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Influence of drought stress on photosynthetic characteristics and protective enzymes in plants

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Abstract

Drought stress as one of the major growth limiting factors in natural environments influences photosynthetic components and electron transfer process, elevating the production of reactive oxygen species (ROS), leading to damage to the cell. Furthermore, ROS are toxic by-products resulted from stress and are involved in signaling pathways, causing major transcriptional changes. ROS scavenging enzymes, localized in the thylakoid membrane of chloroplasts, play a key role in the detoxification of ROS. The capacity of ROS-scavenging enzymes depends on several factors including plant species, duration and intensity of drought stress, stages of plant development, and gene expression patterns of various isoforms. In this regard, novel functional and regulatory genes related to ROS-scavenging enzymes in plants are identified that play a key role in response to drought stress. These genes are differentially expressed in sensitive and tolerant species that may be related to the drought tolerance level of plant species themselves; but the overexpression of those genes in transgenic plants mainly improves drought stress tolerance. However, in some conditions, high drought stress severely damages the photosynthesis apparatus. This damage has a direct relationship to photochemical activities of both PSII and PSI that are required for protecting photosystems against photoinhibition. The photosystem protections are related to precise regulation in D1 protein accumulation under high light conditions, contributing to avoid excessive ROS accumulation. This review describes the influence of drought stress on photosynthetic characteristics, also discusses that the overexpression of genes associated with ROS scavenging enzymes in transgenic plants results in higher drought tolerance and improved photosynthetic characteristics.

***Key words*:** Antioxidant enzymes, Drought stress, Photosystem II, ROS metabolism, ROS scavenging.

ABBREVIATIONS

ROS (Reactive oxygen species), SOD (Superoxide dismutase), Cu/Zn-SOD (copper/zinc superoxide dismutase), Fe-SOD (iron superoxide dismutase), APX (ascorbate peroxidase), Trx (thioredoxin), Prx (peroxiredoxin), PCD (programmed cell death), tAPX (thylakoid ascorbate peroxidase), AOX (alternative oxidase), TF (transcription factor), PS (photosystem), LHC (light-harvesting complexes), PQ (plastoquinone), QA (quinone A), CAT (catalase), AsA (ascorbic acid), GSH (glutathione), MDA (monohydroascorbate radical), MDAR (MDA reductase), Fd (ferredoxin), DHA (Dehydroascorbate), DHAR (DHA reductase), TrxR (thioredoxin reductase), MDA (membrane lipid peroxide), Mn-SOD (manganese SOD), Ni-SOD (nickel SOD), cAPX (cytosolic APX), mitAPX (mitochondria APX), sAPX (stromal APX), microbody membrane-attached APX (mAPX), chlAPX (chloroplastic APX), NTR (NADPH-dependent thioredoxin reductase), Grx (glutaredoxin), RC (reaction centers), OEC (the oxygen-evolving complex), Chl (chlorophyll).

INTRODUCTION

Drought stress is the most severe environmental factor that inhibits photosynthesis and limits plant productivity in both natural and agricultural systems (Chaves *et al.*, 2009). Plants exposed to drought stress often grow in the sunny areas, accordingly, drought stress is accompanied with high light intensity stress and heat stress in the leaves, limiting the CO_2 availability due to the stomatal closure increases the generation of ROS in chloroplasts (Kleine and Leister, 2016; Mignolet-Spruyt *et al.*, 2016). During evolution, plants have adapted to the favorable physiological, biochemical and molecular properties as well as epigenetic regulation to elude lethal effects of ROS and to recognize them as signaling molecules (Foyer and Noctor, 2016; Mignolet-Spruyt *et al.*, 2016). Imbalance between ROS production and detoxification will cause oxidative damage to sensitive macromolecules including lipids, proteins, DNA and RNA leading to programmed cell death (PCD) (Raja *et al.*, 2017). Therefore, it is vital to regulate ROS to a suitable level by enzymatic and non-enzymatic antioxidant defense systems during drought stress (Miller *et al.*, 2010).

Enzymatic antioxidants system for scavenging ROS are located in different cellular compartments. In photosynthesis apparatus, these are embedded in chloroplast thylakoids, a major source of ROS generation, consisting of copper/zinc superoxide dismutase (Cu/Zn-SOD), thylakoid ascorbate peroxidase (tAPX), thioredoxin (Trx), peroxiredoxin (Prx) and alternative oxidase (AOX) (Miller *et al.*, 2010). Drought stress enhances the protective enzymes levels associated to changes in gene expression levels of responsive to stress (Caverzan *et al.*, 2012; Zhang *et al.*, 2019a). Additionally, regulatory genes such as transcription factors (TFs) regulate the protective enzymes levels and other functional proteins involved in these processes (Marinho *et al.*, 2014). If the drought stress is severe, the balance between ROS production and ROS scavenging is disturbed. Because the ROS molecules attack the photosystem II (PSII), oxidation of the D1 and D2 proteins and the inhibition of de novo protein synthesis occur causing oxidative damage and photoinhibition. (Kale *et al.*, 2017). Some compounds such as sodium silicate might decrease drought stress damages by raising the activity of the antioxidant enzymes and preventing the oxidative membrane damage (Tale Ahmad and Haddad, 2011; Kamangar and Haddad, 2016). In the evaluation of influence of drought stress in plant cells, Chl fluorescence is a suitable measurement for the estimation of damage or inhibition in the PSII electron transfer chain. It is well determined that drought stress causes serious damages to photosynthetic pigments and decline in Chl content (Salekjalali *et al.*, 2012; Brestic *et al.*, 2015; Zhao *et al.*, 2017). Thus, the comprehensive study on photosynthesis, metabolism of ROS and scavenging of ROS can help elucidate the mechanism of the light energy conversion and utilization as well as the mechanism of drought resistance and yield increase.

This review gives a broad overview on the effect of drought stress on ROS production during photosynthetic electron transport chain in thylakoid membrane, ROS scavenging enzymes, molecular mechanism in thylakoid membrane and disturbed balance between this two processes caused by the oxidative damage. This review also demonstrates that severe drought in higher plants associated with photoinhibition of photosystem II causes decreases in photosynthetic pigments and chloroplast proteins. The understanding of the hub genes involved in this mechanism is of critical importance for the production of transgenic plants. Transferring a specific drought-tolerance gene can improve drought tolerance in plants.

ROS METABOLISM DURING DROUGHT STRESS IN THYLAKOIDS

Under normal growth conditions, ROS are generated at a low level in cellular compartments such as chloroplasts, mitochondria and peroxisomes because of their higher oxidization activities and rapid electron transfer rates (Demidchik, 2015). Chloroplast thylakoids, the reaction centers of PSI and PSII, are a major source of ROS production. During photosynthesis, reduction of O_2 on the acceptor side of PSI causes the formation of the superoxide radical (O^{2-}), which subsequently can be changed to hydrogen peroxide (H_2O_2), and the hydroxyl radical ($OH^{\bullet}$). At PSII, transfer of excitation energy from excited triplet-state chlorophyll to oxygen at the P680 reaction center and in the light-harvesting complexes (LHC) creates singlet-state oxygen ($^1O_2$) (Miller *et al.*, 2010). ROS can also react with Fe^{2+} leading to the generation of the highly toxic $OH^{\bullet}$ and damage to the cell. Thus, regulating iron levels in response to abiotic stress is vital. (Le *et al.*, 2016).

Under stressful growth conditions such as, salinity, drought, chilling, wounding, pathogen attacks and high light intensity, ROS production rate is dramatically increased. Drought and high light intensity stress affects the photoproduction of ROS via limiting the CO_2 approachability associated with over reduction of the electron transport chain, due to stomatal closure

(Miller *et al.*, 2010; Raja *et al.*, 2017). The increased ROS can begin retrograde and anterograde signaling, also balance the dissemination of energy between PSII and PSI, and impact on photosystem stoichiometry (Kleine and Leister, 2016; Mignolet-Spruyt *et al.*, 2016). These signals induce major transcriptional changes reprogramming plant cells that can either protect them or cause PCD (Rhoads *et al.*, 2006). The enhanced levels of ROS adjust the stress response by changing proteins, which regulates the binding of TFs to DNA, modulating the transcription (Dietz, 2016; Dietz *et al.*, 2016). The production of $^1O_2$ as a signal in chloroplasts can activate reprogramming of nuclear gene expression causing chlorosis and PCD, also induce a wide range of responses associated with different stresses by the function of EXECUTER1 (EX1) and EX2, two chloroplast proteins associated with thylakoid membranes, being encoded in the nucleus (Kleine and Leister, 2016). A study of transcriptome of Arabidopsis under various stresses shows that out of 286 O^{2-}-responsive transcripts overlapped with 180 H_2O_2 -responsive transcripts. Thus, it is comprehensible why O_2 and H_2O_2 signaling functions in the same pathway, because the maximum O_2 generated in the plant cells is converted to H_2O_2 either spontaneously or through SOD activity (Raja *et al.*, 2017). Treatment with exogenous H_2O_2 and Ca^{2+} alleviated drought stress in *Brassica* seedlings grown normally (Khan *et al.*, 2017). Also, exogenous H_2O_2 increased the oxidation of quinone A (QA), enhanced the photosynthetic electron transport flow, and reduced the generation of $^1O_2$ during the stress; thus, the water–water cycle repress the photoproduction of^1 O_2 (Asada, 2006). The redox state of the chloroplast is well known in comprehending redox-regulated gene expression and any modification in its redox homeostasis states leads to changes in chloroplast proteins, ascorbate, glutathione, plastoquinone (PQ), and ROS coupled with ferredoxin system proposing their key signaling role (Foyer and Noctor, 2016).

ROS-SCAVENGING ENZYMES DURING PHOTOSYNTHESIS

Detoxification mechanisms in plants during normal conditions are able to scavenge toxic ROS molecules and reduce the tolerable levels (Nishiyama *et al.*, 2006). These detoxification mechanisms have been evolved by extensive enzymatic systems, such as superoxide SOD, Prx, APX, and catalase (CAT), and non-enzymatic systems, including glutathione, ascorbic acid (AsA), alkaloids, β-carotene, α-tocopherol and non-protein amino acids. In addition, Chloroplastic ROS is also alleviated by pathways such as the Foyer– Haliwell–Asada pathway (Miller *et al.*, 2010).

Generally, SOD catalyzes the conversion of O^{2-} to H_2O_2 and O_2 (Fridovich, 1995), which is further converted to H_2O by thioredoxin/peroxiredoxin (Trx/Prx) or glutathione (GSH) pathway (Rhoads *et al.*, 2006). In Trx/Prx system, APX generates monohydroascorbate radical (MDA) using oxidation AsA, while MDA is catalysed by MDA reductase (MDAR) to reduce back to AsA through either reduced ferredoxin (Fd), or through NAD(P)H (Miller *et al.*, 2010). Due to disability of MDAR, Dehydroascorbate (DHA) is generated and is reduced to AsA by DHA reductase (DHAR) via reduced GSH. Trx itself is maintained in the reduced form by thioredoxin reductase (TrxR), and aids the reduced Prx and Trx (Drechsel and Patel, 2010). In the chloroplast, although CAT has not been found, but is very important and synergies among CAT, SOD and enzymes involved in the ascorbate–glutathione pathway protect cells from ROS damage (Asada, 1994). In the water deficiency conditions, the equilibrium of the production and scavenging of the ROS is disrupted that causes excess accumulation of ROS and the intensification of membrane lipid peroxidation. There will be an elevation in membrane lipid peroxide (MDA) levels and the reduction of the photosynthetic rate of the leaves (Salekjalali *et al* , 2011).

Overexpression of ROS-scavenging enzymes in different compartments can mitigate oxidative stress potentially improving tolerance to drought, salt or the combined stresses. In contrast, imperfection in ROS-scavenging mechanisms of chloroplast increases the stress sensitivity to either drought or salinity (Miller *et al.*, 2010). For instance, the ectopic expression of genes of ROS-scavenging enzymes such as *APX*s and *SOD*s were demonstrated to improve photosynthesis by decreasing ROS levels and declining the inhibition of photosynthesis, under hyperosmotic conditions (Lu *et al.*, 2007). In additional to increased expression of TFs such as *NtERF172*, *Zat10*, *Zat12* or *JERF3* elevated the expression of ROS-scavenging enzymes genes, leading to tolerance to drought, salt or osmotic stresses (Davletova *et al.*, 2005; Wu *et al.*, 2008; Zhao *et al.,* 2020). Thus, detoxification of ROS is necessary for cell survival. According to many researches, ROS-scavenging enzymes found in thylakoids of chloroplasts, the origin of photosynthesis are as follows:

Cu/Zn-SOD or Fe-SOD

SODs (EC 1.15.1.1) as the first line of defense protect plant cells against highly toxic O^{2-} by rapidly converting

superoxide to H_2O_2 and O_2 (Fridovich, 1995). Based on the metal cofactor in their active site, SODs have been categorized into four types: copper–zinc SOD (Cu/Zn-SOD); iron SOD (Fe-SOD); manganese SOD (Mn-SOD); and nickel SOD (Ni-SOD) (Abreu and Cabelli, 2010). Cu/Zn-SOD is very abundant in the cytosol, chloroplast, and peroxisome compartments and is closely associated with enzymes involved in plant stress resistance and anti-aging (Song *et al.*, 2006). Neto *et al.* (2018) reported that RcCuZnSOD3 and RcCuZnSOD4 from *Ricinus communis* are located in the chloroplast according to subcellular predictions of SOD proteins from *Arabidopsis thaliana*, rice, sorghum, poplar and tomato. Fe-SOD is mainly found in chloroplasts (e.g. RcFeSOD7 in *Ricinus communis*), whereas Mn-SOD is located in the mitochondria and peroxisomes (Ueda *et al.*, 2013). Ni-SOD is also found in the genus Streptomyces (Choudhury *et al.*, 1999).

SOD comprises of gene families characterized in several plant species, for example, *Medicago truncatula* possesses seven *MtSOD* genes (1 *MnSOD*, 2 *Fe-SOD*s, and 4 *Cu/ZnSOD*s), most of which were differentially expressed under drought, salt, and cold stress (Song *et al.*, 2018), *Salvia miltiorrhiza* has eight *SOD* genes (3 *Cu/Zn-SOD*s, 2 *Fe-SODs* ,and 3 *Mn-SOD*s). Thirty one types of potential TFs regulate the *SmSOD*s (Han *et al.*, 2020). A genome-wide analysis in *Larix kaempferi* demonstrated six *SOD* genes and proteins, localized in different subcellular compartments. Three out of six proteins (*LkSOD2*, 5 and 6) were identified in chloroplast with catalytic activities (Han *et al.*, 2019). SOD isoenzymes play a substantial role in plant tolerance to abiotic stress, including improved drought tolerance by overexpression of various SODs, elevated oxidative stress tolerance by the expression of Cu/Zn-SOD and *Fe-SOD* genes (Prashanth *et al.*, 2008). Besides, the ability of ROS scavenging may be related to drought tolerance of plant species themselves (Zhang *et al.*, 2019a). Yao *et al.* (2018) identified two *Cu/Zn-SOD* genes, *SaSOD-1a* and *SoSOD1a* from *Saccharum arundinaceus* with strong resistance and *Saccharum officinarum*, respectively. The expression of *SaSOD-1a* under more drought stress duration was up-regulated, but *SoSOD1a* was down-regulated. Therefore, *S. arundinaceus* has a higher ability to scavenge superoxide radicals than *S. officinarum*. Signorelli *et al.* (2013b) showed that drought caused oxidative stress in the *Lotus japonicas* photosynthetic compartments. In lotus as a tolerant species, Mn-SOD and Fe-SOD were induced while, in clover as a sensitive species, the SOD isoforms were not affected by drought stress, and hasd a lower total SOD activity than lotus (Signorelli *et al.*, 2013a). The primed plants of sensitive of *olive* cv. Chétoui showed high efficiency in oxygen scavenging systems and enhanced activities of CAT, SOD, GP and high accumulation of polyphenols, leading to a better retention of homeostasis of ROS (Abdallah *et al.*, 2017)2017. Drought stress also preferentially increased the activities of SOD in some traditional rice cultivars from Assam, India, and in somatic hybrid offspring lines of *Brassica napus* and *Sinapis alba* during vegetative growth, rspectively (Xia *et al.*, 2016; Nahar *et al.*, 2018). TaMnSOD transgenic cotton possessed improved drought tolerance by the regulation of superoxide detoxifying, also developed root and leaf organs (Zhang *et al.*, 2014).

Recent studies have clearly demonstrated functions of SOD in chloroplast. When the Cu/Zn-SOD attached to thylakoids in Arabidopsis was knocked down, it showed abnormal chloroplasts and its growth slowed down (Rizhsky *et al.*, 2003). In contrast, the overexpression of an *Avicennia marina* Cu/Zn-SOD gene in transgenic rice improved drought stress tolerance in comparison to wild plants (Prashanth *et al.*, 2008). Tang and Yang (2008) expressed tomato *Cu/Zn SOD* gene in transgenic potato which enhanced resistance to salt and oxidative stress. *SiCSD*, a *Saussurea involucrata* Kar. & Kir novel Cu/Zn-SOD gene, in transgenic tobacco increased tolerance to freezing, drought, and oxidative stresses, and showed higher activities of SODs and other photosynthetic parameters (Zhang *et al.*, 2017). It has been investigated that the overexpression of *Arachis hypogaea Cu/Zn-SOD* gene in tobacco mitigates salinity and drought stress (Negi *et al.*, 2015). Transgenic Arabidopsis and yeast overexpressing *PutCu/Zn-SOD* gene, demonstrated higher identities with the chloroplast of other plants, from *Puccinella tenuiflora* and *TdMnSOD* from durum wheat exhibited better multiple abiotic stress resistance (Kaouthar *et al.*, 2016; Wu *et al.*, 2016). Transgenic Arabidopsis seedlings showed elevated total SOD activity under salt and oxidative stress. *PutCu/Zn-SOD* gene demonstrated higher identities with the chloroplast *Cu/Zn-SOD* gene of other plants (Wu *et al.*, 2016). *ThDREB* expression in *T. hispida* increased SOD and POD activities leading to a decline in the ROS accumulation and improved tolerance to abiotic stress. Therefore, *ThDREB* as an excellent favorable gene for molecular breeding of *T. hispida*, increases plant stress tolerance (Yang *et al.*, 2017). However, it has been presented in several studies that the increased tolerance of various transgenic plants under extragenetic SODs was not obtained (Pitcher *et al.*, 1991; Payton *et al.*, 1997). This phenomenon may

be related to the complexity of the ROS scavenging mechanism and the discrepancy between SOD isoenzymes.

APX

APX (EC 1.11.1.11), class I heme-peroxidases, is found in higher plants, red algae, chlorophytes, and some protists (Caverzan *et al.*, 2012). APX as a key enzyme of the ascorbate-glutathione cycle utilizes AsA to reduce H_2O_2 to H_2O. This process is not limited to chloroplasts; it also scavenges ROS in other compartments. Plants have evolved five isoforms of APX in distinct subcellular compartments including soluble isoforms, cytosolic APX (cAPX: APX 1&2), mitochondria (mitAPX) and chloroplast stromal APX (sAPX), and membrane-bound isoforms, chloroplast thylakoid membrane-attached APX (tAPX) and microbody membrane- attached APX (mAPX) (Duan *et al.*, 2012). The thylakoidal isoforms are found to be the first one to prevent an H_2O_2 molecule as it is located nearby to the acceptor of PSI (Huseynova *et al.*, 2014). The cytosolic isoforms of APX are more susceptible to reduction in ascorbate than chloroplastic APX (chlAPX), both stromal and thylakoid membrane- attached APX. APX isoforms have also been characterized from several plant species such as olive (Lopez-Huertas and Luis, 2014), rice (Vighi *et al.*, 2017), *Vigna unguiculata* (D'Arcy-Lameta *et al.*, 2005), and ber (Yadav *et al.*, 2014).

Interestingly, all of the APX isoforms develop from alternative splicing, which involves the differential modification of expression of different isoforms (Caverzan *et al.*, 2012). The chlAPX isoenzyme genes are categorized into two major groups. The first group includes spinach, tobacco, pumpkin and ice plant, consists of single genes encoding two isoenzymes via a post-transcriptional alternative splicing. In the second group such as Arabidopsis, rice, and tomato, individual genes encode various isoenzymes, individually regulated (Ishikawa and Shigeoka, 2008). In the first group, An assumed splicing regulatory cis element exists in the upstream of the acceptor position in intron 12 of *chAPX* genes, is extremely conserved in plant species and adjusts alternative splicing (Teixeira *et al.*, 2004). There are four types of mRNA, one type (*tAPX-I*) encodeing thylakoid-attached APX and the other three types (*sAPX-I*, *sAPX-II*, and *sAPX-III*) encode the sAPX (Yoshimura *et al.*, 2002).

APX comprises of multigenic families characterized in several plant species, for example, Arabidopsis as a model plant has nine APX isoforms (*AtAPX1-6*, *sAPX*, *tAPX*, *lAPX*) and *Oryza sativa* as another important model plant has eight isoforms (*OsAPX1-8*). *OsAPx5* to *OsAPx8* genes of rice code APX associated with chloroplast, which OSAPX8 particularly characterized as a putative thylakoid-attached isoform (Teixeira *et al.*, 2004). It is anticipated that *OSAPX6* localized in the chloroplast, but OSAPX6-GFP fusion proteins were identified in mitochondria of the BY-2 tobacco cells (Teixeira *et al.*, 2006). Lazzarotto *et al.* (2011) reported a new class of APX in rice, called APX-related (APx-R), which interact with chlAPx proteins. Other plant species APX isoforms have also been characterized, however, we exclusively will review chlAPX. In spinach (Ishikawa *et al.*, 1998) and *Eucalyptus grandis* (Teixeira *et al.*, 2005) two chlAPX isoforms have been identified.

The expression of APX genes is affected by several environmental factors, including drought, salt and high light stress, H_2O_2 and ABA, and is specified in tissues in developmental stages (Teixeira *et al.*, 2006; Rosa *et al.*, 2010). However, in drought stress no increases were observed in APX activity, in *Vigna radiata* and rapeseed seedlings (Nahar *et al.*, 2015; Hasanuzzaman and Fujita, 2011). In tolerant cultivars of *Vigna unguiculata*, the APX activity was higher in stress conditions than in non-stress conditions. When exposed to drought stress, chlAPX of tolerant cultivars was upregulated, however, it upregulated mAPX and cAPX in the sensitive cultivars (D'Arcy-Lameta *et al.*, 2005). Therefore, enhanced drought tolerance indicated the capacity of APX to efficiently scavenge ROS at their generation sites. Under mild water deficit, wheat genotypes showed differential antioxidative responses and APX expression (Sečenji *et al.*, 2010; Suneja *et al.*, 2017). The transcript level of *cAPX1* was up-regulated in both wheat genotypes, *tAPX* and *cAPX2* were enhanced in the tolerant genotypes, while *sAPX2* indicated higher levels of expression in the sensitive cultivars (Sečenji *et al.*, 2010). In contrast with wheat genotypes, *OsAPX8* expression was down-regulated under drought stress, but the *OsAPX1*, *OsAPX2*, *OsAPX5*, *OsAPX6* and *OsAPX7* expression were up-regulated. The peroxisomal *OsAPX3* expression was not influenced, while *OsAPX4* was slightly but significantly down-regulated (Rosa *et al.*, 2010). Jardim-Messeder *et al.* (2018) demonstrated that *OsAPX8* silencing (RNAiOsAPX8) in rice altered the expression of photosynthesis-related genes and signal transduction, leading to high stomatal restriction accompanied by increased H_2O_2 accumulation. Proteomic and physiological analyses of OsApx8 RNAi-silenced in rice (*apx8*) plants revealed that tAPX have a key role in maintaining of H_2O_2 homeostasis

in cells and regulating the abundance of crucial proteins involved in multiple metabolic pathways. This essential role triggered maintaining growth and photosynthesis in response to drought stress (Cunha *et al.*, 2019). Seedlings of the stress-tolerant varieties of *Eleusine coracana* L., exposed to several polyethylene glycol 6000 concentrations demonstrated higher APX and MDAR activities than seedlings of the stress-susceptible varieties (Bartwal and Arora, 2017). This inconsistency can depend on different responses of APX genes in various species or on stress conditions. In Arabidopsis it is demonstrated that the *cAPX1* gene expression may play a crucial role in the adjustment of plants to a combination of stresses such as heat and drought, and according to another study, the combination of stresses has a more negative effect on plants (Zandalinas *et al.*, 2017). Overexpression of *PcAPX*, a cAPX gene from *Populus tomentosa*, in transgenic tobacco protected the plants from drought, salt and oxidative stress (Cao *et al.*, 2017). Gene expression patterns of *ScAPX6*, located in the chloroplast of sugarcane, showed different responses to abiotic stress. *ScAPX6* gene was down-regulated by H_2O, polyethylene glycol, NaCl and salicylic acid, but was up-regulated by ABA and methyl jasmonate (Liu *et al.*, 2018). APX transcript levels are justly enhanced under drought stress in transgenic soybean and tobacco with overexpression of the *P5CS* gene (Ehsanpour *et al.*, 2012). Transgenic tobacco overexpressing *PpAPX*, *Populus peroxisomal* APX gene, improved plant protection against water deficiency (Li *et al.*, 2009). The overexpression of tomato *StAPX* gene in tobacco increased the resistance to salt and osmotic stress (Sun *et al.*, 2010). Overexpression of *SbpAPX* gene, halophyte *Salicornia brachiata* APX gene, showed improved tolerance to salt and drought stress compared to the non-transgenic plants (Singh *et al.*, 2014). In a recent study, *SlCOR413IM1* overexpression in transgenic tobacco increased SOD and APX activities under drought stress, indicating the decreased accumulation of $O_2^{\bullet-}$ and H_2O_2 in this plant. In the WT lines, the expression of *NtFeSOD*, *NtCu/ZnSOD*, *NtAPX1*, and *NtAPX2* genes did not show superior to the transgenic lines. Thus, high activities of these scavenging enzymes were independent of their expression levels (Ma *et al.*, 2017). Since drought stress is accompanied by photooxidative stress, in some studies the responses of spinach leaf APX isoforms to photooxidative stress were examined. cAPX activity and transcript levels elevated during high light intensity stress, while chlAPX isoforms activities exhibited a gradual decline, and the other isoforms exhibited no significant variation (Yoshimura *et al.*, 2000). The mutants lacking tAPX in Arabidopsis and wheat showed increased H_2O_2 accumulation and oxidized proteins (Danna *et al.*, 2003; Maruta *et al.*, 2009). In contrast, a study examined *tapx/sapx* double mutants subjected to photooxidative stress. These mutants showed susceptibility and different signals associated to photosynthetic characteristics indicating that the APX isoforms are necessary under environmental stresses in various species, particularly under light stress (Caverzan *et al.*, 2012).

APX1 complements chlAPX and mAPX in light intensity tolerance and its absence causes protein oxidation and photosynthetic failure. Nevertheless, unlike cAPX, the transcript levels of chlAPX or mAPXs are not enhanced in response to stress. Therefore, APX isoforms play important roles in scavenging cellular ROS and improving the photosynthetic characteristics of higher plants under drought stress.

Trx

Trxs, small ubiquitous oxidoreductases, reduce disulfide bonds and regulate the cellular redox status of many target proteins. Next, the Trxs are reduced by Trx reductases (for example. Fdx–Trx reductase) through NADPH or reduced Fdx as electron donors (Cejudo *et al.*, 2012). Trxs exist in prokaryotic and eukaryotic organisms, such as animals, plants, bacteria and fungi (Haddad and Japelaghi, 2014). In higher plants, Trxs are expressed by a large gene family comprising of Trxs *f*, *h*, *m*, *o*, *s*, *x*, *y*, *z*, and Trx-like proteins (Meyer *et al.*, 2012; Haddad *et al*., 2018). Arabidopsis possesses 20 various Trx isoforms, localized in the plastids (Trxs *f1-2*, *m1-4*, *x, y1-2*, and *z*), and Trx *o1-2* is localized in nucleus and mitochondria, while the eight Trx *h* are distributed between different compartments of the cell (Meyer *et al.*, 2012; Delorme-Hinoux *et al.*, 2016). The grape Trx *h* consists of multiple forms involved in different processes and expressed in all cellular tissues with differential expression patterns (Japelaghi *et al*., 2011). In previous studies, expression analysis of three *h*-type thioredoxin isoforms (VvTrx *h1*, VvTrx *h2*, and Vv*CxxS2*) of three Iranian grape cultivars was examined at six growth stages and various tissues. The highest level of expression was observed at the veraison stage. VvTrx *h2* showed the highest level of expression in different tissues compared to VvTrx *h1* and Vv*CxxS2* isoforms (Haddad *et al*., 2010). Due to the presence of several potential cis-acting elements, it plays a role in response to environmental signals, anticipating that Trxs *h* may respond to a diversity of environmental signals, such as dehydration, salinity, light, heat, cold, heavy metals, pathogen attacks, and plant hormones (Haddad and Japelaghi, 2014; Haddad *et al*., 2018). In Arabidopsis, isoenzymes of Trx *m* demonstrate about

70% of the total Trxs in the chloroplast. Trxs *m1, m2,* and *m4* have similar levels, while Trx *m3* is much less abundant (Okegawa and Motohashi, 2015). Trxs *m1* and *m2* influence on photosynthetic parameters particularly in light stress (Thormählen *et al.*, 2017). In the *trx m1m2* mutants, due to the decreased ability in prompt light activation of NADP-MDH to export extra reductive power from the chloroplast, they indicated lower photosynthetic performance in the high light intensity than WT (Thormählen *et al.*, 2017). Trx *m4* involves in regulating cyclic electron transport vicinity PSI (Courteille *et al.*, 2013). Other plastidial isoforms of Trxs were mainly utilized as reducing substrates for protective enzymes, including 2-Cys Prx, methionine sulfoxide reductases and thiol peroxidases and played a role in response to oxidative stress (Meyer *et al.*, 2012). It has been also reported that Trxs *f* plays a role in the short-term light-activation of carbon fixation and storage during photosynthetic to intercept feedback inhibition of electron transport in response to a swiftly elevate in light intensity (Geigenberger *et al.*, 2017).

In addition to the literature reviewed above, NADPH-dependent thioredoxin reductases (NTRs) are important key-regulatory enzymes modulating the redox state of the Trx system in plants. NTRs directly reduce ROS, leading to stress tolerance in plants. There are three conserved NTRs including NTRA and NTRB located outside the chloroplast, and NTRC located in chloroplast. Lack of NTRC disadjust redox homeostasis of chloroplast. This may indirectly influence the reduction state of other Trxs, such as Trx *f1*. Thus, it is important for ROS scavenging, optimum photosynthesis and continuance growth in fluctuating light environment (Carrillo *et al.*, 2016; Thormählen *et al.*, 2017). In another study, *ntrc* mutants showed more susceptibility against oxidative, salt and drought stresses (Lepistö *et al.*, 2009). Overexpression of NTRC in *Arabidopsis thaliana* increased tolerance to drought and photo-oxidative stresses with enhanced expression of drought-responsive genes such as *RD29A* and *DREB2A*, compared to *NTRC* mutants (Kim *et al.*, 2017). In Arabidopsis, *ntra* and *ntrb* single mutants demonstrated no obvious phenotypic changes, although lines overexpressing *NTRA* improve tolerance to drought and oxidative stress by increased survival rates, decreased water loss and reduced ROS accumulation compared to WT and *ntra* mutants (Cha *et al.*, 2014). Therefore, abiotic stresses lead to increased Trx either on the gene expression level or on protein level. Increased Trx gene expression was identified in rice under biotic and abiotic stress (Nuruzzaman *et al.*, 2012). In the latter level, Trxs repair the oxidized proteins by assigning reducing power to reductases to decrease toxicity of lipid hydroperoxides (Dos Santos and Rey, 2006).

In some plants subjected to drought stress, different Trx isoforms demonstrated tolerant and sensitive cultivar specific responses. Proteomics analyses using iTRAQ-based protein labeling technology in leaves *Nicotiana tabacum* under drought stress showed that Trxs, ascorbate-, glutathione-, and proteins are associated with H_2O_2 up- or down-regulation. Therefore, chaperones and redox signaling involve in tobacco tolerance system during drought, and it anticipates that post translational modifications resulted from redox play a significant role in modulating protein activity (Xie *et al.*, 2016).

Prx

Prxs (EC 1.11.1.15) are ubiquitous thiol peroxidases with various functions in the antioxidant defense system and redox signaling pathway of the plant cells that show cysteine-dependent peroxidase activity with H_2O_2 and larger hydroperoxide substrates (Liebthal *et al.*, 2017). These antioxidative enzymes found firstly in barley, exist in many organisms, including plants, animals, and bacteria (Stacy *et al.*, 1996). Prxs are classified into six distinguished groups based on their structure, amino acid sequence, molecular interaction, and cysteine localization. Type A (2-cysteine Prx), B (1-cysteine Prx), C (PrxQ) and D (type II Prx). Prxs are identified in the nucleus, plastid, mitochondrion and cytosol in plants, but type E and F are just found in several bacteria (Liebthal *et al.*, 2017). Electron donors such as Trx, NTRC and glutaredoxin (Grx)/glutathione (GSH) restore the catalytically active Cys_P in the type A, C and D Prx. Cys_R-free type B Prx the sulfenic acid primly reacts with a thiol or another reductant (for example ascorbate). Usually, the thiol peroxidase cycle comprises of three steps: the reduction of the peroxide substrate and production of the sulfenic acid form of Cys_P, then the decomposition of the sulfenic acid to release H_2O and finally the regeneration of the thiol reductant by electron transmitters (Liebthal *et al.*, 2017). 2-Cys Prx is abundant in the chloroplast and found in PSII-enriched fractions located near thylakoid membranes, likely plays a role in redox status regulation, as primary ROS sensor, both in the thylakoids and the stroma. PrxIIE and PrxQ, like 2-CysPrx is part of the redox-regulatory network of chloroplast and is targeted by ROS. *2-cysprx A/B* mutant lines showed increased photooxidative damage and higher H_2O_2 rates in high light intensity. This analysis also demonstrated that regulation of marker genes responded to ROS such as *ZAT12*, *BAP1*, *HSFA2*

or *OXI1* were unchanged in *2cysprxA/B* mutants compared to WT and just responded when additional knock-out mutations were introduced in the *tApx* gene. This might represent a synergistic dam control by thiol- and APXs and reciprocal compensation of the missing another enzyme (Awad *et al.*, 2015). Lack of PrxQ in *A. thaliana* leads to a decrease in chlorophyll, indicating its role in scavenging ROS and protection of photosynthetic enzymes (Lamkemeyer *et al.*, 2006). Prx and Trx family cooperate with each other. Prxs in Chloroplast and glutathione peroxidase are individually reduced by several members of the whole chloroplast Trx family including Trx *f1-2*, *m1-4*, *x*, *y1-2*, *z*, Trx-like proteins (NTRC, CDSP32, atypical Cys His-rich Trx-*1-4* and protein disulfide isomerase-like proteins-1-3). The thiol peroxidases and tApx and sApx determine distinguished sub-organellar localization in the plastids (Bernal-Bayard *et al.*, 2014; Mock and Dietz, 2016).

Under normal conditions, thiol peroxidases scavenge ROS and maintain it at low levels, while increased ROS under stress may attack susceptible thiols of other proteins (Dietz, 2016). *Tamarix hispida* plants were subjected to abiotic stresses such as salinity, drought, oxidative and ABA. Expression of all the *ThPrx*s (*Tamarix hispida* Prx) was increased under salinity stress. Expression profiles of *ThPrxs* were differed under ABA, drought and oxidative stress (Gao *et al.*, 2012). In addition, different isoforms of Prx were identified. For instance, seven Prx genes were identified in *Vitis vinifera* (*vvprx*) under irradiance, water and heat stresses. Two of vvprx genes were specifically responsive to water stress, the first one, *vvprxIIF* targeted to mitochondria played an important role in water stress and is assumed to be involved in tolerance to drought via H_2O_2 signaling. The second one, a chloroplastic *vvprxII-2*, was most responsive to the heat stress, and probably is related to ABA-dependent thermo-tolerance (Vidigal *et al.*, 2013). *vvPrxII C* may also respond to a variety of environmental signals, including dehydration, heat, heavy metals, light, pathogens, wounding, and plant hormones. These responsive reactions are said to be due to the presence of different regulatory elements in their promoter (Haddad and Japelaghi, 2015). The overexpression of *Suaeda salsa* PrxQ (*SsPrxQ*) gene in *Eustoma grandiflorum* Shinn enhanced antioxidant activity and Trx dependent peroxidase activity under abiotic stress, as well as increased high light intensity and salinity tolerance (Guan *et al.*, 2014). It has been also represented that in Chinese cabbage species subjected to heat shock and oxidative stress, structure of 2-Cys Prx protein was altered from low molecular weight to high molecular weight (Kim *et al.*, 2009). Under abiotic stress, overexpression of mung bean *VrPrx* gene encoding the 2-Cys Prx in transgenic Arabidopsis indicated enhanced photosynthetic efficiency and antioxidant activities (Cho *et al.*, 2012). Zhang *et al.* (2019b) studied the *2-Cys Prx* overexpression in tobacco seedlings under drought stress. In transgenic seedlings H_2O_2 accumulation was reduced the, PSII electron transfer and photosynthetic rate increased, and oxidative damage was mitigated.

PHOTOSYSTEM II RESPONSES TO OXIDATIVE DAMAGE DURING DROUGHT STRESS

PSII is a multi-subunit pigment-protein complex found in the thylakoid membrane of all aerobic photosynthetic organisms such as cyanobacteria, algae, and higher plants, and acts as a water- PQ oxidoreductase that catalyzes H_2O resulted from light oxidation to O_2 and PQ reduction to plastoquinol (Suga *et al.*, 2015; Najafpour *et al.*, 2016). PSII consists of reaction centers (RCs), the oxygen-evolving complex (OEC) and the chlorophyll (Chl) a/b light-harvesting complex (LHCII) (Chen *et al.*, 2016). Due to extreme susceptibility to environmental adverse factors, photosynthesis is often limited by various stresses, especially high light and drought stress. Water shortage leads to the suppression of the progress of photosynthesis by destruction of all main components such as the transport of thylakoid electron, the photosynthetic carbon reduction cycle, and the control of the CO_2 in stoma, along with the increase in the accumulation of sugars, produced excessive ROS (Farooq *et al.*, 2009). In plants under drought stress and high light intensity, absorption of light through the chlorophyll antenna is higher than energy consumption. During such conditions, singlet-state chlorophyll might be altered to detrimental triplet-state chlorophyll. To intercept formation of triplet-state chlorophyll, quenching of singlet-state chlorophyll to heat is kept directly by xanthophyll pigments or indirectly by the rearrangement of proteins of LHCII (Lhcb) via PsbS protein (Ruban *et al.*, 2012). The PsbS, a chlorophyll-binding protein of PSII, plays a crucial role of a kinetic regulator of the energy dispersal process. If PsbS protein protonated, it binds to LHCII trimers, then antenna system rearrangements induces the formation of non-photochemical quenching. Non-photochemical quenching and PsbS protein level after long-term drought stress were significantly enhanced. Protein analysis of the thylakoid membrane represented that most of the PS proteins declined after

the stress, particularly for Lhcb5, Lhcb6 and PsbQ proteins (Chen *et al.*, 2016). In Arabidopsis mutants with impairement in non-photochemical quenching, PSII exhibited increased sensitively to photoinhibition, while transgenic plants with overexpression of *PsbS*, improved PSII tolerance to photoinhibition (Li *et al.*, 2002). In additional to *PsbS*, drought by accumulated ROS inhibits Chl synthesis and reduces the content of proteins binding to Chl, causing a reduction of LHCII (Farooq *et al.*, 2009). On the other hand, chloroplast development under drought cause light-harvesting capacity and components of photosynthetic system to downsize by down-regulating proteins involved in electron transport and upregulation of antioxidative enzymes to prevent photooxidative and excess ROS damages (Dalal and Tripathy, 2018). Since Chl and other photosynthetic pigments during drought stress are substantially damaged, thereby, Chl fluorescence is a proper measurement for the evaluation of inhibition or damage in electron transfer chain of PSII (Brestic *et al.*, 2015). Several studies on drought stress response have shown that drought causes a large decrease in chl a, chl b and total chl content in sunflower (Zlatev and Lidon, 2012), *Euterpe oleracea* Mart (Silvestre *et al.*, 2017), and peanut (Shivakrishna *et al.*, 2017). Unlike chl, an enhancement in xanthophyll pigments including zeaxanthin and antheraxanthin in plants subjected to water stress conditions has been represented (Batra *et al.*, 2014). The xanthophyll pigments play a protective role for plants against stress, and several of these exist in the xanthophyll cycle to inhibit ROS production (Brestic and Zivcak, 2013).

Under stress conditions, scavenging system is incapable to sufficiently detoxify excessive ROS formation, leading to photoinhibition and oxidative damage. Due to the unbalance between the photo-damage rate to PSII and damaged PSII repair rate, photoinhibition occurs (Nishiyama *et al.*, 2006). It has been reported that ROSs act in photoinhibition by D1 and D2 residues oxidation and de novo protein synthesis inhibition (Nishiyama *et al.*, 2006; Kale *et al.*, 2017). The D1 and D2 proteins of RC are sensitive to oxidative alteration by ROS under abiotic stress. Analysis of tandem mass spectroscopy illustrated some of the modifications in the amino acid oxidation of D1 and D2 proteins on the donor side of the PS along with the formation of $HO^{\bullet}$. Therefore, damage to D1 and D2 proteins leads to cleavage and collection of the D1 subunit. This process has also been observed in the D2 protein similar to the D1 protein but at a slower speed (Kale *et al.*, 2017). The last case of ROS functions in photoinhibition suggests that de novo synthesis of D1 protein suppressed by inhibiting elongation factor 2 of *psbA* mRNA, resulted in preventing the repair of PSII (Nishiyama *et al.*, 2006). SlCOR413IM1 is a chloroplast protein responsive to drought and cold stresses. *SlCOR413IM1* overexpression in transgenic tobacco mitigated the accumulation of ROS in cell and therefore, mitigated the photoinhibition of PSII by decreasing the damage to D1 protein, increased drought tolerance (Ma *et al.*, 2017). Steady levels of D1 ,D2 and LHCII is also extremely reduced under short-term drought stress) Chen *et al.*, 2016).

Drought stress can damage other photosynthetic compartments. It destroys the OEC and inactivates RCs of PSII, influences protein phosphorylation and PSII photochemistry (Sperdouli and Moustakas, 2012; Chen *et al.*, 2016; Zhou *et al.*, 2019). It has been demonstrated that phosphorylation and dephosphorylation of PSII proteins are involved in response to abiotic stresses. In pea under long-term drought stress, the PSII core proteins phosphorylation, such as D1, D2, CP43 and LHCII increases, while in Arabidopsis, the phosphorylation of D1 protein levels decreases. Also, PSII proteins in barley under such a condition illustrated rapid dephosphorylation (Liu *et al.*, 2009). Zhou *et al.* (2019) reported that drought stress decreased the connection between independent PSII units, prevented electron transport from Q_A to Q_B, and damaged electron transporters of PSI in leaves of maize. A study showed that severe water shortage resulted in photoinhibitory quenching in the RC of PSII, which is often demonstrated as a decrease in F_v/F_m (Sperdouli and Moustakas, 2012). Thus, expression of *LHC* gene has frequently been considered as stress marker for chloroplast function and photosynthetic efficiency. This gene in *H. rhodopensis* upon exposure to drought stress was downregulated (Mihailova *et al.*, 2017). On the contrary, Charuvi *et al*. (2015) have detected no notable changes in *Craterostigma pumilum*. To elucidate the impact of drought stress on the activity of the photosynthetic apparatus, Yi *et al.* (2018) investigated photochemical activities such as the photochemical quenching coefficient, quantum efficiency of PSII and electron transport rate through PSII, the quantum efficiency of PSI and the electron transport rate through PSI in field-grown cotton. The photochemical activities of both PSII and PSI are stable under mild drought, but decreased under moderate drought. Moderate drought stimulates cyclic electron flow, required for protecting photosystems against photoinhibition. Lv *et al.* (2020) investigated the response of ginger to drought and shading. Proteomic analysis indicated that the expression of *LHC* was

enhanced and the effects of drought on photosynthetic proteins decreased by shading. Photosynthesis rate of two potato varieties under severe drought stress was reduced by damage to PSII and antioxidant enzyme (Li *et al.*, 2017). In four wolfberry species, chlorophyll content, net photosynthesis rate, transpiration rate, and lipid peroxidation declined under drought stress, but under severe drought conditions, their decline was different. The decrease in two wolfberry species was lower, indicating that they had stronger drought resistance (Zhao *et al.*, 2017). The comparative proteomic study was examined on two grapevine accessions (tolerant and sensitive to salt) under drought stress. Some drought-responsive proteins and the three ROS scavenging proteins APX, ASR2, and GRXS17 were up-regulated in salt tolerant accession, whereas they were down-regulated in salt sensitive accessions. Therefore, salt tolerant accessions may alleviate drought stress through the degradation of damaged proteins or the activation of photosynthesis and redox reactions (Azri *et al.*, 2020). Drought or salinity stresses declined growth in barley, photosynthetic rate, chl content, maximal photochemical efficiency of PSII, water and osmotic potential, however, the combinational stress had a more negative impact than each of those (Zandalinas *et al.*, 2017). The study on cashew, as semiarid adapted species, demonstrated that effective photoprotective mechanisms are able to avoid photo-oxidative damage induced by drought along with high light. Due to the increased activities of ROS-scavenging enzymes and non-enzymatic systems, cashew plants exposed to these stresses did not show alterations in F_v/F_m, cellular integrity, H_2O_2 and thiobarbituric acid reactive species contents, but they showed decreased PSII and PSI activities and increased in heat dissipation. These protections were related to precise regulation in D1 protein accumulation under high light conditions, contributing to avoid excessive ROS accumulation (Lima *et al.*, 2018).

CONCLUSIONS

Drought stress is usually accompanied with stresses including oxidative, high light intensity and heat stress. Therefore, understanding the mechanism of production and scavenging of ROS during photosynthesis helps to achieve high efficiency of photosynthesis. The major site of ROS production is chloroplast thylakoid membranes of plants, which keep ROS at a low level in normal conditions. Under drought stress conditions, the produced ROS in PSI and PSII increases leading to the expression of responsive genes to drought, which are classified mainly in functional and regulatory groups. Besides, ROS leads to oxidative damage, and subsequently damages to the D1 and D2 proteins and pigments of photosynthesis such as Chl. The antioxidant enzymatic systems of the plants evolved to compensate for these damages. The four enzymes, Cu/Zn-SOD, APX, Trx and Prx localized in the thylakoid membrane scavenge excess ROS to harmless molecules. As represented in this review, several key genes control or contribute to drought responses in various plants. Using genetically modifications of plants through genetic engineering and increasing the expression of genes, tolerance to drought stress can be increased.

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