An Overview of Roles of Enzymatic and Nonenzymatic Antioxidants in Plant

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Abstract

The postindustrial age radically altered global climate conditions, posing a difficult task for plants and crops to thrive under stress environments like high temperatures, salt, waterlogging, heavy metals, drought, and so on. A small period of poor weather had a substantial impact on the development and growth of plants, eventually influencing crop quality, yield, and agricultural sustainability as a whole. Plant cells produce free oxygen (O_2) radicals and their derivatives, known as reactive oxygen species (ROS), as by-products of other reactions in such hostile environments. Furthermore, these ROS molecules are used as signaling molecules in plants for signal transduction in response to changing environmental conditions. The cytoplasmic balance that triggers the antioxidant defense mechanisms is disrupted as a result of the excessive accumulation of ROSs inside the cell. Plants have developed a complicated ROS scavenging system to avoid sensitive cellular components from being damaged

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by reactive oxygen species. Enzymatic antioxidants, like catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), glutathione peroxidases (GPX), and ascorbate peroxidases (APX), and nonenzymatic antioxidants, like glutathione, ascorbate, tocopherols, and phenolic compounds, are important antioxidants that play key roles in eliminating superoxide (O_2^-) and (H_2O_2). The antioxidant capacity of plants is the sum of the activities of all enzymatic and nonenzymatic antioxidant systems. This chapter seeks to provide fundamental information on enzymatic and nonenzymatic antioxidants, their occurrence, characteristics, and the antioxidant defense system involved in reactive oxygen species (ROS) detoxification under various stresses, as well as their interactions with cellular components.

Keywords

ROS · Abiotic stress · Oxidative stress · Enzymatic antioxidants · Nonenzymatic antioxidants

1.1   Introduction

Based on their biochemical nature, antioxidants are divided into two categories: enzymatic and nonenzymatic. While substantial anabolic and catabolic reactions are occurring, these chemicals are engaged in the detoxification of free radicals or reactive oxygen species (ROS). Both classes of antioxidants are capable of efficiently neutralizing ROS and converting them into relatively stable nontoxic molecules, preventing oxidative damage to cellular apparatuses. As a result, antioxidants are the most important first line of defense against the oxidative stress-induced cell damage. Antioxidants, both enzymatic and nonenzymatic, are electron-rich compounds that readily share electrons with highly energetic ROS and free radicals, stabilizing cellular randomness.

Furthermore, they may interfere with the oxidizing chain reaction in order to reduce free radical damage (Apel and Hirt 2004). Antioxidants are also known as ROS scavengers because they use dynamic and synergistic processes to keep the intracellular concentration of ROS in check. It (antioxidant) is a substance that may scavenge reactive oxygen species (ROS) without being converted into a harmful radical (Noctor and Foyer 1998). As a result, antioxidant enzymes are crucial for sustaining good cellular and systemic health and well-being. All highly reactive, oxygen-containing molecules, including the free radicals, are referred to as ROS. The hydroxyl radical (OH^-), singlet oxygen, superoxide anion radical, H_2O_2 (hydrogen peroxide), hypochlorite radicals, lipid peroxides, and nitric oxide radical are all examples of reactive oxygen species. All have the ability to react with membrane lipids, enzymes, and other molecules, resulting in the loss of critical cellular structures and functions and a variety of negative consequences for plants and animals. As previously stated, free radicals or ROS are highly reactive compounds that are released directly or as a by-product during normal metabolic processes in
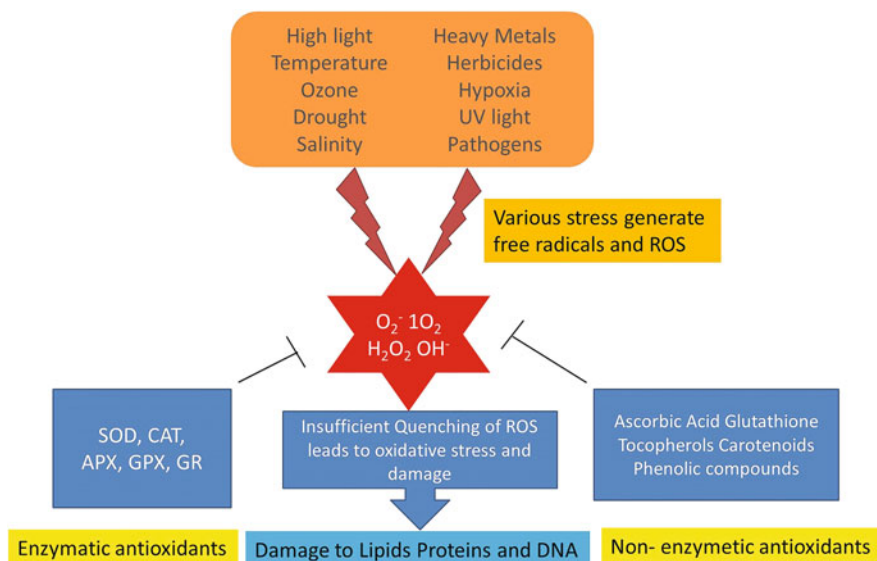
Fig. 1.1 Illustrative representation of different agents generating free radicals and reactive oxygen species in plants and different antioxidants scavenging agents

various cellular compartments like mitochondria, chloroplast, peroxisomes, and apoplast (Panieri and Santoro 2015), but their synthesis is accelerated during extreme conditions. Because these compounds have a lone pair of electrons, they are very unstable and thus highly reactive (Del Río and López-Huertas 2016). ROS-induced oxidative stress is a well-controlled process, and the balance in-between the ROS and its quenching define a plant's and any other organism's well-being. If antioxidants reach a condition of disequilibrium, meaning they are unable to destroy free radicals, the cell and tissue suffer oxidative damage. The degree of oxidative stress caused by free radicals/ROS is determined by their concentration, kind, synthesis site, and developmental stage (Møller et al. 2007). Plants exposed to ROS for a long time period can suffer considerable damage to their cell machinery and biomolecules, including protein oxidation, lipid peroxidation (Mittler 2002), PCD (programmed cell death), and inhibition of the enzymes and also damages nucleic acid, which can lead to tissue necrosis or plant death (Fig. 1.1) (Pérez-Pérez et al. 2012).

1.2   Enzymatic Antioxidants

Several enzymes, like GPX, SOD, glutathione reductase, APX, and CAT (catalase), are the enzymatic components of the antioxidant defense system found in diverse subcellular compartments. In plants under oxidative stress, these enzymatic antioxidant molecules are critical for maintaining cellular homeostasis.

1.2.1   SOD (Superoxide Dismutases)

SODs are enzymes which can catalyze the dismutation/partitioning of O_2^- to H_2O_2 and molecular oxygen (O_2). Because O_2^- is a typical consequence of oxygen metabolism, SOD is thought to be the first line of defense against the reactive O_2 species-induced damage. By neutralizing the superoxide radical, the Haber–Weiss reaction eliminates the possibility of hydroxyl ion production. These enzymes are classed as metalloenzymes based on metal cofactors, subcellular distribution, and protein folds. Cu-/Zn-containing SODs have been found in prokaryotic and eukaryotic organisms, and in plant cells, they can be found in the cytoplasm, extracellular space, or chloroplasts and can also be found in lysosomes, cytoplasm, and nuclear compartments in mammalian cells. Plant cytoplasm and chloroplasts have been found to have Fe-containing SODs. MnSODs are found in all kingdoms but particularly in eukaryotic mitochondria, where they play a critical role in preserving mitochondria by scavenging ROS (Pilon et al. 2011) and initiating cellular differentiation (Moller 2001, 2012). According to Feng et al. (2016), SODs are found in different organisms, such as mammals, yeast, bacteria, and plants. Multiple genes producing SODs exist in plants, and their expression can be influenced by developmental stage, tissue type, and environmental cues (Scandalios 2005; Menezes-Benavente et al. 2004). There are nine SOD genes in tomatoes, which are unevenly distributed across 12 chromosomes and include four Cu/ZnSODs, one MnSOD, and three FeSODs (Feng et al. 2016). Various investigations revealed that different types of SOD genes had varied levels of expression under harsh environmental conditions. Underwater stress, for example, the expression patterns of the banana genes like MaCSD1B and MaMSD1A, which are involved in SOD production, were utterly incompatible (Feng et al. 2015).

Furthermore, SODs with the same cofactor may not necessarily have the same role in various species. MnSOD expression was not affected by oxidative stress in *Arabidopsis*, but it was affected significantly by drought and cold stress in wheat and salt stress in pea (Baek and Skinner 2003). Additionally, alternative splicing and miRNAs have been implicated in the regulation of SOD gene expression (Lu et al. 2010). Various plant species, such as *Populus trichocarpa*, *Sorghum bicolor*, *Musa acuminata*, and *Arabidopsis thaliana*, have been found to contain the SOD genes (Srivastava et al. 2009).

1.2.2   CAT (Catalases)

These are tetrameric enzymes, with iron as a prosthetic group attached to each monomer; they catalyze the energy-efficient disproportionation of H_2O_2 into water molecules (H_2O) and molecular oxygen (Regelsberger et al. 2002; Zamocky et al. 2008). In contrast to H_2O_2, it has a lower affinity for R-O-O-R (organic peroxides) and also has a higher turnover rate among antioxidant enzymes and is unique among antioxidant enzymes because it does not need a reducing counterpart. Unfavorable conditions necessitate increased energy generation, and expenditure by plants and

other organisms leads to an increase in catabolic reactions, which yields H_2O_2. CATs are predominantly attached to peroxisomes, where they execute β-oxidation of fatty acid, photorespiration, and purine catabolism, all of which produce a considerable amount of H_2O_2 (Mittler 2002). Hydrogen peroxide (H_2O_2) is also a key signaling molecule in plant development and plant response to the environment (Mhamdi et al. 2010). Plants have numerous CATs, each produced by a separate gene, that respond differently to different stressors that are known to cause ROS. Recent investigations reveal that CAT is also prevalent in other subcellular compartments like the mitochondria, chloroplast, and cytosol, albeit no evidence of substantial CAT activity has been observed (Mhamdi et al. 2010). CAT1 is mostly expressed in plant pollen and seeds; on the other side, CAT2 is not only expressed in photosynthetic tissues (mostly) but also expressed in seeds and roots, while CAT3 is predominantly expressed in vascular tissues and leaf in angiosperms (McClung 1997; Frugoli et al. 1996).

1.2.3 APX (Ascorbate Peroxidases)

Ascorbate peroxidases are the heme peroxidase superfamily that is involved in the recycling of AsA and the response to environmental stress in plants (Ishikawa and Shigeoka 2008; Lazzarotto et al. 2011). These enzymes catalyze the conversion of H_2O_2 to water and monodehydroascorbate (MDHA) using ascorbate (AsA) as an electron donor (Caverzan et al. 2012). Plants have five different isoforms of APX, which are found in diverse subcellular compartments like the cytosol, mitochondria, peroxisomes, and chloroplast (Sharma and Dubey 2005). These enzymes are divided into groups based on the amino acids they contain and the cell compartments in which they are found. Several abiotic stressors in plants have varied effects on the APX genes (Rosa et al. 2010; Caverzan et al. 2014). APXs, CATs, and SODs must be in balance to determine the effective intracellular level of H_2O_2 and oxygen, and variations in this equilibrium appear to trigger compensation processes (Apel and Hirt 2004; Scandalios 2002, 2005). Under a normal and stressful environment, APX is a key component of the ASC–GSH (ascorbate–glutathione) cycle, which eliminates excess H_2O_2 from plant cells (Mittler and Zilinskas 1991). Because APX is more broadly distributed and also has a higher affinity for hydrogen peroxide than CAT, it is a more effective H_2O_2 scavenger during stressful situations. APX is a chloroplastic isoenzyme expressed by a single gene in higher plants (apx1).

1.2.4 GPx (Glutathione Peroxidases)

The term glutathione peroxidases collectively describe the group of phylogenetically related nonheme and thiol-containing peroxidase enzymes. It was called after GPx-1, the mammalian tetrameric seleno enzyme, which was the first to be defined and reported. More than 700 members of the GPx family have been identified so far, overall domains of life. G. C. Mills discovered its activity in red blood cells in 1957,

where it protected hemoglobin from oxidative degradation. The biological function of GPxs is to catalyze the H_2O_2 reduction or lipid hydroperoxides into H_2O or the corresponding alcohols by using GSH (glutathione) as a reducing agent. The catalytic moiety of selenium was later identified as selenocysteine, the 21st naturally occurring amino acid. Selenocysteine was recommended as a way to ensure a rapid reaction with the hydroperoxide and glutathione reducibility. GPx1 is found in the mitochondria, chloroplasts, and cytosol of a wide range of plants and animals, and it serves as an antioxidant in several cellular compartments. In human beings, there are eight distinct glutathione peroxidase isoforms (GPx1-8) that have been found. The mechanism of reaction comprises oxidation of the selenol of a selenocysteine residue by H_2O_2. The RSeOH (selenenic acid) group is formed as a result of this action. A two-step mechanism converts selenenic acid back to selenol, starting with a reaction with GSH to create the GS-SeR and H_2O. The GS-SeR intermediate is reduced back to selenol by a second GSH molecule, releasing a by-product GS-SG.

1.3   Nonenzymatic Antioxidants

Antioxidants that are generally nonenzymatic in nature are found in all subcellular parts of plants. These antioxidants help to detoxify reactive O_2 species and free radicals and can also help to reduce the substrates from antioxidant enzymes (Mittler 2002). The primary cellular redox buffers GSH and ascorbate, along with carotenoids, tocopherol, and polyphenolic compounds, are different forms of non-enzymatic defense pathways (Scandalios 2002).

1.3.1   Vitamin C (Ascorbic Acid)

Ascorbate is a well-known vitamin having anti-oxidizing properties that have been found in a variety of organelles and even apoplast. It occurs in different reduced and oxidized forms, as ascorbic acid (90% of the ascorbate pool) and mono- and dehydroascorbic acid (Smirnoff 2011). The ratio of oxidized to reduced ascorbate is a key element that influences plant oxidative stress resistance (Conklin et al. 2000; Cruz-Rus et al. 2012). Glutathione reductase, dehydroascorbate reductase, and monodehydroascorbate reductase are among the NAD(P)H-dependent enzymes that keep AsA in its reduced state (Mittler 2002; Foyer and Noctor 2011). According to the Horemans et al. (2000), the mitochondria are the major site for ascorbate production, from which it is transferred to other cell organs via a proton-electron gradient. Due to its ability to transfer electrons in enzymatic and nonenzymatic processes, AsA is a critical component for ROS detoxification in the aqueous phase. AsA can quickly remove O_2^-, hydroxide ions, and $1O_2$, and therefore, it can reduce H_2O_2 to H_2O by the ascorbate peroxidase mechanism, protecting membranes (Blokhina et al. 2003). In the ascorbate–glutathione cycle, APX utilizes two AsA molecules to decrease H_2O_2 to water, with the intermediate monodehydroascorbate, which is a short-lived radical that is further disproportionated into dehydroascorbate

(DHA) and AsA. Furthermore, it plays a crucial role in the dynamic and control of the cell cycle, the advancement of the G1 to S stage of the cell division pathway, and cellular elongation, as well as many photosynthetic functions (Smirnoff 2011). Although the exact biosynthetic process for ascorbate is unknown, it is speculated that D-glucose may be used as a precursor.

1.3.2 Glutathione

Glutathione (GSH) oxidation by ROS results in the formation of GSSG, which is present in all plant cell compartments. In cellular compartments, GSH, together with its oxidized counterpart, GSSG, maintains a redox balance. It has been revealed that the GSH/GSSH pair is involved in gene regulation and cell cycle pathways (Mittler 2002). The antioxidant glutathione and ascorbic acid are prolific and stable, and they have the right redox potential to react with different varieties of substrate and compounds. Glutathione is a tripeptide molecule made up of three amino acids, glutamine, cysteine, and glycine, that are found in all plant cell parts, including the cytoplasm, vacuoles, chloroplasts, mitochondria, and endoplasmic reticulum (Millar et al. 2003). In most plant cells, glutathione is the important source of nonprotein thiols. Glutathione is appropriate for a wide range of metabolic actions in all organisms due to the presence of a thiol group and its reactivity. The reduced form of glutathione (GSH) is found at higher concentrations in chloroplasts. Unlike the ascorbate biogenesis system, the glutathione biosynthetic pathway is well-established and identical throughout all domains of life. The amino acids are linked to produce the full tripeptide in two ATP-dependent stages catalyzed by GSHS and γ-ECS. These events take place in chloroplastic and non-chloroplastic segments, and glutathione concentrations and redox status play a crucial role in different pathways. GSH is used to reduce DHA both in an enzymatic and nonenzymatic way in the ascorbate–glutathione pathway, and it is then oxidized to GSSG. Glutathione reductase catalyzes the regeneration of GSH from GSSG, with NADPH as the reducing agent. The cysteine residue in GSH's tripeptide has a high reactivity potential. GSH scavenges harmful H_2O_2 by reacting nonenzymatically with O_2^-, OH^-, and $1O_2$. The ability of GSH to replenish another potent antioxidant, ascorbic acid, via the ascorbate–glutathione cycle gives it a crucial role in antioxidative defense (Millar et al. 2003). It has been observed that the antioxidant property of glutathione was utilized to achieve transgenic lines of tobacco (Foyer and Noctor 2005), which can withstand oxidative stress (Del Río and López-Huertas 2016). GSH has been involved in sensing alterations in redox equilibrium and transferring these alterations to appropriate target proteins, in addition to being a co-substrate and reducing agent in defense against reactive oxygen species.

1.3.3 Vitamin E

All types of tocopherols are methylated fat-soluble phenols that have similar to vitamin E (Sharma et al. 2012). They primarily function as antioxidants in plants, algae, and mammals, but they may also have additional functions. In lipid bilayers, α-tocopherol is the most effective for the removal of peroxyl radicals. Tocopherols are the most powerful scavengers of free radicals. At the energy of 323 kJ mol^{-1}, the hydroxyl bond present in vitamin E becomes weaker than in the majority of phenols and readily liberates hydrogen atom and thereby helps in quenching peroxyl radicals and other free radicals, decreasing their harmful effect (Lide 2006). The produced tocopheryl radical is generally nonreactive, and through redox interaction with a hydrogen donor such as ascorbate or other antioxidants, it reverts to tocopherol (Igamberdiev and Hill 2004; Traber and Stevens 2011). Tocopherols are integrated into cell membranes and thereby protect the chloroplast membrane from oxidative damage due to their fat-soluble nature (Blokhina et al. 2003). α-Tocopherols are significantly bioactive and prominent antioxidants in the chloroplast lamina and are primarily utilized for defending them against the photooxidative effect. It has been observed that a single α-tocopherol molecule may neutralize one 20 singlet oxygen and also act as reusable chain reaction terminators for PUFA radicals synthesized during oxidation of lipids (Hare et al. 1998; Wu and Tang 2004; Ledford and Niyogi 2005). Photosynthesis and other metabolic processes in chloroplasts produce ROS, which causes lipid peroxidation in plant cells. To cope up with a range of abiotic stress conditions, the content of α-tocopherol in photosynthetic plant tissues increases dramatically (Noctor 2006). The ability of α-tocopherols to scavenge and quench ROS aids in the modulation of signal transduction and the stabilization of membranes (Kruk et al. 2005; Noctor 2006). They work as a free radical capturing process by preventing the chain extension stage in lipid autooxidation. Plants respond to oxidative stress by expressing genes involved in tocopherol production (Table 1.1) (Giacomelli et al. 2007; Wu and Tang 2004).

1.3.4 Carotenoids

Carotenoids, also known as tetra terpenoids, are pigments that naturally occur in plants and microorganisms (Otles and Cagindi 2008). To date, more than 750 natural carotenoids have been discovered. These chemicals give different vegetables and fruits their distinct colors. Xanthophylls and carotenes are the two broad categories of carotenoids. Carotenoids are classified into two broad subclasses, xanthophylls and carotenes; the former class contains oxygen, whereas the latter class is purely hydrocarbons and contains no oxygen (Ngamwonglumlert et al. 2017). Carotenoids found in the human diet may help to prevent cancer, age-related muscle degeneration, atherosclerosis, and other disorders. These pigments are lipid-soluble and are absorbed together with fats through the gut tract. Carotenoids have a variety of beneficial activities in plants, including attracting pollinators, indicating fruit development, assisting in photosynthesis, and protecting cells from light-induced damage

Table 1.1 ROS and their characteristics

ROS	Site of generation	Mode of action	Interaction with protein	Interaction with DNA	Scavenging systems
O_2^-	Membranes, mitochondria, chloroplast	The reaction occurs with a double bond having molecules such as iron–sulfur proteins	Through Fe-center	Excessively low	Super oxide dismutase
OH^-	Membranes, chloroplast, mitochondria	Highly reactive with different biomolecules	Fast reacting	Quick reacting	Flavonoid and proline
H_2O_2	Membranes, mitochondria, chloroplasts peroxisomes	Oxidizes proteins and help in the generation of OH^- through O_2^-	Reacts with Cys residue	Excessively low	CAT and flavonoid
O_2	Membranes, mitochondria chloroplasts	Oxidizes proteins, polyunsaturated fatty acid, and deoxyribonucleic acid	Highly reactive for Trp, Met, His, Tyr, and Cys amino acids moties	Polyunsaturated fatty acid	Carotenoids and vitamin E

in plants and in photosynthetic bacteria and algae (Lerfall 2016). The ability of β-carotene to quench free radicals such as O_2^-, OH^-, and $1O_2$ without undergoing any changes or degradation is largely due to its highly delocalized polyene backbone or conjugated double bond structure, which is primarily responsible for its antioxidant behavior. Carotenoids found in higher concentrations in particular tissues and organs can protect lipids against oxidative damage.

1.3.5   Phenolic Compounds

Tannins, flavonoids, lignins, and stilbenes are examples of phenolic compounds, which constitute a varied group of naturally occurring secondary metabolites common in plants. Multiple phenol rings distinguish these compounds, making them suited for free radical scavenging in both de novo and in vitro conditions. Over 8000 phenolic bioactive substances have been detected in different plant families. Phenylalanine/shikimic acid is the common intermediate precursor for all plant phenolic compounds. Under in vitro conditions, polyphenols have been shown to be more potent antioxidants than ascorbate and tocopherols. Phenols are the most significant dietary elements for humans, providing bitterness, color, astringency, flavor, odor, and oxidative stability in food (Schroeter et al. 2002). Antioxidative activities of polyphenols are characterized by the presence of readily available donor hydrogen or electron (Rice-Evans et al. 1997). In another way, phenols alter the peroxidation kinetics of lipid membrane and packaging, thereby protecting the membrane integrity (Schroeter et al. 2002). Furthermore, phenolics have been implicated in the H_2O_2 scavenging cascade in plant cells. Polyphenols play different functions in plants, which include pigmentation to plants; increase and decrease of plant growth regulators, for example, auxin; UV protectants against ionizing light; deterrence to herbivores; phytoalexins; and signaling compounds in ripening and other plant developmental activities (Huber et al. 2003; Lattanzio et al. 2006).

1.4   Conclusion

Antioxidants are created normally, but they are triggered and upregulated in stressful situations, which help to retain the structural firmness of cell organelles while probably reducing oxidative damage. Plant defense is aided by a number of antioxidant enzymes. The production and activation of ROS scavenging enzyme systems in transgenic plants to increase their tolerance to a variety of stress conditions. Furthermore, because numerous enzymes and their different isoforms are involved and reactive oxygen species is only one of the major factors of plant resistance to unfavorable environmental and biotic stimuli, further research is needed in this field. The increasing number of articles addressing superoxide dismutase, common antioxidant enzyme, ascorbate peroxidase, glutathione peroxidase enzyme, and glutathione reductase enzymes demonstrates these enzymes' favorable responses to biotic and abiotic stressors. These findings highlight the need to investigate these

enzymes in order to better understand their role in the scavenging of hazardous cell products in a variety of species and the relationship between biological processes and oxidative stress.

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