

Standard Review

Recent molecular advances to combat abiotic stress tolerance in crop plants

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Accepted 28 June, 2010

Abiotic stress negatively influences survival, biomass production and crop yield. Being multigenic as well as a quantitative trait, it is a challenge to understand the molecular basis of abiotic stress tolerance and to manipulate it as compared to biotic stresses. Abiotic stresses including drought are serious threats to the sustainability of crop yields accounting for more crop productivity losses than any other factor in rainfed agriculture. Success in breeding for better adapted varieties to abiotic stresses depend upon the concerted efforts by various research domains including plant and cell physiology, molecular biology, genetics, and breeding. Use of modern molecular biology tools for elucidating the control mechanisms of abiotic stress tolerance, and for engineering stress tolerant crops is based on the expression of specific stress-related genes. Plant responses to water deficit can be analysed by systematically identifying genes that relate to drought tolerance followed by analysis to the cellular, biochemical and molecular basis of the gene (traits). Mechanism of drought tolerance and expression of these drought resistance genes in high yielding varieties will help to improve the drought condition. The genes conferring drought resistance provide foundation for scientific improvement of the crop's productivity under arid conditions and contribute to improvement and stabilization of cotton yield and farmers' income. Stress-induced gene expressions are of genes encoding proteins with known enzymatic or structural functions, proteins with as yet unknown functions, and regulatory proteins.

Key words: Abiotic stress, stress induced genes, regulatory proteins, transgenics.

INTRODUCTION

Drought plays a major role in destabilizing the productivity in crop plants. Regardless of whether it is irrigated or not, plants are often exposed to drought, which adversely affects both yield and lint quality. In this regard, conscious efforts are required to improve production in areas commonly exposed to abiotic stress especially drought. Yield improvement in crop plants may be possible by incorporating stable and ideal plant traits pertaining to drought tolerance in the plant system. The development of drought-tolerant crops through a direct selection has been hampered by the low heritability of traits such as

yield, particularly under drought, and by its large 'genotype × environment' interaction (Blum, 1988; Ceccarelli and Grando, 1996). The rainfed ecosystem has characteristic abiotic stress influences, particularly during reproductive ontogeny leading to considerable yield realization. Levit (1980) opined that resistance to water stress might be related to capacity to escape or tolerate adverse environments. In this context, the ability of crop to overcome drought impact is affected by its indeterminate growth habit, longer duration, and osmotic adjustments (Oosterhuis and Wullschlegel, 1987). Maintenance of relatively higher leaf water potential may be a desirable trait in lowering desiccation (Turner, 1986). Drought tolerance in plants is mostly characterized by avoidance and tolerance mechanisms. Morphological adaptations under stress environment generally on

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avoidance in nature, whereas dehydration tolerance under low water potential may be a tolerance features. In this context osmo regulation is sustainable drought tolerant mechanism of dehydration tolerance when the plant water potential is extremely low.

Now it is realized that high throughput expression analysis of stress-specific genes is important for understanding gene function (Cushman and Bohnert, 2000). The recent years an enormous number drought stress response genes have been isolated and characterized using molecular techniques. Despite the fact that a large number of genes have to be contributing to the overall phenotypes, investigations on plant responses to environmental stresses have revealed relatively small number of major quantitative trait loci (Yano and Saski, 1997). The prospects of changing the phenotype through manipulation techniques of genetic engineering become much greater if one or few defined regions of chromosomes are of crucial importance. The identifications of QTLs have therefore practical importance in attempts to enhance stress tolerance (Koyama et al., 2001).

PLANT RESPONSES TO WATER DEFICIT

Plant resistance to water deficit may arise from escape, avoidance or tolerance strategies (Levitt, 1972; Turner, 1986). In most cases, plants may combine a range of response types (Chaves et al., 2003).

Drought escape

Drought escape relies on successful reproduction before the onset of severe stress. The plants combine short life cycles with high rates of growth and gas exchange, using maximum available resources while moisture in the soil lasts (Mooney et al., 1987; Maroco et al., 2000).

Drought avoidance

Drought avoidance involves minimizing water loss (closing stomata, reducing light absorbance through rolled leaves, and decreasing canopy leaf area) and maximizing water uptake (increasing investment in the root, reallocation of nutrients stored in older leaves, and higher rates of photosynthesis) (Chaves et al., 2003).

Drought tolerance

Drought tolerance appears to be the result of coordination of physiological and biochemical alternation at the cellular and molecular levels. These alterations may involve osmotic adjustment (Morgan, 1984), more rigid cell walls, or smaller cells (Wilson et al., 1980). Changes

occurring rapidly at the mRNA and protein levels lead to tolerant state (Ingram and Bartels 1996).

PHYSIOLOGICAL RESPONSES

Plants subjected to water stress, respond by number of physiological responses at the molecular, cellular, and whole-plant levels (Bray, 1993; Bartels et al., 1996; Chaves et al., 2003). Two physiological mechanisms, most relevant will be discussed subsequently.

Water use efficiency (WUE)

Water use efficiency (WUE) is a key factor determining plant productivity under limited water supply. In agronomic terms, it is defined as the ratio between total dry matter (DM) produced (or yield harvested) and water used (or applied) (Jones, 1993). In physiological terms, however, WUE is defined as the ratio between the rate of carbon fixed and the rate of water transpired. Index representing the number of moles of CO₂ assimilated by photosynthesis per mole of water transpired by the plant. C₄ plants and succulent plants with CAM metabolism show higher WUE than do C₃ plants. Carbon isotope ratio (¹³C/¹²C, δ¹³C) is commonly used as an indirect indicator of WUE (Araus et al., 2003). Water use efficiency (WUE), measured as the biomass produced per unit transpiration, describes the relationship between water use and crop production.

In water-limiting conditions, it would be important to produce a high amount of biomass, which contributes to crop yield, using a low or limited amount of water. Water scarcity can impose abiotic stresses like drought and salinity, which are among the most important factors limiting plant performance and yield worldwide. Plant resistance to drought stress can be improved through drought avoidance or drought tolerance, among which drought avoidance mechanisms tend to conserve water by promoting WUE.

Osmotic adjustment

Osmotic adjustment (OA) is the net increase in intercellular solutes in response to water stress (Morgan, 1984), which allows turgor maintenance at lower water potential. OA has been considered one of the crucial processes in plant adaptation to drought, because it sustains tissue metabolic activity and enables regrowth upon rewetting but varies greatly among genotypes. Plant productivity under arid conditions has been associated with OA in a number of species such as sorghum (Tangpremsri et al., 1995), wheat (Morgan, 1984; El Hafid et al., 1998) and oilseed brassicas (Kumar and Singh, 1998).

MOLECULAR RESPONSES

Genes induced during water-stress conditions are thought to function in protecting cells from water deficit by production of important metabolic proteins and regulation of genes for signal transduction in water-tress response. Recently, a number of droughts - responsive genes were cloned and characterized from different plant species (Nepomuceno et al., 2000). Transcription of many of these genes is unregulated by drought stress. Initial attempts to develop transgenics (mainly tobacco) for abiotic stress tolerance involved "single action genes" that is, genes responsible for modification of a single metabolite that would confer increased tolerance to salt or drought stress. Stress-induced proteins with known functions such as water channel proteins, key enzymes for osmolyte (proline, betaine, sugars such as trehalose, and polyamines) biosynthesis, detoxification enzymes, and transport proteins were the initial targets of plant transformation.

Stress-induced gene expression can be broadly categorized into three groups: (1) genes encoding proteins with known enzymatic or structural functions, (2) proteins with as yet unknown functions, and (3) regulatory proteins.

Osmoprotectants

Osmoprotectants are proteins that probably function in stress tolerance. They are water channel proteins involved in movement of water through membranes, the enzymes required for the biosynthesis of various osmoprotectants (sugars, Pro, and Gly-betaine). Stress tolerant transgenic plants to engineer genes that encode enzymes for the synthesis of selected osmolytes (Bray, 1993) or osmoprotectants such as glycine-betaine (Sakamoto et al., 1998, 2000; Holmstrom, 2000; McNeil et al., 2000) and proline (Zhu et al., 1998; Yamada et al., 2005). Also, a number of "sugar alcohols" (mannitol, trehalose, myo-inositol and sorbitol) have been targeted for the engineering of compatible-solute overproduction, thereby protecting the membrane and protein complexes during stress (Gao et al., 2000; Zhao et al., 2000; Garg et al., 2002; Cortina and Culiañez, 2005). Transgenics were engineered for the overexpression of polyamines have also been developed (Roy and Wu, 2001; 2002; Kumria and Rajam, 2002; Waie and Rajam, 2003; Capell et al., 2004). Similarly, transgenics engineered for Genes encoding enzymes that synthesize osmotic and other protectants are *adc* (Arginine decarboxylase), *Adc* (Polyamine synthesis), *Apo-Inv* (Apoplatic invertase), *AtHAL3a* (Phosphoprotein phosphatase), *AtGoIS2* Galactinol and raffinose accumulation), *AtTPS1* (trehalose-6-phosphate synthase), *beta* [Choline dehydrogenase (glycinebetaine synthesis)], *BADH-1* (Betaine aldehyde dehydrogenase), *CHIT33*, *CHIT42*

(Endochitinase synthesis), *codA* [Choline oxidase (glycine betaine synthesis)], *COX* (Choline oxidase (glycine betaine synthesis), *CMO* [Choline monooxygenase (glycine betaine synthesis)], *Ect A...ect C* (Edtoin accumulation in chloroplasts), *GS2* (Chloroplastic glutamine synthetase), *IMT1*[Myo-inositol o-methyltransferase (D-ononitol synthesis)], *M6PR*(Mannose-6-phosphate reductase), *mt1D* [Mannitol-1-phosphate dehydrogenase (mannitol synthesis)], *mt1D* and *GutD* [Mannitol-1-phosphate dehydrogenase and glucitol-6-phosphate dehydrogenase], *Osm1 ...Osm4* [Osmotin protein accumulation], *OsP5CS2* (Highly homologous to P5CS), *otsA* [Trehalose-6-phosphate synthase (trehalose synthesis)], *otsB* [Trehalose-6-phosphate synthase (trehalose synthesis)], *P5CS* [Pyrroline carboxylate synthase(proline synthesis)], *PPO* (Polyphenol oxidases suppression), *SAMDC* [S-adenosylmethioninedecarboxylase (polyamine synthesis)], *spe1-1*; *spe2-1* (Spermidine non-accumulating), *SPE* (Spermidine synthase), *SST/FFT* (Fructan accumulation), *TPSP*; *TPS1* and *TPS2* (Trehalose synthesis), *PpDHNA* (Dehydrin protein accumulation) in crops plants and they were mentioned in Table 1.

Late embryogenesis abundant (LEA) proteins

Proteins that may protect macromolecules and membranes (LEA protein, osmotin, antifreeze protein, chaperon, and mRNA binding proteins). LEA proteins represent another category of high molecular weight proteins that are abundant during late embryogenesis and accumulate during seed desiccation and in response to water stress (Galau et al., 1987). Amongst the several groups of LEA proteins, those belonging to group 3 are predicted to play a role in sequestering ions that are concentrated during cellular dehydration. These proteins have 11-mer amino acid motifs with the consensus sequence TAQAAKEKAGE repeated as many as 13 times (Dure, 1993). The group 1 LEA proteins are predicted to have enhanced water-binding capacity, while the group 5 LEA proteins are thought to sequester ions during water loss. Constitutive over expression of the HVA1, a group 3 LEA protein from barley conferred tolerance to soil water deficit and salt stress in transgenic rice plants (Xu et al., 1996). Constitutive or stress induced expression of the HVA1 gene resulted in the improvement of growth characteristics and stress tolerance in terms of cell integrity in wheat and rice under salt- and water-stress conditions (Sivamani et al., 2000; Rohilla et al., 2002). The water use efficiency (WUE) was extremely low when compared to other data reported in wheat cultigens, transgenic rice (TNG67) plants expressing a wheat LEA group 2 protein (PMA80) gene or the wheat LEA group 1 protein (PMA1959) gene resulted in increased tolerance to dehydration and salt stresses (Cheng et al. 2002).

Table 1. Gene encoding enzymes that synthesize osmotic and other protectants (www.plantstress.com; I.D. designate ID numbers in reference database).

Gene	Gene action	Species	Phenotype	References	ID
<i>adc</i>	Arginine decarboxylase	Rice	Reduced chlorophyll loss under drought stress	Capell et al., 1998	5607
<i>Adc</i>	Polyamine synthesis	Rice	Drought resistance	Capell et al., 2004	7290
<i>Apo-Inv</i>	Apoplastic invertase	Tobacco	Salt tolerance, high "osmotic pressure"	Fukushima et al., 2001	5202
<i>AtHAL3a</i>	Phosphoprotein phosphatase	<i>Arabidopsis</i>	Regulate salinity and osmotic tolerance and plant growth	Espinosa-Ruiz et al., 1999	4601
<i>AtHAL3</i>	Phosphoprotein phosphatase	Tobacco	Improved salt, osmotic and Lithium tolerance of cell cultures	Yonamine et al., 2004	6947
<i>AtGolS2</i>	Galactinol and raffinose accumulation	<i>Arabidopsis</i>	Reduced transpiration	Taji et al., 2002	5884
<i>AtTPS1</i>	Trehalose-6-phosphate synthase	Tobacco	Drought resistance; sustained photosynthesis	Almeida et al., 2007	8668
<i>BADH-1</i>	Betaine aldehyde dehydrogenase	Tobacco	Heat tolerance in photosynthesis	Xinghong Yang, et al., 2005	7858
<i>BADH-1</i>	Betaine aldehyde dehydrogenase	Tomato	Maintenance of osmotic potential	Moghaieb et al., 2000	5094
<i>BADH-1</i>	Betaine aldehyde dehydrogenase	Carrot	Salinity tolerance	Kumar et al., 2004	7353
<i>betA</i>	Choline dehydrogenase (glycinebetaine synthesis)	Tobacco	Increased tolerance to salinity stress	Lilius et al., 1996	3287
<i>betA</i>	Choline dehydrogenase (glycinebetaine synthesis)	Maize	Drought resistance at seedling stage and high yield after drought	Ruidang et al., 2004	7409
<i>CHIT33, CHIT42</i>	Endochitinase synthesis	Tobacco	Salt and metal toxicity resistance (and disease)	Dana et al., 2006	8504
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	<i>Brassica juncea</i>	Tolerance to stress induced photoinhibition	Prasad and Saradhi, 2004	7094
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	Rice	Increased tolerance to salinity and cold	Sakamoto et al., 1998	3859
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	Rice	Recovery from a week long salt stress	Mohanty et al., 2003	6347
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	<i>Arabidopsis</i>	Increased stress tolerance	Huang et al., 2000	4731
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	<i>Arabidopsis</i>	Salt tolerance in terms of reproduction	Ronan et al., 2003	6822
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	<i>Arabidopsis</i>	Seedlings tolerant to salinity stress and increased germination under cold	Hayashi et al., 1997 ; Alia et al., 1998	4571
<i>COX</i>	Choline oxidase (glycine betaine synthesis)	Rice	Salt and 'stress' tolerance	Su et al., 2006	8227
<i>CMO</i>	Choline monooxygenase (glycine betaine synthesis)	Tobacco	Better <i>in vitro</i> growth under salinity and osmotic (PEG6000) stress	Yi-Guo et al., 2002	6285

Table 1. Contd.

<i>Ect A...ect C</i>	Edtoin accumulation in chloroplasts	Tobacco	Salt and cold tolerance	Rai et al., 2006	8090
<i>GS2</i>	Chloroplastic glutamine synthetase	Rice	Increased salinity resistance and chilling tolerance	Hoshida et al., 2000	4792
<i>IMT1</i>	Myo-inositol o-methyltransferase (D-ononitol synthesis)	Tobacco	Better CO ₂ fixation under salinity stress. Better recovery after drought stress.	Sheveleva et al., 1997	3660
<i>M6PR</i>	Mannose-6-phosphate reductase	<i>Arabidopsis</i>	Mannitol accumulation under salt stress leading to salt tolerance	Zhifang and Loescher, 2003	6343
<i>M6PR</i>	Mannose-6-phosphate reductase	<i>Arabidopsis</i>	Mannitol accumulation and salt tolerance due to chloroplast protection	Sickler et al., 2007	6533
<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase (mannitol synthesis)	<i>Arabidopsis</i>	Increased germination under salinity stress	Thomas et al., 1995	5620
<i>mt1D and GutD</i>	Mannitol-1-phosphate dehydrogenase & glucitol-6-phosphate dehydrogenase	loblolly pine	High salt tolerance due to mannitol and glucitol accumulation	Tang et al., 2005	7614
<i>mtID</i>	Mannitol-1-phosphate dehydrogenase (mannitol synthesis)	<i>Populus tomentosa</i>	Salinity tolerance	Chiang et al., 2005	7751
<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase (mannitol synthesis)	Tobacco	Increased plant height and fresh weight under salinity stress	Hu et al., 2005	7946
<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase (mannitol synthesis)	Tobacco	No contribution to sustained growth under salinity and drought stress.	Tarczynski et al., 1993	2383
<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase (mannitol synthesis)	Wheat	Drought and salinity tolerance of calli and plants	Abebe et al., 2003	6533
<i>Osm1 ...Osm4</i>	Osmotin protein accumulation	Tobacco	Drought and salt tolerance in plant water status and proline accumulation	Barthakur et al., 2001	5560
<i>OsP5CS2</i>	Highly homologous to P5CS	Rice	Cold and salinity tolerance	Hur et al., 2004	7264
<i>otsA</i>	Trehalose-6-phosphate synthase (trehalose synthesis)	Tobacco	Increased leaf dry weight and photosynthetic activity under drought. Increased carbohydrate accumulation.	Pilon-smits et al., 1998	3101
<i>otsB</i>	Trehalose-6-phosphate synthase (trehalose synthesis)	Tobacco	Increased leaf dry weight and photosynthetic activity under drought. Increased carbohydrate accumulation.	Pilon-smits et al., 1998	3101
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis) (tomato)	Citrus	Osmotic adjustment and drought resistance	Molinari et al., 2004	7361
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis)	<i>Petunia</i>	Drought resistance and high proline	Yamada et al., 2005	7750
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis)	Potato	Salinity tolerance	Hmida-Sayari et al., 2005	7864
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis)	Rice	Increased biomass production under drought and salinity stress	Zhu et al., 1998	3871

Table 1. Contd.

<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis)	Rice	Reduced oxidative stress under osmotic stress	Hong Zong Lie et al., 2000	5562
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis)	Rice	Resistance to water and salinity stress	Su and Wu, 2004	7034
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis)	Soybean	Resistance to osmotic stress and heat	De Ronde et al., 2001	5767
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis) (tomato)	Soybean	Drought resistance, high RWC, high proline	De Ronde et al., 2004	7383
<i>P5CS</i>	Pyrroline carboxylate synthase (proline synthesis) (tomato)	Sugarcane	Drought resistance via antioxidant role of proline	Molinari et al., 2007	8859
<i>PPO</i>	Polyphenol oxidases suppression	Tomato	Drought resistance	Thipyapong et al., 2004	7267
<i>SAMDC</i>	S-adenosylmethioninedecarboxylase (polyamine synthesis)	Rice	Better seedling growth under a 2 day NaCl stress	Malabika and Wu, 2002	6252
<i>SAMDC</i>	S-adenosylmethioninedecarboxylase (polyamine synthesis)	Tobacco	drought, salinity, Verticillium and Fusarium wilts resistance	Waie and Rajam, 2003	6538
<i>spe1-1; spe2-1</i>	Spermidine non-accumulating	<i>Arabidopsis</i>	Decreased salt tolerance	Vasuki and Astrid, 2004	7089
<i>SPE</i>	Spermidine synthase	<i>Arabidopsis</i>	Chilling, freezing, salinity, drought hyperosmosis	Kasukabe et al., 2004	7277
<i>SST/FFT</i>	Fructan accumulation	Potato	Reduced proline accumulation at low water status	Knipp and Honermeier, 2006	8144
<i>TPSP</i>	Trehalose synthesis	Rice	Drought, salt and cold tolerance expressed by chlorophyll fluorescence	In-Cheol Jang et al., 2003	6389
<i>TPS1</i>	Trehalose synthesis	Tomato	Drought, salt and oxidative stress tolerance	Cortina and Culiáñez-Macià, 2005	7788
<i>TPS1 and TPS2</i>	Trehalose synthesis	Tobacco	Maintenance of water status under drought stress	Karim et al., 2007	8913
<i>PpDHNA</i>	Dehydrin protein accumulation	Moss	Salt and osmotic stress tolerance	Saavedra et al., 2006	8082

Besides, protective chaperone like function of LEA pro-teins acting against cellular damage has been proposed (Vincour and Altman, 2005), indicating the role of LEA proteins in anti aggregation of enzymes under desiccation and freezing stresses (Goyal et al., 2005). Some more genes are *DQ663481* (Lea gene), *HVA1* (Group 3 LEA protein gene), *OsLEA3-1* (Lea protein), Rab17 (LEA protein), *ME-leaN4* (LEA protein) and the crops transformed are given in Table 2.

Detoxifying genes

The higher stress tolerance and the accumulation of compatible solutes may also protect plants against damage by scavenging of reactive oxygen species (ROS), and by their chaperone-like activities in maintaining pro-teins structures and functions (Hare et al., 1998; Bohnert and Shen, 1999; McNeil et al., 1999; Diamant et al., 2001). In most of the aerobic organisms, there is a

need to effectively eliminate reactive oxygen species (ROS) generated as a result of environmental stresses. Depending on the nature of the ROS, some are highly toxic and need to be rapidly detoxified. In order to control the level of ROS and protect the cells from oxidative injury, plants have developed a complex antioxidant defense system to scavenge the ROS. These antioxidant systems include various enzymes and non-enzymatic metabolites that may also play a

Table 2. Late embryogenesis abundant (LEA) related genes (www.plantstress.com).

Gene	Gene action	Species	Phenotype	References	ID
<i>DQ663481</i>	Lea gene	Tobacco	Drought resistance via cell membrane stability	Wang et al., 2006	8510
<i>HVA1</i>	Group 3 LEA protein gene	Oat	Delayed wilting under drought stress	Maqbool et al., 2002	6146
<i>HVA1</i>	Group 3 LEA protein gene	Oat	Salinity tolerance in yield/plant	Oraby et al., 2005	7971
<i>HVA1</i>	Group 3 LEA protein gene	Rice	Dehydration avoidance and cell membrane stability	Babu et al., 2004	7030
<i>HVA1</i>	Group 3 LEA protein gene	Rice	Drought and salinity tolerance	Rohila et al. 2002	6185
<i>HVA1</i>	Group 3 LEA protein gene	Wheat	Increased biomass and WUE under stress	Sivamani et al. 2000	4781
<i>HVA1</i>	Group 3 LEA protein gene	Wheat	Improved plant water status and yield under field drought conditions	Bahieldin et al., 2005	7618
<i>OsLEA3-1</i>	Lea protein	Rice	Drought resistance for yield in the field	Xiao et al., 2007	8926
<i>Rab17</i>	LEA protein	<i>Arabidopsis</i>	Resistance to osmotic and salinity stress	Figueras et al., 2004	7204
<i>ME-leaN4</i>	LEA protein	Lettuce	Enhanced growth and delayed wilting under drought. Salt resistance	Park et al., 2005	7671
<i>ME-leaN4</i>	LEA protein	Chinese cabbage	Drought and salt resistance	Park et al., 2005	7794

that may also play a significant role in ROS signaling in plants (Vranova et al., 2002). A number of transgenic improvements for abiotic stress tolerance have been achieved through detoxification strategy. These include transgenic plants over expressing enzymes involved in oxidative protection, such as glutathione peroxidase, superoxide dismutase, ascorbate peroxidases and glutathione reductases (Zhu et al., 1999; Roxas et al., 1997). Transgenic tobacco over expressing SOD in the chloroplast, mitochondria and cytosol have been generated (Bowler et al., 1991; Van Camp et al., 1996) and these have been shown to enhance tolerance to oxidative stress induced by methyl viologen (MV) in leaf disc assays. Overexpression of chloroplast Cu/Zn SOD showed a dramatic improvement in the photosynthetic performance under chilling stress conditions in transgenic tobacco (Sen et al., 1993) and potato plants (Perl et al., 1993). While transgenic alfalfa (*Medicago sativa*) plants cv. RA3 over expressing MnSOD in chloroplasts showed lower membrane injury (McKersie et al., 1996), the tobacco transgenic plants overproducing alfalfa aldose reductase gene (MsALR) showed lower concentrations of reactive aldehydes and increased tolerance against oxidative agents and drought stress (Oberschall et al., 2000). Tobacco transgenic plants over expressing MnSOD rendered enhanced tolerance to oxidative stress only in the presence of other antioxidant enzymes and substrates (Slooten et al., 1995), thereby, showing that the genotype and the isozyme composition also have a profound effect on the relative tolerance of the transgenic plants to abiotic stress (Rubio et al., 2002). Oxidative stress related genes like *ApGPX2* and *AcGPX2*

(Glutathione peroxidase (GPX)-like proteins), *ALR* (Aldose/aldehyde reductase), *Apx1* (Ascorbate peroxidase peroxidase), *APX2* (Ascorbate peroxidase), *Apx3* (Ascorbate peroxidase), *Apx3* (Ascorbate peroxidase), *Apx* (Ascorbate peroxidase), *AO* (Ascorbate oxidase), *AtMDAR1* (Monodehydroascorbate reductase; Ascorbate regeneration) *DHAR* (regeneration of ascorbate), *Gly1;gly2* (Glutathione-based detoxification of methylglyoxal), *GmTP55* (Antiquitin-like protein), *GST* (glutathione S-transferase overexpression), *GST/GPX* (Glutathione S-transferase with Glutathione peroxidase), *GPX* (Glutathione peroxidase), *katE* (Escherichia coli catalase), *ndhCKJ* [NADPH dehydrogenase], *NtPox* (Glutathione peroxidase), *Nt107* (Glutathione S-transferase), *parB* (glutathione S-transferase), *SOD*(Cu, MN, Fe. Zn-SOD), *SOD*(Cu/Zn superoxide dismutase), *SOD*(Fe superoxide dismutase), *SOD* (Mn superoxide dismutase), *vtc1;vtc2;npq1*; *cad2* (reactive oxygen metabolism mutants), *vtc-1* (ascorbate deficient mutant) were transferred in many crops and given in Table 3.

Multifunctional genes for lipid biosynthesis

Multifunctional genes are those genes that improve photosynthesis under abiotic stress conditions through changes in the lipid biochemistry of the membranes (Grover and Minhas, 2000). Adaptation of living cells to chilling temperatures is a function of alteration in the membrane lipid composition by increased fatty acid unsaturation. Genetically engineered tobacco plants over-expressing chloroplast glycerol-3-phosphate

Table 3. Oxidative stress related genes (www.plantstress.com).

Gene	Gene action	Species	Phenotype	References	ID*
<i>ApGPX2</i> and <i>AcGPX2</i>	Glutathione peroxidase (GPX)-like proteins	<i>Arabidopsis</i>	Oxidative stress, drought and salt resistance	Gaber et al., 2006	8466
<i>ALR</i>	Aldose/aldehyde reductase	Tobacco	Drought and UV-B tolerance	Hideg et al., 2003	6524
<i>ALR</i>	Aldose/aldehyde reductase	Tobacco	Cold and cadmium stress tolerance	Hegedüs et al., 2004	7098
<i>APX2</i>	Ascorbate peroxidase	<i>Arabidopsis</i>	High light and drought tolerant mutant	Rossel et al., 2006	8164
<i>Apx3</i>	Ascorbate peroxidase	Tobacco	Increased protection against oxidative stress	Wang et al., 1999	4531
<i>Apx3</i>	Ascorbate peroxidase	Tobacco	Drought resistance in photosynthesis	Juqiang Yan et al., 2003	6614
<i>Apx</i>	Ascorbate peroxidase	Tomato	Chilling and salt tolerance	Kornyeyev et al., 2003	6769
'AO'	Ascorbate oxidase	Tobacco and <i>Arabidopsis</i>	Salt sensitivity in germination, photosynthesis, and seed yield	Yamamoto et al., 2005	7744
<i>AtMDAR1</i>	Monodehydroascorbate reductase; Ascorbate regeneration	Tobacco	Ozone, salt and polyethylene glycol tolerance	Eltayeb et al., 2007	8814
<i>DHAR</i>	Regeneration of ascorbate	Tobacco	Tolerance to ozone, drought, salt, and PEG	Elsadig et al., 2006	8297
<i>DHAR</i>	Regeneration of ascorbate	<i>Arabidopsis</i>	Salt tolerance	Ushimaru et al., 2006	8492
<i>Gly1; gly2</i>	Glutathione-based detoxification of methylglyoxal	Tobacco	Salt tolerance	Singla-Pareek et al., 2006	8261
<i>GmTP55</i>	Antiquitin-like protein	Soybean Tobacco	Resistance to drought, salt and oxidative stress	Rodrigues et al., 2006	8330
<i>GST</i>	Glutathione S-transferase overexpression	<i>Arabidopsis</i>	No whole-plant salt resistance despite antioxidant activity	Katsuhara et al., 2005	7793
<i>GST</i>	Glutathione S-transferase overexpression	Cotton	No whole-plant salt resistance and no antioxidant activity	Light et al., 2005	8032
<i>GST</i>	Glutathione S-transferase overexpression	Rice	Salt and chilling resistance	Zhao and Zhang, 2006	8555
<i>GPX</i>	Glutathione peroxidase	Tobacco	Chilling and salt resistance	Kazuya et al., 2004	6921
<i>katE</i>	<i>Escherichia coli</i> catalase	Tobacco	Salt tolerance by hydrogen peroxide scavenging	Al-Taweel et al., 2007	9030
<i>ndhCKJ</i>	NAD(P)H dehydrogenase	Tobacco	Photosystem function under heat stress	Wang et al., 2006	8353
<i>NtPox</i>	Glutathione peroxidase	<i>Arabidopsis</i>	Protect against Al toxicity and oxidative stress	Ezaki et al., 2001	5664
<i>Nt107</i>	Glutathione S-transferase	Tobacco	Sustained growth under cold and salinity stress	Roxas et al., 1997	5616
<i>parB</i>	Glutathione S-transferase	<i>Arabidopsis</i>	Protect against Al toxicity and oxidative stress	Ezaki et al., 2000	4728
<i>parB</i>	Glutathione S-transferase	<i>Arabidopsis</i>	Protect against Al toxicity and oxidative stress	Ezaki et al., 2001	5664
<i>SOD</i>	Cu, MN, Fe. Zn-SOD	Alfalfa, rye grass	Increased winter hardiness	McKersie, 2001	5614
<i>SOD</i>	Cu/Zn superoxide dismutase	Tobacco, Tomato	No protection seen against superoxide toxicity	Tepperman and Dunsmuir, 1990	5619

Table 3. Contd.

<i>SOD</i>	Cu/Zn superoxide dismutase	Tobacco	Retained photosynthesis under chilling and heat stress	Gupta et al., 1993	5609
<i>SOD</i>	Cu/Zn superoxide dismutase	Tobacco	Enhanced tolerance to salt, water, and PEG stresses,	Badawi et al., 2004	7033
<i>SOD</i>	Fe superoxide dismutase	Tobacco	Protected plants from ozone damage	Van Camp et al., 1994	5621
<i>SOD</i>	Mn superoxide dismutase	Tobacco	Reduced cellular damage under oxidative stress	Bowler et al. 1991	5606
<i>SOD</i>	Mn superoxide dismutase	Alfalfa	Tolerance to freezing stress	McKersie et al., 1993	5615
<i>SOD</i>	Mn superoxide dismutase	Alfalfa	Tolerance to water deficit	McKersie et al., 1996	3345
<i>SOD</i>	Mn superoxide dismutase	Alfalfa	Winter survival	McKersie et al., 1999	3894
<i>SOD</i>	Mn superoxide dismutase	Tobacco	Tolerance to Mn deficiency	Yu et al., 1999	4512
<i>SOD</i>	Mn superoxide dismutase	Canola	Aluminum tolerance	Basu et al., 2001	5684
<i>SOD</i>	Mn superoxide dismutase	<i>Arabidopsis</i>	Salt tolerance	Wang et al., 2004	7266
<i>SOD</i>	Mn superoxide dismutase	Rice	Reduced injury and sustained photosynthesis under PEG stress	Wang et al., 2005	7724
<i>SOD</i>	Mn/Fe superoxide dismutase	Alfalfa	Background dependent increased photosynthesis under drought stress	Maria et al., 2002	6103
vtc1, vtc2, npq1, cad2	Reactive oxygen metabolism mutants	<i>Arabidopsis</i>	Heat tolerance/sensitivity	Larkindale et al., 2005	7783
vtc-1	Ascorbate deficient mutant	<i>Arabidopsis</i>	Sensitivity to salinity stress	Huang et al., 2005	7990

acyltransferase (GPAT) gene (involved in phosphatidyl glycerol fatty acid desaturation) from squash (*Cucurbita maxima*) and *A. thaliana* (Murata et al., 1992) showed an increase in the number of unsaturated fatty acids and a corresponding decrease in the chilling sensitivity. Besides transgenic tobacco plants with silenced expression of chloroplast x3-fatty acid desaturase (Fad7, which synthesizes trienoic fatty acids) were able to acclimate to high temperature as compared to the wild type (Murakami et al., 2000).

Heat shock protein genes

The heat shock response, increased transcription of a set of genes in response to heat or other toxic

agent exposure is a highly conserved biological response, occurring in all organisms (Waters et al., 1996). The response is mediated by heat shock transcription factor (HSF) which is present in a monomeric, non-DNA binding form in unstressed cells and is activated by stress to a trimeric form which can bind to promoters of heat shock genes. The induction of genes encoding heat shock proteins (Hsps) is one of the most prominent responses observed at the molecular level of organisms exposed to high temperature (Kimpel and Key, 1985; Lindquist, 1986; Vierling 1991). Genetic engineering for increased thermo-tolerance by enhancing heat shock protein synthesis in plants has been achieved in a number of plant species (Malik et al., 1999; Li et al., 2003; Katiyar-Agarwal et al., 2003). There

have been a few reports on positive correlations between the levels of heat shock proteins and stress tolerance (Sun et al., 2001; Wang et al., 2005). Although the precise mechanism by which these heat shock proteins confer stress tolerance is not known, a recent study demonstrated that *in vivo* function of thermoprotection of small heat shock proteins is achieved via their assembly into functional stress granules (HSGs; Miroshnichenko et al., 2005). Genes encoding for molecular chaperones are *APG6* (Chloroplast structure), *AtDjA2* and *atDjA3* (J-domain molecular chaperone family), *AtMTP3* (Metal tolerance Protein), *Atsbp1* (Selenium binding protein), *atRZ-1a* (RNA chaperone protein), *BiP* [Endoplasmic reticulum binding protein (BiP)], *CaHSP26* [Chloroplast (CP)-localized small heat shock

protein], *hs* (Heat shock transcription factor), *Hsp101* (Heat shock protein), *Hsp17.7* (Heat shock protein), *Hsp70* (Heat-inducible antisense HSP70), *LeHSP100/CpB* (Chloroplast HSP), *mHSP22* (Mitochondrial small HSP), *P5CR* [Inducible heat shock promoter (IHSP)], *pBE2113/hiC6* (Overexpressed HIC6 cryoprotective protein), *S1pt::ECS* (glutamylcysteine synthetase), *TLHS1* (Over expressed class I cytosolic small HSP), *wx* (Control amylose synthesis) were used for transformation in crop plants are given in Table 4.

Hormone regulatory genes

Many genes that respond to multiple stresses like dehydration and low temperature at the transcriptional level are also induced by ABA (Mundy and Chua 1988), which protects the cell from dehydration (Dure et al., 1989; Skriver and Mundy, 1990). In order to restore the cellular function and make plants more tolerant to stress, transferring a single gene encoding a single specific stress protein may not be sufficient to reach the required tolerance levels (Bohnert et al., 1995). To overcome such constraints, enhancing tolerance towards multiple stresses by a gene encoding a stress inducible transcription factor that regulates a number of other genes is a promising approach (Yamaguchi-Shinozaki et al., 1994; Chinnusamy et al., 2005). Therefore, a second category of genes of recent preference for crop genetic engineering are those that switch on transcription factors regulating the expression of several genes related to abiotic stresses. Another ABA-independent, stress-responsive and senescence-activated gene expression involves ERD gene, the promoter analysis of which further identified two different novel cis acting elements involved with dehydration stress induction and in dark-induced senescence (Simpson et al., 2003). Similarly, transgenic plants developed by expressing a drought-responsive AP2-type TF, SHN1-3 or WXP1, induced several wax-related genes resulting in enhanced cuticular wax accumulation and increased drought tolerance (Aharoni et al., 2004; Zhang et al., 2005). Thus, clearly, the over expression of some drought-responsive transcription factors can lead to the expression of downstream genes and the enhancement of abiotic stress tolerance in plants (Zhang et al., 2004). The regulatory genes/factors reported so far not only play a significant role in drought and salinity stresses, but also in submergence tolerance. More recently, an ethylene response-factor-like gene Sub1A, one of the cluster of three genes at the Sub1 locus have been identified in rice and the over expression of Sub1A-1 in a submergence-intolerant variety conferred enhanced submergence tolerance to the plants (Xu et al., 2006), thus confirming the role of this gene in submergence tolerance in rice. Various other hormone regulating genes are *ABI1*, *ABI2* (ABA regulation), *ABA2* (ABA regulation), *hab1 group* (ABA hypersensitivity), *AtNCED3* (Increased ABA synthesis), *AtPP2CA* (Reduce ABA

sensitivity), *EIN2* (Ethylene and ABA signaling pathways), *Eto 1-1* (Ethylene over-production), *CYP707A3* (Regulate ABA levels), *LLA23* (Reduced ABA sensitivity), *NTHK1* (Ethylene receptor), *PSAG12-IPT* (Over production of cytokinins), *PLD alpha* (Phospholipase D (alpha) expression), *sp12 and sp5* (ABA overproduction), *tos1* (Increased ABA sensitivity), *ZmACS6* (Ethylene synthesis) are listed in Table 5.

Transcription factors

Transcription factors an attractive target category for manipulation and gene regulation is the small group of transcription factors that have been identified to bind to promoter regulatory elements in genes that are regulated by abiotic stresses (Shinozaki and Yamaguchi-Shinozaki, 1997; Winicov and Bastola, 1997). The transcription factors activate cascades of genes that act together in enhancing tolerance towards multiple stresses. Individual members of the same family often respond differently to various stress stimuli. On the other hand, some stress responsive genes may share the same transcription factors, as indicated by the significant overlap of the gene expression profiles that are induced in response to different stresses (Seki et al., 2001; Chen and Murata 2002). Dozens of transcription factors are involved in the plant response to drought stress (Vincour and Altman, 2005; Bartels and Sunkar, 2005). Most of these falls into several large transcription factor families, such as AP2/ERF, bZIP, NAC, MYB, MYC, Cys2His2 zinc-finger and WRKY (Umezawa et al., 2006).

A cis-acting element, dehydration responsive element (DRE) identified in *A. thaliana*, is also involved in ABA-independent gene expression under drought, low temperature and high salt stress conditions in many dehydration responsive genes like rd29A that are responsible for dehydration and cold-induced gene expression (Yamaguchi-Shinozaki and Shinozaki, 1993; Iwasaki et al., 1997; Nordin et al., 1991). DREB1/CBFs are thought to function in cold-responsive gene expression, whereas DREB2s are involved in drought-responsive gene expression. The transcriptional activation of stress-induced genes has been possible in transgenic plants over-expressing one or more transcription factors that recognize regulatory elements of these genes. Subsequently, the overexpression of DREB1A has been shown to improve the drought- and low-temperature stress tolerance in tobacco, wheat and groundnut (Kasuga et al., 2004; Pellegrineschi et al., 2004; Behnam et al., 2006; Bhatnagar-Mathur et al., 2004, 2006). The use of stress inducible rd29A promoter minimized the negative effects on plant growth in these crop species. However, over-expression of DREB2 in transgenic plants did not improve stress tolerance, suggesting involvement of post-translational activation of DREB2 proteins (Liu et al.,

Table 4. Genes encoding for molecular chaperones (www.plantstress.com).

Gene	Gene action	Species	Phenotype	References	ID*
<i>APG6</i>	Chloroplast structure	<i>Arabidopsis</i>	Heat tolerance	Myouga et al., 2006	8474
<i>AtDjA2 & atDjA</i>	J-domain molecular chaperone family	<i>Arabidopsis</i>	Heat tolerance	Li et al., 2007	9034
<i>AtMTP3</i>	Metal tolerance protein	<i>Arabidopsis</i>	Zinc tolerance	Arrivault et al., 2006	8307
<i>Atsbp1</i>	Selenium binding protein	<i>Arabidopsis</i>	Selenium tolerance	Agalou et al., 2005	7899
<i>atRZ-1a</i>	RNA chaperone protein	<i>Arabidopsis</i>	Cold tolerance	Kim and Kang, 2006	8338
<i>BiP</i>	Endoplasmic reticulum binding protein (BiP)	Tobacco	Maintenance of plant water status under drought stress and antioxidative defence	Alvim et al., 2001	5433
<i>CaHSP26</i>	Chloroplast (CP)-localized small heat shock protein	Tobacco	Protection of PSII and PSI during chilling	Guo et al., 2007	8673
<i>hs</i>	Heat shock transcription factor	<i>Arabidopsis</i>	Increased thermotolerance in transgenic plants	Lee et al., 1995	5612
<i>Hsp101</i>	Heat shock protein	<i>Arabidopsis</i>	Decreased Thermotolerance in Hsp101 deficient (hot1) mutant	Hong and Vierling, 2000	5363
<i>Hsp101</i>	Heat shock protein	<i>Arabidopsis</i>	Manipulated themotolerance in transgenic plants	Queitsch et al., 2000	4733
<i>Hsp101</i>	Heat shock protein	Rice	Heat tolerance in plant growth	Katiyar-Agarwal et al., 2003	6430
<i>Hsp17.7</i>	Heat shock protein	Carrot	Increased or decreased thermotolerance	Malik et al., 1999	4526
<i>Hsp70</i>	Heat-inducible antisense HSP70	<i>Arabidopsis</i>	Increased thermotolerance in transgenic plants	Lee and Schoof., 1999	5613
<i>LeHSP100/Cipl</i>	Chloroplast HSP	<i>Tomato</i>	Heat tolerance	Yang et al., 2006	8468
<i>mHSP22</i>	Mitochondrial small HSP	<i>Arabidopsis</i>	Heat tolerance (high leaf mass after heat stress)	Rhoads et al., 2005	7619
<i>P5CR</i>	Inducible heat shock promoter (IHSP)	Soybean	Increased proline accumulation	de Ronde et al., 2000	4936
<i>pBE2113/ hiC6</i>	Overexpressed HIC6 cryoprotective protein	Tobacco	Freezing tolerance; reduced membrane injury	Honjoh et al., 2001	5531
<i>S1pt::ECS</i>	glutamylcysteine synthetase	<i>Arabidopsis</i>	Metal tolerance	Li et al., 2006	8310
<i>TLHS1</i>	Overexpressed class I cytosolic small HSP	Tobacco	Seedling thermotolerance	Park and Hong, 2002	5811
<i>wx</i>	Control amylose synthesis	Rice	Increased amylose content at low temperature	Hirano and Sano, 1998	5610

1998). Recently, an active form of DREB2 was shown to transactivate target stress-inducible genes and improve drought tolerance in transgenic *Arabidopsis* (Sakuma et al., 2006). The DREB2 protein is expressed under normal growth conditions and activated by osmotic stress through post-translational modification in the early stages of the osmotic stress response. To date, 55 members belonging to the DREB subfamily have been isolated from *Arabidopsis* (Sakuma et

al., 2002) and divided into six sub-groups, A-1, A-2, A-3, A-4, A-5 and A-6, based on the homology of the AP2 conserved domains (Seki et al., 2003; Sakuma et al., 2002; Ito et al., 2006). Among them, the A-1 and A-2 subgroups, harboring the DREB1-type and DREB2-type genes, respectively, were the two largest ones that are involved in two different ABA-in-dependent pathways (Liu et al., 1998; Shinwari et al., 1998; Yamaguchi-Shinozaki et al., 2002). Currently, three DRE-binding

transcription factors from *Gossypium hirsutum*, designated GhDREB1L, GhDBP2 and GhDBP3, are isolated and classified into the A-1, A-4 and A-6 groups of DREB subfamilies (Huang and Liu 2006; Huang et al., 2007, 2008).

Various regulatory genes are *AB13*(Transcription factor), *ABF3*(Transcription factor), *ADC*(Arginine decarboxylase overexpression), *ADH1*; *ADH2*(alcohol dehydrogenase), *ALDH3*(aldehyde dehydrogenase),

Table 5. Hormone regulating genes (www.plantstress.com).

Gene	Gene action	Species	Phenotype	References	ID*
<i>ABI1, ABI2</i>	ABA regulation	<i>Arabidop:</i>	Heat tolerance	Larkindale et al., 2005	7783
<i>ABA2</i>	ABA regulation	<i>Arabidop:</i>	Tolerance to various prolonged stresses?	Lin et al., 2007	8734
<i>hab1 group</i>	ABA hypersensitivity	<i>Arabidop:</i>	Dehydration avoidance	Saez et al., 2006	8435
<i>AtNCED3</i>	Increased ABA synthesis	<i>Arabidop:</i>	Reduced transpiration and drought resistance	Iuchi et al., 2001	5527
<i>AtPP2CA</i>	Reduce ABA sensitivity	<i>Arabidop:</i>	Induce cold sensitivity	Tahtiharju and Palva, 2001	5437
<i>EIN2</i>	Ethylene and ABA signaling pathways	<i>Arabidop:</i>	Salt and osmotic stress responses	Wang et al., 2007	8975
<i>Eto 1-1</i>	Ethylene over-production	<i>Arabidop:</i>	Reduced ABA sensitivity and greater transpiration	Tanaka et al., 2005	7859
<i>CYP707A3</i>	Regulate ABA levels	<i>Arabidop:</i>	Dehydration and rehydration responses	Umezawa et al. 2006	8245
<i>LLA23</i>	Reduced ABA sensitivity	<i>Arabidop:</i>	Drought and salt resistance	Nakajima et al., 2002	6007
<i>NTHK1</i>	Ethylene receptor	<i>Arabidop:</i>	Salt sensitivity	Cao et al., 2007	8733
<i>PSAG12-IPT</i>	Over production of cytokinins	<i>Petunia</i>	Delayed leaf senescence (not tested under stress)	Clark et al., 2004	6904
<i>PLD alpha</i>	Phospholipase D (alpha) expression	<i>Arabidop:</i>	Increase sensitivity to ABA and reduce transpiration	Sang et al. 2001	5635
<i>sp12 and sp5</i>	ABA overproduction	Tomato	High water-use efficiency, low transpiration and greater root hydraulic conductance	Thompson et al., 2007	8805
<i>tos1</i>	Increased ABA sensitivity	Tomato	Hypersensitive to osmotic stress and exogenous ABA	Borsani et al., 2002	6330
<i>ZmACS6</i>	Ethylene synthesis	<i>Maize</i>	Non-functional mutant expressed drought induced senescence	Todd et al., 2004	7471

ALDH3I1 and *ALDH7B4* (aldehyde dehydrogenase), *Alx8* (High APX2 and ABA), *AREB1* (ABA hypersensitivity), *AREB1* (ABRE-dependent ABA signaling), *ASR1* (Undetermined), *AtAOX1* [alternative oxidase (AOX) pathway of plant mitochondria], *AtCBF1-3* (Transcription factor), *AtGluR2* (Transcription factor), *AtGSK1* (Homologue of GSK3/shaggy-like protein kinase), *Atnoa1* (Impaired Nitric Oxide synthesis), *AtPCS1* (Phytochelatin synthesis), *ATP-PRT* (Free His accumulation), *AtRabG3e* (Intracellular vesicle trafficking), *atRZ-1a* (Zinc finger glycine-rich RNA-binding protein), *ATTS244* and *ATTS405* (FtsH protease protecting photosystem), *AZF1*, *AZF2*, *AZF3*, *STZ* (Cys2/His2-Type Zinc-Finger and Proteins), *atRZ-1a* [zinc finger-containing glycine-rich RNA-binding proteins (GR-RBPs)], *AtSZF1* and *AtSZF2* (CCCH-type zinc finger proteins,

involved in salt stress responses), *BNCBF5*, (CBF/DREB1-like transcription factors), *CaBZIP1* [Plant development (dwarf phenotype)], *CAP2* (Transcription factor), *CaPF1* (Transcription factor), *CaPIF1* (Cys-2/His-2 zinc finger protein), *CBF1* (Transcription factor), *CBF1*; *CBF3* (Transcription factor), *CBF3* (Transcription factor), *CBF4* (Transcription factor), *CBL1* (Ca sensing protein), *CBP20* (cap binding complex), *CGS* (Cystathionine-synthase), *CIT1* (Mitochondrial citrate synthase), *CpMYB10* (Glucose sensitive and ABA hypersensitive), *cpSL* [Selenocysteine lyase (mouse)], *CRYOPHYTE/ LOS4* (RNA helicase), *CUP1* (metallothionein accumulation), *Cys* (Enhanced cysteine synthase activity), *desC* (Acyl-lipid 9-desaturase), *DREB* (Transcription factor), *DREB1* or *OsDREB1* (Transcription

factor), *DREB1A* (Transcription factor), *DREB2A* (Transcription factor), *EhCaBP* (Calcium binding protein), *ERA1* (Farnesyl transferase), *FAD3* and *FAD8* (Increased fatty acid desaturation), *FAD7* (Increased fatty acid desaturation under COR15a), *FLD* (Flavodoxin expression in chloroplasts), *Gal* (Raffinose hydrolysis), *Gli1* (Mutant lack glycerol catabolism), *GhDREB1* (Transcription factor), *GPAT* (glycerol-3-phosphate acyltransferase of chloroplasts), *HAL1* (Promote K⁺/Na⁺ selectivity), *HAL2* (Yeast) [Promote K⁺/Na⁺ selectivity], *HOS9* (Transcription factor), *HOS10* (Transcription factor), *HOT2* (Encode a chitinase-like protein), *HsfA2* (Transcription factor), *HsfA2* (Heat-inducible transactivator), *HvCBF4* (Transcription factor), *ISPS* (Isoprene synthesis), *JERF3* (Jasmonate

and ethylene-responsive factor 3), JERF1 (Jasmonate and ethylene-responsive factor 1), LeGPAT (Glycerol-3-phosphate acyltransferase), *lew2* (Wilting allele; cellulose synthesis complex), *MBF1c* (Transcriptional coactivator multiprotein bridging factor), *ME* (NADP-malic enzyme which converts malate and NADP to pyruvate, NADPH, and CO₂), *NADP-ME 2* (NADP-malic enzyme), *MIZ1* (Hydrotropism of root), *MKK9* (MAP Kinase), *MsPRP2* (Transcription factor), *NahG* (salicylate hydroxylase expression), *NPK1* (mitogen-activated protein kinase), *NtC7* (Trans-membrane protein, osmotic adjustment), *OsCDPK7* (Transcription factor), *OsCIPK01-OsCIPK30* (Calcineurin B-like protein-interacting protein kinases), *OsCOIN* (RING finger protein), *OCPI1* (Transcription factor), *OPBP1* (Transcription factor), *OsSbp* (Calvin cycle enzyme sedoheptulose-1,7-bisphosphatase), *OsDREB1A* (Transcription factor), *OsMYB3R-2* (MYB homeodomain and zinc finger proteins), *SIZ1* (SUMO E3 ligase), *SNAC1* (Stomatal activity), *PARP1*; *PARP2* (Poly(ADP-ribose) polymerase), *PDH45* (DNA helicase 45), *RGS1* (Regulation of G-protein signaling), *S851* (Encodes 8 sphingolipid desaturase in cell membranes), *SacB* (Fructan synthesis), *SCABP8* (Interacts with SOS2), *SCOF1* (Transcription factor), *Shn* (Increased epicuticular wax), *SPS* (sucrose phosphate synthase), *SRK2C* (Protein kinase), *STO* (Protein binds to a Myb transcription factor), *Sto1* (Reduced ABA accumulation), *TaPP2Ac-1* (catalytic subunit (c) of protein phosphatase 2A), *TaSTK* (serine/threonine protein kinase), *TaSrg6* (Transcription factor), *TERF1* (ERF transcription activator), *Tsi1* (Transcription factor), *uvi1* (Transcription factor), *VuNCED1* (Involved in ABA biosynthesis), *WXP1* (Epicuticular wax accumulation), *WXP1*; *WXP2* (Epicuticular wax accumulation), *ZmDR EB2A* (Encodes HSP and LEA proteins), *ZPT2-3* (Encodes a Cys2/His2-type zinc finger protein), *MiZpt2* (zinc finger protein) are listed in the Table 6.

Signal transduction genes

Genes involved in stress signal sensing and a cascade of stress-signaling in *A. thaliana* has been of recent research interest (Winicov and Bastola, 1997; Shinozaki and Yamaguchi-Shinozaki, 1999). Components of the same signal transduction pathway may also be shared by various stress factors such as drought, salt and cold (Shinozaki and Yamaguchi-Shinozaki, 1999). Although there are multiple pathways of signal-transduction systems operating at the cellular level for gene regulation, ABA is known component acting in one of the signal transduction pathways, while others act independently of ABA. The early response genes have been known to encode transcription factors that activate downstream delayed response genes (Zhu, 2002). Although, specific branches and components exist (Lee et al., 2001), the

signaling pathways for salt, drought, and cold stresses all interact with ABA, and even converge at multiple steps (Xiong et al., 1999). Abiotic stress signalling in plants involves receptor-coupled phospho-relay, phosphoinositol-induced Ca²⁺ changes, mitogen activated protein kinase (MAPK) cascade, and transcriptional activation of stress responsive genes (Xiong and Zhu, 2001). A number of signaling components are associated with the plant response to high temperature, freezing, drought and anaerobic stresses (Grover et al., 2001). One of the merits for the manipulation of signaling factors is that they can control a broad range of downstream events that can result in superior tolerance for multiple aspects (Umezawa et al., 2006). Alteration of these signal transduction components is an approach to reduce the sensitivity of cells to stress conditions, or such that a low level of constitutive expression of stress genes is induced (Grover et al., 1999). Overexpression of functionally conserved At-DBF2 (homolog of yeast DBF2 kinase) showed striking multiple stress tolerance in *Arabidopsis* plants (Lee et al., 1999). Pardo et al. (1998) also achieved salt stress-tolerant transgenic plants by over expressing calcineurin (a Ca²⁺/Calmodulin dependent protein phosphatase), a protein phosphatase known to be involved in salt-stress signal transduction in yeast. Transgenic tobacco plants produced by altering stress signaling through functional reconstitution of activated yeast calcineurin not only opened-up new routes for study of stress signaling, but also for engineering transgenic crops with enhanced stress tolerance (Grover et al., 1999). Overexpression of an osmotic-stress-activated protein kinase, SRK2C resulted in a higher drought tolerance in *A. thaliana*, which coincided with the upregulation of stress-responsive genes (Umezawa et al., 2004). Similarly, a truncated tobacco mitogen-activated protein kinase kinase kinase (MAPKKK), NPK1, activated an oxidative signal cascade resulting in cold, heat, salinity and drought tolerance in transgenic plants (Kovtun et al., 2000; Shou et al., 2004). However, suppression of signaling factors could also effectively enhance tolerance to abiotic stress (Wang et al., 2005).

SALT TOLERANCE

Transporter genes for salt tolerance

An important strategy for achieving greater tolerance to abiotic stress is to help plants to re-establish homeostasis under stressful environments, restoring both ionic and osmotic homeostasis. This has been and continues to be a major approach to improve salt tolerance in plants through genetic engineering, where the target is to achieve Na⁺ excretion out of the root, or their storage in the vacuole. A number of abiotic stress tolerant transgenic plants have been produced by increasing the cellular levels of proteins (such as vacuolar antiporter

Table 6. Various regulatory genes (www.plantstress.com).

Gene	Gene action	Species	Phenotype	References	ID*
--	Overexpression of nicotianamine synthase	Tobacco and Arabidopsis	Heavy metal tolerance by chelation	Kim et al., 2005	8006
<i>AB13</i>	Transcription factor	<i>Arabidopsis</i>	Enhanced freezing tolerance	Tamminen et al., 2001	5217
<i>ABF3</i>	Transcription factor	Rice	Drought resistance	Oh et al., 2005	7780
<i>ADC</i>	Arginine decarboxylase overexpression	Rice	Polyamine accumulation and salt resistance in biomass accumulation	Roy and Wu, 2001	5561
<i>ALDH3I1 & ALDH7B4</i>	aldehyde dehydrogenase	<i>Arabidopsis</i>	Salt, dehydration and oxidative stress tolerance	Kotchoni et al., 2006	8303
<i>Alx8</i>	High APX2 and ABA	<i>Arabidopsis</i>	Drought resistance	Rossel et al., 2006	8164
<i>AREB1</i>	ABA hypersensitivity	<i>Arabidopsis</i>	Dehydration survival	Fujita et al., 2005	8099
<i>AREB1</i>	ABRE-dependent ABA signaling	<i>Arabidopsis</i>	Drought resistance	Fujita et al., 2006	8099
<i>ASR1</i>	Undetermined	Tobacco	Decreased water loss; salt tolerance	Perlson et al., 2004	7462
<i>AtAOX1</i>	Alternative oxidase (AOX) pathway of plant mitochondria	<i>Arabidopsis</i>	Cold acclimation	Fiorani et al., 2005	8085
<i>AtCBF1-3</i>	Transcription factor	potato	Promoter driven freezing tolerance in yield	Kim et al., 2006	8253
<i>AtGluR2</i>	Transcription factor	<i>Arabidopsis</i>	Calcium utilization under ionic stress	Kim et al., 2001	5172
<i>AtGSK1</i>	Homologue of GSK3/shaggy-like protein kinase	<i>Arabidopsis</i>	Salt tolerance in whole plant and root growth	Piao et al., 2001	5526
<i>Atnoa1</i>	Impaired Nitric Oxide synthesis	<i>Arabidopsis</i>	Salt tolerance	Zhao et al., 2007	8866
<i>AtPCS1</i>	Phytochelatin synthesis	<i>Arabidopsis</i>	Paradoxically showed hypersensitivity to Cd stress	Lee et al., 2003	6387
<i>AtPCS1</i>	Phytochelatin synthesis	<i>Arabidopsis</i>	Arsenic tolerance and cadmium hypersensitivity	Li et al., 2004	7513
<i>AtPCS1</i>	Phytochelatin synthesis	Tobacco	Cadmium tolerance	Pomponi et al., 2006	8092
<i>AtPCS1</i>	Phytochelatin synthesis	Indian mustard	As and Cd tolerance	Gasic et al., 2007a	8912
---	Phytochelatin synthesis (3 genes)	Tobacco	Cadmium tolerance	Wawrzyski et al., 2006	8372
<i>ATP-PRT</i>	Free His accumulation	Alyssum	Nickel tolerance	Ingle et al., 2005	7812
<i>AtPCS1</i>	Phytochelatin synthesis	Indian Mustard	Cadmium and zinc tolerance	Gasic and Korban, 2007b	8815
<i>AtRabG3e</i>	Intracellular vesicle trafficking	<i>Arabidopsis</i>	Salt and osmotic stress tolerance	Mazel et al., 2004	6975
<i>atRZ-1a</i>	Zinc finger glycine-rich RNA-binding proteins	<i>Arabidopsis</i>	Negative effect on germination and seedling growth under salt stress	Kim et al., 2007	9026
<i>atRZ-1a</i>	zinc finger-containing glycine-rich RNA-binding proteins (GR-RBPs)	<i>Arabidopsis</i>	Freezing tolerance	Yeon-Ok et al., 2005	7773
<i>AtSZF1 & AtSZF2</i>	CCCH-type zinc finger proteins, involved in salt stress responses	<i>Arabidopsis</i>	Salt tolerance	Sun et al., 2007	9025
<i>BNCBF5- and 17 17</i>	CBF/DREB1-like transcription factors	<i>Brassica napus</i>	Freezing tolerance and photosynthetic capacity	Savitch et al., 2005	7926

Table 6. Contd.

<i>CAbZIP1</i>	Plant development (dwarf phenotype)	<i>Arabidopsis</i>	Disease, drought and salt tolerance	Lee et al., 2006	8477
<i>CAP2</i>	Transcription factor	Tobacco	Drought and salt tolerance	Shukla et al., 2006	8470
<i>CaPF1</i>	Transcription factor	Virginia pine	Antioxidant activity and metal tolerance	Tang et al., 2005	8022
<i>CaPIF1</i>	Cys-2/His-2 zinc finger protein	Tomato	Chilling and disease resistance	Seong et al., 2007	8716
<i>CBF1</i>	Transcription factor	<i>Arabidopsis</i>	Cold tolerance	Jaglo-Ottosen et al., 1998	5611
<i>DREB</i>	Transcription factor	<i>Arabidopsis</i>	Increased tolerance to cold, drought and salinity	Kasuga et al., 1999	4534
<i>DREB1 or OsDREB1</i>	Transcription factor	Rice	Drought, salt and cold tolerance with reduced growth under non-stress	Ito et al., 2006	8176
<i>DREB1A</i>	Transcription factor	Tobacco	Drought and cold tolerance	Kasuga et al., 2004	7091
<i>DREB1A</i>	Transcription factor	wheat	Delayed wilting under drought stress	Pellegrineschi et al., 2004	7443
<i>DREB2A</i>	Transcription factor	<i>Arabidopsis</i>	Drought resistance	Sakuma et al., 2006	8302
<i>FAD3 & FAD8</i>	Increased fatty acid desaturation	Tobacco	Drought resistance	Meng et al., 2005	8020
<i>GhDREB1</i>	Transcription factor	Tobacco	Chilling tolerance, negatively regulated by gibberellic acid	Shan et al., 2007	9012
<i>MKK9</i>	MAP Kinase	<i>Arabidopsis</i>	Salt resistance in germination	Alzwiya et al., 2007	8979
<i>OsDREB1A</i>	Transcription factor	<i>Arabidopsis</i>	Drought, salt, freezing tolerance	Dubouzet et al., 2003	6429
<i>OsMYB3R-2</i>	MYB homeodomain, and zinc finger proteins	<i>Arabidopsis</i>	Drought, salt, freezing tolerance	Dai et al., 2007	8803
<i>SCABP8</i>	Interacts with SOS2	<i>Arabidopsis</i>	Salt tolerance	Quan et al., 2007	8908
<i>TaPP2Ac-1</i>	catalytic subunit (c) of protein phosphatase 2A	Tobacco	Drought resistance; maintain RWC and membrane stability	Xu et al., 2007	8658
<i>ZIF1</i>	Zn sequestration	<i>Arabidopsis</i>	Zinc tolerance	Haydon and Cobbett, 2007	8802
<i>ZmDREB2A</i>	Encodes HSP & LEA proteins	<i>Arabidopsis</i>	Drought and heat tolerance	Qin et al., 2007	8829
<i>ZPT2-3</i>	Encodes a Cys2/His2-type zinc finger protein	Petunia	Dehydration tolerance	Shoji et al., 2004	6920
<i>MtZpt2</i>	zinc finger protein	Medicao	Recover root growth under salt stress	Merchan et al., 2007	8911

proteins) that control the transport functions. For example, transgenic melon (Borda's et al., 1997) and tomato (Gisbert et al., 2000) plants expressing the HAL1 gene showed a certain level of salt tolerance as a result of retaining more K⁺ than the control plants under salinity stress. A vacuolar chloride channel, AtCLC_d gene, which is involved in cation detoxification, and AtNHX1 gene which is homologous to Nhx1 gene of yeast have been cloned and over expressed in *Arabidopsis* to

confer salt tolerance by compartmentalizing Na⁺ ions in the vacuoles. Transgenic *Arabidopsis* and tomato plants that over express AtNHX1 accumulated abundant quantities of the transporter in the tonoplast and exhibited substantially enhanced salt tolerance (Apse et al., 1999; Quintero et al., 2000; Zhang and Blumwald, 2001). Salt Overly Sensitive I (SOSI) locus in *A. thaliana*, which is similar to plasma membrane Na⁺/H⁺ antiporter from bacteria and fungi, was

cloned and over expressed using CaMV 35S promoter. The up-regulation of SOSI gene was found to be consistent with its role in Na⁺ tolerance, providing a greater proton motive force that is necessary for elevated Na⁺/H⁺ antiporter activities (Shi et al., 2000).

Genes encoding proton pumps, antiporters and ion trans-porters are AtMRP4 (Stomatal guard cell plasma membrane ABC-type ABC transporter), AtNHX1 (Vacuolar Na⁺/H⁺ antiporter), AtNHX2;

AtNHX5 (Vacuolar Na⁺/H⁺ antiporter), *AVP1* (AVP1 proton pump overexpression), *GmCAX1* (Cation/proton antiporter), *HKT1* (Potassium transporter), *AtHKT1* (Sodium and Potassium transporter), *AtHKT1* (Reduction in Sodium in root), *GhNHX1* (Vacuolar Na⁺/H⁺ antiporter), *HvAACT1* (Citrate transporter), *HvPIP2;1* (PIP2 plasma membrane aquaporin Overexpression), *IRT1* (Divalent cation transporter), *NtAQP1* (PIP1 plasma membrane aquaporin), *NtPT1* (Phosphate transporter), *NRT2.1* (Nitrate transporter), *OsNHX1* (Vacuolar Na⁺/H⁺ antiporter), *OsSOS1* (Plasma membrane Na⁺/H⁺ exchanger), *PcSrp* (Serine rich protein (enhancing ion homeostasis)), *Pht1*, *Pht1;4* (Phosphate acquisition by roots), *PIP* (Plasma membrane aquaporin over expression), *PgTIP1* (Tonoplast intrinsic protein), *PIP2;2* (Plasma membrane aquaporin knockout), *PIP1b* (Plasma membrane aquaporin over expression), *PIP1bn* (Plasma membrane aquaporin over expression), *PIP1;4* and *PIP2;5* (Plasma membrane aquaporin over expression), *RWC3* (Aquaporin overexpression), *SOS4* (Involved in the synthesis of pyridoxal-5-phosphate which modulates ion transporters), *SOS3* (Sodium accumulation in roots), *SOS1* (Na⁺-H⁺ antiporter), *SOD2* (Vacuolar Na⁺/H⁺ antiporter), *SsVP-2* (Vacuolar Na⁺/H⁺ antiporter), *SsNHX1* (Vacuolar Na⁺/H⁺ antiporter), *SULTR1;2* (High affinity root sulfate transporter), *TNHX1* and *H⁺-PPase TVP1* (Vacuolar Na⁺/H⁺ antiporter), *TsVP* (Vacuolar Na⁺/H⁺ antiporter), *YCF1* (Sequester glutathione-chelates of heavy metals into vacuoles), *ZntA* (Regulation of Cd, PB and Zn pump) are listed in Table 7.

Antioxidant protection

Stress induces production of reactive oxygen species (ROS) including superoxide radicals, hydrogen peroxide (H₂O₂) and hydroxyl radicals (OH⁻) and these ROS cause oxidative damage to different cellular components including membrane lipids, protein and nucleic acids (Halliwell and Gutteridge, 1986). Reduction of oxidative damage could provide enhanced plant resistance to salt stress. Plants use antioxidants such reduced glutathione (GSH) and different enzymes such as superoxide dismutases (SOD), CAT, APX, glutathione-S-transferases (GST) and glutathione peroxidases (GPX) to scavenge ROS. Transgenic tobacco plants over expressing both GST and GPX showed improved seed germination and seedling growth under stress (Roxas et al., 1997). A major function of glutathione in protection against oxidative stress is the reduction of H₂O₂ (Foyer and Halliwell, 1976). Ruiz and Blumwald (2002) investigated the enzymatic pathways leading to glutathione synthesis during the response to salt stress of wild-type and salt-tolerant *B. napus* L. (Canola) plants over expressing a vacuolar Na⁺/H⁺ antiporter (Zhang et al.,

2001).

Ion homeostasis

Plants respond to salinity using two different types of responses. Salt-sensitive plants restrict the uptake of salt and adjust their osmotic pressure through the synthesis of compatible solutes (e.g. proline, glycinebetaine, soluble sugars; Greenway and Munns, 1980). Salt-tolerant plants sequester and accumulate salt into the cell vacuoles, controlling the salt concentrations in the cytosol and maintaining a high cytosolic K⁺/Na⁺ ratio in their cells. The maintenance of a high cytosolic K⁺/Na⁺ ratio and precise regulation of ion transport is critical for salt tolerance (Glenn et al., 1999). The alteration of ion ratios in plants could result from the influx of Na⁺ through pathways that also function in the uptake of K⁺ (Blumwald et al., 2000). This can be achieved by extrusion of Na⁺ ions from the cell or vacuolar compartmentation of Na⁺ ions. Three classes of low-affinity K⁺ channels have been identified (Sanders, 2001), these are K⁺ Inward rectifying channels (K⁺ IRC); K⁺ outward rectifying channels (KORCs) and Voltage-independent cation channels (VIC). K⁺ outward rectifying channels (KORCs) could play a role in mediating the influx of Na⁺ into plant cells.

These channels, which open during the depolarization of the plasma membrane, could mediate the efflux of K⁺ and the influx of Na⁺ ions. Na⁺ competes with K⁺ uptake through Na⁺ - K⁺ co-transporters and may also block the K⁺ specific transporters of root cells under salinity (Zhu, 2003). This could result in toxic levels of sodium as well as insufficient K⁺ concentration for enzymatic reactions and osmotic adjustment. The influx of Na⁺ is controlled by *AtHKT1*, a low affinity Na⁺ transporter (Rus et al., 2001; Uozumi et al., 2000). The knockout mutant (*hkt1*) from *Arabidopsis* suppressed Na⁺ accumulation and sodium hypersensitivity (Rus et al., 2001), suggesting that *AtHKT1* is a salt tolerance determinant, while the efflux is Hussain et al. (2009) controlled by Salt Overly Sensitive1 (*SOS1*), a plasma membrane Na⁺/H⁺ antiporter (Shi et al., 2000). This antiporter is powered by the operation of H⁺ -ATPase (Blumwald et al., 2000).

In addition to its role as an antiporter, the plasma membrane Na⁺/K⁺ *SOS1* may act as a Na⁺ sensor (Zhu, 2003). The overexpression of *SOS1* improved salt tolerance in *Arabidopsis* (Shi et al., 2003) The compartmentation of Na⁺ ions in vacuoles provides an efficient and cost effective mechanism to prevent the toxic effects of Na⁺ in the cytosol. The overexpression of *AtNHX1*, resulted in the generation of transgenic *arabidopsis* (Apse et al., 1999), tomato (Zhang and Blumwald, 2001), *Brassica napus* (Canola) (Zhang et al., 2001), rice (Ohta et al., 2002), tobacco (Wu et al., 2004), maize (Yin et al., 2004), tall fescue plants (Luming et al., 2006) that were not only able to grow in significantly higher salt concentration (200 mM NaCl) but could also flower and set fruit.

Table 7. Genes encoding proton pumps, antiporters and ion transporters (www.plantstress.com).

Gene	Gene action	Species	Phenotype	References	ID*
AtMRP4	Stomatal guard cell plasma membrane ABCC-type ABC transporter,	<i>Arabidopsis</i>	Drought susceptibility due to loss of stomatal control	Markus et al., 2004	8917
<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Salt tolerance	Yokoi et al., 2002	8872
<i>AtNHX2</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Salt tolerance	Yokoi et al., 2002	7515
<i>AtNHX5</i>					
<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Brassica napus	Salt tolerance, growth, seed yield and seed oil quality	Zhang et al., 2001	8219
<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Cotton	Salt tolerance in photosynthesis and yield	He et al., 2005	7024
<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Tomato	Salt tolerance, growth, fruit yield	Apse et al., 1999	7428
<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Wheat	Salt tolerance for grain yield in the field	Xue et al., 2004	8362
<i>AVP1</i>	AVP1 proton pump overexpression	<i>Arabidopsis</i>	Salt tolerance in growth and sustained plant water status	Gaxiola et al., 2001	6970
GmCAX1	Cation/proton antiporter	<i>Arabidopsis</i>	Salt tolerance	Luo et al., 2005	8231
<i>HKT1</i>	Potassium transporter	Wheat	Salt tolerance in growth and improved K ⁺ /Na ⁺ ratio	Laurie et al., 2002	8568
<i>AtHKT1</i>	Sodium and Potassium transporter	cells	Reduced sodium accumulation	Tomoaki et al. 2005	7252
<i>AtHKT1</i>	Reduction in Sodium in root	<i>Arabidopsis</i>	Salt tolerance	Horie et al. 2006	8981
<i>GhNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i> (cotton)	Salt tolerance	Wu et al., 2004	6120
<i>HvAACT1</i>	Citrate transporter	Tobacco	Aluminum tolerance	Furukawa et al., 2007	6120
<i>IRT1</i>	Divalent cation transporter	<i>Arabidopsis</i>	Iron uptake by root and elimination of iron deficiency	Vert et al., 2002	8007
<i>NtAQP1</i>	PIP1 plasma membrane aquaporin	Tobacco	High root hydraulic conductance and reduced plant water deficit under drought stress	Siefritz et al., 2002	5523
<i>NtPT1</i>	Phosphate transporter	Rice	Phosphate acquisition	Park et al., 2007	7270
<i>NRT2.1</i>	Nitrate transporter	<i>Arabidopsis</i>	Root architecture and nitrate uptake under N stress	Remans et al., 2006	7781
<i>OsNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	rice	Salt tolerance	Fukuda et al., 2004	7254
<i>OsSOS1</i>	Plasma membrane Na ⁺ /H ⁺ exchanger	rice	Salt tolerance	Martínez-Atienza et al., 2007	7256
<i>PcSrp</i>	Serine rich protein (enhancing ion homeostasis?)	Finger millet	Salt tolerance	Mahalakshmi et al., 2006	8830
<i>Pht1, Pht1;4</i>	Phosphate acquisition by roots	<i>Arabidopsis</i>	Phosphate efficiency	Shin et al., 2004	5597
<i>PIP</i>	Plasma membrane aquaporin overexpression	Soybean, lettuce	Downregulated by arbuscular mycorrhiza causing water conservation	Porcel et al., 2006	8352
<i>PgTIP1</i>	Tonoplast intrinsic protein	<i>Arabidopsis</i>	Salt tolerance; root dependant drought tolerance	Peng et al., 2007	6871

Table 7. Genes encoding

<i>PIP2;2</i>	Plasma membrane aquaporin knockout	<i>Arabidopsis</i>	Reduced hydraulic conductivity of root cortex cells	Javot et al., 2003	8591
<i>PIP1b</i>	Plasma membrane aquaporin overexpression	Tobacco	No effect under salt and negative effect under drought stress	Aharon et al. 2003	6659
<i>PIP1bn</i>	Plasma membrane aquaporin overexpression	Tobacco	Tolerance to osmotic stress	Yua et al., 2005	7863
<i>PIP1;4 & PIP2;5</i>	Plasma membrane aquaporin overexpression	Tobacco	Excessive water loss and retarded seedling growth under drought stress	Jang et al., 2007	8974
<i>RWC3</i>	Aquaporin overexpression	Rice	Maintenance of leaf water potential and transpiration under 10 h PEG stress	Lian et al., 2004	7177
<i>SOS4</i>	Involved in the synthesis of pyridoxal-5-phosphate which modulates ion transporters	<i>Arabidopsis</i>	Salt tolerance through Na ⁺ /K ⁺ homeostasis	Shi et al., 2002	5931
<i>SOS3</i>	Sodium accumulation in roots	<i>Arabidopsis</i>	Salt tolerance	Horie et al. 2006	8335
<i>SOS1</i>	Na ⁺ -H ⁺ antiporter	<i>Arabidopsis</i>	Protect K ⁺ permeability during salt stress	Qi and Spalding, 2004	7350
<i>SOD2</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Salt tolerance; higher plant K/Na ratio	Gao et al., 2004	6924
<i>SOD2</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Rice	Salt tolerance	Zhao et al. 2006	8088
<i>SsVP-2</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Salt tolerance	Guo et al. 2006	8166
<i>SsNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Rice	Salt tolerance	Zhao et al. 2006	8216
<i>SULTR1;2</i>	High affinity root sulfate transporter	<i>Arabidopsis</i>	Selenate sensitivity	El Kassis et al., 2007	8800
<i>TNHX1 and H⁺-PPase TVP1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Salt tolerance	Brini et al. 2007	8697
<i>TsVP</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Tobacco	Salt tolerance	Gao et al., 2006	8462
<i>YCF1</i>	Sequester glutathione-chelates of heavy metals into vacuoles	<i>Arabidopsis</i>	Heavy metal and salt tolerance	Koh et al. 2006	8172
<i>ZntA</i>	Regulation of Cd, PB and Zn pump	<i>Arabidopsis</i>	Cd and Pb resistance; reduced metal accumulation	Lee et al., 2003	6824

Synthesis/over expression of compatible solutes

The cellular response of salt-tolerant organisms to both long- and short-term salinity stresses includes the synthesis and accumulation of a class of osmoprotective compounds known as compatible solutes. These relatively small organic molecules are not toxic to metabolism and include proline, glycinebetaine, polyols, sugar

alcohols, and soluble sugars. These osmolytes stabilize proteins and cellular structures and can increase the osmotic pressure of the cell (Yancey et al., 1982). This response is homeostatic for cell water status, which is perturbed in the face of soil solutions containing higher amounts of NaCl and the consequent loss of water from the cell. Glycinebetaine and trehalose act as stabilizers of quaternary structure of proteins and highly ordered states of membranes. Mannitol serves as a free

radical scavenger. It also stabilizes sub cellular structures (membranes and proteins), and buffers cellular redox potential under stress. Hence these organic osmolytes are also known as osmoprotectants (Bohnert and Jensen, 1996; Chen and Murata, 2000). Genes involved in osmoprotectant biosynthesis are upregulated under salt stress and concentrations of accumulated osmo-protectants correlate with osmotic stress tolerance (Zhu, 2002). Although

enhanced synthesis and accumulation of compatible solutes under osmotic stress is well known, little is known about the signaling cascades that regulate compatible solute biosynthesis in higher plants.

Salt tolerance of transgenic tobacco engineered to overaccumulate mannitol was first demonstrated by Tarczynski et al. (1993). The other examples of compatible solute genetic engineering includes the transformation of genes for Ectoine synthesis with enzymes from the halophilic bacterium *Halomonas elongata* (Nakayama et al., 2000; Ono et al., 1999) and trehalose synthesis in potato (Yeo et al., 2000), rice (Garg et al., 2002), and sorbitol synthesis in plantago (Pommerrenig et al., 2007) (Table 1). Initial strategies aimed at engineering higher concentrations of proline began with the overexpression of genes encoding the enzymes pyrroline-5-carboxylate (P5C) synthetase (P5CS) and P5C reductase (P5CR), which catalyze the two steps between the substrate (glutamic acid) and the product (proline). P5CS overexpression in transgenic tobacco dramatically elevated free proline (Kishor et al., 1995). However there is strong evidence that free proline inhibits P5CS (Roosens et al., 1999). Hong et al. (2000) achieved a two-fold increase in free proline in tobacco plants by using a P5CS modified by site directed mutagenesis. The procedure alleviated the feedback inhibition of P5CS activity by proline and resulted in improved germination and growth of seedlings under salt stress.

In spinach and sugar beet which naturally accumulate glycinebetaine, the synthesis of this compound occurs in the chloroplast. The first oxidation to betaine aldehyde is catalyzed by choline mono-oxygenase (CMO). Betaine aldehyde oxidation to glycinebetaine is catalyzed by betaine aldehyde dehydrogenase (BADH) (Rathinasabapathi, 2000). In *Arthrobacter globiformis*, the two oxidation steps are catalyzed by one enzyme, choline oxidase (COD), which is encoded by the *codA* locus (Sakamoto and Murata, 2000). Hayashi et al. (1997) used choline oxidase of *A. globiformis* to engineer glycinebetaine synthesis in *Arabidopsis* and subsequently tolerance to salinity during germination and seedling establishment was improved markedly in the transgenic lines. Huang et al. (2000) used COX from *A. panescens*, which is homologous to the *A. globiformis* COD, to transform *arabidopsis*, *B. napus* and tobacco. In this set of experiments COX protein was directed to the cytoplasm and not to the chloroplast. Improvements in tolerance to salinity, drought and freezing were observed in some transgenics from all three species, but the tolerance was variable. The results offered the possibility that the protection offered by glycinebetaine is not only osmotic but also function as scavengers of oxygen radicals. The level of glycinebetaine production in transgenics could be limited by choline. A dramatic increase in glycinebetaine levels (to 580 mmol/g dry weight in *Arabidopsis thaliana*) was achieved when the growth medium was supplemented with choline (Huang et al.,

2000). The enhancement of glycinebetaine syntheses in target plants has received much attention (Rontein et al., 2002).

Conclusions

This review summarizes the recent efforts to improve abiotic stress tolerance in crop plants by employing some of the stress-related genes and transcription factors. There is a clear and urgent need to begin to introduce stress tolerance genes into crop plants, in addition to establishing gene stacking or gene pyramiding. Although progress in improving stress tolerance has been slow, there are a number of reasons for optimism. The use of transgenes to improve the tolerance of crops to abiotic stresses remains an attractive option. Options targeting multiple gene regulation appear better than targeting single genes. An important issue to address is how the tolerance to specific abiotic stress is assessed, and whether the achieved tolerance compares to existing tolerance. A well focused approach combining the molecular physiological and metabolic aspects of abiotic stress tolerance is required for bridging the knowledge gaps between the molecular or cellular expression of the genes and the whole plant phenotype under stress.

ACKNOWLEDGMENTS

The authors thank the Indo-US collaboration with Agricultural knowledge initiative programme in Biotechnology that is jointly funded by the Indian Council of Agricultural Research, Government of India.

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