

ANTIOXIDANTS: NATURE'S SHIELD AGAINST PLANT STRESS

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ABSTRACT

Plants face a multitude of challenges in their environment, categorized into biotic and abiotic stresses. Abiotic stresses include extreme in temperature, water excess and deficit, salinity stress, nutrient imbalance and light stress whereas, biotic stresses encompass pathogens like bacteria, fungi, and viruses that cause diseases, herbivores that damage plant tissues and reduce photosynthetic efficiency, and weed competition for resources. These stresses change profoundly impacts plants in various ways, altering their growth, development, distribution, and overall ecosystem dynamics. Plants have evolved various adaptive mechanisms to cope with these stresses, including changes in morphology, physiology, and biochemistry. Environmental stressors such as extreme temperatures, drought, pollutants, and UV radiation can trigger the production of reactive oxygen species (ROS) in plants. ROS, including superoxide radicals, hydrogen peroxide, and hydroxyl radicals, are highly reactive molecules that can cause oxidative damage to cellular components like proteins, lipids, and DNA. To counteract this oxidative stress, plants have evolved a sophisticated antioxidant defense system. Antioxidants such as ascorbate (vitamin C), tocopherols (vitamin E), glutathione, and enzymes like superoxide dismutase and catalase play crucial roles in scavenging ROS and maintaining cellular redox balance. Antioxidants play a crucial role in mitigating plant stress by neutralizing reactive oxygen species (ROS) that accumulate under adverse environmental conditions, by scavenging ROS, maintaining redox homeostasis, protecting membrane integrity, regulating signalling pathway, and enhancing antioxidant enzyme activity. Understanding the intricate mechanisms of antioxidant defense in plants is crucial for developing strategies to enhance crop resilience and productivity in the face of ongoing climate change and environmental challenges. The goal of this review is to go over the several antioxidants defense strategies and the underlying enzymatic mechanisms that help plants become more resilient towards abiotic stresses.

Keywords: Antioxidants, Reactive Oxygen Species, Abiotic Stress, Defense Mechanism

Abbreviations: ROS: Reactive Oxygen Species; DNA: Deoxyribonucleic acid; SOD: Superoxide dismutase; CAT: Catalase; POX: Peroxidases; RNS: Reactive nitrogen species;

GR: Glutathione reductases; DHAR: Dehydroascorbate reductases; MDHAR: Monodehydroascorbate reductases; GPX: Glutathione peroxidases; APX: Ascorbate peroxidases; MDHA: Monodehydroascorbate; DHA: Dehydroascorbate; NAD(P)H: Nicotinamide adenine dinucleotide phosphate hydrogen; GSH: Glutathione; GSSG: Glutathione disulfide; ASA: Dehydroascorbic acid; PC: Phytoalexins; UV: Ultraviolet; AA: Ascorbic acid; ROO•: Peroxyl radicals; NPQ: Non-photochemical quenching; ABA: abscisic acid; JA: Jasmonic acid.

1. INTRODUCTION

Stress in plants can be broadly categorized into biotic and abiotic types, each posing unique challenges to plant health and productivity. Biotic stresses originate from living organisms such as pathogens (e.g., fungi, bacteria, viruses) and pests (e.g., insects, mites), which can directly damage plants, inhibit growth, and reduce yields. Abiotic stresses, on the other hand, arise from non-living environmental factors like extremes in temperature (heat, cold), water availability (drought, flooding), soil salinity, nutrient imbalances, light intensity variations, air pollutants, and mechanical damage (e.g., wind, hail). Both types of stress can disrupt plant metabolism, hinder nutrient uptake, and lead to physiological disorders (Nawaz et al., 2023). Plants respond to biotic stresses by activating defense mechanisms such as the production of antimicrobial compounds and initiating immune responses (Mishra et al., 2021).

In contrast, abiotic stress responses involve adaptive changes in morphology (e.g., root architecture), physiology (e.g., osmotic adjustment), and biochemical processes (e.g., antioxidant production) to enhance resilience (Ghosh and Majee, 2023). Effective management strategies, including crop breeding for stress tolerance and integrated pest management practices, aim to mitigate these stresses and ensure sustainable agricultural production. Abiotic stress in plants encompasses a range of non-living environmental factors that can significantly impact their growth and productivity (Zaidi et al., 2014). These include extremes in temperature both heat waves and cold snaps alongside water deficiencies like drought and excesses such as flooding. Salinity in soils, nutrient imbalances, and variations in light intensity also pose challenges. Furthermore, air pollutants and mechanical stress from wind or abrasion can further hinder plant health. Plants respond to these stresses through various adaptive mechanisms, adjusting their morphology, physiology, and biochemical processes. Strategies include altering root architecture for better water uptake, adjusting osmotic balance to cope with drought or salinity, and producing stress-related proteins and antioxidants. Research and breeding efforts continue to focus on developing resilient crop varieties capable of thriving under diverse and challenging environmental conditions.

Antioxidants play essential roles in plant defense against both biotic and abiotic stresses by neutralizing reactive oxygen species (ROS) that can damage cellular components under stress conditions. ROS encompass a variety of highly reactive molecules derived from molecular oxygen (O₂). In plants, ROS are generated as natural byproducts of metabolic processes, including photosynthesis, respiration, and various enzymatic reactions. These ROS play essential roles in signaling and defense mechanisms but can also cause oxidative damage to cellular components when present in excess (Figure 1).

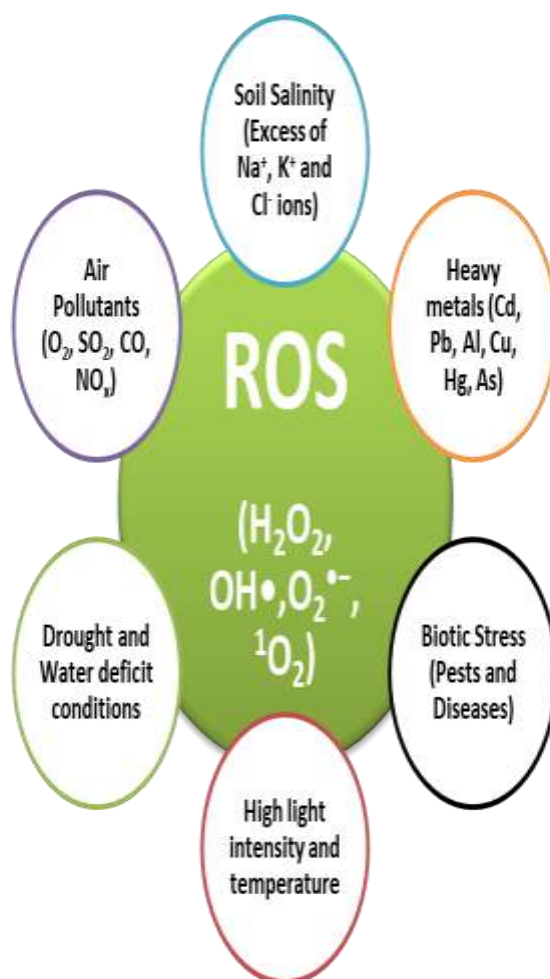


Figure 1: Various causes responsible for the generation of ROS (Source: Das and Roychoudhury, 2014)

In plants, the production and scavenging of ROS are in balance under normal circumstances. But when under stress, this equilibrium is thrown off, which raises ROS levels and causes oxidative damage to cell components (Pang and Wang, 2008). However, more advanced plants have an internal defense system to offset this increase in ROS concentrations (Sharma et al., 2019). The ROS defense mechanism is essential to lowering ROS level in plants during abiotic stresses. These defence systems work synergistically to maintain ROS levels within a tolerable range and protect plants from oxidative damage. By pre-emptively regulating ROS production and accumulation, plants enhance their resilience to various environmental stresses and optimize their growth and development in challenging conditions. Over time, plants have evolved complex defense system to combat the accumulation and production of reactive oxygen species (Figure 2) (Berni et al., 2019)

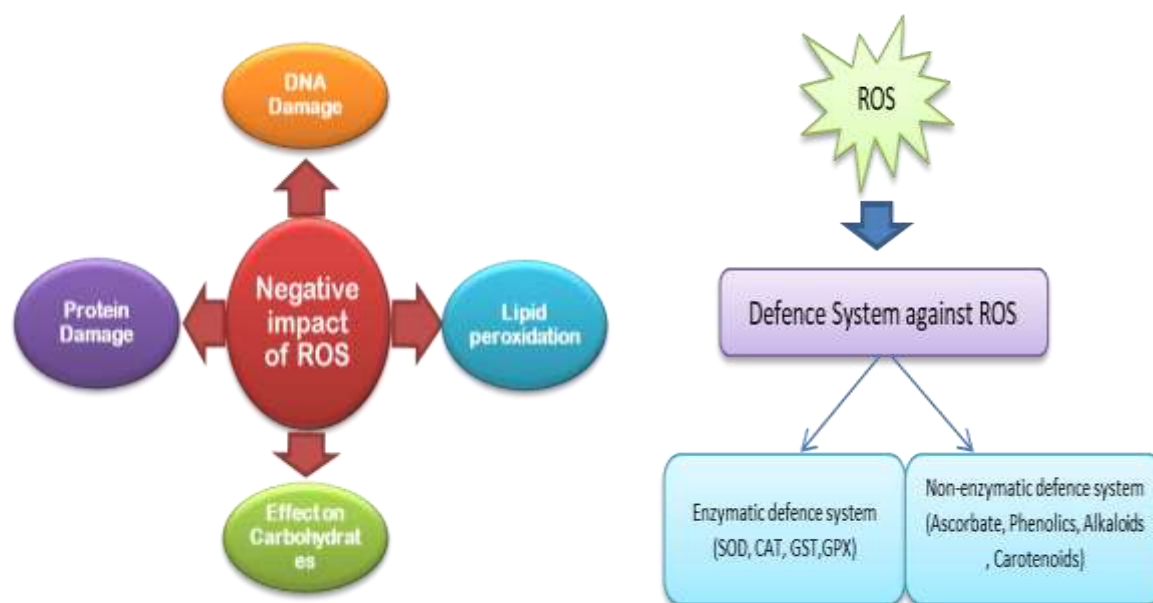


Figure 2: Oxidative stressors' effects on various plant defense mechanisms. By blocking proteins, DNA, and other metabolic pathways, reactive oxygen species (ROS) seriously harm plant cells. On the other hand, plants' defense mechanisms against ROS are triggered by several enzymatic and non-enzymatic antioxidant substances, which control the plants' functional activity (Source: Mansoor et al., 2022).

Antioxidants include non-enzymatic antioxidants like ascorbic acid, glutathione, tocopherols, and enzymatic antioxidants like superoxide dismutase, catalase, and peroxidases, which scavenge ROS and maintain cellular redox balance (Rezayian et al., 2019). Antioxidants also induce defense pathways by signaling and regulating stress-responsive genes, protect against lipid peroxidation to maintain membrane integrity, and possess antimicrobial properties that inhibit pathogen growth (Pathak et al., 2019). Additionally, they mediate crosstalk with phytohormones to coordinate various defense mechanisms, thereby enhancing plant resilience and survival in challenging environments (Raza et al., 2022).

Under stress conditions, plants often accumulate reactive oxygen species (ROS) such as superoxide radicals ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\cdot OH$), which can damage cellular components like proteins, lipids, and DNA (Das and Roychoudhary, 2014). Antioxidants like ascorbic acid (vitamin C), glutathione, tocopherols (vitamin E), and enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidases (POX) help neutralize these ROS, thereby protecting cells from oxidative damage (Mehla et al., 2017). Antioxidants participate in maintaining cellular redox balance by regulating the levels of ROS and reactive nitrogen species (RNS). This balance is crucial for signaling pathways involved in stress responses and defense mechanisms (Hunyadi, 2019). Some antioxidants, particularly ascorbic acid and glutathione, have been implicated in signaling pathways that activate defense genes and proteins (Scandalios, 2005). They can act as signaling molecules or co-factors in enzymatic reactions that regulate stress-responsive gene expression. Lipid peroxidation, caused by oxidative stress, leads to membrane damage and disruption of cellular integrity. Antioxidants like tocopherols and carotenoids protect membranes by scavenging lipid peroxy radicals and stabilizing lipid bilayers (Sisein, 2014). Certain

antioxidants, such as phenolic compounds and flavonoids, possess antimicrobial properties that directly inhibit the growth of pathogens (Lima et al., 2019). They can disrupt microbial cell membranes, interfere with enzymatic activities, and inhibit spore germination (Li et al., 2022). Antioxidants can interact with phytohormones (e.g., salicylic acid, jasmonic acid, ethylene) and other signaling molecules involved in plant defense responses. This crosstalk helps coordinate different defense pathways and optimize the plant's response to stress (Yang et al., 2015). Antioxidants in plants serve as critical defenders against oxidative stress induced by both biotic and abiotic factors. By scavenging ROS, maintaining redox homeostasis, inducing defense pathways, protecting membranes, and enhancing antimicrobial activity, antioxidants play a multifaceted role in enhancing plant resilience and survival under adverse environmental conditions.

Many stressors, such as pathogen infection, salt, dehydration, high temperatures, heavy metals, pollution and high levels of radiation upset the delicate balance between the production and scavenging of ROS (Xie et al., 2019). Thus a variety of critical parameters including modifications to growth settings and intensity and length of stress conditions and the plants ability to adjust to shifting energy equations, are necessary for the plants to survive (Prasad et al., 2008). Only 1% to 2% of the oxygen consumed by plant tissue is thought to result in the production of ROS. This review aims to provide a comprehensive analysis of the role of antioxidants in mitigating plant stress and their potential for use in enhancing crop productivity under stress conditions.

2. ANTIOXIDANTS AND PLANT STRESS

The end of the 20th century saw the discovery of the ROS defense system in plants, along with its different components and activities (Bowler et al., 1994; Karpinska et al., 2001; Baba et al., 2019). It was recently determined that the defense mechanism against ROS is not solely attributed to the scavenging system, but also includes both enzymatic and non-enzymatic defense mechanisms, both of which are triggered by different environmental stressors (Noctor et al., 2018). This section of the review highlights the roles of the main enzymatic and non-enzymatic antioxidants as crucial regulators of plant growth and development and important determinants of cell fate. On the other hand, the present review also offers a thorough examination of ROS's fate in plants and its useful function in stress and other abnormalities management. The adverse effects of the producing sites are also described. Furthermore, covered are the molecular characteristics and origins of ROS production, capture mechanisms, the impact of ROS on cell biochemistry, and the interactions of ROS with other signaling molecules and pathways.

2.1. ENZYMATIC ANTIOXIDANTS AND THEIR ROLE DURING PLANT STRESS

The enzymatic defense system against reactive oxygen species (ROS) comprise a range of enzymes, such as glutathione reductases (GRs), dehydroascorbate reductases (DHARs), superoxide dismutases (SODs), monodehydroascorbate reductases (MDHARs), glutathione peroxidases (GPXs), catalases (CATs), and ascorbate peroxidases (APXs). Plants need enzymatic defense mechanisms against ROS in order to preserve cellular homeostasis and shield them from oxidative stress, which can be brought on by a variety of environmental stressors as well as physiological activities. ROS, such as superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radicals ($\bullet OH$), and singlet oxygen (1O_2), are byproducts of aerobic metabolism and can accumulate to harmful levels under stress conditions. Here are the key enzymatic components of ROS defense systems in plants:

2.1.1 Superoxide dismutase (SOD)

An essential antioxidant enzyme called superoxide dismutase (SOD) is involved in plant's defense against environmental stress, especially oxidative stress brought on by reactive oxygen species (ROS). SOD is a metalloenzyme that is one of the most effective components of a plant cell's antioxidant defense against ROS toxicity. SOD are thought to be present in all oxygen-metabolizing cells and subcellular compartments, including cytoplasm, apoplast, mitochondria, nuclei, peroxisomes and chloroplast (Fink and Scandalios, 2002; Mahanty et al., 2012). Alscher et al (2002) stated that SOD is divided into three isoenzymes depending on the presence of a metal cofactor. According to their location, structure and functions in plants, the three isoenzymes that make up SOD are Cu/Zn-SOD, Mn-SOD and Fe-SOD (Corpas et al., 2006). Mn-SOD can also be found in mitochondrial peroxisomes and apoplast; Cu/Zn-SOD has been found in peroxisomes, chloroplast and the cytoplasm (Pan et al., 2006). Fe-SOD is primarily found in chloroplast, with apoplast and peroxisomes containing lower levels of the compound. Since SODs are a crucial part of the plant defense system, they serve as the first line of defense against abiotic stress. Stress raised ROS and its reaction products, and SODs catalysed the dismutation of O_2 into hydrogen peroxide and Oxygen.

One of the most significant abiotic factors influencing crop quality and yield is salinity (Mittler, 2006). Salinity changes the activity of ROS-scavenging enzymes and increases the renewal of reactive oxygen species. In certain plants, abiotic stress causes a reduction in SOD activity or no change at all, whereas, salt stress causes an increase in SOD activity overall in other plants (Hernandez et al., 2006; Sheokand et al., 2008; Kumar et al, 2013; Rasool et al., 2013). The significant differences in SOD activities amongst salt-stressed plants offer evidence that it acts intra or inter specifically. Numerous factors, including the type of plant species which may be tolerant or sensitive, the intensity and duration of stress, and the plant organ used in the experiment, influence SOD activity (Mishra et al., 2023).

Mishra et al. (2023) reported that *Oryza sativa* cultivars that are sensitive to salt and tolerant to it exhibited a greater response to Cu/Zn-SOD, while the cytosolic fraction exhibited a notable level of Mn-SOD activity. Furthermore, the cytosolic MN-SOD's incredibly low activity implies that it does not perform much to scavenge the generation of oxygen O_2 free radicals brought on by salt. An additional isozyme called Cu/Zn-SOD is found in all the three cell compartments, with the maximum concentration found in the chloroplast, cytosol and mitochondria. Apart from the physiological alternations resulting from salt stress, plants undergo other physiological changes due to drought stress. According to Anjum et al. (2011) stomatal closure caused by abscisic acid decreases CO_2 fixation, which lowers photosynthetic rate and causes morphological defects, most notably reduced organ growth. Research indicates that SOD can shield photosystem II from reactive O_2 brought on by oxidative and hydrostatic stress (Deeba et al., 2012; Mishra et al., 2023).

SOD catalyzes the dismutation (conversion) of superoxide radicals ($O_2^{\cdot-}$) into oxygen (O_2) and hydrogen peroxide (H_2O_2). Superoxide radicals are highly reactive and can cause damage to cellular components such as lipids, proteins, and DNA. By converting superoxide radicals into hydrogen peroxide, SOD reduces the levels of this harmful ROS, thereby protecting the cell from oxidative damage (Bhattacharya, 2015). SOD is essential for maintaining cellular redox balance. ROS are produced as natural by-products of metabolic processes, and their levels increase under environmental stress conditions such as high light intensity, drought, heat, cold, and pollutants (Ali and Alquraini, 2006). SOD helps regulate ROS levels to prevent oxidative stress, which can impair cellular function and lead to cell

death. SOD works in conjunction with other antioxidant enzymes and molecules to scavenge ROS effectively. For example, hydrogen peroxide produced by SOD can be further detoxified by enzymes like catalase (CAT) or peroxidases (POX), converting it into water and oxygen (Rajput et al., 2021). In photosynthetic tissues, SOD plays a crucial role in protecting chloroplasts from photooxidative damage caused by excess light energy (Asada, 2019). It helps prevent the formation of harmful ROS that can damage photosynthetic pigments and proteins. Plants can upregulate SOD expression and activity in response to environmental stressors (Xie et al., 2019). This adaptive response enhances the plant's ability to withstand adverse conditions and maintain cellular integrity under stress. Superoxide dismutase (SOD) is a key player in the antioxidant defense system of plants, particularly against oxidative stress induced by environmental factors. Thus, by catalyzing the breakdown of superoxide radicals into less harmful molecules, SOD helps protect cellular structures and maintain physiological processes essential for plant growth, development, and stress tolerance. Understanding the role of SOD and its interactions with other antioxidants provides insights into plant adaptation mechanisms and informs strategies for enhancing crop resilience in challenging environmental conditions.

2.1.2 Catalases

The main scavenging enzyme that may dismutate H_2O_2 directly is catalase which is also necessary for the detoxification of reactive oxygen species under stress (Ben-Amer et al., 2005). Plant catalases are divided into three groups based on their structural makeup: class 1 catalase is found in photosynthetic tissue and helps remove excess H_2O_2 produced during photorespiration, class 2 catalase is found in vascular tissues and may play a role in lignification, though its exact biological function is unknown, and class 3 catalase is found in seeds and young plants and its activity is linked to removing excess H_2O_2 produced during fatty acid degradation in the glyoxylate cycle in glyoxisomes (Ben-Amer et al., 2005; Mishra et al., 2023).

Increased catalase activity is thought to be an adaptive characteristic that could aid in overcoming tissue metabolic damage by lowering harmful levels of H_2O_2 (Mhamdi et al., 2010). Many studies have focused on the importance of the catalase catalysis under drought and salt stress because of the critical function that catalase plays in photorespiration. Indeed, the persistence of CAT activity in drought stressed plant leaves is likely the reason of the removal of photorespiratory H_2O_2 . Generated when plants are confronted to increased degree of salt and water deficiency problems. In these conditions, photorespiration acts as an energy sink to prevent photoinhibition and an excessive reduction in photosynthetic electron transport chain, as stated by Bauwe et al. (2012). As a result, photorespiration and CAT pathway are no longer regarded as inefficient processes but rather as necessary and supporting components of photosynthesis and stress response of green tissue designed to prevent the accumulation of ROS (De Pinto et al., 2013; Rahman et al., 2013). Previous researches have been demonstrated that the degree of dryness that plants experience is often correlated with a higher level of catalytic activity (Grover et al., 2011. Mittler et al., 2011).

Catalase plays a significant role in combating environmental stresses, particularly oxidative stress induced by reactive oxygen species (ROS). Catalase catalyzes the decomposition of hydrogen peroxide (H_2O_2) into water (H_2O) and oxygen (O_2). Hydrogen peroxide is a by-product of various metabolic processes in plants and can accumulate to harmful levels under environmental stresses such as high light intensity, drought, heat, cold, and pollutants. Catalase ensures that excess hydrogen peroxide is rapidly converted into

water and oxygen, thereby preventing the formation of hydroxyl radicals (OH•) through the Fenton reaction, which can cause oxidative damage to cellular components (Ofoedu, 2021). By detoxifying hydrogen peroxide, catalase helps maintain the cellular redox balance. ROS are constantly generated as part of normal cellular metabolism, and their levels increase under stress conditions. Catalase activity ensures that ROS levels are kept within manageable limits, preventing oxidative stress-induced damage to lipids, proteins, nucleic acids, and other cellular structures (Das and Roychoudhary, 2014). Catalase activity is particularly important for protecting cellular organelles, such as chloroplasts and mitochondria, from oxidative damage (Rezaiyan et al., 2019). These organelles are highly sensitive to ROS and oxidative stress, which can disrupt photosynthesis, respiration, and overall cellular metabolism. By neutralizing hydrogen peroxide, catalase helps preserve the structural integrity and functional efficiency of these organelles (Singh et al., 2022).

Like other antioxidant enzymes, catalase expression and activity can be induced in response to environmental stresses. Plants can upregulate catalase production to cope with increased oxidative stress levels, thereby enhancing their resilience and survival under adverse conditions. Catalase works synergistically with other antioxidant enzymes, such as superoxide dismutase (SOD) and peroxidases (POX), to detoxify ROS effectively (Shah and Gupta, 2020). SOD converts superoxide radicals ($O_2^{\cdot-}$) into hydrogen peroxide, which is then decomposed by catalase into water and oxygen. Additionally, peroxidases can utilize hydrogen peroxide as a substrate for detoxification reactions. Its role in maintaining cellular redox balance, protecting organelles, and responding to environmental stresses highlights its importance in plant adaptation and survival. Understanding catalase function and regulation contributes to strategies aimed at enhancing plant resilience to diverse environmental challenges in agriculture and natural ecosystems.

2.1.3 Ascorbate peroxidase (APX)

Ascorbate Peroxidase is a crucial antioxidant enzyme in plants that plays a significant role in combating environmental stresses, particularly oxidative stress induced by reactive oxygen species (ROS). Higher plants, chlorophytes, red algae and protists, all contain APX which is essential for regulating growth (Wang et al., 2004; Chen et al., 2013). The subcellular location of each APX isoform in the cell is used to characterize them. Soluble isoforms are located in cytosol, mitochondria and chloroplast stroma, whereas, membrane bound isoform are found in microbodies, such as peroxisomes and glyoxysomes and Chloroplast thylakoid (Yoshimura and Ishikawa, 2024). Ascorbate peroxidase catalyzes the detoxification of hydrogen peroxide (H_2O_2) by utilizing ascorbate (vitamin C) as an electron donor. The reaction converts hydrogen peroxide into water (H_2O) and oxygen (O_2), thereby reducing the levels of this harmful ROS in plant cells.

This process helps prevent oxidative damage to cellular components such as lipids, proteins, and DNA. Ascorbate peroxidase plays a crucial role in maintaining the pool of ascorbate within plant cells (Maruta et al., 2016). Ascorbate is an important antioxidant molecule itself, capable of scavenging ROS directly and also regenerating other antioxidants like tocopherols (vitamin E) from their oxidized forms (Ali et al., 2020). By utilizing ascorbate to detoxify hydrogen peroxide, APX helps ensure the availability of active antioxidant molecules for continuous ROS scavenging. In photosynthetic tissues, ascorbate peroxidase is particularly important for protecting chloroplasts from photooxidative damage. During photosynthesis, chloroplasts generate ROS as by-products, especially under conditions of excess light intensity or environmental stresses. APX helps maintain the

balance between ROS production and scavenging within chloroplasts, thereby preserving the efficiency of photosynthetic electron transport and preventing photoinhibition (Foyer and Shigeoka, 2011). The expression and activity of ascorbate peroxidase can be induced in response to various environmental stresses, including drought, high light intensity, cold, heat, and pollutants (Hasanuzzaman et al., 2017). This adaptive response allows plants to increase their antioxidant capacity and mitigate oxidative damage under stress conditions. Ascorbate peroxidase works in concert with other antioxidant enzymes and molecules to protect plants from oxidative stress. It collaborates with enzymes such as superoxide dismutase (SOD) and catalase to detoxify ROS efficiently (Mehla et al., 2017). Additionally, ascorbate peroxidase interacts with the ascorbate-glutathione cycle, where it plays a key role in maintaining the redox status and cellular homeostasis (Pandey et al., 2015). Its ability to utilize ascorbate as an electron donor, protect chloroplasts from photooxidative stress, and respond to environmental stresses underscores its importance in plant adaptation and survival (Fortunato et al., 2023). Understanding APX function and regulation provides insights into enhancing plant resilience to oxidative stress and developing strategies for improving crop productivity in changing environmental conditions.

Numerous environmental conditions, including as pathogen attack, H₂O₂, abscisic acid, high light level, drought stress, salt stress, and high and low temperature affects the expression of genes that make APX (Teixeira et al., 2004; Passardi et al., 2007; Anjum et al., 2016). Additionally, Teixeira et al. (2005) found that the tissue and developmental stage influence the transcriptional expression of APX genes. In response to salinity stress, which causes an ion imbalance and physiological conditions similar to drought, APX confers a degree of salt tolerance on the affected plants (Mishra et al., 2023). Chloroplast APX activity rises in response to salt stress, defending against ROS produced in peroxisomes and mitochondria. Additionally, soil contamination by heavy metal ions is a significant issue that lower crop yield. *Brassica napus* leaves expressed less APX in response to cadmium and arsenic stress compared to those of *Solanum nigrum*, *Brassica juncea* and *Arabidopsis thaliana* (Smeets et al., 2008; Khan et al., 2009; Markovska et al., 2009, Nouairi et al., 2009; Pinto et al., 2009; Ansari et al., 2015).

2.1.4 Monodehydroascorbate reductase (MDHAR)

Monodehydroascorbate reductase (MDHAR) is an important enzyme in the antioxidant defense system of plants, specifically involved in combating oxidative stress induced by reactive oxygen species (ROS) under various environmental stresses. MDHAR catalyzes the reduction of monodehydroascorbate (MDHA) to ascorbate (vitamin C) using NAD(P)H as a reducing agent (Sano, 2017). Ascorbate is a potent antioxidant in plants that scavenges ROS directly and regenerates other antioxidants like tocopherols (vitamin E). By converting MDHA back to ascorbate, MDHAR maintains the pool of active ascorbate within plant cells, ensuring continuous ROS scavenging capacity (Anjum et al., 2014). Ascorbate, regenerated by MDHAR, serves as an essential antioxidant that neutralizes various ROS, including hydrogen peroxide (H₂O₂), superoxide radicals (O²⁻), and hydroxyl radicals (OH•) (Zandi and Schnug, 2022). By participating in the ascorbate-glutathione cycle, MDHAR contributes to the overall antioxidant defense network of the plant, helping to detoxify ROS and prevent oxidative damage to cellular components.

In photosynthetic tissues, MDHAR plays a critical role in protecting chloroplasts from photooxidative damage. During photosynthesis, chloroplasts generate ROS as by-products, especially under conditions of high light intensity or environmental stresses. MDHAR

ensures that the ascorbate pool is maintained within chloroplasts, thereby preserving the efficiency of photosynthetic electron transport and preventing photoinhibition (Asthir et al., 2020). The expression and activity of MDHAR can be induced in response to environmental stresses such as drought, heat, cold, salinity, and pollutants. This adaptive response allows plants to enhance their antioxidant capacity and cope with increased ROS production under stress conditions. MDHAR works synergistically with other antioxidant enzymes and molecules to protect plants from oxidative stress. It collaborates with enzymes like ascorbate peroxidase (APX) and glutathione reductase (GR) in the ascorbate-glutathione cycle, where MDHAR helps maintain the redox status and antioxidant capacity of the cell (Asthir et al., 2020). Monodehydroascorbate reductase (MDHAR) plays a crucial role in the antioxidant defense system of plants by regenerating ascorbate, scavenging ROS, and protecting cellular components from oxidative damage under environmental stresses. Its ability to maintain the ascorbate pool, particularly in photosynthetic tissues, ensures optimal photosynthetic efficiency and overall plant health in challenging environmental conditions. Understanding MDHAR function and regulation provides insights into enhancing plant resilience to oxidative stress and developing strategies for improving crop productivity in diverse environmental settings.

2.1.5 Dehydroascorbate reductase (DHAR)

Dehydroascorbate reductase (DHAR) is a key enzyme in the antioxidant defense system of plants, playing a significant role in combating oxidative stress induced by environmental factors. DHAR catalyzes the reduction of dehydroascorbate (DHA) back to ascorbate (vitamin C) using reduced glutathione (GSH) as a cofactor (Anjum et al., 2014). Ascorbate is a crucial antioxidant in plants that scavenges reactive oxygen species (ROS) directly and regenerates other antioxidants such as tocopherols (vitamin E) (Dumanovic et al., 2021). By converting DHA to ascorbate, DHAR helps maintain the pool of active ascorbate within plant cells, ensuring continuous ROS scavenging capacity. Ascorbate, regenerated by DHAR, plays a vital role in neutralizing various ROS, including hydrogen peroxide (H_2O_2), superoxide radicals ($O_2^{\cdot-}$), and hydroxyl radicals ($OH^{\cdot}$) (Zandi and Schnug, 2022). This antioxidant activity helps protect cellular components such as lipids, proteins, and DNA from oxidative damage induced by environmental stresses. In photosynthetic tissues, DHAR is particularly important for protecting chloroplasts from photooxidative damage (Garcia-Caparras, 2021). Chloroplasts produce ROS as natural by-products of photosynthesis, and excessive ROS production can occur under high light intensity or environmental stresses. DHAR ensures that the ascorbate pool is maintained within chloroplasts, thereby preserving the efficiency of photosynthetic electron transport and preventing photoinhibition (Asthir et al., 2020). The expression and activity of DHAR can be induced in response to various environmental stresses, including drought, heat, cold, salinity, and pollutants.

This adaptive response allows plants to enhance their antioxidant capacity and cope with increased ROS production under stress conditions (Hasanuzzaman et al., 2012). DHAR interacts closely with the glutathione-ascorbate cycle, which involves the interconversion of ascorbate and glutathione (GSH) to detoxify ROS. DHAR uses GSH to reduce DHA to ascorbate, while the resulting oxidized glutathione (GSSG) is converted back to reduced GSH by glutathione reductase (GR). This cycle helps maintain the redox balance and antioxidant capacity of plant cells. Dehydroascorbate reductase (DHAR) plays a crucial role in the antioxidant defense mechanism of plants by regenerating ascorbate and scavenging ROS under environmental stresses. Its ability to maintain the ascorbate pool, particularly in chloroplasts, ensures optimal photosynthetic efficiency and protects cellular integrity from

oxidative damage. Understanding DHAR function and regulation provides insights into enhancing plant resilience to oxidative stress and developing strategies for improving crop productivity in challenging environmental conditions.

2.1.6 Glutathione reductase (GR)

Glutathione reductase (GR) is a vital enzyme in the antioxidant defense system of plants, playing a crucial role in combating oxidative stress induced by various environmental factors. NADPH is used as a reductant by glutathione reductase, also known as GSR or GR, a flavoprotein oxide reductase, to help catalyse the reduction of glutathione disulfide (GSSG) to its reduced sulfhydryl form (GSH) (Hasanuzzaman et al., 2019). Monodehydroascorbate (MDHA) and dehydroascorbic acid (ASA) from the reduced GSH that has been produced, converting GSH to GSSG (Jiang et al., 2022).

Studies have shown that glutathione reductase is actually an abiotic stress defense mechanism. GR efficiently maintains a relatively high cellular GSH/GSSG ratio by speeding up the formation of disulfide link in glutathione disulfide (Gondim et al., 2012; Aftab and Hakeem, 2022). The possible mechanism exists by which GSH shields the plants cellular machinery from ROS-oxidative damage:

- 1) Directly suppressing reactive oxygen species (ROS)
- 2) Coupling heavy metals and xenobiotics to GS and
- 3) Serving as a precursor to the production of phytoalexins (PCs)

Plant can resist heavy metal stress by retaining high PC levels. In order for plants to be resistant to heavy metal, GR is essential. One important component of the rate-limiting phase in the synthesis of phytochelatins is GSH (Inouche et al., 2015). The resulting phytochelatins reduce oxidative damage by forming complexes with different heavy metal ions and being sequestered to the vacuole for breakdown (Nahar et al., 2016).

GR catalyzes the reduction of oxidized glutathione (GSSG) back to its reduced form (GSH) using NADPH as a reducing agent. Glutathione (GSH) is a tripeptide (γ -glutamyl-cysteinyl-glycine) that serves as a major antioxidant in plants. It directly scavenges reactive oxygen species (ROS) and also participates in the detoxification of xenobiotics and heavy metals. By maintaining a high ratio of GSH to GSSG, GR ensures the availability of active antioxidant molecules for continuous ROS scavenging and detoxification (Jozefczak et al., 2012). GSH, regenerated by GR, plays a critical role in protecting cellular components such as p roteins, lipids, and DNA from oxidative damage induced by ROS (Averill-Bates, 2023). This antioxidant activity is essential for maintaining cellular redox balance and preserving cellular integrity under environmental stresses such as drought, heat, cold, salinity, pollutants, and UV radiation. GR interacts closely with the ascorbate-glutathione cycle, a crucial antioxidant pathway in plants (Kuzniak et al., 2017). In this cycle, ascorbate peroxidase (APX) and dehydroascorbate reductase (DHAR) use ascorbate (vitamin C) and glutathione (GSH), respectively, to detoxify hydrogen peroxide (H_2O_2) and regenerate antioxidants. GR ensures the efficient recycling of GSH within this cycle, thereby enhancing the overall antioxidant capacity of plant cells. The expression and activity of GR can be induced in response to environmental stresses. Increased oxidative stress leads to higher production of ROS, which in turn stimulates the expression of GR to enhance the plant's antioxidant defenses. This adaptive response allows plants to cope with oxidative stress and maintain cellular homeostasis under adverse conditions. Besides its role in antioxidant defense, GR is

involved in various metabolic processes such as sulfur metabolism, amino acid biosynthesis, and redox signaling (Garcia-Caparros et al., 2021). These functions contribute to overall plant growth, development, and stress tolerance. Glutathione reductase (GR) is a critical enzyme in the antioxidant defense system of plants, responsible for maintaining the redox balance by recycling glutathione and protecting cellular components from oxidative damage induced by environmental stresses (Gill et al., 2013). Its interaction with the ascorbate-glutathione cycle and its role in ROS detoxification highlight its importance in plant adaptation and survival under changing environmental conditions. Understanding GR function and regulation provides insights into enhancing plant resilience to oxidative stress and developing strategies for improving crop productivity in diverse environmental settings.

2.1.7 Guaiacol peroxidase (GPX)

Guaiacol peroxidase (GPX) also known as class III peroxidase, is an important enzyme in plants involved in the defense against environmental stresses. GPX catalyzes the reduction of hydrogen peroxide (H_2O_2) using a variety of substrates, including guaiacol, phenolic compounds, and organic acids (Rajput et al., 2021). This enzymatic reaction converts hydrogen peroxide into water and oxygen, thereby reducing the levels of this harmful reactive oxygen species (ROS) in plant cells. By detoxifying hydrogen peroxide, GPX helps prevent oxidative damage to cellular components such as lipids, proteins, and DNA. GPX plays a crucial role in maintaining cellular redox balance under environmental stresses such as drought, heat, cold, salinity, pollutants, and UV radiation (Gill and Tuteja, 2010). These stressors can lead to increased ROS production, which GPX helps to neutralize, thus protecting cellular integrity and function. In addition to its role in ROS detoxification, GPX is involved in the cross-linking of cell wall components, particularly lignin biosynthesis (Barcelo and Laura, 2009). Lignin deposition in cell walls strengthens plant tissues and provides structural support, which is important for plant defense against biotic and abiotic stresses (Yadav and Chatopadhyay, 2023). The expression and activity of GPX can be induced in response to environmental stresses.

Increased ROS levels trigger the upregulation of GPX expression, enhancing the plant's antioxidant capacity and enabling it to cope with oxidative stress more effectively (Rajput et al., 2021). GPX works synergistically with other antioxidant enzymes and molecules, such as superoxide dismutase (SOD), catalase (CAT), and various peroxidases, to maintain cellular redox homeostasis. These interactions contribute to the overall antioxidant defense network of the plant, ensuring robust protection against oxidative damage (Hasanuzzaman et al., 2012). Guaiacol peroxidase (GPX) is a critical component of the antioxidant defense system in plants, involved in ROS detoxification, cell wall strengthening, and adaptation to environmental stresses. Its ability to neutralize hydrogen peroxide and participate in lignin biosynthesis underscores its importance in plant resilience and survival under adverse conditions (Yadav and Chatopadhyay, 2023). Understanding GPX function and regulation provides insights into enhancing plant stress tolerance and developing strategies for improving crop productivity in challenging environmental environments.

2.2 NON-ENZYMATIC ANTIOXIDANTS AND THEIR ROLE DURING STRESS

Non-enzymatic defense systems against Reactive Oxygen Species (ROS) in plants are equally important and complement enzymatic mechanisms in mitigating oxidative stress. These non-enzymatic antioxidants play crucial roles in scavenging ROS, maintaining redox balance, and protecting cellular components. The complement to enzymatic antioxidants

consists of non-enzymatic antioxidants, such as ascorbic acid (AA), glutathione (GSH), α -tocopherol, carotenoids, phenolics, flavonoids, and the amino acid osmolyte proline. These substances influence cellular functions like cell division, elongation, aging, and programmed cell death. Their primary function is to protect cellular components from damage and support essential processes in plant growth and development (de Pinto and DeGara, 2004). Here are the key non-enzymatic defense systems against ROS in plants:

2.2.1 Ascorbic acid (AA)

Ascorbic acid (AA) also known as vitamin C, is a powerful antioxidant molecule in plants that plays a crucial role in combating environmental stresses, particularly oxidative stress induced by reactive oxygen species (ROS). Ascorbic acid directly scavenges reactive oxygen species (ROS) such as superoxide radicals ($O_2^{\cdot-}$), hydroxyl radicals ($OH^{\cdot}$), and singlet oxygen (O_2) (Edge and Truscott, 2021). By donating electrons, AA neutralizes these harmful ROS, thereby preventing oxidative damage to cellular components such as lipids, proteins, and DNA (Gegotek and Skrzydlewska, 2022). Ascorbic acid regenerates other antioxidants within the plant, such as tocopherols (vitamin E) and glutathione (GSH) (Chen et al., 2003). For example, AA can reduce oxidized tocopherol radicals back to their active reduced forms, enhancing their antioxidant capacity (Khan et al., 2011). Similarly, AA acts as a cofactor for enzymes like monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR), which regenerate ascorbate from its oxidized forms, ensuring a continuous supply of active antioxidant molecules (Smirnoff, 2018).

In photosynthetic tissues, ascorbic acid protects chloroplasts from oxidative damage induced by excess light energy and environmental stresses. AA helps maintain the integrity of photosynthetic membranes, photosystems, and pigments, thereby preserving photosynthetic efficiency and preventing photoinhibition. Environmental stresses such as drought, heat, cold, salinity, pollutants, and UV radiation can increase ROS production in plants. In response, plants may upregulate the biosynthesis of ascorbic acid to enhance their antioxidant defenses (Orabi and Abou-Hossein, 2019). This adaptive response helps plants cope with oxidative stress and maintain cellular homeostasis under adverse environmental conditions. Ascorbic acid is involved in regulating various signaling pathways associated with stress responses, hormone signaling, and defense mechanisms (Akram et al., 2017). Its role in modulating gene expression, enzymatic activities, and metabolic processes contributes to plant adaptation and survival under stress (Akram et al., 2017). Its involvement in signaling pathways and stress responses underscores its importance in plant adaptation to environmental challenges. Understanding the functions and regulation of ascorbic acid provides insights into enhancing plant resilience, improving crop productivity, and developing strategies for sustainable agriculture in changing environmental conditions.

2.2.3 Alpha tocopherol

Alpha tocopherol, a form of vitamin E, plays a crucial role in plant defense against environmental stresses. Alpha tocopherol acts as an antioxidant, scavenging harmful ROS such as superoxide radicals ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) that accumulate under stress conditions (Orabi et al., 2017). By neutralizing ROS, alpha tocopherol helps prevent oxidative damage to cellular structures such as proteins, lipids, and DNA (Ozougwu, 2016). Environmental stresses such as high light intensity and drought can lead to lipid peroxidation, which damages cell membranes. Alpha tocopherol protects membranes by preventing the propagation of lipid peroxidation chain reactions, thereby maintaining membrane integrity

and cellular function (Munne Bosch, 2007). Photosynthesis is sensitive to environmental stresses, and alpha tocopherol helps maintain photosynthetic efficiency by protecting chloroplast membranes and photosynthetic pigments from oxidative stress (Ali et al., 2020). Alpha tocopherol interacts with signaling molecules and pathways involved in stress responses, such as phytohormones and transcription factors (Ali et al., 2022). This regulation helps coordinate the plant's adaptive responses to environmental challenges. By mitigating oxidative stress and protecting cellular structures, alpha tocopherol supports overall plant growth and development under adverse environmental conditions (Hasanuzzaman et al., 2014). Thus, alpha tocopherol in plants functions as a potent antioxidant that protects against oxidative damage, maintains membrane integrity, enhances photosynthetic efficiency, regulates signaling pathways, and promotes resilience to environmental stresses. Its multifaceted role contributes significantly to plant adaptation and survival in challenging environments.

2.2.4 Carotenoids

Carotenoids play a critical role in plant defense against environmental stresses primarily through their antioxidant properties and other protective mechanisms. Carotenoids act as antioxidants, scavenging harmful ROS such as singlet oxygen ($^1\text{O}_2$), peroxy radicals ($\text{ROO}\cdot$), and other free radicals generated under stress conditions. By neutralizing ROS, carotenoids prevent oxidative damage to cellular components like lipids, proteins, and DNA (Dawanjee et al., 2021). Environmental stresses such as high light intensity and drought can lead to photooxidative damage in the photosynthetic apparatus. Carotenoids, particularly β -carotene and xanthophylls (e.g., lutein, zeaxanthin), protect photosynthetic pigments (chlorophylls) and membranes from oxidative stress, thereby maintaining photosynthetic efficiency (Klasinac et al., 2021). Carotenoids are integral components of thylakoid membranes in chloroplasts. They stabilize these membranes under stress conditions, thereby maintaining membrane fluidity and integrity. Non-photochemical quenching (NPQ) is a mechanism that dissipates excess excitation energy as heat to protect against photodamage. Carotenoids play a crucial role in NPQ by participating in the dissipation of excess light energy, thus preventing the formation of ROS (Faraloni and Torzillo, 2017). Carotenoids, especially β -carotene, are efficient scavengers of singlet oxygen ($^1\text{O}_2$), a highly reactive species produced during photosynthesis under stress conditions (Parvez et al., 2022). This scavenging action protects chloroplasts and other cellular components from oxidative damage. Carotenoids can influence the levels and activities of phytohormones such as abscisic acid (ABA), which regulates plant responses to environmental stresses like drought and salinity. Overall, carotenoids in plants serve as crucial antioxidants and photoprotective agents that protect against oxidative stress, maintain photosynthetic efficiency, stabilize membranes, enhance non-photochemical quenching, and regulate stress-responsive pathways. Their presence and function are essential for plant adaptation and survival in diverse environmental conditions.

2.2.5 Flavonoids

Flavonoids are a diverse group of secondary metabolites found in plants that play significant roles in combating environmental stresses through various mechanisms. Flavonoids possess strong antioxidant properties, scavenging reactive oxygen species (ROS) such as superoxide radicals ($\text{O}_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\cdot\text{OH}$) (Wang et al., 2007). By neutralizing ROS, flavonoids protect cellular structures from oxidative damage induced by environmental stresses such as high light intensity, drought, and pollutants. UV-B radiation can cause DNA damage and oxidative stress in plants. Flavonoids, particularly UV-

absorbing flavonols like quercetin and kaempferol, act as sunscreen compounds by absorbing and dissipating UV-B radiation, thereby protecting plant tissues from UV-induced damage (Agati and Tattani, 2010). Flavonoids can chelate metals such as iron and copper, which are involved in generating ROS through Fenton chemistry under stress conditions. By sequestering these metals, flavonoids reduce the formation of harmful ROS and mitigate oxidative stress (Flora et al., 2013). Flavonoids can modulate signaling pathways involved in stress responses. They interact with enzymes and receptors, influence gene expression related to stress defense, and regulate the production of phytohormones such as abscisic acid (ABA), which coordinates responses to drought and other stresses (Parvez et al., 2022). Some flavonoids exhibit antimicrobial properties that help plants defend against pathogens and pests (Treutter, 2006).

They can disrupt microbial cell membranes, inhibit enzyme activities essential for pathogen survival, and suppress fungal spore germination (Das et al., 2024). Flavonoids in pollen grains protect against oxidative stress during pollen development and germination. They maintain pollen viability and fertility under adverse environmental conditions. Flavonoids often work synergistically with other antioxidants and protective compounds in plants, enhancing overall stress tolerance and resilience (Sharma et al., 2019). Flavonoids contribute significantly to plant defense against environmental stresses by acting as antioxidants, UV protectants, metal chelators, regulators of signaling pathways, antimicrobial agents, and protectors of pollen viability. Their multifaceted roles make them integral components of plant adaptation strategies in challenging environmental conditions.

2.2.6 Proline

Proline, a unique amino acid, plays a crucial role in plant defense against environmental stresses, particularly abiotic stresses such as drought, high salinity, extreme temperatures, and heavy metal toxicity (Hosseinifard, 2022). Proline acts as an osmolyte, accumulating in plant cells under stress conditions to maintain cellular osmotic balance. This accumulation helps plants retain water and turgor pressure, thereby preventing dehydration and wilting during drought stress (Hemati et al., 2022). Proline stabilizes proteins, membranes, and other cellular structures under stress conditions. It protects enzymes and cellular components from denaturation and maintains their functional integrity, even at high temperatures or in the presence of high concentrations of salts or metals (Shafi et al., 2019).

Proline plays a role in scavenging ROS such as hydrogen peroxide (H_2O_2) and hydroxyl radicals ($\cdot OH$) that accumulate under stress conditions. By reducing ROS levels, proline helps minimize oxidative damage to cellular components such as lipids, proteins, and nucleic acids (Hossain et al., 2014). Proline metabolism is closely linked to cellular redox status. It participates in redox signaling and maintains redox balance within cells, which is critical for activating stress-responsive gene expression and antioxidant defense pathways (Liang et al., 2013). Proline interacts with phytohormones such as abscisic acid (ABA) and jasmonic acid (JA), which are involved in signaling pathways that regulate plant responses to environmental stresses (Wang et al., 2020). This interaction helps coordinate adaptive responses and enhance stress tolerance. Under stress conditions, proline accumulation can protect chloroplasts and photosynthetic machinery from damage, thereby maintaining photosynthetic efficiency and ensuring continued carbon assimilation (Zahra et al., 2022). Proline accumulation in roots enhances root growth and increases the uptake of water and nutrients, which are crucial for plant survival under stressful conditions such as drought and salinity (El Moukhtari et al., 2020). Overall, proline serves as a versatile molecule in plant adaptation to

environmental stresses by acting as an Osmo protectant, stabilizing biomolecules, scavenging ROS, regulating redox balance, interacting with phytohormones, improving photosynthetic efficiency, and enhancing root growth and nutrient uptake. Its multifaceted roles make proline a key component of plant resilience and survival in adverse environmental conditions.

3. CONCLUSION

Reactive oxygen species (ROS) are highly reactive molecules and free radicals derived from molecular oxygen. ROS are produced naturally in plant cells during various metabolic processes such as photosynthesis, respiration, and photorespiration. However, environmental stresses such as high light intensity, drought, extreme temperatures, pollutants, and pathogen attack can significantly increase ROS production in plants. The accumulation of ROS beyond a certain threshold can cause oxidative stress, damaging cellular components such as lipids, proteins, and DNA. This oxidative damage can impair cellular function and ultimately lead to cell death if not mitigated. Plants have evolved a sophisticated antioxidant defense system to counteract the harmful effects of ROS that neutralize ROS and prevent oxidative damage. Under stress conditions, plants often upregulate the production of antioxidants to maintain cellular redox homeostasis and protect themselves from oxidative stress. This antioxidant defense system helps plants adapt to environmental challenges and maintain their growth and productivity. Plants often employ both enzymatic and non-enzymatic defense mechanisms in a coordinated manner to combat stresses effectively. The activation of these defense systems is tightly regulated and can vary depending on the type of stress and the specific plant species. Understanding these defense mechanisms is crucial for developing strategies to enhance plant resistance to diseases and environmental stresses, which is essential for sustainable agriculture and natural ecosystems.

4. FUTURE CONSIDERATION

Future research on antioxidants in plant stress can focus on several critical areas to advance our understanding and improve stress tolerance in crops. Firstly, identifying and exploring novel antioxidant compounds, both natural and synthetic, could offer new avenues for enhancing protection against oxidative stress. Understanding the regulation of antioxidant enzyme expression and activity under stress conditions is essential, as it involves unraveling signaling pathways and genetic mechanisms that control antioxidant synthesis. Investigating antioxidant interaction networks and their role in signaling pathways will help optimize antioxidant mixtures for effective stress management. Genetic engineering approaches can be utilized to manipulate antioxidant defense systems, potentially boosting stress resilience in crops. Omics technologies offer opportunities to dissect comprehensive changes in antioxidant metabolism during stress, identifying biomarkers and targets for genetic manipulation. Field studies are crucial for validating antioxidant-based strategies in real-world conditions, assessing long-term effects on crop performance and stress resilience. Integrating antioxidant research into breeding programs can facilitate the development of stress-tolerant crop varieties. Exploring interactions between antioxidants and other stressors, such as pathogens and climate change, will provide insights into holistic stress management approaches. Lastly, developing innovative application technologies for antioxidants can ensure their effective delivery and uptake in plants across diverse environmental contexts.

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