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The Pharma Innovation



ISSN (E): 2277-7695 ISSN (P): 2349-8242 NAAS Rating: 5.23 TPI 2022; SP-11(8): 494-499 © 2022 TPI www.thepharmajournal.com

Received: 22-05-2022 Accepted: 25-06-2022

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Oxidative stress in plants: A delicate balance between life and death

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Abstract

It is well known that several reactive oxygen species (hydroxyl peroxide and superoxide anion) are produced as a consequence of normal metabolic activities such as photosynthesis, respiration, and cellular metabolism. Plants can suffer oxidative stress due to reactive oxygen species, which means they are exposed to unhealthful conditions, and this can result in their death. It is believed that ROS are produced by the cell endogenously as a result of lipid accumulations in the cell membrane. There is a consequent reduction in the production of soluble proteins and sugars, as well as a reduction in the absorption of elements throughout the cell membrane as a result. In order to regulate the whole process of ROS production, there is a signal protein that acts as a signal that signal when the body is under stress. This oxidative stress in agriculture crops can be attributed to the accumulation of heavy metal ions in the rhizosphere. During periods of stress in the rhizosphere, these ions cause damage to the plant's normal metabolism, causing damage to the plant's health. As a result of this, there is insufficient photosynthesis, which further results in inadequate yields as a result. There are some physiological changes that occur in plants as a result of oxidative stress. Throughout this paper, we will be exploring a range of topics, such as the introduction of ROS (reactive oxygen species) to crops, the production of ROS, the production of free radicals, mitochondrial oxidative stress, signalling, and the phytotoxic effects of ROS. At both the molecular and enzymatic levels of the cell, plants have evolved mechanisms to scavenge free radicals in order to protect themselves against ROS damage.

Keywords: Agriculture, biotic, crop, rhizosphere, toxicity, hunger, poverty, reactive oxygen species, sustainability, poverty, hunger

Introduction

Among the most common abiotic stresses that we face today are heavy metals, salinity, drought, heat, and salinity. As a result of such environmental stresses, crop production is affected in a negative way. Due to the disruption of normal metabolic activities, plants undergo a variety of physiological changes when they are under stressed conditions. It is known that reactive oxygen species, that is, hydrogen peroxide, hydroperoxide, and hydroxyl, cause oxidative stress on plant cells when they interact with oxygen. A stress-induced disruption of a whole physiological cycle results in the breakdown of low-energy molecules, causing reactive oxygen species, as well as free radicals to form (Mishra et al., 2011)^[16]. The electron transport system in the mitochondria is disrupted when the mitochondrial membrane is damaged. As a result, ROS ions accumulate within the cellular system, which causes toxicity, a reduction in chlorophyll in the cell membrane, and a reduction in protein levels due to low chlorophyll and low protein concentrations within the cells. There are a number of factors to consider, including photosynthesis, protein content, etc. (Evans, 2004)^[5]. There are several enzymes in the body that are activated during stress, including catalase, peroxidase, amylase, and superoxide dismutase. As a result of the actions of these enzymes, ROS concentration is regulated by enabling reduction reactions (Mishra et al., 2011)^[16]. Both enzymatic and nonenzymatic mechanisms play a role in maintaining ROS levels within the body. In order to be able to grow and develop properly, the body needs to be able to regulate the levels of ROS. There is a defence mechanism in plants, but it is managed by the cells themselves in order to scavenge ROS (Meriga et al., 2004)^[15]. Photobleaching and the production of ROS are two of the most common disturbances of the cell, and they ultimately kill the cell. Under conditions of stress, the nuclei of the cells begin to undergo enzymatic reactions in response to the situation. As a result of environmental factors always taking precedence over the factors associated with stress, ROS are the first to react.

Reactive Oxygen Species: ChemistryS and Biology

It is estimated that oxygen occupies about 20.95 per cent of the atmosphere, placing it third after hydrogen and helium in terms of volume. In the earth's crust, there are a number of compounds that are present. One of these substances is calcium carbonate. In order to determine the reactivity of oxygen, both the number of unpaired electrons within the spin and the number of unpaired electrons within the spin must be considered. It is believed that mitochondria and chloroplasts are the primary sources of ROS production. The chlorophyll pigment absorbs the light quantum in the triplet state when it is absorbed by chlorophyll during photosynthesis. During the diffusion of oxygen molecules into the nuclei, oxygen molecules diffuse between the plasma membrane and the nuclei in a very short period of time (3.1-3.9*s) (Meriga et al., 2004)^[15]. In the electron transport chain, oxygen is released at the end of the electron transport chain as a result of plasma membrane oxidation. As a result, hydrogen peroxide will be formed when it is combined with it. Several ROS species, including hydrogen peroxide, ozone, and hydroxide, do not belong to the radical family. There are also carbonyls, hypochlorous acids, and many other types of compounds that can be found in plants. In addition to carbonyl, hypobromous acid, carbonate, hypoiodous acid, and others, reactive oxygen species exist as well. Incomplete reductions result in the production of ROS species.

There is no doubt that whenever a plant experiences abiotic stress, it will also undergo oxidative stress, which will lead to the evolution of ROS species. There is a close relationship between redox potential and enzyme activity in stressful situations. In order for plants to maintain their metabolism during times of stress, they contain a number of enzymes. As a result of the metabolic functions performed by plant cells, a critical amount of ROS is required. It has been shown that signal proteins are both involved in controlling the production and scavenging of ROS in cells. According to Evans (2004) ^[5], ROS itself has been described as a signalling molecule that controls the activity of cells. Cells are damaged by reactive oxygen species (ROS). As a result of the proper regulation of concentration and the concomitant processes ROS (phenomena caused by natural processes), a strong correlation has been established. The presence of abiotic stress disrupts the equilibrium between the generation of ROS and their scavenging, leading to a build-up of ROS. There is also a disruption in the metabolism of the cells. The amount of lipid peroxidase activity, the protein content, and the membrane injury index of chlorophyll are increased when chlorophyll is photobleached. It is through enzymes like catalase, lipid peroxidase, and superoxide dismutase that cells mitigate the effects of stress.

Abiotic Stress and the Oxidative Stress

Abiotic stress in plants can be caused by both natural and anthropogenic factors. Plants are normally grown in fields, and soil and water provide the major source of energy for plants. Plants, as well as humans, are at risk from changing weather conditions and contamination of soil and water. There is also an issue of industrial waste being imported directly into rivers, resulting in eutrophication and excessive levels of heavy metals in soil and water as a consequence. It seems that this condition could be characterized as heavy metal stress (Mishra *et al.*, 2011) ^[16]. In addition to heavy metal stress, ROS are also produced in cells by other sources. Other stresses like drought, salinity, and heat also contribute

to ROS formation inside the cell. ROS are made in a variety of locations, including the apoplast, chloroplast, mitochondria, plasma membrane, and peroxisomes. Abiotic stresses disrupt photosynthesis when carbon dioxide and oxygen concentrations are reduced. ROS production varies considerably among species due to morphology, genetic resilience, and stress levels.

Stress Caused by Oxidative Activity under Salinity

A plant's rhizosphere, as well as the plant itself, can be affected by the effects of salinity stress. It has been shown that excessive ROS production is a consequence of ion toxicity in the soil, as well as an insufficient supply of water, leading to nutritional deficiencies in the plant (Evans, 2004) ^[15]. Observations in the field have shown that young leaves of a plant are more prone to being affected by salinity stress than older leaves, as a result of changes in their environment. There was a significant increase in ROS production and electrolyte leakage in rice grown under salinity stress, as well as a marked increase in lipid peroxidase activity in rice grown under control conditions.

A Description of How Plants Fight against Antioxidants

Antioxidants are able to slow down the production of ROS by either indirectly or directly inhibiting them. As a result of their lower molecular weight, some anti-oxidant enzymes play an important role in the regulation of oxidative stress responses in plants. Natural antioxidants such as alkaloids, phenolic compounds, flavonoids, and alkaloids are some of the nonenzymatic antioxidants that protect our cells from the free radicals in the environment. There are a lot of amino acids that become active during the process of abiotic stress, which includes catalase, superoxide dismutase, peroxidase, polyphenol oxidase (PPO), GPX, GR, GPX, GST, TRX, and PRX.

Plant Defense Signaling - A Re-Evaluation of ROS Signaling

In the presence of abiotic stress, excessive amounts of ROS are produced as a consequence of disturbances in various metabolic functions and physiological imbalances as a result of abiotic stress. In antioxidant defence pathways such as AsA-GSH, NADPH is crucial for the production of antioxidants. Once this energy has been depleted, these pathways cannot protect against ROS toxicity once this energy has been depleted (Evans, 2004)^[5]. Until the end of the 20th century and the beginning of the 21st century, ROS (especially H2O2) had only gained significant attention as a mechanism for regulating plant stress responses. It has been shown that H2O2 confers tolerance to biotic and abiotic stresses by acting as a signalling molecule. In order to prevent overloading of the photosynthetic machinery due to reactive oxygen species, chloroplasts produce reactive oxygen species. It is also known that ROS protect mitochondria from damage. By activating the Ca²⁺ and MAPK pathways, H2O2 triggers downstream signalling cascades by activating downstream signalling cascades that depend on the source of ROS. It is also important to notice that plant hormone that is related to stress, such as ethylene (ET) and abscisic acid (ABA), have a significant influence on both stress response and stress tolerance. The role of ROS in the body is not only to transduce signals and communicate with hormones, but it is also to regulate metabolic processes. As part of the process of plant acclimation, redox reactions play a role that regulating stress acclimation proteins and enzymes, thereby preventing damage to the plant as a result. NO, and Ca2+ signalling pathways are also involved in both the production and degradation of H2O2. In addition to controlling plant growth and development, they also play an important role in controlling cellular and physiological responses to adverse abiotic conditions. A few reports examine the effects of H2O2 treatment under abiotic stress conditions, since endogenous H2O2 increases tolerance to abiotic stress. Recently, studies have shown that exogenous H2O2 increases tolerance to abiotic stress. As a signal transduction pathway under stress, ROS collaborates with RNS, RSS, and RCS. Because cellular antioxidant levels can affect ROS generation and signalling, antioxidant levels may also influence ROS generation. RCS is involved in the downstream perception and mediation of ROS, whereas RSS is involved in the production. The cytosol, mitochondria, thylakoids, peroxisomes, chloroplasts, and vacuoles of plant cells are all known to produce enzymatic antioxidants, as well as nonenzymatic antioxidants, thylakoids, peroxisomes, chloroplasts, and vacuoles. Catalase is another enzyme that plays a vital role in the activation of superoxide dismutase.

ROS Have a Hazardous Effect on the Environment

The reaction of incomplete reduction of molecular oxygen in the cell results in reactive oxygen species. These highly active molecules contain oxygen due to the incomplete reduction of molecular oxygen during the manufacturing process (Santos et al., 2018). There are a number of free radical species that are known as reactive oxygen species (ROS), which may be synthesized from other free radical species or compounds. In the cellular environment, antioxidant substances and enzymes play an important role in the synthesis and clearance of reactive oxygen species (ROS). Since the discovery of ROS in biological materials more than a decade ago, they were thought to be harmful substances. There are a number of diseases associated with them that have been linked to them. An oxidative stress reaction occurs when ROS production exceeds the antioxidant defence mechanisms, leading to damage to nucleic acids, proteins, and lipids as a result. There is evidence that ROS are related to cancer, neurotoxicity, cholesterol, diabetes, and ageing. According to research, ROS are thought to have evolved in cells to perform certain crucial functions that are crucial to their survival.

Damage Caused by Oxidative Stress as a Biomarker of Aging

Due to the fact that free radicals are electron-borrowing molecules, they have the potential to damage macromolecules within cells that may include DNA, proteins, and lipids (Pham-Huy et al., 2008)^[20]. When DNA is exposed to ROS, it becomes 8-oxoguanine, which enables cytosine and adenine to mate with each other. It has been reported that this mutation can lead to genomic instability and double-strand breaks in the DNA (Kregel et al., 2007)^[11]. As a result of ROS oxidizing amino acid side chains and backbones, proteins can sometimes be damaged, especially the thiol residues in cysteine and methionine. This causes the proteins to break down rapidly. Consequently, structural changes in proteins can lead to a loss of functionality (Sohal, 2002)^[23] or can be used to manipulate their ability to transmit signals (Sohal, 2002)^[23]. Additionally, ROS in the environment can also cause lipid peroxidation, which may cause further damage to the cell membrane due to reactive byproducts

resulting from the peroxidation of the lipids (Mylonas and Kouretas, 1999)^[18]. As a result of the research carried out by Moskalev *et al.*, 2013^[17], researchers have found that DNA damage, protein carbonisation, lipid peroxidation, and mitochondrial DNA damage are all linked (Moskalev *et al.*, 2013)^[17]. According to Liguori *et al.* (2018)^[12], several biomarkers have been identified as markers of ageing. A key signalling molecule in plants is ROS, which is responsible for normal cell development and stress responses, as well as for causing permanent DNA damage and cell death through the generation of ROS.

Oxidative and ROS-related damage

Considering the fact that cells contain both reactive oxygen species (ROS) as well as antioxidant defence systems, there is a delicate balance between them that needs to be maintained. As a result of oxygenation, inflammation, hypoperfusion, and excessive ROS production, this equilibrium is disturbed by oxygenation, inflammation, hypoperfusion, as well as abnormal ROS production. It is believed that there are a number of mechanisms that are believed to be involved in the process of ROS-induced cell death. The presence of ROS results in the damage of proteins, lipids, and nucleic acids directly as a result of the presence of ROS. Clearly, proteins can be oxidized and nitrosylated (carbonylation, nitration, and nitrotyrosine production, for example) in such a way that adversely affects their function (as well as their ability to produce growth factors for the cell) in a way that adversely affects their function as well as their ability to produce growth factors. According to Frischwirth and Hermetter (2008)^[7], lipoperoxidation triggers the release of ceramide from the cell and activates the enzyme sphingomyelinase, which then triggers apoptosis (Fruhwirth and Hermetter, 2008) [7]. In apoptosis and necrosis, it is the oxidation of phosphate groups in nucleic acids that results in the oxidation of their molecules (Auten et al., 2002)^[1]. It depends upon the severity of the alteration and the consequences of the alteration to determine how long it will take the cells to heal.

An Overview of the Role Played by ROS in Damage to Biomolecules

As a matter of fact, there is no doubt that oxidative stress can be prevented by ensuring that ROS are effectively secreted and disposed of. In order for a cell to be considered to have experienced "oxidative stress", there must be a sufficient amount of ROS present in the cell in order to overwhelm the cell's defence mechanisms (Meriga, et al., 2004) [15]. In addition to salt, drought, strong light, metal toxicity, viruses, and other stress factors, there are many other factors that can affect the balance between ROS generation and scavenging breakdowns, such as salt, drought, strong light, metal toxicity, and viruses. A variety of biomolecules such as lipids, proteins, DNA, as well as other biomolecules are damaged in a variety of ways as a result of reactive oxygen species (ROS). We can see these changes in terms of fluidity, ion transport, enzyme activity loss, protein cross-linking, protein synthesis suppression, DNA damage, and other intrinsic membrane properties that are affected by these changes.

Oxidative damage to lipids

It is a well-known fact that when ROS levels exceed a threshold, lipid peroxidation occurs in both cellular and organelle membranes, which can negatively impact the normal function of a cell when ROS levels are high. As a result of the peroxidation of lipids, lipid-derived radicals are formed, which can interact with proteins and DNA, causing oxidative stress as a result of their reaction with them. To detect ROS-mediated damage to cell membranes under stress conditions, we can measure lipid peroxidation in the membrane in order to identify ROS-mediated damage to the membrane during stress conditions. In plants, stress causes oxidation (degradation) of body fats as a result of stress (Mishra *et al.*, 2011) ^[16]. As a result of the high level of lipid peroxidation and the presence of reactive oxygen species (ROS), a high level of ROS is produced as a result of the high level of lipid peroxidation. It has been found that malondialdehyde (MDA) is one of the end products of unsaturated fatty acid peroxidation (Halliwell and Gutteridge, 1989)^[9]. It is proven that ROS attack the unsaturated (double) bonds between two carbon atoms as well as the ester bonds between glycerol and the fatty acid in phospholipid molecules. The ROS attack on polyunsaturated fatty acids (PUFAs) and membrane phospholipids is particularly damaging. As a result of polyunsaturated fatty acids peroxiding, reactive oxygen species (ROS) are released, thereby increasing the effectiveness of cellular processes.

Damage to proteins caused by ROS

It has been shown that ROS can alter proteins directly or indirectly depending on how they react to the ROS with respect to how they react to the ROS. There are several direct changes that lead to the alteration of a protein's function, such as nitrogenation, carbonylation, disulfide bond formation, and glutathionylation. By interacting with the breakdown products of fatty acid peroxidation, proteins can be indirectly altered because they can be directly affected by the breakdown products of fatty acid peroxidation (Yamauchi et al., 2008). A protein that has been exposed to ROS is more likely to be proteolyzed. This is because the generation of ROS leads to the fragmentation of amino acids, fragmentation of peptide chains, and aggregation of crosslinked reaction products. These are all involved in the proteolysis of proteins. The damage caused to tissues by oxidative stress is reflected in their higher levels of carbonated proteins than those that are not damaged by oxidative stress, according to Romero-Puertas et al. (2002) [22]. There is a possibility that plant proteins are modified when plants are exposed to adverse environments (Romero-Puertas et al., 2002)^[22] when plants are exposed to adverse environments. It has been shown that the level of resistance of amino acids in peptides to ROS varies considerably among them. It is possible for ROS to damage sulfur-containing amino acids and thiol groups in thiol groups. It is possible to remove hydrogen atoms from cysteine residues by activating oxygen, in order to form thiol radicals, whose reaction is then followed by the formation of disulfide bridges with another thiol radical. Heavy metal exposure has been noted to cause the depletion of active thiol groups in proteins and this has been observed to occur as a result of exposure to heavy metals such as Cd, Pb, and Hg (Stohs and Bagchi, 1995)^[26]. The methionine sulphoxide derivatives can also be synthesized by adding oxygen to a molecule of methionine to obtain methionine sulphoxide derivatives (Brot and Weissbach, 1982)^[2]. A rapid crosslinking occurs between tyrosine and ROS when the two substances are present together (Davies, 1987)^[3], leading to the formation of tyrosine products. Different enzymes are activated as a result of the reaction between ROS and iron and sulfur in the body when ROS react with iron and sulfur

(Gardner and Fridovich, 1991) ^[8]. During the process of oxidizing amino acid residues around proteins, a divalent bond is formed between Iron (Fe) and the amino acid residues surrounding the protein due to the formation of the OH ion formed by the iron (Fe) (Stadtman 1986) ^[25].

Risks to DNA from ROS

In order for DNA damage to occur, Relative Oxygen Species (ROS) need to be present. DNA in the nucleus, mitochondria, and chloroplasts are all susceptible to oxidative damage due to free radicals. In the event of damage to a cell's DNA, the proteins encoded in the DNA can be drastically altered, resulting in problems, as well as the complete inactivation of the genes that are encoded in the DNA. Besides oxidation of deoxyribose, DNA oxidation can also cause strand breaks, nucleotide loss, modifications in the organic bases of nucleotides, as well as changes in the cross-links between DNA and proteins. A change in one nucleotide may also cause a conflict with another nucleotide, which will result in mutations in the other strand as a result of the change in one nucleotide. A significant increase in the rate of DNA degradation occurs in plants when salinity and metal toxicity are present (Meriga et al., 2004)^[15]. Unlike sugar moieties, both the base and sugar moieties of DNA have a very high sensitivity to the oxidation caused by ROS. There are several causes of sugar degradation, but the most common one is deoxyribose, whereas hydroxyl radicals also cause DNA bases to undergo oxidative stress. In nature, a deoxyribose backbone is a form of purine and pyrimidine bases that react with the hydroxyl radical in the presence of a hydroxyl radical (Halliwell and Gutteridge, 1999)^[9]. There are a number of ways in which DNA bases can be converted to OH, with the most common being hydroxymethyl urea, urea, thymine glycol, thymine and adenine ring-opened products, and saturated products. In this way, 8-Hydroxyguanine is the most prevalent by-product as a result of this reaction. The name H2O2 is drawn from the fact that it does not react with bases at all, whereas the name O2 is derived from the fact that it interacts exclusively with guanine (Dizdaroglu, 1993)^[4]. As a result of ROS-induced DNA damage, mutagenic changes may also occur. In particular, mutations caused by selective alteration of the G: C regions, in particular, are indicative of oxidative DNA damage. Indirectly, ROS attacks DNA bases through the production of reactive products produced by ROS attacking other macromolecules like lipids. The ROS attack on DNA sugars results in the breaking of single-strand DNA strands. A radical deoxyribose is formed when the oxidative stress of deoxyribose is broken down, resulting in the loss of a hydrogen atom from deoxyribose's C4 position, resulting in the generation of the radical of deoxyribose, which is then responsible for DNA strand breaks (Evans, 2004)^[5]. It has been demonstrated that neither H2O2 nor O2• can break strands in vitro under healthy conditions, causing strand breaks in the process. The DNA and protein crosslinks are produced when OH oxidizes DNA and proteins linked to it. It is difficult to repair DNA protein chains if replication or transcription occurs before the repair has taken place. This result is due in part to the lack of protective proteins, including histones, and the proximity of ROS-producing systems to mitochondrial and chloroplast DNA (Richter 1992) ^[21]. It is important to note that although damaged DNA has a repair system, excessive ROS can result in irreversible DNA damage that may adversely affect the cell as a whole.

Conclusion

Stress causes the production of ROS to be influenced by a signal protein within the body. This protein acts as a signal, which affects the whole process of ROS production within the body. The electron transport system in mitochondria is affected by damaged mitochondria that generate ROS. It has been found that ROS ions overabundant in cell membranes are toxic, increases membrane lipids, and decrease chlorophyll levels, ultimately affecting photosynthesis as well as total protein levels. In response to abiotic stress, a plant becomes oxidatively stressed, resulting in a build-up of reactive oxygen species (ROS). In order for a system to remain in equilibrium, there exists a partnership between the redox potential and the enzymatic activity that takes place when stress is applied. In contrast, stress, on the other hand, promotes a group of enzymes within plant cells to become active in order to maintain cellular metabolism. It is essential for a plant cell to have a certain level of ROS in order to function correctly. In order for a cell to function properly, it is vital that it has a certain level of ROS. The production of ROS as well as the scavenging of ROS are both controlled by signal proteins.

Acknowledgement: All authors of this paper are thanked for their support and encouragement during its preparation. Thank you to Lovely Professional University, Punjab, India, for your support and encouragement.

Conflict of Interest: We confirm no conflicts of interest exist with this publication.

List of Abbreviation

ROS: Reactive oxygen species; DNA: deoxyribonucleic acid; H_2O_2 : Hydrogen peroxide NADPH: Nicotinamide Adenine Dinucleotide Phosphate; ADP: Adenosine diphosphate; ABA: Abscisic acid; GSH: glutathione; GST: glutathione-S-transferases; MDA: malondialdehyde; O2: Oxygen; PPO: polyphenol oxidase; Pb: Lead; Cd: Cadmium; Hg: Mercury GPX: glutathione peroxidase; MDHAR: monodehydroascorbate reductase; DHAR: dehydroascorbate reductase; Ca^{2+:} Calcium; Na⁺: Sodium

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