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Review Article

MECHANISM OF STRESS SIGNAL TRANSDUCTION AND INVOLVEMENT OF STRESS INDUCIBLE TRANSCRIPTION FACTORS AND GENES IN RESPONSE TO ABIOTIC STRESSES IN PLANTS

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ABSTRACT

The genetic architecture of plant growth and development of cereal crops are greatly affected by abiotic stress conditions such as drought, salinity, and low temperature. Plants respond to these environmental challenges through a number of molecular and physiological mechanisms that alter the signal transduction pathways and expression of different genes. These stress inducible genes are altered in order to sustain under adverse climatic factors. Several regulatory of molecular and metabolic pathways that activate or repress the stress tolerance genes with the help of transcription factors and *cis*-acting elements in the stress-responsive promoters function for the plant adaptation to environmental stresses. Here, we summarize recent studies highlighting the role of stress signaling molecules and specific members of transcription factors and genes expression in the adaptive responses to abiotic stresses.

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INTRODUCTION

Abiotic stresses, such as drought, salinity, low and high temperature and floods, seriously hamper the yield of major cereal crops all over the world, especially in developing countries. It is estimated that average major crop yield loss is less than 50% worldwide (Bray *et al.* 2000). Furthermore, world food production needs to be doubled by the year 2050 to meet the ever-growing demands of the population (Tilman *et al.* 2002). For these reasons, understanding the mechanisms underlying plant abiotic stress responses and the generation of stress tolerant plants has received much attention in recent years. The tolerant plants can initiate a variety of changes at the molecular, cellular and physiological traits and signal transduction pathways, to survive under adverse climatic factors. All of these adaptive processes universally include changes in the expression of specific genes and transcription factors (Thomashow 1999; Shinozaki *et al.* 2003). However, the complexity of abiotic stress tolerance traits, conventional

approaches are less effective at directly connecting tolerance traits to the determinant genes that play key roles in the stress response. Recent progress in advance genomics and high throughput sequence technologies, genes involved in many of the essential steps regulating the molecular mechanism and stress responsive genes have been identified and characterized. In particular, stress signaling molecules, transduction pathways and discovery of ABA receptors play a major role in understanding the transcriptional and post-transcriptional regulation of stress-responsive gene expressions.

Factors involving in tolerance to abiotic stresses

The rice crop responds to these environmental challenges through a number of defense mechanisms to maintain the optimal growth conditions and involves many changes at whole plant, tissue, cellular, physiological and molecular levels. The exposure of plants to a different combination of stress factors may trigger agonistic, antagonistic, or potentially unrelated responses. Such interaction between multiple biotic and/or abiotic stresses is coordinated by a complex signaling crosstalk

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of phyto-hormones (Mundy et al. 2006). Phytohormones such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and abscisic acid (ABA) are major players that regulate the defense responses of plants against both biotic and abiotic stresses via synergistic and antagonistic actions, which are referred to as signaling crosstalk (Fujita et al. 2005) and modified the regulate pathways in terms of metabolic, physiological and molecular pathways in plant growth and its leading to serious yield losses in crops (Bray et al. 2000; Sakamoto et al. 2004). The increases in rice production can only be achieved by using both conventional breeding methods and modern technologies. Tolerance or susceptibility to these abiotic stresses is a very complex phenomenon, because of stress may occur at multiple stages of plant development and more than one stress simultaneously affects the plant. Therefore, the perception of abiotic stresses and signal transduction to switch on adaptive responses are critical steps in determining the survival and reproduction of plants exposed to adverse environments (Chinnusamy et al. 2004). The abiotic stress effects depend on the various stages in crop growth such as, seed germination, seedling establishment, genotypic capacity of species, vegetative or post-emergence growth, flowering or reproduction, and grain filling period (Mittler et al. 2004). Improvement of stress tolerance crops is largely dependent on exploiting genetic variation in landrace and wild germplasm and this has been achieved in the past through traditional plant breeding methods (Langridge and Fleury 2011).

Developments of tolerant/resistant crops, requires broader inter disciplinary approaches as involving an understanding molecular mechanisms, signaling process and the effect of QTLs/gene in stress regulation pathways (Fig. 1). Collins et al. (2008) reported in the alteration of gene expression pathways with switch off/on transcription factors and physiological adjustment, which determining yield in a particular target population of environments.

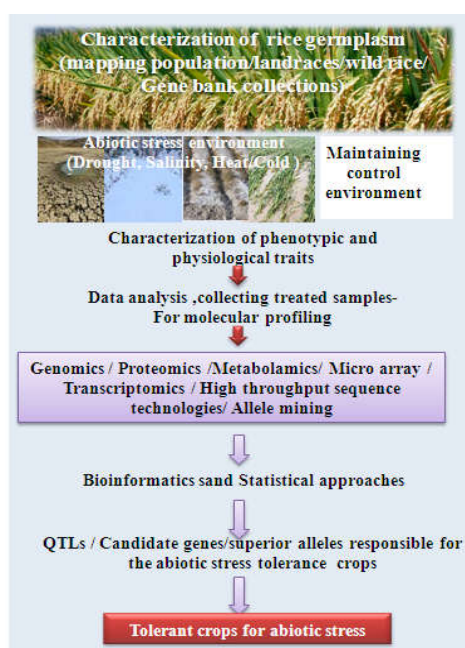


Fig. 1 Integration of molecular biology, physiology and phenotypic approaches to development of abiotic stress tolerance crops with assist of insilico tools

Recent functional and comparative genomic studies show considerable overlap of plant responses to osmotic stresses such as drought, and salinity (Chen et al. 2002; Kreps et al. 2002; Buchanan et al. 2005). The drought, salinity, high temperature stresses leads to changes in metabolic toxicity, membrane disorganization, generation of reactive oxygen species (ROS), inhibition of photosynthesis and altered nutrient acquisition (Hasegawa et al. 2000). The molecular level, abiotic stress tolerance can be achieved through gene transformation by changing the accumulation of osmoprotectants, production of chaperones, superoxide radical scavenging mechanisms (Zhu 2002; Valliyodan and Nguyen 2006). A promising strategy to deal with adverse scenario is to take advantage of the flexibility that biodiversity (genes, species, ecosystems) offers and increase the ability of crop plants to adapt to abiotic stresses. Henceforth, this paper aims to consolidate the molecular mechanism and their regulation of transcription factors and genes to know the stress tolerance in the genotypes and their feasibility in developing cultivars suitable for the abiotic stress condition by utilizing of MAS and genomic technologies.

Regulation of ABA signaling pathways

The phytohormone Abscisic acid (ABA) plays a significant role in physiological processes such as seed dormancy, development of seeds, stomatal closure, synthesis of storage proteins and lipids, leaf senescence and also defense against pathogens. Also it plays an important role in integrating various stress signals and controlling downstream stress responses (Chinnusamy et al. 2004) in the process of signal transduction. Plants are perceiving and adapting to dangerous climatic factors as drought, cold/high temperature, salinity and flooding. These are controlled by abscisic acid (ABA) (Mahajan and Tuteja 2005) and also regulation of ABA responsive genes through the transcription factors. The expression of stress responsive genes can be followed by two approaches as ABA dependent or ABA independent pathway (Xiong et al. 2002). The “direct” pathway involves cis-acting ABA-responsive elements (ABREs), which are directly activated by binding with transcription factors such as basic domain leucine zipper (bZIP)-type DNA binding proteins (Kobayashi et al. 2004). Alternatively, the “indirect” ABA-dependent transcription pathway involves other cis-acting elements, such as MYC and MYB. The transcription factors regulate almost every aspect of the plant life cycle by regulating the expression of specific genes, including the stress responsive genes. These transcription factors have been shown to play a variety of roles in many essential plant life processes (Abe et al. 2005; Alonso et al. 2009). Importantly, the molecular and physiological traits of a number of genes and transcription factors have been investigated in different crops and transgenic model plants. The present review describes recent progress towards understanding of molecular mechanism, signal recognition and transduction via ABA pathways and stress-responsive gene expression by different transcription factors (TFs) and their corresponding cis-acting elements associated with the abiotic stresses in plant.

Stress signaling

In response to environmental adversities, plants have developed several strategies to cope with these challenges either by

adaptation mechanisms, which help them to survive the adverse conditions, or specific growth habits to avoid stress conditions. Stress tolerant plants have evolved certain adaptive mechanisms, displayed by different degrees of tolerance, which are largely determined by their genetic plasticity. This differential stress tolerance could be due to difference in terms of perception of stress, signal transduction and appropriate gene expression patterns, or presence of novel metabolic pathways restricted to tolerant plants (Bartels and Sunkar 2005). Plants can perceive environmental stresses and elicit appropriate responses with altered metabolism, growth and development. The regulatory circuits include stress sensors, signaling pathways comprising network of protein-protein interactions, transcription factors (TFs) and finally proteins or metabolites which impart stress tolerance to plants. The products of stress inducible genes can be classified into two groups; (i) those that function directly in protecting against stresses also termed as functional or downstream genes, and (ii) those that regulate gene expression and signal transduction in response to stress termed as regulatory or upstream genes (Shinozaki *et al.* 2003).

Integrated circuits of most complicated plant's stress responses involve various pathways in a compartmentalized fashion including the interaction of signaling molecules/additional cofactors to coordinate a specified response to a given stimulus (Dombrowski 2003). As the signals, in form of ligands or elicitors, transduce through the cellular membrane, electrochemical gradient across over it has a great impact. The sensitivity of the electrical membrane potential to different external stimuli suggests that ion exchange could serve for the membrane perceived signals.

Thus a hyper polarization-activated influx of Ca^{2+} into the host cell could provide a pathway for the elevation of cytosolic free Ca^{2+} concentrations that mediate the induction of several biochemical pathways that are a part of plant's defense response (Rodrigues *et al.* 2009). Sensor molecules can catch the stress signal coming first and regulate the mesh of different interconnecting pathways via initiation and/or suppression of a cascade of intercellular signal transportation and to induce specific set of genes by the production of active nuclear TFs (Fig. 2). Ca^{2+} ions also act as secondary messengers as Ca^{2+} ion concentration is geared up in the cytoplasm when the cell senses stress.

The principal molecular machine in plant's two-component signaling system is a membrane bound receptor (with kinase activity of histidine) that has an extracellular domain which can act as a ligand binding site (or protein-protein interactions), a transmembrane domain and an intracellular kinase domain. When the extracellular sensor domain perceives a signal, the cytoplasmic histidine residue is autophosphorylated and the phosphoryl moiety is then passed to an aspartate receiver in a response regulator, which may constitute a part of the sensor protein or a separate protein. The sensors may couple with a downstream mitogen-activated protein kinase (MAPK) cascade or directly phosphorylate specific targets to initiate cellular responses. Upon receiving a signal from membrane receptors, cells often utilize multiple phosphoprotein cascades to transduce and amplify the information. Phosphorylation and dephosphorylation of active proteins are perhaps the most common intracellular signaling modes. They regulate a wide range of cellular processes such as enzyme activation, assembly of macromolecules, protein localization and degradation. Secondary signals (i.e., phytohormones and second messengers, inositol phosphates and reactive oxygen species or ROS) can initiate another cascade of signaling events, which can differ from the primary signaling in spatio-temporal manner (Xiong and Zhu 2002).

There are various networks of signal transduction. Oxidative and osmotic stress signaling uses MAPK modules, involves the generation of ROS scavenging enzymes and antioxidant compounds as well as osmolytes. Ca^{2+} dependent signaling leads to activation of the late embryogenesis abundant (LEA)-type genes, such as the dehydration responsive elements (DRE) and cold responsive sensitive transcription factors (CRT) class of genes, involves the production of stress-responsive proteins. Salt overlay sensitive (SOS) signaling with the help of Ca^{2+} ions regulates ion homeostasis and involves the SOS pathway specific to ionic stress (Xiong *et al.* 2002). Due to high and low temperature, water scarcity, prolonged under water condition and high salty environments forcibly produce reactive oxygen species (ROS), one type of secondary messenger, such as hydrogen peroxide (H_2O_2), hydroxyl radicals (OH^\cdot), singlet oxygen ($O^{\cdot-}$), superoxide ($O_2^{\cdot-}$) etc. that may cause extensive damages in the plant cell. Some enzymes, osmolytes and some other macromolecules can also function as ROS scavengers (Xiong *et al.* 2002) to protect the plants. Signaling in this condition is done by a phosphoprotein modulated cascade using MAPK which is activated by receptors (tyrosine kinases, G-protein coupled receptors, histidine kinases etc.). The core MAPK cascades consist of 3 kinases that are activated sequentially by an upstream kinase. The MAP kinase

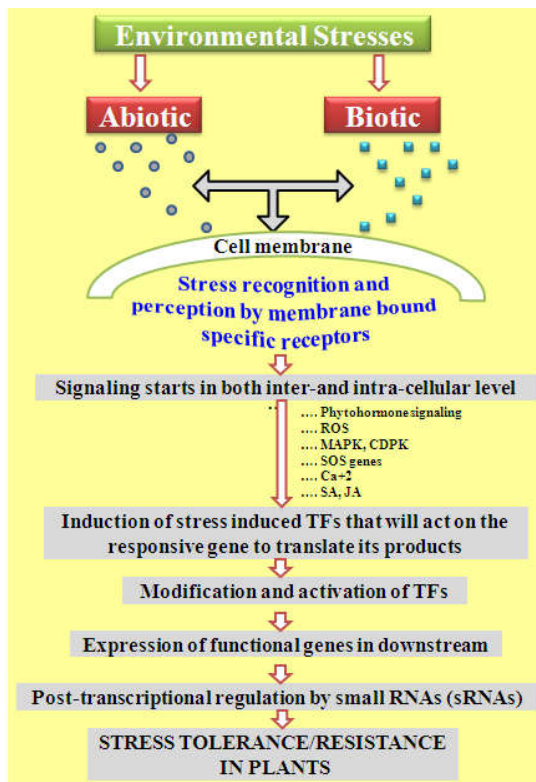


Fig. 2 Sequential steps involved in signaling cascade for stress (both abiotic and biotic) tolerance/resistance in crop plants

kinasekinase (MAPKKK), upon activation, phosphorylates a MAP kinase kinase (MAPKK) on serine and threonine residues. This dual-specificity MAPKK in turn phosphorylates a MAP kinase (MAPK) on conserved tyrosine and threonine residues.

The activated MAPK can then either migrate to the nucleus to activate the transcription factor directly, or activate additional signal components to regulate gene expression, cytoskeleton-associated proteins or enzyme activities, or target certain signal proteins for degradation (Xiong et al. 2002). Osmotic stress activates several protein kinases including mitogen-activated kinases, which may mediate osmotic homeostasis and/or detoxification responses. Abscisic acid biosynthesis is regulated by osmotic stress at multiple steps. Both ABA -dependent and -independent stress signaling first modify constitutively expressed transcription factors, leading to the expression of early response transcriptional activators, which then activate downstream stress tolerance effector genes (Zhu 2001). On the other hand, calcium-dependent protein kinases (CDPKs) are implicated as important sensors of Ca^{2+} influx in plants in response to such stresses. CDPKs are serine/threonine protein kinases with a C-terminal calmodulin-like domain with up to 4 EF-hand motifs that can directly bind Ca^{2+} (Rodrigues et al. 2009). Salt stress-induced Ca^{2+} signals are perceived by SOS3 which activates the SOS2 kinase. The SOS3-SOS2 kinase complex regulates cellular Na^+ levels by stimulating Na^+ transport out of the cytoplasm (e.g. by increasing the expression and activity of SOS1) and conceivably by restricting Na^+ entry into the cytosol. An additional target of the SOS2 kinase, NHX (vacuolar Na^+/H^+ exchanger), also contributes to Na^+ ion homeostasis by transporting Na^+ from the cytoplasm into the vacuole (Chinnusamy et al. 2004).

Transcription factors in abiotic stresses

Transcriptional regulation, also known as transcriptome reprogramming/ gene switches, is essential for plant adaptation to abiotic stresses. The transcription factors are proteins with a DNA domain, which are involved in recognizing a short (usually 4-8bp) DNA sequences of cis-acting elements present in the promoter of a target gene and it can induce (activators) or repress (repressors) the activity of the RNA polymerase, thus regulating gene expression against presence or absence of stress condition (Liao et al. 2008). Based on the structure of the DNA-binding domain, transcription factors are classified into 50 to 60 different families, and in plants, 5% to 7% of all the protein-encoding genes are transcription factors. The regulation of transcription factor is a potential area for coordination of regulated genes relevant to abiotic stress tolerance in different crops.

An abiotic stress response as plant's regulatory mechanism and signal transduction pathways turns out to be very complex phenomenon. Generally stress tolerance seems to be controlled mostly at transcriptional levels and it's depending on TFs activity of DNA binding domain and a protein-protein interaction domain which mediates, directly or indirectly, the activation or repression of transcription (Brivanlou and Darnell 2002). Approximately 2000 plant TFs were *in silico* identified in plants and classified into families and subfamilies according to the similarity of binding domain, their gene structure, their

function and other structural features (Abdelaty 2003). Among these identified TFs, only a few transcription factors has been functionally characterized and validated in model plants.

Transcription factors (TFs) are master regulators that control structural and regulator genes. A single TF can control the expression of many target genes through specific binding of the TF to the cis-acting element in the promoters of respective target genes. The regulation of TFs activity modified by phosphorylation, ubiquitination and sumoylation, which play a critical role in the fine-tuned regulation of the relevant genes under abiotic stresses (Nakashima et al. 2012) (Fig.3). Recently several transcription factors have been characterized and functionally validated in many transcription factors as dehydration-responsive element-binding (DREB) or C-repeat binding factor (CBF), MYB, basic-leucine zipper (bZIP), AP2/ERF, NAC, WRKY and C2H2 zinc (ZFP252, ZFP245, ZFP179 and DST) finger families play a critical role in the abiotic stress response (Bartels and Sunkar 2005; Hu et al. 2006) and it activates the cascades of genes that act together in enhancing tolerance towards multiple stresses. Most of these transcription factors (TFs) regulate their target gene expression through binding to the linked *cis*-elements in the promoters of the stress-related genes. Several major regulons that are active in response to abiotic stress have been identified in various crops. Dehydration-responsive element binding protein 1 (DREB1)/C-repeat binding factor (CBF) and DREB2 regulons function in ABA-independent gene expression, whereas the ABA-responsive element (ABRE) binding protein (AREB)/ABRE binding factor (ABF) regulon functions in ABA-dependent gene expression (Fig.3). In addition to these major pathways, other regulons, including the NAC and MYB/MYC regulons, are involved in abiotic stress-responsive gene expression. Recent studies demonstrated that DREB1/CBF, DREB2, AREB/ABF, and NAC regulons have important roles in response to abiotic stresses in cereal crops.

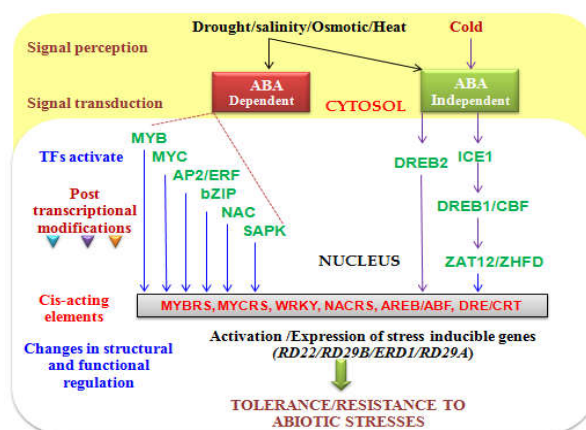


Fig. 3. A schematic representation of major transcriptional regulatory networks of cis-acting elements and transcription factors involved in abiotic stress-responsive gene expression. Abiotic stress signaling perception and their transduction and transcriptional regulation of stress-responsive genes followed by the interaction between in response to abiotic stresses are indicated by lines with arrows. Interaction between the transcription factor families (shown by green color) and the corresponding cis-acting elements (shown by red color) in the promoter region of stress inducible genes (shown by *italics*). Rectangles () are indicated that modification of the TFs through the phosphorylation, sumoylation and ubiquitination.

Regulation of transcription domains

The essence of transcriptional activation of target gene expressions involves interaction between the trans-sequence with specific DNA-binding transcription factors and cis promoter regulatory sequences. The binding of regulatory elements play a key role in modulating plant stress responses and result in increasing tolerance to various environmental stresses. The regulation of transcription factors as specific domains are involved in the activation or repression of transcription. Several different types of activation domains have been identified in known transcription factors and they do not appear to possess any consensus sequences. Instead, they have been classified as acidic, glutamine-rich, proline-rich, serine- and threonine-rich domains on the basis of their amino acid composition (Pater *et al.* 1996).

Mechanism of regulation of transcription factors belong to many different families. However, there are certain families that include a relatively large number of members that have been implicated in environmental stress responses. These include the DREB1/CBF family of cis-acting element, DRE/CRT transcription factors (Lata and Prasad 2011) as well as other DREB2, belonging to the ERF/AP2 family (Yamaguchi and Shinozaki 2005), Class I homeodomain-leucine zipper proteins (Elhiti and Stasolla 2009), WRKY family transcription factors (Rushton *et al.* 2012; Chen *et al.* 2012), NAC family (Nakashima *et al.* 2012). bZip family (Choi *et al.* 2000), MYC family (Abe *et al.* 2003), MYB family (Yanhui *et al.* 2006), ZFP family (Mukhopadhyay *et al.* 2004) have been well characterized under abiotic stress conditions. Although there are some other multiple transcription factors, including ICE (inducer of CBF expression), CBFs/DREBs, AREB/ABF/ABI/bZip, MYC/ MYB and NACs, have been well characterized (Chinnusamy *et al.* 2004) under salt and drought stress. Interestingly, the families mentioned here are all plant-specific (Riechmann *et al.* 2000) suggesting that they may have evolved to help plants deal with the stress tolerance. However, members of transcription factor families that are found outside of plants have also been implicated in control of stress-inducible gene expression.

Stress-inducible genes for abiotic stress

The complex plant response to abiotic stress involves many genes that are induced by cold as well as induced by both drought and salinity (Shinozaki and Yamaguchi-Shinozaki 2000), probably because many cold-inducible genes encode different types of proteins to protect the plant cell that follow specific signal transduction in the response to abiotic stresses. Generally the stress inducible gene products are classified into three major groups.

1. Gene encoding products of heat stress proteins (HSPs) or chaperones, LEA proteins, osmo-protectants, anti freeze proteins, detoxification enzymes and free-radical scavengers directly protect plant cells against stresses (Bray *et al.* 2000).
2. Encoding products are involved in signaling cascades and in controlling transcriptional regulation and network pathways as MAPK,CDPK (Ludwig *et al.* 2004) and SOS kinase (Zhu 2001), phospholipases (Frank *et al.* 2000) and transcriptional factors (Choi *et al.* 2000).

3. Involved in water uptake and transport of aquaporins and ion transporters (Blumwald 2000).

The stress-inducible gene products are involved in the generation of regulatory molecules as ethylene (ET), jasmonic acid (JA) and salicylic acid (SA) that play a major role in response to biotic stress.

Table 1 List of abiotic stress tolerance gene/transcription factors studied in various crops

Type of abiotic stress tolerance	Crop	Genes/transcription factor	References	
Drought, Cold and Salinity	Rice	OsCDPK7	Sajjo <i>et al.</i> 2000	
		OsDREB1B	Ito <i>et al.</i> 2006	
		OsCOIN	Liu <i>et al.</i> 2007	
		OsDREB1F	Wang <i>et al.</i> 2008	
		OsiSAP8	Kanneganti and Gupta 2008	
		OsDREB1F	Wang <i>et al.</i> 2008	
		OsABF2	Hossain <i>et al.</i> 2010	
		OsDREB1	Fukao <i>et al.</i> 2011	
		WDREB2	Egawa <i>et al.</i> 2006	
		ABF4	Choi <i>et al.</i> 2000	
	Maize	ZmbZIP17	Jia <i>et al.</i> 2009c	
	Wheat A. thaliana	OsCDPK7	Sajjo <i>et al.</i> 2000	
		Osmotin	Barthakur <i>et al.</i> 2001	
		OsDREB2A	Dubouzet <i>et al.</i> 2003	
		OsRacB	Luo <i>et al.</i> 2006	
OsAB15		Zou <i>et al.</i> 2008		
Drought and Salinity	Rice	OsbZIP23	Xiang <i>et al.</i> 2008	
		ONAC045	Zheng <i>et al.</i> 2009	
		OsDHODH1	Liu WY <i>et al.</i> 2009	
		OsNAC6/SNAC2	Lu <i>et al.</i> 2009	
		OsAREB1	Jin <i>et al.</i> 2010	
		OsLEA3	Fukao <i>et al.</i> 2011	
		OSRIP18	Jiang <i>et al.</i> 2012	
		OsCam3	Phean-O-Pas <i>et al.</i> 2005	
		OSRIP18	Jiang <i>et al.</i> 2011	
		OsHsfA7	Liu <i>et al.</i> 2013	
	Wheat	PSP 1015	Hollung <i>et al.</i> 1994	
	A. thaliana	RD26	Fujita <i>et al.</i> 2004	
		AhDREB1	Shen <i>et al.</i> 2003b	
	Tobacco	Mn-SOD	Tanaka <i>et al.</i> 1999	
	Salinity	Wheat	OsA1/ OsA2	Zhang <i>et al.</i> 1999
OsGS2			Hoshida <i>et al.</i> 2000	
Mt1D			Li <i>et al.</i> 2004	
OsNHX1			Fukuda <i>et al.</i> 2004	
OsHKT1			Kader <i>et al.</i> 2006	
Rice		OsBZ8	Kakali <i>et al.</i> 2006	
		OsMAPK33	Lee <i>et al.</i> 2011	
		OsWRKY45-2	Tao <i>et al.</i> 2009	
		TVPI	Brini <i>et al.</i> 2005	
		AeNHX1	Qiao <i>et al.</i> 2007	
		CaZF	Jain <i>et al.</i> 2009	
		OsSRT1	Huang <i>et al.</i> 2007	
		OsDREB1G	Chen <i>et al.</i> 2008	
		Rab16D	Zou <i>et al.</i> 2008	
		RD22	Hou <i>et al.</i> 2009	
Drought	Rice	Os AP59 /Os AP37	Oh <i>et al.</i> 2009	
		OsNAC10	Jeong <i>et al.</i> 2010	
		Dro1	Uga <i>et al.</i> 2011	
		Oshrf1	Zhang <i>et al.</i> 2011	
		OsGRF8	Shunwu <i>et al.</i> 2014	
	Maize	ZmPLC1	Wang <i>et al.</i> 2008	
		TsVP	Li <i>et al.</i> 2006	
		betA	Quan <i>et al.</i> 2004	
		ZmNF-YB2	Nelson <i>et al.</i> 2007	
		TaLTP1	Pellegrineschi <i>et al.</i> 2004	
	Wheat	DREB1A	Jang <i>et al.</i> 2004	
		mt1D	Abebe <i>et al.</i> 2003	
		PDH	Mani <i>et al.</i> 2002	
		A. thaliana	SbDREB2	Bihani <i>et al.</i> 2011
		Sorghum	SbDREB2	Bihani <i>et al.</i> 2011

		MYBS3	Jang et al. 2003
	Rice	OsDREB1A,	Dubouzet et al. 2003
		OsCtb1	Saito et al. 2001
		OscodA	Sakamoto et al. 1998
		HOS10	Chen et al. 2008
		OsMYB3R-2	Ma et al. 2009
		Osmyb4	Park et al. 2010
Cold		Tacr7	Gana et al. 1997
		ScRPS7	Berberich et al. 2000
	Wheat	CHT9	Yet et al. 2000
		Wlt10	Motomura et al. 2013
		Wdhn13	Motomura et al. 2013
		Wcor14	Motomura et al. 2013
	A. thaliana	GmWRKY21	Zhou et al. 2008
	Tomato	AtCBF2	Hsieh et al. 2002
	Wheat	TaDREB1	Shen et al. 2003
		Wlip19	Kobayashi et al. 2008
Drought and Cold	Rice	HvCBF4	Oh et al. 2007
	Cotton	GhNAC2	Meng et al. 2009
	Sorghum	SbDREB2	Bihani et al. 2011
	Rice	GS2	Hoshida et al. 2000
Salinity and Cold	Wheat	TaSnRK	Zhang et al. 2010
Drought and Heat	Rice	OsDREB2 B	Matsukura et al. 2010
		OsXET9	Jiali Dong et al. 2011

Abscisic acid (ABA) is the most studied stress-responsive hormone for its pivotal roles in the regulation of abiotic stress responses to drought, osmotic and cold stress (Vlot et al. 2009; Peleg and Blumwald 2011). Overall, the stress signal transduction requires exact coordination of all the signaling molecules, including protein modifiers (*methylation, ubiquitination, glycosylation*, etc.), adaptors and scaffolds (Xiong et al. 2002) and many genes which may cross talk with each other. Finally, the stress tolerance response can lead to either growth inhibition or cell death, which depends on what kind of genes are up- or down regulated in response to the stress(es).

Stress-inducible genes have been used to improve the drought, salinity and cold/high temperature stress tolerance of plants by genetic engineering technologies. It is important to analyze the functions of stress-inducible genes, not only to understand the molecular mechanisms of stress tolerance and their responses in higher plants, but also to improve the stress tolerance of crops by gene manipulation. In the last few decades, several genes have been identified and functionally validated in different crops that showed tolerance to abiotic stress responses (Table 1). With the advancement of new and powerful tools such as genomics and proteomics, particularly the high-throughput microarray platform, RNA-Seq, and increasing number of completed genome sequences of major cereal crops, enormous strides have been made to identify genes that are up- or down regulated by abiotic stresses (Fig.1). This allows the simultaneous monitoring of expression profiles for many genes and facilitates the determination of a large spectrum of stress responsive genes, which can greatly broaden and deepen our understanding on the stress response in a comprehensive way. Many studies have reported changes in the expression of individual genes when the plant frequently responds to abiotic and biotic stresses, showing their diverse functions under abiotic stress conditions. Example of such genes are the MAP kinase (Agrawal et al. 2003), DREB genes (Dubouzet et al. 2003), Rab16D (Hou et al. 2009), Calcium-dependent protein kinase (Saijo et al. 2000), OSRIP18 (Shu et al. 2011), OsERF3 (Wan et al. 2011), and OsHsfA7 (Liu et al. 2013), OsSAP8

(Kanneganti and Gupta 2008), OsGRF8 (Shunwu et al. 2014) and signaling (kinases) (Saijo et al. 2000), membrane integrity (LEA protein) (Xu et al. 1996). The promoters of stress responsive genes typically have cis-regulatory elements such as DRE/CRT, ABRE, and MYCRS/MYBRS and are regulated by various upstream transcriptional factors.

Cis-acting elements

Abiotic stress tolerance genes expression can be modulated at different levels in the regulation pathways. Among the types of regulation, transcriptional regulation is important regulatory machinery in higher plants. The expression of abiotic stress tolerance genes depend on the initiation and efficiency of the interaction between the cis-acting elements on their promoters and their interaction with TFs. These DNA-protein interactions are critical for the regulation of expression of the stress responsive genes (Mitsuda et al. 2009). Several types of cis acting elements are involved in abiotic stress responses and their binding with specific transcription factor families (Table 2).

Types of transcription factors

Basic leucine zipper (bZIP) transcription factors

Basic leucine zipper (bZIP) transcription is one of the largest transcription factor families in plants. These transcription factors have been shown to play a variety of roles in many essential plant life processes (Xiang et al. 2008; Alonso et al. 2009) and it is characterized by the presence of a basic region, responsible for DNA-binding of a leucine zipper, involved in protein homo- and heterodimerization (Jakoby et al. 2002). Many bZIP TFs have been linked to the ABA dependent signaling pathway in several plant species, such as rice, Arabidopsis, and maize (Choi et al. 2000).

In the dicotyledonous model plant (*Arabidopsis thaliana*), 75 bZIP transcription factor genes have been designated (AtbZIP1-AtbZIP75) and classified into ten groups according to the sequence similarity of their basic region (Jakoby et al. 2002). In monocotyledonous model plant (*Oryza sativa*), 89 bZIP transcription factors and classified into 11 groups according to their DNA-binding specificity and the amino acid sequences in their basic and hinge regions (Nijhawan et al. 2008). To date, several bZIP transcription factors of have been functionally characterized, including those shown to be responsive to ABA-dependent stress signal transduction, and have thus been designated as ABA-responsive element binding proteins (AREBs), also known as ABRE binding factors (ABFs) in abiotic stresses.

WRKY transcription factors

The WRKY family of TF is one of the largest and oldest families of transcriptional regulators in the plant kingdom (Rushton et al. 2010). The WRKY TFs are characterized by a DNA-binding domain with highly conserved 60 amino acid long WRKY domains, comprising highly conserved WRKYGQK at N-terminus and a novel metal chelating zinc finger signature at C-terminus.

The WRKY TF families were first identified and reported from sweet potato and gradually increasing numbers of WRKY TFs have been identified in various plants. Rice WRKY family

consists (109 members), Arabidopsis (74 members), Wheat (43 members) and Barley (45 members) WRKY domains (Mangelsen *et al.* 2008; Niu *et al.* 2012). In rice WRKY TF families is divided into three groups based on the number of WRKY domains (two domains in Group I and one in Groups II and III), the second group is divided in five subgroups, IIa, IIb, IIc, IId and IIe (Rushton *et al.* 2010). The WRKY domain has been crystallized (Tao *et al.* 2009) and the proposed structures consist the cis-element where it should bind and the highly conserved W-box (TTGACC/T). Because of the conserved cis elements, the specificity of different TFs must be obtained by the neighboring areas of the W-box (Ciolkowski *et al.* 2008). WRKY TFs have been described in having a role in the regulation of biotic and/or abiotic stress responses, germination, senescence, and developmental processes.

The ABFs contain a highly conserved bZIP domain composed of a basic region responsible for DNA binding and three heptad leucine repeats for TF dimerization at the C-terminus. Apart from the bZIP domain, the ABFs contain four highly conserved regions at the N or C-terminus, C1, C2, C3, and C4, containing several serine (S) and threonine (T) residues that have been suggested as the phosphorylation sites of different kinases (Kim 2006; Huang *et al.* 2010).

The ABRE element is always flanked by a distal or proximal coupling element (CE), such as CE3 and CE1 in barley, forming an abscisic acid response complex (ABRC), which might be necessary and sufficient to confer ABA response or trigger ABA-mediated gene expression against abiotic stresses (Kim 2006).

Table 2 List of major transcription factor (TF) families and their interactions with cis acting elements involved in abiotic stress response

Abiotic stress response	TF Families	Cis-acting elements	Reference
Dehydration, Salinity, Cold and Low temperature stress	MYB	MYBR	Abe <i>et al.</i> 2003; Agarwal <i>et al.</i> 2006; Lippold <i>et al.</i> 2009, Yanhui <i>et al.</i> 2006
Drought, Salinity, Cold and Low temperature stress	DREB	DRE	Yamaguchi-Shinozaki and Shinozaki 1994; Gilmour <i>et al.</i> 1998; Dubouzet <i>et al.</i> 2003; Song <i>et al.</i> 2005; Lata and Prasad 2011
Salinity, Osmotic stress, Wounding, Drought, Anoxia and Cold	ERF	GCC box	Dietz <i>et al.</i> 2010; Zhu <i>et al.</i> 2010
Drought, Low phosphate stress, Heat and Salt stress	WRKY	G-box	Yamasaki <i>et al.</i> 2005; Guillaumie <i>et al.</i> 2010
Heat, Drought and Salinity	HsF	HSE	Ogawa <i>et al.</i> 2007; Yoshida <i>et al.</i> 2008; Schmidt <i>et al.</i> 2012; Li <i>et al.</i> 2013
Cold, Drought and Salinity	AP2/ERF	DRE/CRT	Gilmour <i>et al.</i> 1998; Haake <i>et al.</i> 2002; Magome <i>et al.</i> 2004
Drought and cold	AREB or ABF	ABRE	Seki <i>et al.</i> 2002; Niu <i>et al.</i> 2002; Kim 2006; Fujita <i>et al.</i> 2013
Drought, Salt and Heat	CBF	CRT	Sakuma <i>et al.</i> 2006
Drought and Salinity	NAC	NACRS	Hu <i>et al.</i> 2006; Mao <i>et al.</i> 2012
Drought and Salinity	DST	DBS	Huang <i>et al.</i> 2009
Cold	bHLH	ICEr1	Chinnusamy <i>et al.</i> 2003
Cold	bHLH	E-box	Chinnusamy <i>et al.</i> 2003; Feng <i>et al.</i> 2012; Peng <i>et al.</i> 2013
Drought	NAC	NACR	Tran <i>et al.</i> 2004
Drought	ZFHD	rps1 site	Tran <i>et al.</i> 2004
Drought	bZIP	ABRE	Choi <i>et al.</i> 2000; Uno <i>et al.</i> 2000

WRKY transcription factors play major task in regulating the transcriptional reprogramming associated with multiple plant processes as WRKY TFs have been shown to play multiple roles in various developmental and physiological processes, such as ABA signaling (Rushton *et al.* 2012), lignifications and xylem development (Guillaumie *et al.* 2010), leaf senescence (Besseau *et al.* 2012), root development (Zhou *et al.* 2008), seed germination (Rushton *et al.* 2012), and hormone signaling (Zhou *et al.* 2008). Moreover, WRKYs are also shown to be involved in regulation of other abiotic stresses, such as low phosphatestress (Chen *et al.* 2009), heat and salinity stress (Jiang and Deyholos 2009; Li *et al.* 2011), and osmotic stress (Liu *et al.* 2011).

AREB or ABF family transcription factor

Interaction between the ABA-responsive TFs and the target genes is linked by different cis -acting elements, among which ABA-responsive element (ABRE) with the core sequence of PyACGTGGC initially was identified on the promoter region of wheat EM gene (Marcotte *et al.* 1989). The proteins binding to ABRE element are a group of basic domain/leucine zipper (bZIP) TFs, particularly ABRE binding protein (AREB)/ABRE-binding factor (ABF), which have been demonstrated to play in vivo roles in ABA and stress responses (Choi *et al.* 2000; Fujita *et al.* 2005; Nakashima *et al.* 2009).

The conserved regions of different types ABF/AREBs family members have been also reported and fallowed displayed different expression patterns in various crops, such as, rice, barley, wheat, tomato, trifoliolate orange, and potato (Hobo *et al.* 1999; Choi *et al.* 2000; Johnson *et al.* 2002; Kobayashi *et al.* 2008; Huang *et al.* 2010; Garcia *et al.* 2012).

AP2/ERF family

The AP2/ERF (APETALA2/ethylene response factor) family of transcription factors is characterized by the presence of the highly conserved AP2 DNA-binding domain and it was initially characterized as plant specific transcription factor (Dietz *et al.* 2010). Several AP2/ERF TFs have been isolated from various plants such as rice (Dubouzet *et al.* 2003), Arabidopsis (Sakuma *et al.* 2002), tobacco (Wu *et al.* 2007), wheat (Agarwal *et al.* 2006), and poplar (Dietz *et al.* 2010). Based on the sequence similarity of the DNA binding domains, AP2/ERF family is divided into five subfamilies: AP2, RAV, ERF, DREB, and "others" (Sakuma *et al.* 2002). The members of the DREB, ERF and other subgroups contain a single AP2/ERF domain, such as ZmDBFs, NtERFs, AtDREBs, AtCBFs, LePtis, AtEBP and AtERFs (Riechmann *et al.* 2000; Sakuma *et al.* 2002). However, the RAV subfamily (RAV: for Related to ABI3/VP1) includes genes that two different conserved cis elements DNA-binding domains,

AP2/ERF and B3. B3 DNA binding domain is conserved in VP1/ABI3 (Kagaya et al. 1999).

The AP2/ERF transcription factors have several members in many plant species of monocots and dicots playing important roles in plant development and in the responses of plants to biotic and abiotic stresses. The ERF subfamily subfamilies contains proteins that can bind to cis-acting elements regulating many pathogenesis-related (PR) protein responses to biotic stresses (Woo et al. 2010) and regulation of stress tolerance proteins involved in response to various abiotic stresses, such as high salinity, osmotic stress, injuries, drought, anoxia, and cold (Xu et al. 2007; Zhang et al. 2009; Zhu et al. 2010; Zhang and Huang 2010; Park et al. 2011), and the enhancement of stress tolerance when over expressed (Xu et al. 2007; Zhang and Huang 2010). While, the RAV subfamily proteins are likely to be involved in some biological processes as they coordinate the brassinosteroid biosynthetic and signaling pathways, indicating a putative function evolved in higher plants. The ERF abundance and activity are also regulated by other factors, such as the post-transcriptional modification and protein-protein interaction (Licausi et al. 2013). The ERFs functions in stress tolerance by regulating the stress-responsive genes through interacting with the cis - elements.

DREB1

DREB proteins interact with the DRE/CRT cis-element usually present in the promoter of genes, involved in cold, drought, and high salinity responses. Transcription factors belonging to the DREB subfamily have been extensively studied in several plants, such as Arabidopsis, rice, wheat, tomato, and barley (Agarwal et al. 2006; Yamaguchi-Shinozaki and Shinozaki 2006; Dietz et al. 2010;). Based on studies in Arabidopsis, this subfamily was further divided in two subclasses, DREB1/CBF and DREB2, according to their transcriptional response to abiotic stress conditions (Agarwal et al. 2006; Yamaguchi-Shinozaki and Shinozaki 2006).

The initially identified DREB1/CBF genes, DREB1A, DREB1B, and DREB1C were rapidly and transiently induced by cold, but not by drought or high salt stress, suggesting that in Arabidopsis they may be involved in cold stress responses. Contrastingly, DREB2 genes, DREB2A and DREB2B, were induced by drought and high salt, but not by cold, indicating a putative function in the tolerance to drought and high salt stress (Agarwal et al. 2006; Nakashima et al. 2009). The identification of new members of the DREB1/CBF subclass, DREB1D and DREB1F, which respond to drought and salt stress, respectively, may suggest a crosstalk between DREB1/CBF and DREB2 pathways in response to those abiotic stresses (Sakuma et al. 2002; Nakashima et al. 2009;). Most of the DREBs are involved in ABA independent stress responses; however, some studies have reported DREBs that are responsive to ABA (Yamaguchi-Shinozaki and Shinozaki 2006). Genetic and molecular approaches have been used in combination to characterize a series of DREB family regulatory genes involved in many different pathways, including genes related to cold, drought, high salinity, heavy metals, and abscisic acid (ABA) (Peng et al. 2013).

MYB family

MYB transcription factors are characterized by the presence of MYB repeats (R) involved in DNA-binding and protein-protein interactions. In plants, MYB proteins can be classified into three subfamilies, R-MYB, R2R3-MYB, and R1R2R3-MYB (MYB3R) depending on the presence of one, two, or three tandems MYB repeats contains 50 to 53 amino acids of each subfamily (Feller et al. 2011).

Several members of this family were identified in rice, Arabidopsis, maize, and soybean, and shown to be involved in a wide variety of cell processes and tolerance to abiotic stresses as cell cycle and cell morphogenesis (Feller et al. 2011;), freezing tolerance (Agarwal et al. 2006), stomata movements in drought (Jung et al. 2008), ABA and auxin signals (Seo et al. 2009), transcriptional activation of cuticular wax biosynthesis in drought resistance (Seo et al. 2011). The number of MYB TF subfamilies varies in different crops such as Arabidopsis (126), Rice (109), and Poplar (192) and recently identified in soybean (252) (Wilkins et al. 2009; Du et al. 2012). Liao et al. (2008) reported, in soybean MYB TFs as GmMYB76, GmMYB92, and GmMYB177 are induced by several abiotic stress conditions and over expression of these TFs improves tolerance to salt and freezing in Arabidopsis. In rice, few studies reported that MYB TFs regulate a variety of target genes and it plays an important role in the regulation of various physiological and molecular processes under abiotic stresses. The above findings suggest the role of much MYB transcription factors in regulating the diversity of target genes and thus play a part in the regulation of various physiological and molecular processes under the abiotic stresses.

NAC

Plants hold several families of plant-specific transcription factors, among NACs constitute one of the largest gene families that are ubiquitously distributed in wide range of plant species. The NAC TFs derived from three genes that were initially discovered to contain a particular domain (the NAC domain): NAM (for no apical meristem), ATAF1 and 2, and CUC2 (for cup-shaped cotyledon) (Souer et al. 1996; Aida et al. 1997).

The number of NAC domains in a plant genome varies greatly among plant species as 151 NAC family members in rice, 117 in Arabidopsis, 101 in Soybean, 152 in tobacco, 101 in Soybean, 79 in grape, 26 in citrus and recently 40 NAC family members in tomato have been identified in various crops (Ooka et al. 2003; Rushton et al. 2008; Fang et al. 2008; Hu et al. 2010; Nuruzzaman et al. 2012; Huang et al. 2013)

Many NAC transcription factors have been shown to be involved in plant responses to drought and salinity stress and also involved in diverse aspects of plant growth and development, such as floral morphogenesis (Sablowski and Meyerowitz 1998), seed germination (Park et al. 2011), embryo and shoot apical meristem development (Hao et al. 2011), secondary wall formation (Zhong et al. 2011), hormonal signaling (Yang et al. 2011). Moreover, enormous research and public databases have shown that NACs play critical roles in responses to abiotic stresses in plants (Pinheiro et al. 2009). So far, a number of abiotic stress-responsive NAC genes have

been identified and functionally characterized, such as SNAC1, SNAC2, OsNAC9, and OsNAC10 of rice (Hu *et al.* 2008; Redillas *et al.* 2012), TaNAC2, TaNAC4, TaNAC8, TaNAC69 of wheat (Xia *et al.* 2010; Mao *et al.* 2012), SINAC1 of tomato (Huang *et al.* 2013), ANAC019, ANAC055 and ANAC072 of Arabidopsis (Tran *et al.* 2004), and BnNAC of Brassica (Hegeudus *et al.* 2003). These NAC genes are considered as stress-responsive ones because of their up-regulation by various abiotic stresses or the competence of conferring enhanced stress tolerance when over expressed in the transgenic plants (Mao *et al.* 2012).

Heat stress transcription factor (HsFs)

The elevation of temperature causes a heat-shock response, accompanied by the transcriptional reprogramming of a myriad of heat stress-responsive genes. Extensive analysis of the promoter regions of these heat stress-responsive genes revealed the existence of an important motif called heat shock elements (HSE) containing the palindromic consensus sequence, (AGAAnnTTCT), a highly conserved element among the genes of different systems. Transcription factors binding to the HSE are so-called heat stress transcription factor (HsFs), which are known to function in the terminal position of the signal transduction cascade mediating the responses of heat responsive genes (Von Koskull-Doring *et al.* 2007).

Recent studies of functional genomics analysis has demonstrated that some of the HsFs act as the master regulators of heat stress-responsive gene expression and play critical roles in the basal or acquired thermo tolerance (Yoshida *et al.* 2008; Liu *et al.* 2009; Li *et al.* 2013) and the interaction between Hsfs, such as HsfA1 with HsfA2, and HsfA5 with HsfA4, function in synergy for transcriptional regulation of the target genes (Baniwal *et al.* 2007). Generally the HsFs are not specifically induced by heat shock, but also activated by other abiotic stresses, such as high salinity and drought. In addition, over expression of the HsF genes has been found to confer enhanced tolerance to heat stress and other abiotic stresses (Ogawa *et al.* 2007; Schmidt *et al.* 2012; Li *et al.* 2013), suggesting that the targets of the HsFs may exhibit protective roles in a wide range of physiological processes.

Basic/Helix-Loop-Helix (bHLHs)

The basic/helix-loop-helix (bHLH) domain contains approximately 60 amino acids with two functionally distinct regions, the N-terminal basic region and the HLH region. The basic region, nearly 15 amino acids, functions as a DNA-binding motif and determines the specificity of the DNA-protein interactions. The HLH region, adjacent to the basic one, contains two amphipathic α -helices connected by a loop region of variable length. The amphipathic α -helices of two bHLH proteins can interact with each other, suggesting that they are implicated in the formation of homo- or heterodimers (Li *et al.* 2006).

The bHLH TFs are extensively distributed in eukaryotes but found in lesser extent in plants. They play a transcriptional regulatory role in the network pathways. The bHLH TFs are genes existing as large families in plant genomes. Li *et al.* (2006) and Benedito *et al.* (2008) reported that 167 bHLH genes exist in Arabidopsis and 162 bHLH genes exist in rice genomes, respectively. The plant bHLH proteins have been

functionally characterized during the past decade suggesting their diverse roles in the transcriptional regulation of various biological processes, such as development (Tominaga-Wada *et al.* 2012), secondary metabolite synthesis (Xie *et al.* 2012), photo induced signal transduction (Huq and Quail 2002), and hormone signaling (Nakata *et al.* 2013). Several other bHLH genes involved in drought tolerance, salt tolerance and heavy metal detoxification and cold response have also been identified in different plants, including Arabidopsis (Lingam *et al.* 2011; Sivitz *et al.* 2012), Rice (Jiang and Deyholos 2009; Seo *et al.* 2011), Apple (Feng *et al.* 2012), Banana (Huang *et al.* 2013) and Trifoliate orange (Peng *et al.* 2013). All these findings suggest that the plant bHLH TFs play critical roles in the regulation of responses to various abiotic stresses.

Zinc fingers

The zinc-finger proteins play a major role in many cellular pathways and are present in all eukaryotic organisms. Zn finger TFs have been implicated in distinct pathways, such as nutrient homeostasis and root development (Devaiah *et al.* 2007), flower development (Wu *et al.* 2008), and light and hormonal signaling (Feurtado *et al.* 2011). The C2H2-type Zn finger TFs are one of the most abundant Zn finger TFs and have been described to be involved in the response of different plants to abiotic stress conditions (Sakamoto *et al.* 2004; Mittler *et al.* 2006). These TFs, also referred to as TFIIIA-type finger, are characterized by two cysteine and two histidine residues that bind to a zinc ion to form a structure that binds to the major groove of DNA (Pavletich and Pabo 1991). The first of such TFs identified in plants was the petunia ZPT2-1, a zinc-finger protein TFIIIA type (Takatsuji *et al.* 1992). In rice, despite the high number of genes encoding C2H2-type Zn finger TFs (Agarwal *et al.* 2006), only a few have been functionally characterized: Zinc Finger Proteins 182 (ZFP182), ZFP245, ZFP252 in drought and salt tolerance (Huang *et al.* 2009). The over expression of the first three of these TFs in rice plants yielded similar phenotypes: increased tolerance to abiotic stress conditions (Huang *et al.* 2009).

CONCLUSIONS AND FUTURE PERSPECTIVES

Many physiological traits and stress inducible genes that are regulated by abiotic stresses have been reported in different crops. The regulation of gene expression and modification of the biochemical and physiological components, have revealed the presence of multiple signal transduction pathways, between the perceptions and signal transduction process of major abiotic stresses. The regulation of gene expressions occurs by ABA and it plays an important role following two mechanisms: ABA dependent and ABA independent.

Molecular analyses of these transcription factors and stress inducible genes provide a better understanding of the signal transduction cascades during drought, salt and cold stresses. The development of transgenic plants that modify the expression of these genes and transcription factors will give more information about the function of their gene products. Recently, many abiotic stress tolerance genes and transcription factors have been identified in different crops and when transferred into major cereal crops, have showed high level of tolerance to abiotic stresses, but the association of physiological and molecular mechanism still needs to be

understood in signal networking pathways. In conclusion, combination of powerful molecular tools, advance genomic technologies as transcriptome and proteome analyses, comparative sequence analysis, cis-motif and GO annotations and functional studies will give more insight into the molecular mechanisms and helps to identify regulation of stress responsive TF genes in abiotic stresses signaling in plants.

Conflict of interest

The authors declare that they have no conflict interest.

References

- Abdelaty S, Montserrat P (2003) Plant AP2/ERF Transcription factors. *Genetica* 35(1): 37-50.
- Abe H, Urao T, Ito T, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2003) Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. *Plant Cell* 5: 63-78.
- Abe M, Kobayashi Y, Yamamoto S, Daimon Y, Yamaguchi A, Ikeda Y, Ichinoki H, Notaguchi M, Goto K, Araki T, FD (2005) A bZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. *Science* 309: 1052-1056.
- Abebe T, Guenzi AC, Martin B, Chushman JC (2003) Tolerance of mannitol-accumulating transgenic wheat to water stress and salinity. *Plant Physiol* 131: 1748-1755.
- Agarwal M, Hao YJ, Kapoor A, Dong CH, Fujii H, Zheng X, Zhu JK (2006) A R2R3 type MYB transcription factor is involved in the cold regulation of CBF genes and in acquired freezing tolerance. *J Biol Chem* 281: 37636-37645.
- Agrawal GK, Iwahashi H, Rakwal R (2003) Rice MAPKs. *Biochem Biophys Res Commun* 302: 171-180.
- Aida M, Ishida T, Fukaki H, Fujisawa H, Tasaka M (1997) Genes involved in organ separation in Arabidopsis: an analysis of the cup-shaped cotyledon mutant. *Plant Cell* 9: 841-857.
- Alonso RL, Onate-Sanchez F, Weltmeier A, Ehlert I, Diaz K, Dietrich J, Vicente-Carbajosa W, Droge-Laser (2009) A pivotal role of the basic leucine zipper transcription factor bZIP53 in the regulation of Arabidopsis seed maturation gene expression based on heterodimerization and protein complex formation. *Plant Cell* 21: 1747-1761.
- Baniwal SK, Chan KY, Scharf KD, Nover L (2007) Role of heat stress transcription factor HsfA5 as specific repressor of HsfA4. *J Biol Chem* 282: 3605-3613.
- Barthakur S, Babu V, Bansal KC (2001) Over-expression of Osmotin induces proline accumulation and confers tolerance to osmotic stress in transgenic tobacco. *J Plant Biochem Biotechnol* 10: 31-37.
- Benedito VA, Torres-Jerez I, Murray JD, Andriankaja A, Allen S, Kakar K, Wandrey M, Verdier J, Zuber H, Ott T, Moreau S, Niebel A, Frickey T, Weiller G, He J, Dai X, Zhao PX, Tang Y, Udvardi MK (2008) A gene expression atlas of the model legume *Medicago truncatula*. *Plant J* 55: 504-513.
- Berberich T, Uebeler M, Feierabend J (2000) cDNA cloning of cytoplasmic ribosomal protein S7 of winter rye (*Secale cereale*) and its expression in low-temperature-treated leaves. *Biochim Biophys Acta* 1492: 276-279.
- Besseau S, Li J, Palva ET (2012) WRKY54 and WRKY70 co-operate as negative regulators of leaf senescence in Arabidopsis thaliana. *J Exp Bot* 63: 2667-2679.
- Bihani P, Char B, Bhargava S (2011) Transgenic expression of sorghum DREB2 in rice improves tolerance and yield under water limitation. *J Agr Sci* 149: 95-101.
- Blumwald E (2000) Sodium transport and salt tolerance in plants. *Curr Opin Cell Biol* 12: 431-4.
- Bray EA, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stresses. In: Grissem W, Buchannan B, Jones R (eds.) Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville, MD P: 1158-249.
- Brini F, Gaxiola RA, Berkowitz GA, Masmoudi K (2005) Cloning and characterization of a wheat vacuolar cation/proton antiporter and pyrophosphatase proton pump. *Plant Physio Biochem* 43: 347-354.
- Brivanlou AH, Darnell JE (2002) Signal transduction and the control of gene expression. *Science* 295: 813-8
- Buchanan CD, Lim SY, Salzman RA, Kagiampakis L, Morishige DT, Weers BD, Klein RR, Pratt LH, Cordonnier-Pratt MM, Klein PE, Mullet JE (2005) Sorghum bicolor's transcriptome response to dehydration, high salinity and ABA. *Plant Molecular Biology* 58: 699-720.
- Chen JQ, Meng XP, Zhang Y, Xia M, Wang XP (2008) Over-expression of OsDREB genes lead to enhanced drought tolerance in rice. *Biotechnol Lett* 30: 2191-2198.
- Chen L, Song Y, Li S, Zhang L, Zou C, Yu D (2012) The Role of WRKY Transcription Factors in Plant Abiotic Stresses. *Biochimica et Biophysica Acta* 1819(2): 120-128.
- Chen QQ, Yu SB, Li CH, Mou TM (2008) Identification of QTLs for heat tolerance at flowering stage in rice. *Sci Agric Sin* 41: 315-321.
- Chen W, Provart NJ, Glazebrook J, Katagiri F, Chang HS, Eulgem T, Mauch F, Luan S, Zou G, Whitham SA, Budworth PR, Tao Y, Xie Z, Chen X, Lam S, Kreps JA, Harper JF, Si-Ammour A, Mauch-Mani B, Heinlein M, Kobayashi K, Hohn T, Dangl JL, Wang X, Zhu T (2002) Expression profile matrix of Arabidopsis transcription factor genes suggests their putative functions in response to environmental stresses. *Plant Cell* 14: 559-574.
- Chen YF, Li LQ, Xu Q, Kong YH, Wang H, Wu WH (2009) The WRKY6 transcription factor modulates PHOSPHATE1 expression in response to low Pi stress in Arabidopsis. *Plant Cell* 21: 3554-3566.
- Chinnusamy V, Ohta M, Kanrar S, Lee BH, Hong X, Agarwal M, Zhu JK (2003) ICE1: a regulator of cold-induced transcriptome and freezing tolerance in Arabidopsis. *Gene Dev.* 17:1043- 54.
- Chinnusamy V, Schumaker K, Zhu JK (2004) Molecular genetic perspectives on cross-talk and specificity in

- abiotic stress signalling in plants. *J Exp Bot* 55: 225-236.
- Choi HI, Hong JH, Ha J, Kang JY, Kim SY. (2000) ABFs, a family of ABA-responsive element binding factors. *J Biol Chem* 275: 1723-30.
- Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? *Plant Physiol* 147: 469-486.
- Devaiah BN, Nagarajan VK, Raghothama KG (2007) Phosphate homeostasis and root development in Arabidopsis are synchronized by the zinc finger transcription factor ZAT6. *Plant Physiol* 145: 147-159.
- Dietz K-J, Vogel MO, Viehhauser A (2010) AP2/EREBP transcription factors are part of gene regulatory networks and integrate metabolic, hormonal and environmental signals in stress acclimation and retrograde signalling. *Protoplasma* 245: 3-14.
- Dombrowski JE (2003) Salt Stress Activation of Wound-Related Genes in Tomato Plants. *Plant Physiol* 132: 2098-2107.
- Du H, Yang SS, Liang Z, Feng BR, Liu L, Huang YB (2012) Genomewide analysis of the MYB transcription factor superfamily in soybean. *BMC Plant Biol* 12: 106.
- Dubouzet JG, Sakuma Y, Ito Y, Kasuga M, Dubouzet EG, Miura S, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2003) OsDREB genes in rice, *Oryza sativa* L., encode transcription activators that function in drought-, high salt- and cold-responsive gene expression. *Plant J* 33: 751-763.
- Egawa C, Kobayashi F, Ishibashi M, Nakamura T, Nakamura C, Takumi S (2006) Differential regulation of transcript accumulation and alternative splicing of a DREB2 homolog under abiotic stress conditions in common wheat. *Genes Genet Syst* 81: 77-91.
- Elhiti M, Stasolla C (2009) Structure and function of homodomain-leucine zipper (HDZip) proteins. *Plant Signalling & Behavior* 4(2): 86-88.
- Fang Y, You J, Xie K, Xie W, Xiong L (2008) Systematic sequence analysis and identification of tissue-specific or stress-responsive genes of NAC transcription factor family in rice. *Mol Genet Genomics* 280: 547-563.
- Feller A, Machemer K, Braun EL, Grotewold E (2011) Evolutionary and comparative analysis of MYB and bHLH plant transcription factors. *Plant J* 66: 94-116.
- Feng XM, Zhao Q, Zhao LL, Qiao Y, Xie XB, Li HF, Yao YX, You CX, Hao YJ (2012) The cold-induced basic helix-loop-helix transcription factor gene MdCIBLH1 encodes an ICE-like protein in apple. *BMC Plant Biol* 12: 22.
- Feurtado JA, Huang D, Wicki-Stordeur L, Hemstock LE, Potentier MS, Tsang EW, Cutler AJ (2011) The Arabidopsis C2H2 zinc finger INDETERMINATE DOMAIN1/ENHYDROUS promotes the transition to germination by regulating light and hormonal signaling during seed maturation. *Plant Cell* 23(5):1772-1794.
- Frank W, Munnik T, Kerkmann K, Salamini F, Bartels D (2000) Water deficit triggers phospholipase D activity in the resurrection plant *Craterostigma plantagineum*. *Plant Cell* 12: 111-24.
- Fujita M, Fujita Y, Maruyama K, Seki M, Hiratsu K, Ohme-Takagi M, Tran LS, Yamaguchi-Shinozaki K, Shinozaki K (2004) A dehydration-induced NAC protein, RD26, is involved in a novel ABA-dependent stress-signaling pathway. *Plant J* 39(6): 863-76.
- Fujita Y, Fujita M, Satoh R, Maruyama K, Parvez MM, Seki M, Hiratsu K, Ohme-Takagi M, Shinozaki K, Yamaguchi-Shinozaki K (2005) AREB1 is a transcription activator of novel AREB dependent ABA signaling that enhances drought stress tolerance in Arabidopsis. *Plant Cell* 17: 3470-3488.
- Fujita Y, Yoshida T, Yamaguchi-Shinozaki K (2013) Pivotal role of the AREB/ABF-SnRK2 pathway in ABRE-mediated transcription in response to osmotic stress in plants. *Physiol Plant* 147: 15-27.
- Fukao T, Yeung E, Bailey-Serres J (2011) the submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. *Plant Cell* 23: 412-427.
- Fukuda A, Nakamura A, Tagiri A, Tanaka H, Miyao A, Hirochika H, Tanaka Y (2004) Function, intracellular localization and the importance in salt tolerance of a vacuolar Na⁺/H⁺ antiporter from rice. *Plant Cell Physiol* 45: 146-159.
- Gana JA, Sutton F, Kenefick DG (1997) cDNA structure and expression patterns a low-temperature-specific wheat gene *tacr7*. *Plant Mol Biol* 34: 643-650.
- García MNM, Giammaria V, Grandellis C, Téllez-Iñón MT, Ulloa RM, Capiati DA (2012) Characterization of StABF1, a stress-responsive bZIP transcription factor from *Solanum tuberosum* L. that is phosphorylated by StCDPK2 in vitro. *Planta* 235: 761-778.
- Gilmour SJ, Zarka DG, Stockinger EJ, Salazar MP, Houghton JM, Thomashow MF (1998) Low temperature regulation of Arabidopsis CBF family of AP2 transcriptional activators as an early step in cold-induced COR gene expression. *Plant J* 16:433-42.
- Guillaumie S, Mzid R, Méchin V, Leon C, Hichri I, Destrac-Irvine A, Trossat-Magnin C, Delrot S, Lauvergeat V (2010) The grapevine transcription factor WRKY2 influences the lignin pathway and xylem development in tobacco. *Plant Mol Biol* 72: 215-234.
- Haake V, Cook D, Riechmann JL, Pineda O, Thomashow MF, Zhang JZ (2002) Transcription factor CBF4 is a regulator of drought adaptation in Arabidopsis. *Plant Physiol* 130:639-48
- Hao YJ, Wei W, Song QX, Chen HW, Zhang YQ, Wang F, Zou HF, Lei G, Tian AG, Zhang WK, Ma B, Zhang JS, Chen SY (2011) Soybean NAC transcription factors promote abiotic stress tolerance and lateral root formation in transgenic plants. *Plant J* 68: 302-313.
- Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Mole Biol* 51: 463-499.
- Hegedus D, Yu M, Baldwin D, Gruber M, Sharpe A, Parkin I, Whitwill S, Lydiate D (2003) Molecular

- characterization of Brassica napus NAC domain transcriptional activators induced in response to biotic and abiotic stress. *Plant Mol Biol* 53: 383-397.
- Hobo T, Kowiyama Y, Hattori T (1999) A bZIP factor, TRAB1, interacts with VP1 and mediates abscisic acid-induced transcription. *Proc Natl Acad Sci USA* 96: 15348-15353.
- Hollung K, Espelund M, Jakobsen KS (1994) Another Lea B19 gene (Group 1 barley containing a single 20 amino acid hydrophilic motif) *Plant Mol Biol* 25: 559-564.
- Hoshida H, Tanaka Y, Hibino T, Hayashi Y, Tanaka A, Takabe T, Takabe T (2000) Enhanced tolerance to salt stress in transgenic rice that over expresses chloroplast glutamine synthetase. *Plant Mol Biol* 43: 103-111.
- Hossain MA, Cho JI, Han M, Ahn CH, Jeon JS, An G, Park PB (2010) The ABRE-binding bZIP transcription factor OsABF2 is a positive regulator of abiotic stress and ABA signaling in rice. *J Plant Physiol* 167: 1512-1520
- Hou X, Xie K, Yao J, Qi Z, Xiong L (2009) A homolog of human ski-interacting protein in rice positively regulates cell viability and stress tolerance. *PNAS U S A* 106: 6410-6415.
- Hsieh TH, Lee JT, Charng YY, Chan MT (2002) Tomato plants ectopically expressing Arabidopsis CBF1 show enhanced resistance to water deficit stress. *Plant Physiol* 130: 618-626.
- Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q, Xiong L (2006) Over expressing a NAM, ATAF, and CUC (NAC) Transcription Factor Enhances Drought Resistance and Salt Tolerance in Rice. *Proceedings of the National Academy of Sciences USA* 103(35): 12987-12992.
- Hu H, You J, Fang J, Zhu X, Qi Z, Xiong L (2008) Characterization of transcription factor gene SNAC2 conferring cold and salt tolerance in rice. *Plant Mol Biol* 67: 169-181.
- Hu R, Qi G, Kong Y, Kong D, Gao Q, Zhou G (2010) Comprehensive analysis of NAC domain transcription factor gene family in *Populus trichocarpa*. *BMC Plant Biol*. 10: 145.
- Huang L, Sun Q, Qin F, Li C, Zhao Y, Zhou DX (2007) Down-regulation of a Silent information regulator 2-related histone deacetylase gene, OsSRT1, induces DNA fragmentation and cell death in rice. *Plant Physiol* 144: 1508-1519.
- Huang W, Miao M, Kud J, Niu X, Ouyang B, Zhang J, Ye Z, Kuhl JC, Liu Y, Xiao F (2013) SINAC1, a stress-related transcription factor, is fine-tuned on both the transcriptional and the post-translational level. *New Phytol* 197: 1214-1224.
- Huang XS, Liu JH, Chen XJ (2010) Overexpression of PtrABF gene, a bZIP transcription factor isolated from *Poncirus trifoliata*, enhances dehydration and drought tolerance in tobacco via scavenging ROS and modulating expression of stress-responsive genes. *BMC Plant Biol* 10: 230.
- Huang XY, Chao DY, Gao JP, ZhuMZ, Shi M, Lin HX (2009) A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. *Genes Dev* 23:1805-1817.
- Huq E, Quail PH (2002) PIF4, a phytochrome-interacting bHLH factor, functions as a negative regulator of phytochrome B signaling in Arabidopsis. *EMBO J* 21: 2441-2450.
- Ito Y, Katsura K, Maruyama K, Taji T, Kobayashi M, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2006) Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. *Plant Cell Physiol* 47: 141-153.
- Jain D, Roy N, Chattopadhyay D (2009) CaZF, a plant transcription factor functions through and parallel to HOG and calcineurin pathways in *Saccharomyces cerevisiae* to provide osmotolerance. *Proc Natl Acad Sci USA* 4: e5154.
- Jakoby M, Weisssha B, Droge-Laser W, Vicente-Carbajosa J, Tiedemann J, Kroj T, Parcy F (2002) bZIP transcription factors in Arabidopsis. *Trends in Plant Science* 7: 106-111.
- Jang CS, Lee HJ, Chang SJ, Seo YW (2004) Expression and promoter analysis of the TaLTP1 gene induced by drought and salt stress in wheat (*Triticum aestivum* L.). *Plant Sci* 167: 995-1001.
- Jang IC, Oh SJ, Seo JS, Choi WB, Song SI, Kim CH, Kim YS, Seo HS, Choi YD, Nahm BH, Kim JK (2003) Expression of a bifunctional fusion of the Escherichia coli genes for trehalose-6-phosphate synthase and trehalose-6-phosphate phosphatase in transgenic rice plants increases trehalose accumulation and abiotic stress tolerance without stunting growth. *Plant Physiol* 131: 516-524.
- Jeong JS, Kim YS, Baek KH, Jung H, Ha SH, Do Choi Y, Kim M, Reuzeau C, Kim JK (2010) Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under field drought conditions. *Plant Physiol* 153: 185-197.
- Jia Z, Lian Y, Zhu Y, He J, Cao Z, Wang G (2009) Cloning and characterization of a putative transcription factor induced by abiotic stress in *Zea mays*. *Afr J Biotechnol* 8: 6764-6771.
- Jiali Dong, Yunyun Jiang, Rongjun Chen, Zhengjun Xu, Xiaoling Gao (2011) Isolation of a novel xyloglucan endotransglucosylase (OsXET9) gene from rice and analysis of the response of this gene to abiotic stresses. *Afr J Biotechnol* 10(76): 17424-17434.
- Jiang SY, Bhalla R, Ramamoorthy R, Luan HF, Venkatesh PN, Cai M, Ramachandran S (2012) Over-expression of OSRIP18 increases drought and salt tolerance in transgenic rice plants. *Transgenic Res* 21(4): 785-95.
- Jiang Y, Deyholos MK (2009b) Functional characterization of Arabidopsis NaCl-inducible WRKY25 and WRKY33 transcription factors in abiotic stresses. *Plant Mol Biol* 69: 91-105.
- Jin XF, Jiong AS, Peng RH, Liu JG, Gao F, Chen JM, Yao QH (2010) OsAREB1, an ABREbinding protein responding to ABA and glucose, has multiple functions in Arabidopsis. *BMB Reports* 43: 34-39.

- Johnson RR1, Wagner RL, Verhey SD, Walker-Simmons MK (2002) The abscisic acid-responsive kinase PKABA1 interacts with a seed-specific abscisic acid response element binding factor, TaABF, and phosphorylates TaABF peptide sequences. *Plant Physiol* 130: 837-846.
- Jung C, Seo JS, Han SW, Koo YJ, Kim CH, Song SI, Nahm BH, Choi YD, Cheong JJ (2008) Overexpression of AtMYB44 enhances stomatal closure to confer abiotic stress tolerance in transgenic Arabidopsis. *Plant Physiol* 146: 623-635.
- Kader MA, Seidel T, Gollack D, Lindberg S (2006) Expressions of OsHKT1, OsHKT2, and OsVHA are differentially regulated under NaCl stress in salt-sensitive and salt-tolerant rice (*Oryza sativa* L.) cultivars. *J Exp Bot* 57: 4257-4268.
- Kagaya Y, Ohmiya K, Hattori T (1999) RAV1, a novel DNA-binding protein, binds to bipartite recognition sequence through two distinct DNA-binding domains uniquely found in higher plants. *Nucleic Acids Research*, 27 (2): 470-478.
- Kakali Mukherjee, Aryadeep Roy Choudhury, Bhaskar Gupta, Sudhiranjan Gupta, Dibyendu N Sengupta (2006) An ABRE-binding factor, OSBZ8, is highly expressed in salt tolerant cultivars than in salt sensitive cultivars of *indica* rice. *BMC Plant Biology* 6: 18.
- Kim SY (2006) The role of ABF family bZIP class transcription factors in stress response. *Physiol Plant* 126: 519-527.
- Kobayashi F, Maeta E, Terashima A, Takumi S (2008) Positive role of a wheat HvABI5 ortholog in abiotic stress response of seedlings. *Physiol Plant* 134: 74-86
- Kobayashi Y, Yamamoto S, Minami H, Kagaya Y, Hattori T (2004) Differential activation of the rice sucrose nonfermenting1-related protein kinase2 family by hyperosmotic stress and abscisic acid. *Plant Cell* 16: 1163-1177.
- Kreps JA, Wu Y, Chang HS, Zhu T, Wang X, Harper JF (2002) Transcriptome changes for Arabidopsis in response to salt, osmotic, and cold stress. *Plant Physiology* 130: 2129-2141.
- Kanneganti V, Gupta AK (2008) Overexpression of OsSAP8, a member of stress associated protein (SAP) gene family of rice confers tolerance to salt, drought and cold stress in transgenic tobacco and rice. *Plant Mole Biol* 66: 445-462.
- Lata C, Prasad M (2011) Role of DREBs in regulation of abiotic stress responses in plants. *J Exp Bot* 1460-2431
- Langridge P, Fleury D (2011) Making the most of 'omics' for crop breeding. *Trends in Biotechnol* 29: 33-40.
- Lee SK, Kim BG, Kwon TR, Jeong MJ, Park SR, Lee JW, Byun MO, Kwon HB, Matthews BF, Hong CB, Park SC (2011) Overexpression of the mitogen-activated protein kinase gene OsMAPK33 enhances sensitivity to salt stress in rice (*Oryza sativa* L.). *J Biosci* 36: 139-151.
- Li XX, Duan XP, Jiang HX, Sun YJ, Tang YP, Yuan Z, Guo JK, Liang WQ, Chen L, Yin JY, Ma H, Wang J, Zhang DB (2006) Genome wide analysis of basic/helix-loop-helix transcription factor family in rice and Arabidopsis. *Plant Physiol* 141: 1167-1184.
- Li B, Wei AY, Song CX, Li N, Zhang JR (2008) Heterologous expression of the TsVP gene improves the drought resistance of maize. *Plant Biotechnol J* 6: 146-159.
- Li Z, Zhang L, Wang A, Xu X, Li J (2013) Ectopic overexpression of SlHsfA3, a heat stress transcription factor from tomato, confers increased thermo tolerance and salt hypersensitivity in germination in transgenic Arabidopsis. *PLoS One* 8: e54880.
- Li ZC, Zhang XC, Zhang L, Thuang BC, Zhang CL, Wang GY, Fu YC (2004) Expression of MtD1 gene in transgenic rice leads to enhanced salt-tolerance. *J China Agri University* 9: 38-43.
- Li ZY, Chen SY (2000) Isolation and characterization of a salt- and drought-inducible gene for S-adenosylmethionine decarboxylase from wheat (*Triticum aestivum* L.). *Plant Physiol* 156: 386-393.
- Liao Y, Zou HF, Wei W, Hao YJ, Tian AG, Huang J, Liu YF, Zhang JS, Chen SY (2008) Soybean GmbZIP44, GmbZIP62 and GmbZIP78 genes function as negative regulators of ABA signaling and confer salt and freezing tolerance in transgenic Arabidopsis. *Planta* 228: 225-240.
- Licausi F, Ohme-Takagi M, Perata P (2013) APETALA2/Ethylene Responsive Factor (AP2/ERF) transcription factors: mediators of stress responses and developmental programs. *New Phytol* 199: 639-649.
- Lingam S, Mohrbacher J, Brumbarova T, Potuschak T, Fink-Straube C, Blondet E, Genschik P, Bauer P (2011) Interaction between the bHLH transcription factor FIT and ETHYLENE INSENSITIVE3/ETHYLENE INSENSITIVE3-LIKE1 reveals molecular linkage between the regulation of iron acquisition and ethylene signaling in Arabidopsis. *Plant Cell* 23: 1815-1822.
- Lippold F, Diego H, Sanchez DH, Musialak M, Schlereth A, Scheible WR, Hinch DK, Udvardi MK (2009) AtMyb41 regulates transcriptional and metabolic responses to osmotic stress in Arabidopsis. *Plant Physiol* 149: 1761-1772.
- Liu AL, Zou J, Liu CF, Zhou XY, Zhang XW, Luo GY, Chen XB (2013) Over-expression of OsHsfA7 enhanced salt and drought tolerance in transgenic rice. *BMB Rep* 46(1): 31-6.
- Liu JG, Qin QL, Zhang Z, Peng RH, Xiong AG, Chen JM, Yao QH (2009) OsHSF7 gene in rice, *Oryza sativa* L., encodes a transcription factor that functions as a high temperature receptive and responsive factor. *BMB Rep* 42: 16-21.
- Liu Y, Subhash C, Yan J, Song C, Zhao J, Li J (2011) Maize leaf temperature responses to drought: Thermal imaging and quantitative trait loci (QTL) mapping. *Environmental and Experimental Botany* 71: 158-165.
- Lu G, Gao C, Zheng X, Han B (2009) Identification of OsZIP72 as a positive regulator of ABA response and drought tolerance in rice. *Planta* 229: 605-615.
- Ludwig A, Romeis T, Jones JD (2004) CDPK-mediated signalling pathways: specificity and cross-talk. *Journal of Experimental Botany* 55: 181-8.

- Luo M, Gu SH, Zhao F, Zhang F, Wu NH (2006) Rice GTPase OsRacB: Potential Accessory Factor in Plant Salt-stress Signaling. *Acta Biochimica et Biophysica Sinica* 38(6): 393-402.
- Ma Q, Dai X, Xu Y, Guo J, Liu Y, Chen N, Xiao J, Zhang D, Xu Z, Zhang X, Chong K (2009) Enhanced Tolerance to Chilling Stress in OsMYB3R-2 Transgenic Rice Is Mediated by Alteration in Cell Cycle and Ectopic Expression of Stress Genes. *Plant Physiology* 150(1): 244-256.
- Magome H, Yamaguchi S, Hanada A, Kamiya Y, Oda K (2004) Dwarf and delayed flowering 1, a novel Arabidopsis mutant deficient in gibberellin biosynthesis because of over expression of a putative AP2 transcription factor. *Plant J* 37:720-29.
- Mahajan Shilpi, Tuteja Narendra (2005). Cold, salinity and drought stresses: An overview *Archives of Biochemistry and Biophysics* 444: 139-158.
- Mangelsen E, Kilian J, Berendzen KW, Kolukisaoglu UH, Harter K, Jansson C, Wanke D (2008) Phylogenetic and comparative gene expression analysis of barley (*Hordeum vulgare*) WRKY transcription factor family reveals putatively retained functions between monocots and dicots. *BMC Genomics* 9: 194.
- Mani S, Van de Cotte B, Montagu M, Verbruggen N (2002) Altered levels of proline dehydrogenase cause hypersensitivity to proline and its analogs in Arabidopsis. *Plant Physiol* 128:73-83.
- Mao X, Zhang H, Qian X, Li A, Zhao G, Jing R (2012) TaNAC2 a NAC type wheat transcription factor conferring enhanced multiple abiotic stress tolerances in Arabidopsis. *J Exp Bot* 63: 2933-2946.
- Marcotte WR Jr, Russell SH, Quatrano RS (1989) Abscisic acid responsive sequences from the em gene of wheat. *Plant Cell* 1989: 969-976.
- Matsukura S, Mizoi J, Yoshida T, Todaka D, Ito Y, Maruyama K, Shinozaki K, Yamaguchi-Shinozaki K (2010) Comprehensive analysis of rice DREB2-type genes that encode transcription factors involved in the expression of abiotic stress-responsive genes. *Mol Genet Genomics* 283: 185-196.
- Meng C, Cai C, Zhang T, Guo W (2009) Characterization of six novel NAC genes and their responses to abiotic stresses in *Gossypium hirsutum* L *Plant Sci* 176 352-359.
- Mitsuda N, Ohme-Takagi M (2009) Functional analysis of transcription factors in Arabidopsis. *Plant Cell Physiol* 50: 1232-1248.
- Mittler R (2006) Abiotic stress, the field environment and stress combination. *Trends in Plant Sci* 11: 15-19.
- Mittler R, Vanderauwera S, Gollery M, Van Breusegem F (2004) Reactive oxygen gene network of plants. *Trends in Plant Sci* 9: 490-498.
- Motomura Yoichi, Kobayashi Fuminori, Iehisa Julio CM, Takumi Shigeo (2013) A major quantitative trait locus for cold-responsive gene expression is linked to frost-resistance gene Fr-A2 in common wheat. *Breeding Sci* 63: 58-67.
- Mukhopadhyay A, Vij S, Tyagi AK (2004) Overexpression of a zinc-finger protein gene from rice confers tolerance to cold, dehydration, and salt stress in transgenic tobacco. *PNAS* 101: 6309-6314.
- Mundy J, Nielsen HB, Brodersen P (2006) Crosstalk. *Trends in Plant Sci* 11: 63-64.
- Nakashima K, Ito Y, Yamaguchi-Shinozaki K (2009) Transcriptional regulatory networks in response to abiotic stresses in Arabidopsis and grasses. *Plant Physiol* 149: 88-95.
- Nakashima K, Takasaki H, Mizoi J, Shinozaki K, Yamaguchi-Shinozaki K (2012) NAC transcription factors in plant abiotic stress responses. *Biochim. Biophys. Acta* 1819: 97-103.
- Nakata M, Mitsuda N, Herde M, Koo AJ, Moreno JE, Suzuki K, Howe GA, Ohme-Takagi M (2013) A bHLH-type transcription factor, ABA-INDUCIBLE BHLH-TYPE TRANSCRIPTION FACTOR/ JA-ASSOCIATED MYC2-LIKE1, acts as a repressor to negatively regulate jasmonate signaling in Arabidopsis. *Plant Cell* 25: 1641-1656.
- Nelson DE, Repetti PP, Adams TR, Creelman RA, Wu J, Warner DC, Anstrom DC, Bensen RJ, Castiglioni PP, Donnarummo MG, Hinchey BS, Kumimoto RW, Maszle DR, Canales RD, Krolikowski KA, Dotson SB, Gutterson N, Ratcliffe OJ, Heard JE (2007) Plant nuclear factor Y (NF-Y) B subunits confer drought tolerance and lead to improved corn yields on water-limited acres. *Proc Natl Acad Sci USA* 104: 16450-16455.
- Nijhawan A, Jain M, Tyagi AK, Khurana JP (2008) Genomic survey and gene expression analysis of the basic leucine zipper transcription factor family in rice. *Plant Physiology* 146 (2): 2 333-350.
- Niu CF, Wei W, Zhou QY, Tian AG, Hao YJ, Zhang WK, Mai B, Lin Q, Zhang ZB, Zhang JS, Chen SY (2012) Wheat WRKY genes TaWRKY2 and TaWRKY19 regulate abiotic stress tolerance in transgenic Arabidopsis plants. *Plant Cell Environ* 35: 1156-1170
- Niu X, Helentjaris T, Bate NJ (2002) Maize ABI4 binds coupling element1 in abscisic acid and sugar response genes. *Plant Cell* 14: 2565-2575.
- Nuruzzaman, M, Sharoni AM, Satoh K, Moumeni A, Venuprasad R, Serraj R (2012) Comprehensive gene expression analysis of the NAC gene family under normal growth conditions, hormone treatment, and drought stress conditions in rice using near-isogenic lines (NILs) generated from crossing Aday Selection (drought tolerant) and IR64. *Mol Genet Genomics* 287: 389-410.
- Ogawa D, Yamaguchi K, Nishiuchi T (2007) High-level overexpression of the Arabidopsis HsfA2 gene confers not only increased thermotolerance but also salt/osmotic stress tolerance and enhanced callus growth. *J Exp Bot* 58: 3373-3383.
- Oh SJ, Kwon CW, Choi DW, Song SI, Kim JK (2007) Expression of barley HvCBF4 enhances tolerance to abiotic stress in transgenic rice. *Plant Biotechnol J* 5: 646-656.
- Oh SJ, Kim YS, Kwon CW, Park HK, Jeong JS, Kim JK (2009) Over expression of the transcription factor

- AP37 in rice improves grain yield under drought conditions. *Plant Physiol* 150:1368-1379.
- Ooka H, Satoh K, Doi K, Nagata T, Otomo Y, Murakami K, Matsubara K, Osato N, Kawai J, Carninci P, Hayashizaki Y, Suzuki K, Kojima K, Takahara Y, Yamamoto K, Kikuchi S (2003) Comprehensive analysis of NAC family genes in *Oryza sativa* and *Arabidopsis thaliana*. *DNA Res* 20: 239-247.
- Park HY, Seok HY, Woo DH, Lee SY, Tarte VN, Lee EH, Lee CH, Moon YH (2011a) AtERF71/HRE2 transcription factor mediates osmotic stress response as well as hypoxia response in *Arabidopsis*. *Biochem Biophys Res Commun* 414: 135-141.
- Park MR, Yun KY, Mohanty B, Herath V, Xu F, Wijaya E, Bajic VB, Yun SJ, De Los Reyes BG (2010) Supra-optimal expression of the cold-regulated OsMyb4 transcription factor in transgenic rice changes the complexity of transcriptional network with major effects on stress tolerance and panicle development. *Plant Cell Environ* 33: 2209-2230.
- Pater S, Greco V, Pham K, Memelink J, Kijne J (1996) Characterization of a zinc-dependent transcriptional activator from *Arabidopsis*. *Nucleic Acids Res* 24: 4624-4631.
- Pavletich NP, Pabo CO (1991) Zinc finger-DNA recognition: crystal structure of a Zif268-DNA complex at 2.1 Å. *Science* 252: 809-817.
- Peleg Z, Apse MP, Blumwald E (2011). Engineering Salinity and Water Stress Tolerance in Crop Plants: Getting closer to the Field. *Advance Bot Res* 57: 405-428.
- Pellegrineschi A, Reynolds M, Paceco M, Brito RM, Almeraya R, Yamaguchi-Shinozaki K, Hoisington D (2004) Stress-induced expression in wheat of the *Arabidopsis thaliana* DREB1A gene delays water stress symptoms under greenhouse conditions. *Genome* 47: 493-500.
- Peng HH, Shan W, Kuang JF, Lu WJ, Chen JY (2013) Molecular characterization of cold-responsive basic helix-loop-helix transcription factors MabHLHs that interact with MaICE1 in banana fruit. *Planta*. 238(5): 937-53.
- Peng YL, Wang YS, Cheng H (2013) Characterization and expression analysis of three CBF/DREB1 transcriptional factor genes from mangrove *Avicennia marina*. *Genome* 141: 68-76.
- Phean-O-Pas S, Punteeranurak P, Buaboocha T (2005) Calcium signaling-mediated and differential induction of calmodulin gene expression by stress in *Oryza sativa* L. *J Biochem Mol Biol* 38(4): 432-9.
- Pinheiro GL, Marques CS, Costa MD, Reis PA, Alves MS, Carvalho CM, Fietto LG, Fontes EP (2009) Complete inventory of soybean NAC transcription factors: sequence conservation and expression analysis uncover their distinct roles in stress response. *Gene* 444: 10-23.
- Qiao WH, Zhao XY, Li W, Luo Y, Zhang XS (2007) Over expression of AeNHX1, a root-specific vacuolar Na⁺/H⁺ antiporter from *Agropyron elongatum*, confers salt tolerance to *Arabidopsis* and *festuca* plants. *Plant Cell Rep* 26: 1663-1672.
- Quan R, Shang M, Zhang H, Zhao Y, Zhang J (2004). Engineering of enhanced glycine betaine synthesis improves drought tolerance in maize. *Plant Biotechnol J* 2: 477-486.
- Redillas MCFR, Jeong JS, Kim YS, Jung H, Bang SW, Choi YD, Ha SH, Reuzeau C, Kim JK (2012) The overexpression of OsNAC9 alters the root architecture of rice plants enhancing drought resistance and grain yield under field conditions. *Plant Biotechnol J* 10: 792-805.
- Riechmann JL, Heard J, Martin G, Reuber L, Jiang CZ, Keddie J, Adam L, Pineda O, Ratcliffe OJ, Samaha RR, Creelman R, Pilgrim M, Broun P, Zhang JZ, Gandhari D, Sherman BK, Yu GL (2000) *Arabidopsis* transcription factors: genome-wide comparative analysis among eukaryotes. *Science* 290: 2105-2110.
- Rodrigues MA, Gomes DA, Nathanson MH, Leite MF (2009) Nuclear calcium signaling: a cell within a cell. *Braz J Med Biol Res* 42:17-20
- Rushton DL, Tripathi P, Rabara RC, Lin J, Ringler P, Boken AK, Langum TJ, Smidt L, Boomsma DD, Emme NJ, Chen X, Finer JJ, Shen Q, Rushton PJ (2012) WRKY transcription factors: key components in abscisic acid signaling. *Plant Biotechnol J* 10: 2-11
- Rushton PJ, Somssich IE, Ringler P, Shen QJ (2010) WRKY transcription factors. *Trends in Plant Science* 15: 247-258.
- Rushton, PJ, Bokowiec MT, Han S, Zhang H, Brannock JF, Chen X.(2008) Tobacco transcription factors: novel insights into transcriptional regulation in the Solanaceae. *Plant Physiol*. 147: 280-295.
- Saijo Y, Hata S, Kyojuka J, Shimamoto K, Izui K (2000) Over expression of a single Ca²⁺-dependent protein kinase confers both cold and salt/drought tolerance on rice plants. *Plant J* 23: 319-327.
- Saito K, Miura K, Nagano K, Hayano-Saito Y, Araki H, Kato A (2001). Identification of two closely linked quantitative trait loci for cold tolerance on chromosome 4 of rice and their association with anther length. *Theor Appl Genet* 103: 862-868.
- Sakamoto A, Alia, Murata N (1998) Metabolic engineering of rice leading to biosynthesis of glycinebetaine and tolerance to salt and cold. *Plant Mol Biol* 38: 1011-1019.
- Sakamoto H, Maruyama K, Sakuma Y, Meshi T, Iwabuchi M, Shinozaki K, Yamaguchi-Shinozaki K (2004) *Arabidopsis* Cys2/His2-type zinc finger proteins function as transcription repressors under drought, cold and high-salinity stress conditions. *Plant Physiol* 136: 2734-2746.
- Sakuma Y, Liu Q, Dubouzet JG, Abe H, Shinozaki K, Yamaguchi- Shinozaki K (2002) DNA-binding specificity of the ERF/AP2 domain of *Arabidopsis* DREBs, transcription factors involved in dehydration- and cold-inducible gene expression. *Biochem Biophys Res Commun* 290: 998-1009.
- Sakuma Y, Maruyama K, Qin F, Osakabe Y, Shinozaki K, Yamaguchi- Shinozaki K (2006) Dual function of an *Arabidopsis* transcription factor DREB2A in water-stress- responsive and heat-stress responsive gene

- expression. *Proc Natl Acad Sci USA* 103: 18822–18827.
- Schmidt R, Schippers JHM, Welker A, Mieulet D, Guiderdoni E, Mueller-Roeber B (2012) Transcription factor OsHsfC1b regulates salt tolerance and development in *Oryza sativa* ssp. *japonica*. *AoB Plants* 2012: pls011.
- Seki M, Ishida J, Narusaka M, Fujita M, Nanjo T, Umezawa T, Kamiya A, Nakajima M, Enju A, Sakurai T, Satou M, Akiyama K, Yamaguchi-Shinozaki K, Carninci P, Kawai J, Hayashizaki Y, Shinozaki K (2002) Monitoring the expression pattern of around 7,000 Arabidopsis genes under ABA treatments using a full-length cDNA microarray. *Funct Integr Genomics* 2: 282–291.
- Seo JS, Joo J, Kim MJ, Kim YK, Nahm BH, Song SI, Cheong JJ, Lee JS, Kim JK, Do Choi Y (2011a) OsbHLH148, a basic helix-loop-helix protein, interacts with OsJAZ proteins in a jasmonate signaling pathway leading to drought tolerance in rice. *Plant J* 65: 907–92.
- Seo PJ, Xiang F, Qiao M, Park JY, Lee YN, Kim SG, Lee YH, Park WJ, Park CM (2009) The MYB96 transcription factor mediates abscisic acid signaling during drought stress response in Arabidopsis. *Plant Physiol* 151:275–289
- Shin DJ (2011) Expression of StMYB1R-1, a novel potato single MYB-like domain transcription factor, increases drought tolerance. *Plant Physiol* 155: 421–432.
- Shen YG, Zhang WK, Yan DQ, Du BX, Zhang JS, Liu Q, Chen SY (2003b) Characterization of a DRE-binding transcription factor from a halophyte *Atriplex hortensis*. *Theor Appl Genet* 107: 155–161.
- Shim JS, Jung C, Lee S, Min K, Lee YW, Choi Y, Lee JS, Song JT, Kim JK, Choi YD (2013) AtMYB44 regulates WRKY70 expression and modulates antagonistic interaction between salicylic acid and jasmonic acid signaling. *Plant J*. 73 483–495.
- Shinozaki K and Yamaguchi-Shinozaki K (2000) Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. *Curr Opin Plant Biol*.3: 217–223
- Shinozaki K, Yamaguchi-Shinozaki K, Seki M (2003) Regulatory network of gene expression in the drought and cold stress responses. *Curr Opin Plant Biol* 6: 410–417.
- Shou H, Bordallo P, Wang K (2004) Expression of the nicotiana protein kinase (NPK1) enhanced drought tolerance in transgenic maize. *J Exp Bot* 55: 1013–1019.
- Shu L, Lou Q, Ma C, Ding W, Zhou J, Wu J, Feng F, Lu X, Luo L, Xu G, Mei H (2011) Genetic, proteomic and metabolic analysis of the regulation of energy storage in rice seedlings in response to drought. *Proteomics* 11 4122–4138.
- Sivitz AB, Hermand V, Curie C, Vert G (2012) Arabidopsis bHLH100 and bHLH101 control iron homeostasis via a FIT-independent pathway. *PLoS ONE* 7: e44843.
- Song CP, Agarwal M, Ohta M, Guo Y, Halfter U, Wang P, Zhua JK (2005) Role of an Arabidopsis AP2/EREBP-type transcriptional repressor in abscisic acid and drought stress responses. *Plant Cell* 17:2384–96.
- Souer E, van Houwelingen A, Kloos D, Mol J, Koes R (1996) The no apical meristem gene of *Petunia* is required for pattern formation in embryos and flowers and is expressed at meristem and primordia boundaries. *Cell* 85: 159–170.
- Takatsuji H, Mori M, Benfey P, Ren L, Chua NH (1992) Characterization of a zinc finger DNA-binding protein expressed specifically in *Petunia* petals and seedlings. *EMBO J* 11: 241–249.
- Tanaka K, Hibino T, Hayasi Y, Tanaka A, Kishitani S, Takabe T, Yokota S, Takabe T (1999) Salt tolerance of transgenic rice over expression yeast mitochondrial Mn-SOD in chloroplasts. *Plant Sci* 148: 131–138.
- Tao Z, Liu H, Qiu D, Zhou Y, Li X, Xu C, Wang S (2009) A pair of allelic WRKY genes play opposite roles in rice-bacteria interactions. *Plant Physiol* 151: 936–948
- Thomashow MF (1999) Plant cold acclimation: freezing tolerance genes and regulatory mechanisms, *Annual Review of Plant Physiology and Plant Molecular Biology* 50: 571–599.
- Tilman D., Cassman K.G., Matson P.A., Naylor R., Polasky S. Agricultural sustainability and intensive production practices. *Nature* 2002; 418: 671–677.
- Tominaga-Wada R, Iwata M, Nukumizu Y, Sano R, Wada T (2012) A full-length R-like basic-helix-loop-helix transcription factor is required for anthocyanin upregulation whereas the N-terminal region regulates epidermal hair formation. *Plant Sci* 183: 115–122.
- Tran LS, Nakashima K, Sakuma Y, Simpson SD, Fujita Y, Maruyama K, Fujita M, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2004) Isolation and functional analysis of Arabidopsis stress-inducible NAC transcription factors that bind to a drought-responsive cis element in the early responsive to dehydration stress 1 promoter. *Plant Cell* 16: 2481–2498.
- Uga Y, Okuno K, Yano M (2011) Dro1, a major QTL involved in deep rooting of rice under upland field conditions. *J Exp Bot* 62: 2485–2494.
- Uno Y, Furihata T, Abe H, Yoshida R, Shinozaki K, et al. 2000. Arabidopsis basic leucine zipper transcription factors involved in an abscisic acid-dependent signal transduction pathway under drought and high-salinity conditions. *Proc. Natl. Acad. Sci. USA* 97:11632–37
- Valliyodan B, Nguyen HT (2006) Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Plant Biology* 9:1–7.
- Vlot AC, Dempsey DMA, Klessig DF (2009) Salicylic Acid, a Multifaceted Hormone to Combat Disease. *Annual Review of Phytopathology* 47: 177–206.
- Von Koskull-Döring P, Scharf KD, Nover L (2007) The diversity of plant heat stress transcription factors. *Trends Plant Sci* 12: 452–457.
- Wan L, Zhang J, Zhang H, Zhang Z, Quan R, Zhou S, Huang R (2011) Transcriptional activation of OsDERF1 in OsERF3 and OsAP2-39 negatively modulates ethylene synthesis and drought tolerance in rice. *PLoS ONE* 6: e25216.

- Wang Q, Guan Y, Wu Y, Chen H, Chen F, Chu C (2008) Over expression of a rice OsDREB1F gene increases salt, drought, and low temperature tolerance in both Arabidopsis and rice. *Plant Mol Biol* 67: 589-602.
- Wilkins O, Nahal H, Foong J, Provart NJ, Campbell MM (2009) Expansion and diversification of the Populus R2R3-MYB family of transcription factors. *Plant Physiol* 149: 981–993.
- Woo HA, Yim SH, Shin DH, Kang D, Yu DY, Rhee SG (2010) Inactivation of peroxiredoxin I by phosphorylation allows localized H₂O₂ accumulation for cell signaling. *Cell* 140(4):517-28.
- Wu CY, You CJ, Li CH, Long T, Chen GX, Byrne ME, Zhang QF (2008) RID1, encoding a Cys2/His2-type zinc finger transcription factor, acts as a master switch from vegetative to floral development in rice. *Proc Natl Acad Sci U S A* 105(35):12915-12920.
- Xia N, Zhang G, Liu X, Deng L, Cai G, Zhang Y, Wang X, Zhao J, Huang L, Kang Z (2010a) Characterization of a novel wheat NAC transcription factor gene involved in defense response against stripe rust pathogen infection and abiotic stresses. *Mol Biol Rep* 37: 3703–3712.
- Xiang Y, Tang N, Du H, Ye HY, Xiong LZ (2008) Characterization of OsZIP23 as a key player of the basic leucine zipper transcription factor family for conferring abscisic acid sensitivity and salinity and drought tolerance in rice. *Plant Physiology* 148: 1938–1952
- Xie XB, Li S, Zhang RF, Zhao J, Chen YC, Zhao Q, Yao YX, You CX, Zhang XS, Hao YJ (2012) The bHLH transcription factor MdbHLH3 promotes anthocyanin accumulation and fruit colouration in response to low temperature in apples. *Plant Cell Environ* 35: 1884–1897.
- Xiong L, Schumaker KS, Zhu JK (2002) Cell signaling during cold, drought, and salt stress. *Plant Cell* 165–183.
- Xiong, L., and Zhu, J.K. (2002). Molecular and genetic aspects of plant responses to osmotic stress. *Plant Cell Environ.* 25 131–139.
- Xu K, Mackill DJ (1996) A major locus for submergence tolerance mapped on rice chromosome 9. *Molecular Breeding* 2: 219-224.
- Xu ZS, Xia LQ, Chen M, Cheng XG, Zhang RY, Li LC, Zhao YX, Lu Y, Ni ZY, Liu L, Qiu ZG, Ma YZ (2007) Isolation and molecular characterization of the *Triticum aestivum* L. ethylene-responsive factor 1 (TaERF1) that increases multiple stress tolerance. *Plant Mol Biol* 65: 719–732.
- Yamaguchi-Shinozaki K, Shinozaki K (1994) A novel cis-acting element in an Arabidopsis gene is involved in responsiveness to drought, low temperature, or high-salt stress. *Plant Cell* 6: 251–264.
- Yamaguchi-Shinozaki K, Shinozaki K (2005) Organization of cis-acting regulatory elements in osmotic- and cold-stress-responsive promoters. *Trends Plant Sci* 10: 88–94.
- Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annu Rev Plant Biol* 57: 781–803.
- Yang SD, Seo PJ, Yoon HK, Park CM (2011) The Arabidopsis NAC transcription factor VNI2 integrates abscisic acid signals into leaf senescence via the COR/RD genes. *Plant Cell* 23: 2155–2168.
- Yanhui C, Xiaoyuan Y, Kun H, Meihua L, Jigang L, Zhaofeng G, Zhiqiang L, Yunfei Z, Xiaoxiao W, Xiaoming Q, Yunping S, Xiaohui D, Jingchu L, Xing-Wang D, Zhangliang C, Hongya G, Li-Jia Q (2006). The MYB transcription factor superfamily of Arabidopsis: expression analysis and phylogenetic comparison with the rice MYB family. *Plant Molecular Biology* 60: 107–124.
- Yet S, Moffatt BA, Griffith M, Xiong F, Yang DSC, Wiseman SB, Sarhan F, Danyluk J, Xue YQ, Hew CL, Doeherty-Kirby, A, Lajoie G (2000) Chitinase genes responsive to cold encode antifreeze proteins in winter cereals. *Plant Physiol* 124: 1251–1263.
- Yoshida T, Sakuma Y, Todaka D, Maruyama K, Qin F (2008) Functional analysis of an Arabidopsis heat-shock transcription factor HsfA3 in the transcriptional cascade downstream of the DREB2A stress-regulatory system. *Biochem Biophys Res Commun* 368: 515–521
- Zhang H, Mao X, Wang C, Jing R (2010) Over expression of a common wheat gene TaSnRK2.8 enhances tolerance to drought, salt and low temperature in Arabidopsis. *PLoS ONE* 5(12): e16041
- Zhang J, Nguyen HT, Blum A (1999) Genetic analysis of osmotic adjustment in crop plants. *J Exp Bot* 50: 291–302.
- Zhang Z, Huang R (2010) Enhanced tolerance to freezing in tobacco and tomato overexpressing transcription factor TERF2/LeERF2 is modulated by ethylene biosynthesis. *Plant Mol Biol* 73: 241–249.
- Zhang Z, Zhang H, Quan R, Wang XC, Huang R (2009) Transcriptional regulation of ethylene response factor LeERF2 in the expression of ethylene biosynthesis genes controls ethylene production in tomato and tobacco. *Plant Physiol* 150: 365–377.
- Zheng X, Chen B, Lu G, Han B (2009) Over expression of a NAC transcription factor enhances rice drought and salt tolerance. *Biochem Biophys Res Commun* 379: 985-989.
- Zhong R, McCarthy RL, Lee C, Ye ZH (2011) Dissection of the transcriptional program regulating secondary wall biosynthesis during wood formation in poplar. *Plant Physiol* 157: 1452–1468.
- Zhou QY, Tian AG, Zou HF, Xie ZM, Lei G, Huang J, Wang CM, Wang HW, Zhang JS, Chen SY (2008) Soybean WRKY-type transcription factor genes, GmWRKY13, GmWRKY21, and GmWRKY54, confer differential tolerance to abiotic stresses in transgenic Arabidopsis plants. *Plant Biotechnol J* 6: 486–503.
- Zhu JK (2001) Cell signaling under salt, water and cold stresses. *Curr Opin Plant Biol* 4: 401-6.
- Zhu JK (2002) Salt and drought stress signal transduction in plants. *Annual Review of Plant Biology* 53: 247-273.

Zhu Q, Zhang J, Gao X, Tong J, Xiao L, Li W, Zhang H (2010) The Arabidopsis AP2/ERF transcription factor RAP2.6 participates in ABA, salt and osmotic stress responses. *Gene* 457: 1–12.

Zou M, Guan Y, Ren H, Zhang F, Chen F (2008) A bZIP transcription factor, OsABI5, is involved in rice fertility and stress tolerance. *Plant Mol Biol* 66: 675–683.

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