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Oxidative Stress and Antioxidant Metabolism under Adverse Environmental Conditions: a Review

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Abstract

Reactive oxygen species (ROS) originate as a natural byproduct in standard metabolism of oxygen activities. The principal sites of ROS generation in the cell are apoplast, mitochondria, chloroplasts, and peroxisomes. These ROS can induce cellular injuries by proteins oxidation, lipid peroxidation, and DNA damage, which finally may result in plant cellular death. Under regular circumstances, there is a steadiness between generation and elimination of ROS, but this balance is hampered by different biotic and abiotic stress factors such as exposure to heavy metals, high and low-light conditions, pathogens, insects and temperature extremes, resulting in a high generation of ROS which should be counteracted by the antioxidant machinery in cells. The antioxidant system of defense is composed by two groups: (i) Enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), general peroxidases (PRX) (e.g. guaiacol peroxidase GPX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR); (ii) Non-enzymatic antioxidants such as ascorbic acid (AA), reduced glutathione (GSH), α-tocopherol, carotenoids, plastoquinone/ubiquinone and flavonoids. These two groups of metabolites and enzymes work together with the main aim of ROS scavenging, but also in determining plant signaling, immune response, and plant growth and development. Finally, the molecular genetics of ROS genes and related metabolic pathways are briefly outlined, including gene isoforms, cellular localization,

detection methods used and interactions amongst them. This information is crucial in better understanding and designing procedures for plants´stress tolerance; leading to a better management of agricultural plants under challenging and changing climatic conditions and food security.

Keywords Abiotic and biotic stress · DNA damage · Lipid peroxidation · Molecular genetics · Protein oxidation · Reactive oxygen species (ROS) · Stress response

Introduction

The appearance of reactive oxygen species (ROS) as undesirable byproducts dates back to 2.7 billion years when molecular oxygen (O_2) was introduced into the Earth's atmosphere via photosynthesis (Singh et al., 2016a). It originated through membrane-linked electron transport processes, redox cascades, and metabolic pathways as a natural product of the normal oxygen metabolism, whose generation is exacerbated under adverse conditions. However, the potential for cellular damage from the production of elevated ROS has been moderated through evolutionary pressure to develop and expand a range of ROS scavenging mechanisms. Redox balanceand ROS homeostasis are considered amongst the earliest symptoms following fluctuations in environmental conditions (Berens et al., 2017; Das & Roychoudhury, 2014). In addition, it is well-known that modifications in redox balance and the maintenance of ROS homeostasis are the first marks under changing environmental conditions (Nafees et al., 2019; Waszczak et al., 2018). This capacity of detection of changes in parameters and the corresponding signals are crucial for the regulation of the metabolism from tissue level until subcellular compatments (Nafees et al., 2019). ROS are produced mainly in root and bud meristems and leaves; and in different organelles in cells such as the apoplast, mitochondria, chloroplasts and peroxisomes. Under an increase of ROS, the attendance of antioxidative compounds in these cellular compartments is essential for significant ROS detoxification and continuous cellular existence (Evans et al., 2016; Liu et al., 2016; Pucciariello & Perata, 2017; Sies et al., 2017; Sies, 2018). The last findings have reported reactive oxygen species participates as essential signals since they are involved in a wide range of biomolecules reactions and even in the necrosis and plant death (Nafees et al., 2019). On the other hand, it has also been reported that reactive oxygen species are crucial in several biological processes as well as in the modification of signal transduction pathways and gene expression (Dalton et al., 1999; Nafees et al., 2019).

An increase in the production of ROS such as: superoxide radical ($O_2^{\bullet-}$), singlet oxygen ($^1O_2$), hydroxyl radical ($^*OH$) and hydrogen peroxide (H_2O_2) is one of the main responses under different stressful conditions. All of these species show cytotoxicity in plants (De Gara & Foyer, 2017; Wang et al., 2018).The foremost consequences of ROS at a cellular and biochemical level are:

(a) Disruption in the conformation of nucleic acids through different processes like oxidation of deoxyribose, strand breaks, removal/deletion of nucleotides, modification of bases, and cross-linked protein with DNA (He et al., 2018).
(b) Lipid peroxidation with the consequent break of longer chains and an increase in the fluidity and membranes permeability (Ozgur et al., 2018).

(c) Proteins oxidation resulting in different modifications such as cleavage of the peptide chain, protein crosslinking and modification of the electric charge (Akter et al., 2015).

In the end, when the damage caused by ROS is high, the following consequence can be the programmed cell death (Mittler, 2017). In cells subjected to non-adverse conditions, ROS molecules are not capable of causing any damage as they are scavenged by a range of antioxidative mechanisms. Although initially ROS were regarded as harmful byproducts responibles for the oxidation of several molecules and structures, this concept has changed somewhat to the concept of ROS signaling (Waszczak et al., 2018), keeping ROS concentrations low even under increased ROS production. Therefore, elevation in ROS concentration in different subcellular compartments appears to be transient, reflecting only the efficiency of scavenging systems, rather than directly leading to programmed cell death (PCD) (Conway & McCabe, 2018; Rogers & Moorthy, 2018).

Nevertheless, the balance between ROS scavenging and frequent production may be disrupted under stressful conditions such as the presence of heavy metals, light intensity, temperature extremes, UV-B radiation, air pollutants, water scarcity, salinity and herbicides (Choudhury et al., 2017; Cortese-Krott et al., 2017), and results in their scavenging through plant antioxidative machinery composed of enzymatic and non-enzymatic compounds. Enzymatic compounds include SOD, CAT, APX, PRX, GR, MDHAR and DHAR. Non-enzymatic compounds are comprisedof ascorbic acid (AA), glutathione (GSH), α-tocopherol, carotenoids, flavonoids and plastoquinone/ubiquinone (Das & Roychoudhury, 2014; Hancock, 2016; Sewelam et al., 2016).

In this review, we will mainly emphasize on the types of ROS and especially the damage caused by high concentration of ROS, the subcellular distribution of ROS, and the antioxidant defense systems involving enzymatic and non-enzymatic antioxidants. Attempts will be made to highlight the involvement and role of H_2O_2 (hydrogen peroxide) and other signaling component, different environmental stresses, and the antioxidant machinery counteracting stress at the biochemical and molecular level.

Types of ROS

Reactive oxygen species is a common phrase used to catalogue some reactive molecules and free radicals derived from molecular oxygen; which include $O_2^{\bullet-}$, $^1O_2$, H_2O_2 and $^*OH$. All of these molecules are very dangerous because they are involved in cell molecular and structural damage and eventually cell death (Mittler, 2017) (Fig. 1).

ROS such as H_2O_2, *OH, and $O_2^{\bullet-}$ can be the products of redox reactions or are active forms of O_2. It is necessary to point out that only H_2O_2 is able to cross the plant membrane being essential in cell signaling. The generation of these reactive oxygen species is carried on different cell compartments. They have a high capicity of reactivity and toxicity and can suffer an oxidation process which leads to damage in proteins, nucleic acids, and lipids (Nafees et al., 2019; Singh et al., 2016a; Suzuki et al., 2012). Although it is well-known the toxicity of these compounds, curently there are many papers focused on the role of them in signaling in several crucial physiological pathways in plants (Baxter et al., 2014; Nafees et al., 2019). At evolutionary level, the role of ROS as a signaling molecule evidences the tolerance of plants under these

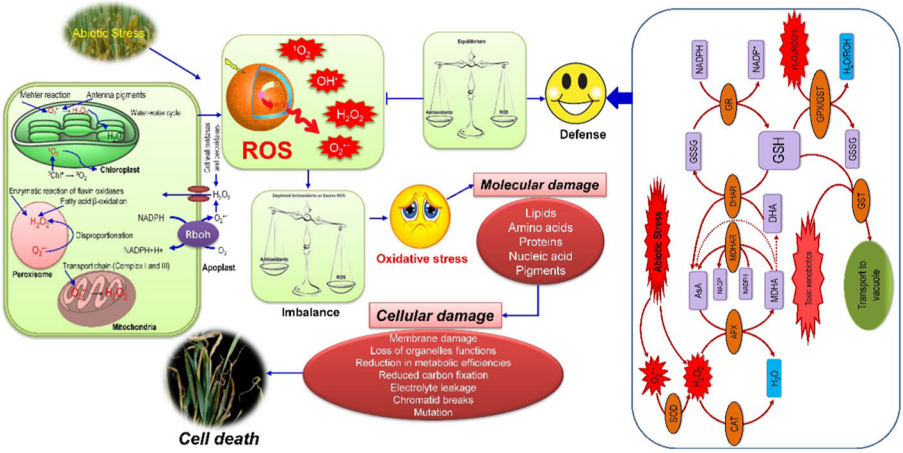

Fig. 1 Schematic representation of ROS response under stressful conditions. Rboh: respiratory burst oxidase homologs, SOD: superoxide dismutase, CAT: catalase, APX: ascorbate peroxidase, AsA: ascorbate, MDHA: monodehydroascorbate, DHA: dehydroascorbate, MDHAR: monodehydroascorbate reductase, DHAR: dehydroascorbate reductase, GSSG: glutathione, GSH: Reduced glutathione, GPX: guaiacol peroxidase, GST: glutathione S-transferase, GR: glutathione reductase

toxic reactive oxygen (Bhattacharjee, 2014; Mattila et al., 2015; Nafees et al., 2019). On the same line, it is necessary to point out that oxygen-metabolizing redox cascades are responsible for the activation of reactive oxygen species (Nafees et al., 2019).

Superoxide Radical ($O_2^{\bullet-}$)

The generation of superoxide radical ($O_2^{\bullet-}$) involves the capture of one electron released in mitochondrial ETC and photosynthetic electron transport (PET). The main sites of generation are the inner mitochondrial membrane (from NADH ubiquinone reductase and ubiquinone cytochrome c reductase) and the photosystem I of Z-scheme (from ferredoxin). At membrane level, the generation of superoxide radicals involves the participation of NADPH oxidases or respiratory burst oxidase homologs (RBOHs) (Fridovich, 1986; Bhattacharjee, 2019). In plants, NADPH oxidases are of special importance since they initiates the production of superoxide (Bhattacharjee, 2019; Suzuki et al., 2012). As a consequence, $O_2^{\bullet-}$ production is considered as the first response in a cell because is involved in the generation of other ROS. Considering the cell type or cellular compartment this generation can be immediate or through enzyme- or metal-catalyzed processes. Upon partial reduction of O_2 during electron transfer some ROS are generated along the photosynthetic electron transport chain (ETC) of chloroplasts, and other sites of the plant cell such as peroxisomes, apoplast and the plasma membrane (Saed-Moucheshi et al., 2014).

Superoxide radical ($O_2^{\bullet-}$) are generated uninterrupted during pseudocyclic electron flow of photosynthetic Z-scheme in the chloroplasts by partial reduction of O_2 molecules or energy transfer to them. During the photosynthesis, the principal sie of $O_2^{\bullet-}$ generation is the photosystem I located in the thylakoid membrane. Therefore, the generation of $O_2^{\bullet-}$ due to a reduction of O_2 throughout the photosynthetic electron transport is recognized as pseudocyclic pathway of chloroplasts. The aerobic

respiration is also involved in the production of superoxide radicals. Under normal conditions, four electrons are transferred consecutively when terminal cytochrome c oxidase or the alternative oxidase interact with O_2 whereas under stressed conditions, O_2 is able to react with other ETC compounds tranferring only one electron which leads to the generation of $O_2^{\bullet-}$. Although superoxide radical is moderately reactive, the generation of this reactive oxygen species may leds to the formation of more active ROS like $OH^{\cdot}$ (responsible for membrane damage by peroxidation) or $HO_2^{\bullet-}$ (responsible for modifications in membrane lipid-associated PUFA) under protonation of $O_2^{\bullet-}$. In addition, $O_2^{\bullet-}$ is able to reduce iron (from Fe^{3+} to Fe^{2+}) which is involved in the reduction of H_2O_2 as a consequence of the activity of the superoxide dismutase which dismutases $O_2^{\bullet-}$ to $OH^{\bullet-}$. These reactions in cell compartments in which there is an accumulation of $OH^{\bullet-}$ is known as Haber and Weiss reaction, where the final step entails the oxidation of Fe^{2+} by H_2O_2 (Fenton's reaction) (Bhattacharjee, 2019).

Moreover, the generation of $O_2^{\bullet-}$ in chloroplasts is mediated by Mehler reactions based on the reduction of O_2, reduced by electrons from the photosynthetic (ETC), and then $O_2^{\bullet-}$ is changed into hydrogen peroxide (H_2O_2), mainly by CuZn-superoxide dismutase (SOD); therefore the lifetime of $O_2^{\bullet-}$ depends on the enzymatic activity of CuZn (SOD) (Takagi et al., 2016). Another important site of $O_2^{\bullet-}$ production are the peroxisomes, where superoxide radicals are generated in three different ways:

(a) Due to the activation of enzyme xanthine oxidase in the peroxisomal matrix and later by the photosynthetic electron transport chain (ETC) in the peroxisomal membrane (del Rio, 2015).
(b) Superoxide radicals are also produced by NADPH oxidases (NOX) or respiratory burst oxidase homologs (RBOHS) (Niu et al., 2018).
(c) Finally, $O_2^{\bullet-}$ is generated by the action of xanthine dehydrogenase and aldehyde oxidase in the cytosol of the cell (Chung, 2017).

It is also necessary to point out some characteristics of this ROS such as very short half-life (2-4 μs) (Bhattacharjee, 2019; Dat et al., 2000), impermeability to biological membranes and extreme reactivity in hydrophobic environments such as the inner membrane or multimeric protein (Bhattacharjee, 2019).

Singlet Oxygen ($^1O_2$)

This reactive oxygen species is crucial in reactions of environmental stress-induced oxidative damages. Under normal conditions, oxygen has two unpaired electrons with parallel spin but a disruption in these conditions like the absorption of a high amount of energy from photoexcited antenna pigments may cause changes in spin configuration. These changes are mainly related to the reversion of the spin of one of these unpaired electrons leading to the generation of a single state (two outermost orbital electrons with opposite spin). As a consequence, synglet oxygen can be involved in reactions where occurs the transference of two electrons (Apel & Hirt, 2004; Bhattacharjee, 2019).

$^1O_2$ is the first excited electron state of O_2 with a high power of reaction. A reaction between O_2 and the chlorophyll triplet state leads to the generation of ROS occurs in during photosynthesis in photosystem II (PS II). The synthesis of $^1O_2$ during the

photosynthetic process has an overwhelming response to both photosystems (PS I and PS II). Also, singlet oxygen has the major destructive effect during cell death in leaf tissues (Wang & Apel, 2016).

PS II has a reaction center complex formed by a heterodimer of D1 and D2 proteins and cytochrome b559 which allows the binding of functional prosthetic groups (e.g. chlorophyll P680, pheophytin, QA, QB, etc.). The production of the triplet state of P680 under high light energy conditions is favoured by the plastoquinone pool, QA and QB overreduce oxidized P680 and recombine with reduced pheophytin. This triplet state results in generation of singlet oxygen by energy transfer (Koh & Fluhr, 2016; Koh et al., 2016). $^1O_2$ can oxidize and react with biomolecules like pigments, nucleic acids and proteins, like other ROS, resulting in damage and even cell death. Moreover, singlet oxygen plays an important role in the activation process of different regulatory genes (Jajic et al., 2015; Laloi & Havaux, 2015).

The half-life of synglet oxygen is very short (from 4 μs to 100 μs in water and polar solvents, respectively) (Bhattacharjee, 2019; Foyer & Harbinson, 1994; Halliwell & Gutteridge, 1984, 1999). Nevertheless, the migration capacity is high between cell with values around several hundred nanometers (nm) (Bhattacharjee, 2019).

Hydroxyl Radical (·OH)

Hydroxyl radicals (*OH) have major toxicity and reactivity effects amongst its family members, since it is responsible for the disturbance of different compounds at cellular level through lipid peroxidation (LPO), protein damage and membrane destruction. The lack of scavengers in the enzymatic system againt these reactive oxygen species can result in cellular damage and death (Bhattacharjee, 2019; Kalyanaraman et al., 2017).

In the Haber-Weiss reaction, there is a reduction of ferric iron to ferrous ($Fe^{2+} + O_2 \rightarrow Fe^{3+} + O_2^{\bullet-}$). A second step is the Fenton reaction, where transition metals catalyse *OH forming H_2O_2 ($Fe^{2+} + H_2O_2 \rightarrow Fe^{3+} + {}^*OH + OH^-$); therefore the complete series of reactions are $H_2O_2 + O_2^{\bullet-} \rightarrow OH^{\bullet} + OH^- + O_2$ (Chakraborty et al., 2016; Gligorovski et al., 2015). The generation of *OH in the cytosol can be ascribed to the liberation of $O_2^{\bullet-}$ or H_2O_2 from ROS-generating cellular compartments like the chloroplast (especially in photosystem II) or mitochondria (Richards et al., 2015).

Hydrogen Peroxide (H_2O_2)

It is moderately reactive, and spreads out from its site of production reacting with other molecules due to its capability to easily cross biomembranes, probably through aquaporins (see below for more details) of cellular membranes (Gupta et al., 2016; Weisz et al., 2017). The structural composition of hydrogen peroxide without unpaired electrons confers to this reactive oxygen species the capacity of permeability between membranes and therefore oxidative damage and signaling in other organelles far from the synthesis site. In addition, the half-life is higher compared to other ROS. The role as a "signal molecule" confers to the hydrogen peroxide an essential role in many physiological and signaling processes involved in seed germination, programmed cell death, senescence, flowering, root system development and stomatal aperture regulation (Niu & Liao, 2016; Waszczak et al., 2018).

The production of H_2O_2 in plant cells takes place under stressful biotic and abiotic conditions. The generation of H_2O_2 is carried out after the reduction of molecular oxygen (O_2) into superoxide anion ($O_2^{\bullet-}$) through two pathways:

(a) Dismutation of $O_2^{\bullet-}$ with the help of SOD and
(b) Via oxidases (e.g. amino and oxalate oxidases) (Qiao et al., 2014).

Hydrogen peroxide is generated in different organelles where there is a membrane-linked electron flows associated with ATP formation such as: chloroplast (ETC), mitochondria (respiratory electron transport chain), peroxisomes (photosynthetic carbon oxidation cycle), nucleus, plasma membranes and the endoplasmic reticulum (ER). Also, metabolic cascades like β-oxidation of fatty acid and photorespiration generate a high amount of H_2O_2 in plants at cellular level (Bhattacharjee, 2019). For superoxide radical production, cytochrome bc1 complex and NAD(P)H dehydrogenases are produced at two sites in the respiratory electron transport chain in the mitochondria. The process of H_2O_2 production in peroxisomes is related to oxygenase activity of ribulose-1,5-bisphosphatecarboxylase/ oxygenase (RuBisCO) (Turkan et al., 2018). In chloroplasts, H_2O_2 production is related to the photosynthetic electron transport chain (ETC), a starting point of O_2. H_2O_2 source is the cell membrane NADPH-dependent oxidase. Finally, in the apoplast, there are two enzymes associated with the generation of H_2O_2; amineoxidase and germin-like oxidase (Hossain et al., 2015).

Subcellular Distribution of ROS

ROS are produced under standard and adverse conditions at different cellular sites, but the chloroplasts and peroxisomes are the main sites of its generation under light conditions and mitochondria under darkness (Apel & Hirt, 2004; Bhattacharjee, 2005, 2019; Chan et al., 2016; Halliwell & Gutteridge, 1999) (Fig. 1). Apart form these organelles, peroxisomes, mitochondria, plasma membranes, apoplast, endoplasmic reticulum, and cytosol are sites with different degrees of ROS generation in fuction of environmental and developmental conditions Fundamentally, the process of ROS generation is based on the release of electrons onto O_2 coming from ETC in chloroplasts, mitochondria, and plasma membranes (Bhattacharjee, 2019; Millar & Leaver, 2000).

Apoplast

Plant apoplast is the compartment outside the cell plasma membrane, where solutes can diffuse freely between cells. This cellular compartment is characterized by a low antioxidant capacity and a pH lesser than the cytoplasm. Under these pH conditions, there is a lessening of cysteine and other antioxidants like ascorbate and glutathione (Qi et al., 2017). However, each ROS production site is equipped with an array of antioxidant systems to buffer the local environment to a relative oxidized state, and the apoplast is estimated to contain most of the leaf H_2O_2 (see Foyer & Noctor, 2016; Noctor et al., 2016 for estimates), while containing low concentrations of ASC and GSH. Therefore, ROS accumulation in the apoplast enables the generation of ROS

signaling pathways to impede the negative consequences of low pH on the redox sensitivity of the apoplastic proteins (Liebthal & Dietz, 2017). Apoplast ROS are involved in acclimation of photosynthesis under changing light conditions (Foyer et al., 2018), lignin cross-linkage to interact with cell walls (Cosio et al., 2017; Moural et al., 2017) and the regulation of stomata (Singh et al., 2017).

Under abiotic and biotic stresses, cells are induced to produce ROS in the apoplast. This generation is carried out by NADPH oxidases, class III cell wall proxidases and amino oxidases. In plants, NADPH oxidases are closely related to the respiratory burst oxidase homolog (RBOH) family. These RBOH proteins are composed by six conserved transmembrane helices, two heme groups maintained by transmembrane helices, the C-terminal hydrophilic domains, and the N-terminal domains (Liu & He, 2016). The transfer of electrons across the membrane to oxygen (O_2 as an electron acceptor) at the apoplast via flavin adenine dinucleotide (FAD) is related to the presence of heme groups in these proteins. The N-terminal domains are composed of two EF-hands (helix loop structural domains) responsible for calcium-binding, whereas terminal domains, the cytosolic C-terminal domains are composed of FAD- and NADPH-binding sites (Waszczak et al., 2018). The crucial role of RBOHs is to convey electrons from cytosolic NADPH or FAD to apoplastic oxygen, leading to $O_2^{\bullet-}$, which is transformed to H_2O_2 voluntarily or by SOD (Kaur et al., 2017; Qu et al., 2017).

Besides RBOH, apoplastic peroxidases contribute intensely in pattern-triggered apoplastic ROS. These aplopastic POXs are heme-containing enzymes associated with ROS generation (in hydroxylic and oxidative cycles) and depletion, and categorized as the intracellular class I POXs, and class II POXs (E.C. 1.11.1.7), and released to the vacuole or transported to the extracellular space. In the oxidative cycle, by using apoplastic reductants POXs are responsible for the reduction of O_2 to $O_2^{\bullet-}$ or H_2O_2. However, in the hydroxylic cycle POXs are involved in reactions in which $^{*}OH$ is produced from H_2O_2 and $O_2^{\bullet-}$ (Mammarella et al., 2015). The activation of peroxidase genes is influenced by a number of stressful conditions (Podgorska et al., 2017), and peroxidases are also implicated in plant developmental processes and germination of seeds (Francoz et al., 2015; Shigeto & Tsutsumi, 2016).

The antioxidant enzymes Amine oxidases (AOs) found in the apoplast are Copper-containing AOs (CuAOs; EC 1.4.3.6) and Flavin-containing polyamine oxidases (PAOs; EC 1.5.3.11).

The first ones are involved in the catalyzation oxidative deamination of aliphatic diamines such as putrescine (Put) and cadaverine (Cad), and to a lesser extent to spermine (Spm) and spermidine (Spd). Second group regulates the oxidation of Spm, Spd, and their acetylated derivatives at the secondary amino group (Angelini et al., 2017; Tavladoraki et al., 2016). PAOs catalyze catabolism of spermidine and spermine generate the production of H_2O_2, which play a role under and stress conditions and plant development, and there are clear implications for cellular metabolism (Yoda et al., 2003; Yoda, 2006). However, it is not clear of their role in antioxidant functions. The apoplast contains a number of cysteine-rich peptides (Tavormina et al., 2015) that could participate in ROS sensing, such a group are the cysteine-rich receptor-like kinases (CRKs); but again it is not clear of their function (Akter et al., 2015).

Chloroplasts

Exposure of chloroplasts to stress decreases the maximal photosynthetic potential eliciting an overexcitation energy that minimizes the photosynthetic electron transport (PET) sections and produces singlet oxygen ($^1O_2$) (Serrano et al., 2016). Chloroplast thylakoids in the photosystems (PSI and PSII) represent a high production of singlet oxygen since the principal place in the generation of ROS is the photosynthetic electron transport chain (ETC), overloading the electron flow in these cellular compartments, enabled by the generation of oxygen in PSII (Dietz et al., 2016). As a consequence of charge recombination of primary radical pair (P680+ pheophytin2) with pheophytin acting as the primary electron acceptor for the generation of triplet state chlorophyll (^{3}Chl) in PSII. Moreover, due to $^1O_2$ originating under high levels in PET the quinone acceptors of PSII (primary electron-accepting plastoquinone of PSII [QA], secondary electron-accepting plastoquinone of PSII, and the plastoquinone pool) are reduced (Ning & Wang, 2016).

The majority transference of electrons occurs from the reduced P700 reaction center to the stromal Fe-S protein ferredoxin in PSI. Being several times superior to the rate of superoxide production, the efficiency of participation of SOD and reactions of the ascorbate–glutathione cycle are determined by the strength of SOD and ascorbate peroxidase activities, where superoxide production is integrated into a known water-water cycle. The photoproduced $O_2^{\bullet-}$ as well as H_2O_2, and generation of *OH radicals are effectively scavenged and suppressed by water–water cycle, theirby blocking their interaction with target molecules and hence photoinhibition (Gautam et al., 2017). ROS production is also participated by the photosynthetic electron transport chain (ETC) following overloading of electron flow in the chloroplasts, and helped by the generation of oxygen in PSII. ROS production in the chloroplast is closely associated with the Mehler reaction, where the electron flow is diverted from ferredoxin to O_2, reducing it to the superoxide anion (Woodson, 2016).

Information about environmental and metabolic changes to the nucleus is now thought to initiate in the chloroplast by a retrograde signaling mechanism (reviews in Chan et al., 2016; Leister, 2017; Waszczak et al., 2018). As a simple and ubiquitous molecule, H_2O_2 cannot carry any information about its function or origin. Signal transduction studies to the nucleus have presented evidence for three possible mechanisms:

(a) The stromules are narrow tubular structures, having stroma surrounded by an envelope membrane, originating from all types of plastids in vascular plants. They directly mediate in the delivery of ROS and proteins to the nucleus (Hanson & Hines, 2018).
(b) Fast regulation of nuclear H_2O_2 concentrations by a population of companion chloroplasts localized around the nucleus.
(c) Signaling via accumulation of chloroplast metabolites, their oxidative derivatives, or both.

The signaling molecule is not clear, but chloroplastic 3-phosphoadenosine 5-phosphate (PAP) phosphatase undergoes redox- or H_2O_2-dependent oxidative inactivation (Chan et al., 2016), leading to the accumulation of PAP, which is suggested to direct H_2O_2

translocation from chloroplasts to nucleus. It appears clear that H_2O_2 as a direct signal to the nucleus does not provide sufficient information which could differentiate chloroplastic and/or peroxisomal H_2O_2 (Hashem, 2018; Waszczak et al., 2018).

Although ROS and redox regulation in mesophyll and bundle sheath cells of C_4 plants differ but several photosynthetic enzymes involved in the light and dark (carbon) reactions are regulated through redox components, like thioredoxins as redox transmitters and peroxiredoxins. Linear and cyclic electron transport in the chloroplasts operates differentially in these two cell types; as compared to C3 chloroplasts; changing the redox needs of the cell photosynthetic light reactions, ROS generation trends, antioxidant defence, and thiol-based redox regulation (Krasensky-Wrzaczek & Kangasjärvi, 2018). CAT activities are higher in C_3 plants whereas APX and GR are higher in C_4 plants which generally have low photorespiratory activity; suggesting the ROS scavenging mechanism depend on the type of photosynthesis (Turkan et al., 2018). In CAM plants the situation is less clear and CAM plants handle the O_2 evolvedin photosynthesis during daytime by a number of mechanisms:

(a) Mitochondrial respiration.
(b) Photorespiration.
(c) Formation of some reactive oxygen species (ROS).

It appears that in the induction of CAM up-regulation of mitochrondrial Mn-SOD is a typical reaction (Males & Griffiths, 2017). More plasticity of CAM plants is especially well equipped to deal with oxidative stress by an increased expression of the antioxidative response systems that are not toxic (Borland et al., 2011). However, O_2 like CO_2 can diffuse through biological membranes when CAM plants have closed stomata, and gases may diffuse through the cuticle (Ceusters & Van de Poel, 2018; Turkan et al., 2018). An unexpoled area of research in photosynthesis and ROS scavenging mechanism is the possible importance of carbonic anhydrase in C_3, C_4 and CAM metabolism (DiMario et al., 2017).

Mitochondria

Mitochondria are another organelle in which there is a high production of ROS due to stress, like H_2O_2 and $O_2^{\bullet-}$ and as a consequence, there is a high risk of oxidative damage. Therefore, these organelles possess many antioxidant defenses to overcome the damage generated by ROS production (Das et al., 2015). A spontaneous dismutation of $O_2^{\bullet-}$ occurs in mitochondria to H_2O_2 or through mitochondrial manganese-SOD, subsequently H_2O_2 is scavenged by Prxrs (Finkemeier et al., 2005) and APX. In plant mitochondria a full set of enzymes necessary for completion of the ascorbate-glutathione (ASC-GSH) cycle have been localized (Huang et al., 2016). To reduce O_2 to form ROS, mitochondrial ETC accommodates electrons with ample amounts of free energy theirby acting as the main source of ROS generation. Several sites in the mitochondrial ETC are closely related to generation of ROS like NADH dehydrogenase (Complex I) and ubiquinone-cytochrome region (Complex III) (Mignolet-Spruyt et al., 2016).

O_2 is reduced to $O_2^{\bullet-}$ spontaneously at its flavoprotein region in the Complex I, where ROS production shows an enhancement in the case of reverse electron flow from

Complex III to Complex I because of lack of NAD^+-linked substrates. ATP hydrolysis supervises this reverse flow of electrons (Liberatore et al., 2016). Alternative oxidases (AOXs) have a major role in this redirection upstream of complex III when, for example, complex III is suboptimal. No major impacts on development, physiology, or metabolism have been shown by altering AOX activities and several other mitochondria-targeted proteins (mitochondrial dysfunction stimulon MDS or motif MDM) through NAC transcription factors ANAC013, ANAC016, ANAC017, ANAC053, and ANAC078, all of which possess C-terminal transmembrane domains and mitochondrial retrograde signaling (Hofmann, 2013).

Presence of ubiquinone in its fully reduced form is related to the generation of $O_2^{\bullet-}$ at Complex III contributing with an electron to cytochrome c_1 originating an unstable ubisemiquinone semi-radical which promotes leakage of electrons to O_2 (Huang et al., 2016). Moreover, there are various other enzymes localized in the mitochondrial matrix responsible for ROS production. For instance, 1-galactono-γ-lactone dehydrogenase (GAL) secondarily produces ROS by passing electrons to the ETC but aconitase is directly connected with reactive oxygen species production (Wang et al., 2016a).

Peroxisomes

These subcellular organelles as important sites for ROS generation are enclosed by a single membrane and devoid of DNA. The generation mainly occurs via photorespiration and the fatty acid β-oxidation pathways a process dependent on light energy, based on the uptake of O_2 and the release of CO_2 that is stored in chloroplasts, peroxisomes and mitochondria (Reumann & Bartel, 2016). The first step of the photorespiratory pathway in peroxisomes is the oxidation of glycolate to glyoxylate through glycolate oxidase (GOX), generating H_2O_2 (del Rio & López-Huertas, 2016).

The fatty acids enter peroxisomes via ATP-binding cassette (ABC) in the pathway of fatty acid β-oxidation, which then get oxidized to fatty acetyl-CoA in peroxisomes, shortened by 2 carbons in each β-oxidation cycle. Finally, glyoxylate cycle under gluconeogenesis in the mitochondria and cytosol converts acetyl-CoA to four-carbon molecules. The results of this pathway are the production of significant amounts of H_2O_2 (Sandalio & Romero-Puertas, 2015).

The glutathione peroxidase requires glutathione as a cellular reductant to reduce H_2O_2 to water and O_2; so far as removal of H_2O_2 in peroxisomes is concerned, catalases are independent of cellular reducing cofactors, like glutathione or thioredoxin, and can catalyze a dismutation reaction converting H_2O_2 to water and O_2 (Wang et al., 2015). Some evidence indicates a relatively low contribution forthe peroxisomal antioxidant system, and conditions shift the redox status of the cellular GSH and ASC pools toward a more oxidized state (Queval et al., 2007), coinciding with rapid transcriptome reprogramming (Kerchev et al., 2016) related to perturbed glycolate metabolism or altered cytoplasmic redox balance rather than H_2O_2 buildup.

The main sites of superoxide radical production in peroxisomes are in the following compartments: in a short electron chain associated with the NADH/NADPH-driven peroxisomal membrane and in the peroxisomal matrix associated with xanthine oxidoreductase (XOD/XDH) and uricase (Corpas et al., 2017).

SA-mediated inhibition of peroxisomal H_2O_2 scavenging inhibits auxin and jasmonic acid (JA) biosynthesis to increase the resistance of plants to biotrophic

pathogens, and it is difficult to differentiate between internal and external ROS and redox signals. Calcium concentration increases in peroxisomes (Costa et al., 2010), which promoted CAT activity possibly via Ca^{2+}-dependent interactions between CAT and calmodulin mediated also by ethylene concentrations (Kazan, 2015).

Oxidative Damage by ROS

Lipid Peroxidation

Lipids are the main components of plasma membrane of the cells and organelles (including phospholipids and galactolipids of plant cells and thylakoid membranes). With an increase in ROS levels normal cellular functions are influenced and the oxidative stress exacerbated through the production of lipid-derived radicals and lipid peroxidation occurs (Pospisil & Yamamoto, 2017). The dipole moment of H_2O_2 is larger than that of H_2O, preventing free diffusion through membranes. However, according to studies of yeast survival, multiple plant aquaporins can transport H_2O_2 (reviews in Bienert & Chaumont, 2014; Waszczak et al., 2018), the main damaging ROS. Hydrogen peroxide (H_2O_2) crosses the membranes through specific channels, called peroxiporins**,** which are recognized as a sub-class of the aquaporin (AQP) protein family of membrane channels (see next paragraph).

Aquaporins as membrane channels allow the transference of H_2O as well as small neutral molecules across biological membranes. These include CO_2, H_2O_2, urea, ammonia, salicylic acid, arsenite and wide range of other small solutes. There are different isoforms of aquaporins in plants located in different cell compartments such as plasma membrane, endoplasmic reticulum, vacuoles, plastids and, in some species, in membrane compartments interacting with symbiotic organisms (Maurel et al., 2015; Noronha et al., 2016). A regulation in response to signaling intermediates such as cytosolic pH and calcium, and reactive oxygen species are also allowed by aquaporins. This knowledge is now integrated with the help of combined genetic and physiological approaches, depicting how aquaporins are involved in hydraulic regulation in roots and leaves under scarce water conditions as well as other abiotic stress conditions like flooding, nutrient availability, temperature or light (Abascal et al., 2014; Ampah-Korsah et al., 2016; Maurel et al., 2015). Aquaporins are accepted as suitable candidate for the generation of transgenic plants with high tolerance under different abiotic stresses because of their versatile functions (Srivastava et al., 2016). A chain reaction is triggered once lipid peroxidation occurs in cellular or organelle membranes, which further aggravates the oxidative stress by generating lipid radicals damaging proteins and DNA biomolecules (Bhattacharjee, 2014; Chmielowska-Bak et al., 2015).

The double bond between C-atoms and the ester linkage between glycerol and fatty acids are involved in the two main effects of ROS on membrane phospholipids. The crucial constituents of the plasma membrane polyunsaturated fatty acids (PUFA) are the main targets for ROS damage. The polyunsaturated fatty acids like linoleic acid are specifically vulnerable to the ROS (e.g.$^{*}OH$ and $^{1}O_{2}$). The hydroxyl radical ($^{*}OH$) causes high damage, and can stimulate a cyclic chain reaction leading towards further peroxidation of other PUFAs (Singh et al., 2015). Membrane lipid peroxidation occurs in three stages; initiation, progression, and termination (El-Beltagi & Mohamed, 2013).

The first stage involves the energization of O_2 to form $O_2^{\bullet-}$ and $^*OH$ radicals, followed by reaction of ROS with PUFA methylene groups, yielding conjugated dienes, lipid peroxyl radical and hydroperoxides, in a series of reactions like: PUFA-H +$^*OH$→ PUFA$^\bullet$ (PUFA alkyl radical) + H_2O and PUFA$^\bullet$ + O_2 → PUFA-OO$^\bullet$ (Peroxyl radical). Latter involves further reactions to form lipid hydroperoxide through the extraction of one H-atom from contiguous PUFA side chains as PUFA-OO$^\bullet$ + PUFA-H → PUFA-OOH + PUFA$^\bullet$. PUFA-OOH (the lipid hydroperoxide) engages in cleavage by reacting with a reduced metal, e.g. Fe^{2+} as here PUFA-OOH + Fe^{2+} → PUFA-O$^\bullet$ + Fe^{3+}. These hydroperoxides can also get decomposed to form different reactive species like lipid alkoxyl radicals, aldehydes, alkanes, lipid epoxides, and alcohols. The last step in LPO is the generation of different lipid dimers induced by different lipid-derived radicals like; PUFA$^\bullet$ + PUFA$^\bullet$ → PUFA + PUFA (Fatty acid dimer), PUFA$^\bullet$ + PUFA-OO$^\bullet$ → PUFA-OO-PUFA (Peroxide bridged dimer) and PUFA-OO$^\bullet$ + PUFA-OO$^\bullet$ → PUFA-OO-PUFA + O_2 .

A decrease in membrane fluidity and an increase in the leakiness of the membrane are the final effects of these series of reactions (Farmer & Mueller, 2013; Sofo et al., 2015, 2016).

Protein Oxidation

This process is chemically based on a covalent modification of proteins generated by reactive oxygen species or byproducts of oxidative stress. This process is frequently irreversible but may also be reversible in the presence of sulfur-containing amino acids. The glycosylation and disulphide bond formation modifications take place in plant secretory proteins before proper folding. These then go over to their final destination through endomembrane system. In the endoplasmic reticulum (ER) a ROS response is triggered by the accumulation of unfolded proteins due to sub-optimal environmental conditions. An important but poorly understood aspect in this connection is the ROS production originating from ER stress, and the interaction between ER stress and overall ROS signaling process in other organelles, such as the mitochondria and chloroplasts (Ozgur et al., 2018).

The process of oxidation of proteins can be categorized in four steps; a-metal-catalyzed oxidation, b-amino acid oxidation, c-oxidation induced cleavage and d-conjugation of lipid peroxidation products (Ahmad et al., 2017). The first stage is characterized by the presence of enzymes like NADH and NADPH oxidase, which catalyze the reduction and oxidation of Fe (III) /Fe (II), and Cu (II)/Cu (I) metal ions to generate H_2O_2. For $^*OH$, generation, oxidized forms of Fe (II) and Cu (I) bind to a specific metal binding site within the protein, react with H_2O_2 followed by attacking of amino acid residues near metal binding sites, resulting in the cleavage of peptide bonds. This can be either carried out by $^*OH$ which reacts with proteins and forms alkyl radicals. In order to form protein aggregates or react with O_2 to generate an alkylperoxide radical it forms cross-links with other similar alkyl-radicals. The reaction of a free radical such as $^*OH$ with the glutamyl, prolyl and aspartyl residues of the protein chain can also lead to the rupture of peptide bond (Anjum et al., 2015).

The peptide bond cleavage and amino acid oxidation into protein carbonyls are main outcomes of protein oxidation. One of the most sensitive targets for ROS-mediated post-translational modifications are cysteine (Cys) residues in proteins, becoming key

residues for ROS signaling. Cys residues reactivity towards ROS, together with their ability to react to different oxidation states permits them to appear at the crossroads of highly dynamic oxidative events. A redox-active cysteine can be present as *S*-glutathionylated (-SSG), disulfide bonded (S-S), sulfenylated (-SOH), sulfinylated (-SO_2H), and sulfonylated (-SO_3H). In ROS-sensing pathways sulfenic acid (-SOH) form is regarded important resulting in more modifications which affects protein structure and function (Akter et al., 2015). Secondary reactions with lipid peroxidation products like HNE (4-hydroxynonenal) or with reducing sugars or their oxidation products can also be generated by carbonyl groups. Therefore, protein carbonylation is much used as an indicator determining the extent of protein oxidation. It can be related to the direct oxidation of amino acid side chains (e.g. proline and arginine to γ-glutamyl semialdehyde, lysine to aminoadipic semialdehyde and threonine to aminoketobutyrate) (Moller et al., 2011; Jung et al., 2014).

DNA Damage

In plants histones and other linked proteins protecte nuclear DNA. However, as a consequence of the low capacity of protection from histones, as well as their proximity with ROS generation systems mitochondrial and chloroplastic DNA are susceptible to ROS attack (Tudek et al., 2017). Various parts of the transcriptional machinery in plants can modify redox-dependent control of nuclear transcription and redox homeostasis (He et al., 2018). Reactive oxygen species and redox homeostasis are of special importance in epigenetic and retrograde control of gene expression and cross-tolerance processes (Locato et al., 2018).

There are single-and double-stranded DNA injuries. First group is composed of interference with only one DNA strand, such as oxidized or alkylated base damage, base loss, DNA adducts, intra-strand cross-links, DNA photoproducts and single-strand DNA breaks (SSBs). Second group includes disturbance to both DNA strands, such as inter-strand cross-links and double-strand DNA breaks (DSBs) (Masova & Gruszka, 2015). As a result of the damage to DNA, many physiological functions are affected such as mutations, disruption to protein synthesis, arrest or induction of transcription, cell membrane changes and genomic instability (Fatima et al., 2016).

DNA damage is endogenously generated by ROS such as $^1O_2$ and $^*OH$. Latter is highly reactive, provoking damage to purine and pyrimidine bases, as well as deoxyribose backbone. Moreover, ROS with DNA or its linked proteins promote the reactions of DNA-protein cross-links (Hu et al., 2016a). Much evidence suggests that a major role in the trans-generational embedding of stress tolerance is played by changes in the reduction/oxidation (redox) status of stress signaling molecules, as well as level of DNA methylation, but little information is available concerning the specific pathways and mechanisms involved (Foyer et al., 2018; Waszczak et al., 2018).

Antioxidant Defense Systems

The maintenance of prevailing homeostasis cell conditions in plants is essential, therefore under changing conditions, enzymatic and nonenzymatic scavenger are synthetized by plants to avoid cell oxidative damage (Hussain et al., 2019).

Enzymatic Antioxidants

Major ones are SOD, CAT, APX, PRX, GR, MDHAR and DHAR.

Superoxide Dismutase (SOD)

These (EC 1.15.1.1) are the first barrier against oxidative damage and are present in every cell. Conversion or dismutation of toxic $O_2^{\bullet-}$ radicals to H_2O_2 and molecular oxygen (O_2) are the main function of these antioxidant enzymes (Chung, 2017). In plants SOD's are classified into 3 groups, depending on the class of prosthetic metals: copper and zinc (Cu/Zn-SODs), manganese (Mn-SODs) and iron (Fe-SODs) (Wang et al., 2016a). Cu/Zn-SOD is displayed in chloroplasts, cytosol and mitochondria. Mn-SOD is mainly placed in mitochondria, but also present in different types of peroxisomes. In chloroplasts, and also in peroxisomes and mitochondria Fe-SOD appears (Wang et al., 2017). A fourth group with Ni (II/III) at the active metal site (Ni-SOD) is present in some species of marine algae (Gill et al., 2015).

Catalase

These (EC 1.11.1.6) are the members of a category of heme-containing enzymes. They are responsible for the dismutation of hydrogen peroxide into water and oxygen, and play important in plant metabolism as well as in signal recognition (Liu et al., 2015). All aerobic eukaryotes possess it. The release of H_2O_2 generated in peroxisomes by oxidases involved in β-oxidation of fatty acids, photorespiration, purine catabolism and during oxidative stress is carried out by these (Sofo et al., 2015). CAT is localized in peroxisomes and also in mitochondria, and are classified into three groups. The group I is located in photosynthetic tissues, whereas group II is related to vascular tissues. The group III are exhibited in seeds and reproductive tissues (Table 1) (Anjum et al., 2016).

Ascorbate Peroxidase

Ascorbate peroxidase (EC 1.11.1.11) belongs to the category of heme-containing peroxidases, responsible for the reduction of hydrogen peroxide (H_2O_2) to water using ascorbate (AsA) as an electron donor. Against the toxic effects of ROS, APX has the main role in removing ROS and in defense in higher plants (Maruta et al., 2016). APXs are present in different cell compartments such as mitochondria, chloroplasts, and peroxisomes (Ozyigit et al., 2016). The classification of different isoforms is based on their subcellular localization. For instance, in the cytosol (cAPX), mitochondria (mitAPX) and chloroplast stroma (sAPX) isoforms with high solubility are present. On the other hand, in the microbodies (including peroxisome and glyoxisome) (mAPX) and chloroplast thylakoids (tAPX) membrane-bound isoforms are present (Table 1) (Anjum et al., 2016). The modulation of quantum efficiency and control of electron transport together with the ascorbate-glutathione (AsA-GSH) cycle are due to the defensive functions of APX through H_2O_2 removal, which (Pandey et al., 2017).

Table 1 Gene isoforms described for various ROS enzymes and metabolites, detection methods, localization, and interactions with other genes and metabolites. For each ROS enzyme and metabolite, plant species list illustrated is not to suggest that all isoforms are present in each plant. It simply demonstrates the species diversity where at least one such isoform has been studied

ROS enzyme and metabolite	Genes and isoforms	Detection and localisation	Plant species and reference genome	References
Superoxide dismutase (SOD)	9 functional isoforms *SOD 1,2,3,4,5,6,7,8,9* Cu/Zn *SOD 1,2,3,4* Mn*SOD 5,6* Fe *SOD 7,8,9*	mRNA, cDNA, RT-PCR, BLAST search/sequencing; chloroplast *SOD 2,3,7,8,9*, mitochondria *SOD2,5,6,* cytosol *SOD 1,2,4,6* extracellular *SOD 3,6*	*Arabidopsis thaliana Glycine max* *Brassica campestris* *Brassica juncea* *Vigna radiata* *Zea mays* *Triticum aestivum* *Medicago sativa* *Oryza sativa* *Hordeum vulgare Rhaphanus sativus Saccharum officinarum Pisum sativum*	Gill et al., 2015 Tamayo et al., 2016 Wang et al., 2016b
Catalase (CAT)	4 functional isoforms *CAT 1,2,3,4* Rice functional categories *CAT A, CAT B*	mRNA, RT-PCR, database search; class I cytosol/ microsome, class II vascular tissue (lignin), class III seeds/ young seedlings (fatty acid)	*Oryza sativa* *Arabidopsis thaliana* *Zea mays* *Nicotiana tabacum Saccharum officinarum Helianthus annuus* *Brassica juncea* *Lycopersicon esculentum* *Pisum sativum* *Raphanus sativus* *Populus nigra* *Hordeum vulgare* *Cucumis sativus*	Anjum et al., 2016 Hu et al., 2016b Zhou et al., 2017
Ascorbate peroxidase (APX)	9 functional isoforms. *APX 1,2,3,4,5,6,7,8,9*	mRNA, RT-PCR, SMART–RACE, adapted primers; cytosol *APX 1,2,6*, chloroplast *APX 5,6,7,8,* peroxisome *APX 3,4,5*, mitochondria *APX 6*	*Arabidopsis thaliana* *Pisum sativum* *Oryza sativa* *Festuca sp.* *Nicotiana tabacum*	Chen et al., 2015 Anjum et al., 2016 Ozyigit et al., 2016

Table 1 (continued)

ROS enzyme and metabolite	Genes and isoforms	Detection and localisation	Plant species and reference genome	References
			Spinacia oleracea *Brassica napus* *Lycopersicon esculentum* *Zea mays* *Eucalyptus grandes* *Olea europaea* *Gossypium hirsutum* ***Camellia sp***	
Peroxidase family (PRX) (also may be called GPX, GPOD)	PRX gene family have general activity using various substrates. Isoforms not described, but isoenzymes described	mRNA, RT-PCR specific primers, isoenzymes have been localized in vacuoles, cytosol and cell walls, gene localization is not available	*Solanum melongena* *Lycopersicon esculentum* *Ralstonia solanacearum. Xanthomonas oryzae Pseudomonas fluorescens*	Ozyigit et al., 2016 Prakasha & Umesha, 2016
Glutathione reductase (GR)	3 functional isoforms. *GR 1,2,3*	mRNA, RT-PCR, sequencing, phylogenetic relationship across plants; chloroplast *GR 1,2* mitochondria *GR 3*,	*Arabidopsis thaliana Nicotiana tabacum* *Zea mays* *Pisumsativum* *Oryza sativa* *Populus trichocarpa* *Vinga unguiculata* *Hevea brasiliensis*	Trivedi et al., 2013 Deng et al., 2015
Dehydroascorbate reductase (DHAR)	4 functional isoforms, *DHRA 1,2,3,4*	EST, cDNA, mRNA, RT-PCR, sequencing, cytosol and chloroplast *DHRA 1,2*, cytosol *DHRA 3*, unknown *DHRA 4*	*Arabidopsis thaliana Nicotiana tabacum* *Zea mays* *Pennisetum glaucum* *Populus sp* *Selaginella moellendorffii* *Populus tomentosa* *Pinus abies* *Pinus taeda*	Zhang et al., 2015 Noshi et al., 2016 Pandey et al., 2017
Ascorbic acid		RNA, cDNA, BLAST similarity and sequencing	*Arabidopsis thaliana Triticum durum* *Lycopersicon esculentum, Oryza sativa*	Chen et al., 2016 Noshi et al., 2017

Table 1 (continued)

ROS enzyme and metabolite	Genes and isoforms	Detection and localisation	Plant species and reference genome	References
	5 functional isoforms. *VTC 1,2,3,4,5*. Other ROS enzymes affect ascorbic acid levels; e.g. APX, AO, MDHRA and DHRA	*VTC* genes are difficult to localiseand describe for regulation, most are based on *Arabidopsis* mutants	*Nicotiana tabacum* *Solanum tuberosum* *Phaseolus vulgaris* *Malus domestica* *Vinga unguiculata* *Actinidia deliciosa* *Fragaria ananassa* *Citrus sinensis*	Kim et al., 2018
Glutathione	6 functional isoforms apparently described. Other ROS enzymes affect glutathione levels, e.g. DHRA and MDHRA	semi-quantitative RT-PCR, fluorescence and enzymatic assays, giving gene activity, but glutathione genes difficult to study at specific level	*Ipomoea batatas* *Solanum tuberosum* *Oryza sativa* *Arabidopsis thaliana*	Zmorzynski et al., 2015 Noshi et al., 2017 Kim et al., 2018
α-Tocopherol	6 functional isoforms. *VTE 1,2,3,4,5* and *PDS 1*. Secondary metabolite genes are usually difficult to assess and quantify	QTL mapping and 'in silico' mapping (cDNA chip) technology; for many plants chip not be available, so nearest plant species used	*Arabidopsis thaliana Brassica napus* *Zea mays* *Oryza sativa*	Wang et al., 2012 De Filippis, 2016 Havlickova et al., 2018
Carotenoids	*CLA 1, CLB 5, CCR 1, CCR 2* carotenoid genes, *LUT 1,2,5* lutein genes, *PDS 1,2* pigment loss, *HP 1,2,3* high pigment content	various methods used for studies on multi-enzymatic metabolites. Most studies on regulation of carotenoids by the *PSY* gene family	*Zea mays* *Oryza sativa* *Triticum aestivum* *Daucus carota* *Arabidopsis thaliana* *Zea mays* *Vitis vinifera* *Brassica napus* *Brassica campestris*	Nisar et al., 2015 Merhan, 2017
Flavonoids	*PAL 1,2,3* isoform genes, *C4H 1,2* isoforms, *4CL 1,2* genes, but other genes affect flavonoids including *FLS, CHS* and *F3H* genes	various methods used for studies on multi-enzymatic pathway	*Arabidopsis thaliana Gerbera sp.* *Antirrhinum majus* *Zea mays*	El-Sayed-Bashandy, 2016 Lan et al., 2017

Table 1 (continued)

ROS enzyme and metabolite	Genes and isoforms	Detection and localisation	Plant species and reference genome	References
		metabolites. Most studies on regulation of flavonoids by *MYB* family	*Nicotiana tabacum Chrysanthemum sp. Brassica oleracea*	
Plastoquinone (PQ) Ubiquinone (UQ)	Over 35 enzymes used. PQ uses tyrosine; UQ uses phenypropanoid. Both use PPS, HST, PPT, family of genes, benzene / quinone	various methods used for studies on multi-enzymatic pathway metabolites. Most studies on regulation of flavonoids by *MYB* family	*Arabidopsis thaliana Brassica napus Brassica campestris Saccharomyces cerevisiae Oryza sativa Zea mays Glycine max Vitis vinifera*	Du et al., 2015 Parmar et al., 2015 Liu & Lu, 2016

Peroxidases (PRX family)

This family (EC 1.11.1.7) forms another group of heme-containing proteins. They show wide structural variability, preferably oxidizing aromatic electron donors like guaiacol and pyragallol at the expense of H_2O_2 (Das & Roychoudhury, 2014). Class III peroxidases are commonly found in apoplast, cell wall or vacuole which catalyze the oxidation of various substrates; and they have essential roles in many biosynthetic pathways and defense systems under stressed conditions (Yadav & Sharma, 2016). The main function of GPX and GOPD (Table 1) in plants is the decomposition of indole-3-acetic acid (IAA). The biosynthesis of lignin and defense against biotic stresses requires the depletion of hydrogen peroxide in different cell sites such as vacuole, cell wall and also in extracellular spaces (Dar et al., 2017).

Glutathione Reductase

This (EC 1.6.4.2) is a flavo-protein oxidoreductase, present in all kingdoms. It is responsible for the reduction of glutathione disulfide (GSSG) to glutathione (GSH), a critical molecule responsible for scavenging of H_2O_2 through the ascorbate-glutathione cycle (Ding et al., 2016; Hasanuzzaman et al., 2017). The main sites of generation of GR are chloroplasts, mitochondria, and cytosol. Glutathione reductase proteins have been categorized into 2 groups depending on the N-terminal prolongation. The first group are known as GR1 and are characterized by a shorter cytosolic enzyme, and the second group are known as GR2 and are characterized by an elongated organellar protein GOR1 (N-terminal sequences), which can target the GR protein to both mitochondria and chloroplasts (Nahar et al., 2016).

Monodehydroascorbate Reductase

It (E.C.1.6.5.4) is a flavin adenine dinucleotide (FAD) enzyme, catalyzing the formation and recycling of ascorbic acid (AsA) from the short-lived MDHA radicals and uses NADPH as a reducing agent/electron donor, eventually refilling AsA pools in the cells. In plants it occurs in different cell sites such as chloroplasts, mitochondria, peroxisomes and the cytosol (Kim et al., 2016).

Dehydroascorbate Reductase

It (EC 1.8.5.1) is involved in the scavenging of ascorbate, catalyzing the glutathione (GSH)-dependent reduction of oxidized ascorbate (dehydroascorbate, DHA). A pool of reduced ascorbate is regenerated by DHAR which detoxifies ROS (Yadav & Sharma, 2016). Formation of MDHA takes place via the univalent oxidation of AsA which through spontaneous disproportionation or further oxidation is converted to the divalent oxidation product dehydroascorbate (DHA) (Chang et al., 2017). DHAR is located mainly in green and etiolated shoots, root tissues and seeds (Dar et al., 2017).

Non-enzymatic Antioxidants

These are other members of the antioxidant machinery like ascorbic acid (AsA), glutathione (GSH), α-Tocopherol, carotenoids, flavonoids and plastoquinone/plastocyanin.

Ascorbic Acid (Vitamin C)

The main roles for ascorbic acid are like a redox buffer. It acts as a cofactor for many enzymes, cell division and growth regulation, as well as in signal transduction. Moreover, in higher plants it is the most abundant water-soluble antioxidant, participating in the detoxification of ROS (Seminario et al., 2017; Ntakgas et al., 2018). It directly scavenges $O_2^{\bullet-}$, $^*OH$ and $^1O_2$, and can reduce H_2O_2 to H_2O via the APX reaction (Liang et al., 2017a). It is generated mainly in mitochondria though several pathways. Smirnoff-Wheeler pathway (D-mannose/L-galactose pathway) is the first one. The second involves cell wall pectins, whereas the third involves the conversion of GDPD-mannose to GDP-L-gulose and subsequent generation of L gulono-1, 4-lactone via L-gulose. The fourth pathway is the synthesis of ascorbate from myo-inositol. Here myo-inositol is converted to L-gulono-1, 4-lactone. Three reactions take place here, catalyzed by myo-inositol oxygenase, glucuronate reductase and aldono lactonase (Akram et al., 2017). Although often considered only as a signalling molecule in plants ascorbate plays novel roles including the induction of cytosolic Ca^{2+} signals and metabolite efflux from cells via anion channels controlling the ionic and electrical equilibrium (together with K^+ efflux via GORK channels) (Makavitskaya et al., 2018).

Glutathione

It is a molecule composed of thiol tripeptide (γ-glutamylcysteinyl-glycine) present in all aerobic organisms. Glutathione reductase converts the oxidized glutathione (GSSG) to the reduced form (GSH), with collateral oxidation of NADPH (Diaz-Vivancos et al., 2015). The -SH groups of some enzymes and structural proteins are also protected by GSH, against oxidation either by acting as a scavenger for oxidizing substances or by repairing the –SH groups through the GSH-disulphide exchange reaction (Gill et al., 2013). This non enzymatic antioxidant participates in several biological processes like regulation of enzymatic activity, xenobiotics detoxification, cell division-differentiation- death-senescence, synthesis of proteins-nucleotides as well as phytochelatins, metabolite conjugation, and finally stress-responsive gene expression (Zeng et al., 2017). Glutathione is generated in several cell sites such as endoplasmic reticulum, chloroplasts, cytosol, mitochondria, peroxisomes, vacuoles, and apoplast (Table 1). These are the main sites for intracellular defence against ROS-induced oxidative damage. GSH scavenges H_2O_2, $^1O_2$, $^*OH$ and $O_2^{\bullet-}$ and binds different biomolecules by forming adducts directly with reactive electrophiles (glutathiolation) or by reducing them in the presence of ROS or organic free radicals, yielding GSSG as a byproduct (Dar et al., 2017). The oxidized form can be converted back to GSH by 'de novo' synthesis or through the participation of glutathione reductase (GR); thus keeping a cellular GSH reserve. The concentrations of GSSG/GSH forms modulate the effective redox potential of the cells, therefore in plants growing under unchallenging conditions, GSH compounds are reduced by cellular antioxidant systems, whereas under suboptimal conditions like abiotic and biotic stresses, GSSG are accumulated to higher levels (Couto et al., 2016).

Tocopherol (Vitamin E)

These are lipophilic antioxidants related to the family of vitamin E, only generated by plants, algae and some cyanobacteria i.e. the photosynthetic organisms (Orabi &

Abdelhamid, 2016). The plastids in plants are the main site for their biosynthesis. The synthesis of precursors derived from 2 different metabolic routes is related to the production of tocopherols. The formation of aromatic ring of tocopherols occurs through the homogentisic acid (2,5-dihydroxyphenylacetate; HGA) synthesized via cytosolic shikimate pathway, whereas the phytyldiphosphate (PDP) for the tocopherol tail originates from the plastid methylerythritol phosphate pathway. Finally, the tocopherols are also produced by the conjugation of HGA and PDP (Ji et al., 2016; Szymanska et al., 2017). The main roles of tocopherols are the quenching and scavenging of $^1O_2$ for the cleavage of polyunsaturated fatty acid (PUFA) radical species produced during lipid peroxidation. The process of deactivation of singlet oxygen can be performed through two systems. In the primary system, tocopherol can physically quench $^1O_2$. This is done by donating an electron to the electron-deficient $^1O_2$, forming a charge transfer complex. Latter undergoes an intersystem crossing subsequently, dissociates into α-tocopherol and $^3O_2$. During the second system, tocopherols can chemically scavenge $^1O_2$ through incorporation of singlet oxygen in the 8th position of the 2 rings of tocopherol structure to form hydroperoxydienone. Latter decomposes with the formation of tocopherol 26uinine and tocopherol 26uinine epoxides (Hasanuzzaman et al., 2014; Mekki et al., 2016).

Carotenoids

Chemically these accessory pigments are C40 lipophilic isoprenoids synthesized in plastids, chloroplasts, and chromoplasts through 2 pathways well-differentiated. These pathways are cytoplasmic mevalonate pathway and the plastid-located pathway (Nisar et al., 2015). They are very important in light harvesting as well as photosynthetic apparatus protection from photo-oxidative damage under excess light conditions (Liang et al., 2017b). The scavenging of $^1O_2$ to inhibit oxidative damage is the main function of carotenoids. To avoid the formation of $^1O_2$ and preserve the photosynthetic apparatus carotenoids are needed to quench triplet chlorophyll ($^3Chl^•$) and excited chlorophyll ($Chl^•$) molecules (Mattos & Moretti, 2015). Oxidative removal of carotenoids in plants results in the generation of apocarotenoid compounds which participate in essential functions like photoprotection, photosynthesis, pigmentation, and signaling (Hou et al., 2016).

Flavonoids

These are comprised of a group of polyphenolic compounds predominantly present in plants and possess a benzo- -pyrone structure. These metabolites are produced via the phenylpropanoid route by the activity of a cytosolic multienzyme complex, known as flavonoid metabolon, related to the cytoplasm and the endoplasmic reticulum (ER). They are found in the mesophyll cell nucleus and within ROS generation centers with an ability to take up the most energetic solar wavelengths (UV-B and UV-A) (Brunetti et al., 2013; Mierziak et al., 2014). The flavonoids participate as signal molecules and mediate the cascades of oxidative stresses. They also act as regulators of intra-cellular and long-distance movements of multifunctional growth regulators, like auxins (Mouradov & Spangenberg, 2014). The flavonoids act as secondary antioxidant defense system as well in plant tissues subjected to stressed conditions (Kumar & Pandey,

2013). They are able to quench H_2O_2 and H_2O_2-generated hydroxyl radical in the nucleus of mesophyll cells (Ozyigit et al., 2016).

The reason being dihydroxy B-ring-substituted flavonoid glycosides have a high potential to complex Fe and Cu ions. Latter catalyze the formation of hydroxyl radical in the presence of H_2O_2 via the Fenton reaction. In the centers of ROS generation, they have capacity to quench singlet oxygen (Schultz et al., 2016).

Plastoquinone (PQ) / Ubiquinone (UQ)

Both are prenylquinones with an antioxidant capacity involved in the transport of electrons in ETC oxygenic photosynthesis as well as aerobic respiratory chain. They play essential roles in plant response to stress, regulation of gene expression together with cell signal transduction. PQ/UQ possess an active benzoquinone ring, which is attached to a polyisoprenoid side chain. Their synthesis is very complicated because over 35 enzymes are involved. PQ is found in plants and UQ in plants, animals and microbes. In PQ and UQ biosynthesis many enzymes and the encoding genes are involved. These have been investigated intensively lately (Liu & Lu, 2016). They are localized in different plant cell compartments; PQ in the thylakoids of chloroplasts and UQ on the inner membrane of mitochondria since both are crucial in photophosphorylation and oxidative phosphorylation. Plastoquinone and ubiquinone are scavengers of free radicals preventing protein oxidation, lipid peroxidation, and DNA damage in plants under adverse conditions. Their reserves can be used for the reduction of O_2 to superoxide by semiquinone in reality, and the reduction of superoxide to hydrogen peroxide by hydroquinone (Liu & Lu, 2016; Ozyigit et al., 2016).

ROS Systemic Signaling and Regulation

Under steady conditions, the rate of ROS production in plants is low, however its production considerably increases in plants under adverse conditions, increasing the normal production of $O_2^{\bullet-}$, $^1O_2$, $^*OH$ and H_2O_2 in the intracellular environment, resulting in the activation of the antioxidant machinery to counteract the imbalances. Sometimes, ROS act as signaling molecules under stress and protect against stress. For instance, hydrogen peroxide has a small molecular size, and high mobility through membranes, therefore, it is often involved in the transmission of information between organelles in a cell. H_2O_2, the most stable form of ROS, and perhaps $O_2^{\bullet-}$ have a sufficiently long (milliseconds to seconds) life to act as regulatory compounds, however this largely depends on the presence and activity of dedicated ROS scavengers (Mattila et al., 2015). Also, H_2O_2 has the ability to regulate the activities of many other signaling compounds and intercalate in somesignaling cascades with different biological consequences, such as its own synthesis.

Modulation of activities of other signaling components, and stomatal closure under drought conditions is a common response of H_2O_2-mediated Ca^{2+} signaling. For an activation of NADPH oxidases positioned at the plasma membrane H_2O_2 generation entails a constant Ca^{2+} influx. At the same time, under water deficit, ABA can get involved to induce stomatal closure by reducing the turgor of guard cells. Researchers have proposed that H_2O_2 may act as an intermediary in ABA signaling. It therefore performs

important role as a second messenger in the stomatal closure produced by ABA (Niu & Liao, 2016; Saxena et al., 2016). Treatment with O_3 (Vahisalu et al., 2010) and H_2O_2 (Price, 1990) induce stomatal closure, indicating the existence of mechanisms for rapid perception of apoplastic ROS and other signaling events required for stomatal closure. However, the actual perception mechanisms remain unclear (Sierla et al., 2016). Recent data indicate that the entry of apoplastic ROS into the cytoplasm of guard cells is facilitated by the aquaporin PIP2;1 as *pip2;1* guard cells failed to accumulate H_2O_2 in response to ABA (Rodrigues et al., 2017). An unidentified H_2O_2-dependent Ca^{2+} influx channel (s) is activated in apoplast by ROS accumulation (Pei et al., 2000). The increase in cytoplasmic Ca^{2+} concentration triggers secondary Ca^{2+} stimulated activity of RBOHs and activate anion channels (Wang et al., 2016a). Also, ROS accumulation in the guard cell chloroplasts increases exposure of plants to pathogens. Latter demands establishment of a systemic acquired resistance (SAR) response. In the latter salicylic acid (SA) and jasmonic acid (JA) are key signaling molecules (Lim et al., 2017). Benzoic acid (the immediate precursor of SA) is involved in the H_2O_2 and SA relationship. There is a convertion into SA by the H_2O_2-mediated activation of benzoic acid 2-hydroxylase. It is also well known that SA is capable of enhancement of endogenous level of H_2O_2, mainly by the initiation of SOD activity (Herrera-Vásquez et al., 2015). A plasma membrane intrinsic protein1 (PIP1;4) imported during apoplastic ROS plant pathogen interactions (Tian et al., 2016) and another PIP2;1 (similar to aquaporin) have been suggested to mediate H_2O_2 transport in guard cell signaling (see Awad et al., 2015). Regulatory roles of NADPH oxidases (Kadota et al., 2015; Kimura et al., 2017), apoplastic peroxidases (Daudi et al., 2012), and polyamine oxidases (PAOs) (Yoda, 2006; Yoda et al., 2003) are now well established. However, it is difficult to determine the relative contributions of apoplastic ROS sources to the development of plant immune responses, because currently available data indicate that all three contribute to plant defense.

ROS systemic signaling and regulation has been extensively reviewed recently by Hancock (2016) and Waszczak et al. (2018), and some important questions remain unresolved (eg. dealing with ROS or redox signaling, intracellular interactions between organelle ROS and redox signaling, and the role of ROS in plant development). The important questions above are not likely to be answered by transcriptional analyses but rather from consideration of the biochemical nature and location of these molecules. Nitric oxide is also an important messenger in plants, which shows pro-oxidant and antioxidant properties in plant response to stress. Nitric oxide is related to H_2O_2 because it is responsible for the induction of the scavenging of excess H_2O_2, thus inhibiting peroxide signaling pathways. Moreover, nitric oxide may also cooperate with H_2O_2 to control biotic and abiotic stress tolerance (Qiao et al., 2014). The post-translational modifications like *S*-nitrosylation, reversible addition of an NO group to a protein cysteine residue are usually transmitted by the bioactivity of nitric oxide (NO), leading to *S*-nitrosothiols (SNOs) and expression of alternative oxidase (AOX) (Gupta et al., 2018). However, its production and role in photosynthetic organisms remains partially unresolved (Astier et al., 2018; Umbreen et al., 2018).

Molecular Genetics

Genes and gene products for many of the ROS enzymes and metabolites above have been studied using available molecular biology methods, however this has only been

possible in the recent decade as the methods have become common in plant research. The most often used study approaches include traditional transcriptomic approaches e.g. mRNA isolation (sometimes difficult to achieve), cDNA synthesis and RT-PCR (reverse transcription - polymerase chain reaction). Lately sequencing and searches in available data banks (e.g. BLAST). Gene chip technology (Tamayo et al., 2016) and NGS (next generation sequencing) studies have begun to influence ROS studies and are providing additional information (Hu et al., 2016a; Ozyigit et al., 2016). To address this in more detail, analysis of mutants, double mutants and triple mutants of known isoforms may clarify the physiological significance of many of the enzymes and metabolites from the point of improved ROS tolerance in plants.

Various fuctional isoforms of specific genes for ROS enzymes and metabolites, methods of detection and cellular localization are summarized in Table 1. However, genes for most secondary metabolites are difficult to assess and their regulation difficult to determine; most have been based on related *Arabidopsis* studies (Lan et al., 2017; Trivedi et al., 2013). Also, the instability of key products like MHAR, a very reactive molecule which is short-lived can be very difficult to measure at the molecular level. What is clear from phylogenetic studies of ROS, following an evolutionary divergence of monocots from dicots, there was consecutive duplications of primordial genes. This was followed by differential loss of non-coding sequences resulting in multiple isoforms. Notably, unlike animals and humans which contain few ROS isoform. Different isoforms residing within cells and organelles signify the important role played by isoenzymes in developmental processes and stress tolerance (Noshi et al., 2016). However, the enigma created by the presence of so many different isoforms of ROS genes need to be resolved. More investigations are needed to delineate the genetic regulation of isoform gene expression in response to different types of stresses.

Transgenic plants, specifically upregulated for increased AsA levels do not often result in elevated amounts of AsA, probably due to feedback mechanisms for the labile pool of AsA and different rate limiting steps in the biosynthetic pathway. Cultivation of plants in tissue culture or growth chambers contain lower amounts of AsA than field (outdoor) grown plants. Ascorbate recycling via cytosolic DHAR is one of the rate limiting steps regulating the ascorbate pool size and its redox states (Noshi et al., 2017). Flavonoid biosynthesis genes may turn-off or down-regulate, and the antioxidant properties of flavonoids that can inhibit ROS accumulation are often inhibited. Plant resistance to cell wall-degrading enzymes increases by phenolic and lignin reinforcement of plant cell walls. The toxins produced by pathogens may cause oxidative cross-linking of proteins and so increase resistance against pathogens (Wang et al., 2012). Tocopherol biosynthetic pathway and its regulation is more complex than expected, although well characterized lately. Many genes have been cloned for encoding the key enzymes of these pathways and used for genetic engineering of biofortified staple crops. In several transgenic plants (with extra-genetic SODs) stress tolerance has been observed and studied well (Gill et al., 2015). Role and complexity of the ROS detoxification systems, as well as differences in gene isoforms have been advocated as major areas for further study.

ROS gene expression is strongly regulated during the development and growth of plants under normal conditions. The activity and expression of these genes (and also their isoenzymes) can be regulated in plants by environmental stressed conditions. A key feature not well appreciated is that the ascorbate-glutathione cycle relatedenzymes in chloroplasts have little effect on ascorbate levels in response to photo-oxidative stress. Literature cited in

this review clearly reflects paucity of information on molecular/genetic insights as major functions (and underlying mechanisms) performed by ROS, and also with the fine regulation of gene isoforms by post-translational modifications.

Environmental Stress Tolerance

Modifications of environmental plant growth conditions such as extremes of temperature and light, heavy metal and UV radiation exposure, drought, flooding, salt stress or air pollution trigger an imbalance of redox homeostasis and the accumulation of reactive oxygen species leading to unwanted oxidative damage in plant cells (Bhattacharjee, 2019).

Heavy Metals

Under heavy metal exposure, plant cells trigger a range of physiological and molecular processes to reduce the cytoplasmatic concentrations of non-essential toxic heavy metals like lead, cadmium, mercury and arsenic (Ashraf et al., 2010, 2015; Aziz et al., 2016; Ghori et al., 2019; Gucel et al., 2009a, b; Hasanuzzaman et al., 2015; Nahar et al., 2015; Sabir et al., 2015; Sharma et al., 2016; Ozturk et al., 2008, 2010, 2017). First barrier in plants against excess metals are physical barriers. If they overcome these barriers and enter tissues and cells, many different types of cellular defense mechanisms in plants are initiated, which reduce their adverse effects. These defense mechanisms are related to the biosynthesis of biomolecules such as metallochaperones, organic acids, glutathione, phytochelatins and flavonoid and phenolic compounds, however if these mechanisms fail to restrain metal poisoning, a disruption in the equilibrium of cellular redox systems in plants takes place, leading to an increased induction of ROS (Singh et al., 2016b).

Heavy metals are classified into 2 categories on the basis of their physicochemical features; redox-active and non-redox active. The former includes Cr, Cu, Mn, Fe and latter Cd, Ni, Hg, Zn, Pb, As, Al. First group metals directly generate oxidative injury following the Haber-Weiss and Fenton reactions. They end up in the production of ROS or oxygen free radical species in plants. This causes cell homeostasis disruption, DNA strand breakage and protein defragmentation. The non-redox group causes oxidative stress indirectly via different mechanisms like glutathione depletion, binding to sulfhydryl groups of proteins, inhibiting antioxidative enzymes, or inducing ROS-producing enzymes like NADPH oxidases (Arif et al., 2016).

Several reports discuss about heavy metal exposure effects and antioxidant potential (production) in plants. Some representative examples are outlined in Table 2. Physiological responses of *Oryza sativa* to lead excess (10 and 50 μM) have been studied by Thakur et al. (2017). Their report regarding the lead (Pb)-treated plants mentions that there is lipid peroxidation enhancement as well as increase in SOD, APX and GR activity. The barley roots subjected to a transient exposure to Cd, Pb, Hg or Cu for 30 min have shown an increase in the reactive oxygen species, mainly superoxide, following marked cell death at the site of their generation in the root tips (Tamas et al., 2017). Other studies have demonstrated that *Petroselinum hortense* plants subjected to different concentrations of $CdCl_2$ have shown an increase in the lipid peroxidation,

SOD activity, but CAT and APX activity have decreased (Ulusu et al., 2017). Guo et al. (2017) have studies Cd and oxidative stress relationship in *Iris lactea*; a perennial halophyte subjected to different concentrations of Cd (0-150 mg L^{-1}) during 21 d. The results have revealed an increase of H_2O_2 and MDA content, as well as SOD and POD activity. Moustaka et al. (2016) also reported a decline in quantum yield of photosystem II and a a gradual increase in leaf membrane lipid peroxidation in wheat cultivars under increasing aluminium concentration.

Light

The light intensity is a factor that affects plant photosynthesis. Under low light conditions there is a decrease in net photosynthetic rate (PNmax), ΦPSII (quantum yield of PSII), as well as electron transport rate (ETR) in plants. Nevertheless, the presence of high light conditions usually provokes an imbalance between energy supply and energy consumption resulting in the process of photoinhibition (Pospisil, 2016). The generation of ROS follows limitations in the energy transfer as well as electron transport. A limitation in energy transference can lead to the deleterious triplet chlorophyll formation from singlet chlorophyll because surplus energy absorbed by chlorophyll in the PSII antennae complex is not completely used in the PSII reaction center by charge separation. The presence of triplet chlorophyll is dangerous for organelle, therefore it is necessary to avoid its generation. One of these methods is the maintenance of the quenching singlet chlorophyll and xanthophylls and carotenoids lead to a direct dissisipation of the extra heat energy, or indirectly by the re-arrangement of Lhcb proteins at the quenching site for PSII by PsbS (pigment binding proteins controlling the organization of the PSII antenna). However, this process is not sufficient sometimes to maintain low levels of singlet chlorophyll, therefore, triplet chlorophyll formation occurs from singlet chlorophyll, transferring energy to O_2 forming $^1O_2$. An electron transport reduction on the PSII electron acceptor is connected with full reduction of PQ pool. Due to the full reduction of PQ pools, QB site becomes unoccupied by PQ, forwarding of an electron from QA to QB is blocked. Therefore, a deleterious triplet chlorophyll can result due to back electron transport from $QA^{\bullet-}$ to Pheo and consequent recombination of $Pheo^{\bullet-}$ with $P680^{\bullet}$ (Shumbe et al., 2016). Many studies have reported on the antioxidant machinery present against light stress (see Table 2). Chen et al. (2016) has studied the consequences of low light stress on the watermelon seedlings grafted onto different rootstocks, and they reported that there was an increase of POD activity and MDA content. Xu et al. (2010) have reported that *Festuca arundinacea* plants show an increase of SOD, CAT and APX activities, and an increase of H_2O_2 content when transferred to high-light (500 μmol m^{-2} s^{-1}) conditions from the relatively low-light intensity (100 μmol m^{-2} s^{-1}) for 21 days. However, as Krasensky-Wrzaczek and Kangasjärvi (2018) have pointed out ROS appears to integrate temperature and light signals in crosstalk to control at least calcium signaling, circadian clocks and trigger programmed cell death (PCD) in plants.

Temperature

Climate change with its negative effects on global crop production has become a topic of great concern for plant scientists, as such much research is done on the temperature

Table 2 Effects of different abiotic stresses on the antioxidant machinery in different crops during 2014-2018

Plant species	Stress level	Response	References
Hibiscus cannabinus	Cadmium stress (10-200 μmol L^{-1}), 6 d	Increase of MDA, AsA and GSH concentrations and increase of SOD and POD activities	(Deng et al., 2017)
Acalypha indica	Lead stress (100-150 mg L^{-1}), 12 d	Decrase of POX, CAT and APX activities and increase of SOD activity. Genotoxicity on DNA.	(Venkatachalam et al., 2017)
Citrus sp.	Heat stress (40°C), 7d	Increase of SOD, APX, CAT and GR activities in order to maintain a favourable GSH/GSSG ratio	(Zandalinas et al., 2017)
Cicer arietinum	Cold stress (4°C), 7d	Increase of SOD, CAT, POX acitivities and increase of ascorbate and proline.	(Karami-Moalem et al., 2018)
Deschampsia antartica	UVB stress (21 kJ m^{-2} day^{-1}), 3h	Increase of SOD activity and increase of total phenolic concentration	(Kohler et al., 2017)
Solanum tuberosum	UVB stress (2 h per day of UV-B (1.5 W m^{-2})), 6 d	Decrease of H_2O_2 concentration and increase of GPX and SOD activities	(Oyarburo et al., 2015)
Vigna radiata	Ozone stress (4 h per day of 10 ppb of O_3), 7 d	Increase of lipid peroxidation and SOD and POD activities	(Mishra & Agrawal, 2015)
Triticum aestivum	Ozone stress (5 to 120 ppb), 65 d	Decrase of SOD, CAT and APX activities and increase of GR activity	(Liu et al., 2015)
Amygdalus mira	Water stress (no water supply), 16 d Water stress (water supply at different	Increase of MDA concentration and increase of POD, CAT and APX activities	(Cao et al., 2017)
Camptotheca acuminate	field capacity), 40 d	Increase of MDA concentration and SOD and POX activities	(Ying et al., 2015)
Brassica juncea	Salt stress (0-200 mM NaCl), 10 d	Increase of MDA concentration and increase of SOD, APX, CAT and GR activities	(Yousuf et al., 2017)
Kandelia candel	Salt stress (0-30 ppt NaCl), 2 months	Decrease of SOD, MDHAR and CAT activities and increase of APX and GPX activities	(Hossain et al., 2017)
Pennisetum glaucum	Herbicide stress (atrazine (0-200 mg kg^{-1}), 68 d	Increase of reduced (AsA) and oxidized (DHA) ascorbate concentration	(Erinle et al., 2016)

stress (Awasthi et al., 2015). Such a stress in plants may be related to high temperatures (heat stress) or low temperatures (cold stress, which both chilling stress (<20°C), and also freezing stress (<0°C). Heat stress causes changes at metabolic and structural level in plants affecting essential physiological processes such as respiration, photosynthesis, and water relations (Sehgal et al., 2016). Both plant metabolism and transcriptomes are affected by the cold stress because of the direct inhibition of metabolic enzymes and reprogramming of gene expression (Zhu, 2016) (see also Table 2). Recent experiments have established that Ca^{2+} and ROS are the initial, indispensable factors that evoke the heat and cold stress responses (Gharechachi et al., 2016; Ohama et al., 2017). Chilling stress also involves an imbalance of redox homeostasis causing a disruption between light absorption and light use by inhibiting PCRC, enhancing photosynthetic ROS formation (Bhattacharjee, 2019; Fadzillah et al., 1996). Under extreme temperature conditions, there is a downregulation of the transcriptional activity of rbcL and rbcS genes reducing the activity and reserves of RUBISCO. This fact leads to an increase in electron flux to O_2 related to the generation of ROS (Bhattacharjee, 2019; Zhou et al., 2006). In this sense, there is a negative correlation between accumulation of reactive oxygen species in chloroplast and RUBISCO kinetics and the rate of PCRC (Bhattacharjee, 2019; Prasad et al., 1994).

There are many types of research studies which have focused on the effect of temperature stress on the antioxidant activity in plants. Heat stress (42 °C for 1hour in a hot air oven for 7 days) in *Vigna aconitifolia* plants has resulted in an increase in the activity of CAT, GPOX and SOD (Harsh et al., 2016). The study with two genotypes of *Brassica campestris*, differing in heat tolerance and subjected to three heat-stress treatments (>30 °C for five days) has revealed that there were higher concentrations of reduced ascorbic acid (AsA) and glutathione (GSH) in heat-tolerant genotypes compared to heat-sensitive plants (Zou et al., 2016).

The studies undertaken on the cold stress in barley tolerant and sensitive genotypes has revealed an increase of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) concentrations, being more accentuated in temperature sensitive genotypes. Moreover, the activity of CAT and POD increased to scavenge H_2O_2 and to prevent damage to cells (Valizadeh-Kamran et al., 2017). Oustric et al. (2017) have used tetraploid citrus seedlings or rootstocks. They studied their response to low temperatures to determine which ones are more tolerant to abiotic stress than their respective diploids. As per their report higher activity of catalase (CAT), ascorbate peroxidase (APX) and dehydroascorbate reductase (DHAR) has been recorded in the tetraploid rootstocks compared to diploid ones. However, H_2O_2 levels and SOD activity have not changed significantly.

Ultraviolet (*UV-B) Radiation*

UV is an electromagnetic radiation categorized as; UV-A (315 to 400 nm), UV-B (280 - 315 nm) and UV-C (100 -280 nm) (Ulm & Jenkins, 2015). UV-B exposure provokes injuries in DNA, proteins, and membranes. It is also involved in the photosynthetic activity reduction as well as plant growth. Moreover, exposure to UV-B radiation involves an increase of ROS generation, which may be formed due to the disruption of metabolic activities or owing to the increased activity of membrane-localized NADPH-oxidase (Sharma et al., 2017). In addition, the exposure under UV-B radiation

downregulates the light-saturated rate of PCRC and RUBISCO carboxylation kynetics (Allen et al., 1997; Bhattacharjee, 2019).

UV-B radiation effects on plants has been studied much. These studies focuss on enzymatic antioxidant capacity (Table 2). An increase in the SOD and APX in *Vaccinium corymbosum* has been reported after being subjected to 0, 0.07, 0.12 and 0.19 W m^{-2} of UV-B irradiance for 0-72 h (Inostroza-Blancheteau et al., 2016). According to Raghuvanshi and Sharma (2016), *Phaseolus vulgaris* exposed to UV-B (ambient + 10.2 kJ m^{-2} day^{-1}) radiation has led to an increase. *Prunella vulgaris* grown under short-term UV-B conditions for 15 days has shown an increase in POD, SOD and GSH activities, as well as H_2O_2 and malondialdehyde (MDA) contents (Zhang et al., 2017). Sankari et al. (2017) have studied exposure of UV-B and UV-C radiations in *Bixa orellana* for 5 days. They have reported an increase in CAT, POX and SOD activity in UV-B treated seedlings compared to the UV-C.

Air Pollutants

The air pollutants like sulfur dioxide, nitrogen oxides, carbon monoxide have increased in the atmosphere following the burning of fossil fuels. There has been a release of unburned hydrocarbons and hydrogen fluoride as well. Anthropogenic activities and the use of motor vehicles are the most significant source of particulate matter and increased ozone concentration in urban environments (Gostin, 2016; Saxena & Kulshrestha, 2016). The main site of entrance of air pollutants into plant tissues is through stomata. This enterance ends up with an increase in ROS, causing severe damages to the DNA, proteins, and lipids. Other effects are frequently observed in leaves subjected to air pollution such as reduction of stomatal and epidermal cell size, lower number of stomata, reduction of thecell wall, epicuticular wax deposition, and chlorosis (Uka et al., 2017). There are many references on the effects of air pollution at the biochemical level in plants. Hassan et al. (2017) has investigated the effects of ambient ozone on antioxidant metabolites in pea plants. They report that an increase of antioxidant metabolite activities such as AsA, GR, SOD, reduced GSH and oxidized GSSG has resulted in a better tolerance of pea to O_3. Latter enters plant tissues mainly through stomata, but may decompose in the cell walls due to various ROS, and triggers active ROS generation; ultimately leading to the formation of hypersensitive response; like cell death (Agus et al., 2018).

Early responses to O_3 include accumulation of ethylene (Vainonen & Kangasjarvi, 2014); however, the regulation of most O_3 responsive transcriptsis independent of ethylene, as well as SA and JA, signaling (Xu et al., 2015), suggesting the existence of ROS-dependent apoplast-to-nucleus signaling pathways independent from hormonal signaling. Similarly, Elloumi et al. (2017) have investigated the biochemical effects of fluoride in *Eriobotrya japonica*. The results obtained depict high oxidative stress indices, an increase of H_2O_2 content and lipid peroxidation, and an increase of SOD, CAT and glutathione peroxidase (GPx) activities in leaves and roots under ozone stress. The study on the effects of SO_2 pollution on biochemical markers in *Trichilia dregeana*, carried out by Appalasamy et al. (2017) has also reported an increase in intracellular H_2O_2 production and electrolyte leakage.

Drought

This phenomenon is observed when plant water potential and turgor decrease. As a consequence, plants face difficulties to execute normal physiological functions. Main reasons for this phenomenon in plants are a high restriction of water supply to the roots and high transpiration rate (Shahzad et al., 2016).The effects of this type of stress in plants are reduction in the rate of cell division and expansion, leaf and stem size, root multiplication, disturbed stomatal oscillations, and poor plant water and nutrient relations; that can result in a decrease of crop productivity and water use efficiency (Verslues, 2017). Reduction of water supply leads to an oxidative stress with overproduction of ROS. Under water stress, there is a generation of a variety of ROS such as $O_2^{\bullet-}$, $^1O_2$, $^*OH$ and H_2O_2 related to the decline of photosynthetic activity. This decline can be due to stomatal closure with the consequent decline of CO_2 influx and damage to the photosynthetic machinery (Kaur & Asthir, 2017) (Table 2).

Many studies have been carried out on the effects of this type of stress on the overproduction of ROS in plants. Celik et al. (2017) have studied its effects (7 days with holding irrigation) on the antioxidant machinery in two different industrial tomato varieties. They have reported an increase in the POX, APX, SOD and CAT activity in both varieties under drought. *Vicia faba* plants have been subjected to 3 water treatments (90%, 60%, and 30% field capacity) to study the drought stress effects on enzymatic activity. The results have shown an increase of SOD, CAT, and GPX under this abiotic stress (Abid et al., 2017). Under drought conditions (7 days of water deprivation), *Punica granatum* plants showed an increase of lipid peroxidation (nearly three-fold compared to control plants) and H_2O_2 intracellular content (Catola et al., 2016). The activity of SOD, POD and CAT has increased even under medium levels of drought (Li et al., 2017) with the aim of determining the effects of different levels of drought stress (four treatments; control (water holding capacity (70-80%), mild drought (60-70%), medium drought (50-60%) and serious drought (35-45%), water holding capacity respectively) in potato seedlings. Lipid peroxidation and H_2O_2 concentration also increased in cucumber under drought conditions as reported by Ouzounidou et al. (2016).

Salinity

Salinity is one of the major environmental threats limiting plant growth and productivity. The effects of salt stress are related to water and ionic stress that result in growth reduction and nutrient imbalances in plants (Giannakoula et al., 2015; Hasanuzzaman et al., 2019; Negrao et al., 2017; Ozturk et al., 2006). Salt stress effects can be overcome by an osmotic adjustment, as well as scavenging of ROS to avoid lipid peroxidation, protein oxidation plus DNA damage in cells (Acosta-Motos et al., 2017). Since salinity is a serious concern for crop production, much work has been published in this connection notable among these being (Hasanuzzaman et al., 2019; Ozturk et al., 2006). Wei et al. (2017) have reported an increase in the H_2O_2 and GSSG contents and a decrease of GSH under saline conditions following an experiment carried out with a wild diploid cotton species (*Gossypium klotzschianum*). Sharp increases in H_2O_2 production was correlated to respiratory burst oxidase homologue (RBOH) genes and a higher NADPH oxidase activity, enhanced Na^+ exclusion from the root and promotion of early stomatal closure (Niu et al., 2018). Farhangi-Abriz and Torabian

(2017) have studied common bean plants under 3 salinity levels (non-saline, 6 and 12 dS m^{-1} of NaCl). The results obtained by them have shown that CAT, APX, SOD and POD activities have increased together with MDA and H_2O_2 content in leaf and root in plants under high salt level. Vighi et al. (2017) determined the activation of the enzymatic antioxidant system under saline conditions (150 to mM NaCl for 0, 6, 24, 48, and 72 h) in two genotypes of rice: BRS Bojuru (tolerant) and BRS Pampa (sensitive). The results report an increase in H_2O_2 content but MDA decreases in the tolerant genotype, but no change has been recorded in the sensitive genotype in H_2O_2 content but an increase of MDA content. Moreover, both genotypes had shown an increase of SOD activity (recent examples are in Table 2).

Herbicide Stress

Weeds in a field are accepted as a great drawback for farmers and crop growers since weeds compete with crops for water, nutrients, and light resulting in a significant yield reduction. As a consequence, growers frequently use herbicides as the quickest chemical solution against weeds (Davis & Frisvold, 2017). Nevertheless, farmer applications frequently cause damage to non-target plants affecting metabolism of the plant, photosynthesis, growth and especially leads to the activation of the antioxidative system and ROS-scavenging systems (Varshney et al., 2015). Herbicides exposure in plants involves reactive oxygen species generation and metabolic imbalances. The ROS generation may be ascribed to the inhibition of the normal flow of electrons during operational Z-scheme showing PSII-mediated reduction of plastoquinone generating then a a monocation radical able to react with molecular oxygen (Arora et al., 2002; Bhattacharjee, 2019).

Concerning herbicide stress, it is possible to find many references to the effects of herbicides on antioxidant machinery in plants. Seven-day-old seedlings of *Pisum sativum* were treated with 10 mM of isoproturon. The application of this herbicide resulted in an increase of H_2O_2 intracellular content, ion leakage and lipid peroxidation due to induction of oxidative stress. Also, SOD, CAT and APX activity increased while GPX activity decreased (Singh et al., 2016c). This study was carried out with wheat plants which were exposed to 0.8 to 8.0 mg kg^{-1} ametrine for 7 d. The high presence of ametrine in the wheat resulted in a high production of ROS causing injuries in membrane lipids. The wheat plants have activated the generation of SOD, CAT, POD, APX, GR and GST antioxidant enzymes (Jiang et al., 2016a). Increase of SOD, APX, CAT and POD activity was exhibited in *Pennisetum americanum* plants treated during 68 days with atrazine at moderate concentrations (20 mg kg^{-1} or below) (Jiang et al., 2016b). In another experiment, rice plants were treated with different butachlor treatments in order to evaluate the effects at biochemical level of this herbicide extensively applied in paddy fields. The results reported an increase of H_2O_2 intracellular content, ion leakage and lipid peroxidation due to the adoption of this herbicide (Islam et al., 2017).

Concluding Remarks and Future Directions

There is an equilibrium between generation and removal of ROS under normal conditions. As such, ROS can be both beneficial and detrimental, but this balance

may be disrupted by an exposure to stressful conditions like heavy metals, light intensity, temperature extremes, resulting in a high ROS generation and subsequent oxidative stress. Latter occurs because of high reactivity and toxicity of ROS species like superoxide radical ($O_2^{\bullet-}$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($^*OH$), produced extra- or intra-cellularly. The main damages of ROS are closely related to the inactivation of nucleic acids, lipids, and proteins. Main sites of ROS generation in the cell include photosynthetic tissue and meristematic areas of shoots and roots; apoplast, mitochondria, chloroplasts, and peroxisomes. In order to detoxify the harmful effects of ROS during oxidative stress, the main response in a cell is to activate the antioxidant machinery. There are 2 groups of antioxidant defenses. First group covers non-enzymatic ones (glutathione, α-tocopherols, carotenoids, plastoquinone/ubiquinone and flavonoids) and second group covers enzymatic ones (superoxide dismutase, catalase, glutathione peroxidase and glutathione reductase). Therefore, knowledge concerning the mechanisms triggered at the cellular level by plants to overcome oxidative stress may be useful in future for the survival of plants.

The cellular and molecular mechanisms acting during the adaptation and acclimation of plants to their environment have been elucidated. These reports fully highlight some important signaling functions for ROS in these processes. In view of this the concept of ROS as a signaling substance has been established. ROS levels are tightly controlled, and increased ROS levels often serve as an initiation for multiple signaling, and ROS signaling specificity is likely determined by local ROS sensors and metabolites. The accumulation of ROS is necessary for multiple metabolic, physiological, and developmental processes that function at the cellular and whole-organism levels. ROS accumulation and signaling is connected with Ca^{2+} signals, and recent documentation of chloroplast-to-nucleus proteins and H_2O_2 transport means that the previously proposed retrograde signaling pathways based on ROS diffusion to thecytoplasm should be re-evaluated. The relationship between compartment-specific changes in redox balance and ROS formation, and how they affect each other are not always clear.

Presently, reports are not exhaustive on the molecular genetics in the current context of ROS and stress. The aspects like biochemical-genomic characterization, techniques for ROS genes and metabolites assays as well as their modulation in plants under stress have not been discussed much. Very few reports have tried to enlighten such topics. Molecular insights into the interaction between ROS enzymes and metabolites, and their potential synergistic role in the control and improvement of plant stress tolerance have yet to be realised. Improved, efficient and reproducible techniques for bioassays of ROS are now required, and better diagnostic methods may lead to biosensors and biomarkers. Plant signal transduction under stress conditions will help in designing better strategies for stress tolerance in plants.

In view of the discussions presented above future investigations must deal with the key questions related to co-ordinated organization of different components of carotenoid pathway and known sub-organellar localisation. These can facilitate further advancement in the field of carotenoid metabolic engineering to improve crop nutritional quality. The response to photo-oxidative stress may be triggered bythe collapse of chloroplastic glutathione redox homeostasis, and information about the physico-chemical properties in these reactions are essential.

Molecular genetics approaches have the ability to identify conserved motif signatures of ROS gene constructs, their phylogenetic trees and 3D protein structures, and

generate data on protein-protein interaction networks. To evaluate the role of specific gene isoforms upon exposure to oxidative stress at a higher level antisense and micro RNA technology can also be employed. The inducing agents and interactions with other metabolites need be considered. Induction and function of key pathway genes suggests, a tremendous genetic potential lays before us for improving plant tocopherol and carotenoid contents. The complex genetic network for secondary metabolite biosynthesis can be elucidated via QTL mapping, association analysis, and homologous gene mapping and alignment. These are important tools for improving plant biotic and abiotic stress tolerance. These will help much in an efficient management of agricultural challenges under changing global climate scenarios.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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