Transcription Factor-Mediated Abiotic Stress Signaling in Rice

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ABSTRACT

Abiotic stresses are the major cause that limits productivity of crop plants worldwide. Plants respond to these stress conditions at physiological and molecular levels. At the molecular level, the expression of thousands of genes is altered in response to various abiotic stress conditions. Several studies have been performed to find out the role of these genes in abiotic stress signaling. However, among these, transcription factor encoding genes are most important because many of them act as 'key or master regulators' of gene expression. Transcription factors appear to be attractive targets to unravel the molecular mechanisms of abiotic stress responses and engineering abiotic stress tolerance in plants. However, the role of only a few transcription factors in abiotic stress responses have been elucidated in rice until now and require a detailed investigation for several such candidate genes. In this review, our endeavour is to develop a comprehensive understanding of the intricate regulatory network of transcription factors operative during abiotic stress responses with greater emphasis on rice.

CONTENTS

INTRODUCTION

Plants are extremely prone to environmental onslaughts like various abiotic stresses and pathogen invasion. Abiotic stress factors such as water-deficit, high salinity and extremes of temperature cause great loss in crop productivity worldwide. Since the food demand is far exceeding the growing population, optimum crop productivity is an immediate matter of concern and needs to be addressed using various biotechnological techniques/applications. Plants have developed intricate machinery to respond and adapt these adverse conditions both at physiological and molecular levels. Hence, it is very important to understand the molecular mechanisms underlying various abiotic stress responses. This knowledge would enable development of stress tolerant crops with optimum yield and better sustenance. Abiotic stress is a multigenic trait and hence, it is difficult to decipher the complete regulatory network involved in abiotic stress responses. Although current research has divulged several key genes, quantitative trait loci and gene regulatory networks that mediate plant responses to various abiotic stresses, the comprehensive understanding of this complex trait has still not been deciphered.

The knowledge available in context of abiotic stress regulatory networks in plants is preliminary. However, over the years, transcriptome analysis of model plant species like *Arabidopsis* and rice have identified thousands of stress-responsive genes involved in various biological processes (Urano *et al.* 2010). Among them, transcription factors are the key regulators of gene expression and uniquely mediate abiotic stress responses in plants via several regulons in the complex signal transduction network. Understanding the molecular basis of signaling cascades is of utmost importance in order to decipher the abiotic stress regulatory network. Considerable work regarding characterization of transcription factors involved in signaling cascades has been carried out in *Arabidopsis* and fundamental knowledge has been established in rice as well. Rice is an annual, monocot model crop plant with great nutritive value. It is consumed as a staple food in large parts of the world (Gao
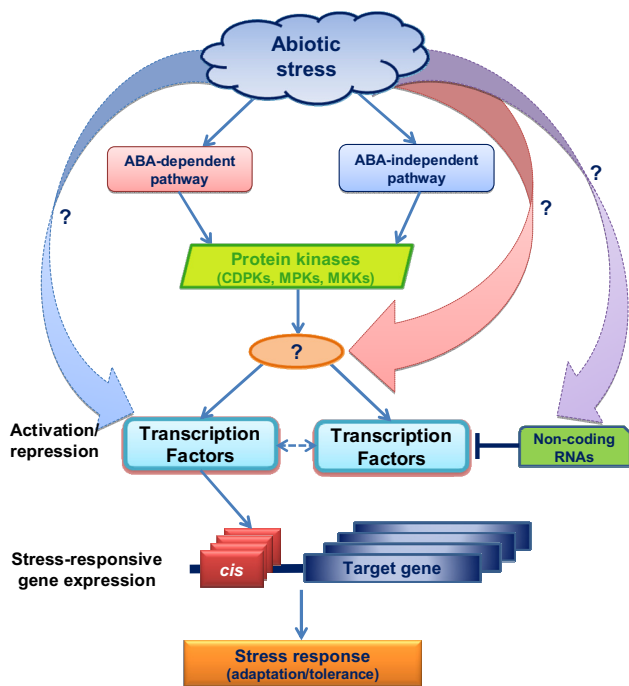
Invited Review

Fig. 1 Model for transcription factor mediated abiotic stress signaling. Abiotic stress response is mediated by ABA-dependent or independent pathways via protein kinases followed by activation/repression of transcription factors directly or indirectly. The transcription factors are also regulated by non-coding RNAs. Transcription factors either independently or in conjunction/coordination with other transcription factors regulate the expression of several downstream target genes, which leads to a stress response.

et al. 2008). Therefore, the biology of abiotic stress responses needs to be understood completely to devise new/better technologies for rice improvement. Previously, several reports have also described abiotic stress signaling and regulatory networks in plants (Chinnusamy *et al.* 2004; Mahajan and Tuteja 2005; Vij and Tyagi 2007; Nakashima *et al.* 2009; Hirayama and Shinozaki 2010; Urano *et al.* 2010; Yang *et al.* 2010; Hardiato and Tran 2011; Qin *et al.* 2011; Todaka *et al.* 2012). However, the complexity of the signaling cascades and regulatory networks in the abiotic stress responses needs to be unfurled exhaustively in the future. This review highlights advances in understanding abiotic stress regulatory networks in plants with a greater emphasis on rice. It aims to provide insights into the abiotic stress signaling mediated by rice transcription factors and focuses on the importance of transcription factors as promising candidates for future biotechnological implications.

IMPORTANCE OF TRANSCRIPTION FACTORS

Transcription factors comprise of a major group of regulatory proteins, which participate in the complex orchestration of the abiotic stress regulatory network (**Fig. 1**). In general, abiotic stress response is mediated via ABA-dependent and independent pathways. The production of several protein kinases is triggered in response to abiotic stress factors and they in turn, act directly or indirectly on transcription factors modulating their action. These transcription factors at the same time can be regulated by other unknown components and small non-coding RNA molecules. Transcription factors act as master regulators controlling the expression of many target genes either singularly or in conjunction with other transcription factors by specific binding to *cis*-regulatory elements in the promoter of downstream target genes (Nakashima *et al.* 2009). The *cis*- and *trans*-acting elements of several transcription factors in plants, especially *Arabidopsis* and rice, have been analyzed in order to decipher the molecular mechanisms involved in

transcriptional regulation (Yamaguchi and Shinozaki 2005; Fujita *et al.* 2006; Zou *et al.* 2011). Transcription factors may coordinate/regulate several pathways in parallel, leading to diverse abiotic stress responses (**Fig. 1**). They regulate the expression of stress-responsive genes and appear to be the link between sensing of the stress signals and generation of abiotic stress responses (Golldack *et al.* 2011). The transcription factors act as molecular switches and culmination points of signal transduction in abiotic stress responses (Yamaguchi and Shinozaki 2005, 2006). Among the numerous plant transcription factors involved in abiotic stress responses, it is particularly important to identify 'key or master regulators' and other associated regulatory components, so that the hierarchy of molecular mechanisms in the regulatory network could be revealed.

DIFFERENTIAL EXPRESSION OF TRANSCRIPTION FACTORS UNDER ABIOTIC STRESS CONDITIONS

The expression profiles of various transcription factors have been studied in different plants at single gene, gene family and whole genome levels. Over the years, numerous transcription factor encoding genes have been reported to be differentially expressed during various abiotic stress conditions. Rice transcription factors induced during drought stress responses at different developmental stages have also been delineated recently (Yue *et al.* 2006; Zhou *et al.* 2007; Rabello *et al.* 2008; Ray *et al.* 2011). Earlier, using microarray technology, Rabbani *et al.* (2003) conducted transcriptome analysis of 1700 independent rice cDNAs under drought, cold and salinity stresses and identified several stress-inducible transcription factors. About 40% of the drought or salinity induced genes were also found to be affected by cold stress. Additionally, >98% and 100% of salinity and abscisic acid (ABA) inducible genes, respectively, were also activated by drought stress suggesting correlation among drought and salinity stress signaling pathways. A comparative transcriptome analysis of *Arabidopsis* and rice revealed that they share common stress-inducible genes and may exhibit conservation in the mechanism of action during abiotic stress responses even though eudicots and monocots separated approximately one million years ago during evolution (Shinozaki and Yamaguchi-Shinozaki 2007).

In *Arabidopsis* and rice, 56 and 63 transcription factor families have been reported, respectively, of which many have been found to be responsive to various abiotic stresses (Guo *et al.* 2005; Gao *et al.* 2006). At least one member of 58 families exhibited differential expression under water-deficit stress in rice (Ray *et al.* 2011). A few of these transcription factors families like dehydration responsive element binding (*DREBs*), belonging to ethylene response factor (ERF) family have been well investigated. For example, *OsDREB1A* to *OsDREB1I*, *OsDREB2A* to *OsDREB2E* and *OsABI4* have been analyzed in rice. Drought stress conditions induced *OsDREB1F*, *OsDREB1G*, *OsDREB2A* and *OsDREB2B* genes, whereas *OsDREB1A* and *OsDREB1B* genes showed upregulation due to low temperature conditions. Additionally, an altered expression level of *OsDREB1F* has been reported after ABA treatment in *Arabidopsis* (Dubouzet *et al.* 2003; Chen *et al.* 2008; Wang *et al.* 2008). Other stress-responsive genes belonging to the Apetalla2 (AP2) transcription factor family like *AP37*, *AP59* and *ABA responsive AP2-like gene* (*ARAG1*) were also found to be induced by water-deficit conditions (Oh *et al.* 2009; Zhao *et al.* 2010).

The basic leucine-zipper (bZIP) domain transcription factor family is comprised of 89 members in rice, harboring a bZIP domain composed of a DNA-binding basic region and the Leu zipper dimerization region (Nijhawan *et al.* 2008). Among 33 abiotic stress-responsive bZIP genes, 24 were found to be upregulated and nine genes showed downregulation in rice (Nijhawan *et al.* 2008). Many of these genes exhibited response to multiple stresses and some of

them showed response to specific stress condition only. *OsbZIP23* was evidenced to be upregulated by salinity, water-deficit, polyethylene glycol (PEG) and ABA treatments, but not due to low temperatures (Xiang *et al.* 2008). In addition, *OsABI5* expression was found to be induced by ABA treatment and high salinity conditions; however the gene was downregulated under water-deficit and low temperature conditions in rice seedlings (Zou *et al.* 2008). The transcription factor responsible for ABA regulation 1 (TRAB1), a *trans*-acting factor involved in the ABA-mediated gene regulation, showed altered expression in drought and salinity stress treated rice seedlings (Hobo *et al.* 1999). Furthermore, rice ABA-responsive element binding transcription factor, *OsAREB1*, was found to be upregulated by ABA and PEG treatments besides heat stress (Jin *et al.* 2009). Differential expression of several NAM, ATAF1/2 and CUC2 {No apical meristem, *Arabidopsis thaliana* activation factor1/2, Cup-shaped cotyledon2} (NAC) transcription factors have also been reported during abiotic stress conditions. It has been observed that exogenous ABA, water-deficit and salinity lead to induction of *ONAC5* and *ONAC6* transcription factors. Similar expression patterns were seen for *OsNAC5* and homologous genes like *OsNAC6*, *stress-responsive NAC1* (*SNAC1*), *OsNAC3* and *OsNAC4* as well (Takasaki *et al.* 2010). Among them, a member of ATAF subfamily, *OsNAC6*, has been found to be localized in the nucleus and acts as a transcriptional activator. It is highly expressed in response to several abiotic and biotic stresses (Ohnishi *et al.* 2005).

Among a total of 107 members of homeobox transcription factors family, at least 37 were also found to be differentially expressed in rice seedlings under various abiotic stress conditions (Jain *et al.* 2008). In addition, a few homeodomain leucine-zipper (HD-Zip) gene family members were reported to have altered expression levels in drought-tolerant and sensitive varieties of rice in the flowering stage (Agalou *et al.* 2008). Based on some evidences, it has been speculated that homeobox transcription factors are involved in regulation of abiotic stress responses via both ABA-dependent and independent pathways (Bhattacharjee and Jain 2012). Likewise, several MCM1, Agamous, Deficiens and SRF (MADS)-box transcription factors were also found to be upregulated under abiotic stress conditions (Arora *et al.* 2007; Ray *et al.* 2011).

Several other rice transcription factor families, including WRKY, zinc-finger homeodomain (ZFHD), plant homeodomain (PHD) zinc-finger, Cys3/His (C3H) and Cys2/His2 (C2H2) zinc-finger transcription factors, etc. have also been reported to be involved in abiotic stress responses (Ray *et al.* 2011). Among the WRKY transcription factors, four were upregulated by drought, 13 were upregulated by drought and salinity, and two were upregulated by drought but downregulated by cold stress, whereas one gene was upregulated by drought but downregulated by cold and salinity stress (Ramamoorthy *et al.* 2008). Besides this, rice seedlings, when exposed to high concentration of PEG, ABA, NaCl treatments and high temperature conditions, exhibited significant induction of *OsWRKY72* (Song *et al.* 2010). So far, 20 TIFY transcription factors (previously known as ZIM {Zinc-finger motif expressed in Inflorescence Meristem} domain transcription factors) have been recognized in rice and six of them were found to be induced prominently by water-deficit conditions (Ye *et al.* 2009). Among myeloblastosis (MYB) transcription factors, only *OsMYB3R-2* was found to be induced by drought, salinity and cold stress (Dai *et al.* 2007). Moreover, transcription factors in *Arabidopsis* belonging to nuclear factor Y (NF-Y) and basic helix-loop-helix (bHLH) family also showed differential expression and have been reported to be involved in multiple stress responses recently (Fujita *et al.* 2011).

STRESS TOLERANCE MEDIATED BY RICE TRANSCRIPTION FACTORS

Several rice transcription factors involved in abiotic stress responses have been functionally characterized so far. Over-expression or knocking out of such transcription factors have been shown to confer abiotic stress tolerance in transgenic plants. Here, we provide a few examples of transcription factor mediated stress responses/tolerance in plants. A plethora of stress-responsive genes get activated due to over-expression of *DREB* transcription factors in transgenic plants resulting in enhanced stress tolerance. *OsDREB1A* over-expression led to upregulation of ten specific genes, including ABA regulated genes, which conferred dehydration tolerance in plants (Dubouzet *et al.* 2003). Moreover, the function of *AtDREB1A* remained conserved when over-expressed in rice, resulting in accumulation of osmolytes like proline and sugars, eventually leading to abiotic stress tolerance (Ito *et al.* 2006). When *AtDREB1A* and *ABRE-binding factor3* (*ABF3*) were over-expressed in rice, 13 and 27 genes were activated during drought conditions, without any compromise in the plant growth and productivity. The transgenic plants exhibited considerable drought tolerance due to the activation and alteration in levels of stress-inducible targets like late embryogenesis abundant (LEA) proteins, cold-inducible (KIN), phospholipase C and others, which led to the development of abiotic stress tolerance in rice (Kasuga *et al.* 1999; Oh *et al.* 2005). Interestingly, barley *C-repeat binding factor4* (*CBF4*) proved to be more potent than *AtDREB1A* in conferring stress tolerance, signifying differences in the functionality of DREB proteins across species, which might depend on the plant genome composition and the ability of transcription factors to activate and repress different sets of target genes (Nakashima *et al.* 2009). *OsDREB1A* and *OsDREB1B* over-expression lines exhibited enhanced drought and low temperature tolerance in rice, respectively, whereas in *Arabidopsis*, the over-expression of *OsDREB2B* enabled better survival during water-deficit and heat stress conditions (Ito *et al.* 2006; Matsukura *et al.* 2010). The over-expression of *OsDREB1F* in rice also resulted in upregulation of downstream target genes involved in both ABA-dependent and ABA-independent transcriptional regulation (Liu *et al.* 1998; Wang *et al.* 2008). In *Arabidopsis*, the over-expression of *DREB2A* without the repressor domain and *DREB2C* resulted in thermotolerance, suggesting a cross-talk between heat and drought stress regulation (Liu *et al*. 1998; Lim *et al.* 2007; Qin *et al.* 2008).

Among other AP2 domain-containing transcription factors, the overexpression of *AP37*, *AP59* and *ARAG1* showed enhanced tolerance to drought stress in transgenic rice plants without any phenotypic abnormality. Contrarily, in several instances, over-expression of transcription factors led to developmental compromise. For example, DREB1A over-expression in *Arabidopsis* was accompanied by reduction in crop yield and stunted growth (Ito *et al.* 2006). Hence, the use of stress-inducible promoter like *response to dehydration 29A* (*rd29A*) has been encouraged with the aim to raise transgenic plants devoid of pleiotropic developmental alterations. For example, the over-expression of *DREB1A* under the control of stress-inducible promoter led to development of abiotic stress tolerant plants with optimum crop yield and normal growth (Kasuga *et al.* 1999).

Recent evidences show that homeobox transcription factors, which are majorly involved in developmental processes, have also been implicated in abiotic stress responses. The over-expression of some homeobox transcription factors has imparted abiotic stress tolerance in *Arabidopsis* transgenic plants (Zhu *et al.* 2004; Tran *et al*. 2006; Yu *et al.* 2008; Bhattacharjee and Jain 2012). Recently, a gain-of-function mutation in homeodomain the lipid sterol- binding StAR-related lipid transfer (START) transcription factor has also been shown to impart drought tolerance to *Arabidopsis* plants (Yu *et al.* 2008). However, only one rice transcription factor, *OsBHD1*, has been analyzed *in planta* so far. The

transgenic tobacco plants were sensitive to salinity and oxidative stress, but developed enhanced tolerance to viral infections. These evidences suggested negative regulatory role of *OsBHD1* in context of abiotic stress responses. It was also speculated that *OsBHD1* regulates abiotic and biotic stress responses independently via different pathways (Luo *et al.* 2005).

The rice bZIP family includes around 100 members and many of them, namely *OsbZIP05/OSBZ8*, *OsbZIP12/OsABF1*, *OsbZIP23*, *OsbZIP38/LIP19*, *OsbZIP66/TRAB1*, *OsbZIP72*, *OsAREB1* and *OsABI5*, have been comprehensively analyzed (Nakagawa *et al.* 1996; Hobo *et al.* 1999; Shimizu *et al.* 2005; Nijhawan *et al.* 2008; Xiang *et al.* 2008; Lu *et al.* 2009; Hossain *et al.* 2010). Among bZIP transcription factors, the negative regulatory role of *OsABI5* was established in abiotic stress responses, when their antisense transgenic plants exhibited improved tolerance to osmotic and salinity stress, but decreased rice fertility. Contrarily, their over-expression lines were more sensitive to ABA, salinity and PEG treatment (Zou *et al.* 2008, 2009). Besides this, Xiang *et al.* (2008) showed that *OsbZIP23* positively regulated the expression of several stress-inducible genes via ABA-dependent pathway in various abiotic stress responses. The over-expression of *OsbZIP23* conferred abiotic stress tolerance and activated several stress-responsive downstream target genes like dehydrins, phosphatases, protein kinases, LEA proteins and other metabolic enzymes in rice leading to stress tolerance without any growth retardation or losses in crop yield. Recently, it has been demonstrated that drought tolerance in rice is significantly improved upon constitutive activation of OsbZIP46 (Tang *et al.* 2012). Similarly, the over-expression of *OsAREB1* in *Arabidopsis* yielded heat and drought stress-tolerant plants (Jin *et al.* 2009). Thus, these transcription factors have proved to be promising targets for engineering stress tolerance in crop plants like rice.

The plant-specific NAC transcription factor family is comprised of numerous genes involved in plant development and abiotic stress responses. The over-expression of several NAC transcription factors led to generation of stress-tolerant rice and *Arabidopsis* transgenic plants (Nakashima *et al.* 2012; Puranik *et al.* 2012). Among 151 NAC genes, at least 45 are induced by various abiotic stress conditions in rice (Fang *et al.* 2008; Nuruzzaman *et al.* 2010). Many of the NAC genes were found to be responsive to multiple abiotic stresses (Ray *et al.* 2011). The *OsNAC6* over-expression transgenic rice lines showed retarded growth and poor grain yield, and altered expression of several target genes like protein kinases, transcription factors, chitinases and peroxidases. However, these plants depicted improved tolerance during abiotic stress conditions (Nakashima *et al.* 2007). Simultaneous investigations suggested that under the control of stress-inducible promoter, *OsNAC6* transgenic rice lines with better productivity and minimal growth retardation could be obtained. Subsequently, suitable evidences revealed that *OsNAC6* acts as a transcriptional activator in both abiotic and biotic stress responses (Ohnishi *et al.* 2005; Nakashima *et al.* 2007). Correspondingly, over-expression of *OsNAC5* in rice showed drought tolerance without developmental defects. This study revealed that both these NAC transcription factors activated different target genes (Takasaki *et al.* 2010). In another study, the over-expression of stress-responsive *NAC1* (*SNAC1*) and stress-responsive *NAC2* (*SNAC2/OsNAC6*) genes in rice imparted enhanced stress tolerance without developmental defects or compromise on the grain yield even in the field conditions (Hu *et al.* 2006, 2008; Nakashima *et al.* 2009). Another NAC protein, ONAC45, when over-expressed in rice showed considerable tolerance to various abiotic stresses at the seedling stage and plants were devoid of phenotypic compromises (Zheng *et al.* 2009).

WRKY transcription factors also consist of a large gene family in *Arabidopsis* (72) and rice (109) and are unique to green lineage of eukaryotes i.e. plant kingdom (Ulker *et al.* 2004; Rushton *et al.* 2010). WRKY family proteins contain highly conserved WRKY domain and a zinc-finger structure distinct from other known zinc-finger motifs (Eulgem *et al.* 2000). WRKY transcription factors play important role in plant stress responses via reprogramming the transcriptional machinery (Chen *et al.* 2012). The over-expression of *OsWRKY72* in transgenic *Arabidopsis* exhibited increased sensitivity of plants to mannitol, NaCl and ABA, and activated ABA-dependent genes like *ABI4* and *ABA2* (Song *et al.* 2010). Besides this, differential salt induced regulation of a WRKY protein has been witnessed in salinity-sensitive rice and its halophytic salt-tolerant relative, suggesting the possibility of WRKY proteins conferring salinity tolerance in transgenic plants (Diedhiou *et al.* 2009). It was evidenced that *OsWRKY45* gets induced by a range of abiotic stress factors and its over-expression in *Arabidopsis* resulted in activation of several stress-responsive genes. In addition, *OsWRKY45* has been speculated to be involved in the ABA-dependent signal transduction pathway mediating drought tolerance (Qiu and Yu 2009). Recently, TIFY transcription factors also have been characterized in rice. Reports showed that the over-expression of *OsTIFY11a* in transgenic rice led to improved drought and salinity tolerance (Ye *et al.* 2009) and its alleles have been found to perform diverse and overlapping roles in abscisic acid signaling and abiotic stress tolerance (Tao *et al.* 2011).

Many zinc-finger-like transcription factors, namely *zinc-finger protein 245* (*ZFP245*), *ZFP252*, members of stress associated protein gene family, namely, *Oryza sativa indica* stress-associated proteins (*OsiSAP1* and *OsiSAP8*), *drought and salt tolerance transcription factor* (*DST*) and *Oryza sativa cold-inducible* (*OsCOIN*) also get induced by abiotic stresses. The over-expression of zinc-finger protein (*ZFP245*), *OsCOIN*, *OsiSAP1* and *OsiSAP8* has been shown to confer abiotic stress tolerance in transgenic plants (Mukhopadhyay *et al.* 2004; Liu *et al.* 2007; Kanneganti and Gupta 2008; Huang *et al.* 2009a). The elevated levels of stress-responsive genes like *OsDREB1A*, *OsLEA3*, *Oryza sativa delta1-pyrroline-5-carboxylate synthetase* (*OsP5CS*) and *Oryza sativa* proline transporter (*OsProT*) in ZFP252 transgenic over-expressing rice lines suggested their potent implications in abiotic stress responses (Xu *et al.* 2008). Additionally, a Cys2/His2 zinc-finger protein, drought and salt tolerance (DST) protein, has been reported to regulate stomatal closure, as it targets reactive oxygen species (ROS) homeostasis related genes in an ABA-independent manner (Huang *et al.* 2009b). In rice, repression of DST further decreases levels of peroxidase 24 precursor, which consequently increases levels of H_2O_2, thereby promoting stomatal closure and enhancing drought stress tolerance (Huang *et al.* 2009b). Recently, it has been found that many zinc-finger transcription factors also act as versatile regulators of OsDREB1B (Figueiredo *et al.* 2012).

MYB transcription factors represent another important family involved in abiotic stress responses that act in ABA-dependent pathway of transcriptional regulation (Martin and Javier 1997; Agarwal and Jha 2010). A low temperature regulated transcription factor, OsMyb4, has been found to intricately affect stress tolerance and panicle development in rice (Park *et al.* 2010). In addition, the over-expression of *OsMYB4* in different host plants like *Arabidopsis* and tomato exhibited varied tolerant phenotypes (Vannini *et al.* 2004, 2007). However, the over-expression of *OsMYB3R-2* in *Arabidopsis* yielded transgenics with stunted growth but greater abiotic stress tolerance (Dai *et al.* 2007). Another MYB family protein, OsMYB2, was also found to impart tolerance to multiple abiotic stresses in rice (Yang *et al.* 2012).

ROLE OF ABSCISIC ACID IN TRANSCRIPTION FACTOR-MEDIATED REGULATORY NETWORK

Several plant hormones influence abiotic stress signal transduction pathways and some of their roles have already been elucidated. While salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) are mainly involved in biotic stress res-

ponses, ABA, cytokinin and auxin have been shown to be predominantly associated with abiotic stress responses (Morgan and Drew 1997; Wang *et al*. 2002; Yang *et al*. 2004; Horvath *et al*. 2007; Grant and Jones 2009; Jain and Khurana 2009; Wasternack and Kombrink 2010; Tran *et al*. 2010; Fujita *et al*. 2011).

Among them, ABA is produced during stress conditions and plays a key role in molecular regulation (Cutler *et al*. 2010; Raghavendra *et al*. 2010; Fujita *et al*. 2011). ABA mediates stomatal closure and regulates several developmental processes like embryo maturation, seed development and dormancy. It even participates in abiotic stress signaling leading to activation of stress-responsive genes. ABA accumulates as a result of dehydration and other abiotic stresses, which in turn triggers expression of several stress-inducible genes. The ABA-dependent transcriptional regulatory pathway involves key transcription factors like DREBs, NACs and MYBs (Shinozaki and Yamaguchi-Shinozaki 2007). An interrelation between water-deficit responses mediated via ABA and JA dependent pathways has been established. This implies crosstalk between biotic and abiotic stress responses (Shinozaki and Yamaguchi-Shinozaki 2007; Wastenack and Kombringe 2010). Based on ABA metabolism studies, it has been deciphered that the ABA catabolic and biosynthetic enzymes like 9-*cis*-epoxy carotenoid dioxygenases (NCEDs) may be critical in mediating enhanced drought tolerance (Iuchi *et al*. 2001).

ABA-mediated transcriptional regulation has been exhaustively studied in response to osmotic stress in plants. A working model of ABA mediated transcriptional control during osmotic stress in *Arabidopsis* highlights the participation of several regulatory molecules like kinases, chromatin remodeling factors, second messengers, *cis*-acting elements and specific transcription factors in osmotic stress regulatory network (Fujita *et al*. 2011). Specifically, sucrose nonfermenting1 (SNF1)-related kinase 2 (SnRK2) are critical to the signaling cascade operative during osmotic stress (Nakashima *et al*. 2009; Fujita *et al*. 2011). Well-defined roles of these molecules have been suggested in post translational modifications like phosphorylation, enabling targeting of downstream transcription factors (Kobayashi *et al*. 2005; Furihata *et al*. 2006). Transgenic over-expression of rice SNF1-type serine-threonine protein kinase (SnRK2-type SAPK4) led to controlled ion and ROS homeostasis under salinity stress conditions (Diedhiou *et al*. 2008). So far, 30 calcineurin B-like protein-interacting protein kinases (CIPK/SnRK3) are known in rice, of which 15 CIPKs are drought-inducible and harbor ABA-responsive element (ABRE) and/or drought-responsive element (DRE), in their promoter region (Xiang *et al*. 2007). In addition, ten SnRK2 kinases primarily induced by hyperosmotic stresses have been identified in rice (Kobayashi *et al*. 2004). Notably, in rice protoplasts, stress/ABA-activated protein kinases (SAPKs) were able to control the downstream target genes containing ABRE elements, signifying their function in an ABA-dependent manner (Kobayashi *et al*. 2005; Nakashima *et al*. 2009; Umezawa *et al*. 2010).

TRANSCRIPTIONAL REGULATORY NETWORKS

A number of transcription factors have been shown to coordinate and/or interact directly or indirectly to generate abiotic stress responses in plants. Inducer of CBF expression 1 (ICE1) has been reported to control the expression of DREB1 transcription factors in *Arabidopsis* (Chinnusamy *et al*. 2003). Dong *et al*. (2006) demonstrated that ICE1 controls the expression of a RING finger protein, high expression of osmotically responsive1 (HOS1) protein. Additionally, Miura *et al*. (2007) also reported enhanced activation of DREB1A by SIZ1 via sumoylation. DREB2 has been shown to act in conjunction with DREB interacting proteins (DRIP), which are enzyme3 (E3) ubiquitin ligases (Qin *et al*. 2008). Responsive to dessication22 (RD22) gets activated by MYB and Myelocytomatosis (MYC) transcription factors during osmotic stress in *Arabi-*

dopsis (Abe *et al*. 2003). Phosphorylation by SnRK2 has been reported to be significant in activating various ABA-dependent transcription factors like ABA responsive element binding1 (AREB1) in *Arabidopsis* and TRAB1 in rice (Kobayashi *et al*. 2005; Furihata *et al*. 2006). Calmodulin-binding transcription activator (*CAMTA*) transcription factors bind to conserved motif and activate Ca^{2+} signaling occurring during abiotic stress responses (Doherty *et al*. 2009). There are reports that during osmotic stress, stress-inducible *NAC* transcription factors bind to MYC type drought-responsive sequence and zinc finger-homeodomain1 (ZF-HD1) transcription factor binds to ZFHD recognition (ZFHDR) sequence in the *early responsive to dehydration1* (*ERD1*) promoter, thereby cooperatively activating its expression (Tran *et al*. 2004, 2006). Moreover, in *Arabidopsis* zinc finger transcription factor, ZAT12 and DREB2 are implicated in drought and salinity stresses respectively, by regulation of *DREB* genes (Vogel *et al*. 2005). Although, these studies provide good examples of coordination and interaction among transcription factors during abiotic stress responses, comprehensive interaction studies among rice transcription factors are still awaited.

The existence of at least four pathways in abiotic stress responses has been proposed (Shinozaki and Yamaguchi-Shinozaki 1997). The ABA-dependent pathway I involves protein synthesis (for example, bZIP and MYC/MYB) for downstream gene expression, whereas in the ABA-dependent pathway II, no protein synthesis is required. In this case, bZIP proteins directly bind to *cis*-acting element, ABRE, mediating gene expression. Further, the existence of ABA-independent pathways III and IV during drought and salinity conditions was suggested. Reports revealed that in ABA-independent pathway IV, DRE motifs were essential for cold stress regulation, apart from drought and salinity responses. In addition, the roles of *cis*- and *trans*-acting elements in abiotic stress responses have been explored and they were found to mediate abiotic stress signaling via transcription factors. ABA-responsive element binding proteins (AREBs) and MYC/MYBs trigger the abiotic stress response via binding to ABRE and MYCRS/MYBRS sequences, respectively, whereas the DREB and NAC transcription factors mediate stress responses by specific binding to DRE/CRT and NAC recognition site (NACRS) motifs present in the promoter of respective target genes (Tran *et al*. 2004; Yamaguchi-Shinozaki and Shinozaki 2005). The analysis of cold stress-inducible gene promoters revealed the existence of DRE and ABRE motifs suggesting that the cold stress response is generated via both ABA-dependent and independent pathways (Yamaguchi-Shinozaki and Shinozaki 1994; Stockinger *et al*. 1997).

Later, Shinozaki and Yamaguchi-Shinozaki (2007) investigated more about gene networks prevalent in drought stress and identified several transcription factors as connecting links in the previously proposed generalized abiotic stress regulatory network. Apart from the existing four pathways of transcriptional regulation, they projected the existence of other ABA-dependent and independent drought related regulatory pathways. In the ABA-dependent pathway, ABREs exist as crucial ABA-responsive elements recognized by AP2 transcription factors. The *RD22* gene gets induced by MYB2/MYC2 transcription factors, which bind to *cis*-acting element, namely MYC/MYC recognition site (MYCRS/MYBRS) (Abe *et al*. 1997). Moreover, *MYC2* and *NAC* (*RD26*) transcription factors were reported to be involved in wounding stresses apart from ABA-dependent abiotic stress signaling (Shinozaki and Yamaguchi-Shinozaki 2007). Particularly, in the *RD26* over-expression plants, activation of prominent stress-inducible genes was not seen. Instead, accumulation of gene products involved in antioxidant defense systems like glyoxylase 1 family proteins (GLY molecules) and JA-induced stress-responsive gene products was reported. The *RD26* promoter was found to be enriched in W boxes and asymmetric1 (AS1) motifs apart from *cis*-acting elements like ABRE, DRE, MYCRS and MYBRS, which are recognition sites involved in ABA-

dependent gene expression (Fujita *et al.* 2004). This suggested crosstalk between ABA- and JA-mediated stress signaling. Hence, it is clear that the ABA-dependent and independent pathways act in coherence and simultaneously coordinate the abiotic stress responses in plants (Shinozaki and Yamaguchi-Shinozaki 2007). Notably, in *Arabidopsis*, another drought and salinity controlled ABA-independent pathway comprising of NAC and homeodomain-leucine zipper (HD-ZIP) transcription factors exists, which activates *ERD1* gene expression ensuring abiotic stress tolerance (Shinozaki and Yamaguchi-Shinozaki 2007). Similar pathways are speculated to exist in rice abiotic stress regulatory network also.

AREB regulon

ABA induces the expression of several stress-responsive genes. These ABA-inducible genes are bZIP-type transcription factors, which exclusively act via ABA-dependent pathways and contain specific *cis*-acting elements known as ABREs in their promoter region. These elements exist in conjunction with coupling elements, which are of utmost importance in the ABA-mediated transcription regulons. For example, in rice, A/GCGT serves as a coupling element (Hobo *et al.* 1999). AREBs are the proteins binding to ABRE elements of ABA-responsive genes. The members of bZIP transcription factor family have been referred to as AREBs in *Arabidopsis*, which were first identified via yeast one-hybrid screening using ABRE element as bait (Choi *et al.* 2000; Uno *et al.* 2000). It has also been reported that these proteins, for example, AREB1, AREB2 and ABRE-binding factor3 (ABF3) undergo homo- or hetero-dimerization in order to attain functional specificity (Yoshida *et al.* 2010). They also interact with SnRK2 protein kinases and mediate ABA-dependent phosphorylation of transcription factors in the signaling cascade (Yoshida *et al.* 2010).

In rice, although all members of bZIP transcription factor family have been identified, their functional analysis still remains to be done (Nijhawan *et al.* 2008). A lot of evidence reveals the vital role of phosphorylation and dephosphorylation in abiotic stress responses (Agarwal and Jha 2010). The conservation of SnRK2-AREB/ABF pathways has been evidenced in rice (Fujita *et al.* 2011). SnKR2 protein kinases like OSRK1 are involved in phosphorylation and lead to subsequent activation of AREB regulons (Chae *et al.* 2007). These kinases get activated by ABA, resulting in phosphorylation of TRAB1 (Kagaya *et al.* 2002; Kobayashi *et al.* 2005). It was demonstrated that mutations in AREB1 and its rice homologue, TRAB1, resulted in transcriptional activation of ABA-responsive genes even in the absence of ABA, leading to enhanced drought tolerance in plants (Kobayashi *et al.* 2005; Furihata *et al.* 2006; Shinozaki and Yamaguchi-Shinozaki 2007). The existence of the AREB pathway was also confirmed by the *OsABI5* knockout plants, which exhibited greater/better salinity tolerance and activated the expression of salt-responsive genes like *SalT* and *SKC1* (Zou *et al.* 2008). These evidences reaffirmed the potential of protein kinases and bZIP transcription factors in developing stress tolerance in crop plants like rice.

DREB regulon

The DREB transcription factors regulate the expression of several stress-responsive genes. They consist of two subclasses, namely, DREB1 and DREB2. These transcription factors may act in ABA-dependent as well as independent pathways of abiotic stress responses, apart from being involved in biotic stress responses (Agarwal *et al.* 2006; Wang *et al.* 2008) The role of *DREB* transcription factors in abiotic stress responses has been extensively studied. OsDREB1A exhibits preferential binding to DRE/CRT core, GCCGAC sequences (Dubouzet *et al.* 2003), whereas AtDREBs show comparable binding affinity for both GCCGAC and ACCGAC sequences (Stockinger *et al.*

1997; Liu *et al.* 1998). There seems to be evolutionary divergence in binding specificities of DREBs among dicots and monocots in the abiotic stress response mechanisms (Stockinger *et al.* 1997; Liu *et al.* 1998). So far, four DREB1/CBF homologous genes, *OsDREB1A*, *OsDREB1B*, *OsDREB1C* and *OsDREB1D* have been characterized in rice (Dubouzet *et al.* 2003). Their over-expression in *Arabidopsis* and rice showed enhanced abiotic stress tolerance. In addition, the over-expression of *Arabidopsis DREB1A* or *OsDREB1A* resulted in accumulation of osmolytes, induction of several stress-responsive genes and considerably improved drought and low temperature tolerance in transgenic rice (Ito *et al.* 2006). This led to the possibility of conservation in the functionality of these stress-inducible genes in monocot and dicot species (Shinozaki and Yamaguchi-Shinozaki 2007) and established that modulation of DREB transcription factors can impart stress tolerance in economically important cereal crops like rice (Oh *et al.* 2005; Ito *et al.* 2006). The stress tolerance was conferred in *Arabidopsis* and tobacco when *DREBs* from other plants like maize or wheat were over-expressed (Dubouzet *et al.* 2003; Shen *et al.* 2003; Qin *et al.* 2007).

NAC regulon

The NAC transcription factors possess specific domains for interaction with other regulators and have been reported to act via ABA-dependent and independent pathways by playing crucial roles in both biotic and abiotic stress responses (Olsen *et al.* 2005; Nakashima *et al.* 2007; Puranik *et al.* 2012) The NAC regulon has been found to be conserved in *Arabidopsis* and rice. Many members of NAC transcription factor family, like SNAC1 and SNAC2 (OsNAC6) upregulated stress-responsive genes facilitating the production of protective molecules, kinases and other enzymes, which eventually attribute abiotic stress tolerance trait in rice (Nakashima *et al.* 2009). *SNAC1*, an ABA-inducible transcription factor, predominantly expressed in guard cells (stomata), regulates stomatal movement during water-deficit conditions and its over-expression triggers stomatal closure. The transgenic plants possessed better seed setting than wild type. Furthermore, SNAC2 (OsNAC6) transgenic plants exhibited considerable abiotic stress tolerance at the seedling stage (Ohnishi *et al.* 2005; Nakashima *et al.* 2007). The transcriptome analysis of transgenic rice revealed that target genes of SNAC1 and SNAC2 (OsNAC6) were not enriched in NACRS element in the promoter region, suggesting the regulation of *NAC* genes via a separate pathway (Simpson *et al.* 2003; Hu *et al.* 2006, 2008). Non-redundancy was observed among various NAC proteins over-expressed in rice, although primarily they were involved in abiotic stress responses (Hussain *et al.* 2011). Instead, the promoter region of *SNAC2* (*OsNAC6*) was found to be enriched in several stress-responsive *cis*-acting elements like ABREs, MYBRSs and MYCRSs suggesting ABA-mediated gene regulation. Differential expression patterns of *OsNAC10* and *ONAC45* were observed due to salinity and cold treatments in rice plants, respectively, whereas both were commonly upregulated during drought treatment. These transcription factors activate the expression of downstream target genes like LEA, transcription factors like WRKY and NAC, cytochrome P450 (CYP450) and mitogen-activated protein kinase kinase (MAPKK) proteins, which probably elicit drought tolerance in transgenic rice (Xiao *et al.* 2007; Zheng *et al.* 2009; Jeong *et al.* 2010). Moreover, *OsNAC10* gene regulates the stress-responsive genes like AP2, WRKY, leaf-specific target gene, leucine-rich repeat (LRR), NAC, zinc-finger type proteins and potassium transporters like *HAK5* (Jeong *et al.* 2010). Evidences of *in vitro* binding of ONAC5 and ONAC6 proteins suggested that their functional dimerization enables transcriptional activation of stress-responsive genes like *OsLEA3* leading to stress tolerance (Rabbani *et al.* 2003; Takasaki *et al.* 2010). This suggests that NAC transcription factors participate in coordinated regulation of molecules in abiotic

stress regulatory network in order to mediate stress tolerance in plants and may be governed by some master regulators simultaneously (Golldack *et al*. 2011). Besides this, co-overexpression of NAC and other transcription factors like zinc-finger homeodomain (ZF-HD) has been reported to confer enhanced abiotic stress tolerance in *Arabidopsis* (Tran *et al*. 2006). This also suggests a critical role of NAC transcription factors in molecular mechanisms of abiotic stress adaptations. Probably, similar cooperative interactions are anticipated to exist in rice as well and such possibilities need to be explored.

MYB/MYC regulon

In plants, MYB/MYC transcription factors exist abundantly and have been reportedly involved in defense responses (Chen *et al*. 2006). These transcription factors have been implicated in ABA-dependent pathway of abiotic stress response. The transcription factors specifically bind to MYBRS/MYCRS *cis*-regulatory elements in the promoters of downstream genes to mediate stress responses (Abe *et al*. 2003; Agarwal and Jha 2011). Several *Arabidopsis* transcription factors, namely MYB102, MYB44, MYB15 and MYB41, have been implicated in diverse abiotic stress responses and their over-expression has enabled development of stress-tolerant plants (Denekamp and Smeekens 2003; Agarwal *et al*. 2006; Jung *et al*. 2008; Lippold *et al*. 2009; Ding *et al*. 2009). The over-expression of *OsMYB3R2* yielded superior transgenics eliciting better stress tolerance phenotype in rice (Dai *et al*. 2007). The components of this regulon need to be elucidated further by more investigations.

NON-CODING RNAs REGULATING TRANSCRIPTION FACTORS

Several regulatory small RNAs play pivotal role in abiotic stress responses by controlling expression of transcription factors. The recently proposed model of transcriptional regulatory network delineates the role of small RNAs (Urano *et al*. 2010). Small RNAs modify major transcriptional regulators like NAC, WRKY and zinc-finger proteins in *Arabidopsis* by post-transcriptional silencing and signaling via ROS (Golldack *et al*. 2011). The transcribed mRNA forms ribonuclear complexes and simultaneously undergoes translation to form functional proteins. Some mRNAs are initially activated by histone modifications, whereas others are regulated post-translationally. However, non-translated mRNA may be processed as P-body, which leads to degradation of useless mRNA or as stress granules which may temporarily store translation initiation factors. These key signaling cytoplasmic complexes are crucial during stress responses (Urano *et al*. 2010). Several transcription factors are targets of stress-inducible microRNAs (miRNAs). For example, NAC transcription factor family members are targeted by miR164 in switchgrass (Matts *et al*. 2010). Similarly in *Arabidopsis*, scarecrow-like (SCL), MYB and TCP transcription factors are targets of drought and salinity-inducible miRNAs, namely miR159, miR168, miR171 and miR396 (Liu *et al*. 2008). Several small RNAs corresponding to many stress-responsive homeobox genes have also been identified (Jain and Khurana 2008). These results suggest miRNA-mediated regulation of transcription factors in abiotic stress responses. In the future, modulation of the miRNA-mediated regulatory pathways may prove to be promising for abiotic stress tolerance in crop plants.

FUTURE PERSPECTIVES

Plants develop diverse strategies to overcome the detrimental effects of abiotic stresses. These adaptive strategies involve action of transcription factors and other regulatory molecules, as they orchestrate complex signaling cascades. Technical advancement has enabled the systematic amalgamation of knowledge pertaining to abiotic stress responses. Moreover, in recent times the integration of transcrip-

tomics, metabolomics and proteomics information has enabled the detailed analysis of the regulatory networks prevalent in abiotic stress responses in plants, including rice. At the transcriptional level, role of several transcription factors and non-protein coding RNAs have been deciphered. The transcription factors are crucial targets for genetic manipulations as they can mediate stress tolerance in plants by directing multiple abiotic stress regulatory pathways singularly or in conjunction with other transcription factors (Nakashima *et al*. 2009; Hussain *et al*. 2011). The knowledge of their binding elements can further highlight the importance of several other key components involved in the transcriptional regulatory network. The ability of any transcription factor to regulate subregulons in the signaling cascade determines its potential as a suitable candidate for engineering stress tolerance in plants. Concurrently, it is also important to compare the abiotic stress induced signaling in the tolerant and sensitive plant species in order to select the most important regulators of abiotic stress responses for biotechnological applications. Eventually, the biotechnological applications leading to stress tolerance must ensure optimum productivity and considerable tolerance in crop plants like rice (Gao *et al*. 2008).

The products of stress-inducible genes involved in signal transduction pathways often have been related to abiotic stress tolerance in plants. Improvement in abiotic stress tolerance has been attained in *Arabidopsis* and crop plants like rice by over-expression of suitable transcription factor encoding genes (Nakashima *et al*. 2009), osmoprotectants like LEA genes (Wang *et al*. 2007; Yang *et al*. 2010), heat shock proteins (Sato and Yokoya 2008), metallothiones (Yang *et al*. 2009), dihydroorotate dehydrogenases (Liu *et al*. 2009), *NCEDs* (Iuchi *et al*. 2001), aquaporins (Capell *et al*. 2004; Li *et al*. 2008), ROS scavenging enzymes like ascorbate peroxidise (Lu *et al*. 2007), kinases like receptor-like kinases (Ouyang *et al*. 2010), MAPKs and SnRK2s (Kim *et al*. 2003; Kobayashi *et al*. 2005; Ning *et al*. 2010).

The need of the hour is to develop stress-tolerant crop plants by modulating transcription factors and other components involved in the abiotic stress signaling network. To achieve this, a comprehensive understanding of the regulatory network operative during abiotic stress response is desirable. The complete elucidation of the transcriptional regulatory network and identification of major molecular switches would be possible, once functional characterization of individual transcription factors and associated regulatory components is accomplished. In addition, the cross-talk among various transcription factor mediated regulatory pathways also need to be understood so that genetic engineering of suitable regulatory components helps in raising transgenics, which ultimately enable restoration of molecular balance in plants.

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