Reactive Oxygen Species: Friend or Foe

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Abstract

Climate change and associated unfavorable abiotic stress conditions, such as drought, salinity, heavy metals, water logging, extreme temperatures, oxygen deprivation, etc., influence plant growth and development to a great extent, eventually disturbing crop yield and quality, finally food security in general. Plant cells produce oxygen radicals and their derivatives, so-called reactive oxygen species (ROS), during different processes related with abiotic stress. Further, the ROS generation is a primary process in higher plants and operates to transmit signaling information at the cellular level in response to the change in environmental conditions. One of the most critical outcomes of abiotic stress is the disruption of the balance between the ROS generation and antioxidant defense systems inducing the excessive ROS accumulation and thus oxidative stress in plants. Remarkably, both enzymatic and nonenzymatic antioxidant defense mechanisms are known to maintain equilibrium between the detoxification and ROS generation under adverse environmental stresses. Even though this area of research has been captivated with massive attention, it mostly remains unfathomed, and our understanding of ROS signaling remains poorly understood.

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In this chapter, we have highlighted the current advancement demonstrating the detrimental effects of ROS, antioxidant defense systems implicated in ROS detoxification during various abiotic stresses, and molecular cross-talk with other key signal molecules such as reactive nitrogen, sulfur, and carbonyl species. Besides, state-of-the-art molecular strategies of ROS-mediated enhancement in antioxidant defense under the acclimation process in response to abiotic stresses in plants have also been covered.

Keywords

Abiotic stress · Antioxidant systems · Oxidative stress · Plant stress tolerance · Reactive nitrogen species · Reactive oxygen species · Stress signaling

6.1 Introduction

Environmental stresses, including salinity, drought, extreme temperature, heavy metals, flooding/waterlogging, etc. are now widespread owing to severe and adverse climate change (Raza et al. 2019; Hasanuzzaman et al. 2020). The aggravation of various abiotic stresses has turned out to be a major menace to global crop production systems. Besides, numerous detrimental effects cause oxidative stress via the overaccumulation of reactive ROS including free radicals (superoxide anion, $O_2^{\bullet -}$; hydroperoxyl radical, $HO_2\bullet$; alkoxy radical, $RO\bullet$; and hydroxyl radical, $\bullet OH$) and nonradical molecules (hydrogen peroxide, H_2O_2 and singlet oxygen, $^1O_2$) (Mehla et al. 2017; Hasanuzzaman et al. 2019a, b). The main ROS generation locations in a plant cell are apoplast, chloroplasts, mitochondria, peroxisomes, and plasma membranes (Singh et al. 2019). While ROS are formed in a normal plant cellular metabolism, overaccumulation as a result of stress severely damages indispensable cellular ingredients including carbohydrates, lipids, proteins, DNA, etc. on account of their highly reactive nature (Berwal et al. 2018; Raja et al. 2017). Plants largely respond to oxidative stress by means of an endogenous defense system comprising of different enzymatic (superoxide dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; glutathione reductase, GR; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione peroxidase, GPX; guaiacol peroxidase, GOPX; glutathione *S*-transferase, GST; Ferritin; nicotinamide adenine dinucleotide phosphate (NADPH) oxidase-like alternative oxidase, AOX; peroxiredoxins, PRXs; thioredoxins, TRXs; glutaredoxin, GRX; etc.) and nonenzymatic (ascorbic acid, AsA; glutathione, GSH; phenolic acids; alkaloids; flavonoids; carotenoids; α-tocopherol; nonprotein amino acids; etc.) antioxidants (Gill and Tuteja 2010; Kumar et al. 2013a, b; Kaur et al. 2019a, b). In plant cells, the antioxidant defensive mechanism and ROS accumulation maintain steady-state equilibrium (Hasanuzzaman et al. 2012). Keeping cellular ROS at an optimum level facilitates accurate redox reactions to take place and the regulation of various processes necessary for growth and development in plants (Mittler 2017). Such optimum level is maintained as a result of equilibrium between ROS production and ROS scavenging (Hasanuzzaman et al. 2019a, b). But, under stress conditions, over-generation of ROS creates imbalance and instigates cell damage, resulting into programmed cell death (PCD), thus reducing crop productivity (Raja et al. 2017). In addition to their damaging activity, ROS are recognized as secondary messengers and are involved in signal transduction to the nucleus via redox reactions using mitogen-activated protein kinase (MAPK) pathway in a number of cellular processes to improve abiotic stress tolerance (Singh et al. 2019). Reactive oxygen species contribute as key molecules during the acclimation process of plants under environmental stimuli by acting as signal transduction molecules, which direct various pathways during the acclimation of the plant under stressed state (Choudhury et al. 2017). A number of investigations have demonstrated that ROS are necessary for the accomplishment of many primary natural processes such as cellular proliferation and differentiation (Mittler 2017). Also, H_2O_2 is an important element in regulation of stress response in plants such as rice (Sohag et al. 2020), wheat (Habib et al. 2020), maize (Terzi et al. 2014), mung bean (Fariduddin et al. 2014), soybean (Guler and Pehlivan 2016), cucumber (Sun et al. 2016), sour orange (Tanou et al. 2012), strawberry (Christou et al. 2014), basil (Gohari et al. 2020), and rapeseed (Hasanuzzaman et al. 2017a, b). Additionally, it is well-known that in addition to ROS, reactive nitrogen species (RNS), reactive sulfur species (RSS), and reactive carbonyl species (RCS) are also involved in signal transduction as well as in a cross-talk in plant tolerance to abiotic stress (Yamasaki et al. 2019). Thus, ROS play a central, dual role in plant biology, exhibiting a fascinating research area for plant biologists. In this chapter, we recapitulate the latest progress of harmful effects of ROS, antioxidant defensive mechanism implicated in ROS detoxification during different abiotic stresses, and as well the cross-talk of RNS, RSS, and RCS with ROS. We also spotlight on development in molecular approaches of ROS-mediated improvement in plant antioxidant defense during the acclimation process against abiotic stress.

6.2 ROS Formation and Types

In plants, ROS are generated in many cellular compartments including chloroplasts, mitochondria, peroxisomes, and plasma membrane (Dmitrieva et al. 2020). In the chloroplast, light quanta are absorbed by chlorophyll (chl) molecules and are excited to their triplet state. If this triplet chl is not quenched well, recombination of charge takes place leading $^3O_2$ to excited $^1O_2$ (Dmitrieva et al. 2020). Though its lifetime is extremely short (3.1–3.9 μs) and diffusion distance is small (190 nm), $^1O_2$ diffuses outside the chloroplast to reach the cell wall, targets plasma membrane, tonoplast, or even cytosolic signaling cascades (Fischer et al. 2013). Furthermore, $^3O_2$ could receive electrons from electron transport chain or nicotinamide adenine dinucleotide phosphate (NADPH) oxidase activity generating $O_2^{\bullet-}$ having a half-life of 1–1000 μs (Hasanuzzaman et al. 2019a, b). Additionally, $O_2^{\bullet-}$ reacts with H+ generating $HO_2^{\bullet-}$, which is far more reactive, stable, and permeable through biological membranes. Likewise, H_2O_2 can be generated during the dismutation of

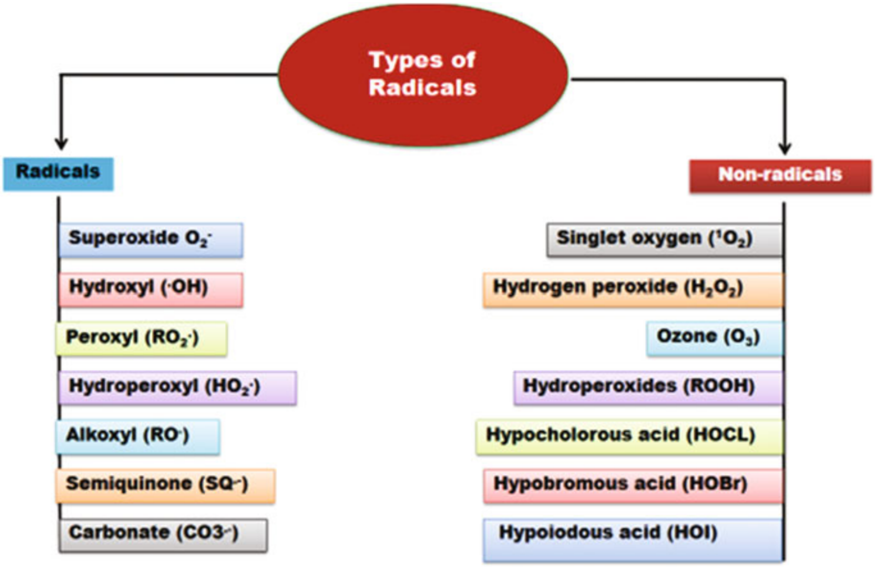

Fig. 6.1 Various types of reactive oxygen species/free radicals generated in plant systems

$O_2^{\bullet-}/HO_2^{\bullet-}$ by SOD isoforms, NADPH oxidases, and heme-containing class III peroxidases (POX) activity (Rejeb et al. 2015; Berwal et al. 2018). Chemically, H_2O_2 is a weak acid with high diffusibility and stability, with a life span of <1 s and can cross the plasma membrane through aquaporins (Mhamdi et al. 2012). Another in place of one more essential ROS •OH can be generated during the Fenton reaction, hydroperoxides activity during sunlight, and inner-sphere electron transfer. Furthermore, proteins, for example heme oxygenases, cytochrome P450s, superoxide reductases, and some photosystem II (PSII) proteins, also generate •OH (Demidchik 2015). The calculated half-life of •HO is about 1 ns and has a short diffusibility of <1 nm.

Cellular ROS constitutes both free radical and non-radicals (Fig. 6.1). Among the free radicals, $O_2^{\bullet-}$, •OH, RO•, and peroxyl radical (ROO•) and non-radicals, H_2O_2, $^1O_2$, and ozone (O_3) are very common (Maurya 2020). Nevertheless, some other non-radicals are also present in plants for example hypochlorous acid (HOCl), hydroperoxides (ROOH), and excited carbonyls (RO*) (Kapoor et al. 2015). In addition, reactive oxygen intermediates (ROI) are also categorized as reactive oxygen molecules generated by incomplete O_2 reduction; thus, ROS comprise all kinds of ROI as well as O_3 and $^1O_2$ (Fig. 6.1). Also, some acids like hypobromous acid (HOBr), hypoiodous acid (HOI), and HOCl and radicals like carbonate radical ($CO_3^{\bullet-}$) and semiquinone ($SQ^{\bullet-}$) are also incorporated into ROS (Waszczak et al. 2018).

Among ROS radicles, $O_2^{\bullet-}$ is a primary reducing agent that forms strong oxidants. Furthermore, RNSs, RSSs, and RCSs are generated on reaction of $O_2^{\bullet-}$

with nitric oxide (NO). These compounds further cause oxidative stress, and play a vital role in "shaping" the intra- and extracellular redox signals (Suzuki et al. 2012).

6.3 Localization and Processes of the Generation of ROS in Plant Cells

In plant cells, ROS is mainly generated in chloroplasts, mitochondria, peroxisomes, plasma membrane, as well as cell wall (Kohli et al. 2019; Kumar et al. 2021). Consequently, compartmental ROS generation in plants sums to its total production (Singh et al. 2019). Chloroplasts are the primary spots for ROS generation depending on the interaction of chl and light, where triplet chl and ETC of PS I and II play main role in main generation of ROS (Dietz 2016; Kim and Dogra 2019; Singh et al. 2019). Mitochondria are considered as the main site of ROS generation in case of nongreen parts of a plant such as roots. In mitochondria, leakage of electrons from both complex I and III of ETC generates $O_2^{\bullet-}$, which later on gets converted into H_2O_2 by Mn-SOD and CuZn-SOD (Singh et al. 2019). The prime source of ROS generation in peroxisomes is glycolate oxidase (GOX) (Kerchev et al. 2016). Also, $O_2^{\bullet-}$ and uric acid are produced in peroxisomal matrix by the activity of xanthine oxidase (XOD), which further dismutates to H_2O_2 by SOD and urate oxidase (UO), respectively (Corpas et al. 2019). In addition to β-oxidation of fatty acids, H_2O_2 is also generated in peroxisomes due to $O_2^{\bullet-}$ disproportionation and flavin oxidase activity (Gilroy et al. 2016). In addition, copper amine oxidase, polyamine oxidase, sulfite oxidase, and sarcosine oxidase enzyme activity also results in generation of H_2O_2 in peroxisome (Corpas et al. 2020). Nevertheless, MDHAR has been established to hydrolyze H_2O_2 through AsA-GSH cycle and regenerate AsA in peroxisomes (Lisenbee et al. 2005), while NADPH oxidase, class III POX, amine and germin-like oxalate oxidases, quinine reductase, and lipoxygenases (LOX) guide the ROS generation in apoplast (Mittler 2017; Choudhary et al. 2020). Fatty acid oxidation as well as also GOX and UO activities produce $O_2^{\bullet-}$ and H_2O_2 in glyoxysomes (Jeevan Kumar et al. 2015). Furthermore, XOD and aldehyde oxidase (AO) potentially contribute to ROS production in cytosol (Jeevan Kumar et al. 2015) (Table 6.1).

6.4 Antioxidant Defense and Plant Abiotic Stress: Recent Approaches

Plants trigger their antioxidant defense system in order to alleviate the unfavorable effects of oxidative stress. However, antioxidant defense role differs between plant species and genotypes, as well as stress types and duration (Table 6.2). Further, various strategies to improve antioxidant defense in plants have also been revealed (Table 6.2).

Table 6.1 Reaction mechanisms of major reactive oxygen species (ROS) scavenging enzymatic antioxidants

Antioxidants	Reactions catalyzed	Catalytic reaction sites
Nonenzymatic		
Ascorbic acid	Scavenges $O_2^{\bullet -}$, H_2O_2, $^{\bullet}OH$, and $^1O_2$	Chloroplast, peroxisomes, cytosol, mitochondria, apoplast
Glutathione	Scavenges H_2O_2, $^{\bullet}OH$, and $^1O_2$	Chloroplast, peroxisomes, cytosol, mitochondria, apoplast
Tocopherol	Scavenges $^{\bullet}OH$, $^1O_2$, $ROO^{\bullet}$, and ROOH	Thylakoid membrane of chloroplast
Carotenoids	Scavenges mainly $^1O_2$	Chloroplast
Flavonoids	Scavenges $O_2^{\bullet -}$, H_2O_2, and $^1O_2$	Chloroplast, vacuole
Phenolic acids	Scavenges $O_2^{\bullet -}$, $^{\bullet}OH$, $ROO^{\bullet}$, and $ONOO^-$	Cell wall
Alkaloids	Scavenges $O_2^{\bullet -}$, $^{\bullet}OH$, H_2O_2, and $^1O_2$	Vacuole
Nonprotein amino acids	Scavenges $O_2^{\bullet -}$, H_2O_2, and $^1O_2$	Cytosol, mitochondria, cell wall
Enzymatic		
Superoxide dismutase (SOD; EC 1.15.1.1)	$^2O_2^{\bullet -} + 2H^+ \rightarrow O_2 + H_2O_2$	Chloroplast, peroxisomes, cytosol, mitochondria, apoplast
Catalase (CAT; EC 1.11.1.6)	$2H_2O_2 \rightarrow 2H_2O + O_2$	Peroxisomes
Peroxidases (POX; EC 1.11.1.7)	$2PhOH + H_2O_2 \rightarrow 2PhO^{\bullet} + 2H_2O$ $2PhO^{\bullet} \rightarrow$ cross-linked substances $PhO^{\bullet} + Asc \rightarrow PhOH + MDHA$ $PhO^{\bullet} + MDHA \rightarrow PhOH + DHA$	Cell wall, apoplast, vacuole
Polyphenol oxidase (PPO; EC 1.14.18.1)	$PhOH + O_2 \rightarrow$ Catechols + $O_2 \rightarrow Q + H_2O$	Thylakoid membrane of chloroplast, cytosol, vacuole
Ascorbate peroxidase (APX; EC 1.11.1.11)	$H_2O_2 + AsA \rightarrow 2H_2O + MDHA$	Chloroplast, peroxisomes, cytosol, mitochondria, apoplast
Monodehydroascorbate reductase (MDHAR; EC 1.6.5.4)	$MDHA + NAD(P)H \rightarrow AsA + NAD(P)^+$	Chloroplast, cytosol, mitochondria
Dehydroascorbate reductase (DHAR; EC 1.8.5.1)	$2GSH + DHA \rightarrow GSSG + AsA$	Chloroplast, cytosol, mitochondria
Glutathione reductase (GR; EC 1.6.4.2)	$GSSG + NADPH + H^+ \rightarrow GSH + NADP^+$	Chloroplast, cytosol, mitochondria
Glutathione peroxidase (GPX; EC 1.11.1.9)	$H_2O_2 + GSH \rightarrow H_2O + GSSG$	Cytosol, mitochondria
Glutathione S-transferase (GST; EC 2.5.1.18)	$R\text{-}X + GSH \rightarrow GS\text{-}R + H\text{-}X$	Chloroplast, cytosol, mitochondria

(continued)

Table 6.1 (continued)

Antioxidants	Reactions catalyzed	Catalytic reaction sites
Peroxiredoxins (PRX; EC 1.11.1.15)	H_2O_2 + PRX-S^- → OH^- + PRX-SOH + GSH → PRX-SSG + H_2O PRX-SSG + GSH → PRX-S^- + GSSG	Cytosol, chloroplasts, mitochondria, nucleus, extracellular spaces
Thioredoxin (TRX; EC 1.8. 1.9)	TRX-RS_2 + NADPH + H^+ → TRX-R$(SH)_2$ + $NADP^+$	Chloroplast, cytosol, mitochondria

6.4.1 Antioxidant Defense in Plants Under Salinity

Regulation of antioxidant mechanism improves the salt stress effects in plants, as delineated in various works (Table 6.2). It has been reported that differential activities of antioxidant enzymes vary in terms of salinity extent, exposure time, and the plant developmental stages (Li et al. 2019). Vighi et al. (2017) recorded differential response in salt-tolerant rice cultivar in contrast to salt-sensitive and revealed that *OsAPX3*, *OsGR2*, *OsGR3*, and *OsSOD3-Cu/Zn* genes were the basic differential markers between tolerant and sensitive rice genotypes. In another study, wheat (salt-tolerant cv. Suntop and salt-sensitive Sunmate) and barley (salt-tolerant cv. CM72) cultivars were compared and revealed that higher antioxidant activity (SOD, peroxidase; POD, APX, GR, and CAT) is strongly associated with the higher tolerance to salinity demonstrating an apparent antioxidant role in enhancement of oxidative stress induced by salinity (Zeeshan et al. 2020). In the same way, Alzahrani et al. (2019) reported higher levels of SOD, CAT, GR, and AsA in *Vicia faba* genotypes, when H_2O_2 concentration increased over 90% during salt stress, thus validating the antioxidant response regulation under salinity stress and its mitigation. Antioxidant activity can be regulated by employing either chemical or natural protectants against salinity has been demonstrated to play vital role in antioxidant response for ameliorating stresses in plants for example salinity (Zulfiqar et al. 2019, 2020). Alsahli et al. (2019) reported that a twofold increase in SOD, CAT, and APX activity resulted into threefold decrease in H_2O_2 in wheat under salinity stress on application of salicylic acid (SA) in contrast to control plants. Also, the application of jasmonic acid (JA) and humic acid together enhanced APX activity, improving salt tolerance in sorghum (Ali et al. 2020), whereas application of polyamines exogenously controlled antioxidant responses in sour orange when grown under high salinity conditions (Tanou et al. 2014).

6.4.2 Role of Antioxidants in Plants Under Water Scarcity and Drought Stress

Various studies have demonstrated the activity of antioxidant defense system under drought stress in various plant species (Table 6.2). In a study carried out by Nahar et al. (2017), decrease in AsA/DHA and GSH/GSSG ratio due to enhanced activities of APX, GR, GPX, and GST in mung bean seedlings compared to control in

Table 6.2 Antioxidant defense in plants under different abiotic stress factors

Plant species	Stress conditions	Antioxidant defense	References
Salinity			
Triticum aestivum	100 mM NaCl; 20 days	Nitrogen supplementations increased the activity of SOD, CAT, GR, MDHAR, and DHAR by twofold and APX threefold, respectively, compared to untreated	Ahanger et al. (2020)
Nicotiana benthamiana	150 mM NaCl; 15 days	Acetylcholine application increased SOD by onefold and POD by twofold	Qin et al. (2020)
Solanum lycopersicum	150 mM NaCl; 5 days	Vanillic acid increased AsA/DHA, GSH/GSSG, MDHAR, GR, GST, SOD, and CAT by 161%, 90%, 18%, 53%, 87%, 43%, and 105%, respectively	Parvin et al. (2020)
Medicago sativa	250 mM NaCl; 2 weeks	Melatonin increased the activities of CAT, POX, and Cu/Zn-SOD	Cen et al. (2020)
Cucumis sativus	150 mM NaCl; 3 days	Melatonin increased CAT, SOD, POD, and APX by 23%, 29%, 15%, and 16%, respectively	Zhang et al. (2020a, b)
T. aestivum	100 mM NaCl; 20 days	Sodium nitroprusside (SNP) and glucose solely increased Cys and GSH content by 86% and 79%, and 19% and 18%, respectively, whereas SOD, CAT, APX, and GR increased by 75% and 65%, 49% and 37%, 97% and 57%, and 60% and 57%, respectively. Combined SNP and glucose application increased the activity of these antioxidant enzymes (SOD, CAT, APX, and GR) by 138%, 61%, 271%, 127% and 44%, 17%, 119%, 23%, respectively, compared to the control and glucose-treated plants	Sehar et al. (2019)
C. sativus	200 mM NaCl; 7 days	H2S increased ASA content by 42.6% and GR activity by 9.1%. Reversed decreased SOD and POD activity	Jiang et al. (2019)
Brassica juncea	100 mM NaCl; 15 days	Nitric oxide increased SOD, CAT, APX, and GR activity by 91%, 33%, 114%, and 49%, respectively	Jahan et al. (2020)

Water deficit and simulated drought			
Zea mays cv. Run Nong 35, Wan Dan 13 and Dong Dan 80	Mild drought (80% FC), moderate drought (60% FC), and severe drought (40% FC)	Increased activities of APX, MDHAR, and DHAR by 24%, 13%, and 29% in Dong Dan. 80% and 16%, 11%, and 10% in Wan Dan 13, respectively, under severe drought. Higher SOD activity as well as AsA and DHA contents under moderate and severe drought in both maize hybrids	Anjum et al. (2017)
Glycine max and *G. tomentella*	Water deficit, flowering stage, 12 days	A substantially increased SOD and GR enzymes activities with the highest value during eighth day of stress treatment in *G. max*. A gradual increase in GR activity till the end of drought treatment was observed in *G. tomentella*	Hamim et al. (2017)
Brassica napus cv. Binasarisha-3	Osmotic stress (10% and 20% PEG), 48 h	MDHAR activity was higher under 10% PEG. DHAR activity increased under both stress level. GR and GST activity was higher by 26% and 23% and 25% and 31% at both stress level, respectively	Hasanuzzaman et al. (2017a, b)
Phaseolus vulgaris cv. Bn-150 (drought-tolerant) and Bn-16 (drought-sensitive)	Moderate drought (50% FC) and severe drought (0% FC), 14 days	Significantly increased total phenolic contents of Bn-150 by 223% and 265%, respectively, under moderate and severe drought. SOD, CAT, APX, and GR activities were increased in tolerant genotypes (Bn-150) than the sensitive one (Bn-16)	Kusvuran and Dasgan (2017)
Vigna radiata cv. BARI Mung-2	Osmotic stress (5% PEG), 48 h	Decreased AsA/DHA ratio by 54%. Increased APX and GR by 20% and 42%, respectively. Reduced CAT and MDHAR activity by 13% and 26%, respectively	Nahar et al. (2017)
B. napus cv. Binasarisha-3	Osmotic stress (10% and 20% PEG), 48 h	Moderate stress increased AsA content, GPX, and GST activity but reduced CAT activity, whereas severe stress enhanced APX activity but reduced MDHAR, DHAR, and GR activities. Both levels of stress increased GSH and GSSG contents by 31% and 26%; and 83% and 225%, respectively, compared to control	Hasanuzzaman et al. (2018a, b)
B. rapa cv. BARI Sharisha-15	Osmotic stress (20% PEG), 2 days	AsA and GSH contents increased by 10% and 72%, respectively. APX, GR, CAT, and GPX activity increased by 23%, 81%, 29%, and 26%, respectively	Bhuiyan et al. (2019)

(continued)

Table 6.2 (continued)

Plant species	Stress conditions	Antioxidant defense	References
Oryza sativa var. *japonica* cv. Nipponbare	Osmotic stress (20% PEG-6000), 5 days	Decreased SOD, APX, and CAT activities, but POD activity increased by 59% compared to control	Liu et al. (2019)
S. lycopersicum cv. Login 935	Drought stress (60% FC), 20 days	Enhanced SOD, CAT, and APX activities by 110%, 66%, and 77%, respectively. Increased AsA, GSH, and α-tocopherol contents by 81%, 93%, and 103%, respectively	Rady et al. (2020)
G. max	Osmotic stress (5%, 10%, and 15% PEG), 3 weeks	Highest activities of CAT, APX, and PPO were observed at mild osmotic stress (5% PEG), whereas increased SOD and POX activities were found at severe osmotic stress (15% PEG). Total phenol and tocopherol contents increased by 51%, 32%, and 44%, and 26%, 26%, and 21% at three levels of osmotic stress intensities, respectively, compared to control	Rezayian et al. (2020)
Toxic metals/metalloids			
Brassica napus cv. BINA Sharisha-3	0.5 and 1.0 mM $CdCl_2$, 2 days	Reduction of AsA content, whereas higher GSSG content and GST activity. APX and GR activity increased, but CAT, MDHAR, and DHAR activity reduced	Hasanuzzaman et al. (2017a, b)
V. radiata cv. BARI mung-2	0.5 mM $AlCl_3$, 2 and 3 days	AsA content reduced, but GSH and GSSG increased. The activity of SOD, GST, GPX, APX, and GR increased, but MDHAR, DHAR, and CAT decreased	Nahar et al. (2017)
Oryza sativa cv. BRRI dhan54	0.25 and 0.5 mM $NiSO_4 \cdot 7H_2O$, 3 days	64% lower AsA and 146% higher GSH content at 0.5 mM Ni stress. APX, MDHAR, DHAR, and GR activities increased by 114%, 116%, 31%, and 104% at 0.5 mM Ni stress, respectively	Hasanuzzaman et al. (2019a, b)
Pisum sativum	100 μM $NiCl_2$, 3 days	GSH accumulation increased by fivefold. SOD activity increased by 14-fold, CAT and APX activities both by sixfold, and GR activity by almost threefold	El-Amier et al. (2019)
P. sativum	100 μM $CdCl_2$, 3 days	GSH accumulation increased by threefold and GSSG by twofold. SOD activity increased by tenfold, CAT and APX activities both by eightfold, and GR activity by almost fourfold	El-Amier et al. (2019)

B. juncea cv. BARI Sharisha-11	0.5 and 1.0 mM CdCl2, 3 days	42% lower AsA and 200% higher DHA at severe stress, whereas 44% and 72% higher GSSG content under mild and severe stress, respectively. 44% higher SOD and 31% higher GPX activity at severe stress	Al Mahmud et al. (2018)
T. aestivum cv. Pradip	0.5 and 1.0 mM $Pb(NO_3)_2$, 2 days	APX activity increased, but MDHAR and DHAR decreased; GR increased initially and then declined. 35% higher SOD, 44% higher GST along with 31% lower CAT, and 28% lower GPX activities were reported	Hasanuzzaman et al. (2018a, b)
Extreme temperature			
Cicer arietinum (sensitive genotype: ICC14183, ICC5912; tolerant genotypes: ICCV07110, ICCV92944)	30/20, 35/25, 40/30, and 45/35 °C; 2 days for flower and 8 days for three leaves stage	Reduced APX (by 38–49% and 43–50% at 40/30 °C) and GR (by 30–46% and 44–49% at 45/35 °C) activity as well as AsA (by 13–18% and 28–32% at 40/30 °C), and GSH (by 24–33% and 37–44% at 45/35 °C) content in sensitive genotypes	Kumar et al. (2013a, b)
Cucumis sativus	35 ± 1 °C; 7 days	Improved SOD (by 16.6%), CAT (by 13%), APX (by 25.2%), GR (by 14.4%), and POD (by 35.4%) activity	Ding et al. (2016)
Sorghum bicolor	36/26 and 39/29 °C; until 7 days after full anthesis	In pollen, decreased the SOD (58–87%), CAT (44–56%), and POX (36–60%) activity. In pistil, decreased the SOD (59–77%), CAT (35–60%), and POX (42–78%) activity	Djanaguiraman et al. (2018)
Gossypium hirsutum	45/30 ± 2 °C; 120 days	Enhanced SOD and CAT activity	Sarwar et al. (2018)
O. sativa	38 °C; 5 days	Decreased the activity of SOD and CAT. Enhanced POD (by 32.1%) activity	Liu et al. (2019)
O. sativa cv. DM You 6188	12 °C; 6 days	Enhanced SOD (by 1.4%), CAT (by 1.58%), and GSH/GSSG (by 2.42-fold)	Han et al. (2017)
Calendula officinalis	4 °C; 24, 48, 72, 96, and 120 h	Elevated GR (161%), SOD (46%), and APX (82%) activity at 120 h	Jan et al. (2018)
Capsella bursa-pastoris	10 °C; 24, 48, 72, 96, and 120 h	Elevated GR (70%), POD (79%), and CAT (70%) activity at 120 h	Wani et al. (2018)
Citrus reticulata	1, −1, and −3 °C; 3 h	Enhanced CAT (1.35-fold) and APX (twofold) activities	Mohammadrezakhani et al. (2019)

(continued)

Table 6.2 (continued)

Plant species	Stress conditions	Antioxidant defense	References
Vitis vinifera	5 °C; 6, 12, 24, 48, and 72 h	Elevated GR (20.26%), DHAR (7.64%), and MDHAR (16.60%) activities with increased AsA (12.13%), DHA (7.89%), and GSH (56.09%) contents	Chen et al. (2019)
Waterlogging			
S. bicolor cv. JN01 and JZ31	Waterlogged soil, 12 days	Increased SOD (by 1.38- and 1.5-fold) and CAT (by 1.43- and 1.36-fold) in JN01 and JZ31, respectively	Zhang et al. (2019)
S. lycopersicum cv. Roma	Waterlogged soil, 15 days	AsA content reduced by 31%. SOD, CAT, and POD activities increased by 7%, 33%, and 57%, respectively, compared with control samples	Rasheed et al. (2018)
Sesamum indicum cv. BARI Til-4	Waterlogged soil, 2, 4, 6, and 8 days	GSH and GSSG increased by 45% and 150%, respectively, whereas AsA content decreased by 38% after 8 days WL. APX and MDHAR activity increased by 61% and 55%, but DHAR and GR activity reduced by 59% and 23%, respectively, after 8 days WL	Anee et al. (2019)
Deschampsia antarctica	Waterlogged soil, 7 days	Increment of CAT activity by 91%	Park and Lee (2019)
Hordeum vulgare cvs. TF57 and TF58	Waterlogged soil, 21 days	SOD, POD, and CAT activities increased in both WL-sensitive TF57 and WL-tolerant TF58 genotype	Luan et al. (2018)

response to drought stress, which resulted into drought-induced tolerance to oxidative stress. Akram et al. (2018) reported the increase in total phenolics and POD and CAT activities in the two *B. napus* cultivars under drought stress (60% FC, 21 days). A group of researchers studied the two *Sorghum bicolor* L. cultivars, M-81E (tolerant) and Roma (sensitive) and observed the increased H_2O_2 concentration in both M-81E and Roma, respectively, in contrast to control, when activities of SOD and APX increased respectively, thus improved tolerance to drought stress (Guo et al. 2018). Another study conducted by Hassan et al. (2020) reported decreased CAT activity but increased GPX activity under drought stress in *Triticum aestivum* cv. Sakha-94 (Hassan et al. 2020).

6.4.3 Antioxidant Defense in Plants Under Toxic Metals/Metalloids

Various investigations have demonstrated the positive correlation between tolerance to metals/metalloids toxicity with improved antioxidant activities for ROS detoxification and metal chelation (Table 6.2) (Gratao et al. 2019). Among major antioxidants, GST assists GSH to reduce toxicity to metals/metalloids on conjugation with them (Kumar and Trivedi 2018). In addition, GSH functions as a cytosolic precursor of phytochelatins (PC), binds to metals and allows the transport of compound into cell vacuole by catalyzing the transport of metal ions and other xenobiotics (Chakravarthi et al. 2006). Hasanuzzaman et al. (2019a, b) reported an increase in both the GSH and GSSG in rice seedlings under Ni stress, but under the application of exogenous Si, GSH content was further enhanced while GSSG level decreased, indicating the function of Si in upregulating GSH. Ahanger et al. (2020) reported an enhancement in both GSH and tocopherol content together with SOD, GST, and DHAR activities with elevated H_2O_2 and $O_2^{\bullet -}$ concentrations in *V. angularis* seedlings under Cd stress, while AsA levels and CAT activity were found to be reduced. On the contrary, activities of SOD, CAT, POX, and GR were increased with elevated levels of H_2O_2 under Cd stress in two *Mentha arvensis* genotypes indicating the induction of an antioxidant defense mechanism in response to Cd toxicity (Zaid et al. 2020). The authors also observed a further upregulation of antioxidant defense activity after application of gibberellic acid, triacontanol, or SA.

6.4.4 Antioxidant Defense in Plants Under High Temperature

Like other abiotic stress factors, the antioxidant defense mechanism is also activated to cope with high temperature (HT) stress in plants (Table 6.2) (Ding et al. 2016), but in general antioxidant activity varies between species as well as tolerant and sensitive genotypes (Hasanuzzaman et al. 2012). According to Kumar et al. (2013a, b), APX and GR activities were considerably reduced in sensitive chickpea cultivars with approximately twofold H_2O_2 increase under high temperature conditions compared to tolerant genotypes. Liu et al. (2019) reported reduced activities of SOD and CAT with subsequent decreased OsSOD, OsCAT, and OsAPX2 expression, causing elevated levels of H_2O_2 in germinating rice seeds in response to high temperature stress. Sarkar et al. (2016) reported increased activity of CAT and POX in wheat in response to high temperature stress. In another study, Zandalinas et al. (2017) reported enhanced GSH and AsA levels in Carrizo citrange under HT stress (40 °C) with enhanced SOD and CAT activities in Cleopatra mandarin.

6.5 Plant Antioxidant Defense System

Antioxidants have been shown to either directly or indirectly scavenge reactive oxygen species (ROS) and/or inhibit ROS generation (Carocho and Ferreira 2013). Nonenzymatic antioxidants such as tocopherols, phenolic compounds (PhOH), flavonoids, alkaloids, AsA, GSH as well as several nonprotein amino acids make up the plant antioxidant defense system (Hasanuzzaman et al. 2019a, b). In order to limit the ROS production, the nonenzymatic antioxidants operate in a coordinated approach with antioxidant enzymes such as SOD, POX, CAT, APX, MDHAR, DHAR, GR, GPX. TRX, GST, PRX, and polyphenol oxidase (PPO) (Fig. 6.2) (Laxa et al. 2019). In plant defense system, the catalytic reactions occur in the cellular organs and between enzymatic and nonenzymatic antioxidants as represented in Table 6.1. In plants, the SOD enzyme plays a crucial role linked directly to the stress tolerance and has been considered as first line of defense by converting O_2 into H_2O_2 (Table 6.1) (Del Río et al. 2018). This generated H_2O_2 further converts into H_2O with the help of enzymes such as CAT, GPX, and APX or it can be catalyzed in the AsA-GSH cycle. The AsA-GSH cycle, also known as the Asada-Halliwell cycle, considered as a major antioxidant defense system in plants and plays a crucial role to catalyze H_2O_2. The cycle consists of four antioxidant key enzymes such as APX, MDHAR, DHAR, and GR as well as low molecular weight nonenzymatic antioxidants like AsA and GSH. In plants, the AsA-GSH cycle plays critical function in the antioxidant defense system by minimizing H_2O_2 concentration and maintaining the redox homeostasis (Fotopoulos et al. 2010). Furthermore, detoxification of H_2O_2 and xenobiotics requires two vital enzymes such as GPX and GST (Fig. 6.2) (Hasanuzzaman et al. 2018a, b). Among the nonenzymatic antioxidants, AsA and GSH are the most abundant soluble antioxidants in the higher plants (Foyer and Noctor 2011). These play an important role as electron donors and actively scavenge ROS via the AsA-GSH cycle (Hasanuzzaman et al. 2019a, b). In addition, the concentration of cellular ROS lowers by interaction of beta-carotene with OH, O_2, and ROOH (Kapoor et al. 2019).

6.5.1 Nonenzymatic Antioxidants

In plants, there are a number of nonenzymatic antioxidants playing an important role in the ROS scavenging. Among the nonenzymatic antioxidants, ascorbate contributes momentous role to scavenge ROS molecules through AsA-GSH cycle by donating electrons and endures stability due to delocalization of electrons caused

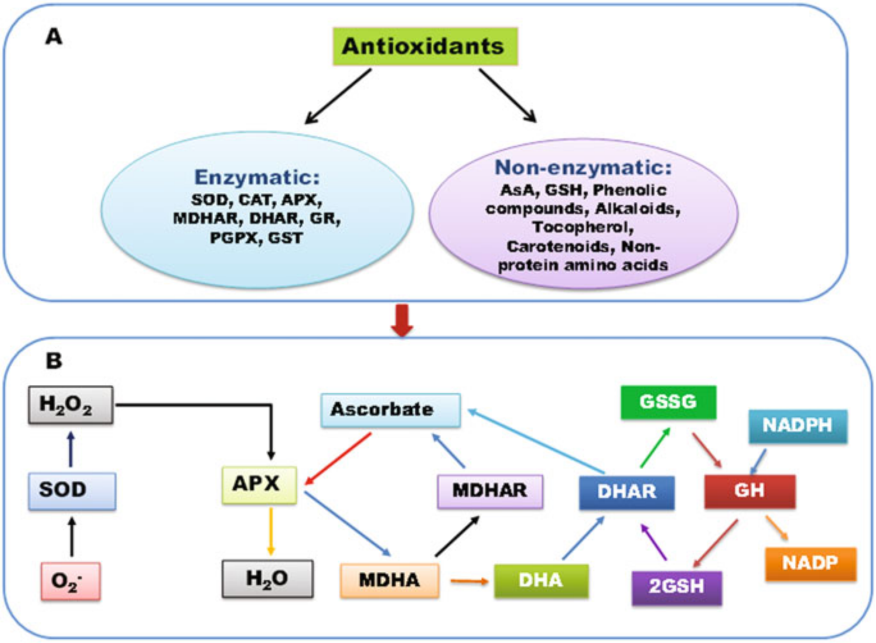

Fig. 6.2 Overview of plant antioxidant defense system: (**a**) types of antioxidants and (**b**) combined mechanisms of enzymatic and nonenzymatic antioxidants. See the text for a more detailed description. APX, ascorbate peroxidase; AsA, ascorbate; CAT, catalase; DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; GPX, glutathione peroxidase; GR, glutathione reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; GST, glutathione S-transferase; H_2O_2, hydrogen peroxide; MDHA, monodehydroascorbate; MDHAR, monodehydroascorbate reductase; NADPH, nicotinamide adenine dinucleotide phosphate; $O_2^{\bullet-}$, superoxide anion; POX, peroxidases; PRX, peroxiredoxins; R, aliphatic, aromatic, or heterocyclic group; ROOH, hydroperoxides; –SH, thiolate; SOD, superoxide dismutase; –SOH, sulfenic acid; TRX, thioredoxin; X, sulfate, nitrite, or halide group

by the resonance phenomenon between the two forms (Hasanuzzaman et al. 2019a, b). AsA regenerates α-tocopherol (Vitamin-E) from tocopheroxyl radical by scavenging •OH and $O_2^{\bullet-}$ radicals and also regulates a number of phytochrome biosynthesis production pathways (Naz et al. 2016). Another important nonenzymatic antioxidant such as GSH also scavenges ROS molecules and maintains homeostasis (Hasanuzzaman et al. 2019a, b). Tocopherol, on the other hand, is an important component of the antioxidant defense system that protects the chloroplast and keeps photosynthesis by scavenging ROS, mainly $O_2^{\bullet-}$ and •OH (Kumar et al. 2013a, b). Another group of nonantioxidant molecules called carotenoids also play an important role to protect light harvesting complex proteins and thylakoid membrane integrity by scavenging free radicals (Terzi et al. 2014). Some other low molecular compounds such as flavonoids, particularly dihydroxy B-ring substituted flavones and flavanols, also play a promising role for scavenging ROS free molecules and reducing lipid peroxidation and induced cell damage (Tiong et al. 2013). Furthermore, abiotic stressors increase the expression of genes which are involved in activated antioxidant defense system and production of flavonoids (Mehla et al. 2017). One more important group of nonenzymatic antioxidants called phenolic acids are made up of hydroxybenzoic and hydroxycinnamic acids, which function as chelators and scavengers of free radicals, particularly $O_2^{\bullet}$, $^{\bullet}OH$, ROOH, and $ONOO^-$ (Carocho and Ferreira 2013). As free radical scavengers, alkaloids also decrease H_2O_2 in the cells and induce oxidation in the plants (Tiong et al. 2013). Nonprotein amino acids (gamma-aminobutyric acid, ornithine, and citrulline) are also thought to be nonenzymatic antioxidants (Vranova et al. 2011).

6.5.2 Antioxidant Enzymes

Antioxidant enzymes are a group of enzymes which scavenge ROS molecules in plants. Among these the most critical antioxidant enzyme called SOD (EC 1.15.1.1) is characterized into three types, namely Cu/Zn-SOD, Fe-SOD, and Mn-SOD, which lead the frontline defense enzyme in the antioxidant defense system in plants (Berwal and Ram 2018; Rai et al. 2017). This enzyme dismutates the $O_2^{\bullet}$ free radical into H_2O_2 and prevents the production of •OH (Gill et al. 2015; Rai et al. 2018). Another important antioxidant enzyme known as catalase (EC 1.11.1.6) is a tetrameric heme-containing enzyme for ROS detoxification in the antioxidant defense system. A research study concluded that this enzyme can catalyze 26 million H_2O_2 molecules into H_2O in one minute (Mehla et al. 2017). Peroxidase (EC 1.11.1.7) primarily oxidizes PhOH to produce phenoxyl radical (PhO•), also known as QA, in which H_2O_2 takes an electron and is transformed to H_2O. Phenoxyl radical (PhO•) cross-interacts producing suberin, lignin, and quinines in the absence of AsA but in the presence of AsA, PhO• reacts with AsA, resulting in monodehydroascorbate (MDHA) and, eventually, DHA (Fig. 6.2 and Table 6.2) (Jovanovic et al. 2018).

Polyphenol oxidase (EC 1.14.18.1) is one more antioxidant enzyme to scavenge ROS molecules. The enzyme is predominantly located in the chloroplast's thylakoid membrane and can directly affect the photosynthesis process. In the ROS scavenging reaction, the enzyme polyphenol oxidase may interact with the peroxidase or water-water cycle. Another important function of PPO is that it oxidizes PhOH to QA and H_2O using available O_2 (Boeckx et al. 2015). Plant cells contain one more antioxidant enzyme known as AsA-dependent APX (EC 1.11.1.1) which is present in various isoforms (mitochondrial APX (mtAPX), chloroplastic APX (chlAPX), and cytosolic APX (cAPX)).The APX is the only enzyme capable of scavenging H_2O_2 in the chloroplasts of plants because CAT enzyme is absent and peroxisomal/glyoxysomal APX (including mAPX) and other H_2O_2 help to produce monodehydroascorbate (MDHA) through AsA-GSH cycle in plants (Pandey et al. 2017). In plants, the produced MDHAR (EC 1.6.5.4), a NADPH-dependent flavin adenine dinucleotide enzyme found in two isoforms found in diverse cellular sites (Hasanuzzaman et al. 2019a, b). The enzyme plays an important role in plant life by converting MDHA to AsA. By phenoxyl radical reduction, monodehydroascorbate reductase enzyme contains a thiol group which regenarates AsA (García-Caparrós et al. 2019). Monodehydroascorbate reductase is further reduced to DHA nonenzymatically, which is then recycled to AsA by the activity of GSH-dependent DHAR (EC 1.8.5.1) (García-Caparrós et al. 2019). Furthermore, GSH is oxidized to GSSH, which is then reduced to GSH by the NADPH-dependent GR (EC1.6.4.2) enzyme, which is also an important enzyme for redox homeostasis regulation (Couto et al. 2016).

In plants, GPX (EC 1.11.1.9) is a nonheme-containing POX family antioxidant enzyme with a highly reactive thiol group that scavenges H_2O_2, reducing lipids, and organic acids via GSH and TRXs (Bela et al. 2015). GST (EC 2.5.1.18) metabolizes xenobiotics (particularly herbicides and other pharmaceutically active compounds) and transports them into plant vacuoles by conjugating GSH and electrophilic substrates at its active sites (Xu et al. 2015; Christou et al. 2016). GST enzyme also plays an important role in peroxide breakdown, hormone production and stress signaling as well as GPX activity acceleration (Nianiou-Obeidat et al. 2017). Another critical antioxidant enzyme in plants which plays an important role in ROS scavenging is TRX (EC 1.8.1.9). The enzyme has different isoforms (f, m, h, o, y, and z) and contains an enzyme active redox site known as (WCG/PPC). This enzyme reduces disulfide bonds into dithiol by H_2O_2 and regulated target proteins quicker than GSH enzyme or dithiothreitol (Calderón et al. 2018). In chloroplast organelle of plants, the two isoforms of TRX enzyme (TRXx and TRXy) regulates the redox homeostasis by reducing 2-Cysteine (Cys) PRX, whereas TRXo1 activates antioxidant defense in mitochondria by interacting with PRX and sulfiredoxin (Sevilla et al. 2015).

Another thiol-based PRX enzyme (EC 1.11.1.15), a POX-like antioxidant enzyme in plant cells, neutralizes peroxides (H_2O_2 and ROOH) in the cytosol, chloroplasts, mitochondria, and nucleus (Liebthal et al. 2018). PRXs enzymes are thiol-dependent (GSH or any other thiol group) and have ability to reduce diverse organic and inorganic peroxides and also play an important role in regulation of ROS molecules (Fig. 6.2 and Table 6.1) (Hasanuzzaman et al. 2017a, b).

6.6 Reactive Oxygen Species Signaling in Plant Defense

Excess ROS are generated in response to various abiotic stresses as a result of the disturbance of various metabolic activities and physiological disorders (Choudhury et al. 2017). The antioxidant defense pathways for example, AsA-GSH pathway uses energy in the form of NADPH, and once this energy is used up, these pathways would be unable of evading ROS toxicity (Choudhury et al. 2017). Though, the functions of ROS (especially H_2O_2) in plant stress biology came into the attention at the end of the twentieth and the beginning of the twenty-first century. Few scientific groups identified H_2O_2 as a signaling molecule, which induces acclimation processes and increases tolerance to various environmental stresses (Neill et al. 2002). Reactive oxygen species evolved in the chloroplast under stress may divert electrons from the photosynthetic apparatus inhibiting overload of the antenna and consequent damage. Reactive oxygen species also guard mitochondria in a same way (Asada 2006). Cell wall peroxidase may contribute to generation of ROS in relation to signaling where H_2O_2 uses Ca^{2+} and MAPK pathway as a downstream signaling cascade. In addition, phytohormones, particularly ethylene (ET) and abscisic acid (ABA), are implicated in various responses to different environmental stresses via cross-talk with ROS and thus augment stress tolerance, which indicates the dual role of ROS under various stresses (Kar 2011). Apart from signal transduction and communication with hormones, ROS can also involve in metabolic fluxes under abiotic stresses, which mutually direct plant acclimation processes where redox reactions check transcription and translation of proteins and enzymes related to stress adaptation, eventually defending plant cells from injury (Choudhury et al. 2017). Moreover, H_2O_2 controls NO and Ca^{2+} signaling pathways, which manage plant growth and development, and other cellular and physiological responses under varied abiotic stresses (Janicka et al. 2019). Since endogenous H_2O_2 plays pivotal role in enhancing abiotic stress tolerance, exogenous application of H_2O_2 is gaining interest and has proved its efficiency at a large scale (Savvides et al. 2016; Hasanuzzaman et al. 2017a, b). In Table 6.3, we have mentioned some key findings highlighting the effect of H_2O_2 treatment in response to various abiotic stress conditions. Furthermore, ROS interact with RNS, RSS, and RCS under stress and collaborate in signal transduction pathways (Kaur et al. 2019a, b). Antioxidant levels in the cell may vary in order to alter generation of ROS and play a specific role to signaling (Hancock and Whiteman 2016). In contrast, RSS affect the generation, perception, and further signaling of ROS and RNS (Kaur et al. 2019a, b), whereas RCS act downstream of ROS as signal mediators in response to a variety of stresses (Biswas et al. 2019).

6.7 Cross-talk of Reactive Nitrogen, Sulfur, and Carbonyl Species with ROS

Apart from ROS, other reactive species are produced in plant cells during adverse environmental conditions, including RNS, RSS, and RCS (Fig. 6.3) (Nawaz et al. 2019). All these reactive species are involved in a molecular cross-talk and have a particular role in cellular signaling cascades [23]. Therefore, the following subsections discuss the intimate relationship among ROS, RNS, RSS, and RCS. Cross-Talk of Reactive Nitrogen, Sulfur, and Carbonyl Species with ROS. Apart from ROS, other reactive species are produced in plant cells during adverse environmental conditions, including RNS, RSS, and RCS (Fig. 6.3) (Nawaz et al. 2019). All these reactive species are involved in a molecular cross-talk and have a particular role in cellular signaling cascades. Therefore, the following subsections discuss the intimate relationship among ROS and RNS.

Table 6.3 Effect of exogenous H_2O_2 in plants under different abiotic stress factors

Plant species	Stress condition	H_2O_2 treatments	Positive effects	References
Triticum aestivum cv. Zhengmai no. 004	150 mM NaCl; 2 days	Cotreatment; 0.05 μM, 2 days	Decreased MDA content and $O_2^{\bullet-}$ generation. Increased GSH and carotene content by 21% and 33%, respectively. Increased SOD, POD, CAT, and APX activity. Increased growth and biomass	Li et al. (2011)
Cucumis sativus cv. Jinchun no. 4 and Lvfeng no. 6	Osmotic stress; (10% PEG 6000); 2 days	Pretreatment as spraying; 1.5 mM	Decreased MDA and H_2O_2 content. Increased AsA and GSH content. Increased activity of GPX, CAT, APX, GR, MDHAR, and DHAR	Liu et al. (2010)
C. sativus cv. Jinchun no. 4	Low light; 100 mol m^{-2} s^{-1}; 144 h	Pretreatment as spraying; 1.5 mM	Decreased $O_2^{\bullet-}$, H_2O_2, and MDA content. Increased CAT, SOD, APX, GR, MDHAR, and DHAR activity	Zhang et al. (2011)
Vigna radiata L. Wilczek) cv. SML-668	Cu ($CuSO_4 \cdot 5H_2O$); 50 and 100 mg kg^{-1} of soil	Spraying; 2.5 mM	Increased relative water content (RWC) and SPAD value. Increased pro content. Enhanced activity of SOD and CAT. Increased growth	Fariduddin et al. (2014)
Zea mays	Osmotic stress (3% PEG 6000), 12 h	Pretreatment; 10 mM, 6 h	Decreased water loss, MDA, and H_2O_2 content. Increased levels of soluble sugars and proline. Increased Put, Spd, and Spm content by 72%, 106%, and 68%, respectively, over control	Terzi et al. (2014)
Glycine max cv. Merrill 537	Drought; withholding irrigation, 4 and 7 days	Foliar spray; 1 mM, 3 days	Improved water status, pigment content, and alleviated lipid peroxidation. Decreased MDA and H_2O_2 content. Increased activity of SOD (by 93% and 190%), CAT (by 49% and 120%), APX (by 106% and 194%), and GR (by 31% and 229%) on day 4 and 7 of the drought period, respectively, over control	Guler and Pehlivan (2016)
C. sativus L.	Drought; 60 ± 5% FC	Spraying; 1.5 mM (100 mL pot^{-1})	Decreased MDA content and ROS ($O_2^{\bullet-}$, H_2O_2) generation. Increased activity of SOD and POD. Increased soluble sugar and proline content. Increased chl and RWC	Sun et al. (2016)

(continued)

Table 6.3 (continued)

Plant species	Stress condition	H_2O_2 treatments	Positive effects	References
Brassica napus cv. Binasarisha-3	Cd; 0.5 mM (mild) and 1.0 mM (severe) $CdCl_2$; 2 days	Pretreatment; 50 µM, 24 h	Decreased MDA content (by 23% and 25%) under both Cd toxicity levels, respectively. Decreased H_2O_2 content. Increased AsA (by 32% and 30%); GSH content (by 38% and 25%) under both Cd stresses, respectively. Enhanced GSH/GSSG ratio. Increased activity of APX (by 40% and 39%), DHAR (by 77% and 67%), GR (by 36% and 79%), GST (by 44% and 43%), CAT (by 79% and 47%), and glyoxalase II (by 47% and 55%) under both Cd stresses, respectively. Enhanced GPX activity (by 40%) under severe stress and glyoxalase I activity (by 35%) under mild stress	Hasanuzzaman et al. (2017a, b)
T. aestivum cv. Fsd-2008 and S-24	Drought; withholding irrigation, 6 weeks	Seed priming; 1.5 mM, 16 h	Decreased MDA and H_2O_2 content. Enhanced the activity of SOD, CAT, and POD. Increased photosynthetic pigments. Increased GB and Pro content	Habib et al. (2020)
Oryza sativa cv. BRRI dhan29	Osmotic stress (15% PEG-6000)	Foliar spray; 5 and 10 mM	Decreased MDA and H_2O_2 content. Increased activity of CAT and GPX. Protected photosynthetic pigments	Sohag et al. (2020)

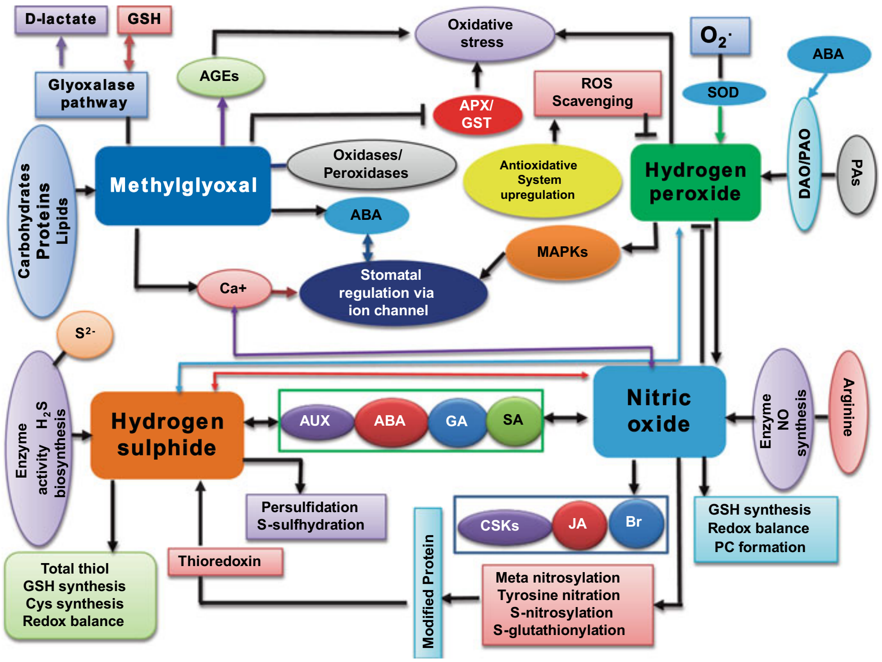

Fig. 6.3 Cross-talk among vital ROS (H_2O_2), RNS (NO), RSS (H_2S), and RCS (MG) in plant cells for oxidative stress and defense response in plants. APX, ascorbate peroxidase; AUX, auxin; ET, ethylene; ABA, abscisic acid; ROS, reactive oxygen species; GSH, reduced glutathione; JA, jasmonates; MAPKs, mitogen-activated protein kinases; SA, salicylic acid; AEGs, advanced glycation end products; PAs, polyamines; MG, methylglyoxal; NO, nitric oxide; H2S, hydrogen sulfide. Dotted lines represent activation/enhancement

6.8 Transgenic Approach in Enhancing Antioxidant Defense in Plants

From the last 20 years, transgenics have been extensively used to improve plants under oxidative stress. Therefore, transgenic plants can be engineered to improve abiotic stress tolerance and the antioxidant enzyme defense mechanism activity. Here, we have highlighted transgenic plants with enhanced responses of antioxidant defense systems under several stresses which are presented in Table 6.4. Kiranmai et al. (2018) observed lower concentrations of MDA, H_2O_2, and $O_2^{\bullet-}$ and increased activities of SOD and APX in groundnut due to overexpression of *MuWRKY3* gene under drought stress. Another study conducted by Sun et al. (2018) demonstrated the enhanced drought stress tolerance and activities of CAT and POD in transgenic apple cultivars due to overexpression of *MdATG18a*. Results also denoted that tolerance to stress was improved because of a high frequency of autophagy and inhibition of oxidative damage. Kumar et al. (2020) demonstrated that chickpea

Table 6.4 Antioxidant defense systems and their expression pattern in crop plants

Stress condition and duration	Plant system	Source plant	Gene	Impact on antioxidant defense systems	References
Salinity					
0, 50,100, and 150 mm Nacl; 7 and 15 days	*Solanum tuberosum*	*Potentilla atrosanguinea* and *Rheum australe*	PaSOD and RaAPX	Enzyme activities are enhanced in transgenic plants as of SOD by two- to sixfold in PaSOD and one- to threefold in double transgenic plants (DTP); APX by 5-fold to 11-fold in APX and four- to eightfold in DTP	Shafi et al. (2017)
100, 200, 400 mm; 1, 5, 10, 15 days	*Chrysanthemum*	*Dendranthema grandiflorum*	*DgNAC1*	Enzyme activities are enhanced in transgenic plants as of SOD by two-, CAT by two-, and POD by threefold	Wang et al. (2017)
150 mM NaCl; 3, 6, 9, 12, and 24 h	*Arabidopsis thaliana*	*Vitis vinifera*	*VvWRKY30*	Enzyme activities are significantly enhanced in transgenic plants, i.e., POD, CAT, and SOD	Zhu et al. (2019)
150 or 200 mM NaCl, till germination	*Glycine max*	*Glycine max*	*GmMYB84*	Enzyme activities are significantly enhanced in transgenic plants, i.e., SOD, POD, and CAT	Zhang et al. (2020a, b)
Water deficit and simulated drought					
Osmotic stress (20% PEG); 1, 3, 6 12, 24, and 48 h	*Nicotiana tabacum*	*Spinacia oleracea*	*SoCYP85A1*	Overexpressed lines improve the activity of POD by 1.3–1.5 and SOD by 1.36–1.39-fold	Duan et al. (2017)
Withholding water for 14 and 21 days	*Malus domestica*	*Malus domestica*	*MdATG18a*	Enzyme activities are enhanced in transgenic plants as of CAT and POD by 1.57–2.05-fold in overexpressed lines	Sun et al. (2018)
Withholding water till the wilting stage	*Arachis hypogaea*	*Macrotyloma uniflorum* Lam. Verdc.	*MuWRKY3*	Enzyme activities are enhanced in transgenic plants as of SOD by three- to five- and APX by three- to sevenfold	Kiranmai et al. (2018)
Osmotic stress (15% PEG); 60 days	*N. tabacum*	*Zea mays*	*ZmSO*	Overexpressed lines increase the activity of GSH 64% and 88%	Xia et al. (2018)

Osmotic stress (15% and 25% PEG); 7 days	*A. thaliana*	*Cicer arietinum*	*CaMT*	Enzyme activities are enhanced in transgenic plants as of APX 488%, POD 135%, GPX 134%, and GRX 186%	Dubey et al. (2019)
Withholding water for 12 days	*A. thaliana*	*Malus prunifolia*	*MpDGK2*	Enzyme activities are enhanced in transgenic plants, i.e., CAT, APX, and POD	Tan et al. (2020)
Drought stress	*Solanum Lycopersicon*	*Tomato*	*Antioxidant gene*	Enhanced the SOD, APX gene expression	Rai et al. (2018)
Toxic metals/metalloids					
As(III) [5 and 10 μM ($NaAsO_2$)], As(V) [50 and 100 μM (Na_2HAsO_4)], Cd [30 and 50 μM ($CdCl_2$)] and Cr($K_2Cr_2O_7$)	*A. thaliana*	*Oryza sativa*	*OsSultr1;1*	Enzyme activity is enhanced in transgenic plants, i.e., GSH with As(III) toxicity	Kumar et al. (2019)
300 μM $CdCl_2$ and 300 μM $NiCl_2 \cdot 6H_2O$; 1, 12, 24, and 48 h	*N. tabacum*	*Salicornia brachiate*	*SbMYB15*	Enzyme activities are enhanced in transgenic plants as of CAT and SOD and also increase the expression of Mn-SOD at 100 μM (1.69-fold) and 300 μM (3.2-fold) of CdCl2 and CAT1 by 62.19- and 9.8-fold at 100 and 300 μM	Sapara et al. (2019)
Extreme temperature					
45 °C; 0.5, 1, 2, 3, 6, 9, 12, and 24 h	*N. tabacum*	*Triticum aestivum*	*TaFBA1*	Enzyme activities are enhanced in transgenic plants, i.e., SOD, POD, and APX, while CAT activity was decreased under heat stress	Li et al. (2018)
48 °C; 6 h	*M. domestica*	*M. domestica*	*MdATG18a*	Enzyme activities are enhanced in transgenic plants, i.e., SOD, POD, CAT, AsA, and GSH, whereas a decreased ratio of GSH/GSSG was reported	Huo et al. (2020)

(continued)

Table 6.4 (continued)

Stress condition and duration	Plant system	Source plant	Gene	Impact on antioxidant defense systems	References
4 °C; 5 days	*Solanum lycopersicum*	*A. thaliana*	*AtDREB1A*	Enzyme activities are enhanced in transgenic plants as of SOD by 29.49% and CAT by 21.34%	Karkute et al. (2019)
4 °C; 6, 12, 24, 36, and 48 h	*S. tuberosum*	*S. tuberosum*	*StSOD1*	Enzyme activities are enhanced in transgenic plants as of SOD by 1.38-, POD by 1.24-, and CAT by 1.37-fold	Che et al. (2020)
Waterlogging					
2 cm waterlogging; 3, 6, 12, 24, and 72 h	*A. thaliana*	*Brassica napus*	*BnERF2.4*	Enzyme activities are enhanced in transgenic plants, i.e., SOD, POD, and CAT	Lv et al. (2016)
Soil–atmosphere interface for 1 weeks	*A. thaliana*	*Mentha arvensis*	*MaRAP2–4*	Enzyme activities are enhanced in transgenic plants, i.e., CAT, GPX, and SOD	Phukan et al. (2018)
5 cm waterlogging; 24 and 48 h	*A. thaliana*	*Dioscorea alata*	*DaAPX*	Enzyme activity is enhanced in transgenic plants, i.e., APX but no significant effect on CAT	Chen et al. (2019)
3 cm standing water; 14 days	*Chrysanthemum morifolium*	*Chrysanthemum morifolium*	*CmSOS1*	Overexpressed plants enhance the activities of SOD and CAT by 171%	Wang et al. (2019)
Overexpressed plants enhance the activities of SOD and CAT by 171%	*A. thaliana*	*Hordeum vulgare*	*HvERF2.11*	Enzyme activities are enhanced in transgenic plants as of SOD by 55%, 48%, and 45%, POD by 64%, 65%, and 70%, CAT by 2.2%, 2.1%, and 2.1%, alcohol dehydrogenases by 2.1-, 2.3-, and 1.9-fold in three transgenic lines, respectively	Luan et al. (2018)

CaGrx gene was overexpressed in *A. thaliana* with maximal activities of GRX, GR, GPX, GST, and APX under heavy metal stress in comparison to controls, while activities of CAT, SOD, and MDHAR were also considerably enhanced. Authors recommended that CaGrx can be an appropriate candidate gene to surmount metal stresses in other crops as well (Kumar et al. 2020). Karkute et al. (2019) reported the increased activities of SOD, CAT, and POD and in turn tolerance to chilling stress due to overexpression of *A. thaliana AtDREB1A* gene in tomato. They observed 29% and 21% increase in activities of SOD and CAT respectively in transgenic plants, demonstrating better chilling stress tolerance. Che et al. (2020) showed that the activities of SOD, POD, and CAT were enhanced on overexpression of the potato *StSOD1* gene during cold stress and enhanced cold tolerance in transgenic potato plants. Similarly, Wang et al. (2019) revealed the overexpression of *CmSOS1* gene increases SOD and CAT by 171% in transgenic Chrysanthemum plants under waterlogging conditions.

6.9 Conclusions and Future Perspectives

Abiotic stresses are major limiting factors that affect growth and development of plants all over the globe. Consequently, there is a need to decipher the physiological, biochemical, molecular, and cellular abiotic stress response mechanisms and tolerance and to establish potential mitigation approaches that would lead to global food and agricultural sustainability. Abiotic stresses cause ROS accumulation, which leads to oxidative injury in plants. In the beginning, ROS were believed to cause toxicity and considered as outcome of aerobic metabolism, present in some subcellular compartments. The ROS metabolism is essential in growth, development, and adaptation of crop plants under various environmental stresses. The generation and scavenging of ROS are of utmost importance to plant defense processes. In order to enhance resistance to various abiotic stresses, modulation and overexpression of candidate genes governing production of various ROS-detoxifying enzymes are extensively used. Nonenzymatic antioxidant systems are known to play dynamic role in maintaining equilibrium between detoxification and ROS generation in plants under stressful conditions. Remarkably, ROS are well-known to play a dual part in plant biology owing to molecular cross-talk with other signaling molecules for example RNS, RSS, and RCS. On the basis of previous works, ROS is incredibly essential player for different biological mechanisms and are well-known for its signaling role at low concentrations. On the other hand, ROS toxicity explicitly destroys cells via oxidative stress as a result of ROS-activated machinery accountable for cellular degradation. Besides, there exists a correlation between ROS, RCS, RSS, and RNS and metabolic activities in normal and stressed conditions; nevertheless, a few reports have addressed these interactions. Both ROS and RNS can generate oxidative and nitrosative stress exclusively or in concert cause nitro-oxidative stress although both are also involved in signaling cascade of higher plant species principally under harsh environment. Alternatively, both ROS and RSS signaling pathways are indistinguishable and signal via interaction with Cys, but the RSS signaling seems to be more widespread in comparison to ROS signaling. On the contrary, RCS can maintain metabolism of ROS as these molecules are direct outcome of oxidative stress and have the capability to operate as its sensors. Thus, these four reactive molecules possibly will be the novel gateway of attention for the plant scientists. Even though amassing of information regarding signaling pathways of such reactive molecules has been accelerated over the period of time, more comprehensive research is desirable to illuminate their roles in plant stress biology. With the latest advances in molecular and genetic techniques, considerable advancement has been made in enhancing plant stress tolerance through transgenics with improved activities of antioxidant enzymes. Based on the available literature, there is a need to identify and report candidate genes that can considerably enhance the tolerance and yield of transgenic plants under stressful environments. Additionally, chemical priming is a smart way to genetic engineering so as to accomplish similar targets, often through the regulation of the antioxidant defense apparatus. At some point, systems biology approaches such as genomics, transcriptomics, proteomics, and metabolomics may possibly help introducing novel alternatives for the improving plant stress tolerance. Integrating abovementioned approaches can be employed to identify key and stress-related regulators, genes, proteins, and metabolites. Moreover, identification and exploitation of pathways related to ROS-detoxifying regulators could be improved to produce genotypes tolerant to abiotic stresses. As we know, plants undergo a wide range of stresses simultaneously; therefore, identification of genes that can confer multiple abiotic stress tolerance is of utmost importance. Also, state-of-the-art genome-editing technologies such as CRISPR/Cas system could modify the plant genome through the development of mutants with single or multiple genes, e.g., ROS-detoxifying regulators for sustainable growth and development in plants and to improve the antioxidant defense mechanisms. Recently, speed breeding has also come to light as a powerful means to enhance the plant growth and development under desired circumstances. Thus, in order to save time plant genome editing could be integrated with speed breeding to generate transgenic plants with induced antioxidant potential that are tolerant to different stresses and will thus contribute to feed ever-growing population and to guarantee global food security.

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