

ANTIOXIDANT DEFENCE SYSTEM AND ITS STRESS FACTORS IN PLANTS

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Abstract

In normal oxygen activity metabolism, reactive oxygen species originate as a natural by-product. Apoplasts, chloroplasts, mitochondria, and peroxisomes are the main sites of the production of reactive oxygen species in the cell. Enzymatic antioxidants like catalase, superoxide dismutase, ascorbate peroxidase, glutathione reductase, general peroxidases, monodehydroascorbate reductase as well as dehydroascorbate reductase and non-enzymatic antioxidants such as ascorbic acid, alpha-tocopherol, glutathione elimination, carotenoids, ubiquinone/plastoquinone and flavonoids; Both metabolite and enzyme classes collaborate to scavenge reactive oxygen species, but also to analyze plant signaling, immunological response, growth, and development.

1. INTRODUCTION

Since the generation of molecular oxygen by photosynthesis (Singh et al., 2016a), reactive oxygen species have occurred as undesirable by-products via redox cascades, electron transport systems, and metabolic pathways, particularly under unfavourable conditions. Scavenging mechanisms for reactive oxygen species can modulate its cellular damaging capability. Fluctuations in homeostasis of reactive oxygen species are known as first marks of heterogeneity in environmental conditions (Berens et al., 2017; Waszczak et al., 2018 and Nafees et al., 2019). The presence of antioxidant compounds in cellular compartments is important for continued cellular survival and detoxification of reactive oxygen species ("Evans et al., 2016; Pucciariello and Perata, 2017 and Sies, 2018"). The generation of reactive oxygen species in plants involves several biomolecule reactions, necrosis, and apoptosis, as well as modification of multiple signaling pathways and gene expression. (Dalton et al., 1999). Reactive oxygen species produce cytotoxicity under adverse conditions ("De Gara and Foyer, 2017 and Wang et al., 2018") by disrupting nucleic acid conformation via processes such as strand breaks, deoxyribose oxidation, nucleotide deletion or removal, base modification, DNA protein cross-linkage (He et al., 2018), increasing fluidity and permeability of membranes through lipid peroxidation (Ozgun et al., 2018), (Mittler, 2017). The stressful conditions for plants that disrupt homeostasis of reactive oxygen species include light intensity, heavy metal presence, high temperatures, air pollution, UV-B radiation, water shortage, herbicides and salinity ("Choudhury et al., 2017 and Cortese-Krott et al., 2017"). Antioxidant machinery that scavenges reactive oxygen species from enzymatic as well as nonenzymatic compounds in plants. Catalase, superoxide dismutase, ascorbate peroxidase, glutathione reductase, general peroxidases, monodehydroascorbate reductase and dehydroascorbate reductase are examples of enzymatic compounds, while glutathione, ascorbic acid, alpha-tocopherol, flavonoids, carotenoids and ubiquinone or plastoquinone are examples of non-enzymatic compounds (Hancock, 2016 and Sewelam et al., 2016).

The key emphasis of this analysis is on the different forms of reactive oxygen species, the "enzymatic and non-enzymatic" antioxidants of antioxidant protection systems and the different environmental stresses that disrupt reactive oxygen species' homeostasis.

2. REACTIVE OXYGEN SPECIES AND ITS TYPES

Free radicals, which are reactive oxygen species produced from molecular oxygen, include superoxide radicals, singlet oxygen, peroxide, and hydroxyl radicals. In nature, these molecules are harmful as they cause structural as well as molecular damage and eventually cell death (Mittler, 2017). The reactive oxygen species also have signalling pathways that show their significance for plants in stress tolerance (Nafees et al., 2019).

1. Superoxide Radical

NADPH oxidases start production in plants and then participate in the production of other superoxides (Bhattacharjee, 2019). Enzymes such as xanthine oxidase, xanthine dehydrogenase and aldehyde oxidase are also involved in peroxisome, mitochondrial and cell cytosol development (Niu et al., 2018 and Chung, 2017). This reactive oxygen species has a very short half-life of about 2-4 μ s ("Dat et al., 2000 and Bhattacharjee, 2019"), intense reactivity in hydrophobic conditions such as the multimeric protein or inner membrane, and membrane impermeability ("Bhattacharjee, 2019").

2. Oxygen singlet

Singlet oxygen is essential in order for the body to react to oxidative damage produced by environmental stress. (Laloi and Havaux, 2015). Singlet oxygen has a relatively short half-life, spanning between 4 and 100 seconds in water and polar solvents (“Bhattacharjee, 2019”).

3. Hydroxyl Radical

Among its family members, these have significant toxicity and reactivity effects, as they are responsible for disrupting various compounds at cellular level. (“Bhattacharjee, 2019 and Kalyanaraman et al., 2017”). The release of superoxides or peroxides from reactive oxygen species-generating cell compartments such as chloroplast or mitochondria can be due to the generation of hydroxyl radical in the cytosol (“Richards et al., 2015”).

4. Hydrogen Peroxide

Hydrogen peroxide is formed in various organelles where membranal electron flows are correlated with the formation of ATP, such as: chloroplast (chain of electron transport), mitochondria (chain of respiratory electron transport), peroxisomes (cycle of photosynthetic carbon oxidation), nuclei, plasma membranes and endoplasmic reticulum. Metabolic cascades such as fatty acid β -oxidation and photorespiration also contain a high amount of hydrogen peroxide in plants at the cellular level (Bhattacharjee, 2019). NADPH-dependent oxidase, which is found in the cell membrane, is the source of hydrogen peroxide. Finally, two enzymes are involved in the formation of hydrogen peroxide in the apoplast: amine oxidase and germ-like oxidase.; (“Hossain et al., 2015”). Under normal and bad settings, reactive oxygen species are formed at a variety of cellular locations, but chloroplasts and peroxisomes generate the majority of them under light settings, whereas mitochondria generate the majority under darkness. (“Bhattacharjee, 2019 and Chan et al., 2016”). In addition to these “organelles, peroxisomes, mitochondria, plasma membranes, apoplastic, endoplasmic reticulum, and cytosol” all create reactive oxygen species in different amounts depending on environmental and developmental conditions. Fundamentally, the mechanism by which reactive oxygen species are formed is dependent on the release of electrons from electron transport into molecular oxygen. (Millar & Leaver, 2000 and Bhattacharjee, 2019).

3. ANTIOXIDANT DEFENCE SYSTEMS

Maintaining the prevailing circumstances of homeostasis cells in plants is critical, thus plants synthesize enzymatic and nonenzymatic scavengers under changing conditions to minimize cell oxidative damage. (“Hussain et al., 2019”).

Enzymatic scavengers: - The following are the main enzymatic reactions: -

Superoxide Dismutase: - This is the first oxidative damage barrier and is present in every cell. The key feature of these antioxidant enzymes is the conversion or dismutation of toxic superoxide radicals to hydrogen peroxide and molecular oxygen (O₂) (Chung, 2017). Depending on the class of prosthetic metals, SODs are categorised into 3 classes in plants (Wang et al., 2016). In chloroplasts, cytosol and mitochondria, Cu/Zn-SOD is shown. Mn-SOD is found predominantly in the mitochondria. Fe-SOD occurs in chloroplasts and also in peroxisomes and mitochondria (Wang et al., 2017). In certain species of marine algae, a fourth category of “Ni (II/III)” is present at the active metal site “(Ni-SOD)” (“Gill et al., 2015”).

Catalase: - The heme-containing enzymes are the members of this group. They are in charge of converting hydrogen peroxide into oxygen and water, and they are crucial in plant metabolism and signal recognition (“Liu et al., 2015”). These oxidases are involved in the release of H₂O₂ from peroxisomes during fatty acid purine catabolism, photorespiration, and under conditions of oxidative stress. (Sofa et al., 2015).

Peroxidases: - This family contains additional heme-containing proteins. They exhibit a broad structural diversity and preferentially oxidize aromatic electron donors such as guaiacol and pyrogallol over hydrogen peroxide. (“Das and Roychoudhury, 2014”). Class III peroxidases located in the apoplast, catalyze the oxidation of a wide range of substrates and are involved in numerous metabolic pathways and stress defense mechanisms... (“Yadav and Sharma, 2016”).

Glutathione Reductase: - This is an oxidoreductase flavo-protein found in all kingdoms. It is in charge of converting glutathione disulfide to “glutathione”, a critical component in the ascorbate-glutathione cycle's hydrogen peroxide scavenging. (“Ding et al., 2016 and Hasanuzzaman et al., 2017”).

Reductase monodehydroascorbate: - It is a “flavin adenine dinucleotide” enzyme that catalyzes ascorbic acid production and recycling from monodehydroascorbate radicals. It also acts as a reduction agent and electron donor, gradually replenishing it as a cellular pool. It is found in a range of structures within plant cells, including “chloroplasts, mitochondria, peroxisomes, and cytosol”... (Kim et al., 2016).

Non-enzymatic antioxidants: - The following are the primary non-enzymatic reactions: -

Ascorbic acid: - The redox buffer relies heavily on ascorbic acid. It is a cofactor for many enzymes and is important in signal transmission, cell division, and growth regulation. Furthermore, the most abundant water-soluble antioxidant in higher plants is engaged in reactive oxidative stress detoxification. (“Seminario et al., 2017 and Ntakgas et al., 2018”). It directly absorbs superoxide, hydroxide and singlet oxygen and, through the

ascorbate peroxide reaction, can reduce hydroperoxide to water (“Liang et al., 2017a”). It is produced mainly through several pathways in mitochondria (Akram et al., 2017 and Makavitskaya et al., 2018).

Glutathione: All aerobic species have the thiol tripeptide (-glutamylcysteinyl-glycine) molecule. (“Gill et al., 2013”). “This non-enzymatic antioxidant is involved in a variety of biological processes, including the regulation of enzymatic activity, xenobiotic detoxification, cell division-differentiation-death-senescence, protein-nucleotide synthesis, phytochelatin synthesis, metabolite conjugation, and stress-responsive gene expression” (“Zeng et al., 2017”). These are key areas for intracellular protection against oxidative damage caused by reactive oxygen species (ROS)..-

Carotenoids: These auxiliary pigments are C40 lipophilic isoprenoids produced by two distinct pathways in “plastids, chloroplasts, and chromoplasts”. (Liang et al., 2017b). Carotenoids' primary purpose is to prevent oxidative damage by scavenging singlet oxygen. In plants, oxidative degradation of carotenoids produces apocarotenoid molecules, which are involved in “photoprotection, photosynthesis, pigmentation, and signalling”. (“Hou et al., 2016”).

Flavonoids: -These are a class of polyphenolic compounds found largely in benzo-pyrone-containing plants. These metabolites are created by the flavonoid metabolone, a cytosolic multienzyme complex that is coupled to the cytoplasm and endoplasmic reticulum via the phenylpropanoid pathway. (“Mierziak et al., 2014”). They also act as regulators of multifunctional growth regulators' intracellular and long-distance movements, such as auxins (Mouradov and Spangenberg, 2014).

Plastoquinone / Ubiquinone: - They play important roles in stress response from plants, controlling gene expression along with transduction of cell signals. Plastoquinone / ubiquinone has an active ring of benzoquinone linked to the side chain of a polyisoprenoid. Their manufacture is extremely complex, requiring approximately 35 enzymes. Plastoquinone is found in plants, whereas ubiquinone is found in plants, animals, and microorganisms. Both plastoquinone, , are present in a variety of plant cell compartments and are essential for photophosphorylation and oxidative phosphorylation.. (“Liu and Lu, 2016 and Ozyigit et al., 2016”).

4. ENVIRONMENTAL STRESS TOLERANCE

Heavy metals:- Plant cells activate a number of physiological and molecular mechanisms when exposed to hazardous heavy metals such as lead, cadmium, mercury, and arsenic, in order to reduce cytoplasmic concentrations of non-essential heavy metals such as lead, cadmium, mercury, and arsenic. (“Ghori et al., 2019; Hasanuzzaman et al., 2015; Sharma et al., 2016 and Ozturk et al., 2017”). “The first line of defense against excess metals in plants is physical barriers. Numerous different types of cellular defense mechanisms are triggered in plants when pathogens break these barriers and enter tissues and cells, therefore mitigating their detrimental effects.” If these processes are not effective in limiting metal poisoning, the balance of cellular redox systems in plants is upset, resulting in an increase in the induction of reactive oxygen species. (Singh et al., 2016b).

Temperature: - Climate change concerns the global crop production, with much of the research done on temperature stress (“Awasthi et al., 2015”). “High temperatures (heat stress) or low temperatures (cold stress, both chilling stress (< 20 ° C) and even freezing stress (< 0 ° C) can be associated with such stress in plants. Heat stress induces metabolic and structural changes in plants that influence important physiological processes such as breathing, photosynthesis, and water relationships (Sehgal et al., 2016). Due to direct inhibition of metabolic enzymes and reprogramming of gene expression, both plant metabolism and transcriptomes are impaired by cold stress (Zhu, 2016). Chilling stress often entails a redox homeostasis imbalance that creates a disturbance between light absorption and light usage by inhibiting PCRC, improving the formation of photosynthetic ROS (Bhattacharjee, 2019 and Fadzillah et al., 1996).”

Ultraviolet (UV-B) Radiation: UV is a type of electromagnetic radiation that comes in three wavelengths: “UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm) (Ulm & Jenkins, 2015)”. Additionally, UV-B light exposure increases the generation of reactive oxygen species (ROS), which may occur as a result of metabolic disruption or increased membrane-localized NADPH oxidase activity. (Sharma et al., 2017).

Air pollution:- Anthropogenic activities are the primary contributors to rising particulate matter and ozone levels in urban areas. (“Saxena and Kulshrestha, 2016”). The key entrance site for air contaminants into the tissues of plants is via stomata. This entry results in an increase in species of reactive oxygen, causing significant DNA, protein, and lipid damage. Other consequences typically found in air-polluted leaves include “decreased stomatal and epidermal cell size, decreased stomatal and epidermal cell number, decreased cell wall, epicuticular wax deposition, and chlorosis” (“Uka et al., 2017”). There are other allusions to air pollution's biochemical impacts on plants. Drought: - When the need for plant water and turgor is constrained, this scenario occurs. (Verslues, 2017). As a result, plants struggle to carry out basic physiological processes (Shahzad et al., 2016). With the overproduction of reactive oxygen species, reducing the availability of water leads to oxidative stress. This drop could be related to stomatal closure, which reduces CO₂ flow and damages photosynthetic machinery. (Kaur and Asthir, 2017).

Salinity: Salinity is a major stressor on the ecosystem, limiting plant growth and productivity. Water and ionic stress are associated with the effects of salt stress on plants, resulting in decreased growth and nutritional imbalances. - (Hasanuzzaman et al., 2019 and Negrao et al., 2017). The activation of the enzymatic antioxidant mechanism in two genotypes of rice under saline conditions was determined by Vighi et al. (2017). Salt stress effects can be controlled in cells through osmotic modification and ROS scavenging, which prevents lipid peroxidation, protein oxidation, and DNA damage. (“Acosta-Motos et al., 2017”). Because salt is a significant hazard to agricultural productivity, a substantial amount of research has been published in this subject, the most famous of which is (Hasanuzzaman et al., 2019).

Herbicide Stress: Field weeds are widely recognized as a significant disadvantage for farmers and crop growers because they compete with crops for water, nutrients, and light, resulting in significant production losses. As a result, farmers use herbicides as the most effective chemical weed control. (“Davis and Frisvold, 2017”). During the operational Z-scheme, the generation of reactive oxygen species may be attributed to an obstruction of the usual flow of electrons, as demonstrated by “PSII-mediated reduction of plastoquinone, resulting in a monocation radical capable of interacting with molecular oxygen”. (Bhattacharjee, 2019).

Light: - The intensity of light is a factor that regulates plant photosynthesis. Under low light conditions, plants' net photosynthetic rate, PSII quantum yield, and electron transport rate all decline. (Pospisil, 2016). There are limits to the production of reactive oxygen species in both energy transfer and electron transport. The deleterious formation of triplet chlorophyll from singlet chlorophyll will lead to a limitation in energy transfer because surplus energy absorbed by chlorophyll in the “PSII antenna complex” is not fully exploited by charge separation in the PSII reaction core. The presence of triplet chlorophyll is hazardous to organelles, hence its synthesis must be avoided. “One of these methods is the preservation of the quenching singlet chlorophyll, xanthophylls, and carotenoids, which contributes directly to heat dissipation or, indirectly, to the rearrangement of Lhcb proteins at the PSII quenching site by pigment-binding proteins that regulate the PSII antenna organization”. However, this strategy is frequently insufficient to sustain low quantities of singlet chlorophyll, and hence triplet chlorophyll is created by transferring energy to molecular oxygen to make singlet oxygen. (Shumbe et al., 2016).

5. CONCLUSION

There is a balance between the creation and elimination of reactive oxygen species under normal conditions. As a result, reactive oxygen species can be both beneficial and detrimental; however, when exposed to stressful environments such as heavy metals, intense light, or extreme temperatures, this equilibrium can be disrupted, resulting in the production of excessive reactive oxygen species. The primary reaction in a cell is the activation of the antioxidant machinery in response to oxidative stress in order to detoxify the harmful effects of reactive oxygen species.

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