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REVIEW

Photosynthesis and antioxidative defense mechanisms in deciphering drought stress tolerance of crop plants

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Abstract

Crop plants are regularly exposed to an array of abiotic and biotic stresses, among them drought stress is a major environmental factor that shows adverse effects on plant growth and productivity. Because of this these factors are considered as hazardous for crop production. Drought stress elicits a plethora of responses in plants resulting in strict amendments in physiological, biochemical, and molecular processes. Photosynthesis is the most fundamental physiological process affected by drought due to a reduction in the CO_2 assimilation rate and disruption of primary photosynthetic reactions and pigments. Drought also expedites the generation of reactive oxygen species (ROS), triggering a cascade of antioxidative defense mechanisms, and affects many other metabolic processes as well as affecting gene expression. Details of the drought stress-induced changes, particularly in crop plants, are discussed in this review, with the major points: *1*) leaf water potentials and water use efficiency in plants under drought stress; *2*) increased production of ROS under drought leading to oxidative stress in plants and the role of ROS as signaling molecules; *3*) molecular responses that lead to the enhanced expression of stress-inducible genes; *4*) the decrease in photosynthesis leading to the decreased amount of assimilates, growth, and yield; *5*) the antioxidant defense mechanisms comprising of enzymatic and non-enzymatic antioxidants and the other protective mechanisms; *6*) progress made in identifying the drought stress tolerance mechanisms; *7*) the production of transgenic crop plants with enhanced tolerance to drought stress.

Additional key words: abiotic stresses, antioxidants, chlorophyll, net photosynthetic rate, osmolytes, PEPC, ROS, RuBPC, water use efficiency.

Introduction

Plants grow well only under an optimum range of environmental factors including radiation, temperature, air humidity, and water supply. Even a slight variation of these factors influences growth and productivity. Changes in the photoperiod, the amount of radiation and its spectral composition, nutrient affluence or starvation, drought or flooding, high-speed wind, UV radiation, anaerobic conditions, extreme temperatures, and air and soil pollution, all these abiotic factors can cause stress on the plants (Versulues *et al.* 2006). Drought stress is one of the most vital, multidimensional abiotic stress factors that adversely affect plant growth, metabolism, and yield (Osakabe *et al.* 2014) and is responsible for decreasing the crop yield by up to 50 % (Zlatev and Lidon 2012). Drought stress is outlined by changes in water relations, physiological processes, alterations in the cell membrane

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Abbreviations: AA - ascorbic acid; ABA - abscisic acid; APX - ascorbate peroxidase; C2H2 - zinc finger domain; DREB - dehydration-responsive element binding; DRO - deeper rooting; GB - glycine betaine; GR - glutathione reductase; GRAS - gibberellic-acid insensitive repressor; GSH - glutathione; GSSG - glutathione disulfide; LEA - late embryogenesis abundant; MDA - monodehydroascorbate; MDHAR - monodehydroascorbate reductase; MYB - myeloblastosis; NADP-ME - nicotinamide adenine dinucleotide phosphate malic enzyme; NAR - net assimilation rate; NCED - 9-*cis*-epoxycarotenoid dioxygenase; NPR - natriuretic peptide receptor; PCR - pentose carbon reduction; PEPC - phospho*enol*pyruvare carboxylase; PPDK - phosphopyruvate dikinase; PS - photosystem; ROS - reactive oxygen species; RWC - relative water content; SOD - superoxide dismutase; SPS - sucrose phosphate synthase; STZ - salt tolerant zinc finger protein; WRKY - transcription factor with conserved sequence; WUE - water use efficiency; YUC - yucasin; ZAT - zinc transporter; ZFP - zinc finger proteins.

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structure, and ultra-structure of cell organelles (Yordanov *et al.* 2003). Plants experience drought stress because of two major reasons: due to a deficit water supply to the roots and high transpiration rates. These conditions mostly prevail under arid and semi-arid climates (Rahdari and Hoseini 2012). To overcome the low water availability, plants adapt using stress avoidance and stress tolerance mechanisms (Lawlor 2013).

Plant growth and water relations under drought stress

A deeper root system, increased root to leaf surface, synthesis of new root tips, increased root length, and increased density are various adaptations of plant's root systems to decreased soil water content also help to increase hydraulic conductivity of the plants (Peña-Valdivia *et al.* 2010). Transport of water in plant roots is achieved either through the apoplastic pathway or the symplastic pathway; the latter of which includes plasma membrane or tonoplast, in which the transport is mediated by the expression of aquaporins (Giuliani *et al.* 2005). The up-regulation of aquaporin genes like *PIP1* and *RWC-3* helps the maize crop to increase water uptake capacity (Giuliani *et al.* 2005). Adaptations of plants to drought can be best understood by studying the genes and transcription factors responsible for root patterning. The transcription factor dehydration-responsive element binding *DREB1A* driven by a stress responsive promoter *rd29* from *Arabidopsis thaliana* helps in the root development of groundnut during drought stress (Shridhar *et al.* 2012). It has been reported that the *Arabidopsis AVP1* gene increases root growth during drought stress (Park *et al.* 2005). The *Deeper Rooting 1* (*DRO1)* gene is responsible for the root depth increase due to the increased gravitropic response in rice root tips. This gene when introduced into IR64 genotype of rice by backcrossing resulted in an increased drought tolerance without any apparent loss in yield (Uga *et al.* 2013).

Plants undergo various changes to avoid water stress induced damage. Some changes are Morphological like increased development of root hairs, deepening of roots, and rolling of leaves. There are also physiological changes like alterations in carbon partitioning, osmotic adjustment, reduced stomatal conductance, and increased water use efficiency (WUE, Taji *et al.* 2004). Water use efficiency is usually calculated as net photosynthetic rate to transpiration rate ratio or also as biomass production to tranpiration rate ratio ($\mathrm{WUE_m}$). In the second case, it is influenced by the relative growth rate, leaf area ratio (LAR), and net assimilation rate (Van den Boogaard *et al.* 1997). Increased WUE is caused by a less reduction in photosynthetic rate than in transpiration rate due to stomatal closure (Chaves *et al.* 2009).

Annual crop plants adapt to drought stress by decreasing their leaf size. This is preceded by a delay in the flowering process (Sujata *et al.* 2013). Drought stress suppresses plant growth and development in crop plants. Water deficiency leads to a reduction in the dry matter of wheat (Ahmad *et al.* 2007). Accumulation of fresh mass in cowpea and common bean is inhibited more than accumulation of dry mass (Augé *et al.* 2001) and so the dry mass/fresh mass ratio in the common bean increases (Ramos *et al.* 1999). Relative growth rate of durum wheat and bean plants decrease during drought stress by 25 % due to a reduction in the net assimilation rate (NAR) and changes in the photosynthetic rate. This is due to a decreased LAR (Lutts *et al.* 2004, Berova and Zlatev 2002).

Drought stress is one of the critical constraints for the growth and production of crop plants. Improvement of drought stress tolerance is dependent on primary factors like osmotic adjustment (Praba *et al.* 2009). Osmotic adjustment is one of the important components of drought resistance in crop plants, this involves accumulation of solutes and thus a decreased osmotic potential as well as increased pressure potential (Martinez *et al.* 2007). Osmotic adjustment helps the plants in maintaining a high relative water content (RWC) at a low leaf water potential, thereby sustaining the growth (Farooq *et al.* 2009). Osmotic adjustment has been observed in the leaves of many crops such as wheat (Budak *et al.* 2013), maize (Pei *et al.* 2010), sorghum (Assefa *et al.* 2010), chickpea (Krouma 2010), field pea (Zlatev and Lidon 2012), sunflower (Rauf and Sadaqat 2008), common bean (Guler *et al.* 2012), rice (Bunnag and Pongthai 2013), barley (Witcombe 2008), and pearl millet (Boyer *et al.* 2008).

Drought stress is associated with changes in the content of phytohormones (Yang *et al.* 2002). Cytokinins and abscisic acid (ABA) are important hormones that play a major role in drought tolerance (Raghavendra *et al.* 2010). Elevated ABA content in response to drought stress leads to many physiological changes like stomatal closure to avoid water loss through transpiration. Abscisic acid sensing and signalling are thought to be mediated according to the current model established in *Arabidopsis thaliana*, which involves: pyrabactin resistance 1 (PYR)/PYR1-like (PYL)/regulatory components of the ABA receptor (RCAR), protein phosphatase 2C (PP2C), and sucrose non-fermenting-1 (SNF1)-related protein kinase 2 (SnRK2) (Yoshida *et al.* 2015). Abscisic acid plays a role in protecting plants during drought depending on the crop, drought stress profile, and season (Blum 2015). Drought stress results in leaf senescence which is related to the decline in cytokinin content in various plant species. The *ipt* gene of cytokinin biosynthesis is reported to delay leaf senescence and promote stress resistance in several plant species (Merewitz *et al.* 2011).

Oxidative stress in plants

Production of reactive oxygen species (ROS): One of the most striking and deleterious results of the abiotic stress in crop plants is the production of toxic ROS in different cellular and sub-cellular compartments (Vaahtera and Brosché 2011). Some ROS are considered to be the most potent reactive ions known. They are generated due to the decreased content of intracellular CO_2, this results in the transfer of electrons from the electron transport chain to oxygen at photosystem I (Reddy *et al.* 2004). Synthesis and production of ROS, such as superoxide radical ($O_2^{\bullet-}$), hydroxyl radical ($OH^{\bullet}$), hydroperoxyl radical ($HO_2^{\bullet}$), hydrogen peroxide (H_2O_2), alkoxy radical ($RO^{\bullet}$), peroxy radical ($ROO^{\bullet}$), singlet oxygen ($^1O_2$), and excited carbonyl (RO^*) leads to the damage of lipids, nucleic acids, and sugars (Vellosillo *et al.* 2010). Reactive oxygen species can damage virtually all macromolecules. This results in a severe damage to cellular components causing DNA lesions. This causes mutations that can often lead to irreparable metabolic dysfunction and cell death (Karuppanapandian *et al.* 2011). The ROS also act as regulators of cell division and differentiation in growing tissues (Schippers *et al.* 2012). The ROS are the by-products of different metabolic pathways and they are produced not only in chloroplasts but also in mitochondria, cell wall, peroxisomes, endoplasmic reticulum, and plasma membrane. During abiotic stresses plants undergo several mechanisms to combat increased ROS production, and in some plants ROS are purposefully generated as signalling molecules to control programmed cell death, pathogen defence, or stomatal closure (Apel and Hirt 2004). The expression of different transcription factors is enhanced by ROS and includes members of the transcription: WRKY transcription factor (consisting of a 60 amino acid domain with conserved amino acid sequence WRKYGQK at its N-terminal end, zinc transporter (ZAT), related to ABI3/VP1 (RAV), GRAS (plant-specific gene family of putative transcription factors whose name derived from its first three identified members, gibberellic acid insensitive (GAI), repressor of GA1 (RGA), and scarecrow (SCR) (Pang and Wang 2010).

Table 1. Localization and functions of ROS in plants.

ROS	Localization	Function
Singlet oxygen ($^1O_2$)	chloroplasts	mediates retrograde signalling through activation of second messengers
Superoxide radical ($O_2^{\bullet-}$)	ETC, mitochondria, chloroplasts, peroxisomes, cytosol	dismutated to H_2O_2
Hydrogen peroxide (H_2O_2)	peroxisomes, mitochondria, chloroplasts	oxidizes proteins; reacts with $O_2^{\bullet-}$ in a Fe catalysed reaction to form $OH^{\bullet}$
Hydroxyl radical ($OH^{\bullet}$)	chloroplasts	originates by Haber-Weiss/Fenton reaction; reacts with all biomolecules

Singlet oxygen ($^1O_2$) is produced by the input of energy to the relatively stable oxygen resulting in removal of spin restriction and rearrangement of electrons. Two forms of $^1O_2$ can be generated according to the access of one electron into the free orbitals. In both forms of $^1O_2$, the spin restriction is eliminated resulting in the increase of oxidizing ability. The chlorophyll pigments associated with the electron transport system are the primary sources of $^1O_2$. Singlet oxygen may also arise as by-product of lipoxygenase activity (Armin *et al.* 2014). Hydroxyl radicals (OH^-) and $^1O_2$ are the most reactive molecular species. The hydroxyl radicals are generated in Fenton reactions in the presence of a suitable chelating agent like iron under a specific temperature and neutral pH conditions. Hydroxyl radicals can even be produced from $O_2^{\bullet-}$ and H_2O_2 (Keles and Unyayar 2004). The ROS are also produced during normal cellular metabolisms, but during drought stress the balance between the ROS production and elimination gets disturbed. The enormous ROS that are produced in young leaf cells during drought stress are eliminated by complex non-enzymatic and enzymatic antioxidant systems.

Role of ROS as signalling molecules: Apart from being the damaging agents, ROS also act as signalling molecules in promoting the adaptation of plants to abiotic stress (Foyer and Noctor 2000, Jaspers and Kangasjärvi 2010). Reactive oxygen species signalling is highly integrated with several plant hormone responses such as ABA induced stomata closure; auxin induced root gravitropism; gibberellic acid induced seed germination and hypersensitive responses; jasmonic acid induced programmed cell death; and salicylic acid induced lignin biosynthesis (Sharma *et al.* 2014). However, to date there is no clear understanding about the mechanism of ROS signalling and the perceiving of ROS signals prior to drought stress adaptation remains elusive. Under biotic stress ROS along with salicylic acid and methyl salicylate; jasmonic acid and methyl jasmonate; azelaic acid; auxin; ethylene; ABA, *etc.*, mediate systemic signals in plants to achieve systemic acquired acclimation (Mittler and Blumwald 2015). Most of the ROS generated by NADPH oxidases act as signaling molecules (Jaspers and Kangasjärvi 2010). Perceiving of extracellular ROS might be done in multiple mechanisms with the possibilities of a protein redox regulation leading to ROS sensing or the oxidation of cell wall components or membranes that in turn is sensed by receptors to transduce the signal into the cytosol (Hancock *et al.* 2006). The intracellular redox status is sensed also by transcription factors such as NPR1, whose monomerization permits the translocation of protein into the nucleus, thereby enhancing the defense response (Tada *et al.* 2008). Candidates for the recognition of ROS in the apoplast include cysteine-rich protein receptor-like kinases (CRKs), small apoplastic proteins, and peptides (Reddie and Carroll 2008). Cysteine-rich protein receptor-like kinases have been found to be transcriptionally regulated by oxidative stress, pathogen attack, and plant hormones. The small extracellular GRIM REAPER (GRI) protein is another candidate for ROS perception. A peptide derived from GRI can induce cell death in plants in the presence of a superoxide radical. However, existing evidence could support the probable role for CRKs and GRI in ROS perception; this hypothesis is yet to be experimentally tested (Wrzaczek *et al.* 2011).

Table 2. Expression of transcription factors in different plants and their functions in stress response.

Gene	Plant	Function
DREB1C	*Arabidopsis*	enhances desiccation tolerance
ABF3	rice	inhibits wilting and rolling
DREB1A	wheat, rice	delays wilting, improves drought tolerance
AREB1	*Arabidopsis*	enhances dehydration tolerance
HARDY	rice	induces high WUE and photosynthesis
ABP9	maize	increases photosynthesis under drought
ABF1, ABF2	rice	improves drought tolerance
bZIP 23	rice	improves drought tolerance
NAC2	rice	induces stomatal closure
NAC6, NAC10	rice	protects against oxidative stress
S1AREB	tomato	improves drought tolerance

Molecular responses to drought stress

The physiological and biochemical responses that are induced during drought are the result of an assortment of genes with diverse functions (Yamaguchi-Shinozaki and Shinozaki 2005). These gene products function in response to drought stress resulting in tolerance at the cellular level. Drought stress triggers certain signals resulting in the activation of transcriptional factors (TFs) involved in drought tolerance. These transcriptional factors include dehydration responsive transcription factors (DREBs) and C-repeat binding factors (CBFa) that bind to the dehydration response element (DRE), C-repeat terminal (CRT) *cis*-acting elements, ethylene responsible element binding factor (ERF), zinc-finger family, WRKY family, basic helix-loop-helix (bHLH) family, basic-domain leucine zipper (bZIP) family, NAC family, and homeodomain transcription family. Drought stress-induced gene expression was seen to be regulated by TFs belonging to bZIP, AP2/ERF, HD-ZIP, MYB, bHLH, NAC, NF-Y, EAR, and ZPT2 families (Rao *et al.* 2015). The consequences of drought stress include variation in the expression of late embryogenesis abundant (*LEA*) genes, leading after this to the synthesis of molecular chaperones that assist to conserve other proteins from degradation (Xoconostle-Cazares *et al.* 2011). The transfer of stress-inducible genes like the 9-*cis*-epoxycarotenoid dioxygenase (*NCED*) gene *via* gene transfer produces stress tolerant plants (Zhang *et al.* 2008b). Microarray analysis of stress-inducible genes from different plant species assist in investigating the functions of these genes to have knowledge of molecular mechanisms governing the drought stress tolerance in plants through genetic manipulation (Table 2).

Genes like *DREB2A*, *RD29B*, and *LEA*s are induced in mature tissues of plants subjected to mild osmotic stress (Skirycz *et al.* 2011). Recent studies reported that *Arabidopsis* plants overexpressing *yucasin 6* (*YUC6*), belonging to the flavin monooxygenases (FMOs) family, exhibits improved drought stress tolerance due to a low rate of water loss and controlled ROS accumulation (Cha *et al.* 2015). During drought, ABA is produced, which not only causes stomatal closure but also activates stress-related genes encoding protein kinases or phosphatases. These genes contain a conserved ABA-responsive element (ABRE)/CRT (C-repeat) that is characterized with the promoter region of RD29A. With the advent of environmental stress in plants, the *cis*-element *trans*-factors CBF/DREB1 and DREB2 are expressed and mediate the up-regulation of genes involved in drought tolerance (Uno *et al.* 2000). Several *cis*-acting basic leucine zipper (bZIP) transcription factors AREB/ABF can bind to ABRE, thus activating ABA-dependent gene expression. The reduced activity of ABA in ABA-deficient *aba2*, ABA-insensitive *abi1*, as well as enhanced activity in the ABA hypersensitive *era1*

Arabidopsis mutants resulted in the different activation of these transcription factors. The ABA-dependent gene expressions depend upon a drought-inducible *RD22* gene. The *RD22* gene is activated by the binding of the MYC transcription factor AtMYC2 (RD22BP1) and MYB transcription factor AtMYB2 with the *cis*-elements of RD22 promoter region, resulting in improved drought tolerance in transgenic plants (Abe *et al.* 2003). The drought inducible gene with NAC transcription factor RD26 is up-regulated with ABA in transgenics and repressed in the RD26 repressor lines. The transcription factors NAC016, NAP, and AREB1 function in the drought stress response in addition to affecting leaf senescence in *Arabidopsis* (Sakuraba *et al.* 2015).

The products of drought-inducible genes identified through microarray analysis in *Arabidopsis* are classified into two groups. The first group includes effector proteins: LEA, osmotin, chaperones, antifreeze proteins, mRNA binding proteins, water channel proteins, sugar and proline transporters, detoxification enzymes, and proteases. The second group includes regulatory proteins: proteins that regulate signal transduction, stress-responsive gene expression, transcription factors, protein kinases, protein phosphatases, enzymes of phospholipid metabolism, and signalling molecules. Ethylene response factors 5 and 6 activate a plethora of osmotic stress tolerance genes such as WRKY33, MYB51, and salt tolerance zinc finger protein (STZ) (Dubois *et al.* 2013) and they were also shown to provide resistance to oxidative stress (Wang *et al.* 2013) and biotic stress (Sun *et al.* 2010).

LEA proteins are extremely hydrophilic proteins, which were first described in cotton as accumulating in late phases of seed development, whose function correlates with the membrane stability; it also possesses resistance to desiccation, thus acting as important source of cellular dehydration tolerance in plants (Sivamani *et al.* 2000). The desiccation sensitive *Lindernia subracemosa* plants under drought stress up-regulate the synthesis of LEA proteins similar to those present in the resurrection plants (Bartels *et al.* 2007). The LEA proteins are encoded by *RD* (responsive to dehydration), *ERD* (early responsive to dehydration), *COR* (cold regulated), *KIN* (cold inducible), and *RAB* (responsive to abscisic acid) genes that are induced during drought stress in different plant species (Shinozaki and Yamaguchi-Shinozaki 2000, Zhu 2002). The LEA proteins are found in a wide range of crop plants like *Gossypium hirsutum* (Galau *et al.* 1993), *Glycine max* (Shih *et al.* 2004), *Oryza sativa* (Moons *et al.* 1997), *Pisum sativum* (Grelet *et al.* 2005), and *Raphanus sativus* (Raynal *et al.* 1990) in response todrought stress (Table 3).

Osmotin is a 24-kDa protein and belongs to dehydrins (LEA2 proteins) that play an important role in stress tolerance mechanisms in plants. Transgenic plants with the over-expressing *OSMOTIN* gene accumulate a significantly more protein under drought stress, determining the role of osmotin in imparting tolerance to drought stress (Barthakur *et al.* 2001). Induction of osmotin transcription is induced by ABA at low leaf water potentials and the amount of osmotin transcript increases with increasing endogenous ABA content (Singh *et al.* 1989). Transcription of osmotin is inhibited by a plethora of tissue specific and hormonal signals that show similarity with ABRE responsive elements; this is associated with osmotic stress tolerance in plants (Raghothama *et al.* 1993). In tomato, water stress causes a substantial rise in the content of osmotin mRNA and protein (Grillo *et al.* 1995). Besides osmotic adjustments, osmotin also safeguards the native structure of proteins during drought stress and is also involved in repairing denatured proteins (Goel *et al.* 2010). Transgenic cotton plants that have been transformed with the tobacco *OSMOTIN* gene have an increased tolerance to osmotic stress (Parkhi *et al.* 2009).

Aquaporins are channel proteins localized in the plasma membrane and intracellular membranes and they facilitate the transport of water, ions, and gases (Maurel *et al.* 2008). The major intrinsic proteins (MIP) family includes aquaporins that control water movement through cells and maintain plant water relations especially during drought in which the water supply is decreased (Šurbanovski *et al.* 2013). Aquaporins regulate water conductance at key "gatekeeper" cell layers; this causes a change in the whole plant water flow and plant water potential (Chaumont *et al.* 2014). Functions of aquaporins are reported to be involved in root hydraulics

Table 3. Expression of genes that encodes polypeptides related to LEA proteins in different plants during drought stress.

Gene	Plant	Related LEA proteins
Em	wheat	D19-LEA-protein (group 1)
pRAB16A	rice	D11-LEA-protein (group 2)
DREB1A	maize	D11-LEA-protein (group 2)
ERD10;ERD14	*Arabidopsis*	D11-LEA-protein (group 2)
Ha ds10	sunflower	D19-LEA-protein (group 1)
HVA1	barley	D19-LEA-protein (group 1)
HVA1	wheat	D7-LEA-protein (group 3)
HVA1	barley	D11-LEA-protein (group 2)
pLE4	tomato	D11-LEA-protein (group 2)
pcECP40	carrot	D11-LEA-protein (group 2)

and in water transport from xylem to stomata, there by facilitating the plant adaptation to short term changes in soil moisture (Gomes *et al.* 2009). The plasmalemma and tonoplast are rich in subfamilies of aquaporins called plasma membrane intrinsic proteins (PIP) and tonoplast intrinsic proteins (TIP), respectively. The PIPs and TIPs mediate the central pathways for transport of water in the cells and maintains intracellular and transcellular water relations during stress. The PIPs are involved in numerous processes in response to drought stress. Drought stress in grape vine causes an increased expression of five *PIP* genes (Galmes *et al.* 2007). However, transcription of the *Arabidopsis AtPIP* aquaporin gene in roots undergo down-regulation under drought stress preventing water back flow from the root to drying soil (Alexandersson *et al.* 2005). But it remains elusive whether the decreased expression of aquaporins during drought is a deliberate or spontaneous phenomenon.

Zinc finger proteins (ZFP) play a crucial role in stress adaptations through their DNA binding or RNA binding interactions. Zinc finger domain (C2H2) families of ZFPs are strongly induced in plants under osmotic stress (Sakamoto *et al.* 2004). About 134 C2H2 ZFPs are reported in the *Arabidopsis* genome. Over-expression of rice *OsZFP252* augments the tolerance of rice seedlings to drought, which is shown by a remarkable survival rate of 79 % (Xu *et al.* 2008). The WRKY transcription factors are involved in the regulation of plant growth and development, and confer tolerance to biotic stresses (Ulker and Somssich 2004). Expression of *OsWRKY11* in rice under the *HSP 101* promoter provides tolerance to drought (Wu *et al.* 2009).

Photosynthesis during drought

Photosynthesis is an important physiological process occurring in all green plants (Ashraf and Harris 2013). The rate of photosynthesis is adversely affected by drought stress due to stomatal and non-stomatal limitations (Kawamitsu *et al.* 2000, Yordanov *et al.* 2003, Samarah *et al.* 2009). A decrease in stomatal conductance with a decrease in leaf water potential results in a reduced net photosynthetic rate and so a decreased assimilate production resulting in a reduced growth and yield (Nikinmaa *et al.* 2013). Stomatal closure is supposed to be one of the main reasons for the decreased net photosynthesis rate (Boyer 1970, Flexas *et al.* 2004). Stomatal closure leads to a decrease in intracellular CO_2 concentrations, which in turn affects Rubisco as well as other enzymes such as sucrose phosphate synthase (SPS) and nitrate reductase. Specific changes in membrane potential and cytosolic pH play an important role in determining the direction and capacity of ion transport in guard and subsidiary cells (Mumm *et al.* 2011). During drought, the activities of different C_4 photosynthetic enzymes like NADP malic enzyme (NADP-ME), phosphopyruvate dikinase (PPDK), and fructose-1,6-bisphosphatase decrease significantly, suggesting the relevance of these enzymes for drought responses (Du *et al.* 1998).

The ability of plants to acclimate to different abiotic stresses varies from species to species depending on the carbon fixation pathways (C_3, C_4, and CAM). About 85 % of higher plants represent C_3, 5 % are C_4, and the rest 10 % belongs to CAM. Drought stress represses cell growth and photosynthesis, and also affects the whole metabolism by adversely affecting the activities of different photosynthetic enzymes. The structural and biochemical impairment of light-dependent reactions as well as carboxylation processes of photosynthesis are the consequences of severe drought stress (Ghotbi-Ravandi *et al.* 2014).

The decrease in the activity of Calvin cycle enzymes has also been observed in drought stressed plants (Maroco *et al.* 2002). Prolonged drought stress decreases the RuBP content due to the inadequate supply of ATP or NADPH to pentose carbon reduction (PCR) cycle. Water deficit affects Rubisco activase which regulates the conformational structure of the Rubisco active site by releasing tight binding inhibitors at the active site utilising ATP (Athar *et al.* 2005). In C_4 plants, fixation of CO_2 in the cytosol of mesophyll cells is mediated by phospho*enol*pyruvate carboxylase (PEPC) to form oxaloacetate. Drought induces the accumulation of *PEPC* transcripts and PEPC proteins as well as an increased activity of PEPC. NADP-malic enzyme (NADP-ME) catalyses the oxidative decarboxylation of malate in the presence of $NADP^+$ to produce pyruvate, CO_2, and NADP(H) (Doubnerová *et al.* 2011). The membrane damage caused during severe drought requires membrane lipid regeneration by synthesising fatty acids. The NADP-ME helps in providing the necessary NADH and pyruvate for the synthesis of fatty acids. The NADPH required for the antioxidative defense systems, like the ascorbate-glutathione cycle involved in plant protection against drought stress, is also produced by NADP-ME (Hernández *et al.* 2012). The up-regulation of NADP-ME during drought stress also helps in modulating organic anionic metabolism in guard cells and in control of stomatal closure by malate degradation during day (Guo *et al.* 2009). The PPDK is found abundantly in C_4 plants and in low quantities in C_3 plants (seeds and mid veins); it helps in catalysing the reversible reaction converting ATP, Pi, phospho*enol*pyruvate (PEP), AMP, and PPi. The cytosolic PPDK plays an important role in transport of amino acids during natural leaf senescence and in accelerating the nitrogen metabolism from leaves, thereby increasing the nitrogen content of seeds (Chastain *et al.* 2006, Taylor *et al.* 2010).

Photosystem (PS) II plays a key role in photosynthetic response to drought stress (Misra *et al.* 2012). Drought stress causes a considerable damage to photosynthetic pigments, which leads to degradation of thylakoid membranes (Kannan *et al.* 2011). The effect of drought on photosynthesis is due to the change in chlorophyll content, by affecting chlorophyll components, and by damaging the photosynthetic apparatus. Drought stress declines the content of chlorophylls in sunflower and the reduction of chlorophyll *b* is greater than of chlorophyll *a* (Jaleel *et al.* 2009).

Antioxidants

The production of ROS is the outcome of a plant metabolism that needs to be controlled to safeguard its cellular components (Saeidnejad *et al.* 2015). The natural antioxidants maintain the cellular redox balance by binding and inactivating the free radicals, which is crucial for the survival of plants during environmental stresses (Most and Jutta 2015). The antioxidant defense system comprising of the co-ordinated action of enzymatic and non-enzymatic antioxidants provide an efficient mechanism of controlling the toxicity rendered by ROS.

Non-enzymatic antioxidants include ascorbic acid (AA), glutathione (GSH), α-tocopherol, and carotenoids among which AA is one of the most important antioxidants synthesised in the majority of plant cell types, organelles, and apoplast (Smirnoff and Wheeler 2000, Giovannoni 2007). The non-enzymatic antioxidants play a vital role in sustaining photosynthetic efficiency and yield stability under severe stress conditions (Gupta and Thind 2015). Except in dry seeds, AA occurs in almost all tissues of plants. Ascorbate can readily donate an electron forming a monodehydroascorbate (MDHA) radical which on further oxidation yields an uncharged radical dehydroascorbate (DHA). The electron donating capability and formation of less reactive MDHA forms the basis for its antioxidant and scavenging activity (Venkataraman *et al.* 2004). Ascorbate reacts with a hydroxyl radical, superoxide, and singlet oxygen. Ascorbic acid provides membrane protection by directly scavenging an OH^- ion and regenerating tocopherol from the tocopheroxy radical. Ascorbate is also an important co-substrate of key antioxidant enzymes such as ascorbate peroxidase (APX) that detoxifies H_2O_2, and 2-oxoacid dependent dioxygenases involved in the biosynthesis of ABA and gibberellic acid (Brossa *et al.* 2011). The role of ethylene and gibberellins in growth regulation has been studied in the leaf tissues of *Brachypodium distachyon* and maize subjected to a mild drought at different developmental stages (Verelst *et al.* 2013). Ascorbic acid is involved in plant cell growth and division, then it is also a co-factor for many enzymes, *e.g.*, AA acts as co-factor in the reaction where APX catalyses the reduction of H_2O_2 to water with concomitant production of MDHA that further yields DHA and AA under catalysis of monodehydroascorbate reductase (MDHAR, Asada 1999).

Glutathione (γ-glutamylcysteinglycine) is another major low molecular mass antioxidant present in plants and occurring in virtually all cellular components, such as chloroplasts, mitochondria, endoplasmic reticulum, vacuoles, and cytosol, performing multiple functions. Glutathione is associated with the storage and transport of reduced sulphur (Kopriva *et al.* 2004), detoxification of xenobiotics *via* glutathione-*S*-transferase (Dixon *et al.* 2002), synthesis of phytochelatins, and in the regulation of redox homeostasis of the cell together with its oxidised form (GSSG) (Cobbett 2000). The central nucleophilic cysteine residue of GSH helps in scavenging cytotoxic H_2O_2 and reacts enzymatically with various other ROS. Glutathione plays a vital role in antioxidative defense by regenerating AA *via* the AA-GSH cycle (Halliwell 2006). Glutathione is precursor for synthesising phytochelatins; this is crucial for controlling cellular heavy metal content (Koffler *et al.* 2014).

Enzymatic antioxidants: Superoxide dismutases (SODs) belong to the family of metallo-enzymes that catalyse the disproportion of superoxide (O_2^-) to O_2 and H_2O_2. All aerobic organisms that are prone to oxidative stress require SODs to dismutate O_2^- yielding H_2O_2. Based on the metal co-factor, SODs are classified into three types: Fe-SOD (localized in chloroplasts), Mn-SOD (localized in mitochondria), and Cu/Zn SOD (localized in chloroplasts, peroxisomes, and cytosol). These three isoenzymes show different sensitivity to H_2O_2. The first plant *SOD* gene was cloned from maize (Cannon *et al.* 1987). Numerous SOD isoenzymes have been reported from plants like nine in maize (Baum *et al.* 1979), seven in *Arabidopsis* (Kliebenstein *et al.* 1999), and two Cu/Zn SODs in *Nelumbo nuceifera* (Dong *et al.* 2011). Several studies indicated that an increased expression of the *MnSOD* gene enhances tolerance to many environmental stresses. The over-expression of *Cu/ZnSOD* enhances the tolerance of potato to drought stress (Kumar *et al.* 2013). The Fe-SOD has been detected only in chloroplasts of limited species and has an inconsistent distribution, but genome analysis in higher plants indicates the wide distribution of chloroplastic *Fe-SOD* genes (Kanematsu and Asada 1994). The role of SOD activity varies with different abiotic stress conditions depending on the distribution as well as the mechanism involved in overcoming stress (Karuppanapandian *et al.* 2011).

Catalase is a tetrameric heme containing enzyme that occurs in all aerobic eukaryotes; it catalyses the dismutation of H_2O_2 generated in peroxisomes into H_2O and O_2 (Moloudi *et al.* 2013). Catalase is a critical enzyme for maintaining the redox balance during oxidative stress. Three isoforms of the catalase enzyme are encoded by *Arabidopsis* genes *CAT-1*, *CAT-2*, and *CAT-3* which are distributed on separate chromosomes and differentially expressed as well as independently regulated. The *CAT* genes are sensitive to numerous abiotic stress signals that regulate their expression (Dat *et al.* 2000). The damage of tissue metabolism in response to stress is overcome by dismutating toxic H_2O_2 due to increased catalase activity.

Ascorbate peroxidase is localised in chloroplasts, cytosol, vacuoles, and extracellular components; it detoxifies H_2O_2 to form H_2O and monodehydroascorbate, using ascorbate as electron donor (Adriano *et al.* 2015). The APX is a key enzyme in the ascorbate-glutathione cycle also known as Halliwell-Asada pathway. It was reported that drought stress up-regulates cytosolic APX in alfalfa nodules (Naya *et al.* 2007). Thylakoid APX (tAPX) and stroma APX (sAPX) are the two isoforms of chloroplastic APX. Thylakoid APX binds to the vicinity of PS I, so that it detoxifies even small quantities of H_2O_2 in its production site (Miyake *et al.* 1993). The expressions of rice thylakoid *OsAPX8* and *OsAPX4* are significantly down-regulated during drought stress, which is due to the distinct responses of *APX* genes in different species and to different magnitudes of stress (Rosa *et al.* 2010). Transgenic plants over-expressing the *SbpAPX* gene show an enhanced drought stress tolerance (Singh *et al.* 2014). The SOD and APX, which are present in chloroplasts and exist in soluble as well as thylakoid-bound forms, expedite rapid scavenging $O_2^{\cdot-}$ generated at the membrane surface and immediately convert it to H_2O_2 (Flexas *et al.* 2004). The over-expression of a key enzyme of ABA biosynthesis 9-cis-epoxy-carotenoid dioxygenase gene (*SgNCED1*) in transgenic tobacco plants results in a higher accumulation of ABA and regulation of APX activity under drought stress (Zhang *et al.* 2008b). The over-expression of the *Solanum lycopersicum* thylakoid-bound APX gene (*StAPX*) in tobacco plants shows a higher APX activity under salinity and drought stress (Sun *et al.* 2010).

Glutathione reductase (GR) is an NAD(P)H-dependent enzyme that catalyses the reduction of GSSG to GSH and thus maintains the reduced pool of GSH. Glutathione reductase plays a vital role in drought tolerance in higher plants by scavenging radicals and safeguarding the -SH group *via* the GSH-disulphide exchange reaction. The rate limiting step of the Halliwell-Asada pathway is catalysed by GR. The maximal activity of GR is observed in photosynthetic tissues that contain chloroplastic isoforms that differ from other GR isoforms from cytosol, mitochondria, and peroxisomes. The GSH and GR are involved in the detoxification of H_2O_2 generated by the Mehler reaction. The onslaught of drought stress enhances GR activity resulting in the accumulation of GSH that acts as a potential antioxidant and radical scavenger. One cytosolic isoform (OsGR2) and two chloroplastic isoforms (OsGR1 and OsGR3) of GR have been reported in rice (Rouhier *et al.* 2006, Monodehydroascorbate reductase (MDHAR) together with dehydroacorbate reductase (DHAR) take part in ascorbate glutathione cycle Over-expression of DHAR and MDHAR in transgenic tobacco and *Arabidopsis* induce an enhanced tolerance against osmotic stresses (Eltayeb *et al.* 2007).

Secondary metabolites that function as antioxidants during drought stress: Tocopherols and tocotrienols, in particular α-tocopherol, are synthesised by all plants and form essential components of biological membranes; they prevent auto-oxidation of lipids thus making it an effective free radical trap. Tocopherols are mainly located in chloroplast membranes and protect lipids and other membrane components of PS II (Igamberdiev *et al.* 2004). During drought, tocopherol and AA content significantly increase in rice (Ahmad *et al.* 2008). In higher plants, oxidative stress triggers the expression of genes that synthesise tocopherols (Wu *et al.* 2007). Tocopherols function in protection against photo-oxidative damage, repairement of oxidizing radicals, and stabilization of membrane structure by changing its fluidity.

Polyphenols or phenolic acids serve as powerful antioxidants because of their ability to eliminate radical ions and function as metal chelators. Phenolics, including flavonoids, tannins, hydroxycinnamate esters, and lignin are distinct secondary metabolites that are abundant in plant tissues (Grace and Logan 2000). Polyphenolic compounds and flavonoids have the capacity to amend peroxidation kinetics by customising lipid packaging in order to decrease the fluidity of membranes thus restraining peroxidation reactions (Arora *et al.* 2000). Flavonoids have been studied extensively for their antioxidant activities (Lambert and Elias 2010). They have been reported to interfere with the activities of enzymes involved in ROS generation, quenching free radicals, chelating transition metals, and rendering them redox inactive in the Fenton reaction (Nakabayashi *et al.* 2014). The conversion of polyunsaturated fatty acids to oxygen containing derivatives is catalysed by lipoxygenase and prostaglandin synthetase. Flavonoids act as potent inhibitors for these enzymes and inhibit the reaction.

Carotenoids are lipophilic organic compounds found in plastids where they play a role in the plant metabolism against oxidative stress in addition to their major role as photosynthetic pigments. Carotenoids react with lipid peroxidation products to terminate chain reactions preventing the formation of $^1O_2$ by depleting excess excitation energy through the xanthophyll cycle (Collins 2001).

Osmolytes

Plants accumulate organic solutes in cytoplasm, such as proline, glycine-betaine, glucose, fructose, mannitol, inositol, valine, isoleucine, *etc*., in response to drought stress. These compatible solutes do not inhibit normal metabolic reactions and act as osmoprotectants under drought, a condition that mediates a change in external osmolarity and maintains osmotic balance and continuous water influx (Tarczynski *et al.* 1993). Osmolytes also increase the stability of macromolecules without interferring with their functional activities (Yancey *et al.* 1982). They also scavenge free radicals under severe drought stress (Padmavathi and Rao 2013).

Proline plays an important role in safeguarding cells from damage caused during drought stress. It scavenges ROS and acts as molecular chaperone stabilizing the structure of proteins (Szabados *et al.* 2010). The activities of Δ1-pyrroline-5-carboxylate (P5C) synthetase and P5C reductase help in increasing proline biosynthesis, whereby plants combat abiotic stresses (Hare and Cress 1997).

Glycine betaine (GB) is an amphoteric quaternary amine that acts as compatible solute in most plants during drought stress. It performs an important function in plants when subjected to abiotic stresses by mediating osmotic adjustments and protecting cells from damage (Chen *et al.* 2008). Plants usually contain a low amount of GB, whereas *Arabidopsis* and few crop plants like rice and tomato do not naturally accumulate GB (Fariduddin *et al.* 2013). Abiotic stresses enhance the accumulation of GB in sugar beet, barley, spinach, sorghum, and maize, which stabilizes the structures and activities of enzymes, thereby maintaining the integrity of membranes (Rhodes *et al.* 1993, Yang *et al.* 2003).

Fructans are polymers of branched fructose molecules that are synthesised in vacuoles and serve as reserve saccharides. Fructans are highly water soluble and are synthesised at low temperatures (Livingston *et al.* 2009). During drought stress, fructans release hexoses thereby stabilise membranes and maintain osmotic adjustment in plants like barley and rye (Spollen and Nelson 1994, Olien and Clark 1995, Valluru and Van den Ende 2008). Fructosyltransferases help in the synthesis of fructans in plants; its introduction to fructan non-accumulating plants like tobacco and rice stimulates fructan production and enhances drought tolerance (Livingston *et al.* 2009).

Another important compatible osmolyte is trehalose, a non-reducing disaccharide that is present in low amounts in many plants but vary during environmental stresses. It helps in maintaining membrane stability and osmotic balance. Trehalose is synthesised in plants through the production of the intermediate trehalose-6-phosphate. Transgenic expressions of trehalose biosynthetic enzymes in various crop plants like rice (Jang *et al.* 2003), tomato (Cortina *et al.* 2005), and potato (Goddijn *et al.* 1997) result in trehalose accumulation leading to stress tolerance.

Mannitol is synthesised naturally in various plant species except a few like wheat. In celery, almost a half of fixed CO_2 is converted to mannitol, equal in proportion to that of sucrose. The low water potential of plants due to drought stress results in an increased accumulation of mannitol that is crucial for maintaining membrane stability. The over-expression of gene encoding mannitol-1-phosphate dehydrogenase results in the enhanced tolerance of *Arabidopsis* (Thomas *et al.* 1995) and tobacco (Tarczynski *et al.* 1992, 1993).

Transgenic plants with enhancing drought stress tolerance

Marked decreases in crop production due to abiotic stresses lead to a demand for the development of drought stress resistant crop plants obtained through transgenic approach (Vinocur *et al.* 2005). The induction of drought stress in plants triggers a plethora of genes which play a crucial role in the defence pathways, these were categorised into three groups: *1*) those involved in the protection of proteins and membranes against damage incurred by ROS; *2*) membrane transporters and ion channels involved in water as well as ion uptake; *3*) transcription factors involved in controlling the transcription of stress related genes.

Different osmolytes have been reported to be associated with drought stress tolerance; enzymes involved in their metabolism represent potential candidates for generating drought stress tolerant transgenic plants (Sharma *et al.* 2011). Plants over-expressing proline biosynthesis genes have an increased tolerance to abiotic stress to some extent (Székely *et al.* 2008). Overproduction of proline in transgenic tobacco and other transgenic plants induces enhanced root biomass under limited water supply (Kishor *et al.* 1995). Transgenic soybean with the P5C reductase (*P5CR*) gene and the antisense construct from *Arabidopsis* prove that proline enhances the survival during drought stress (De Ronde *et al.* 2000). It was found that two transgenic potato lines with enhanced expression of the yeast trehalose-6-phosphate synthase (*TPS1*) gene are more competent at maintaining water content and acceptable photosynthetic rate during drought in comparison with the wild type (Stiller *et al.* 2008). Glycine betaine biosynthetic genes in transgenic *Arabidopsis*, eucalypt, tobacco, rice, tomato, potato, and wheat plants proved to be highly effective in conferring stress tolerance (Goel *et al.* 2011). Several transgenic plants were produced using the genes involved in sorbitol biosynthesis. Transgenic tobacco plants expressing apple cDNA for sorbitol-6-phosphate-dehydrogenase accumulate a varying content of sorbitol. *Diospyros kaki* transformed with sorbitol-6-phosphate dehydrogenase accumulates sorbitol and shows a higher photosynthetic activity compared with control plants (Gao *et al.* 2001).

The increased activities of antioxidant enzymes obtained by the expression of foreign genes for enhancing abiotic stress tolerance have been reported in several plant species (Gupta *et al.* 1993, Allen *et al.* 1997, Payton *et al.* 1997, McKersie *et al.* 2000, Chen and Gallie 2005). Reports have also shown that *SOD* over-expression leads to enhanced tolerance to drought stress (Bohnert and Sheveleva 1998). Alfalfa plants overexpressing the *Mn-SOD* from *Nicotiana plumbaginifolia* have been shown to have an improved yield and enhanced vigour after water deficit (McKersie *et al.* 1996). Over-expression of the *Populus* peroxisomal ascorbate peroxidase (*PpAPX*) gene in transgenic tobacco enhances its drought resistance (Li *et al.* 2009).

Expression of aquaporins was elevated in roots of rice plants grown in the presence of NH_4, resulting in increased water permeability along with hydraulic conductivity (Ding *et al.* 2015). Over-expression of wheat *TaAQP7* confers drought stress tolerance to transgenic tobacco by enhancing water retention, reducing ROS accumulation by enhancing the enzymatic and non-enzymatic antioxidants, and reducing the membrane damage by decreasing lipid peroxidation (Zhou *et al.* 2012). Over-expression of the *Musa acuminata* aquaporin gene *PIP1;1* in *Arabidopsis* results in an increased primary root elongation along with root hair numbers and survival rates compared to the wild type under drought stress (Xu *et al.* 2014).

Transcription activator and suppressor factors are key regulators involved in the induction of changes in the expression of stress related genes during the response to environmental stresses (Sakuma *et al.* 2006). Most of the transcription factors were identified and analysed in *Arabidopsis* using genome-wide microarrays to identify several potential target genes (Ravikumar *et al.* 2014). Over-expression of ABA stress and ripening induced protein 1 (TaASR1) in tobacco results in a decreased lipid peroxidation and membrane damage, as well as higher relative water content and antioxidant enzyme activities than in the wild type under drought stress (Hu *et al.* 2013). Ectopic expressions of *DREB* genes in *Arabidopsis*, wheat, barley, soybean, tomato, tobacco, strawberry, rice, oilseed rape, potato, *etc.*, enhance tolerance to several abiotic stresses (Hussain *et al.* 2011). Constitutive expression of *Arabidopsis DREB1A* and*ABF3* genes in transgenic rice increase tolerance to drought stress (Oh *et al.* 2005). MYB-type proteins are involved in diverse processes of plant growth,

Table 4. Expression of genes in different transgenic plants for enhanced drought tolerance.

Gene	Plant species	Function	Reference
CfPIP2;1	*Arabidopsis*	enhanced drought tolerance	Jang *et al*. 2007
Dehydrin	*Arabidopsis*	enhanced osmotic and salt stress tolerance	Hanin *et al*. 2011
PIP2:2	*Arabidopsis*	enhanced root water uptake capacity	Javot *et al*. 2003
PgTIP1	*Arabidopsis*	improved drought tolerance	Peng *et al*. 2007
Rab 17	*Arabidopsis*	enhanced osmotic stress tolerance	Figueras *et al*. 2004
RcHSP17.8	*Arabidopsis*	drought, salt, and osmotic stress tolerance	Jiang *et al*. 2009
MIZ1	*Arabidopsis*	dehydration avoidance under drought	Iwata *et al*. 2013
CBL1	*Arabidopsis*	enhanced drought tolerance	Cheong *et al*. 2003
ABP9	*Arabidopsis*	improved photosynthetic activity under drought stress	Zhang *et al*. 2008a
OsWRKY45	*Arabidopsis*	enhanced drought tolerance	Qiu *et al*. 2009
AtHSP17.6A	*Arabidopsis*	improved drought tolerance	Sun *et al*. 2001
RWC3	rice	maintenance of water potential and transcription during stress	Lian *et al*. 2004
OsLEA3	rice	enhanced dehydration tolerance	Zhang *et al*. 2009
OsLEA3-1	rice	improved drought resistance	Xiao *et al*. 2007
HVA1	rice	enhanced cell membrane stability	Babu *et al*. 2004
PF00477	rice	improved dehydration tolerance	Cheng *et al*. 2002
sHSP17.7	rice	enhanced drought tolerance	Sato *et al*. 2008
OsiSAP8	rice	drought and salt stress tolerance	Kanneganti *et al*. 2008
OCPI1	rice	enhanced crop yield during drought	Huang *et al*. 2007
HVA1	rice	improved drought and salinity tolerance	Xu *et al*. 1996
SodERF3	tobacco	increased drought tolerance	Trujillo *et al*. 2009
NtAQP1	tobacco	increased root hydraulic conductance and drought tolerance	Siefritz *et al*. 2002
LEA 4	tobacco	improved membrane stability	Liu *et al*. 2009
CaLEA6	tobacco	protection of photosynthetic activity during drought stress	Jun *et al*. 2008
DQ663481	tobacco	improved cell membrane stability	Wang *et al*. 2006
NtHSP70-1	tobacco	regulated water flux and enhanced drought tolerance	Cho *et al*. 2006
HVA1	wheat	increased WUE and biomass	Sivamani *et al*. 2000
LEA3-L2	wheat	increased protein synthesis	NDong *et al*. 2002
HVA1	wheat	increased yield under drought stress	Bahieldin *et al*. 2005
PIP	soybean	enhanced drought tolerance	Porcel *et al*. 2006
HVA1	mulberry	enhanced drought and salt tolerance	Checker *et al*. 2012
ME-leaN4	lettuce	delayed wilting and improved drought tolerance	Park *et al*. 2005b
ME-leaN4	chinese cabbage	improved drought tolerance	Park *et al*. 2005a
CaLEA	chinese cabbage	enhanced dehydration tolerance	Park *et al*. 2003
HVA1	oat	delayed wilting under drought stress	Maqbool *et al*. 2002
NPK1	maize	protect photosynthetic activity during drought	Shou *et al*. 2004

development, and abiotic stress response. Transgenic *Arabidopsis* plants overexpressing the *TaMYB30-B* gene shows an altered expression of drought stress-responsive genes leading to improved drought stress tolerance during the germination and the seedling stages (Zhang *et al.* 2012). A list of genes used for generating the transgenic plants with enhanced drought stress tolerance has been enclosed in Table 5.

Conclusions and future perspectives

Drought stress is one of the harsh environmental factors limiting the production of crop plants globally. The main challenge is to increase the production of plants under decreasing water potential, which can be achieved by understanding the changes in the osmotic potentials that in turn trigger an array of metabolic responses due to the increased expression of genes responsible for the protection of plants under various environmental conditions. The capability of drought stress tolerance in crop plants is more related to the adaptation of plants pertaining to changes in the environment and flexibility of their cellular metabolism, which is considered as key step in tolerance to environmental stresses. Changes in growth and development of plants are always related to changes in their physiological, biochemical, and molecular mechanisms (Fig. 1). For the past two decades, many drought stress inducible genes have been identified in crop plants after the genome sequencing of *Arabidopsis*. In spite of this progress, a critical gaps still remain in identifying mechanisms concerning phyto-hormone dependent and independent gene expression, and the role of enzymes in regulating toxicity of reactive nitrogen species and their metabolism along with identifying the rate limiting enzymes for the synthesis of osmo-protectants. Water deficit induces the expression of specific genes involved in adaptation of plants to stresses; the functions of some of them are not yet established. One way of understanding these functions is by identifying the key rate limiting steps that help in providing drought stress tolerance.

The ROS are important for regulating many cellular processes related to the response to changes in the environment. The ROS were initially recognized as toxic byproducts of an aerobic metabolism eliminated by the coordination of enzymatic and non-enzymatic antioxidants. Apart from their toxicity, the critical role of ROS includes their function as important signaling molecules in different processes involved in growth, development, responses to abiotic and biotic stress stimuli, and programmed cell death. Reactive oxygen species signaling is controlled by the balance of their production and scavenging similarly to calcium signaling which is controlled by storage and release. Still a few connections are missing, regarding the pathways that maintain optimum content of ROS in cells and the role of ROS in mediating the pathways oriented with plant protection mechanisms. Also, the role of ROS in cell to cell communications and integration of networks related to the abiotic stress response and the possible interactions between ROS and reactive nitrogen species is still to be answered. Focus on these aspects will give comprehensive information on understanding drought tolerance mechanisms, and the application of these parameters on crop plants at a global level will lead to the production of crop plants with enhanced drought stress tolerance.

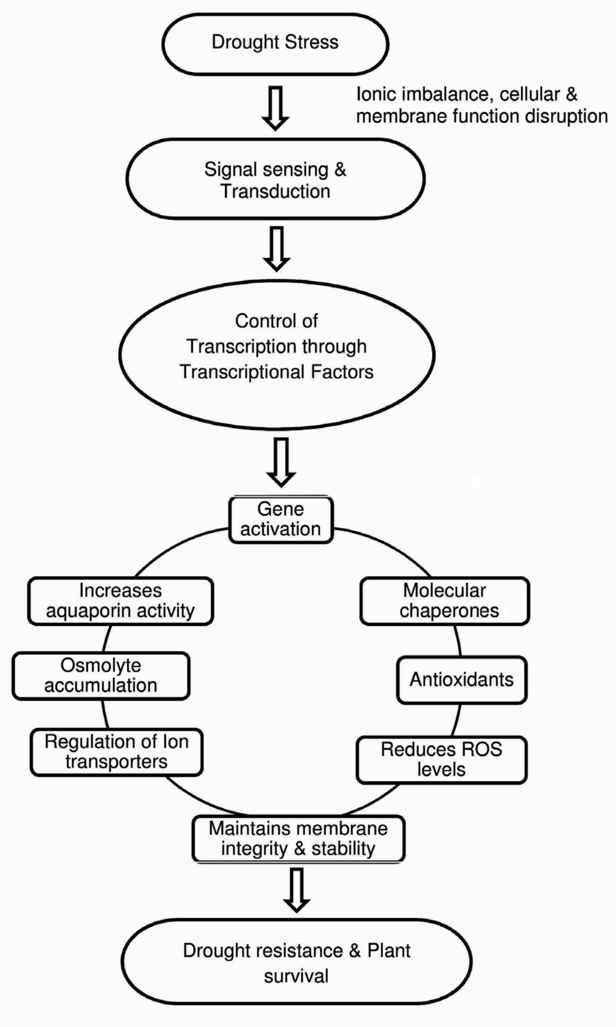

Fig. 1. Drought tolerance mechanisms in plants.

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