Transgenic Approaches for
Abiotic Stress Tolerance in Crop Plants

Sarvajeet Singh Gill[1] • Ritu Gill[1] • Naser A. Anjum[2] • Narendra Tuteja[3*]

[1] Centre for Biotechnology, MD University; Rohtak - 124 001, Haryana, India
[2] Centre for Environmental and Marine Studies (CESAM) and Department of Chemistry, University of Aveiro, 3810-193 Aveiro, Portugal
[3] Plant Molecular Biology Group, International Centre for Genetic Engineering and Biotechnology, Aruna Asaf Ali Marg, New Delhi 110 067, India

Corresponding author: * narendra@icgeb.res.in

ABSTRACT

Modern agriculture practice using genetically engineered crops is emerging as an effective tool to combat the negative impact of abiotic stresses on crop production. Abiotic stresses such as salt, drought, temperature, cold, flooding, heavy metals, etc. remain the greatest constraint to crop production. Estimations revealed that abiotic stresses alone responsible for crop failure and crop productivity loss between 50-70%. Global climate change further aggravating the frequency of abiotic stresses which is a serious challenge to feed the rapidly increasing world population. Plants respond to unfavorable environmental conditions in their habitat by developmental, physiological and biochemical ways to tolerate and/or sustain life. The main goal of modern agricultural research is to improve the potential of crop plants to survive under abiotic stresses for a long time. In this context, transgenic approaches are one of the potential ways for the genetic improvement of crop plants. Furthermore, functional genomics approaches revealed various mechanisms for crop improvement and abiotic stress tolerance. Genetic engineering of major crops such as rice, wheat, maize, soybean, pulses etc with genes from other sources is an extremely powerful tool for molecular plant breeding. Research has already come up with many transgenic crop plants with enhanced abiotic stress tolerance. The present article summarizes recent breakthroughs on the aforesaid aspects highlighting mainly transgenic plants overexpressing various genes for abiotic stress tolerance and improved crop productivity.

CONTENTS

INTRODUCTION

The world's population is increasing at an alarming rate to reach about 9 billion by the end of 2050 (http://www.un.org/esa/population/unpop.htm) but a proportional increase in agricultural productivity is hampered by various environmental factors in the changing climate, which is leading to food crisis. The food crisis is not a transient phenomenon and by 2050 there will be another 2.5 billion people on the planet, therefore, it is a great challenge to feed them (http://environmentalresearchweb.org/cws/article/opinion/48593). Economic agricultural productivity losses due to the occurrence of a combination of abiotic stresses and climate change on crop plants are huge. Overall, reduction in crop productivity caused by abiotic stresses causes losses worth hundreds of millions of dollars each year (Mahajan and Tuteja 2005). According to an estimation, it is reported that global warming decreased the yield of major crops like maize, wheat and barley by ~ 40 million metric tons per year between 1981 and 2002 (http://environmentalresearchweb.org/cws/article/news/27343).

Global effects on desertification, soil salinity, atmospheric CO_2 enrichment and effects of other pollutants are predicted to cause dramatic changes in the climatic conditions of arable lands in this century. Being sessile in nature, plants cannot run away but often encounter and are bound to grow under various adverse environmental conditions, such as salinity, drought, chilling, heat, flooding, heavy metal or extreme light, which adversely affect the plant growth and productivity worldwide (Mahajan and Tuteja 2005; Tuteja 2007; Tuteja *et al*. 2011, 2012a, 2012b). The stress management through avoidance is not applicable in case of plants hence they have developed various systems within to counter those stresses. Plants have developed capacities to sense changes/stress around them and recruit various signalling molecules to transduce these signals locally or systemically to prepare themselves to manage it. Plants can afford only mild abiotic stresses putting in place molecular mechanisms that ensure survival and reproduction. Plants have evolved the ability to reprogram the expression of their genome in response to environmental changes. It has been estimated that the relative decreases in potential maximum yields

Invited Review

associated with abiotic stress factors account for more than 70% (Bray *et al.* 2000). Therefore, it is clear that there is an urgent need to produce abiotic stress tolerant crops. Among abiotic stresses, salinity, drought and cold are of wide occurrence and have significant impact on crop productivity; therefore, tolerance to these stresses is a critical condition for yield stability. Plants respond to various stresses through multifaceted molecular signalling pathways. Where, the significant changes at the molecular, cellular, physiological and biochemical levels enable plants to respond to and/or adapt/survive under stressful conditions (Mishra *et al.* 2006; Tuteja and Mahajan 2008; Tuteja and Sopory 2008a, 2008b; Tuteja *et al.* 2011, 2012a, 2012b).

In general, the stress signal is first perceived by the receptors present on the membrane of the plant cells. Following this, the signal information is transduced downstream resulting in the activation of various stress responsive genes. The products of these stress genes ultimately lead to stress tolerance response or plant adaptation and help the plant to survive and surpass unfavourable conditions (Tuteja and Sopory 2008a, 2012b; Tuteja *et al.* 2011, 2012a, 2012b). The various stress responsive genes can be broadly categorized as early and late induced genes. Early genes are induced within minutes of stress signal perception, which include various transcription factors. Late genes include the major stress responsive genes such as RD (responsive to dehydration)/KIN (cold induced)/COR (cold responsive), which encodes and modulate the proteins needed for synthesis, for example LEA-like proteins, antioxidants, membrane stabilizing proteins and osmolytes (Tuteja and Sopory 2008a, 2008b). Understanding of molecular signalling pathways and identification of key molecules and their specific roles may provide a treasure trove of opportunity for molecular breeding approaches to increase the efficiency of crop plants under stressful conditions without yield penalty. Therefore, efforts should be taken to reduce hunger and promote growth and development of crop plants for sustainable agriculture.

In this article, we discuss some of the genetic engineering approaches significant for crop improvement and abiotic stress tolerance. In addition, various genes potentially important for the development of abiotic stress tolerant crop plants are also highlighted.

TRANSGENIC APPROACHES FOR ABIOTIC STRESS TOLERANCE IN CROP PLANTS

Transgenic approaches are one of the many tools available for modern plant improvement programs. After the green revolution, now it's the turn of gene revolution, which is basically the use of gene discovery and functional genomics strategies to reveal multitudinous mechanisms and gene families; hence to confer improved productivity and adaptation to abiotic stresses. These gene families can further be manipulated into novel combinations, expressed ectopically, or transferred to species in which they do not naturally occur or vary. The post genomics era, enhancement of high-throughput facilities which includes, computational biology, metabolomics, and phenomics, has enabled continuously improving capabilities to explore functional plant biology and to develop stress tolerant crops. This makes it possible to address hitherto unexplored aspects of fundamental and applied crop research at high levels of throughput, though not without challenges (Bhatnagar-Mathur *et al.* 2008; Jewell *et al.* 2010).

It is well documented that among abiotic stresses extreme temperatures (freezing, cold, heat), water availability (drought, flooding), and ion toxicity (salinity, heavy metals) are the major causes, which adversely affect the plant growth and productivity worldwide (Mahajan and Tuteja 2005; Tuteja 2007; Tuteja *et al.* 2011, 2012a, 2012b). Nevertheless, it is also predicted that the aforesaid environmental stresses will become more intense and frequent with climate change. To sense these environmental signals, higher plants have evolved a complex signaling network.

Stress signal transduction pathways starts with signal perception by receptors. Following this, the signals activate the generation of second messangers such as calcium and this secondary signaling molecules, which can modulate the intracellular Ca^{2+} level by receptor mediated Ca^{2+} release or it can bypass Ca^{2+} in early signaling steps and initiate a protein phosphorylation cascade (protein phosphatase, MAPK, CDPK, SOS3/PKS, etc.), which activates specific stress-responsive genes for cellular protection through transcription control (MYC/MTB, CBF/DREB) (Mishra *et al.* 2006; Tuteja and Mahajan 2008; Tuteja and Sopory 2008a, 2008b; Tuteja *et al.* 2011). Stress injury may occur through denaturation of cellular proteins/enzymes or through the production of ROS, Na^+ toxicity and disruption of membrane integrity. In response to injury, plants trigger a detoxification process, which may include changes in the expression of LEA/dehydrin type gene, synthesis of molecular chaperones, proteinases, enzymes for scavenging ROS and other detoxification proteins. This process functions in the control and repair of stress induced damage and results in stress tolerance (**Fig. 1**). The complete understanding of the molecular mechanism for abiotic stress tolerance is still a major challenge in biology. Overall, the stress response could be a coordinated action of many genes, which may cross-talk with each other. The stress-induced gene products are also involved in the generation of regulatory molecules like ABA, salicylic acid and ethylene, which can initiate the second round of signaling events. Recently, ABA has been mostly implicated to play a cricial role biotic stress tolerance process (Bhatnagar-Mathur *et al.* 2008). In the following sections, some of the aforesaid transgenic approaches including transcription factors (TFs), transporters, osmolytes, and genes discovered in plants in context with their role in reactive oxygen species (ROS)-perception, impacts and/or detoxification, and antioxidant defense system components modulation will be critically discussed.

TRANSCRIPTION FACTORS

The perception of environmental stresses (including salinity, drought and cold) and the downstream signalling cascades to activate adaptive stress responses are key steps to acquire stress resistance (**Fig. 1**; Seki *et al.* 2003; Yamaguchi-Shinozaki and Shinozaki 2006; Ishida *et al.* 2012). In the signal transduction network that leads from the perception of stress signals to the expression of stress-responsive genes, transcription factors (TFs) play an essential role.

TFs are proteins that act together with other transcriptional regulators, including chromatin remodeling/modifying proteins, to employ or obstruct RNA polymerases to the DNA template; and it is estimated that plant genomes assign approximately 7% of their coding sequence to TFs, which proves the complexity of transcriptional regulation (Udvardi *et al.* 2007). Moreover, TFs were shown to interact with *cis*-elements in the promoter regions of several stress-related genes and in this way, up-regulate the expression of many downstream genes resulting in imparting abiotic stress tolerance (Agarwal and Jha 2010). Because TFs, as opposed to most structural genes, tend to control multiple pathways steps, they have emerged as powerful tools for the manipulation of complex metabolic pathways in plants (Hussain *et al.* 2011). In fact, the transcriptional control is typically exerted through the action of TFs that are specifically involved in particular signal responses. It has been found that TF genes constitute a significant proportion of stress-inducible genes, suggesting that gene transcriptional regulation of stress responses is a crucial mechanism for stress adaptation (Seki *et al.* 2003; Ishida *et al.* 2012). Different families of TFs such as ERF/AP2, HSF, bZIP, MYB, MYC, NFY, NAC,WRKY, Cys2His2, MADS-box and zinc-finger have been shown to regulate the expression of stress-responsive genes (Yamaguchi-Shinozaki and Shinozaki 2006; Hirayama and Shinozaki 2010). Based on the presence of their DNA-binding domains the TFs can be classified into >50 different families, which mainly
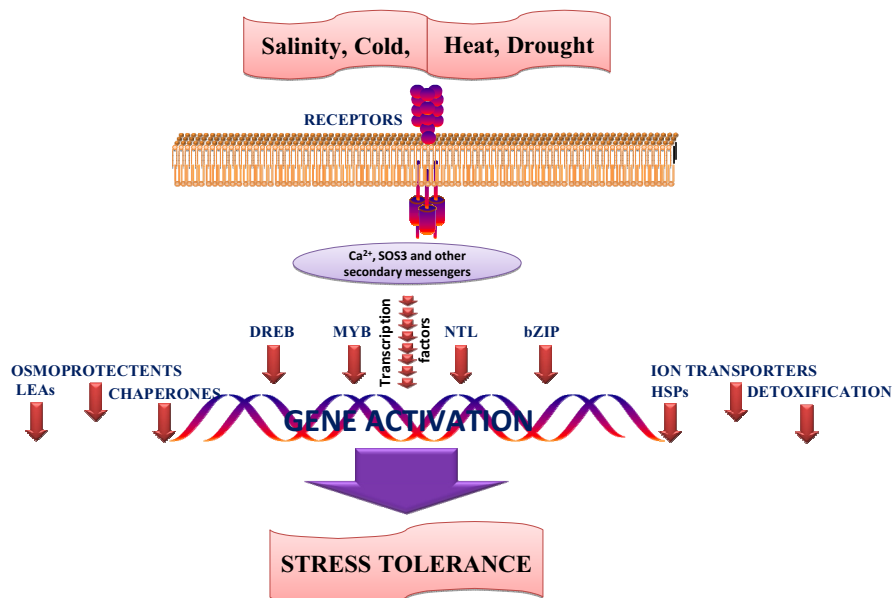
Fig. 1 Generic pathway under salinity, drought cold and heat stress. Stress signal transduction pathways starts with signal perception by receptors. After this the signals activate the signaling mechanism, which helps to generate secondary signaling molecules, and activates specific stress-responsive genes for cellular protection through transcription control. In response to injury, plants trigger a detoxification process, which may include change in the expression of LEA/dehydrin type gene, synthesis of molecular chaperones, proteinases, enzymes for scavenging ROS and other detoxification proteins. This process functions in the control and repair of stress induced damage and results in stress tolerance.

includes MYB, NAM/ATAF1,2/CUC2 (NAC), WRKY, APETALA2/ethylene-responsive element binding factor (AP2/ERF), basic leucine zipper (bZIP), basic helix-loop-helix (bHLH), homeodomain, and zinc finger transcription factors (Riechmann*et al*. 2000; Yamaguchi-Shinozaki and Shinozaki 2006). In the genome of the model plant, *Arabidopsis thaliana*, about 1500 TFs are described which are considered to be involved in stress responsive gene expression (Riechmann *et al*. 2000). Extensive reports are now available conforming important role of TFs in the development of abiotic stress tolerant transgenic crop plants (**Table 1**). The phytohormone ABA-dependent signaling systems have been illustrated as pathways that have been reported to mediate stress adaptation by induction of at least two separate regulons (a group of genes controlled by a certain TF): (a) the AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor) regulon; and (b) the MYC (myelocytomatosis oncogene)/MYB (myeloblastosis oncogene) regulon (Saibo *et al*. 2009; Cutler *et al*. 2010). While the CBF/DREB regulon; and (2) the NAC (NAM, ATAF and CUC) and ZF-HD (zincfinger homeodomain) regulon represent the ABA-independent regulons (Nakashima *et al*. 2009; Saibo *et al*. 2009). The NAC [NAM (No Apical Meristem), ATAF1-2, and CUC2 (Cup-Shaped Cotyledon)] TF have been reported to be associated with abiotic stress (Reguera *et al*. 2012). NAC regulates both the ABA-dependent and independent genes. Salinity and drought stress conditions are mediated by ABA that induces expression of various genes. Dehydration-responsive element (DRE)/C-repeat (CRT) proteins have been indentified to play important roles in drought, cold and salinity response (Yamaguchi-Shinozaki and Shinozaki 1994). In addition, The DRE-binding (DREB) and ethylene responsive element binding factors (ERF) subfamilies that belong to the large family of TFs APETALA2/ethylene-responsive (AP2/EREBP), mediate plant signal transduction pathways in response to environmental cues (Reguera *et al*. 2012). The presence of DRE/CRT and ABRE has been noted in many stress-responsive gene promoters, suggesting that ABRE also plays a role in stress-responsive transcription (Yamaguchi-Shinozaki and Shinozaki 2006). ABRE binding proteins/ABRE binding factors have also been identified in *Arabidopsis*, and both are bZIP-type TFs (Choi *et al*. 2000; Uno *et al*. 2000). MYB, NAC, and other families have also been suggested to play important roles in the stress response

especially drought in various crop plants. The ABA-independent stress-responsive genes are regulated by DREB proteins, which bind to DRE *cis*-elements and has also been reported that DREB1/CBF proteins (DREB1A-C/CBF1-3) is induced by cold stress (Liu *et al*. 1998; Nakashima *et al*. 2000). A number of downstream genes get activated by overexpression of DREB transcription factors leading to enhanced abiotic stress tolerance (**Table 1**). Overexpression of SNAC1 (STRESS-RESPONSIVE NAC 1) in *Oryza sativa* reported to protect against drought and salinity stress (Hu *et al*. 2006, 2008; Jeong *et al*. 2010; Takasaki *et al*. 2010). Moreover, the overexpression of NAC genes including OsNAC5, OsNAC6 and OsNAC10 was shown to improved environmental stress tolerance in transgenic *O. sativa* (Hu *et al*. 2008; Jeong *et al*. 2010; Takasaki *et al*. 2010). Yokotani *et al*. (2009) reported that OsNAC063 from rice showed enhanced tolerance to salt and osmotic stress in *A. thaliana*. DREB1/CBF overexpression in *Arabidopsis*, triggers the upregulation of not only various stress-responsive genes including LEA protein and cold-inducible KIN protein genes but also a C_2H_2 zinc finger transcription factor gene. This gene, termed STZ, is one of the direct target genes of DREB1/CBF (Maruyama *et al*. 2004; Sakamoto *et al*. 2004). Because the overexpression of STZ, which functions as a transcriptional repressor, also enhances the tolerance to drought stress (Sakamoto *et al*. 2004), the transcriptional cascade including DREB/CBF and STZ appears to play a key role in the cold stress response in *A. thaliana*. CAMTA3 (Calmodulin Binding Transcription Activator) has been shown to be a positive regulator of the DREB1C/ CBF2 gene (Doherty *et al*. 2009). The heat-inducible expression of HSP genes is regulated by heat shock transcription factors (HSFs). R2R3-MYB transcription factors play wide functional roles, and involved in imparting stress tolerance against various abiotic stresses in transgenic plants (**Table 1**). Dai *et al*. (2007) reported that MYB3R-2I from *O. sativa* found to enhance salinity, dehydration and freezing stress tolerance and decreased sensitivity to ABA in transgenic *Arabidopsis*. The overexpression of GmMYB76, GmMYB92, or GmMYB177 in *Arabidopsis* resulted in significantly higher seed germination under salinity (Liao *et al*. 2008). Overexpression of apple Myb 10 resulted in osmotic stress tolerance (Gao *et al*. 2010). A heat stress-induced HSF, AtHsfA2, has also been shown to activate HSP expression and then enhance

Table 1 Transgenic plants overexpressing various enzymes (oxidative stress, antioxidants, osmolytes, transporters, transcription factors) for abiotic stress tolerance in crop plants. Gene sources are abbreviated as *Ag*, *A. globiformis*; *Ah*, *Atriplexhortensis*; *Al*, *Aeluropus littoralis*; *Am*, *Avicennia marina*; *At*, *Arabidopsis thaliana*; *Bj*, *Brassica juncea*; *Bn*, *Brassica napus*; *Ec*, *E. coli*; *Eg*, *E. gunnii*; *Gm*, *Glycine max*; *Hv*, *Hordeum vulgare*; *Ib*, *Ipomoea batatas*; *Lb*, *Limonium bicolour*; *Mp*, *Malus pumila*; *Nt*, *Nicotiana tabacum*; *P*, *Populus*; *Pf*, *Pyrococcus furiosus*; *Pg*, *Pennisetum glaucum*; *Ps*, *Pisum sativum*; *Pv*, *Pteris vittata*; *S*, *Synechocystis PCC 6803*; *Sb*, *Salicornia brachiata*; *So*, *Spinacia oleracea*; *Ss*, *Suaeda salsa*; *Ta*, *Tamarix androssowii*; *Ta*, *Triticum aestivum*; *Th*, *Tamarix hispida*; *Va*, *Vigna aconitifolia*.

Source/Gene	Transgenic	Response	Reference
At2-Cys Prx (2-cysteine peroxiredoxin)	*Solanum tuberosum* L. cv. Atlantic	Oxidative stress tolerance	Kim *et al.* 2011
BjOXS3 (Oxidative stress 3)	*Schizosaccharomyces pombe*	Enhanced tolerance to a range of metals and oxidizing chemicals	Blanvillain *et al.* 2009
PvGrx5 (Glutaredoxin)	*Arabidopsis thaliana*	High temperature stress and reduces oxidative damage to proteins	Sundaram and Rathinasabapathi 2010
PsMCM6 (Mini chromosome maintenance protein)	*Nicotiana tabacum*	Enhanced salt stress tolerance without yield penalty	Dang *et al.* 2011
TaALMT1 (Aluminum-activated malate transporter)	*Hordeum vulgare* cv. Golden Promise	Increase grain production on an acid soil	Delhaize *et al.* 2009
SsNHX1 (vacuolar Na^+/H^+ antiporter)	*Medicago sativa*	Salt tolerance	Li *et al.* 2010
ThSOS1-RNAi/Thellungiella halophilla (Salt overly sensitive)	*Thellungiella halophilla*	Salt tolerance	Oh *et al.* 2009
AtAvp1 (H^+-PPases)	*Medicago sativa*	Salt tolerance	Bao *et al.* 2009
AtCLCc (Chloride channel)	*A. thaliana*	Salt tolerance	Jossier *et al.* 2010
AtNHX3 (Na^+/H^+ antiporter)	*A. thaliana*	Tolerance to low potassium	Liu *et al.* 2010
AtCBL5 (CalcinurinB-like protein)	*A. thaliana*	Dehydration and salinity stress tolerance	Cheong *et al.* 2010
MAPKKK/DSM1 (MAPK kinase kinase)	*Oryza sativa*	Dehydration stress tolerance	Ning *et al.* 2010
CaCIPK6 (CBL interacting protein kinases)	*N. tabacum*	Salinity stress tolerance	Tripathi *et al.* 2009
AlSAP (A20/AN1 zinc-finger)	*N. tabacum*	Improved drought and salt stress tolerance	Ben Saad *et al.* 2010
OsAP37 (Transcription Factor)	*O. sativa*	Salt, low temperature and drought tolerance	Oh *et al.* 2009
AtAZI1 (Azelaic acid induced 1)	*A. thaliana* and *Saccharomyces cerevisiae*	Freezing stress tolerance	Xu *et al.* 2011
LbDREB (Drought Responsive Element Binding Protein)	*N. tabacum*	Copper stress tolerance	Ban *et al.* 2011
HvDREB2	*O. sativa*	Improved tolerance under water limitation	Bihani *et al.* 2011
PgDREB2A	*N. tabacum*	Salt and dehydration tolerance	Agarwal *et al.* 2010
SbDREB2A	*Escherichia coli* (BL21DE3)	Salt and dehydration tolerance	Gupta *et al.* 2010
OsDREB2B	*A. thaliana*	Dehydration and heat stress tolerance	Matsukura *et al.* 2010
GmERF3	*N. tabacum*	Salt and dehydration stress tolerance	Zhang *et al.* 2009
CBF/DREB1 and *COR15*	*Brassica oleracea* var. *botrytis*	Enhanced proline production and frost resistance	Hadi *et al.* 2011
TaDREB2 and *TaDREB3*	*Triticum aestivum* L. cv. Bobwhite and *H. vulgare* L. cv. Golden Promise	Significant improvement in frost tolerance	Morran *et al.* 2011
MpMyb10 (Myeloblastoma)	*A. thaliana*	Osmotic stress	Gao *et al.* 2010
OsSNAC2 (No apical meristem)	*O. sativa* Zhonghua 11	Salt and cold stress tolerance	Hu *et al.* 2008
AtNTL8(NAC)	*A. thaliana*	GA mediated salt signaling	Kim *et al.* 2008
OsONAC063	*A. thaliana*	Salt and osmotic stress tolerance	Yokotani *et al.* 2009
EguCBF1a/b (C-repeat binding factor genes)	*Eucalyptus*	Low temperature stress tolerance	Navarro *et al.* 2011
ATHB6 (Transcription Factor)	*Lycopersicon esculentum*	Drought tolerance	Mishra *et al.* 2011
ThbZIP (Basic leucine zipper proteins)	*N. tabacum*	Salt stress tolerance by enhancing ROS scavenging system	Wang *et al.* 2010
BF1-3 (C-repeat binding factors)	*A. thaliana*	Frost tolerance	Sharabi-Schwager *et al.* 2010
DDF1 (Dwarf and delayed flowering 1)	*A. thaliana*	Cold, drought, and heat stress tolerance	Kang *et al.* 2011
LeSOD (Superoxide dismutase)	Pepper	Drought tolerance	Chatzidimitriadou *et al.* 2009
AmCu/Zn SOD	*O. sativa* Pusa Basmati-1	MV, salinity and drought stress tolerance	Prashanth *et al.* 2008
NtMn SOD + APX	*Festuca arundinacea* Schreb. cv. Kentucky-31	MV, H_2O_2, Cu, Cd and As tolerance due to increased SOD and APX activity	Lee *et al.* 2007
BjCAT3 (Catalase)	*N. tabacum*	Cd stress tolerance	Guan *et al.* 2009
Cytsod + cytapx	*N. tabacum* 'Xanthi	Less oxidative stress and drought tolerance	Faize *et al.* 2011
PpAPX (Ascorbateperoxidase)	*N. tabacum*	Drought resistance and salt tolerance	Li *et al.* 2009
BntAPX	*Brassica napus*	Salt and drought stress tolerance	Wang *et al.* 2011
EcGR (Glutathione reductase)	*T. aestivum* cv. Oasis protoplast	Salt stress tolerance with higher GSH content	Melchiorre *et al.* 2009
AmMDAR	*N. tabacum*	Salt tolerance	Kavitha *et al.* 2010
AtDHAR (Dehydroascorbatereductase)	*N. tabacum*	Drought and salt tolerance with higher DHAR activity	Eltayeb *et al.* 2007
SsGST (Glutathione-S-transferase)	*Arabidopsis*	Salt tolerance	Qi *et al.* 2010
SGPX-2	*A. thaliana*	Tolerance to H_2O_2, Fe ions, MV, chilling, high salinity or drought stresses	Gaber *et al.* 2006
TaP5CR (Δ^1-pyrroline-5-carboxylate reductase)	*A. thaliana*	Salt tolerance	Ma *et al.* 2008

Table 1 (Cont.)

Source/Gene	Transgenic	Response	Reference
SoBADH-1 (*Betaine aldehyde dehydrogenase*)	*N. tabacum*	Salt tolerance	Yang *et al*. 2008
betA (*Choline dehydrogenase*)	*Gossypium hirsutum* L.	Improved salt tolerance and seed cotton yield	Zhang *et al*. 2011
AhCMO (*Choline monooxygenase*)	*G. hirsutum* L.	Salt tolerance	Zhang *et al*. 2009
AgcodA (*Choline oxidase*)	*L. esculentum*	Drought and salt stress tolerance	Goel *et al*. 2011
AgcodA	*Brassica chinensis*	Enhanced tolerance to extreme temperature and high salinity	Wang *et al*. 2010
AtADC2 (*Arginine decarboxylase*)	*A. thaliana*	Drought tolerance	Alcazar *et al*. 2010

acquired thermotolerance in *A. thaliana* (Charng *et al*. 2007). Improved water use-efficiency but decreased transpiration have been achieved in *O. sativa* through over-expressing HARDY (HRD), encoding a AP2/ERE-like TF (Karaba *et al*. 2007).

TRANSPORTERS

Plants suffer from dehydration or osmotic stress under salinity, drought, and also under low-temperature conditions, which causes reduced availability of water for cellular function and maintenance of cellular turgor pressure. Salinity imposes severe deleterious effects on crop productivity in most plant species, mainly through osmotic stress and ion (Na^+)-specific toxicity (Blumwald 2000; Blumwald *et al*. 2000; Munns and Tester 2008; Tuteja *et al*. 2011). The accumulation of Na^+ in the cytosol causes serious damage *via* inhibition of essential cellular processes, including protein synthesis and vital enzyme reactions (Flowers and Lauchli 1983; Murguia *et al*. 1995). It has been revealed from the recent studies that some classes of Na^+ transporters play crucial roles in Na^+ homeostasis during salinity stress (Horie *et al*. 2010; Hauser and Horie 2010; Uozumi and Schroeder 2010; Yamaguchi *et al*. 2012). Transporters vary in their structure and size from small organic molecules and peptides to multisubunit complexes. Membrane transport proteins are divided into three categories: pump, channel, and secondary transporters. The *Arabidopsis* plasma membrane Na^+/H^+ antiporter SOS1 (salt overly sensitive 1), the Na^+ transporter AtHKT1;1, and the tonoplast Na^+/H^+ antiporter AtNHX1 have drawn particular interest due to their capacity to transport Na^+, and their molecular functions and physiological roles have been extensively studied (Rai *et al*. 2012). The AtNHX1 gene was identified by sequence homology to the *Nhx1* gene in *Saccharomyces cerevisiae*. The AtNHX1 transporter functions in Na^+ sequestration into the vacuole during salinity stress to maintain a high K^+/Na^+ ratio in the cytosol (Apse *et al*. 1999; Gaxiola *et al*. 2001). Transgenic *Arabidopsis* and *Lycopersicon esculentum* plants overexpressing AtNHX1 were reported to accumulate abundant quantities of the transporter in their tonoplast; hence, exhibited substantially enhanced salt tolerance (Apse *et al*. 1999; Quintero *et al*. 2000; Zhang and Blumwald 2001). Salt Overly Sensitive 1 (SOS1) encodes a membrane protein that is homologous to plasma membrane Na^+/H^+ antiporters from bacteria and fungi (Shi *et al*. 2002). Mutant analyses of *sos1* plants have led to a working model of the SOS1 transporter under salinity stress, where SOS1 prevents Na^+ level in xylem sap by unloading/loading of Na^+ into xylem vessels decided by the strength of salinity stress, and influenced Na^+ transport from roots to shoots (Shi *et al*. 2002). SOS1 also functions in direct Na^+ extrusion to outer environment from the root tip where meristematic cells do not have large vacuoles for Na^+ sequestration (Shi *et al*. 2002). Plants possess a large number of genes encoding K^+ transporters, including high-affinity transporters and ion channels (Maser *et al*. 2002). K^+ constitutes the most important macronutrients taken up by plants, and serve essential roles as osmoticum and charge carriers. The mechanisms of K+ uptake and its sensitivity to salt stress in the model plant species is largely known today. HKT (High-affinity K^+ transporter) is a group of well-studied plant Na+

transporters identified in several species (Platten *et al*. 2006). HKT transporters are involved in root Na^+ uptake in wheat (Laurie *et al*. 2002), rice (Garciadeblás *et al*. 2003) and barley (Haro *et al*. 2005). HKT1 (a wheat K^+ transporter) was shown to mediate K^+/Na^+ symport when expressed in *Xenopus oocytes* (Schachtman and Schroeder 1994; Rubio *et al*. 1995; Gassmann *et al*. 1996), and the Arabidopsis and rice homologues are now known to sustain substantial sodium currents (Uozumi *et al*. 2000; Horie *et al*. 2001). Moreover, mutant analysis in Arabidopsis recently indicated significant contribution of AtHKT1 for Na^+ influx *in planta* (Rus *et al*. 2001). Arabidopsis AKT1 and KAT1 (inward-rectifying K^+ channels) have been functionally characterized (Bauer *et al*. 2000; Buschmann *et al*. 2000). The exhibition of topological homology of plant K^+ channels of the AKT/KAT family to animal (outward-rectifying) Shaker-type K^+ channels has been reported (Zimmermann and Sentenac 1999). Moreover, plant inward-rectifying K^+ channels were shown to exhibit high selectivity for K^+ over other monovalent cations, and to specifically mediate K^+ uptake and transport in plant cells (Schachtman *et al*. 1992). The K^+ channels of the AKT/KAT subfamily are differently expressed in root and leaf tissues. In this context, Arabidopsis KAT1 and its potato homologue KST1 were successfully expressed in guard cells (Nakamura *et al*. 1995; Müller-Röber *et al*. 1995). Cao *et al*. (1995) and Lagarde *et al*. (1996) reported that Arabidopsis AKT1 can primarily be expressed in root tissue and localized to epidermis, cortex, and endodermis by promoter activity analysis; whereas in tomato, Hartje *et al*. (2000) reported the localization of LKT1 to root hairs. Additionally, salinity stress-tolerant and -sensitive *O. sativa* were reported to differentially regulate AKT1-type K^+ channel transcripts (Golldack *et al*. 2003). *A. thaliana* AKT1 (*Arabidopsis* K^+ Transporter 1) was reported to be channel mediated that is regulated by voltage (a process known as gating in which the channels open and close), and in this case to favour channel opening at negative voltages that promote net K^+ influx. AKT1 and its relatives are members of the Kv-like (Shaker-like) family of channel proteins that form functional units as tetrameric assemblies around a central pore (Dubey *et al*. 2008; Jeanguenin *et al*. 2008). Nevertheless, MATE (Multidrug And Toxic compound Extrusion Transporters or Multidrug And Toxin Efflux) - a family of small organic molecule transporters and consisting of 400-700 amino acids with 9-12 transmembrane domains, functions actively in the detoxification of xenobiotics, transport of a wide range of metabolites such as cations, organic acids and secondary metabolites and also in heavy metal translocation and hyperaccumulation in plants (Yazaki 2005; Yazaki *et al*. 2008; Gill *et al*. 2012). There are reports of 56 MATE transporter genes in *A. thaliana* plant genome (Li *et al*. 2002; Yazaki *et al*. 2008). AtDTX1 (*A. thaliana* detoxification 1) is a member of the MATE family and serves as a carrier for a range of toxic compounds and is also capable of the detoxification of Cd^{2+} (Li *et al*. 2002). Whereas, FRD3 (ferric reductase defective 3) - a gene encoding a member of MATE family, has been reported to be localized at root pericycle plasma membranes; and functions in Fe homeostasis in Arabidopsis (Rogers and Guerinot 2002; Durrett *et al*. 2007), and also for translocation of other metals, such as Zn (Krämer *et al*. 2007). Additionally, MATE family gene was reported to

protect sorghum against Al stress (Magalhães *et al.* 2007). Genetic engineering studies reported that overexpression of transporter genes in plants results in stress tolerance to various abiotic stresses (**Table 1**).

OSMOLYTES

Abiotic stress factors are menace for agricultural productivity. To cope with these stresses, plants have developed adaptive strategies by expressing specific genes and synthesizing compatible solutes like proline, glycine betaine, trehalose and sugars (Djilianov *et al.* 2005). Glycine betaine (N,N,N-trimethylglycine-betaine; GB) and proline are two major osmoprotectant osmolytes, which are synthesized by many plants (but not all) in response to abiotic stress factors (Vinocur and Altman 2005). Many important agronomical crops, such as rice, potato, tomato and tobacco cannot synthesize GB. Therefore, such plants overexpressing GB synthesizing genes can result in the production of enough amount of GB, which lead plants to tolerate stresses including salinity stress. The overexpression of the genes encoding betaine aldehyde decarboxylase from halophyte *Suaedaliao tungensis* improved the salinity tolerance in tobacco plants. The choline dehydrogenase gene (*codA*) from *Arthrobacter globiformis* helped salinity tolerance in rice (Vinocur and Altman 2005). The overexpression of the genes encoding betaine aldehyde decarboxylase from halophyte *S. tungensis* improved the salinity tolerance in tobacco plants. The choline dehydrogenase gene (*codA*) from *A. globiformis* helped salinity tolerance in rice (Vinocur and Altman 2005). The overexpression of N-methyl transferase gene in cyanobacteria and *Arabidopsis* resulted in accumulation of GB in higher levels and improved salinity tolerance (Waditee *et al.* 2005). Overexpression of *betA* from *E. coli* in *Triticum aestivum* resulted in better salt tolerance and accumulated higher level of GB (He *et al.* 2010).

It is well documented that following salt, drought and metal stress there is a dramatic accumulation of proline. Free proline has been proposed to act as an osmoprotectant, a protein stabilizer, a metal chelator, an inhibitor of lipid peroxidation, OH· and $^1O_2$ scavenger (Ashraf and Foolad 2007; Trovato *et al.* 2008). The overexpression of the genes of its biosynthetic pathway showed better tolerance to plants under various environmental stresses (**Table 1**). The function of proline is thought to be an osmotic regulator under water stress, and its transportation into cells is mediated by a proline transporter. Proline is not only an important molecule in redox signaling, but also an effective quencher of ROS formed under salt, metal and dehydration stress conditions in all plants, including algae (Alia and Pardha Saradhi 1991). Su and Wu (2004) reported that both constitutive expression and stress-inducible expression of the *P5CS* cDNA in transgenic *O. sativa* have led to the accumulation of *P5CS* mRNA and proline, which resulted in higher salt and water deficiency stress tolerance. *T. aestivum* plants overexpression of *Vigna aconitifolia* Δ^1-pyrroline-5-carboxylate synthetase (*P5CS*) cDNA under the control of a stress-induced promoter complex-AIPC resulted in enhanced proline accumulation under water deficit. The tolerance to water deficit in transgenic plants was mainly due to protection mechanisms against oxidative stress and not caused by osmotic adjustment. Overexpression of *P5CS* gene in transgenic tobacco resulted in increased production of proline and salinity/drought tolerance. Ueda *et al.* (2008) have reported that altered expression of barley proline transporter (HvProT) causes different growth responses in *Arabidopsis*, as it leads to the reduction in biomass production and decreased proline accumulation in leaves. Impaired growth of *HvProT* transformed plants was restored by exogenously adding proline, which suggested that growth reduction was caused by a deficiency of endogenous proline. The overexpression of GB and proline biosynthetic pathway genes enhances the abiotic stress tolerance in transgenic plants (**Table 1**).

OXIDATIVE STRESS AND ANTIOXIDANT DEFENSE SYSTEM

Abiotic stresses cause oxidative stress by the generation and/or accumulation of reactive oxygen species (ROS), which basically includes superoxide anion ($O_2\cdot^-$), hydroxyl radicals (OH·) and hydrogen peroxide (H_2O_2) (Gill and Tuteja 2010; Anjum *et al.* 2012; Gill *et al.* 2012) (**Fig. 2**). ROS react with organic molecules and causes membrane lipid peroxidation, protein oxidation, enzyme inhibition and DNA, RNA damage, etc. (Gill and Tuteja 2010; Gill *et al.* 2012). Plants possess very efficient enzymatic (superoxide dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; glutathione reductase, GR; monodehydroascorbatereductase, MDHAR; dehydroascorbatereductase, DHAR; glutathione peroxidase, GPX; guaicolperoxidase, GOPX and glutathione-*S*-transferase, GST) and non-enzymatic (ascorbic acid, ASH; glutathione, GSH; phenolic compounds, alkaloids, non-protein amino acids and α-tocopherols) antioxidant defense systems, which work in concert to control the cascades of uncontrolled oxidation and protect plant cells from oxidative damage by scavenging of ROS (Gill and Tuteja 2010; Anjum *et al.* 2012; Gill *et al.* 2012). Therefore, the overexpression of ROS scavengers can increase the plant resistance to various stresses such as salinity, drought, heat, cold, etc. (**Table 1**).

Overexpression of a Mn-SOD in transgenic *Arabidopsis* plants also showed increased salt tolerance (Wang *et al.* 2004). Furthermore, they showed that Mn-SOD activity as well as the activities of Cu/Zn-SOD, Fe-SOD, CAT and POD (peroxidase) was significantly higher in transgenic *Arabidopsis* plants than control (Wang *et al.* 2004). Cu/Zn-SOD overexpressing transgenic tobacco plants showed multiple stress tolerance (Badawi *et al.* 2004). Overexpression of Mn-SOD in transformed *L. esculentum* plants also showed enhanced tolerance against salt stress (Wang *et al.* 2007). Further, the combined expression of Cu/Zn-SOD and APX in transgenic *Festuca arundinacea* plants led to increased tolerance to MV (methyl viologen), H_2O_2, Cu, Cd and As (Lee *et al.* 2007). Pyramiding of antioxidative enzyme Cu/ZnSOD, APX, and DHAR in tobacco chloroplasts showed salinity and oxidative stress tolerance compared to those plants expressing single or double gene (Lee *et al.* 2007). The overexpression of Cu/ZnSOD, APX, and DHAR resulted in ~1.6-2.1 times higher DHAR activity, higher ratios of reduced ascorbate to DHA, and oxidized glutathione (GSSG) to reduced glutathione (GSH) (Lee *et al.* 2007). Maize Cu/ZnSOD and/or CAT genes were targeted to the chloroplasts of *Brassica campestris* and it was noted that exposure of transgenic plants to 400 ppb SO_2 showed enhanced tolerance than wild type (Tseng *et al.* 2007). Transgenic *Arabidopsis* plants overexpressing OsAPXa or OsAPXb exhibited increased salt tolerance. It was found that the overproduction of OsAPXb enhanced and maintained APX activity to a much higher extent than OsAPXa in transgenic plants under different NaCl concentrations (Lu *et al.* 2007). Overexpression of a eukaryotic GR from *B. campestris* (BcGR) and *E. coli* GR (EcGR) was studied in *E. coli* in pET-28a. It was found that BcGR-overproducing *E. coli* showed better growth and survival rate than the control but far better growth was noted in *E. coli* strain transformed with the inducible EcGR in the presence of paraquat, SA and Cd (Yoon *et al.* 2005). In an interesting study, transgenic *Nicotiana tabacum* plants with 30-70% less GR activity were used to find out the possible mechanism of GR against oxidative stress. Transgenic plants with less GR activity showed enhanced sensitivity to oxidative stress. It was suggested that GR plays an important role in the regeneration of GSH and thus protects against oxidative stress also by maintaining the ASH pool (Ding *et al.* 2009). It has also been noted that the overexpression of DHAR in tobacco protected the plants against ozone toxicity (Chen and Gallie 2005). Overexpression of DHAR increased salt tolerance in *A. thaliana* (Ushimaru *et al.* 2006) and drought and ozone stress tolerance in tobacco (Eltayeb *et al.* 2006).
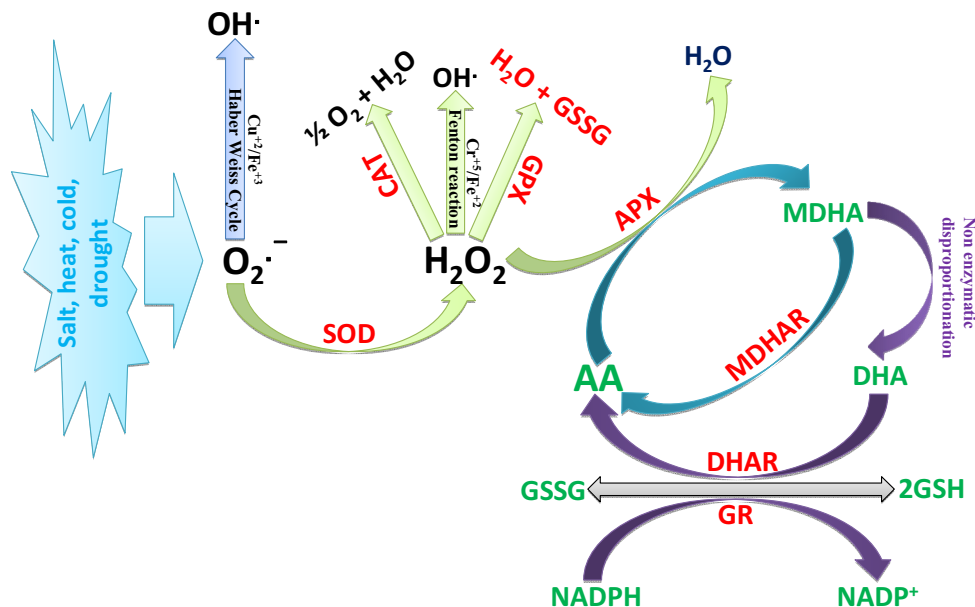
Fig. 2 Generation of reactive oxygen species (ROS) by abiotic stresses and their scavenging mechanism by antioxidants. ROS: $O_2^{\cdot-}$, superoxide radicals; H_2O_2, hydrogen peroxide; $OH\cdot$, hydroxyl radical. Antioxidants: SOD, superoxide dismutase; CAT, catalase, APX, ascorbate peroxidase; GPX, DHAR, dehydroascorbatereductase; MDHAR, mono dehydroascorbatereductase; GR, glutathione reductase; AA, ascorbic acid; GSH, reduced glutathione; GSSG, oxidised glutathione.

GST Nt107 expressing transgenic cotton lines were used to investigate the tolerance potential under various stresses like chilling, salinity, and herbicides and it was noted that transgenic seedlings exhibited ten-fold and five-fold higher GST activity under control and salt stress conditions, respectively (Light *et al.* 2005). Transgenic tobacco plants overexpressing *Prosopisjuli flora* GST survived better than control plants under 15% PEG stress (George *et al.* 2010). It was noted that GPX activity in transgenic cotton seedlings was 30-60% higher under normal conditions, but was not different than GPX activity in wild type seedlings under salt stress conditions (George *et al.* 2010). Overexpression of various antioxidant enzymes has been found to enhance abiotic stress tolerance in transgenic plants (**Table 1**).

CONCLUSIONS

Comprehensive efforts have been made to unravel plant abiotic tolerance mechanisms in model as well as crop plants but still our understanding of the underlying molecular basis of abiotic stress tolerance is not very well clear yet. As plants are sessile, stress is an unavoidable and integral part in the plant growth, development and evolution. Though it causes great deal of losses towards the yield in crop plants, the recent studies in this respect are providing leads to develop sustainable varieties. Functional genomics and high throughput analysis including microarray, transcriptomics, metabolomics, reverse genetics etc. supported by a high quality bioinformatics should answer some of these questions related to stress response. It has been revealed that transcription factors also play important role by activating/repressing target genes to help produce metabolites, enzymes, osmolytes, osmoprotectants and other chaperon molecules, which provide protection to cell components from the stress. Genetic engineering has opened up a new opportunity in crop improvement allowing the transfer of desirable gene(s) across species and genera for developing transgenic plants with novel traits, such as built-in protection, improved nutritional qualities, and so on. The major attempt to enhance plant tolerance is the manipulation of genes that are either directly involved in protection of cells against water loss or the genes that are involved in regulating signal transduction pathways in response to water stress. Much effort isstill required to uncover detail of a gene induced by cold, salinity, and drought stress, and their interacting partners to understand the complexity of the stress signal transduction pathways. Overall, a combination of a good genetic background with multiple transgenes/alleles mining and promising performance in field conditions will reveal the success of the development of abiotic stress-tolerant plants.

REFERENCES

Agarwal P, Agarwal PK, Joshi AJ, Reddy MK, Sopory SK (2010) Overexpression of PgDREB2A transcription factor enhances abiotic stress tolerance and activates downstream stress-responsive genes. *Molecular Biology Reports* **37**, 1125-1135

Agarwal PK, Jha B (2010) Transcription factors in plants and ABA dependent and independent abiotic stress signalling. *Biologia Plantarum* **54**, 201-212

Alcázar R, Planas J, Saxena T, Zarza X, Bortolotti C, Cuevas JC, Bitrián M, Tiburcio AF, Altabella T (2010) Putrescine accumulation confers drought tolerance in transgenic *Arabidopsis* plants overexpressing the homologous Arginine decarboxylase 2 gene. *Plant Physiology and Biochemistry* **48**, 547-552

Alia, Pardha Saradhi P (1991) Proline accumulation under heavy metal stress. *Journal of Plant Physiology* **138**, 554-558

Anjum NA, Ahmad I, Mohmood I, Pacheco M, Duarte AC, Pereira E, Umar S, Ahmad A, Khan NA, Iqbal M, Prasad MNV (2012) Modulation of glutathione and its related enzymes in plants' responses to toxic metals and metalloids - a review. *Environmental and Experimental Botany* **75**, 307-324

Apse M, Aharon G, Sneddon W, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na^+/H^+ antiport in *Arabidopsis*. *Science* **285**, 1256-1258

Ashraf M, Foolad MR (2007) Roles of glycinebetaine and proline in improving plant abiotic stress tolerance. *Environmental and Experimental Botany* **59**, 206-216

Badawi GH, Yamauchi Y, Shimada E, Sasaki R, Kawano N, Tanaka K, Tanaka K (2004) Enhanced tolerance to salt stress and water deficit by overexpressing superoxide dismutase in tobacco (*Nicotiana tabacum*) chloroplasts. *Plant Science* **166**, 919-928

Ban Q, Liu G, Wang Y (2011) A DREB gene from *Limonium bicolor* mediates molecular and physiological responses to copper stress in transgenic tobacco. *Journal of Plant Physiology* **168**, 449-458

Bao AK, Wang SM, Wu GQ, Xi JJ, Zhang JL, Wang CM (2009) Overexpression of the *Arabidopsis* H^+-PPase enhanced resistance to salt and drought

stress in transgenic alfalfa (*Medicago sativa* L.). *Plant Science* **176**, 232-240

Bauer CS, Hoth S, Haga K, Philippar K, Aoki N, Hedrich R (2000) Differential expression and regulation of K(+) channels in the maize coleoptile: Molecular and biophysical analysis of cells isolated from cortex and vasculature. *Plant Journal* **24**, 139-145

Ben Saad R, Zouari N, Ben Ramdhan W, Azaza J, Meynard D, Guiderdoni E, Hassairi A (2010) Improved drought and salt stress tolerance in transgenic tobacco overexpressing a novel A20/AN1 zinc-finger "AlSAP" gene isolated from the halophyte grass *Aeluropus littoralis*. *Plant Molecular Biology* **72**, 171-90

Bhatnagar-Mathur P, Vadez V, Sharma KK (2008) Transgenic approaches for abiotic stress tolerance in plants: Retrospect and prospects. *Plant Cell and Reports* **27**, 411-424

Bihani P, Char B, Bhargava S (2011) Transgenic expression of sorghum DREB2 in rice improves tolerance and yield under water limitation. *Journal of Agriculture Science* **149**, 95-101

Blanvillain R, Kim JH, Wu S, Lima A, Ow DW (2009) OXIDATIVE STRESS 3 is a chromatin-associated factor involved in tolerance to heavy metals and oxidative stress. *Plant Journal* **57**, 654-665

Blumwald E (2000) Salt transport and salt resistance in plants and other organisms. *Current Opinion in Cell Biology* **12**, 431-434

Blumwald E, Aharon GS, Apse MP (2000) Na$^+$ transport in plant cells. *Biochimica et Biophysica Acta* **1465**, 140-151

Bray EA, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stresses. In: Gruissem W, Buchannan B, Jones R (Eds) *Biochemistry and Molecular Biology of Plants*, American Society of Plant Physiologists, Rockville, MD, pp 1158-1249

Buschmann PH, Vaidyanathan R, Gassmann W, Schroeder JI (2000) Enhancement of Na(+) uptake currents, timedependent inward-rectifying K(+) channel currents, and K(+) channel transcripts by K(+) starvation in wheat root cells. *Plant Physiology* **122**, 1387-1398

Cao Y, Ward JM, Kelly WB, Ichida AM, Gaber RF, Anderson JA, Uozumi N, Schroeder JI, Crawford NM (1995) Multiple genes, tissue specificity, and expression dependent modulation contribute to the functional diversity of potassium channels in *Arabidopsis thaliana*. *Plant Physiology* **109**, 1093-1106

Charng Y-Y, Liu H-C, Liu N-Y, Chi W-T, Wang C-N, Chang S-H, Wang T-T (2007) A heat-inducible transcription factor, HsfA2, is required for extension of acquired thermotolerance in *Arabidopsis*. *Plant Physiology* **143**, 251-262

Chatzidimitriadou K, Nianiou-Obeidat I, Madesis P, Perl-Treves R, Tsaftaris A (2009) Expression of SOD transgene in pepper confer stress tolerance and improve shoot regeneration. *Electronic Journal of Biotechnology* **12**, 4

Chen Z, Gallie DR (2005) Increasing tolerance to ozone by elevating folia ascorbic acid confers greater protection against ozone than increasing avoidance. *Plant Physiology* **138**, 1673-1689

Cheong YH, Sung SJ, Kim BG, Pandey GK, Cho JS, Kim KN, Luan S (2010) Constitutive overexpression of the calcium sensor CBL5 confers osmotic or drought stress tolerance in *Arabidopsis*. *Molecular Cells* **29**, 159-165

Choi H-I, Hong J-H, Ha J-O, Kang J-Y, Kim SY (2000) ABFs, a family of ABA-responsive element binding factors. *Journal of Biological Chemistry* **275**, 1723-1730

Cutler SR, Rodriguez PL, Finkelstein RR, Abrams SR (2010) Abscisic acid: emergence of a core signaling network. *Annual Reviews of Plant Biology* **61**, 651-679

Dai XY, Xu YY, Ma QB, Xu WY, Wang T, Xue YB, Chong K (2007) Overexpression of an R1R2R3 MYB gene, OsMYB3R-2, increases tolerance to freezing, drought, and salt stress in transgenic *Arabidopsis*. *Plant Physiology* **143**, 1739-1751

Dang HQ, Tran NQ, Gill SS, Tuteja R, Tuteja N (2011) A single subunit MCM6 from pea promotes salinity stress tolerance without affecting yield. *Plant Molecular Biology* **76**, 19-34

Delhaize E, Taylor P, Hocking PJ, Simpson RJ, Ryan PR, Richardson AE (2009) Transgenic barley (*Hordeum vulgare* L.) expressing the wheat aluminium resistance gene (TaALMT1) shows enhanced phosphorus nutrition and grain production when grown on an acid soil. *Plant Biotechnology Journal* **7**, 391-400

Ding S, Lu Q, Zhang Y, Yang Z, Wen X, Zhang L, Lu C (2009) Enhanced sensitivity to oxidative stress in transgenic tobacco plants with decreased glutathione reductase activity leads to a decrease in ascorbate pool and ascorbate redox state. *Plant Molecular Biology* **69**, 577-592

Djilianov D, Georgieva T, Moyankova D, Atanassov A, Shinozaki K, Smeeken SCM, Verma DPS, Murata N (2005) Improved abiotic stress tolerance in plants by accumulation of osmoprotectants - gene transfer approach. *Biotechnology and Biotechnological Equipment* **19**, 63-71

Doherty CJ, Van Buskirk HA, Myers SJ, Thomashow MF (2009) Roles for *Arabidopsis* CAMTA transcription factors in cold-regulated gene expression and freezing tolerance. *Plant Cell* **21**, 972-984

Duby G, Hosy E, Fizames C, Alcon C, Costa A, Sentenac H, Thibaud J-B (2008) AtKC1, a conditionally targeted Shaker-type subunit, regulates the activity of plant K$^+$ channels. *Plant Journal* **53**, 115-123

Durrett TP, Gassmann W, Rogers EE (2007) The FRD3-mediated efflux of

citrate into the root vasculature is necessary for efficient iron translocation. *Plant Physiology* **144**, 197-205

Eltayeb AE, Kawano N, Badawi GH, Kaminaka H, Sanekata T, Morishima I, Shibahara T, Inanaga S, Tanaka K (2006) Enhanced tolerance to ozone and drought stresses in transgenic tobacco overexpressing dehydroascorbate-reductase in cytosol. *Physiologia Plantarum* **127**, 57-65

Eltayeb AE, Kawano N, Badawi GH, Kaminaka H, Sanekata T, Shibahara T, Inanaga S, Tanaka K (2007) Overexpression of monodehydroascorbate-reductase in transgenic tobacco confers enhanced tolerance to ozone, salt and polyethylene glycol stresses. *Planta* **225**, 1255-1264

Faize M, Burgos L, Faize L, Piqueras A, Nicolas E, Barba-Espin G, Clemente-Moreno MJ, Alcobendas R, Artlip T, Hernandez JA (2011) Involvement of cytosolic ascorbate peroxidase and Cu/Zn-superoxide dismutase for improved tolerance against drought stress. *Journal of Experimental Botany* **62**, 2599-2613

Flowers TJ, Lauchli A (1983) Sodium versus potassium: substitution and compartmentation. In: Lauchli A, Bieleski RA (Eds) *Inorganic Plant Nutrition*, New Series, vol. 15B, Encyclopedia of Plant Physiology, Springer, Berlin, pp 651-681

Gaber A, Kazuya Y, Takashi Y, Yukinori Y, Toru T, Hitoshi M, Yoshihisa N, Shigeru S (2006) Glutathione peroxidase-like protein of *Synechocystis* PCC 6803 confers tolerance to oxidative and environmental stresses in transgenic *Arabidopsis*. *Physiologia Plantarum* **128**, 251-262

Gao JJ, Zhang Z, Peng RH, Xiong AS, Xu J, Zhu B, Yao QH (2010) Forced expression of Mdmyb10, a myb transcription factor gene from apple, enhances tolerance to osmotic stress in transgenic *Arabidopsis*. *Molecular Biology Reports* **38**, 205-211

Gao JJ, Zhang Z, Peng RH, Xiong AS, Xu J, Zhu B, Yao QH (2010) Forced expression of Mdmyb10, a myb transcription factor gene from apple, enhances tolerance to osmotic stress in transgenic *Arabidopsis*. *Molecular Biology Reports* **38**, 205-211

Garciadeblás B, Senn ME, Bañuelos MA, Rodríguez-Navarro A (2003) Sodium transport and HKT transporters: The rice model. *Plant Journal* **34**, 788-801

Gassmann W, Rubio F, Schroeder JI (1996) Alkali ion selectivity of the wheat root high-affinity potassium transporter HKT1. *Plant Journal* **10**, 869-882

Gaxiola RA, Li J, Undurraga S, Dang LM, Allen GJ, Alper SL, Fink GR (2001) Drought- and salt-tolerant plants result from overexpression of the AVP1 H$^+$-pump. *Proceedings of the National Academy of Sciences USA* **98**, 11444-11449

George S, Venkataraman G, Parida A (2010) A chloroplast-localized and auxin induced glutathione *S*-transferase from phreatophyte *Prosopisjuli flora* confer drought tolerance on tobacco. *Journal of Plant Physiology* **167**, 311-318

Gill SS, Anjum NA, Ahmad I, Pacheco M, Duarte AC, Umar S, Khan NA, Pereira ME (2012) Metal hyperaccumulation and tolerance in *Alyssum*, *Arabidopsis* and *Thlaspi*. In: Anjum NA, Ahmad I, Pereira ME, Duarte AC, Umar S, Khan NA (Eds) *The Plant Family Brassicaceae: Contribution towards Phytoremediation*, Springer, Dordrecht, The Netherlands, pp 99-137

Gill SS, Singh LP, Gill R, Tuteja N (2012) Generation and scavenging of reactive oxygen species in plants under stress. In: Tuteja N, Gill SS, Tiburcio AF, Tuteja R (Eds) *Improving Crop Resistance to Abiotic Stress*, Wiley-VCH Verlag GmbH and Co. KGaA, Germany, pp 49-70

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry* **48**, 909-930

Goel, D Singh AK, Yadav V, Babbar SB, Murata N, Bansal KC (2011) Transformation of tomato with a bacterial *codA* gene enhances tolerance to salt and water stresses. *Journal of Plant Physiology* **168**, 1286-1294

Golldack D, Quigley F, Michalowski CB, Kamasani UR, Bohnert HJ (2003) Salinity stress-tolerant and -sensitive rice (*Oryza sativa* L.) regulate AKT1-type potassium channel transcripts differently. *Plant Molecular Biology* **51**, 71-81

Gupta K, Agarwal PK, Reddy MK, Jha B (2010) SbDREB2A, an A-2 type DREB transcription factor from extreme halophyte *Salicornia brachiata* confers abiotic stress tolerance in *Escherichia coli*. *Plant Cell Reports* **29**, 1131-1137

Hadi F, Gilpin M, Fuller MP (2011) Identification and expression analysis of CBF/DREB1 and COR15 genes in mutants of *Brassica oleracea* var. botrytis with enhanced proline production and frost resistance. *Plant Physiology and Biochemistry* **49**, 1323-1332

Haro R, Bañuelos MA, Senn ME, Barrero-Gil J, Rodríguez-Navarro A (2005) HKT1 mediates sodium uniport in roots. Pitfalls in the expression of HKT1 in yeast. *Plant Physiology* **139**, 1495-1506

Hartje S, Zimmermann S, Klonus D, Müller-Röber B (2000) Functional characterisation of LKT1, a K+ uptake channel from tomato root hairs, and comparison with the closely related potato inwardly rectifying K+ channel SKT1 after expression in *Xenopus* oocytes. *Planta* **210**, 723-731

Hauser F, Horie T (2010) A conserved primary salt tolerance mechanism mediated by HKT transporters: a mechanism for sodium exclusion and maintenance of high K$^+$/Na$^+$ ratio in leaves during salinity stress. *Plant Cell and Environment* **33**, 552-565

He C, Yang A, Zhang W, Gao Q, Zhang J (2010) Improved salt tolerance of transgenic wheat by introducing *betA* gene for glycine betaine synthesis. *Plant Cell, Tissue and Organ Culture* **101**, 65-78

Hirayama T, Shinozaki K (2010) Research on plant abiotic stress responses in the postgenome era: past, present and future. *Plant Journal* **61**, 1041-1052

Horie T, Hauser F, Schroeder JI (2009) HKT transporter-mediated salinity resistance mechanisms in *Arabidopsis* and monocot crop plants. *Trends in Plant Sciences* **14**, 660-668

Horie T, Yoshida K, Nakayama H, Yamada K, Oiki S, Shinmyo A (2001) Two types of HKT transporters with different properties of Na$^+$ and K$^+$ transport in *Oryza sativa*. *Plant Journal* **27**, 129-138

Hu H, You J, Fang Y, Zhu X, Qi Z, Xiong L (2008) Characterization of transcription factor gene SNAC2 conferring cold and salt tolerance in rice. *Plant Molecular Biology* **67**, 169-181

Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q, Xiong L (2006) Overexpressing 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**, 12987-12992

Hussain SS, Kayani MA, Amjad M (2011) Transcription factors as tools to engineer enhanced drought stress tolerance in plants. *Biotechnology Progress* **27**, 297-306

Ishida T, Osakabe Y, Yanagisawa S (2012) Transcription factors: Improving abiotic stress tolerance in plants. In: Tuteja N, Gill SS, Tiburcio AF, Tuteja R (Eds) *Improving Crop Resistance to Abiotic Stress*, Wiley-VCH Verlag GmbH and Co. KGaA, pp 589-619

Jeanguenin L, LebaudyA, Xicluna J, Alcon C, Hosy E, Duby G, Michard E, Lacombe B, Dreyer I, Thibaud J-B (2008) Heteromerization of *Arabidopsis* Kv channel α-subunits: data and prospects. *Plant Signaling and Behavior* **3**, 622-625

Jeong JS, Kim YS, Baek KH, Jung H, Ha S-H, Do Choi Y, Kim M, Reuzeau C, Kim J-K (2010) Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under field drought conditions. *Plant Physiology* **153**, 185-197

Jewell MC, Campbell BC, Godwin ID (2010) Transgenic plants for abiotic stress resistance. In: Kole C, Michler C, Abbott AG, Hall TC (Eds) *Transgenic Crop Plants*, Springer-Verlag Berlin Heidelberg, pp 67-132

Jossier M, Kroniewicz L, Dalmas F, Le Thiec D, Ephritikhine G, Thomine S, Barbier-Brygoo H, Vavasseur A, Filleur S, Leonhardt N (2010) The *Arabidopsis* vacuolar anion transporter, AtCLCc, is involved in the regulation of stomatal movements and contributes to salt tolerance. *Plant Journal* **64**, 563-576

Kang H-G, Kim J, Kim B, Jeong H, Choi SH, Kim EK, Lee H-Y, Lim PO (2011) Overexpression of FTL1/DDF1, an AP2 transcription factor, enhances tolerance to cold, drought, and heat stresses in *Arabidopsis thaliana*. *Plant Science* **180**, 634-641

Karaba A, Dixit S, Greco R, Aharoni A, Trijatmiko KR, Marsch-Martinez N, Krishnan A, Nataraja KN, Udayakumar M, Pereira A (2007) Improvement of water use efficiency in rice by expression of HARDY, an Arabidopsis drought and salt tolerance gene. *Proceedings of the National Academy of Sciences USA* **104**, 15270-15275

Kavitha K, George S, Venkataraman G, Parida A (2010) A salt-inducible chloroplastic monodehydroascorbate reductase from halophyte *Avicennia marina* confers salt stress tolerance on transgenic plants. *Biochimie* **92**, 1321-1329

Kim MD, Kim Y-H, Kwon S-Y, Jang B-Y, Lee S-Y, Yun D-J, Cho J-H, Kwak S-S, Lee H-S (2011) Overexpression of 2-cysteine peroxiredoxin enhances tolerance to methyl viologen-mediated oxidative stress and high temperature in potato plants. *Plant Physiology and Biochemistry* **49**, 891-897

Kim SG, Lee AK, Yoon HK, Park CM (2008) A membrane-bound NAC transcription factor NTL8 regulates gibberellic acid-mediated salt signaling in *Arabidopsis* seed germination. *Plant Journal* **55**, 77-88

Kim YH, Kim CY, Song WK, Park DS, Kwon SY, Lee HS, Bang JW, Kwak SS (2008) Overexpression of sweetpotato swpa4 peroxidase results in increased hydrogen peroxide production and enhances stress tolerance in tobacco. *Planta* **227**, 867-881

Krämer U, Talke IN, Hannikenne M (2007) Transition metal transport. *FEBS Letters* **581**, 2263-2272

Lagarde D, Basset M, Lepetit M, Conejero G, Gaymard F, Astruc S, Grignon C (1996) Tissue-specific expression of Arabidopsis AKT1 gene is consistent with a role in K$^+$ nutrition. *Plant Journal* **9**, 195-203

Laurie S, Feeney KA, Maathuis FJM, Heard PJ, Brown SJ, Leigh RA (2002) A role for HKT1 in sodium uptake by wheat roots. *Plant Journal* **32**, 139-149

Lee SH, Ahsan N, Lee KW, Kim DH, Lee DG, Kwak SS, Kwon SY, Kim TH, Lee BH (2007) Simultaneous overexpression of both CuZn superoxide dismutase and ascorbate peroxidase in transgenic tall fescue plants confers increased tolerance to a wide range of abiotic stresses. *Journal of Plant Physiology* **164**, 1626-1638

Lee SH, Ahsan N, Lee KW, Kim DH, Lee DG, Kwak SS, Kwon SY, Kim TH, Lee BH (2007) Simultaneous overexpression of both CuZn superoxide dismutase and ascorbate peroxidase in transgenic tall fescue plants confers increased tolerance to a wide range of abiotic stresses. *Journal of Plant Physiology* **164**, 1626-1638

Li L, He Z, Pandey GK, Tsuchiya T, Luan S (2002) Functional cloning and characterization of a plant efflux carrier for multidrug and heavy metal detoxification. *Journal of Biological Chemistry* **277**, 5360-5368

Li Y, Zang Y, Feng F, Liang D, Cheng L, Shi SM (2010) Overexpression of a *Malus* vacuolar Na$^+$/H$^+$ antiporter gene (*MdNHX1*) in apple rootstock M.26 and its influence on salt tolerance. *Plant Cell, Tissue and Organ Culture* **102**, 337-345

Li Y-J, Hai R-L, Du X-H, Jiang X-N (2009) 1 and H. LU Over-expression of a *Populus* peroxisomalascorbate peroxidase (*PpAPX*) gene in tobacco plants enhances stress tolerance. *Plant Breeding* **128**, 404-410

Liao CCY, Chen ZH, Chan TW (2008) My-Mini-Pet: The design of pet-nurturing handheld game. In: Eisenberg M, Kinshuk, Chang M, Mcgreal R (Eds) *Digital Game and Intelligent Toy Enhanced Learning, IEEE International Workshop*, IEEE Computer Society, Los Alamitos, CA, pp 138-140

Light GG, Mahan JR, Roxas VP, Allen RD (2005) Transgenic cotton (*Gossypium hirsutum* L.) seedlings expressing a tobacco glutathione *S*-transferase fail to provide improved stress tolerance. *Planta* **222**, 346-354

Liu H, Tang R, Zhang Y, Wang C, Lv Q, Gao X, Li W, Zhang H (2010) *AtNHX3* is a vacuolar K$^+$/H$^+$antiporter required for low-potassium tolerance in *Arabidopsis thaliana*. *Plant Cell and Environment* **33**, 1989-1999

Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchi-Shinozaki K, Shinozaki K (1998) Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low temperature responsive gene expression, respectively, in *Arabidopsis*. *Plant Cell* **10**, 1391-1406

Lu ZQ, Liu D, Liu SK (2007) Two rice cytosolic ascorbate peroxidases differentially improve salt tolerance in transgenic *Arabidopsis*. *Plant Cell Reports* **26**, 1909-1917

Ma L, Zhou E, Gao L, Mao X, Zhou R, Jia J (2008) Isolation, expression analysis and chromosomal location of P5CR gene in common wheat (*Triticum aestivum* L.). *South African Journal of Botany* **74**, 705-712

Magalhães JV, Liu J, Guimarães CT, Lana UGP, Alves VMC, Wang YH, Schaffert RE (2007) A gene in the multidrug and toxic compound extrusion (MATE) family confers aluminum tolerance in sorghum. *Nature Genetics* **39**, 1156-116

Mahajan S, Tuteja N (2005) Cold, salinity and drought stress: An overview. *Archives of Biochemistry and Biophysics* **444**, 139-158

Maruyama K, Sakuma Y, Kasuga M, Ito Y, Seki M, Goda H, Shimada Y, Yoshida S, Shinozaki K, Yamaguchi-Shinozaki K (2004) Identification of cold-inducible downstream genes of the *Arabidopsis* DREB1A/CBF3 transcriptional factor using two microarray systems. *Plant Journal* **38**, 982-993

Maser P, Eckelman B, Vaidyanathan R, Horie T, Fairbairn DJ, Kubo M, Yamagami M, Yamaguchi K, Nishimura M, Uozumi N, Robertson W, Sussman MR, Schroeder JI (2002) Altered shoot/root Na$^+$ distribution and bifurcating salt sensitivity in *Arabidopsis* by genetic disruption of the Na$^+$ transporter AtHKT1. *FEBS Letters* **531**, 157-161

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. *Molecular Genetics and Genomics* **283**, 185-196

Melchiorre M, Robert G, Trippi V, Racca R, Lascano HR (2009) Superoxide dismutase and glutathione reductase overexpression in wheat protoplast: Photooxidative stress tolerance and changes in cellular redox state. *Plant Growth Regulation* **57**, 57-68

Mishra KB, Iannacone R, Petrozza A, Mishra A, Armentano N, Vecchia GL, Trtílek M, Cellini F, Nedbal L (2012) Engineered drought tolerance in tomato plants is reflected in chlorophyll fluorescence emission. *Plant Science* **182**, 79-86

Mishra NS, Tuteja R, Tuteja N (2006) Signaling through MAP kinase networks in plants. *Achieves of Biochemistry and Biophysics* **452**, 55-68

Morran S, Eini O, Pyvovarenko T, Parent B, Singh R, Ismagul A, Eliby S, Shirley N, Langridge P, Lopato S (2011) Improvement of stress tolerance of wheat and barley by modulation of expression of DREB/CBF factors. *Plant Biotechnology Journal* **9**, 230-249

Müller-Röber B, Ellenberg J, Provart N, Willmitzer L, Busch H, Becker D, Dietrich P, Hoth S, Hedrich R (1995) Cloning and electrophysiological analysis of KST1, an inward rectifying K$^+$ channel expressed in potato guard cells. *EMBO Journal* **14**, 2409-2416

Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**, 651-681

Murguia JR, Belles JM, Serrano R (1995) A salt-sensitive 3'(2'),5'-bisphosphate nucleotidase involved in sulfate activation. *Science* **267**, 232-234

Nakamura RL, McKendree WL, Hirsch RE, Sedbrook JC, Gaber RF, Sussman MR (1995) Expression of an Arabidopsis potassium channel gene in guard cells. *Plant Physiology* **109**, 371-374

Nakashima K, Ito Y, Yamaguchi-Shinozaki K (2009) Transcriptional regulatory networks in response to abiotic stresses in Arabidopsis and grasses. *Plant Physiology* **149**, 88-95

Nakashima K, Shinwari ZK, Sakuma Y, Seki M, Miura S, Shinozaki K, Yamaguchi-Shinozaki K (2000) Organization and expression of two *Arabidopsis* DREB2 genes encoding DRE-binding proteins involved in dehydration- and high-salinity responsive gene expression. *Plant Molecular Biology*

42, 657-665

Navarro M, Ayax C, Martinez Y, Laur J, El Kayal W, Marque C, Teulires C (2011) Two EguCBF1 genes overexpressed in *Eucalyptus* display a different impact on stress tolerance and plant development. *Plant Biotechnology Journal* **9**, 50-63

Ning J, Li X, Hicks LM, Xiong L (2010) A Raf-like MAPKKK gene DSM1 mediates drought resistance through reactive oxygen species scavenging in rice. *Plant Physiology* **152**, 876-890

Oh DH, Leidi E, Zhang Q, Hwang SM, Li Y, Quintero FJ, Jiang X, D'Urzo MP, Lee SY, Zhao Y, Bahk JD, Bressan RA, Yun DJ, Pardo JM, Bohnert HJ (2009) Loss of halophytism by interference with SOS1 expression. *Plant Physiology* **151**, 210-222

Oh S-J, Kim Y-S, Kwon C-W, Park HK, Jeong JS, Kim J-K (2009) Overexpression of the transcription factor AP37 in rice improves grain yield under drought conditions. *Plant Physiology* **150**, 1368-1379

Platten JD, Cotsaftis O, Berthomieu P, Bohnert H, Davenport RJ, Fairbairn DJ et al. (2006) Nomenclature for HKT transporters, key determinants of plant salinity tolerance. *Trends in Plant Sciences* **11**, 372-374

Prashanth SR, Sadhasivam V, Parida A (2008) Over expression of cytosolic copper/zinc superoxide dismutase from a mangrove plant *Avicennia marina* in indica rice var Pusa Basmati-1 confers abiotic stress tolerance. *Transgenic Research* **17**, 281-291

Qi YC, Liu WQ, Qiu LY, Zhang SM, Ma L, Zhang H (2010) Overexpression of glutathione *S*-transferase gene increases salt tolerance of *Arabidopsis*. *Russian Journal of Plant Physiology* **57**, 233-240

Quintero FJ, Blatt MR, Pardo JM (2000) Functional conservation between yeast and plant endosomal Na($^+$)/H($^+$) antiporters. *FEBS Letters* **471**, 224-228

Rai V, Tuteja N, Takabe T (2012) Transporters and abiotic stress tolerance in plants. In: *Improving Crop Resistance to Abiotic Stress*, Tuteja N, Gill SS, Tiburcio AF, Tuteja R (Eds) Wiley-VCH Verlag GmbH and Co. KGaA, Berlin, pp 505-520

Riechmann JL, Heard J, Martin G, Reuber L, Jiang C, Keddie J, Adam L, Pineda O, Ratcliffe OJ, Samaha RR (2000) *Arabidopsis* transcription factors: Genome-wide comparative analysis among eukaryotes. *Science* **290**, 2105-2110

Reguera M, Peleg Z, Blumwald E (2012) Targeting metabolic pathways for genetic engineering abiotic stress-tolerance in crops. *Biochimica et Biophysica Acta - Gene Regulatory Mechanisms* **1819**, 186-194

Riechmann JL, Heard J, Martin G (2000) Arabidopsis transcription factors: genomewide comparative analysis among eukaryotes. *Science* **290**, 2105-2110

Rogers EE, Guerinot ML (2002) FRD3, a member of the multidrug and toxin efflux family, controls iron deficiency responses in Arabidopsis. *Plant Cell* **14**, 1787-1799

Rubio F, Gassmann W, Schroeder JI (1995) Sodium-driven potassium uptake by the plant potassium transporter HKT1 and mutations conferring salt tolerance. *Science* **270**, 1660-1663

Rus A, Yokoi S, Sharkuu A, Reddy M, Lee BH, Matsumoto TK, Koiwa H, Zhu JK, Bressan RA, Hasegawa PM (2001) AtHKT1 is a salt tolerance determinant that controls Na$^+$ entry into plant roots. *Proceedings of the National Academy of Sciences USA* **98**, 14150-14155

Saibo NJM, Lourenco T, Oliveira MM (2008) Transcription factors and regulation of photosynthetic and related metabolism under environmental stresses. *Annals of Botany* **103**, 609-623

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 Physiology* **136**, 2734-2746

Schachtman DP, Schroeder JI (1994) Structure and transport mechanism of a high-affinity potassium uptake transporter from higher plants. *Nature* **370**, 655-658

Schachtman DP, Schroeder JI, Lucas WJ, Anderson JA, Gaber RF (1992) Expression of an inward-rectifying potassium channel by the Arabidopsis KAT1 cDNA. *Science* **258**, 1654-1658

Seki M, Kamei A, Yamaguchi-Shinozaki K, Shinozaki K (2003) Molecular responses to drought, salinity and frost: Common and different paths for plant protection. *Current Opinion in Biotechnology* **14**, 194-199

Sharabi-Schwager M, Samach A, Porat R (2010) Overexpression of the CBF2 transcriptional activator in *Arabidopsis* suppresses the responsiveness of leaf tissue to the stress hormone ethylene. *Plant Biology* **12**, 630-638

Shi H, Quintero FJ, Pardo JM, Zhu J-K (2002) The putative plasma membrane Na$^+$/H$^+$antiporter SOS1 controls long-distance Na$^+$ transport in plants. *Plant Cell* **4**, 465-477

Su J, Wu R (2004) Stress-inducible synthesis of proline in transgenic rice confers faster growth under stress conditions than that with constitutive synthesis. *Plant Science* **166**, 941-948

Sundaram S, Rathinasabapathi B (2010) Transgenic expression of fern *Pteris vittata* glutaredoxin PvGrx5 in *Arabidopsis thaliana* increases plant tolerance to high temperature stress and reduces oxidative damage to proteins. *Planta* **231**, 361-369

Takasaki H, Maruyama K, Kidokoro S, Ito Y, Fujita Y, Shinozaki K, Yamaguchi-Shinozaki K, Nakashima K (2010) The abiotic stress-responsive NAC-type transcription factor OsNAC5 regulates stress-inducible genes and

stress tolerance in rice, Mol. Genet. *Genomics* **284**, 173-183

Tripathi V, Parasuraman B, Laxmi A, Chattopadhyay D (2009) CIPK6, a CBL interacting protein kinase is required for development and salt tolerance in plants. *Plant Journal* **58**, 778-790

Trovato M, Mattioli R, Costantino P (2008) Multiple roles of proline in plant stress tolerance and development. *Rendiconti Lincei - Scienze Fisiche e Naturali* **19**, 325-346

Tseng MJ, Liu CW, Yiu JC (2007) Enhanced tolerance to sulfur dioxide and salt stress of transgenic Chinese cabbage plants expressing both superoxide dismutase and catalase in chloroplasts. *Plant Physiology and Biochemistry* **45**, 822-833

Tuteja N (2007) Mechanisms of high salinity tolerance in plants. *Methods of Enzymology* **428**, 419-438

Tuteja N, Gill SS, Tiburcio AF, Tuteja R (2012) (Eds) *Improving Crop Resistance to Abiotic Stress*, Wiley-VCH Verlag GmbH and Co. KGaA, Germany, 1460 pp

Tuteja N, Gill SS, Tuteja R (2011) Plant responses to abiotic stresses: Shedding light on salt, drought, cold and heavy metal stress. In: Tuteja N, Gill SS, Tuteja R (Eds) *Omics and Plant Abiotic Stress Tolerance*, Bentham Science Publishers Ltd., pp 39-64

Tuteja N, Gill SS, Tuteja R (2012) (Eds) *Omics and Plant Abiotic Stress Tolerance*, Bentham Science Publishers, UAE, 176 pp

Tuteja N, Mahajan S (2007) Calcium signaling network in plants: an overview. *Plant Signaling and Behavior* **2**, 79-85

Tuteja N, Sopory SK (2008a) Plant signaling in stress: G-protein coupled receptors, heterotrimeric g-proteins and signal coupling via phospholipases. *Plant Signaling and Behavior* **3**, 79-86

Tuteja N, Sopory SK (2008b) Chemical signaling under abiotic stress environment in plants. *Plant Signaling and Behavior* **3**, 525-536

Udvardi MK, Kakar K, Wandrey M, Montanari O, Murray J, Andriankaja A, Zhang JY, Benedito V, Hofer JM, Chueng F, Town CD (2007) Legume transcription factors: Global regulators of plant development and response to the environment. *Plant Physiology* **144**, 538-549

Ueda A, Shi W, Shimada T, Miyake H, Takabe T (2008) Altered expression of barley proline transporter causes different growth responses in *Arabidopsis*. *Planta* **227**, 277-286

Uno Y, Furihata T, Abe H, Yoshida R, Shinozaki K, Yamaguchi-Shinozaki K (2000) *Arabidopsis* basic leucine zipper transcription factors involved in an abscisic acid-dependent signal transduction pathway under drought and high-salinity conditions. *Proceedings of the National Academy of Sciences USA* **97**, 11632-11637

Uozumi N, Schroeder JI (2010) Ion channels and plant stress: Past, present and future. In: Demidchik V, Maathuis F (Eds) *Ion Channels and Plant Stress Responses*, Springer, Berlin, pp 1-22

Uozumi N, Kim EJ, Rubio F, Yamaguchi T, Muto S, Tsuboi A, Bakker EP, Nakamura T, Schroeder JI (2000) The Arabidopsis HKT1 gene homolog mediates inward Na(+) currents in *Xenopus laevis* oocytes and Na(+) uptake in *Saccharomyces cerevisiae*. *Plant Physiology* **122**, 1249-1259

Ushimaru T, Nakagawa T, Fujioka Y, Daicho K, Naito M, Yamauchi Y, Nonaka H, Amako K, Yamawaki K, Murata N (2006) Transgenic *Arabidopsis* plants expressing the rice dehydroascorbatereductase gene are resistant to salt stress. *Journal of Plant Physiology* **163**, 1179-1184

Vinocur B, Altman A (2005) Recent advances in engineering plant tolerance to abiotic stress: Achievements and limitations. *Current Opinion in Biotechnology* **16**, 123-132

Waditee R, Bhuiyan MNH, Rai V, Aoki K, Tanaka Y, Hibino T, Suzuki S, Takano J, Jagendorf AT, Takabe T, Takabe T (2005) Genes for direct methylation of glycine provide high levels of glycine betaine and abiotic-stress tolerance in *Synechococcus* and *Arabidopsis*. *Proceedings of National Academy of Sciences USA* **102**, 1318-1323

Wang J-M, Fan Z-Y, Liu Z-B, Xiang J-B, Chai L, Li X-F, Yang Y (2011) Thylakoid-bound ascorbate peroxidase increases resistance to salt stress and drought in *Brassica napus*. *African Journal of Biotechnology* **10**, 8039-8045

Wang Q-B, Xu W, Xue Q-Z, Su W-A (2010) Transgenic *Brassica chinensis* plants expressing a bacterial codA gene exhibit enhanced tolerance to extreme temperature and high salinity. *Journal of Zhejiang University Science B* **11**, 851-861

Wang Y, Gao C, Liang Y, Wang C, Yang C, Liu G (2010) A novel bZIP gene from *Tamarix hispida* mediates physiological responses to salt stress in tobacco plants. *Journal of Plant Physiology* **167**, 222-230

Wang Y, Wisniewski M, Meilan R, Uratsu SL, Cui MG, Dandekar A, Fuchigami L (2007) Ectopic expression of Mn-SOD in *Lycopersicon esculentum* leads to enhanced tolerance to salt and oxidative stress. *Journal of Applied Horticulture* **9**, 3-8

Wang Y, Ying Y, Chen J, Wang XC (2004) Transgenic *Arabidopsis* overexpressing Mn-SOD enhanced salt-tolerance. *Plant Science* **167**, 671-677

Xu ZY, Zhang X, Schläppi M, Xu ZQ (2011) Cold-inducible expression of AZI1 and its function in improvement of freezing tolerance of *Arabidopsis thaliana* and *Saccharomyces cerevisiae*. *Journal of Plant Physiology* **168**, 1576-87

Yamaguchi T, Uozumi N, Horie T (2012) Potassium and sodium transporters: Improving salinity tolerance in plants. In: Tuteja N, Gill SS, Tiburcio AF, Tuteja R (Eds) *Improving Crop Resistance to Abiotic Stress*, Wiley-VCH Ver-

lag GmbH and Co. KGaA, Berlin, pp 521-540

Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology* **57**, 781-803

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

Yang X, Liang Z, Wen X, Lu C (2008) Genetic engineering of the biosynthesis of glycinebetaine leads to increased tolerance of photosynthesis to salt stress in transgenic tobacco plants. *Plant Molecular Biology* **66**, 73-86

Yokotani N, Ichikawa T, Kondou Y, Matsui M, Hirochika H, Iwabuchi M, Oda K (2009) Tolerance to various environmental stresses conferred by the salt-responsive rice gene *ONAC063* in transgenic *Arabidopsis*. *Planta* **229**, 1065-1075

Yokotani N, Ichikawa T, Kondou Y, Matsui M, Hirochika H, Iwabuchi M, Oda K (2009) Tolerance to various environmental stresses conferred by the salt-responsive rice gene *ONAC063* in transgenic *Arabidopsis*. *Planta* **229**, 1065-1075

Yoon HS, Lee IA, Lee H, Lee BH, Jo J (2005) Overexpression of a eukaryotic glutathione reductase gene from *Brassica campestris* improved resistance to oxidative stress in *Escherichia coli*. *Biochemical and Biophysical Research Communications* **326**, 618-623

Yazaki K (2005) Transporters of secondary metabolites. *Current Opinion in Plant Biology* **8**, 301-307

Yazaki K, Sugiyama A, Morita M, Shitan N (2008) Secondary transport as an efficient membrane transport mechanism for plant secondary metabolites. *Phytochemistry Reviews* **7**, 513-524

Zhang H-X, Blumwald E (2001) Transgenic salt-tolerant tomato plants accumulate salt in foliage but not in fruit. *Nature Biotechnology* **19**, 765-768

Zhang G, Chen M, Li L, Xu Z, Chen X, Guo J, Ma Y (2009) Overexpression of the soybean GmERF3 gene, an AP2/ERF type transcription factor for increased tolerances to salt, drought, and diseases in transgenic tobacco. *Journal of Experimental Botany* **60**, 3781-3796

Zhang H, Dong H, Li W, Sun Y, Chen S, Kong X (2009) Increased glycine betaine synthesis and salinity tolerance in AhCMO transgenic cotton lines. *Molecular Breeding* **23**, 289-298

Zhang K, Guo N, Lian L, Wang J, Lv S, Zhang J (2011) Improved salt tolerance and seed cotton yield in cotton (*Gossipium hirsutum* L.) by transformation with *betA* gene for glycinebetaine synthesis. *Euphytica* **181**, 1-16

Zimmermann S, Sentenac H (1999) Plant ion channels: From molecular structures to physiological functions. *Current Opinion in Plant Biology* **2**, 477-482