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Review

Antioxidant Defense System in Plants: Reactive Oxygen Species Production, Signaling, and Scavenging During Abiotic Stress-Induced Oxidative Damage

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Abstract: Plants face various abiotic stresses in their natural environments that trigger the production of reactive oxygen species (ROS), leading to oxidative stress and potential cellular damage. This comprehensive review examines the interplay between plant antioxidant defense systems and ROS under abiotic stress conditions. We discuss the major enzymatic antioxidants, including superoxide dismutase, catalase, reductases, and peroxidases, as well as non-enzymatic antioxidants, such as ascorbic acid, glutathione, polyphenols, and flavonoids, which play crucial roles in ROS detoxification. This review elaborates on different types of ROS, their production sites within plant cells, and their dual role as both damaging oxidants and key signaling molecules. We discuss how various abiotic stresses—including heat, cold, drought, flooding, salinity, and heavy metal toxicity—induce oxidative stress and trigger specific antioxidant responses in plants. Additionally, the mechanisms of ROS generation under these abiotic stress conditions and the corresponding activation of enzymatic and non-enzymatic scavenging systems are discussed in detail. This review also discusses recent advances in understanding ROS signaling networks and their integration with other stress-response pathways. This knowledge provides valuable insights into plant stress-tolerance mechanisms and suggests potential strategies for developing stress-resistant crops by enhancing antioxidant defense systems. Moreover, the strategic ROS modulation through priming, exogenous antioxidants, nanoparticles, or genetic tools can enhance plant resilience. Integrating these methods with agronomic practices (e.g., irrigation management) offers a sustainable path to climate-smart agriculture. Our review reveals that ROS accumulation can be detrimental; however, the coordinated action of various antioxidant systems helps plants maintain redox homeostasis and adapt to environmental stress.

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1. Introduction

Environmental stresses have emerged as significant threats to global agricultural productivity and sustainability [1]. The severity of climate change has a significant effect on plants' ecosystems, with an increasing susceptibility of plants to multiple abiotic stresses, which influences their survival and productivity [1–3]. Abiotic stress includes temperature stress (heat and cold), drought, flooding, soil salinity, nutrient deficiency, heavy metal toxicity, and xenobiotic compounds [4–6]. These stresses are collectively responsible for approximately a 50% or more reduction in crop production [4,7,8]. Under field conditions, the combined abiotic stresses result in complex and synergistic effects on plant physiology, development, and metabolic processes, posing significant challenges for maintaining agricultural productivity and food security [1].

Plants have endogenous defense mechanisms that include both enzymatic and non-enzymatic antioxidant systems [9,10]. The enzymatic components consist of multiple specialized enzymes, including superoxide dismutase, catalase, various peroxidases, and reductases. Additionally, protective enzymes such as glutathione S-transferase, ferritin, polyphenol oxidase, and alternative oxidase play crucial roles during stress [10]. The non-enzymatic antioxidant molecules further strengthen the endogenous defense. These molecules include ascorbic acid, amino acids, phenolic acids, flavonoids, anthocyanins, carotenoids, vitamin E, and mineral elements [11–16]. These molecules are responsible for maintaining cellular redox homeostasis. Under normal conditions, plants maintain an optimal equilibrium between reactive oxygen species generation and neutralization. This equilibrium is essential for cellular signaling and regulating fundamental physiological processes, including plant growth and development [17,18]. However, the unfavorable environmental situation can disrupt this equilibrium by the excessive production of ROS, which leads to cellular damage and programmed cell death [18,19].

ROS serve a dual function in plant systems—while potentially harmful during stress (due to the overproduction of ROS that leads to oxidative stress), they also act as crucial signaling molecules that transmit stress signals to the nucleus via redox-mediated mitogen-activated protein kinase (MAPK) cascades. ROS can oxidize specific redox-sensitive proteins, initiating the MAPK cascade, and the activated MAPK can then phosphorylate transcription factors or other regulatory proteins, leading to changes in gene expression that help the plant adapt to stress [17–19]. These ROS molecules are involved in plant acclimation to environmental stress and function as key signal transducers that interact with several pathways [19]. ROS signaling is essential for fundamental biological processes such as cell division and cell differentiation [18]. Hydrogen peroxide (H_2O_2), a type of ROS, plays a central role in stress response across crop species, including cereals (rice, wheat, maize), legumes (mung bean, soybean), vegetables (cucumber), fruits (sour orange and strawberry), and herbs (basil) [20–25]. Recent studies showed complex crosstalk between ROS and other reactive species, such as reactive nitrogen species (RNS), reactive carbonyl species (RCS), and reactive sulfur species (RSS), in mediating plant responses to abiotic stresses [26–28]. This complex signaling network between ROS and other reactive species signifies a promising area of ongoing research in plant stress biology.

Our review examines the complex interplay of the enzymatic and non-enzymatic antioxidant defense of plants under various abiotic stresses. We highlight the types, production sites, ROS signaling, and their regulation in different stress conditions. In addition,

we discuss the oxidative stress induced by different abiotic factors such as heat, chilling or cold stress, water scarcity, flooding, salinity, and heavy metal toxicity. By understanding these mechanisms, this review provides valuable insights for developing stress-tolerant crops and enhancing agricultural productivity in challenging environmental conditions.

2. Antioxidative Defense Mechanisms in Plants

Antioxidant defense mechanisms enable plants to cope with oxidative stress and maintain the redox balance during normal or unfavorable environmental conditions. Under abiotic stress, plants can upregulate their antioxidative machinery by activating the gene expression and post-translational modifications of key enzymes. This adaptive response enables plants to reduce oxidative damage at cellular levels (such as proteins, lipids, membranes, and nucleic acids) and maintain normal growth and development [29–32]. The enzymatic and non-enzymatic antioxidant defense system in plants operates in different cellular organelles. Enzymatic antioxidants directly neutralize reactive oxygen species or repair oxidative damage. Non-enzymatic antioxidants, including carotenoids, polyphenols, amino acids, vitamins, and minerals, also scavenge ROS and support enzymatic antioxidant activities to maintain the redox balance [1,2,33–35]. The antioxidant defense system is regulated by complex signaling networks involving various transcription factors, phytohormones, and secondary messengers that work collectively to maintain redox homeostasis at the cellular level.

2.1. Enzymatic Antioxidants

Enzymatic antioxidants directly quench the ROS or convert them to be the least reactive in order to protect cellular organelles during oxidative stress [9] (Figure 1). These enzymatic antioxidants include several enzymes such as superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), guaiacol peroxidase (GPx), glutathione S-transferase (GST), alternative oxidase (AOX), polyphenol oxidase (PPO), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR), thioredoxin (Trx) including its multiple isoforms (f, m, h, s, o, x, y, and z), peroxiredoxin (PRX), and glutaredoxin (GRX) [9,10,33–35] (Figure 1). These enzymes can work independently or synergistically to maintain redox homeostasis (Table 1).

Superoxide dismutase (SOD) is the primary antioxidant defense enzyme that exists in three distinct metalloenzyme forms: Cu/Zn-SOD, Fe-SOD, and Mn-SOD [36]. These isoforms are in cytosol, chloroplasts, peroxisomes, and mitochondria [36,37]. The catalase, glutathione reductase, and ascorbate peroxidase work together to detoxify the H_2O_2 into water and oxygen molecules [38]. CAT and APX are metalloenzymes, which are located in peroxisomes and mitochondria [38]; however, APX is also found in cytosol, chloroplasts, microbodies, and in peroxisomal/glyoxysomal isoforms [39]. In chloroplasts, APX is a key component of the ascorbate–glutathione pathway (to produce monodehydroascorbate (MDHA)), requiring ascorbate as an electron donor [39]. This pathway, also known as the Foyer–Halliwell–Asada pathway, has both enzymatic (APX, DHAR, GPX, MDHAR) and non-enzymatic antioxidants (ascorbic acid and glutathione) that mainly regulate hydrogen peroxide levels in different cellular organelles [40]. The NADPH-dependent flavoprotein MDHAR produces ascorbate from MDHA by its thiol-mediated mechanism (Table 1). Spontaneous MDHA disproportionation yields dehydroascorbate (DHA), which is reduced to ascorbate via DHAR using glutathione as the electron donor. This process produces oxidized glutathione (GSSG), which is reduced to glutathione by NADPH-dependent glutathione reductase, thus maintaining redox equilibrium in the plant cells [41].

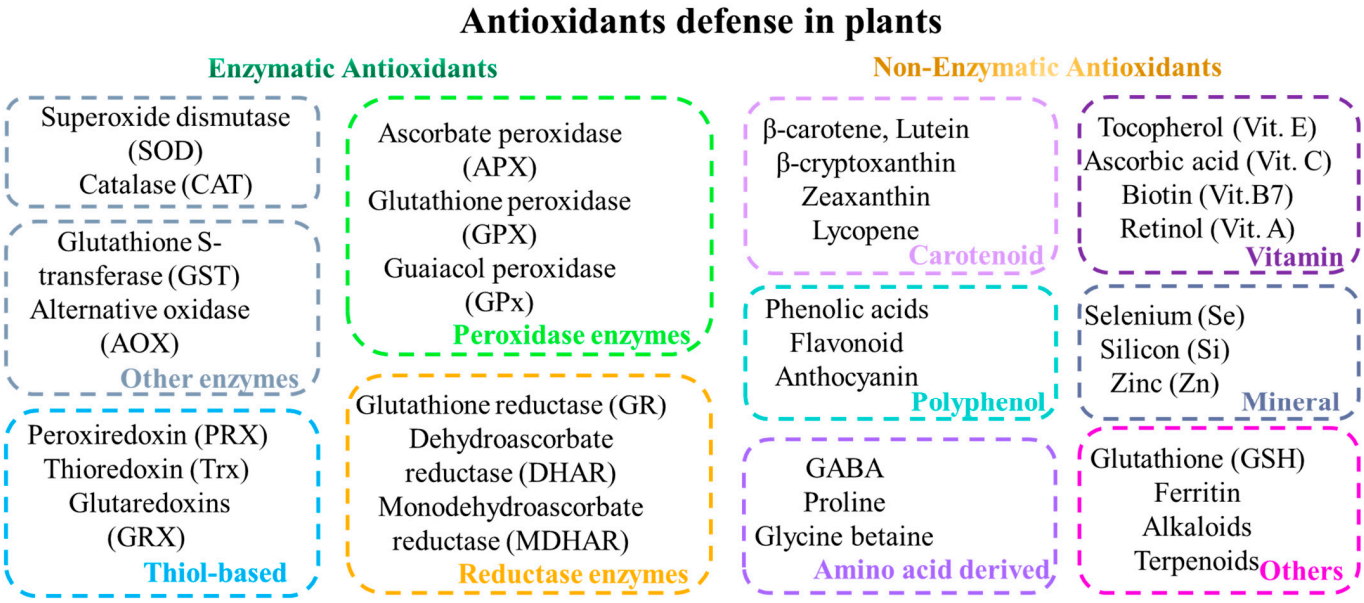

Figure 1. Illustrates the key components of enzymatic and non-enzymatic antioxidant defense machinery in plants [9,10,33–35].

Glutathione reductase (GR) is a key enzyme that plays a vital role in cellular defense systems and exhibits the highest activity in chloroplasts (70–80%). However, GR is also present in other parts of the plant cell [42]. Several factors affect the function of GR, such as the environmental pH and availability of NADPH and oxidized glutathione. It maintains redox homeostasis during oxidative stress by catalyzing GSSG reduction using NADPH as the electron donor [42,43]. Meanwhile, GPX is another critical player in this system and a member of the thiol-containing peroxidase family; it neutralizes harmful ROS by using glutathione and thioredoxins (Table 1). GST facilitates the conjugation between glutathione (GSH) and various electrophilic compounds at its catalytic sites, enabling the detoxification of xenobiotics, particularly herbicides and pharmaceutical compounds, followed by their vacuolar sequestration [44]. Additional protective mechanisms include peroxiredoxins (Prx) and thioredoxins (Trx) [34,35]. Prx is a thiol-dependent enzyme that exhibits peroxidase-like functionality in cellular compartments such as cytosol, chloroplasts, mitochondria, and nucleus, whereas Trx proteins regulate cellular redox status through disulfide bond reduction [35]. Polyphenol oxidase (PPO) is localized in the thylakoid membranes of chloroplasts and exhibits direct modulatory effects on photosynthetic processes [45]. This enzyme demonstrates multifaceted antioxidant capabilities through its interactions with peroxidase systems and the water–water cycle [45]. These systems collectively form an intricate antioxidant network essential for cellular stress tolerance.

Table 1. Enzymatic antioxidants' function during plant abiotic stress.

Serial No.	Enzymatic Antioxidant	Location	Function	Stress Response	Reference
1	Superoxide Dismutase (SOD)	Chloroplasts, mitochondria, cytosol	Catalyzes dismutation of $O_2\bullet^-$ to H_2O_2 and O_2	Increases during drought, salinity, and heat stress	[9,46]
2	Catalase (CAT)	Peroxisomes	Converts H_2O_2 to H_2O and O_2	Upregulated during oxidative stress conditions	[47–49]

Table 1. *Cont.*

Serial No.	Enzymatic Antioxidant	Location	Function	Stress Response	Reference
3	Guaiacol Peroxidase (GPx)	Cell wall, cytosol	Lignification Cell wall strengthening H_2O_2 scavenging	Response to mechanical stress and heavy metal stress	[9,50]
4	Ascorbate Peroxidase (APX)	Chloroplasts, cytosol	Reduces H_2O_2 to H_2O using ascorbate as an electron donor	Enhanced activity during cold and drought stress	[9,40]
5	Glutathione Peroxidase (GPX)	Cytosol, chloroplasts	Reduces H_2O_2 and lipid hydroperoxides	Activated during heavy metal and UV stress	[9,40]
6	Glutathione Reductase (GR)	Chloroplasts, mitochondria	Maintains GSH/GSSG ratio by reducing GSSG to GSH	Elevated levels of salt and metal stress	[42]
7	Dehydroascorbate reductase (DHAR)	Chloroplasts, cytosol, mitochondria	Regenerates ascorbate from dehydroascorbate Maintains ascorbate pool	Enhances drought and salt tolerance; protects photosynthetic machinery	[42,51]
8	Monodehydro-ascorbate reductase (MDHAR)	Chloroplasts, cytosol, mitochondria, peroxisomes	Reduces mono-dehydroascorbate to ascorbate using NADPH Maintains cellular redox balance	Improves tolerance to oxidative stress Enhances aluminum stress tolerance	[9,52]
9	Peroxiredoxin (PRX)	Chloroplasts, mitochondria, nucleus	Reduces hydrogen peroxide and organic hydroperoxides	Scavenges peroxides and peroxynitrite ($ONOO^-$); enhances heat drought, and cold tolerance	[34]
10	Thioredoxin (Trx)	Chloroplasts, mitochondria, cytosol	Maintains protein thiol–disulfide balance Maintains protein redox homeostasis and regulates enzyme activities	Protein disulfide reduction and redox regulation; improves drought and salt tolerance	[35]
11	Glutaredoxins (GRX)	Chloroplasts, mitochondria, nucleus, cytosol	Catalyzes thiol–disulfide exchange reaction Protein deglutathionylation	Glutathione-dependent protein repair, and iron–sulfur (Fe-S) assembly; enhances heavy metal tolerance	[53]
12	Glutathione S-transferase (GST)	Cytosol, chloroplasts	Conjugates glutathione to various substrates for detoxification	GSH conjugation and detoxification of lipid peroxidation products; improves drought and salt resistance	[54]
13	Alternative oxidase (AOX)	Mitochondrial inner membrane	Alternative respiratory pathway enzyme Reduces ROS production	Bypasses complexes III/IV in the mitochondrial electron transport chain; enhances drought and salinity stress tolerance	[55]
14	Polyphenol oxidase (PPO)	Chloroplasts	Oxidizes phenolic compounds into quinones	Oxidizes phenolics to quinones	[45].

2.2. Non-Enzymatic Antioxidants

Non-enzymatic antioxidants play a crucial role in ROS detoxification through chain reaction interruption mechanisms [10]. Several key compounds, including ascorbic acid (AsA), glutathione (GSH), compatible solutes, phenolics, α-tocopherol, carotenoids, flavonoids, anthocyanins, and proline, work together to neutralize stress-induced ROS accumulation [56–59]. GSH, a vital thiol tripeptide, facilitates H_2O_2 degradation via glutathione peroxidase (GPX)-mediated reactions [13]. It functions within the AsA-GSH pathway as a reducing agent for dehydroascorbate reductase (DHAR) while also participating in H_2O_2 and lipid peroxide elimination through GPX and glutathione S-transferase (GST) conjugation reactions [13,60]. Ascorbic acid serves dual roles as an electron donor for ascorbate peroxidase (APX) and as a peroxidase cofactor [61]. Additionally, AsA supports tocopherol regeneration and xanthophyll synthesis, contributing to energy dissipation [62]. Carotenoids function as specialized light-harvesting pigments that mitigate oxidative stress under high light conditions through thermal energy dissipation [63]. These compounds also protect photosystem II by effectively quenching singlet chlorophyll, triplet chlorophyll, and singlet oxygen species in thylakoid membranes [63,64].

Osmoprotective compounds such as proline and glycine betaine significantly accumulate in plants during stress (Table 2). The exogenous application of proline and glycine betaine represents a promising strategy for mitigating the detrimental impacts of environmental stresses on plants [65]. Glycine betaine (GB) has remarkable capabilities in enhancing plant tolerance to various abiotic stresses, especially high-temperature stress [66]. Extensive research has established GB as a crucial mediator of multiple physiological and molecular responses to heat stress, encompassing improvements in growth parameters, the protection of protein structures, the maintenance of photosynthetic efficiency, the modulation of stress-responsive gene expression, and the enhancement of antioxidant defense mechanisms [66,67]. Gamma-aminobutyric acid (GABA), an essential non-protein amino acid, demonstrates significant accumulation in plants during stress conditions, contributing to stress tolerance through its dual role in free radical scavenging and enzymatic regulation [68]. As an osmolyte, GABA either functions directly or stimulates the synthesis of other osmolytes like proline during drought conditions, facilitating osmotic adjustment for stress adaptation [69]. The GABA shunt pathway, comprising three key enzymes—glutamate dehydrogenase (GDH), GABA transaminase (GABA-T), and succinic semialdehyde dehydrogenase—mediates GABA metabolism [70]. Research on *Arabidopsis thaliana* has revealed that *GABA-T* gene deficiency results in decreased GABA and chlorophyll levels, impaired photosynthetic efficiency, and reduced GDH activity, while simultaneously increasing membrane ion leakage, malondialdehyde content, and accelerating leaf senescence under stress conditions [71]. Furthermore, GABA plays a crucial role in stress signal transduction through enhanced cytosolic calmodulin-dependent glutamate decarboxylase activity [72].

Table 2. Non-enzymatic antioxidants' functions during plant abiotic stress.

Serial No.	Non-Enzymatic Antioxidant	Location	Function	Stress Tolerance	Reference
1	Ascorbic Acid (Vitamin C)	Chloroplasts, cytosol, vacuoles, mitochondria	Neutralizes ROS Regenerates vitamin E Acts as an enzyme cofactor in various physiological processes Key role in photoprotection	Acts as the first line of defense against ROS Protects photosynthetic machinery during heat/drought Maintains cell membrane integrity under salt stress Enhances cold tolerance Crucial for stomatal regulation during water stress	[61]
2	Glutathione (GSH)	Chloroplasts, mitochondria, cytosol, nucleus	Maintains cellular redox balance Detoxifies heavy metals Protects proteins from oxidation Regenerates ascorbate (AsA-GSH cycle)	Primary defense against heavy metal toxicity Maintains cellular redox state during oxidative stress Key role in xenobiotic detoxification Protects protein thiols during heat stress Essential for drought-tolerance mechanisms	[13]
3	Tocopherols (Vitamin E)	Cell membranes, chloroplast membranes, thylakoids	Protects membrane lipids Scavenges lipid peroxyl radicals (prevents lipid peroxidation) Maintains membrane stability Protects photosystem II	Prevents lipid peroxidation under stress Stabilizes membranes during temperature extremes Protects chloroplast function during high light stress Enhances drought resistance Critical for cold stress tolerance	[73]
4	Carotenoids	Chloroplasts, chromoplasts	Quenches singlet oxygen Protects chlorophyll Dissipates excess light energy	Protects photosynthetic apparatus from photo-oxidation Dissipates excess light energy as heat Stabilizes thylakoids under high temperatures Light stress adaptation by dissipating energy as heat	[63,64,74]
5	Phenolic Compounds	Vacuoles, cell walls, cytosol	ROS scavenging Metal chelation UV screening Cell wall lignification UV-B radiation protection	Abiotic stress protection Enhanced pathogen resistance UV radiation screening Antioxidant activity Strong UV-B radiation protection	[75,76]
6	Flavonoids	Vacuoles, cell wall	ROS scavenging Osmolyte function during drought Metal chelation Regulates stomatal closure	Drought stress tolerance Salt-stress amelioration Metal toxicity chelation	[58,77]
7	GABA (Gamma-aminobutyric acid)	Cytosol, mitochondria	Protects cellular membranes Maintains ion homeostasis Stabilizes membrane integrity Scavenges ROS Enhances antioxidant enzyme activities Maintains redox homeostasis	Chelates heavy metals Enhances frost tolerance Improves salt and drought tolerance Acts as a heat shock protectant Maintains photosynthetic efficiency under stress	[68–70]

Table 2. *Cont.*

Serial No.	Non-Enzymatic Antioxidant	Location	Function	Stress Tolerance	Reference
8	Proline	Cytosol, chloroplasts	Osmolyte function Membrane stabilizer ROS scavenger Metal chelator Protein structure stabilizer	Osmolyte function during drought/salt stress Membrane stabilization under extreme temperatures ROS scavenging during oxidative stress Protein stabilization during dehydration Metal stress tolerance	[65]
9	Glycine Betaine	Chloroplasts, cytosol	Osmotic adjustment Protein structure protection Membrane integrity maintenance Photosynthetic apparatus protection	Temperature stress tolerance Minimizes ROS during water deficit conditions. Cold stress protection	[66,67]
10	Selenium (Se)	Throughout plant tissues	ROS detoxification Activates antioxidant defense mechanisms Enhances photosynthetic efficiency Enhances selenoproteins which combat ROS	Increases drought tolerance by regulating water status Protects against oxidative damage during salt stress Improves heavy metal stress tolerance	[78–80]
11	Zinc (Zn)	Cell wall, membranes, cytoplasm	Cofactor for antioxidant enzymes Maintains membrane stability Regulates stomatal function under drought Enhances root growth and water uptake	Regulates stomatal function during drought Involved in auxin metabolism and stress signaling Protects chloroplast structures during heat stress	[81]
12	Silicon (Si)	Cell walls, epidermis	Strengthens cell walls Improves water retention Forms a protective layer in cell walls Improves nutrients and water uptake	Improves water use efficiency during drought Reduces metal toxicity through complexation Enhances structural stability against lodging Regulates osmolyte accumulation under salt stress	[82,83]
13	Thiamine and nicotinic acid	Chloroplasts, mitochondria, and cytoplasm	Modulates MAPK and ABA pathways Upregulates phytochelatins Enhances GR, APX, and phenolic compounds Chelates lead (Pb) via phenolics/NADPH systems	Reduced Pb-induced oxidative damage (lower H_2O_2 and MDA) Enhanced activity of SOD, CAT, and POD, improving redox balance Higher photosynthetic efficiency	[84]

Recent advances in plant stress biology have highlighted the significance of vitamins and mineral elements in stress tolerance (Table 2). Some vitamins, such as thiamine (vitamin B_1) and nicotinic acid (vitamin B_3), enhance plant heavy metal stress tolerance by modulating antioxidant defense systems and redox homeostasis. Their exogenous application improves growth, reduces oxidative damage, and restricts Pb accumulation in *Lens culinaris*, offering a sustainable strategy for crop protection in contaminated soils [84]. Similarly, mineral elements such as silicon (Si) application have emerged as a promising approach for enhancing plant drought stress tolerance [82]. Additionally, the foliar application of zinc particles enhanced the antioxidative defense of sunflower plants against drought stress [81]. Similarly, selenium nanoparticles demonstrated superior bioactivity and safety profiles at

low concentrations, exhibiting enhanced biocompatibility and reduced toxicity compared to conventional selenium forms like selenate and selenite [85]. The integration of these non-enzymatic antioxidant compounds in agricultural practices represents a sustainable approach to enhancing crop resilience against various abiotic stresses, ultimately contributing to global food security in the face of climate change.

3. Types, Production Sites, and Signaling of Reactive Oxygen Species

Reactive oxygen species exhibit dual functionality in plant cells based on their concentration levels [17]. At lower levels, they serve as vital signaling molecules, facilitating cellular responses to environmental stress through complex signaling cascades [17]. However, during severe abiotic stress, excessive ROS accumulation leads to cellular toxicity and triggers programmed cell death [86]. The cellular impact of ROS regulatory, harmful, or signal mediating is determined by the precise equilibrium between their generation and scavenging processes [19]. The endogenous antioxidative defense systems scavenge ROS and maintain cellular redox homeostasis [87–89]. To enhance plant stress tolerance, cellular antioxidant capacity can be improved by genetic modifications (transgenic plants) or foliar application, thereby fortifying the plant's defense against environmental stress.

3.1. Types of ROS

Reactive oxygen species are a diverse group of molecules that include free radicals and non-radical compounds [90]. The free radicals include superoxide ($O_2\bullet^-$), alkoxyl (RO•), hydroxyl (•OH), and peroxyl (ROO•) radicals, whereas H_2O_2, singlet oxygen ($^1O_2$), and ozone (O_3) are considered non-radical molecules. The non-radical ROS molecules are less reactive but play important roles in plants. Beyond these, there are other non-radical ROS molecules such as organic hydroperoxides (ROOH), excited carbonyls (RO*), and hypochlorous acid (HOCl) [90,91].

Reactive oxygen intermediates (ROIs) are a specific subset of ROS that form when O_2 is partially reduced. This group includes O_3 and $^1O_2$ molecules. The ROS family is quite extensive and further includes reactive species such as hypohalous acids (HOBr, HOI, HOCl) and radical forms like carbonate ($CO_3\bullet^-$) and semiquinone ($SQ\bullet^-$) [90,92,93]. These molecules play various roles in biological and chemical processes, often acting as signaling molecules or contributing to oxidative stress.

The superoxide radical is a unique molecule that acts as a reducing agent but can also give rise to powerful oxidants [90]. When it interacts with nitric oxide (NO), it sets off a chain reaction that produces other reactive molecules such as RNS, RSS, and RCS [27,28,92]. These reactive species are often seen as harmful during oxidative stress, where they can negatively affect plant growth and development. However, they are essential players in modulating redox signaling pathways, inside and outside of cells [90,91]. This means that they help maintain balance and communication within biological systems—harmful in excess but vital for normal cellular functions.

3.2. Production Sites of ROS

Reactive oxygen species are generated in several cellular organelles, including peroxisomes, chloroplasts, plasma membrane, cell wall, and mitochondria (Table 3). The integrated contribution of ROS from these organelles determines the total cellular ROS levels [90]. Notably, chloroplasts are the principal ROS production sites, generating 30–100-fold higher levels than mitochondria [94–96]. This enhanced ROS generation in chloroplasts occurs through the interaction between chlorophyll molecules and light, particularly involving the triplet chlorophyll and electron transport chains of both photosystems I and II. During photosynthesis in PSII, chlorophyll molecules within the light-harvesting

complex (PSII-LHC) become activated to an energized singlet state (1Chl*), characterized by a brief lifetime of approximately ~10^{-8} s [97]. While a significant portion of this energy drives photosynthetic electron transport through P680 via photochemical quenching (pQ), excess energy beyond the pQ capacity dissipates through alternative pathways such as heat emission, fluorescence, or conversion to triplet chlorophyll (3Chl*) through intersystem crossing. This 3Chl* state, though lower in energy, exhibits a longer half-life of about ~10^{-3} s [97]. Under normal conditions, carotenoid pigments (specifically lutein and zeaxanthin) within the LHC effectively quench 3Chl*, preventing energy transfer to other molecules. However, the inefficient quenching of 3Chl* can lead to interactions with molecular oxygen ($^3O_2$) released from water-splitting reactions in the oxygen-evolving complex (OEC), resulting in singlet oxygen formation [98].

Table 3. Reactive oxygen species production, function, signaling, and scavenging mechanisms in plants.

Serial No.	ROS Type	ROS Production Sites	Primary Function	Cellular Reactions and Damage	Effects on Plants	Key Signaling Roles	Scavenging Mechanisms
1	Superoxide ($O_2\bullet^-$)	Chloroplasts, mitochondria, cell membrane	Electron transport chain byproduct, signaling molecule	Damages Fe-S centers, membrane lipid peroxidation	Membrane damage, protein oxidation	Pathogen defense, cell death signaling, growth regulation	Superoxide dismutase
2	Hydrogen Peroxide (H_2O_2)	Peroxisomes, chloroplasts, cytosol	Cell signaling, pathogen defense	Oxidizes protein thiols, inactivates enzymes, DNA damage	Cell wall modification, root growth, stress signaling	Stress-response signaling, root growth regulation, stomatal closure	Catalase, ascorbate peroxidase
3	Hydroxyl Radical (•OH)	Cell wall, all cellular compartments	Highly reactive oxidant	Severe DNA/RNA damage, protein oxidation, cell death	DNA damage, lipid peroxidation	Programmed cell death, stress response, defense activation	Non-enzymatic antioxidants
4	Singlet Oxygen ($^1O_2$)	Photosystem II, chloroplasts	Light harvesting byproduct	Chlorophyll bleaching, lipid peroxidation, PSII damage	Chloroplast damage, PSII inhibition	Photosynthetic signaling, chloroplast-nucleus communication, stress acclimation	Carotenoids, tocopherols

In the photosystem II (PSII) reaction center, P680 undergoes photoexcitation to its singlet state (1P680*) and forms a complex with pheophytin (Pheo), resulting in 1(P680 + Pheo−) [99,100]. Subsequently, electron transfer to quinone A (QA) occurs, generating P680+ QA−. Under stress conditions where QA is pre-reduced and unable to accept electrons, 3(P680 + Pheo−) undergoes recombination with P680 to form the triplet state 3P680* [101]. Although PSII contains two β-carotene molecules capable of quenching 3P680*, their spatial separation exceeds the critical Van der Waals distance (3.6 Å), preventing effective quenching and leading to $^1O_2$ formation [99,100]. Furthermore, abiotic stress-induced stomatal closure reduces chloroplastic CO_2 concentration, causing electron transport chain (ETC) over-reduction and increasing charge recombination between 1P680* and QA− in PSII, thereby enhancing $^1O_2$ production [102,103]. While $^1O_2$ generation is absent in PSI, ferrous iron (Fe^{2+}) mediates the conversion of $O_2\bullet^-$ and H_2O_2 to hydroxyl radicals (•OH). In non-photosynthetic tissues, such as roots, mitochondrial electron leakage

from complexes I and III generates $O_2\bullet^-$, which is converted to H_2O_2 by manganese and copper–zinc superoxide dismutases [103]. In peroxisomes, glycolate oxidase is the primary ROS-generating enzyme [90,103].

In peroxisomes, xanthine oxidase (XOD) generates superoxide radicals and uric acid, which are subsequently converted to hydrogen peroxide through the actions of SOD and urate oxidase [104,105]. In the peroxisome, hydrogen peroxide is produced by fatty acid β-oxidation, superoxide dismutation, and flavin oxidase activity [105]. Additionally, peroxisomal enzymes such as polyamine oxidase, copper amine oxidase, sulfite oxidase, and sarcosine oxidase also produce hydrogen peroxide [104,106]. Notably, in peroxisomes, monodehydroascorbate reductase (MDHAR) functions to neutralize hydrogen peroxide via the ascorbate–glutathione cycle [107]. The apoplastic space harbors multiple ROS-generating enzymes, including NADPH oxidase, class III peroxidases, amine oxidases, germin-like oxalate oxidases, quinone reductase, and lipoxygenases [108]. The cell wall produces ROS by peroxidases, amine oxidases, and lipoxygenases. The plasma membrane ROS generation involves NADPH oxidase and quinone reductase activities [108,109]. The endoplasmic reticulum produces superoxide via cytochrome P450, involving a complex electron transfer process [110]. Glyoxysomes produce superoxide and hydrogen peroxide via fatty acid oxidation and by the activity of glycolate oxidase and urate oxidase [18]. In the cytosol, the xanthine oxidase and aldehyde oxidase are responsible for ROS production [90,106]. In short, peroxisomes are involved in photorespiration and fatty acid oxidation, producing ROS like H_2O_2 and $O_2\bullet^-$. Mitochondria are the powerhouses of the cell, where ROS ($O_2\bullet^-$ and H_2O_2) are produced due to electron leakage from the ETC during stress. Chloroplasts are responsible for photosynthesis, where ROS ($^1O_2$, $O_2\bullet^-$, H_2O_2) are produced under excess light or drought stress. The endoplasmic reticulum is involved in protein folding and lipid synthesis, producing ROS ($O_2\bullet^-$, H_2O_2) during protein misfolding stress (Figure 2).

3.3. Signaling of Reactive Oxygen Species

Plants can transmit stress signals from affected tissues to healthy tissues under stress conditions. These signals trigger the defense responses and enhance resilience via signal transduction pathways, with ROS playing a central role as messengers [18,106]. However, under prolonged stress, the excessive production of ROS can cause oxidative damage and harm the cells [17]. Under these conditions, the regulation of ROS signaling pathways is important to mitigate the damage caused by stress [18,90]. Both biotic (insects/pests) and abiotic stressors can trigger ROS production in plant cells [111,112]. This disrupts the balance of ROS and activates a chain reaction of signals. These signals involve feedback and feed-forward mechanisms that help the plants adapt to stress [90,113]. The time and location of (when and where ROS production play crucial roles in how effectively the plant's signaling networks work, which is crucial for the plant's survival.

The plant stress response involves complex signaling cascades initiated by ROS. ROS act as cellular messengers, spreading stress signals to neighboring cells from one cell to another; this coordinated signaling effort helps the plants adapt to stress conditions. Plants use a variety of molecules, such as phytohormones, amino acids, and polyphenols, which act as signals in response to environmental stress [13,114]. During stress, ROS causes protein oxidation, creating smaller peptides that act as a secondary messenger in the signaling process. H_2O_2 (mobile molecule) is the key signaling molecule due to its non-ionic nature, relative stability, and ability to move through cellular membranes with the help of aquaporin channels [115]. ROS-mediated signaling regulates a range of cellular responses. These include activating antioxidant systems, defense-related genes, calcium ion mobilization, kinase pathways, and protein phosphorylation, all of which assist plants in withstanding stress conditions [115]. ROS signaling also increases jasmonic

acid, salicylic acid, and ethylene stress hormone concentration, which play critical roles in the plant's defense (Figure 2). During biotic stress, ROS signaling induces the production of defense proteins and phytoalexin protective compounds and reinforces the plant cell wall [116]. Additionally, ROS signaling also regulates the activity of enzymes. During stress, glutamate dehydrogenase shifts from its role in ammonia metabolism to produce the proline compound, which contributes to stress tolerance. At lower levels, ROS supports lignin production, tracheary element formation, and programmed cell death, all of which enhance plant tolerance against abiotic stress [117,118]. In short, ROS signaling is a complex and dynamic network that facilitates plants to adapt and survive under unfavorable conditions.

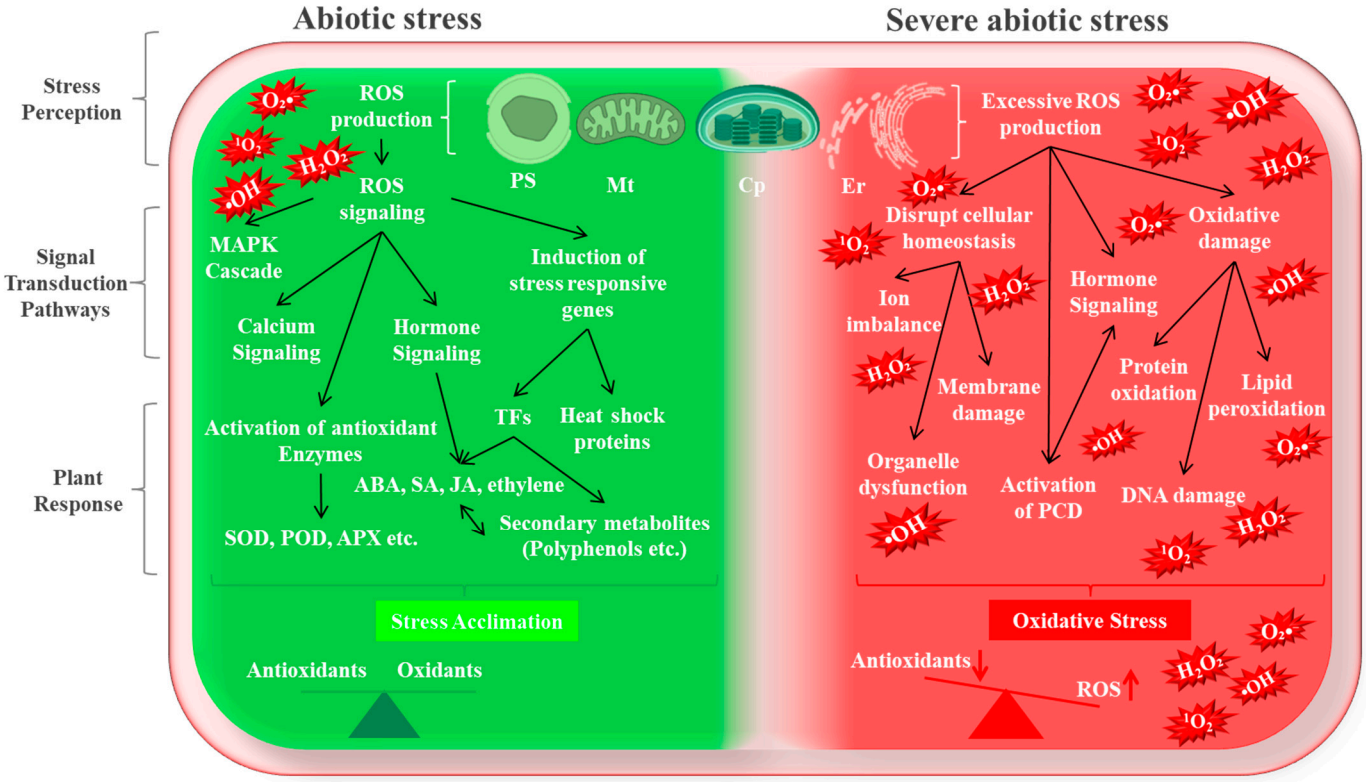

Figure 2. ROS signaling in plants in response to abiotic stress. Abbreviations: ROS, reactive oxygen species; MAPK, mitogen-activated protein kinase; TFs, transcription factors; SOD, superoxide dismutase; POD, peroxidase; APX, ascorbate peroxidase; PCD, programmed cell death; ABA, abscisic acid; SA: salicylic acid; JA: jasmonic acid; Ps: peroxisomes; Mt: mitochondria; Cps: chloroplasts; ER: endoplasmic reticulum. On the left, low/moderate abiotic stress triggers stress perception and signal transduction pathways, including MAPK cascades, calcium signaling, ROS production, and hormone signaling. These pathways activate transcription factors (TFs), heat shock proteins (HSPs), the activation of antioxidant enzymes (e.g., SOD, POD, APX), and secondary metabolites (e.g., polyphenols), leading to stress acclimation. On the right, severe abiotic stress produces excessive ROS, which disrupts cellular homeostasis, causing ion imbalance, membrane damage, organelle dysfunction, and the activation of programmed cell death (PCD). This results in oxidative damage to proteins, DNA, and lipids, ultimately leading to oxidative stress and eventually cell death. The balance between ROS production and antioxidant defense determines the plant's ability to cope with abiotic stress.

Under stress conditions, ROS generated in cellular organelles facilitate retrograde signaling to the nucleus at approximately 8.4 cm per minute, functioning as crucial secondary messengers in plant stress responses [109,117]. This retrograde communication facilitates the nuclear modification of anterograde signals, allowing plants to adapt to stress conditions [119]. In an unfavorable environment, the elevated ROS levels trigger the expression of stress-response heat shock genes. During temperature stress, the heat

shock proteins (HSPs) are key molecular chaperones that prevent protein aggregation and assist in protein folding [109]. In addition to heat tolerance, HSPs are regulated in response to various abiotic stresses such as light, oxygen deprivation, and cold stress [120]. In *Arabidopsis thaliana*, cell cultures have shown that higher hydrogen peroxide induces heat shock gene expression and causes an increased activity of ascorbate peroxidase 2 (APX2) and small HSPs such as *HSP17.6* and *HSP18.2* [121]. In addition, the Arabidopsis H_2O_2-mediated signaling enhances ascorbate peroxidase 1 (APX1) activity, induces light stress tolerance, and improves adaptation to combined heat and drought stresses [122,123]. During hypoxia stress, respiratory burst oxidase homologs regulate ROS production, with this ROS signaling being essential for hypoxic stress management [124].

Hydrogen peroxide is an essential signaling molecule during oxygen-deficient conditions (anoxia/hypoxia). It enhances the transcription of heat shock proteins and fermentation-related genes such as alcohol dehydrogenase [125,126]. In addition, H_2O_2 modulates ZAT10 and ZAT12 transcription factors and other proteins that contribute to stress adaptation [125,126]. Reactive oxygen species demonstrate intercellular communication capabilities through wave-like propagation to surrounding tissues [117,124]. This systemic signaling mechanism, mediated by superoxide and hydrogen peroxide, has been revealed in waterlogged rice roots and Arabidopsis systems. In salt-stress responses, NADPH oxidase genes, specifically *AtrbohF* and *AtrbohD*, generate ROS that regulate cellular Na+/K+ equilibrium, thereby conferring salt tolerance [127]. Research has shown that Arabidopsis mutants deficient in AtrbohF exhibit increased salt sensitivity due to impaired ROS accumulation in root vascular tissues [127]. Under nutrient stress conditions, particularly potassium deficiency, elevated hydrogen peroxide levels in roots promote *HAK5* gene expression while simultaneously activating calcium signaling pathways [128,129]. Further research into ROS-mediated molecular mechanisms and their interactions with other signaling cascades could enhance our ability to develop stress-resistant crop varieties.

4. Abiotic Stress-Induced Oxidative Stress

Plants exhibit sedentary growth patterns in natural environments [130]. However, the environmental stressors driven by anthropogenic activities and climate change trigger oxidative stress through elevated reactive oxygen species production [109]. Multiple cellular compartments are recognized as ROS generation sites (Table 3), including chloroplasts, mitochondria, peroxisomes, apoplast, and plasma membranes, with chloroplasts as the predominant source [95]. Abiotic stress typically restricts CO_2 availability, disrupting carbon fixation mechanisms. This disruption leads to oxygen reduction reactions and elevates ROS levels that compromise chloroplast function and photosynthetic efficiency [6]. ROS accumulation patterns depend on plant species, genetic makeup, stress-resistance capabilities, and exposure duration.

4.1. Heat (High Temperature) and Chilling (Low Temperature) Condition-Induced Oxidative Stress

High-temperature stress induces oxidative damage in plants through excessive ROS generation, which disrupts cellular homeostasis and leads to extensive cellular injury [79,131]. Research has demonstrated that exposure to elevated temperatures (35 °C/32 °C day/night cycles) impairs photosystem II functionality by inhibiting the reaction center and electron transport chain, resulting in decreased quantum efficiency (Fv/Fm) and compromised PSII photochemistry in rice varieties [132]. Studies in cucumber seedlings revealed that high-temperature stress (35 ± 1 °C for 7 days) triggered $O_2\bullet^-$ production, reaching nearly 80% higher than control levels [133]. In addition, malondialdehyde (MDA) levels increased by 60.6% under high-temperature stress than control cucumber seedlings [133]. Similarly, tobacco cells exposed to 50 °C exhibited a 50% eleva-

tion in $O_2^{\bullet -}$ levels within just 5 min of treatment, indicating the rapid onset of oxidative stress [134]. In field experiments with sorghum, high-temperature conditions (36/26 °C and 39/29 °C) caused dramatic increases in $O_2^{\bullet -}$ accumulation, with 3.5-fold and 2.3-fold higher levels detected in pollen and pistil tissues during the post-anthesis period, respectively [135]. Similarly, the extended exposure of *Gossypium hirsutum* to 45/30 ± 2 °C for 120 days led to a 0.78% rise in MDA content, negatively impacting fiber characteristics and boll development [136]. In *Oryza sativa*, heat stress at 38 °C for 5 days doubled H_2O_2 accumulation [137]. However, some studies present contrasting findings—for instance, while high-temperature treatment (38 °C for 5 days) elevated H_2O_2 levels by 27% in rice seeds, researchers observed no significant changes in $O_2^{\bullet -}$ content or lipid peroxidation markers compared to controls [137]. These studies showed that high temperature or heat stress induces ROS production, "creates redox imbalance", and causes significant oxidative damage in various crop species.

Low-temperature stress induces excessive reactive oxygen species production in plants through several mechanisms, including compromised membrane fluidity, impaired photosynthetic machinery function, and disrupted ROS homeostasis, ultimately resulting in cellular membrane damage and electrolyte leakage [25,138]. Research has demonstrated significant oxidative stress markers in cold-stressed plants. For instance, the exposure of 14-day-old rice (*O. sativa* cv. DM You 6188) seedlings to cold stress (12 °C for 6 days) resulted in substantial increases in MDA levels (180%) and electrolyte leakage (49%) [139]. These findings collectively underscore the complex interplay between temperature stress and oxidative damage in plants. In another study investigating cold sensitivity, *Solanum lycopersicum* cv. Jinpeng No. 1 subjected to low-temperature conditions (15 °C/8 °C day/night cycle for 24–48 h) exhibited significantly higher levels of MDA and hydrogen peroxide by 62% and 34%, respectively, compared to control plants [140]. Similarly, the tomato (*Lycopersicon esculentum*) showed a significant increase of 32% in H_2O_2 levels under cold stress (of 4 °C for 24 h). Under cold stress, *L. esculentum* cv. C.H. Falat showed a 100% increase in H_2O_2 content and a 20% increase in electrolyte leakage (at 3 °C for 6 h over 6 days) [141,142]. Under progressive cold stress (4 °C for 24 h, followed by 0 °C for 12 h, and −6 °C for 12 h), comparative analysis between wild-type and transgenic *Ammopiptanthus mongolicus* revealed that wild-type plants showed an increased accumulation of H_2O_2 (confirmed by 3,3′-diaminobenzidine staining), indicating enhanced oxidative stress in control than transgenic lines [143]. These insights into plant responses to cold stress provide valuable directions for future research in improving stress management strategies and promoting sustainable agricultural practices under cold stress.

4.2. Drought (Water Scarcity) and Flooding (Waterlogging)-Induced Oxidative Stress

Water scarcity has a significant impact on plant cellular processes. The water deficit condition mainly disrupts photosynthesis and triggers oxidative stress [144]. Under drought stress, plants close their stomata to safe water, which limits CO_2 uptake and reduces photosynthetic efficiency. This disruption affects the light-harvesting complexes and photochemical processes in chloroplasts, leading to an overproduction of ROS [145]. In plants, several changes at the molecular level occur in response to water stress. These changes include protein denaturation, membrane damage, impaired TCA cycle enzymes, and reduced carboxylation efficiency. These alterations, coupled with reduced NADP+ regeneration, cause the electron transport chain's over-reduction. This leads to increased electron leakage and causes excessive ROS accumulation, resulting in oxidative damage [146,147].

Different studies across various plant species have consistently shown increased ROS accumulation and oxidative damage under water deficit conditions. After 14 days of prolonged drought stress, all the wild-type *Arabidopsis thaliana* plants showed a more than

2-fold increase in H_2O_2, superoxide radical, MDA contents, and electrolytic leakage [57]. Correspondingly, *Phragmites karka* exhibited a significant increase of 22% in MDA content under 40% water-holding capacity for 35 days [148]. *Coffea arabica* L. also showed elevated MDA levels when exposed to prolonged drought stress for 20 days [149]. Similarly, when rice plants were subjected to 8 days of water scarcity, they showed an increase in superoxide (1.8-fold), hydrogen peroxide (2.1-fold), and MDA (1.66-fold) contents compared to control plants [150]. Finger millet under severe water deficit (75% reduction) showed significantly higher electrolyte leakage and H_2O_2 contents than the control [151]. Likewise, tomato plants exposed to 6 days of drought stress showed increased MDA content and a 39% increase in electrolyte leakage [152]. Understanding the oxidative stress regulation in plants under drought stress would be helpful to work on strategies to mitigate oxidative stress and improve drought resilience in crops.

Drought stress significantly influences oxidative stress markers in different plant species [77,144,153]. Polyethylene glycol (PEG)-induced osmotic stress in *Brassica napus* L. and *Vigna radiata* L. consistently showed enhanced ROS accumulation and membrane damage [154,155]. In soybeans, 15% PEG-induced osmotic stress significantly increased MDA, H_2O_2, and lipoxygenase (LOX) activity compared to the control soybean plants [156]. Also, tomato plants exposed to water deficit conditions (60% field capacity for 20 days) exhibited significant increases in superoxide ($O_2^{\bullet -}$) by 75%, H_2O_2 by 37%, and MDA levels by 83% [157]. Severe drought stress in *Medicago truncatula* increased MDA and H_2O_2 levels; however, these parameters normalized upon rewatering [158]. The plant's inherent genetic makeup is crucial for drought tolerance, as shown in *Phaseolus vulgaris* (common bean) genotypes [159]. A comparative analysis of drought-tolerant (Bn-150) and drought-sensitive (Bn-16) common bean varieties under 50% field capacity for 14 days showed that the sensitive genotype had doubled MDA content and increased ROS levels, including $O_2^{\bullet -}$, H_2O_2, and •OH [159].

Waterlogging conditions create hypoxic or anoxic environments, mainly affecting plant roots. The hypoxia/anoxia disrupts mitochondrial respiration, leading to electron leakage from ETC (Complex I/III) and enhanced ROS ($O_2\bullet^-$ and H_2O_2) production via NADPH oxidase (RBOH) activation. The impaired antioxidant system (SOD, CAT, APX) further exacerbates ROS accumulation, triggering oxidative damage [160]. Recent research has shown significant differences in how various plant species respond to oxidative stress under waterlogging conditions. For example, a comparative analysis of waterlogging-tolerant (JN01) and -sensitive (JN31) genotypes of *Sorghum bicolor* revealed that the sensitive genotype has increased MDA levels compared to the tolerance genotype when exposed to waterlogging for 6, 9, and 12 days [161]. In the waterlogging-sensitive *Sesamum indicum* L. cv. BARI Til-4, MDA and hydrogen peroxide levels increased significantly under 2 to 8 days of flooding stress [162]. This pattern of enhanced oxidative stress markers has been consistently observed in *Solanum lycopersicum* [163]. Similarly, barley (*Hordeum vulgare*) waterlogging-susceptible TF57 showed pronounced increases in MDA content and the superoxide generation rate compared to the minimal changes in waterlogging-tolerant TF58 under 21-day waterlogging stress [164]. Notably, the Antarctic species *Deschampsia antarctica* exhibited elevated MDA and H_2O_2 levels under 7 days of waterlogging stress [165]. These indicate the universal nature of oxidative stress responses to waterlogging across diverse plant species.

4.3. Salt Stress-Induced Oxidative Stress

Salt stress induces several detrimental effects in plants, including ionic imbalance, osmotic pressure disruption, nutrient deficiencies, and genetic damage. These harmful effects collectively lead to enhanced ROS generation and cause severe oxidative damage

in plants [166]. Under 100 mM and 200 mM, NaCl stress resulted in 2.5-fold and 3-fold increases in H_2O_2 production, respectively, accompanied by increases in lipid peroxidation [167]. The impact of salt stress varies across plant tissues and organs, with the roots generally showing the highest sensitivity, followed by older and younger leaves in a decreasing order of susceptibility. Recent studies in rice showed that salt stress doubled ROS accumulation, lipid peroxidation, and membrane damage in root tissues compared to control plants [168]. Similarly, when tomato plants were exposed to 100 mM NaCl stress, they showed significant increases in superoxide (157%), H_2O_2 (176%), lipid peroxidation (94%), and electrolyte leakage (158%) [169]. Similar responses were observed in *Capsicum annuum* (sweet pepper), where moderate salinity stress (0.4%) led to a 100% increase in lipid peroxidation and electrolyte leakage [170]. In addition, mung bean (*Vigna radiata* (L.)) plants showed a two-fold increase in H_2O_2, lipid peroxidation, membrane damage, and superoxide, under 100 mM NaCl stress [171].

Salt stress significantly increases the key oxidative stress markers, restricting plant growth and development [172]. Maize (*Zea mays*) plants under 120 mM NaCl stress showed increased H_2O_2 and MDA by 50% and 25%, respectively, compared to control plants [173]. The genetic background is crucial in salt stress-tolerance mechanisms, as shown by differential responses among plant species. Sunflower genotypes such as FH-572 (a salt-sensitive genotype) revealed a 78% increase in H_2O_2 levels, while FH-621 (salt tolerant) showed enhanced salt tolerance with a 20% reduction in H_2O_2, under 120 mM NaCl treatment [174]. Similarly, the TS-5 sesame varieties exhibited a higher tolerance to salt stress than TH-6 under 70 mM NaCl stress [175]. Moreover, *Medicago truncatula* also showed genotype-specific responses between salt tolerance and oxidative stress markers like MDA and H_2O_2, [176]. Faba bean (*Vicia faba*) genotypes exposed to NaCl stress showed that the hydrogen peroxide, superoxide, MDA, electrolyte leakage, and lipid peroxidation were significantly increased in all the salt-sensitive genotypes with severe oxidative damage [177]. Notably, *Ailanthus altissima* showed high salinity (150 mM NaCl) tolerance by enhanced antioxidant enzyme activity while maintaining H_2O_2 levels [178]. This suggests complex stress-response mechanisms for salt-stress adaptability. These findings highlight the universal nature of salt-induced oxidative stress across plant species while indicating significant variations in stress-tolerance mechanisms.

4.4. Heavy Metal Toxicity-Induced Oxidative Stress

Heavy metal toxicity in plants has a wide range of detrimental effects such as stunted growth, chlorosis, and root browning. The presence of heavy metals in soils reduces nutrient and water uptake, disrupts the electron transport chains in chloroplasts and mitochondria, and impairs peroxisomal metabolism, leading to enhanced oxidative damage [179]. The absorption of toxic metals triggers ROS levels in plants and causes significant oxidative damage in plant species [180,181]. Under nickel sulfate (0.25–0.5 mM, 72 h) stress, *Oryza sativa* seedlings showed enhanced lipid peroxidation and hydrogen peroxide [182]. Similarly, the pea (*Pisum sativum*) plants increased ROS and lipid peroxidation under mild nickel stress (100 µM $NiCl_2$) [183]. Cadmium stress also causes oxidative damage by accumulating malondialdehyde, H_2O_2, and superoxide in several crop species [184]. Exposure to 100 µM $CdCl_2$ stress resulted in a significant increase in MDA and H_2O_2 levels in *Arabidopsis thaliana* and cucumber seedlings [185,186]. The adzuki bean (*Vigna angularis*) exhibited higher lipid peroxidation, electrolyte leakage, ROS, and lipoxygenase activity under cadmium stress (100 µM $CdCl_2$) for 20 days [187]. Similar results were observed in *Mentha arvensis* under 50 µM $CdCl_2$ stress [188].

$AlCl_3$ stress in *V. radiata* induced an 83% increase in H_2O_2, a 110% increase in $O_2^{\bullet -}$, and a 72% increase in LOX activity, resulting in a 97% higher lipid peroxidation compared

to control samples [189]. Under lead stress (0.5–1.0 mM $Pb(NO_3)_2$), wheat plants showed a severe increase in oxidative stress [190]. Moreover, pigeon pea plants exposed to arsenic toxicity (10 µM Na_3AsO_4) exhibited a 4-fold increase in lipoxygenase activity and elevated oxidative stress levels [191]. Similarly, quinoa varieties showed increased H_2O_2 and thiobarbituric acid reactive molecules under high (150–300 µM) arsenic (Na_3AsO_4) stress [192]. Copper toxicity in basil revealed a positive correlation between the copper concentration and MDA and H_2O_2 levels; as the copper levels increase, the MDA and H_2O_2 levels increase, with 1000 ppm showing the highest oxidative stress and vice versa [193]. Heavy metals (e.g., Al, Cd, As) disrupt redox homeostasis by inactivating antioxidant enzymes (SOD and CAT) and inducing Fenton/Haber–Weiss reactions, leading to excessive H_2O_2 and •OH generation. Metal-induced ROS also arise from NADPH oxidase (RBOH) activation and impaired mitochondrial electron transport [194]. To conclude, the cadmium, nickel, aluminum, and arsenic stress consistently resulted in elevated levels of hydrogen peroxide, superoxide, and malondialdehyde across different plant species. Additionally, studies revealed that even at relatively low concentrations, metals such as cadmium and arsenic can significantly trigger oxidative stress responses. This suggests a common underlying mechanism of metal-induced oxidative stress in plants, despite variations in plant species and metal types.

5. Antioxidant Enzymatic and Non-Enzymatic Scavenging of ROS and Free Radicals

Antioxidant enzymes play crucial roles in cellular defense mechanisms against ROS. SOD's primary function involves the dismutation of superoxide radicals to hydrogen peroxide and molecular oxygen, thereby preventing hydroxyl radical formation [36]. Catalase, a tetrameric enzyme containing heme groups, detoxifies the H_2O_2. CAT exhibits remarkable efficiency in H_2O_2 degradation, converting approximately 26 million H_2O_2 molecules to water per minute [195]. Additionally, peroxidase facilitates the oxidation of phenols (PhOH) to generate phenoxyl radicals (PhO•), commonly known as quinone acceptors (QA). During this process, H_2O_2 acts as an electron acceptor and is reduced to H_2O [196]. In the absence of ascorbic acid (AsA), phenoxyl radicals undergo cross-reactions to form essential compounds such as suberin, lignin, and quinones. However, in the presence of AsA, these radicals interact with it to form monodehydroascorbate (MDHA), which further converts to dehydroascorbate (DHA) [196]. The PPO catalytic activity involves the oxidation of phenolic compounds to quinones using molecular oxygen, which significantly detoxifies ROS and produces water as a byproduct [45]. In chloroplasts, catalase is absent, and APX is the key enzyme that scavenges H_2O_2 molecules [38,195]. Moreover, the GPX enzyme uses glutathione and thioredoxins to detoxify hydrogen peroxide and several other organic hydroperoxides, including lipid peroxides. The GST enzyme performs multiple roles, such as peroxide degradation, phytohormone synthesis, stress-response signaling, and increases glutathione peroxidase activity [13]. In addition, TRX is characterized by a conserved redox-active center (WCG/PPC) that catalyzes the reduction of disulfide bonds to dithiol groups by H_2O_2. TRX showed superior efficiency compared to GSH or dithiothreitol [35]. In chloroplasts, TRX x and y isoforms maintain a cellular redox equilibrium via 2-Cysteine (Cys) peroxiredoxin reduction. In mitochondria, the TRXo1, peroxiredoxin, and sulfiredoxin collectively provide an antioxidant defense [35]. Furthermore, PRX enzymes effectively neutralize H_2O_2 and ROOH, and they require thiol cofactors (such as GSH) and have a significant ability to reduce organic and inorganic peroxides [34,35].

To conclude, plants' enzymatic antioxidant defense system effectively quenches the ROS during oxidative stress. SOD converts superoxide to hydrogen peroxide and oxygen, CAT converts H_2O_2 into water and oxygen, peroxidases utilize different electron donors

to reduce H_2O_2, and APX plays an important role in chloroplasts and cytosol [195,197]. The ascorbate–glutathione cycle enzymes such as MDHAR, DHAR, and GR maintain the reduced forms of these antioxidant enzymes [13,70]. In addition, the glutathione peroxidases, peroxiredoxins, and thioredoxins provide additional enzymatic protection by thiol-based catalysis in various cellular compartments.

Non-enzymatic antioxidants, including low-molecular-weight compounds, represent the crucial components of plant defense mechanisms against oxidative stress [75]. Ascorbate is a key electron donor in the ascorbate–glutathione cycle, maintaining stability through electron resonance between its oxidized and reduced forms [107,198]. Ascorbate regulates phytohormone pathways and regenerates α-tocopherol (from its radical form), which neutralizes free radicals (hydroxyl and superoxide). Glutathione efficiently scavenges ROS and functions as an essential regulator of cellular redox homeostasis via the ascorbate–glutathione cycle [42,199]. The antioxidant tocopherol maintains photosynthetic efficiency by protecting chloroplasts and targeting singlet oxygen and hydroxyl radicals [200]. Carotenoids provide dual protection by scavenging harmful free radicals and stabilizing light-harvesting complexes and thylakoid membranes [73,200]. Flavonoids, particularly those containing dihydroxy B-ring substitutions, demonstrate significant free radical scavenging capacity and inhibit membrane lipid peroxidation [75]. Environmental stress enhances flavonoid biosynthesis gene expression, strengthening antioxidant defenses. Phenolic compounds, including hydroxy-benzoic and -cinnamic acids, exhibit antioxidant properties through metal chelation and neutralize various reactive species [75]. Additionally, alkaloids and non-protein amino acids like GABA, ornithine, and citrulline contribute to the non-enzymatic antioxidant network through distinct protective mechanisms [69,201,202].

Non-enzymatic antioxidants such as ascorbic acid scavenge multiple ROS ($O_2\bullet^-$, H_2O_2, •OH, $^1O_2$) across various cellular compartments including chloroplasts, peroxisomes, and mitochondria [198]. Glutathione functions primarily against H_2O_2 and hydroxyl radicals, while membrane-bound tocopherols and carotenoids protect against singlet oxygen and lipid peroxyl radicals in chloroplast membranes [44,198]. Secondary metabolites like flavonoids and non-protein amino acids provide additional protection by scavenging the $O_2\bullet^-$, H_2O_2, and $^1O_2$ in vacuoles, chloroplast, cytoplasm, mitochondria, and cell wall. Polyphenolic compounds detoxify several reactive oxygen species such as $O_2\bullet^-$, •OH, ROO•, and ONOO– in the cell wall [75]. Some phenolic compounds have potent antioxidant activity to quench ROS and maintain cellular homeostasis under oxidative stress caused by abiotic factors (Table 4). Moreover, the $O_2\bullet^-$, •OH, H_2O_2, and $^1O_2$ in the vacuoles are neutralized by alkaloid compounds [203]. This integrated network of bioactive non-enzymatic antioxidant systems protects plants against oxidative damage by direct ROS scavenging and the regeneration of antioxidant molecules.

Table 4. Specific functional roles of key polyphenols in quenching ROS under stress conditions.

Serial No:	Compound	Primary Functions During Stress	Specific Roles	Response Mechanisms	Antioxidant Activity	Modulation of Stress-Responsive Pathways	Improvement of Physiological Parameters	References
1-	Quercetin	-ROS scavenging -Membrane stabilization -Osmolyte accumulation -Metal ion chelation	-Enhances drought tolerance -Improves salt resistance -Mediates temperature stress response -Protects UV radiation	-Regulates stress-responsive genes -Enhanced enzyme activities -Aids cellular homeostasis -Membrane integrity maintenance	-Direct ROS scavenging -SOD, CAT, and POD enzyme activation -Reduced lipid peroxidation -Protection of cellular components	-ABA signaling pathway regulation -MAPK cascade activation -Calcium signaling enhancement -Transcription factor regulation	-Enhanced photosynthetic efficiency -Better water relations -Improved nutrient uptake -Increased chlorophyll content	[204–207]
2-	Kaempferol	-ROS scavenging -Membrane stability enhancement -Osmolyte regulation -Signal molecule activation -Stress-tolerance improvement	-Direct scavenging of free radicals -Prevention of lipid peroxidation -Protection of cellular membranes -Enhancement of antioxidant enzyme activities	-Upregulation of stress-responsive genes -Activation of defense pathways -Modulation of hormone signaling -Enhancement of stress-tolerance genes	-Direct free radical neutralization -Support of enzymatic antioxidants -Protection of cellular components -Reduction in oxidative damage	-MAPK signaling cascade activation -ABA-dependent pathway regulation -Stress-responsive transcription factors -Heat shock protein expression	-Enhanced photosynthetic efficiency -Enhanced growth -Better water relations -Improved nutrient uptake	[11,77,153,205,208]
3-	Luteolin	-Acts as ROS scavenger -Maintains cell membrane integrity -Enhances stress tolerance -Regulates osmolytes	-Protects photosynthetic machinery -Stabilizes cellular proteins -Reduces lipid peroxidation -Enhances membrane stability	-Activates stress-responsive genes -Induces enzymatic antioxidants -Modulates hormone signaling -Enhances proline accumulation	-Directly scavenges free radicals -Increases SOD, CAT, and POD activities -Reduces H_2O_2 accumulation -Prevents oxidative damage	-Activates MAPK signaling -Regulates ABA-dependent pathways -Enhances calcium signaling -Influences transcription factors	-Maintains water relations -Enhances photosynthetic efficiency -Improves nutrient uptake -Stabilizes chlorophyll content	[209,210]
4-	Apigenin	-ROS scavenging -Membrane stability enhancement -Osmolyte regulation -Signal molecule activation	-Increases antioxidant defense -Reduces reactivity of free radicals -Increases antioxidant enzyme activities -Protection of cellular membranes	-Activation of stress-responsive genes -Upregulation of heat shock proteins -Enhancement of proline accumulation -Modulation of ion channels	-Quench free radicals -Photosystem II protection -Membrane thermostability -Minimizes oxidative damage -Osmolyte accumulation	-MAPK cascade activation -ABA signaling pathway modulation -Calcium signaling enhancement -Hormone crosstalk regulation	-Improved water retention -Enhanced photosynthetic efficiency -Better nutrient uptake -Increased chlorophyll content	[210,211]

Table 4. *Cont.*

Serial No:	Compound	Primary Functions During Stress	Specific Roles	Response Mechanisms	Antioxidant Activity	Modulation of Stress-Responsive Pathways	Improvement of Physiological Parameters	References
5-	Naringenin	-Acts as a potent ROS scavenger -Functions as stress-signaling molecules -Enhances membrane stability -Regulates osmolyte production -Maintains cellular homeostasis	-Drought-tolerance enhancement -Temperature stress mitigation -Salinity stress protection -Heavy metal stress resistance -UV radiation protection	-Regulates stress-responsive genes -Activation of antioxidant enzymes -Membrane lipid preservation -Ion homeostasis regulation -Photosynthetic efficiency maintenance	-Direct ROS neutralization -Antioxidant enzyme activation -Lipid peroxidation reduction -Free radical chain-breaking -Metal ion chelation	-ABA signaling modulation -MAPK cascade regulation -Heat shock protein induction -Transcription factor activation -Hormone signaling crosstalk	-Enhanced water retention -Better nutrient uptake -Improved growth parameters -Higher photosynthetic rate -Increased stress tolerance	[212,213]
6-	Ferulic acid	-Acts as a potent antioxidant -Membrane stabilizer -Osmolyte accumulation -Cell wall strengthening -Signal molecule	-Direct neutralization of ROS -Scavenges peroxyl radicals -Prevention of lipid peroxidation -Protection of cellular membranes	-Enhancement of SOD, CAT, and POD -Upregulation of stress-responsive genes -Improvement in osmolyte synthesis -Strengthening of cell wall structure	-Electron donation capacity -Free radical neutralization -Metal ion chelation -Prevention of oxidative damage	-Activation of MAPK cascades -Regulation of transcription factors -Hormonal signaling modulation	-Enhanced photosynthetic efficiency -Better water relations -Improved nutrient uptake -Increased biomass accumulation	[12,214–216]
7-	Chlorogenic acid	-Acts as a powerful antioxidant -Protection from oxidative damage -Maintains cellular homeostasis -Contributes to stress-tolerance mechanisms	-Scavenges reactive oxygen species -Stabilizes cell membranes -Protects photosynthetic machinery -Enhance stress-signaling pathways	-Accumulates rapidly during stress exposure -Activates defense-related genes -Triggers enzymatic antioxidants -Modulates hormone signaling	-Directly neutralizes free radicals -Reduces lipid peroxidation -Prevents oxidative damage to proteins -Maintains redox balance	-Activates MAPK signaling cascades -Induces stress-responsive transcription factors -Enhances expression of defense genes -Regulates stress hormone synthesis	-Maintains membrane integrity -Enhance water retention -Improves photosynthetic efficiency -Promotes osmolyte accumulation	[215,217]
8-	Caffeic acid	-Acts as a natural antioxidant -Precursor for lignin biosynthesis -Strengthens cell wall and its stability -Functions as a stress-signaling molecule	-UV radiation protection by absorption -Membrane integrity maintenance -Osmolyte accumulation support -Free radical scavenging -Cell wall reinforcement	-Activates phenylpropanoid pathway -Synthesized protective compounds -Cross-linking of cell wall components -Activation of stress-responsive genes	-Direct ROS scavenging -Reduction in oxidative damage -Protection of cellular components -Regulates antioxidant enzymes -Prevention of lipid peroxidation	-Regulate phenylpropanoid pathway -Activation of defense genes -Interacts with hormone signaling -Stress-responsive protein regulation -Enhanced secondary metabolites	-Better water retention efficiency -Increased membrane stability -Enhanced photosynthetic efficiency -Improved nutrient uptake -Better growth maintenance under stress	[218]

6. Antioxidative Defense Mechanisms Under Abiotic Stress

The enzymatic and non-enzymatic antioxidant defense mechanisms work synergistically to scavenge ROS via progressive reduction reactions, ultimately converting harmful reactive oxygen species to water [33], maintaining cellular plant homeostasis, and providing critical protection under different abiotic stresses [172,203]. Under field conditions, plants frequently experience different abiotic stresses that trigger specific antioxidant responses [6]. For example, heat-tolerant *Brassica juncea* genotypes show enhanced resistance by regulating the peroxidase enzyme activity and increased glutathione levels [219]. Under heat stress, lentils elevated SOD, and other antioxidant activities show an inverse correlation with malondialdehyde and hydrogen peroxide levels, confirming their protective function [220]. Similarly, heat-tolerant wheat varieties (HD 2815 and HDR 77) demonstrate superior stress adaptation through the maintained activities of SOD, CAT, and APX, resulting in the better preservation of chlorophyll content and membrane integrity compared to susceptible genotypes [221]. The protective role of antioxidants extends to metal stress tolerance, as evidenced in rice plants where the coordinated activation of enzymatic (SOD, GPX, APX, GR) and non-enzymatic (ascorbate and GSH) antioxidants, along with proline accumulation, provides a defense against copper-induced oxidative stress [222]. These findings collectively determine that synchronized antioxidant responses are essential for plant survival under adverse environmental conditions.

Research has shown that when *Portulaca oleracea* was simultaneously exposed to heat and drought conditions, it showed elevated activities of SOD and POX enzymes [223]. The cytosolic APX1 enzyme detoxifies the H2O2 and facilitates plant adaptation against drought and high-temperature stress. Similarly, the Arabidopsis mutants lacking APX1 showed increased sensitivity to these combined stresses [224]. Carrizo citrange citrus varieties showed enhanced ROS scavenging capacity and stress tolerance against combined heat and drought stresses [225]. This stress tolerance is from efficient coordination between antioxidant enzymes SOD, CAT, APX, and GR while maintaining glutathione homeostasis. In contrast, Cleopatra mandarin showed high susceptibility under these identical stresses, caused unbalanced antioxidant responses with elevated SOD activity but reduced CAT levels, impaired GR function, and insufficient APX activity, resulting in severe oxidative damage [225].

Under drought stress, *Triticum aestivum* showed increased APX activity and maintained AsA and glutathione redox states, strengthening photosynthetic and mitochondrial functions [226]. Under heat stress, the *Triticum aestivum*-tolerant genotype C306 showed increased activities of SOD, APX, CAT, POX, and GR enzymes [227]. The *Zea mays* seedlings showed increased SOD and peroxidase activities when treated with nitric acid before cold exposure, resulting in reduced ROS generation and membrane lipid peroxidation [228]. When exposed to copper stress, *Oryza sativa* exhibited elevated activities of SOD, GP, APX, and GR, along with increased AsA, GSH, and proline levels, while maintaining stable CAT activity [222]. This resulted in decreased hydrogen peroxide accumulation and reduced lipid peroxidation. Salinity-stressed *Oryza sativa* seedlings treated with manganese showed enhanced levels of both non-enzymatic (phenolics, flavonoids, AsA) and enzymatic (monodehydroascorbate reductase, dehydroascorbate reductase, SOD, CAT) antioxidants [229].

Plants exhibit diverse antioxidant responses when subjected to combined abiotic stresses. *Triticum aestivum* seedlings under concurrent low temperature and isoproturon stress showed enhanced antioxidant activity following AsA application [230]. Similarly, *Oryza sativa* exposed to combined salinity and 2,4-dichlorophenoxyacetic acid stress exhibited modulated enzymatic and non-enzymatic antioxidant responses, effectively reducing oxidative damage [231]. In *Cucumis sativus* exposed to chilling stress, enhanced activities of SOD, APX, GR, and GPx were observed, while CAT activity decreased in leaf

tissues [232]. Similarly, UV-B radiation exposure in *Helianthus annuus* cotyledons increased CAT, glutathione dehydrogenase, and GP activities, with elevated GSH/GSSG ratios [233]. In *Spinacia oleracea* seedlings, the ectopic expression of cytosolic heat shock protein 70 (SoHSC70) enhanced antioxidant enzyme activities, effectively reducing oxidative damage and ROS accumulation [234]. *Artemisia annua* increased the activities of SOD, POX, and CAT enzymatic antioxidants in response to boron stress [235]. The transgenic *Arabidopsis thaliana* plants showed an increase in non-enzymatic antioxidants such as flavonoids and anthocyanins with lower ROS, under drought and high light stress [57,58]. We summarize the intricacy of plant enzymatic and non-enzymatic antioxidants working together to maintain cellular homeostasis under environmental stress, as well as plant survival in hostile conditions.

7. Conclusions

This review summarizes the enzymatic and non-enzymatic antioxidants that work in concert to neutralize the ROS and maintain the cellular redox homeostasis under oxidative stress. The key enzymatic antioxidants such as SOD, CAT, APX, and GR form the first line of defense by directly neutralizing the ROS. Non-enzymatic antioxidants such as ascorbate, glutathione, and bioactive polyphenols, including flavonoid compounds, provide additional protection through their radical scavenging abilities. The production and accumulation of ROS in different cellular organelles serve dual functions—as important signaling molecules at lower concentrations and as damaging oxidative agents (at higher concentrations) under severe stress conditions. Understanding these context-dependent functions is crucial for developing stress-tolerant crops. Our review revealed that the oxidative stress response shares common elements under various abiotic stresses, and each stress type triggers specific antioxidant responses depending on the nature and severity of the stress.

ROS can boost plant stress tolerance when managed strategically. Seed priming with mild ROS (like H_2O_2 or NO) activates defense genes, while antioxidants (ascorbic acid and glutathione) prevent oxidative damage. Tailoring these methods to crop needs, such as appropriate timing and crop-specific dosage, can improve the resilient and sustainable path to climate-smart agriculture. Recent advances in understanding ROS signaling networks and antioxidant systems will be invaluable for engineering stress-resistant crops with enhanced adaptability to changing environmental conditions, ultimately contributing to global food security.

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References

1. Yang, Y.; Tilman, D.; Jin, Z.; Smith, P.; Barrett, C.B.; Zhu, Y.-G.; Burney, J.; D'Odorico, P.; Fantke, P.; Fargione, J. Climate Change Exacerbates the Environmental Impacts of Agriculture. *Science* **2024**, *385*, eadn3747. [CrossRef] [PubMed]
2. Yuan, X.; Li, S.; Chen, J.; Yu, H.; Yang, T.; Wang, C.; Huang, S.; Chen, H.; Ao, X. Impacts of Global Climate Change on Agricultural Production: A Comprehensive Review. *Agronomy* **2024**, *14*, 1360. [CrossRef]
3. Kumar, P.; Tokas, J.; Kumar, N.; Lal, M.; Singal, H.; Praveen Kumar, C. Climate Change Consequences and Its Impact on Agriculture and Food Security. *Int. J. Chem. Stud.* **2018**, *6*, 124–133.
4. Liaqat, W.; Altaf, M.T.; Barutçular, C.; Nawaz, H.; Ullah, I.; Basit, A.; Mohamed, H.I. Ultraviolet-B Radiation in Relation to Agriculture in the Context of Climate Change: A Review. *Cereal Res. Commun.* **2024**, *52*, 1–24. [CrossRef]
5. Rane, J.; Jangid, K.K. Impacts of Abiotic Stresses on Eco-Physiology of Crop in Changing Climate. In *Climate Change Impacts on Soil-Plant-Atmosphere Continuum*; Springer: Berlin/Heidelberg, Germany, 2024; pp. 427–445.
6. Nawaz, M.; Sun, J.; Shabbir, S.; Khattak, W.A.; Ren, G.; Nie, X.; Bo, Y.; Javed, Q.; Du, D.; Sonne, C. A Review of Plants Strategies to Resist Biotic and Abiotic Environmental Stressors. *Sci. Total Environ.* **2023**, *900*, 165832. [CrossRef]
7. Wu, W.; Ma, B.-L. Assessment of Canola Crop Lodging under Elevated Temperatures for Adaptation to Climate Change. *Agric. Meteorol.* **2018**, *248*, 329–338. [CrossRef]
8. Mansoor, S.; Ali, A.; Kour, N.; Bornhorst, J.; Al Harbi, K.; Rinklebe, J.; Abd El Moneim, D.; Ahmad, P.; Chung, Y.S. Heavy Metal Induced Oxidative Stress Mitigation and ROS Scavenging in Plants. *Plants* **2023**, *12*, 3003. [CrossRef]
9. Rajput, V.D.; Harish; Singh, R.K.; Verma, K.K.; Sharma, L.; Quiroz-Figueroa, F.R.; Meena, M.; Gour, V.S.; Minkina, T.; Sushkova, S. Recent Developments in Enzymatic Antioxidant Defence Mechanism in Plants with Special Reference to Abiotic Stress. *Biology* **2021**, *10*, 267. [CrossRef]
10. Irato, P.; Santovito, G. Enzymatic and Non-Enzymatic Molecules with Antioxidant Function. *Antioxidants* **2021**, *10*, 579. [CrossRef]
11. Shen, N.; Wang, T.; Gan, Q.; Liu, S.; Wang, L.; Jin, B. Plant Flavonoids: Classification, Distribution, Biosynthesis, and Antioxidant Activity. *Food Chem.* **2022**, *383*, 132531. [CrossRef]
12. Zhang, B.; Xia, T.; Duan, W.; Zhang, Z.; Li, Y.; Fang, B.; Xia, M.; Wang, M. Effects of Organic Acids, Amino Acids and Phenolic Compounds on Antioxidant Characteristic of Zhenjiang Aromatic Vinegar. *Molecules* **2019**, *24*, 3799. [CrossRef]
13. Rai, G.K.; Kumar, P.; Choudhary, S.M.; Singh, H.; Adab, K.; Kosser, R.; Magotra, I.; Kumar, R.R.; Singh, M.; Sharma, R. Antioxidant Potential of Glutathione and Crosstalk with Phytohormones in Enhancing Abiotic Stress Tolerance in Crop Plants. *Plants* **2023**, *12*, 1133. [CrossRef] [PubMed]
14. Zagoskina, N.V.; Zubova, M.Y.; Nechaeva, T.L.; Kazantseva, V.V.; Goncharuk, E.A.; Katanskaya, V.M.; Baranova, E.N.; Aksenova, M.A. Polyphenols in Plants: Structure, Biosynthesis, Abiotic Stress Regulation, and Practical Applications. *Int. J. Mol. Sci.* **2023**, *24*, 13874. [CrossRef] [PubMed]
15. Renu, K.; Mukherjee, A.G.; Gopalakrishnan, A.V.; Wanjari, U.R.; Kannampuzha, S.; Murali, R.; Veeraraghavan, V.P.; Vinayagam, S.; Paz-Montelongo, S.; George, A. Protective Effects of Macromolecular Polyphenols, Metal (Zinc, Selenium, and Copper)-Polyphenol Complexes, and Pectin in Different Organs with an Emphasis on Arsenic Poisoning: A Review. *Int. J. Biol. Macromol.* **2023**, *253*, 126715. [CrossRef] [PubMed]
16. Rao, M.J.; Duan, M.; Shad, M.A.; Aslam, M.Z.; Wang, J.; Wang, L. Widely Targeted LC-MS/MS Approach Provides Insights into Variations in Bioactive Flavonoid Compounds and Their Antioxidant Activities in Green, Red, and Purple Sugarcane. *LWT Food Sci. Technol.* **2024**, *209*, 116792. [CrossRef]
17. Mittler, R. ROS Are Good. *Trends Plant Sci.* **2017**, *22*, 11–19. [CrossRef]
18. Sachdev, S.; Ansari, S.A.; Ansari, M.I.; Fujita, M.; Hasanuzzaman, M. Abiotic Stress and Reactive Oxygen Species: Generation, Signaling, and Defense Mechanisms. *Antioxidants* **2021**, *10*, 277. [CrossRef]
19. Choudhury, F.K.; Rivero, R.M.; Blumwald, E.; Mittler, R. Reactive Oxygen Species, Abiotic Stress and Stress Combination. *Plant J.* **2017**, *90*, 856–867. [CrossRef]
20. Hasanuzzaman, M.; Nahar, K.; Gill, S.S.; Alharby, H.F.; Razafindrabe, B.H.N.; Fujita, M. Hydrogen Peroxide Pretreatment Mitigates Cadmium-Induced Oxidative Stress in *Brassica Napus*, L.: An Intrinsic Study on Antioxidant Defense and Glyoxalase Systems. *Front. Plant Sci.* **2017**, *8*, 115. [CrossRef]
21. Tanou, G.; Filippou, P.; Belghazi, M.; Job, D.; Diamantidis, G.; Fotopoulos, V.; Molassiotis, A. Oxidative and Nitrosative-based Signaling and Associated Post-translational Modifications Orchestrate the Acclimation of Citrus Plants to Salinity Stress. *Plant J.* **2012**, *72*, 585–599. [CrossRef]
22. Sun, Y.; Wang, H.; Liu, S.; Peng, X. Exogenous Application of Hydrogen Peroxide Alleviates Drought Stress in Cucumber Seedlings. *South Afr. J. Bot.* **2016**, *106*, 23–28. [CrossRef]
23. Guler, N.S.; Pehlivan, N. Exogenous Low-Dose Hydrogen Peroxide Enhances Drought Tolerance of Soybean (*Glycine max* L.) through Inducing Antioxidant System. *Acta Biol. Hung.* **2016**, *67*, 169–183. [CrossRef]
24. Basal, O.; Zargar, T.B.; Veres, S. Elevated Tolerance of Both Short-Term and Continuous Drought Stress during Reproductive Stages by Exogenous Application of Hydrogen Peroxide on Soybean. *Sci. Rep.* **2024**, *14*, 2200. [CrossRef] [PubMed]

25. Zhang, S.; Shan, Y.; Li, Y.; He, J.; Jiang, Y. Hydrogen Peroxide Receptors Regulate Chilling Injury of Banana Fruit during Low-Temperature Storage. *Postharvest Biol. Technol.* **2024**, *214*, 112985. [CrossRef]
26. Yamasaki, H.; Ogura, M.P.; Kingjoe, K.A.; Cohen, M.F. D-Cysteine-Induced Rapid Root Abscission in the Water Fern *Azolla Pinnata*: Implications for the Linkage between d-Amino Acid and Reactive Sulfur Species (RSS) in Plant Environmental Responses. *Antioxidants* **2019**, *8*, 411. [CrossRef]
27. Sonmez, M.C.; Yirmibesoglu, S.S.S.; Ozgur, R.; Uzilday, B.; Turkan, I. Roles of Reactive Carbonyl Species (RCS) in Plant Response to Abiotic Stress. In *ROS Signaling in Plants: Methods and Protocols*; Springer: Berlin/Heidelberg, Germany, 2024; pp. 101–130.
28. Dutta, S.; Sengupta, P.; Samrot, A. V Physiological and Pathological Functions of Reactive Nitrogen Species (RNS) and Reactive Sulphur Species (RSS) on Male Reproductive Functions. *J. Integr. Sci. Technol.* **2024**, *12*, 755. [CrossRef]
29. Rao, M.J.; Wu, S.; Duan, M.; Wang, L. Antioxidant Metabolites in Primitive, Wild, and Cultivated Citrus and Their Role in Stress Tolerance. *Molecules* **2021**, *26*, 5801. [CrossRef]
30. Rao, M.J.; Ahmed, U.; Ahmed, M.H.; Duan, M.; Wang, J.; Wang, Y.; Wang, L. Comparison and Quantification of Metabolites and Their Antioxidant Activities in Young and Mature Leaves of Sugarcane. *ACS Food Sci. Technol.* **2021**, *1*, 362–373. [CrossRef]
31. Rao, M.J.; Tahir Ul Qamar, M.; Wang, D.; Ali, Q.; Ma, L.; Han, S.; Duan, M.; Hu, L.; Wang, L. A High-Throughput Lipidomics and Transcriptomic Approach Reveals Novel Compounds from Sugarcane Linked with Promising Therapeutic Potential against COVID-19. *Front. Nutr.* **2022**, *9*, 988249. [CrossRef]
32. Acosta-Motos, J.R.; Ortuño, M.F.; Bernal-Vicente, A.; Diaz-Vivancos, P.; Sanchez-Blanco, M.J.; Hernandez, J.A. Plant Responses to Salt Stress: Adaptive Mechanisms. *Agronomy* **2017**, *7*, 18. [CrossRef]
33. Rai, K.K.; Kaushik, P. Free Radicals Mediated Redox Signaling in Plant Stress Tolerance. *Life* **2023**, *13*, 204. [CrossRef] [PubMed]
34. Vidigal, P.; Carvalho, R.; Amâncio, S.; Carvalho, L. Peroxiredoxins Are Involved in Two Independent Signalling Pathways in the Abiotic Stress Protection in *Vitis vinifera*. *Biol. Plant* **2013**, *57*, 675–683. [CrossRef]
35. Calderón, A.; Sevilla, F.; Jiménez, A. Redox Protein Thioredoxins: Function under Salinity, Drought and Extreme Temperature Conditions. In *Antioxidants and Antioxidant Enzymes in Higher Plants*; Springer: Berlin/Heidelberg, Germany, 2018; pp. 123–162.
36. Jiang, J.; Zhang, N.; Srivastava, A.K.; He, G.; Tai, Z.; Wang, Z.; Yang, S.; Xie, X.; Li, X. Superoxide Dismutase Positively Regulates Cu/Zn Toxicity Tolerance in Sorghum Bicolor by Interacting with Cu Chaperone for Superoxide Dismutase. *J. Hazard. Mater.* **2024**, *480*, 135828. [CrossRef]
37. Carmo de Carvalho e Martins, M.d.; Martins; da Silva Santos Oliveira, A.S.; da Silva, L.A.A.; Primo, M.G.S.; de Carvalho Lira, V.B. Biological Indicators of Oxidative Stress [Malondialdehyde, Catalase, Glutathione Peroxidase, and Superoxide Dismutase] and Their Application in Nutrition. In *Biomarkers in Nutrition*; Springer: Berlin/Heidelberg, Germany, 2022; pp. 1–25.
38. Su, T.; Wang, P.; Li, H.; Zhao, Y.; Lu, Y.; Dai, P.; Ren, T.; Wang, X.; Li, X.; Shao, Q. The Arabidopsis Catalase Triple Mutant Reveals Important Roles of Catalases and Peroxisome-derived Signaling in Plant Development. *J. Integr. Plant Biol.* **2018**, *60*, 591–607. [CrossRef]
39. Li, S. Novel Insight into Functions of Ascorbate Peroxidase in Higher Plants: More than a Simple Antioxidant Enzyme. *Redox. Biol.* **2023**, *64*, 102789. [CrossRef]
40. Ozyigit, I.I.; Filiz, E.; Vatansever, R.; Kurtoglu, K.Y.; Koc, I.; Öztürk, M.X.; Anjum, N.A. Identification and Comparative Analysis of H2O2-Scavenging Enzymes (Ascorbate Peroxidase and Glutathione Peroxidase) in Selected Plants Employing Bioinformatics Approaches. *Front. Plant Sci.* **2016**, *7*, 301. [CrossRef]
41. Couto, N.; Wood, J.; Barber, J. The Role of Glutathione Reductase and Related Enzymes on Cellular Redox Homoeostasis Network. *Free Radic. Biol. Med.* **2016**, *95*, 27–42. [CrossRef]
42. Rao, A.S.V.C.; Reddy, A.R. Glutathione Reductase: A Putative Redox Regulatory System in Plant Cells. In *Sulfur Assimilation and Abiotic Stress in Plants*; Springer: Berlin/Heidelberg, Germany, 2008; pp. 111–147.
43. Edwards, E.A.; Rawsthorne, S.; Mullineaux, P.M. Subcellular Distribution of Multiple Forms of Glutathione Reductase in Leaves of Pea (*Pisum sativum* L.). *Planta* **1990**, *180*, 278–284. [CrossRef]
44. Madhu; Kaur, A.; Tyagi, S.; Shumayla; Singh, K.; Upadhyay, S.K. Exploration of Glutathione Reductase for Abiotic Stress Response in Bread Wheat (*Triticum aestivum* L.). *Plant Cell Rep.* **2022**, *41*, 639–654. [CrossRef]
45. Zhang, S. Recent Advances of Polyphenol Oxidases in Plants. *Molecules* **2023**, *28*, 2158. [CrossRef]
46. Nimse, S.B.; Pal, D. Free Radicals, Natural Antioxidants, and Their Reaction Mechanisms. *RSC Adv.* **2015**, *5*, 27986–28006. [CrossRef]
47. Polidoros, A.N.; Scandalios, J.G. Role of Hydrogen Peroxide and Different Classes of Antioxidants in the Regulation of Catalase and Glutathione S-transferase Gene Expression in Maize (*Zea mays* L.). *Physiol. Plant* **1999**, *106*, 112–120. [CrossRef]
48. Mittler, R. Oxidative Stress, Antioxidants and Stress Tolerance. *Trends Plant Sci.* **2002**, *7*, 405–410. [CrossRef] [PubMed]
49. Hasanuzzaman, M.; Hossain, M.A.; da Silva, J.A.T.; Fujita, M. Plant Response and Tolerance to Abiotic Oxidative Stress: Antioxidant Defense Is a Key Factor. In *Crop Stress and Its Management: Perspectives and Strategies*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 261–315.

50. Uarrota, V.G.; Moresco, R.; Schmidt, E.C.; Bouzon, Z.L.; da Costa Nunes, E.; de Oliveira Neubert, E.; Peruch, L.A.M.; Rocha, M.; Maraschin, M. The Role of Ascorbate Peroxidase, Guaiacol Peroxidase, and Polysaccharides in Cassava (*Manihot Esculenta Crantz*) Roots under Postharvest Physiological Deterioration. *Food Chem.* **2016**, *197*, 737–746. [CrossRef]
51. Romero-Puertas, M.C.; Corpas, F.J.; Sandalio, L.M.; Leterrier, M.; Rodríguez-Serrano, M.; Del Río, L.A.; Palma, J.M. Glutathione Reductase from Pea Leaves: Response to Abiotic Stress and Characterization of the Peroxisomal Isozyme. *New Phytol.* **2006**, *170*, 43–52. [CrossRef]
52. Yin, L.; Wang, S.; Eltayeb, A.E.; Uddin, M.I.; Yamamoto, Y.; Tsuji, W.; Takeuchi, Y.; Tanaka, K. Overexpression of Dehydroascorbate Reductase, but Not Monodehydroascorbate Reductase, Confers Tolerance to Aluminum Stress in Transgenic Tobacco. *Planta* **2010**, *231*, 609–621. [CrossRef]
53. Li, S. Redox Modulation Matters: Emerging Functions for Glutaredoxins in Plant Development and Stress Responses. *Plants* **2014**, *3*, 559–582. [CrossRef]
54. Muslu, S.; Kasapoğlu, A.G.; Güneş, E.; Aygören, A.S.; Yiğider, E.; İlhan, E.; Aydın, M. Genome-Wide Analysis of Glutathione S-Transferase Gene Family in P. Vulgaris under Drought and Salinity Stress. *Plant Mol. Biol. Rep.* **2024**, *42*, 57–76. [CrossRef]
55. Aziz, S.; Germano, T.A.; Thiers, K.L.L.; Batista, M.C.; de Souza Miranda, R.; Arnholdt-Schmitt, B.; Costa, J.H. Transcriptome Analyses in a Selected Gene Set Indicate Alternative Oxidase (AOX) and Early Enhanced Fermentation as Critical for Salinity Tolerance in Rice. *Plants* **2022**, *11*, 2145. [CrossRef]
56. Mariz-Ponte, N.; Mendes, R.J.; Sario, S.; De Oliveira, J.M.P.F.; Melo, P.; Santos, C. Tomato Plants Use Non-Enzymatic Antioxidant Pathways to Cope with Moderate UV-A/B Irradiation: A Contribution to the Use of UV-A/B in Horticulture. *J. Plant Physiol.* **2018**, *221*, 32–42. [CrossRef]
57. Rao, M.J.; Xu, Y.; Tang, X.; Huang, Y.; Liu, J.; Deng, X. CsCYT75B1, a Citrus CYTOCHROME P450 Gene, Is Involved in Accumulation of Antioxidant Flavonoids and Induces Drought Tolerance in Transgenic Arabidopsis. *Antioxidants* **2020**, *9*, 161. [CrossRef] [PubMed]
58. Rao, M.J.; Xu, Y.; Huang, Y.; Tang, X.; Deng, X.; Xu, Q. Ectopic Expression of Citrus UDP-GLUCOSYL TRANSFERASE Gene Enhances Anthocyanin and Proanthocyanidins Contents and Confers High Light Tolerance in Arabidopsis. *BMC Plant Biol.* **2019**, *19*, 603. [CrossRef] [PubMed]
59. Rao, M.J.; Duan, M.; Yang, M.; Li, M.; Wang, L. Sugarcane Rind Secondary Metabolites and Their Antioxidant Activities in Eleven Cultivated Sugarcane Varieties. *Sugar Tech.* **2022**, *24*, 1570–1582. [CrossRef]
60. Szalai, G.; Kellős, T.; Galiba, G.; Kocsy, G. Glutathione as an Antioxidant and Regulatory Molecule in Plants under Abiotic Stress Conditions. *J. Plant Growth Regul.* **2009**, *28*, 66–80. [CrossRef]
61. Wang, C.; García-Caparros, P.; Li, Z.; Chen, F. A Comprehensive Review on Plant Ascorbic Acid. *Trop. Plants* **2024**, *3*, e042. [CrossRef]
62. Wu, P.; Li, B.; Liu, Y.; Bian, Z.; Xiong, J.; Wang, Y.; Zhu, B. Multiple Physiological and Biochemical Functions of Ascorbic Acid in Plant Growth, Development, and Abiotic Stress Response. *Int. J. Mol. Sci.* **2024**, *25*, 1832. [CrossRef]
63. Caferri, R.; Guardini, Z.; Bassi, R.; Dall'Osto, L. Assessing Photoprotective Functions of Carotenoids in Photosynthetic Systems of Plants and Green Algae. In *Methods in Enzymology*; Elsevier: Amsterdam, The Netherlands, 2022; Volume 674, pp. 53–84, ISSN 00766879.
64. Zulfiqar, S.; Sharif, S.; Saeed, M.; Tahir, A. Role of Carotenoids in Photosynthesis. In *Carotenoids: Structure and Function in the Human Body*; Springer: Berlin/Heidelberg, Germany, 2021; pp. 147–187.
65. Hosseinifard, M.; Stefaniak, S.; Ghorbani Javid, M.; Soltani, E.; Wojtyla, Ł.; Garnczarska, M. Contribution of Exogenous Proline to Abiotic Stresses Tolerance in Plants: A Review. *Int. J. Mol. Sci.* **2022**, *23*, 5186. [CrossRef]
66. Zulfiqar, F.; Ashraf, M.; Siddique, K.H.M. Role of Glycine Betaine in the Thermotolerance of Plants. *Agronomy* **2022**, *12*, 276. [CrossRef]
67. Zhang, Y.; Dai, T.; Liu, Y.; Wang, J.; Wang, Q.; Zhu, W. Effect of Exogenous Glycine Betaine on the Germination of Tomato Seeds under Cold Stress. *Int. J. Mol. Sci.* **2022**, *23*, 10474. [CrossRef]
68. Hasan, M.M.; Alabdallah, N.M.; Alharbi, B.M.; Waseem, M.; Yao, G.; Liu, X.-D.; Abd El-Gawad, H.G.; El-Yazied, A.A.; Ibrahim, M.F.M.; Jahan, M.S. GABA: A Key Player in Drought Stress Resistance in Plants. *Int. J. Mol. Sci.* **2021**, *22*, 10136. [CrossRef]
69. Ashraf, U.; Anjum, S.A.; Naseer, S.; Abbas, A.; Abrar, M.; Nawaz, M.; Luo, K. Gamma Amino Butyric Acid (GABA) Application Modulated the Morpho-Physiological and Yield Traits of Fragrant Rice under Well-Watered and Drought Conditions. *BMC Plant Biol.* **2024**, *24*, 569. [CrossRef] [PubMed]
70. Qian, Z.; Lu, L.; Zihan, W.; Qianyue, B.; Chungang, Z.; Shuheng, Z.; Jiali, P.; Jiaxin, Y.; Shuang, Z.; Jian, W. Gamma-Aminobutyric Acid (GABA) Improves Salinity Stress Tolerance in Soybean Seedlings by Modulating Their Mineral Nutrition, Osmolyte Contents, and Ascorbate-Glutathione Cycle. *BMC Plant Biol.* **2024**, *24*, 365. [CrossRef] [PubMed]
71. Xu, B.; Feng, X.; Piechatzek, A.; Zhang, S.; Konrad, K.R.; Kromdijk, J.; Hedrich, R.; Gilliham, M. The GABA Shunt Contributes to ROS Homeostasis in Guard Cells of Arabidopsis. *New Phytol.* **2024**, *241*, 73–81. [CrossRef] [PubMed]

72. Kaspal, M.; Kanapaddalagamage, M.H.; Ramesh, S.A. Emerging Roles of γ Aminobutyric Acid (GABA) Gated Channels in Plant Stress Tolerance. *Plants* **2021**, *10*, 2178. [CrossRef]
73. Faizan, M.; Alam, P.; Rajput, V.D.; Shareen; Kaur, K.; Faraz, A.; Minkina, T.; Maqbool Ahmed, S.; Rajpal, V.R.; Hayat, S. Potential Role of Tocopherol in Protecting Crop Plants against Abiotic Stresses. *Physiol. Mol. Biol. Plants* **2023**, *29*, 1563–1575. [CrossRef]
74. Stahl, W.; Sies, H. Antioxidant Activity of Carotenoids. *Mol. Asp. Med.* **2003**, *24*, 345–351. [CrossRef]
75. Rao, M.J.; Zheng, B. The Role of Polyphenols in Abiotic Stress Tolerance and Their Antioxidant Properties to Scavenge Reactive Oxygen Species and Free Radicals. *Antioxidants* **2025**, *14*, 74. [CrossRef]
76. Naikoo, M.I.; Dar, M.I.; Raghib, F.; Jaleel, H.; Ahmad, B.; Raina, A.; Khan, F.A.; Naushin, F. Role and Regulation of Plants Phenolics in Abiotic Stress Tolerance: An Overview. In *Plant Signaling Molecules*; Elsevier: Amsterdam, The Netherlands, 2019; pp. 157–168.
77. Rao, M.J.; Duan, M.; Eman, M.; Yuan, H.; Sharma, A.; Zheng, B. Comparative Analysis of Citrus Species' Flavonoid Metabolism, Gene Expression Profiling, and Their Antioxidant Capacity under Drought Stress. *Antioxidants* **2024**, *13*, 1149. [CrossRef]
78. Bai, Y.; Wang, X.; Wang, X.; Dai, Q.; Zhan, X.; Gong, H.; Guo, J. Effects of Combined Application of Selenium and Various Plant Hormones on the Cold Stress Tolerance of Tomato Plants. *Plant Soil* **2024**, *509*, 471–489. [CrossRef]
79. Omar, A.A.; Heikal, Y.M.; Zayed, E.M.; Shamseldin, S.A.M.; Salama, Y.E.; Amer, K.E.; Basuoni, M.M.; Abd Ellatif, S.; Mohamed, A.H. Conferring of Drought and Heat Stress Tolerance in Wheat (*Triticum aestivum* L.) Genotypes and Their Response to Selenium Nanoparticles Application. *Nanomaterials* **2023**, *13*, 998. [CrossRef]
80. Zeeshan, M.; Wang, X.; Salam, A.; Wu, H.; Li, S.; Zhu, S.; Chang, J.; Chen, X.; Zhang, Z.; Zhang, P. Selenium Nanoparticles Boost the Drought Stress Response of Soybean by Enhancing Pigment Accumulation, Oxidative Stress Management and Ultrastructural Integrity. *Agronomy* **2024**, *14*, 1372. [CrossRef]
81. Jan, A.U.; Hadi, F.; Ditta, A.; Suleman, M.; Ullah, M. Zinc-Induced Anti-Oxidative Defense and Osmotic Adjustments to Enhance Drought Stress Tolerance in Sunflower (*Helianthus annuus* L.). *Environ. Exp. Bot.* **2022**, *193*, 104682. [CrossRef]
82. Malik, M.A.; Wani, A.H.; Mir, S.H.; Rehman, I.U.; Tahir, I.; Ahmad, P.; Rashid, I. Elucidating the Role of Silicon in Drought Stress Tolerance in Plants. *Plant Physiol. Biochem.* **2021**, *165*, 187–195. [CrossRef] [PubMed]
83. Zhang, F.; Zhao, Y.; Zhang, Y.; Shi, Y.; Hou, L.; Khan, A.; Zhang, R.; Zhang, Y. Mechanism of Exogenous Silicon in Enhancing Cold Stress Tolerance in *Solanum Lycopersicum* L. Seedlings: Insights from Resistance and Quality Indicators. *Horticulturae* **2024**, *11*, 4. [CrossRef]
84. Bouhadi, M.; El Kouali, M.; Samir, K.; Elbouhmadi, K.; Talbi, M.; Fougrach, H. Exogenous Application of Thiamine and Nicotinic Acid Improves Tolerance and Morpho-Physiological Parameters of Lens Culinaris Under Lead (Pb) Exposure. *J. Plant Growth Regul.* **2024**, *43*, 4185–4198. [CrossRef]
85. Alvi, G.B.; Iqbal, M.S.; Ghaith, M.M.S.; Haseeb, A.; Ahmed, B.; Qadir, M.I. Biogenic Selenium Nanoparticles (SeNPs) from Citrus Fruit Have Anti-Bacterial Activities. *Sci. Rep.* **2021**, *11*, 4811. [CrossRef]
86. Maurya, A.K. Oxidative Stress in Crop Plants. In *Agronomic Crops: Volume 3: Stress Responses and Tolerance*; Springer: Berlin/Heidelberg, Germany, 2020; pp. 349–380.
87. Scalbert, A.; Johnson, I.T.; Saltmarsh, M. Polyphenols: Antioxidants and beyond 1–3. *Am. J. Clin. Nutr.* **2005**, *81*, 215–217. [CrossRef]
88. Canan, İ.; Gündoğdu, M.; Seday, U.; Oluk, C.A.; Karaşahin, Z.; Eroğlu, E.Ç.; Yazici, E.; Ünlü, M. Determination of Antioxidant, Total Phenolic, Total Carotenoid, Lycopene, Ascorbic Acid, and Sugar Contents of Citrus Species and Mandarin Hybrids. *Turk. J. Agric. For.* **2016**, *40*, 894–899. [CrossRef]
89. Mishra, B.; Sangwan, R.S.; Mishra, S.; Jadaun, J.S.; Sabir, F.; Sangwan, N.S. Effect of Cadmium Stress on Inductive Enzymatic and Nonenzymatic Responses of ROS and Sugar Metabolism in Multiple Shoot Cultures of Ashwagandha (*Withania Somnifera Dunal*). *Protoplasma* **2014**, *251*, 1031–1045. [CrossRef]
90. Mittler, R.; Zandalinas, S.I.; Fichman, Y.; Van Breusegem, F. Reactive Oxygen Species Signalling in Plant Stress Responses. *Nat. Rev. Mol. Cell Biol.* **2022**, *23*, 663–679. [CrossRef]
91. Kapoor, D.; Sharma, R.; Handa, N.; Kaur, H.; Rattan, A.; Yadav, P.; Gautam, V.; Kaur, R.; Bhardwaj, R. Redox Homeostasis in Plants under Abiotic Stress: Role of Electron Carriers, Energy Metabolism Mediators and Proteinaceous Thiols. *Front. Environ. Sci.* **2015**, *3*, 13. [CrossRef]
92. Wani, K.I.; Naeem, M.; Castroverde, C.D.M.; Kalaji, H.M.; Albaqami, M.; Aftab, T. Molecular Mechanisms of Nitric Oxide (NO) Signaling and Reactive Oxygen Species (ROS) Homeostasis during Abiotic Stresses in Plants. *Int. J. Mol. Sci.* **2021**, *22*, 9656. [CrossRef] [PubMed]
93. Singhal, R.K.; Jatav, H.S.; Aftab, T.; Pandey, S.; Mishra, U.N.; Chauhan, J.; Chand, S.; Indu; Saha, D.; Dadarwal, B.K. Roles of Nitric Oxide in Conferring Multiple Abiotic Stress Tolerance in Plants and Crosstalk with Other Plant Growth Regulators. *J. Plant Growth Regul.* **2021**, *40*, 2303–2328. [CrossRef]
94. Dogra, V.; Kim, C. Singlet Oxygen Metabolism: From Genesis to Signaling. *Front. Plant Sci.* **2020**, *10*, 1640. [CrossRef]
95. Dietz, K.-J. Thiol-Based Peroxidases and Ascorbate Peroxidases: Why Plants Rely on Multiple Peroxidase Systems in the Photosynthesizing Chloroplast? *Mol. Cells* **2016**, *39*, 20–25. [CrossRef]

96. Tano, D.W.; Kozlowska, M.A.; Easter, R.A.; Woodson, J.D. Multiple Pathways Mediate Chloroplast Singlet Oxygen Stress Signaling. *Plant Mol. Biol.* **2023**, *111*, 167–187. [CrossRef]
97. Muller, P.; Li, X.-P.; Niyogi, K.K. Non-Photochemical Quenching. A Response to Excess Light Energy. *Plant Physiol.* **2001**, *125*, 1558–1566. [CrossRef]
98. Li, Z.; Wakao, S.; Fischer, B.B.; Niyogi, K.K. Sensing and Responding to Excess Light. *Annu. Rev. Plant Biol.* **2009**, *60*, 239–260. [CrossRef]
99. Krieger-Liszkay, A.; Fufezan, C.; Trebst, A. Singlet Oxygen Production in Photosystem II and Related Protection Mechanism. *Photosynth. Res.* **2008**, *98*, 551–564. [CrossRef]
100. Goggin, F.L.; Fischer, H.D. Singlet Oxygen Signalling and Its Potential Roles in Plant Biotic Interactions. *Plant Cell Environ.* **2024**, *47*, 1957–1970. [CrossRef]
101. Krieger-Liszkay, A. Singlet Oxygen Production in Photosynthesis. *J. Exp. Bot.* **2005**, *56*, 337–346. [CrossRef] [PubMed]
102. Flors, C.; Fryer, M.J.; Waring, J.; Reeder, B.; Bechtold, U.; Mullineaux, P.M.; Nonell, S.; Wilson, M.T.; Baker, N.R. Imaging the Production of Singlet Oxygen in Vivo Using a New Fluorescent Sensor, Singlet Oxygen Sensor Green®. *J. Exp. Bot.* **2006**, *57*, 1725–1734. [CrossRef] [PubMed]
103. Li, M.; Kim, C. Singlet Oxygen in Plants: From Genesis to Signaling. In *Advances in Botanical Research*; Elsevier: Amsterdam, The Netherlands, 2023; Volume 105, pp. 1–42, ISSN 00652296.
104. Huang, L.; Liu, Y.; Wang, X.; Jiang, C.; Zhao, Y.; Lu, M.; Zhang, J. Peroxisome-Mediated Reactive Oxygen Species Signals Modulate Programmed Cell Death in Plants. *Int. J. Mol. Sci.* **2022**, *23*, 10087. [CrossRef]
105. He, A.; Dean, J.M.; Lodhi, I.J. Peroxisomes as Cellular Adaptors to Metabolic and Environmental Stress. *Trends Cell. Biol.* **2021**, *31*, 656–670. [CrossRef]
106. Averill-Bates, D. Reactive Oxygen Species and Cell Signaling. Review. *Biochim. Biophys. Acta (BBA)-Mol. Cell Res.* **2024**, *1871*, 119573. [CrossRef]
107. Kunert, K.J.; Foyer, C.H. The Ascorbate/Glutathione Cycle. In *Advances in Botanical Research*; Elsevier: Amsterdam, The Netherlands, 2023; Volume 105, pp. 77–112, ISSN 00652296.
108. Petřivalský, M. Compartmentalization in the Production of ROS and RNS in Horticultural Crops. In *Oxygen, Nitrogen and Sulfur Species in Post-Harvest Physiology of Horticultural Crops*; Elsevier: Amsterdam, The Netherlands, 2024; pp. 141–162.
109. Lennicke, C.; Cochemé, H.M. Redox Metabolism: ROS as Specific Molecular Regulators of Cell Signaling and Function. *Mol. Cell* **2021**, *81*, 3691–3707. [CrossRef]
110. Gideon, D.A.; Nirusimhan, V.; E., J.C.; Sudarsha, K.; Manoj, K.M. Mechanism of Electron Transfers Mediated by Cytochromes c and b 5 in Mitochondria and Endoplasmic Reticulum: Classical and Murburn Perspectives. *J. Biomol. Struct. Dyn.* **2022**, *40*, 9235–9252. [CrossRef]
111. Duan, M.; Bao, L.; Eman, M.; Han, D.; Zhang, Y.; Zheng, B.; Yang, S.; Rao, M.J. The Ectopic Expression of the MpDIR1(t) Gene Enhances the Response of Plants from Arabidopsis Thaliana to Biotic Stress by Regulating the Defense Genes and Antioxidant Flavonoids. *Plants* **2024**, *13*, 2692. [CrossRef]
112. Rao, M.J.; Ding, F.; Wang, N.; Deng, X.; Xu, Q. Metabolic Mechanisms of Host Species Against Citrus Huanglongbing (Greening Disease). *CRC Crit. Rev. Plant Sci.* **2018**, *37*, 496–511. [CrossRef]
113. Gill, S.S.; Tuteja, N. Reactive Oxygen Species and Antioxidant Machinery in Abiotic Stress Tolerance in Crop Plants. *Plant Physiol. Biochem.* **2010**, *48*, 909–930. [CrossRef]
114. Rao, M.J.; Duan, M.; Wang, J.; Han, S.; Ma, L.; Mo, X.; Li, M.; Hu, L.; Wang, L. Transcriptomic and Widely Targeted Metabolomic Approach Identified Diverse Group of Bioactive Compounds, Antiradical Activities, and Their Associated Genes in Six Sugarcane Varieties. *Antioxidants* **2022**, *11*, 1319. [CrossRef]
115. Sewelam, N.; Kazan, K.; Schenk, P.M. Global Plant Stress Signaling: Reactive Oxygen Species at the Cross-Road. *Front. Plant. Sci.* **2016**, *7*, 187. [CrossRef] [PubMed]
116. Andersen, E.J.; Ali, S.; Byamukama, E.; Yen, Y.; Nepal, M.P. Disease Resistance Mechanisms in Plants. *Genes* **2018**, *9*, 339. [CrossRef] [PubMed]
117. Miller, G.; Schlauch, K.; Tam, R.; Cortes, D.; Torres, M.A.; Shulaev, V.; Dangl, J.L.; Mittler, R. The Plant NADPH Oxidase RBOHD Mediates Rapid Systemic Signaling in Response to Diverse Stimuli. *Sci. Signal.* **2009**, *2*, ra45. [CrossRef] [PubMed]
118. Ye, C.; Zheng, S.; Jiang, D.; Lu, J.; Huang, Z.; Liu, Z.; Zhou, H.; Zhuang, C.; Li, J. Initiation and Execution of Programmed Cell Death and Regulation of Reactive Oxygen Species in Plants. *Int. J. Mol. Sci.* **2021**, *22*, 12942. [CrossRef]
119. Woodson, J.D.; Chory, J. Coordination of Gene Expression between Organellar and Nuclear Genomes. *Nat. Rev. Genet.* **2008**, *9*, 383–395. [CrossRef]
120. Ahuja, I.; de Vos, R.C.H.; Bones, A.M.; Hall, R.D. Plant Molecular Stress Responses Face Climate Change. *Trends Plant Sci.* **2010**, *15*, 664–674. [CrossRef]
121. Heidarvand, L.; Maali Amiri, R. What Happens in Plant Molecular Responses to Cold Stress? *Acta Physiol. Plant* **2010**, *32*, 419–431. [CrossRef]

122. Volkov, R.A.; Panchuk, I.I.; Mullineaux, P.M.; Schöffl, F. Heat Stress-Induced H_2O_2 Is Required for Effective Expression of Heat Shock Genes in Arabidopsis. *Plant Mol. Biol.* **2006**, *61*, 733–746. [CrossRef]
123. Pnueli, L.; Liang, H.; Rozenberg, M.; Mittler, R. Growth Suppression, Altered Stomatal Responses, and Augmented Induction of Heat Shock Proteins in Cytosolic Ascorbate Peroxidase (Apx1)-deficient Arabidopsis Plants. *Plant J.* **2003**, *34*, 187–203. [CrossRef]
124. Yamauchi, T.; Yoshioka, M.; Fukazawa, A.; Mori, H.; Nishizawa, N.K.; Tsutsumi, N.; Yoshioka, H.; Nakazono, M. An NADPH Oxidase RBOH Functions in Rice Roots during Lysigenous Aerenchyma Formation under Oxygen-Deficient Conditions. *Plant Cell* **2017**, *29*, 775–790. [CrossRef]
125. Yang, C.-Y.; Hong, C.-P. The NADPH Oxidase Rboh D Is Involved in Primary Hypoxia Signalling and Modulates Expression of Hypoxia-Inducible Genes under Hypoxic Stress. *Environ. Exp. Bot.* **2015**, *115*, 63–72. [CrossRef]
126. Banti, V.; Mafessoni, F.; Loreti, E.; Alpi, A.; Perata, P. The Heat-Inducible Transcription Factor HsfA2 Enhances Anoxia Tolerance in Arabidopsis. *Plant Physiol.* **2010**, *152*, 1471–1483. [CrossRef] [PubMed]
127. Ma, L.; Zhang, H.; Sun, L.; Jiao, Y.; Zhang, G.; Miao, C.; Hao, F. NADPH Oxidase AtrbohD and AtrbohF Function in ROS-Dependent Regulation of Na+/K+ Homeostasis in Arabidopsis under Salt Stress. *J. Exp. Bot.* **2012**, *63*, 305–317. [CrossRef] [PubMed]
128. Li, L.; Kim, B.-G.; Cheong, Y.H.; Pandey, G.K.; Luan, S. A Ca2+ Signaling Pathway Regulates a K+ Channel for Low-K Response in Arabidopsis. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 12625–12630. [CrossRef]
129. Shin, R.; Schachtman, D.P. Hydrogen Peroxide Mediates Plant Root Cell Response to Nutrient Deprivation. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 8827–8832. [CrossRef]
130. Rao, M.J.; Wang, H.; Lei, H.; Zhang, H.; Duan, X.; Bao, L.; Yang, C.; Han, D.; Zhang, Y.; Yang, S.; et al. LC-MS/MS-Based Metabolomic Study Provides Insights into Altitude-Dependent Variations in Flavonoid Profiles of Strawberries. *Front. Plant Sci.* **2025**, *15*, 1527212. [CrossRef]
131. Hendrix, S.; Dard, A.; Meyer, A.J.; Reichheld, J.-P. Redox-Mediated Responses to High Temperature in Plants. *J. Exp. Bot.* **2023**, *74*, 2489–2507. [CrossRef]
132. Fahad, S.; Hussain, S.; Saud, S.; Khan, F.; Hassan, S.; Amanullah; Nasim, W.; Arif, M.; Wang, F.; Huang, J. Exogenously Applied Plant Growth Regulators Affect Heat-stressed Rice Pollens. *J. Agron. Crop Sci.* **2016**, *202*, 139–150. [CrossRef]
133. Ding, X.; Jiang, Y.; He, L.; Zhou, Q.; Yu, J.; Hui, D.; Huang, D. Exogenous Glutathione Improves High Root-Zone Temperature Tolerance by Modulating Photosynthesis, Antioxidant and Osmolytes Systems in Cucumber Seedlings. *Sci. Rep.* **2016**, *6*, 35424. [CrossRef]
134. Vacca, R.A.; de Pinto, M.C.; Valenti, D.; Passarella, S.; Marra, E.; De Gara, L. Production of Reactive Oxygen Species, Alteration of Cytosolic Ascorbate Peroxidase, and Impairment of Mitochondrial Metabolism Are Early Events in Heat Shock-Induced Programmed Cell Death in Tobacco Bright-Yellow 2 Cells. *Plant Physiol.* **2004**, *134*, 1100–1112. [CrossRef] [PubMed]
135. Djanaguiraman, M.; Perumal, R.; Jagadish, S.V.K.; Ciampitti, I.A.; Welti, R.; Prasad, P.V. V Sensitivity of Sorghum Pollen and Pistil to High-temperature Stress. *Plant Cell Environ.* **2018**, *41*, 1065–1082. [CrossRef] [PubMed]
136. Sarwar, M.; Saleem, M.F.; Ullah, N.; Rizwan, M.; Ali, S.; Shahid, M.R.; Alamri, S.A.; Alyemeni, M.N.; Ahmad, P. Exogenously Applied Growth Regulators Protect the Cotton Crop from Heat-Induced Injury by Modulating Plant Defense Mechanism. *Sci. Rep.* **2018**, *8*, 17086. [CrossRef] [PubMed]
137. Liu, J.; Hasanuzzaman, M.; Wen, H.; Zhang, J.; Peng, T.; Sun, H.; Zhao, Q. High Temperature and Drought Stress Cause Abscisic Acid and Reactive Oxygen Species Accumulation and Suppress Seed Germination Growth in Rice. *Protoplasma* **2019**, *256*, 1217–1227. [CrossRef]
138. Fan, Y.; Wang, K.; Wang, M.; Wang, X.; Li, H.; Wu, Y. Production, Functions and Scavenging Mechanisms of Reactive Oxygen Species in Plants under Low-Temperature Stress. *Maejo Int. J. Sci. Technol.* **2023**, *17*, 210.
139. Han, Q.-H.; Huang, B.; Ding, C.-B.; Zhang, Z.-W.; Chen, Y.-E.; Hu, C.; Zhou, L.-J.; Huang, Y.; Liao, J.-Q.; Yuan, S. Effects of Melatonin on Anti-Oxidative Systems and Photosystem II in Cold-Stressed Rice Seedlings. *Front. Plant Sci.* **2017**, *8*, 785. [CrossRef]
140. Liu, T.; Ye, X.; Li, M.; Li, J.; Qi, H.; Hu, X. H_2O_2 and NO Are Involved in Trehalose-Regulated Oxidative Stress Tolerance in Cold-Stressed Tomato Plants. *Environ. Exp. Bot.* **2020**, *171*, 103961. [CrossRef]
141. Ghanbari, F.; Sayyari, M. Controlled Drought Stress Affects the Chilling-Hardening Capacity of Tomato Seedlings as Indicated by Changes in Phenol Metabolisms, Antioxidant Enzymes Activity, Osmolytes Concentration and Abscisic Acid Accumulation. *Sci. Hortic.* **2018**, *229*, 167–174. [CrossRef]
142. Diao, Q.; Song, Y.; Shi, D.; Qi, H. Interaction of Polyamines, Abscisic Acid, Nitric Oxide, and Hydrogen Peroxide under Chilling Stress in Tomato (*Lycopersicon Esculentum* Mill.) Seedlings. *Front. Plant Sci.* **2017**, *8*, 203. [CrossRef]
143. Xue, M.; Guo, T.; Ren, M.; Wang, Z.; Tang, K.; Zhang, W.; Wang, M. Constitutive Expression of Chloroplast Glycerol-3-Phosphate Acyltransferase from *Ammopiptanthus Mongolicus* Enhances Unsaturation of Chloroplast Lipids and Tolerance to Chilling, Freezing and Oxidative Stress in Transgenic Arabidopsis. *Plant Physiol. Biochem.* **2019**, *143*, 375–387. [CrossRef]
144. Hasanuzzaman, M.; Nahar, K.; Gill, S.S.; Fujita, M. Drought Stress Responses in Plants, Oxidative Stress, and Antioxidant Defense. In *Climate Change and Plant Abiotic Stress Tolerance*; Wiley: Hoboken, NJ, USA, 2013; pp. 209–250.

145. Mirza, H.; Kamrun, N.; Mahabub, A.M.; Masayuki, F. Regulation of Reactive Oxygen Species Metabolism and Glyoxalase Systems by Exogenous Osmolytes Confers Thermotolerance in Brassica Napus. *Gesunde Pflanz.* **2020**, *72*, 3–16.
146. Hasanuzzaman, M.; Nahar, K.; Rahman, A.; Inafuku, M.; Oku, H.; Fujita, M. Exogenous Nitric Oxide Donor and Arginine Provide Protection against Short-Term Drought Stress in Wheat Seedlings. *Physiol. Mol. Biol. Plants* **2018**, *24*, 993–1004. [CrossRef] [PubMed]
147. Fahad, S.; Bajwa, A.A.; Nazir, U.; Anjum, S.A.; Farooq, A.; Zohaib, A.; Sadia, S.; Nasim, W.; Adkins, S.; Saud, S. Crop Production under Drought and Heat Stress: Plant Responses and Management Options. *Front. Plant Sci.* **2017**, *8*, 1147. [CrossRef]
148. Abideen, Z.; Koyro, H.; Huchzermeyer, B.; Ansari, R.; Zulfiqar, F.; Gul, B. Ameliorating Effects of Biochar on Photosynthetic Efficiency and Antioxidant Defence of Phragmites Karka under Drought Stress. *Plant Biol.* **2020**, *22*, 259–266. [CrossRef]
149. Campos, C.N.; Ávila, R.G.; de Souza, K.R.D.; Azevedo, L.M.; Alves, J.D. Melatonin Reduces Oxidative Stress and Promotes Drought Tolerance in Young *Coffea arabica* L. Plants. *Agric. Water Manag.* **2019**, *211*, 37–47. [CrossRef]
150. Saha, I.; De, A.K.; Sarkar, B.; Ghosh, A.; Dey, N.; Adak, M.K. Cellular Response of Oxidative Stress When Sub1A QTL of Rice Receives Water Deficit Stress. *Plant Sci. Today* **2018**, *5*, 84–94. [CrossRef]
151. Satish, L.; Rency, A.S.; Ramesh, M. Spermidine Sprays Alleviate the Water Deficit-Induced Oxidative Stress in Finger Millet (*Eleusine Coracana* L. Gaertn.) Plants. *3 Biotech* **2018**, *8*, 63. [CrossRef]
152. Malhotra, C.; Kapoor, R.T.; Ganjewala, D.; Singh, N. Sodium Silicate Mediated Response of Antioxidative Defense System in Lycopersicon Esculentum Mill. under Water Stress. *Int. J. Phytomed.* **2017**, *9*, 364–378. [CrossRef]
153. Rao, M.J.; Feng, B.; Ahmad, M.H.; Tahir Ul Qamar, M.; Aslam, M.Z.; Khalid, M.F.; Hussain, S.B.; Zhong, R.; Ali, Q.; Xu, Q.; et al. LC-MS/MS-Based Metabolomics Approach Identified Novel Antioxidant Flavonoids Associated with Drought Tolerance in Citrus Species. *Front. Plant Sci.* **2023**, *14*, 1150854. [CrossRef]
154. Hasanuzzaman, M.; Nahar, K.; Anee, T.I.; Khan, M.I.R.; Fujita, M. Silicon-Mediated Regulation of Antioxidant Defense and Glyoxalase Systems Confers Drought Stress Tolerance in *Brassica napus* L. *S. Afr. J. Bot.* **2018**, *115*, 50–57. [CrossRef]
155. Hasanuzzaman, M.; Nahar, K.; Hossain, M.S.; Anee, T.I.; Parvin, K.; Fujita, M. Nitric Oxide Pretreatment Enhances Antioxidant Defense and Glyoxalase Systems to Confer PEG-Induced Oxidative Stress in Rapeseed. *J. Plant Interact.* **2017**, *12*, 323–331. [CrossRef]
156. Rezayian, M.; Ebrahimzadeh, H.; Niknam, V. Nitric Oxide Stimulates Antioxidant System and Osmotic Adjustment in Soybean under Drought Stress. *J. Soil Sci. Plant Nutr.* **2020**, *20*, 1122–1132. [CrossRef]
157. Rady, M.M.; Belal, H.E.E.; Gadallah, F.M.; Semida, W.M. Selenium Application in Two Methods Promotes Drought Tolerance in *Solanum Lycopersicum* Plant by Inducing the Antioxidant Defense System. *Sci. Hortic.* **2020**, *266*, 109290. [CrossRef]
158. Filippou, P.; Antoniou, C.; Fotopoulos, V. Effect of Drought and Rewatering on the Cellular Status and Antioxidant Response of *Medicago Truncatula* Plants. *Plant Signal Behav.* **2011**, *6*, 270–277. [CrossRef]
159. Kusvuran, S.; Dasgan, H.Y. Effects of Drought Stress on Physiological and Biochemical Changes in *Phaseolus Vulgaris* L. *Legume Res.-Int. J.* **2017**, *40*, 55–62.
160. Nurrahma, A.H.I.; Putri, H.H.; Syahadat, R.M. Scientific Research Trends of Flooding Stress in Plant Science and Agriculture Subject Areas (1962–2021). *ASEAN J. Sci. Eng.* **2023**, *3*, 163–178. [CrossRef]
161. Zhang, R.D.; Zhou, Y.F.; Yue, Z.X.; Chen, X.F.; Cao, X.; Xu, X.X.; Xing, Y.F.; Jiang, B.; Ai, X.Y.; Huang, R.D. Changes in Photosynthesis, Chloroplast Ultrastructure, and Antioxidant Metabolism in Leaves of Sorghum under Waterlogging Stress. *Photosynthetica* **2019**, *57*, 1076–1083. [CrossRef]
162. Anee, T.I.; Nahar, K.; Rahman, A.; Mahmud, J.A.; Bhuiyan, T.F.; Alam, M.U.; Fujita, M.; Hasanuzzaman, M. Oxidative Damage and Antioxidant Defense in *Sesamum Indicum* after Different Waterlogging Durations. *Plants* **2019**, *8*, 196. [CrossRef]
163. Rasheed, R.; Iqbal, M.; Ashraf, M.A.; Hussain, I.; Shafiq, F.; Yousaf, A.; Zaheer, A. Glycine Betaine Counteracts the Inhibitory Effects of Waterlogging on Growth, Photosynthetic Pigments, Oxidative Defence System, Nutrient Composition, and Fruit Quality in Tomato. *J. Hortic. Sci. Biotechnol.* **2018**, *93*, 385–391. [CrossRef]
164. Luan, H.; Shen, H.; Pan, Y.; Guo, B.; Lv, C.; Xu, R. Elucidating the Hypoxic Stress Response in Barley (*Hordeum vulgare* L.) during Waterlogging: A Proteomics Approach. *Sci. Rep.* **2018**, *8*, 9655. [CrossRef]
165. Park, J.S.; Lee, E.J. Waterlogging Induced Oxidative Stress and the Mortality of the Antarctic Plant, *Deschampsia antarctica*. *J. Ecol. Environ.* **2019**, *43*, 29. [CrossRef]
166. Wang, R.R.-C.; Xu, S.S.; Monaco, T.A.; Robbins, M.D. Dual Mechanisms of Salinity Tolerance in Wheat Germplasm Lines W4909 and W4910. *Int. J. Mol. Sci.* **2024**, *25*, 12892. [CrossRef] [PubMed]
167. Rehman, S.; Abbas, G.; Shahid, M.; Saqib, M.; Farooq, A.B.U.; Hussain, M.; Murtaza, B.; Amjad, M.; Naeem, M.A.; Farooq, A. Effect of Salinity on Cadmium Tolerance, Ionic Homeostasis and Oxidative Stress Responses in Conocarpus Exposed to Cadmium Stress: Implications for Phytoremediation. *Ecotoxicol. Environ. Saf.* **2019**, *171*, 146–153. [CrossRef] [PubMed]
168. Cheng, Y.-W.; Kong, X.-W.; Wang, N.; Wang, T.-T.; Chen, J.; Shi, Z.Q. Thymol Confers Tolerance to Salt Stress by Activating Anti-Oxidative Defense and Modulating Na+ Homeostasis in Rice Root. *Ecotoxicol. Environ. Saf.* **2020**, *188*, 109894. [CrossRef]

169. Ahanger, M.A.; Mir, R.A.; Alyemeni, M.N.; Ahmad, P. Combined Effects of Brassinosteroid and Kinetin Mitigates Salinity Stress in Tomato through the Modulation of Antioxidant and Osmolyte Metabolism. *Plant Physiol. Biochem.* **2020**, *147*, 31–42. [CrossRef]
170. Abdelaal, K.A.; El-Maghraby, L.M.; Elansary, H.; Hafez, Y.M.; Ibrahim, E.I.; El-Banna, M.; El-Esawi, M.; Elkelish, A. Treatment of Sweet Pepper with Stress Tolerance-Inducing Compounds Alleviates Salinity Stress Oxidative Damage by Mediating the Physio-Biochemical Activities and Antioxidant Systems. *Agronomy* **2019**, *10*, 26. [CrossRef]
171. Ahmad, P.; Ahanger, M.A.; Alam, P.; Alyemeni, M.N.; Wijaya, L.; Ali, S.; Ashraf, M. Silicon (Si) Supplementation Alleviates NaCl Toxicity in Mung Bean [*Vigna radiata* (L.) Wilczek] through the Modifications of Physio-Biochemical Attributes and Key Antioxidant Enzymes. *J. Plant Growth Regul.* **2019**, *38*, 70–82. [CrossRef]
172. Hindala, M.R.; Joshi, R.; Patni, V. Reactive Oxygen Species and Oxidative Damage in Halophytes Under Salt Stress. In *Physiology of Halophytes*; Apple Academic Press: New Jersey, NJ, USA, 2025; pp. 337–372.
173. Arora, M.; Saxena, P.; Abdin, M.Z.; Varma, A. Interaction between *Piriformospora Indica* and *Azotobacter Chroococcum* Diminish the Effect of Salt Stress in *Artemisia Annua* L. by Enhancing Enzymatic and Non-Enzymatic Antioxidants. *Symbiosis* **2020**, *80*, 61–73. [CrossRef]
174. Lalarukh, I.; Shahbaz, M. Response of Antioxidants and Lipid Peroxidation to Exogenous Application of Alpha-Tocopherol in Sunflower (*Helianthus annuus* L.) under Salt Stress. *Pak. J. Bot.* **2020**, *52*, 75–83. [CrossRef]
175. Tariq, A.; Shahbaz, M. Glycinebetaine Induced Modulation in Oxidative Defense System and Mineral Nutrients Sesame (*Sesamum indicum* L.) under Saline Regimes. *Pak. J. Bot.* **2020**, *52*, 775–782. [CrossRef]
176. Mhadhbi, H.; Fotopoulos, V.; Mylona, P.V.; Jebara, M.; Aouani, M.E.; Polidoros, A.N. Alternative Oxidase 1 (Aox1) Gene Expression in Roots of *Medicago truncatula* Is a Genotype-Specific Component of Salt Stress Tolerance. *J. Plant Physiol.* **2013**, *170*, 111–114. [CrossRef] [PubMed]
177. Alzahrani, S.M.; Alaraidh, I.A.; Migdadi, H.; Alghamdi, S.; Khan, M.A.; Ahmad, P. Physiological, Biochemical, and Antioxidant Properties of Two Genotypes of *Vicia Faba* Grown under Salinity Stress. *Pak. J. Bot.* **2019**, *51*, 786–798. [CrossRef] [PubMed]
178. Filippou, P.; Bouchagier, P.; Skotti, E.; Fotopoulos, V. Proline and Reactive Oxygen/Nitrogen Species Metabolism Is Involved in the Tolerant Response of the Invasive Plant Species *Ailanthus altissima* to Drought and Salinity. *Environ. Exp. Bot.* **2014**, *97*, 1–10. [CrossRef]
179. Das, A.; Pal, S.; Hasanuzzaman, M.; Adak, M.K.; Sil, S.K. Mitigation of Aluminum Toxicity in Rice Seedlings Using Biofabricated Selenium Nanoparticles and Nitric Oxide: Synergistic Effects on Oxidative Stress Tolerance and Sulfur Metabolism. *Chemosphere* **2025**, *370*, 143940. [CrossRef]
180. Mahajan, P.; Khanna, V. Nanoparticle-Mediated Regulation of Chromium Toxicity in Plants: Unveiling the Mechanism at Cellular Level. In *Sustainable Development Goals Towards Environmental Toxicity and Green Chemistry*; Springer: Berlin/Heidelberg, Germany, 2025; pp. 269–290, ISBN 3031773276.
181. Kumar, U.; Kumar, I.; Singh, P.K.; Dwivedi, A.; Singh, P.; Mishra, S.; Seth, C.S.; Sharma, R.K. Nickel Contamination in Terrestrial Ecosystems: Insights into Impacts, Phytotoxicity Mechanisms, and Remediation Technologies. *Rev. Environ. Contam. Toxicol.* **2025**, *263*, 2. [CrossRef]
182. Hasanuzzaman, M.; Alam, M.M.; Nahar, K.; Mohsin, S.M.; Bhuyan, M.H.M.B.; Parvin, K.; Hawrylak-Nowak, B.; Fujita, M. Silicon-Induced Antioxidant Defense and Methylglyoxal Detoxification Works Coordinately in Alleviating Nickel Toxicity in *Oryza sativa* L. *Ecotoxicology* **2019**, *28*, 261–276. [CrossRef]
183. El-Amier, Y.; Elhindi, K.; El-Hendawy, S.; Al-Rashed, S.; Abd-ElGawad, A. Antioxidant System and Biomolecules Alteration in *Pisum Sativum* under Heavy Metal Stress and Possible Alleviation by 5-Aminolevulinic Acid. *Molecules* **2019**, *24*, 4194. [CrossRef]
184. Nahar, K.; Rahman, M.; Hasanuzzaman, M.; Alam, M.M.; Rahman, A.; Suzuki, T.; Fujita, M. Physiological and Biochemical Mechanisms of Spermine-Induced Cadmium Stress Tolerance in Mung Bean (*Vigna radiata* L.) Seedlings. *Environ. Sci. Pollut. Res.* **2016**, *23*, 21206–21218. [CrossRef]
185. Gupta, D.K.; Pena, L.B.; Romero-Puertas, M.C.; Hernández, A.; Inouhe, M.; Sandalio, L.M. NADPH Oxidases Differentially Regulate ROS Metabolism and Nutrient Uptake under Cadmium Toxicity. *Plant Cell Environ.* **2017**, *40*, 509–526. [CrossRef]
186. Kabała, K.; Zboińska, M.; Głowiak, D.; Reda, M.; Jakubowska, D.; Janicka, M. Interaction between the Signaling Molecules Hydrogen Sulfide and Hydrogen Peroxide and Their Role in Vacuolar H+-ATPase Regulation in Cadmium-stressed Cucumber Roots. *Physiol. Plant* **2019**, *166*, 688–704. [CrossRef]
187. Ahanger, M.A.; Aziz, U.; Alsahli, A.A.; Alyemeni, M.N.; Ahmad, P. Combined Kinetin and Spermidine Treatments Ameliorate Growth and Photosynthetic Inhibition in Vigna Angularis by Up-Regulating Antioxidant and Nitrogen Metabolism under Cadmium Stress. *Biomolecules* **2020**, *10*, 147. [CrossRef] [PubMed]
188. Zaid, A.; Mohammad, F.; Fariduddin, Q. Plant Growth Regulators Improve Growth, Photosynthesis, Mineral Nutrient and Antioxidant System under Cadmium Stress in Menthol Mint (*Mentha Arvensis* L.). *Physiol. Mol. Biol. Plants* **2020**, *26*, 25–39. [CrossRef] [PubMed]

189. Nahar, K.; Hasanuzzaman, M.; Suzuki, T.; Fujita, M. Polyamines-Induced Aluminum Tolerance in Mung Bean: A Study on Antioxidant Defense and Methylglyoxal Detoxification Systems. *Ecotoxicology* **2017**, *26*, 58–73. [CrossRef] [PubMed]
190. Hasanuzzaman, M.; Nahar, K.; Rahman, A.; Mahmud, J.A.; Alharby, H.F.; Fujita, M. Exogenous Glutathione Attenuates Lead-Induced Oxidative Stress in Wheat by Improving Antioxidant Defense and Physiological Mechanisms. *J. Plant Interact.* **2018**, *13*, 203–212. [CrossRef]
191. Yadu, B.; Chandrakar, V.; Tamboli, R.; Keshavkant, S. Dimethylthiourea Antagonizes Oxidative Responses by Up-Regulating Expressions of Pyrroline-5-Carboxylate Synthetase and Antioxidant Genes under Arsenic Stress. *Int. J. Environ. Sci. Technol.* **2019**, *16*, 8401–8410. [CrossRef]
192. Parvez, S.; Abbas, G.; Shahid, M.; Amjad, M.; Hussain, M.; Asad, S.A.; Imran, M.; Naeem, M.A. Effect of Salinity on Physiological, Biochemical and Photostabilizing Attributes of Two Genotypes of Quinoa (*Chenopodium Quinoa* Willd.) Exposed to Arsenic Stress. *Ecotoxicol. Environ. Saf.* **2020**, *187*, 109814. [CrossRef]
193. Georgiadou, E.C.; Kowalska, E.; Patla, K.; Kulbat, K.; Smolińska, B.; Leszczyńska, J.; Fotopoulos, V. Influence of Heavy Metals (Ni, Cu, and Zn) on Nitro-Oxidative Stress Responses, Proteome Regulation and Allergen Production in Basil (*Ocimum Basilicum* L.) Plants. *Front. Plant Sci.* **2018**, *9*, 862. [CrossRef]
194. Keunen, E.; Remans, T.; Bohler, S.; Vangronsveld, J.; Cuypers, A. Metal-Induced Oxidative Stress and Plant Mitochondria. *Int. J. Mol. Sci.* **2011**, *12*, 6894–6918. [CrossRef]
195. Smejkal, G.B.; Kakumanu, S. Enzymes and Their Turnover Numbers. *Expert Rev. Proteom.* **2019**, *16*, 543–544. [CrossRef]
196. Veljović Jovanović, S.; Kukavica, B.; Vidović, M.; Morina, F.; Menckhoff, L. Class III Peroxidases: Functions, Localization and Redox Regulation of Isoenzymes. In *Antioxidants and Antioxidant Enzymes in Higher Plants*; Springer: Berlin/Heidelberg, Germany, 2018; pp. 269–300.
197. Mehla, N.; Sindhi, V.; Josula, D.; Bisht, P.; Wani, S.H. An Introduction to Antioxidants and Their Roles in Plant Stress Tolerance. In *Reactive Oxygen Species and Antioxidant Systems in Plants: Role and Regulation Under Abiotic Stress*; Springer: Berlin/Heidelberg, Germany, 2017; pp. 1–23.
198. Singh, A.; Satheeshkumar, P.K. Reactive Oxygen Species (ROS) and ROS Scavengers in Plant Abiotic Stress Response. In *Stress Biology in Photosynthetic Organisms: Molecular Insights and Cellular Responses*; Springer: Berlin/Heidelberg, Germany, 2024; pp. 41–63.
199. Dixon, D.P.; Skipsey, M.; Edwards, R. Roles for Glutathione Transferases in Plant Secondary Metabolism. *Phytochemistry* **2010**, *71*, 338–350. [CrossRef]
200. Smirnoff, N. Ascorbate, Tocopherol and Carotenoids: Metabolism, Pathway Engineering and Functions. In *Antioxidants and Reactive Oxygen Species in Plants*; Wiley: Honoken, NJ, USA, 2005; pp. 53–86.
201. Sita, K.; Kumar, V. Role of Gamma Amino Butyric Acid (GABA) against Abiotic Stress Tolerance in Legumes: A Review. *Plant Physiol. Rep.* **2020**, *25*, 654–663. [CrossRef]
202. Gutiérrez-Grijalva, E.P.; López-Martínez, L.X.; Contreras-Angulo, L.A.; Elizalde-Romero, C.A.; Heredia, J.B. Plant Alkaloids: Structures and Bioactive Properties. In *Plant-Derived Bioactives*; Springer: Berlin/Heidelberg, Germany, 2020; pp. 85–117.
203. Hasanuzzaman, M.; Bhuyan, M.H.M.B.; Zulfiqar, F.; Raza, A.; Mohsin, S.M.; Mahmud, J.A.; Fujita, M.; Fotopoulos, V. Reactive Oxygen Species and Antioxidant Defense in Plants under Abiotic Stress: Revisiting the Crucial Role of a Universal Defense Regulator. *Antioxidants* **2020**, *9*, 681. [CrossRef] [PubMed]
204. Cizmarova, B.; Hubkova, B.; Birkova, A. Quercetin as an Effective Antioxidant against Superoxide Radical. *Funct. Food Sci.-Online* **2023**, *3*, 15–25. [CrossRef]
205. Jan, R.; Khan, M.; Asaf, S.; Lubna; Asif, S.; Kim, K.-M. Bioactivity and Therapeutic Potential of Kaempferol and Quercetin: New Insights for Plant and Human Health. *Plants* **2022**, *11*, 2623. [CrossRef] [PubMed]
206. Erlund, I. Review of the Flavonoids Quercetin, Hesperetin, and Naringenin. Dietary Sources, Bioactivities, Bioavailability, and Epidemiology. *Nutr. Res.* **2004**, *24*, 851–874. [CrossRef]
207. Saviranta, N.M.M.; Veeroos, L.; Granlund, L.J.; Hassinen, V.H.; Kaarniranta, K.; Karjalainen, R.O. Plant Flavonol Quercetin and Isoflavone Biochanin a Differentially Induce Protection against Oxidative Stress and Inflammation in ARPE-19 Cells. *Food Res. Int.* **2011**, *44*, 109–113. [CrossRef]
208. Wang, F.; Ren, X.; Zhang, F.; Qi, M.; Zhao, H.; Chen, X.; Ye, Y.; Yang, J.; Li, S.; Zhang, Y. A R2R3-Type MYB Transcription Factor Gene from Soybean, GmMYB12, Is Involved in Flavonoids Accumulation and Abiotic Stress Tolerance in Transgenic Arabidopsis. *Plant Biotechnol. Rep.* **2019**, *13*, 219–233. [CrossRef]
209. Jomova, K.; Hudecova, L.; Lauro, P.; Simunková, M.; Barbierikova, Z.; Malcek, M.; Alwasel, S.H.; Alhazza, I.M.; Rhodes, C.J.; Valko, M. The Effect of Luteolin on DNA Damage Mediated by a Copper Catalyzed Fenton Reaction. *J. Inorg. Biochem.* **2022**, *226*, 111635. [CrossRef]
210. Vafadar, F.; Amooaghaie, R.; Ehsanzadeh, P.; Ghanadian, M.; Talebi, M.; Ghanati, F. Melatonin and Calcium Modulate the Production of Rosmarinic Acid, Luteolin, and Apigenin in *Dracocephalum Kotschyi* under Salinity Stress. *Phytochemistry* **2020**, *177*, 112422. [CrossRef]

211. Zhou, L.-J.; Geng, Z.; Wang, Y.; Wang, Y.; Liu, S.; Chen, C.; Song, A.; Jiang, J.; Chen, S.; Chen, F. A Novel Transcription Factor CmMYB012 Inhibits Flavone and Anthocyanin Biosynthesis in Response to High Temperatures in Chrysanthemum. *Hortic. Res.* **2021**, *8*, 248. [CrossRef]
212. Kejík, Z.; Kaplánek, R.; Masařík, M.; Babula, P.; Matkowski, A.; Filipenský, P.; Veselá, K.; Gburek, J.; Sýkora, D.; Martásek, P. Iron Complexes of Flavonoids-Antioxidant Capacity and Beyond. *Int. J. Mol. Sci.* **2021**, *22*, 646. [CrossRef] [PubMed]
213. Borges Bubols, G.; da Rocha Vianna, D.; Medina-Remon, A.; von Poser, G.; Maria Lamuela-Raventos, R.; Lucia Eifler-Lima, V.; Cristina Garcia, S. The Antioxidant Activity of Coumarins and Flavonoids. *Mini Rev. Med. Chem.* **2013**, *13*, 318–334.
214. Dędek, K.; Rosicka-Kaczmarek, J.; Nebesny, E.; Kowalska, G. Characteristics and Biological Properties of Ferulic Acid. *Biotechnol. Food Sci.* **2019**, *83*, 71–85.
215. Kaurinovic, B.; Vastag, D. *Flavonoids and Phenolic Acids as Potential Natural Antioxidants*; IntechOpen: London, UK, 2019; ISBN 1789239206.
216. Marchiosi, R.; dos Santos, W.D.; Constantin, R.P.; de Lima, R.B.; Soares, A.R.; Finger-Teixeira, A.; Mota, T.R.; de Oliveira, D.M.; Foletto-Felipe, M.d.P.; Abrahão, J. Biosynthesis and Metabolic Actions of Simple Phenolic Acids in Plants. *Phytochem. Rev.* **2020**, *19*, 865–906. [CrossRef]
217. Xu, J.-G.; Hu, Q.-P.; Liu, Y. Antioxidant and DNA-Protective Activities of Chlorogenic Acid Isomers. *J. Agric. Food Chem.* **2012**, *60*, 11625–11630. [CrossRef]
218. Mughal, A.; Jabeen, N.; Ashraf, K.; Sultan, K.; Farhan, M.; Hussain, M.I.; Deng, G.; Alsudays, I.M.; Saleh, M.A.; Tariq, S. Exploring the Role of Caffeic Acid in Mitigating Abiotic Stresses in Plants: A Review. *Plant Stress* **2024**, *12*, 100487. [CrossRef]
219. Wilson, R.A.; Sangha, M.K.; Banga, S.S.; Atwal, A.K.; Gupta, S. Heat Stress Tolerance in Relation to Oxidative Stress and Antioxidants in *Brassica juncea*. *J. Environ. Biol.* **2014**, *35*, 383.
220. Chugh, P.; Kaur, J.; Grewal, S.K.; Singh, S.; Agrawal, S.K. Upregulation of Superoxide Dismutase and Catalase along with Proline Accumulation Mediates Heat Tolerance in Lentil (*Lens culinaris* Medik.) Genotypes during Reproductive Stage. *Indian J. Agric. Biochem.* **2017**, *30*, 195–199. [CrossRef]
221. Almeselmani, M.; Deshmukh, P.S.; Sairam, R.K.; Kushwaha, S.R.; Singh, T.P. Protective Role of Antioxidant Enzymes under High Temperature Stress. *Plant Sci.* **2006**, *171*, 382–388. [CrossRef]
222. Thounaojam, T.C.; Panda, P.; Mazumdar, P.; Kumar, D.; Sharma, G.D.; Sahoo, L.; Sanjib, P. Excess Copper Induced Oxidative Stress and Response of Antioxidants in Rice. *Plant Physiol. Biochem.* **2012**, *53*, 33–39. [CrossRef]
223. Jin, R.; Wang, Y.; Liu, R.; Gou, J.; Chan, Z. Physiological and Metabolic Changes of Purslane (*Portulaca Oleracea* L.) in Response to Drought, Heat, and Combined Stresses. *Front. Plant Sci.* **2016**, *6*, 1123. [CrossRef] [PubMed]
224. Koussevitzky, S.; Suzuki, N.; Huntington, S.; Armijo, L.; Sha, W.; Cortes, D.; Shulaev, V.; Mittler, R. Ascorbate Peroxidase 1 Plays a Key Role in the Response of Arabidopsis Thaliana to Stress Combination. *J. Biol. Chem.* **2008**, *283*, 34197–34203. [CrossRef]
225. Zandalinas, S.I.; Balfagón, D.; Arbona, V.; Gómez-Cadenas, A. Modulation of Antioxidant Defense System Is Associated with Combined Drought and Heat Stress Tolerance in Citrus. *Front. Plant Sci.* **2017**, *8*, 953. [CrossRef]
226. Selote, D.S.; Khanna-Chopra, R. Drought Acclimation Confers Oxidative Stress Tolerance by Inducing Co-ordinated Antioxidant Defense at Cellular and Subcellular Level in Leaves of Wheat Seedlings. *Physiol. Plant* **2006**, *127*, 494–506. [CrossRef]
227. Almeselmani, M.; Deshmukh, P.; Sairam, R. High Temperature Stress Tolerance in Wheat Genotypes: Role of Antioxidant Defence Enzymes. *Acta Agron. Hung.* **2009**, *57*, 1–14. [CrossRef]
228. Esim, N.; Atici, O. Nitric Oxide Improves Chilling Tolerance of Maize by Affecting Apoplastic Antioxidative Enzymes in Leaves. *Plant Growth Regul.* **2014**, *72*, 29–38. [CrossRef]
229. Rahman, A.; Hossain, M.S.; Mahmud, J.-A.; Nahar, K.; Hasanuzzaman, M.; Fujita, M. Manganese-Induced Salt Stress Tolerance in Rice Seedlings: Regulation of Ion Homeostasis, Antioxidant Defense and Glyoxalase Systems. *Physiol. Mol. Biol. Plants* **2016**, *22*, 291–306. [CrossRef]
230. Wang, X.; Wu, L.; Xie, J.; Li, T.; Cai, J.; Zhou, Q.; Dai, T.; Jiang, D. Herbicide Isoproturon Aggravates the Damage of Low Temperature Stress and Exogenous Ascorbic Acid Alleviates the Combined Stress in Wheat Seedlings. *Plant Growth Regul.* **2018**, *84*, 293–301. [CrossRef]
231. Islam, F.; Ali, B.; Wang, J.; Farooq, M.A.; Gill, R.A.; Ali, S.; Wang, D.; Zhou, W. Combined Herbicide and Saline Stress Differentially Modulates Hormonal Regulation and Antioxidant Defense System in *Oryza Sativa* Cultivars. *Plant Physiol. Biochem.* **2016**, *107*, 82–95. [CrossRef]
232. Lee, D.H.; Lee, C.B. Chilling Stress-Induced Changes of Antioxidant Enzymes in the Leaves of Cucumber: In Gel Enzyme Activity Assays. *Plant Sci.* **2000**, *159*, 75–85. [CrossRef]
233. Costa, H.; Gallego, S.M.; Tomaro, M.L. Effect of UV-B Radiation on Antioxidant Defense System in Sunflower Cotyledons. *Plant Sci.* **2002**, *162*, 939–945. [CrossRef]

234. Qi, C.; Lin, X.; Li, S.; Liu, L.; Wang, Z.; Li, Y.; Bai, R.; Xie, Q.; Zhang, N.; Ren, S. SoHSC70 Positively Regulates Thermotolerance by Alleviating Cell Membrane Damage, Reducing ROS Accumulation, and Improving Activities of Antioxidant Enzymes. *Plant Sci.* **2019**, *283*, 385–395. [CrossRef] [PubMed]
235. Aftab, T.; Khan, M.M.A.; Idrees, M.; Naeem, M.; Ram, M. Boron Induced Oxidative Stress, Antioxidant Defence Response and Changes in Artemisinin Content in *Artemisia annua* L. *J. Agron. Crop Sci.* **2010**, *196*, 423–430. [CrossRef]

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