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Review

Abiotic Stress: Interplay Between ROS Production and Antioxidant Machinery, Signaling, and ROS Homeostasis

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Abstract

Climate change poses a substantial threat to global crop yield. Moreover, crop production is likely to reduce in the near future because of increasing average temperatures, widespread extreme climate events, and the loss of agricultural land. Abiotic stresses are the major factors limiting the growth and development of various crops worldwide. They cause the buildup of reactive oxygen species (ROS), which leads to cellular damage in a variety of subcellular compartments in plants. The metabolic rate of ROS is critical for crop yield, development, acclimation, and survival under a continuously changing environment. The modulation and enhancement of the expression of genes that encode ROS detoxifying enzymes are commonly used to increase the tolerance against abiotic stresses. Under stressful conditions, however, both enzymatic and nonenzymatic antioxidant systems maintain the balance between ROS elimination and production. At low concentrations, ROS play a signaling role and is important for a variety of biological processes, such as rapid cell growth and differentiation. The consequence of ROS toxicity is the ROS-activated cell damage triggered by the activation of signaling pathways, such as MAPKS and other calcium-dependent pathways. In this review, recent progress on the unfavorable effects of ROS, antioxidant defense mechanisms participating in ROS detoxification in various abiotic stresses, and cross-talk between different signaling pathways have been discussed. Furthermore, advancements in the molecular perspective of ROS-mediated antioxidant defense of plants under abiotic stresses have been discussed.

Keywords

Climatic challenges; plant defense; plant molecular mechanism; stress-tolerant crops

1. Introduction

Plants endure a variety of adverse environmental conditions during their life span. Under suboptimal growing conditions, the survival chances of the plants are dependent on the induction of secondary chemical messengers by environmental impulses; these messengers assist plants in adapting to the changing environment. Secondary messengers, including calcium message carrier systems, activated nitrogen oxide species, and the most common reactive oxygen species (ROS), are one of the most adaptable molecules or intermediates [1].

Abiotic stresses, such as drought, cold, heat, and salinity, are directly or indirectly related to global climate change [2]. Moreover, they disturb agricultural production worldwide, threaten food security [3], and hinder sustainable crop production. Several unfavorable consequences result in oxidative pressure because of the overaccumulation of ROS, free radicals (superoxide anion, hydroperoxyl radical, alkoxy radical, and hydroxyl radical), and nonradical molecules (hydrogen peroxide and singlet oxygen) [4, 5]. High-power initiation or electron switch reactions convert atmospheric oxygen (O_2) into somewhat reduced or activated species of molecular oxygen [6]. Although ROS accumulates in plants as a result of everyday cell metabolism, stress-induced overaccumulation critically damages essential cell elements together with lipids, carbohydrates, DNA, and proteins because of their exceptionally active nature [7].

ROS are oxygen-containing reactive species that are maintained at an optimum concentration by various antioxidant enzymes [8]. The major sites for ROS synthesis are chloroplasts, mitochondria, peroxisomes, endoplasmic reticulum, and plasma membranes [9]. In cells, several enzymatic and nonenzymatic antioxidant compounds act as ROS scavengers and are generated under a variety of stressful conditions [1]. Plants often withstand oxidative stress through several enzymatic antioxidants consisting of ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), dehydroascorbate reductase (DHAR), glutaredoxin (GRX), glutathione S-transferase (GST), oxidase-like alternative oxidase (AOX), peroxiredoxins (PRXs), nicotinamide adenine dinucleotide phosphate (NADPH), and thioredoxins (TRXs). Various nonenzymatic antioxidants are also involved in the maintenance of plants' performance under oxidative stress; these antioxidants include α-tocopherol, glutathione, phenolic acids, carotenoids, ascorbic acid, alkaloids, flavonoids, and nonprotein amino acids [10-12]. In plants, the antioxidant protection structure and ROS buildup maintain a balanced system [11]. An optimal ROS concentration facilitates the functioning of redox reactions and numerous pathways crucial for flora development and growth [13]. This transitional degree is achieved through the balance between ROS manufacturing and scavenging processes [4]. However, stress disturbs the ROS equilibrium, leading to cell destruction, programmed cellular death (PCD), and reduction in plant productivity [7].

During oxidative stress in plants, the function of ROS as supplementary messenger molecules is closely intertwined with downstream signaling pathways and transcriptional regulation. The growth features of a plant under stress are determined by a delicate balance between ROS as a secondary signaling molecule and ROS as causative agents for oxidative damage [1]. The signaling cascade of mitogen-activated protein kinase (MAPK) is structurally similar across species; this cascade activates cells' self-adjustment by transferring information from the environment to the nucleus [14]. In addition to their adverse actions, ROS function as supplementary messengers or signaling compounds, which transfer the indication to the nucleus through redox responses and the MAPK pathway to raise tolerance toward various abiotic stresses [9]. The role of ROS may first increase and then decrease in the reproductive phase of plant development, such as the initiation of flower buds till the maturity of reproductive organs. They mainly act as signaling cascades to manage various metabolic pathways during the adaptation of plants to stressful conditions [6, 15]. Therefore, ROS is vital for the proliferation and differentiation of plant cells, tissues, and organs [13]. In addition, H_2O_2 is a crucial element produced in the crops, such as rice, maize, mung bean, bitter orange, wheat, soybean, strawberry, basil, cucumber, and rapeseed under stressful conditions [16]. Moreover, in addition to ROS, reactive carbonyl species (RCS), reactive nitrogen species [17], and reactive sulfur species (RSS), play a key role in the development of abiotic stress tolerance in plants [18].

ROS has a crucial role in plants' life cycle and in the adaptation to abiotic stresses, which is a major concern because of global warming. In addition to applying ROS as signaling molecules, plants maintain their growth in the presence of ROS and shield themselves from the harmful effects of ROS [19, 20]. If ROS accumulates, it causes oxidative harm to nucleic acid molecules, membranes (lipid peroxidation), and other cellular components, leading to oxidative stress [6]. This review summarizes the mechanism of ROS production and elimination in plants' systems; moreover, it discusses the role of ROS during various developmental phases.

1.1 Biochemistry of ROS

Reactive oxygen species (e.g., OH, $O_2^{\cdot-}$, H_2O_2, and $^1O_2$) are activated or partially reduced forms of atmospheric oxygen [21]. These molecules are the dangerous byproduct of basic cell metabolism in aerobically respiring organisms [22] and are produced in many plant organelles, such as peroxisomes, chloroplasts, plasma membranes, and mitochondria [23]. Cellular ROS are produced from free radicals and nonradicals (Figure 1). Among the free radicals, peroxyl radical ($ROO\bullet$), $^\bullet OH$, $RO^\bullet$, and $O_2^{\bullet-}$ are widely studied, whereas among the nonradicals, O_2, ozone (O_3), and H_2O_2 are commonly studied [24]. A few different nonradical ROS, including hydroperoxides (ROOH), excited carbonyls (RO*), and hypochlorous acid (HOCl), are also observed in flowers [25]. Furthermore, reactive oxygen intermediates (ROI) are related to reactive oxygen molecules produced through the partial reduction of O_2; therefore, ROS consist of ROI in addition to O_2 and O_3 [26]. Moreover, a few acids, such as hypoiodous acid (HOI), HOCl, and hypobromous acid (HOBr), and radicals, such as semiquinone ($SQ^{\bullet-}$) and carbonate radical ($CO_3^{\bullet-}$), come under ROS

[27-29]. Three primary forms of ROS manufacturers have been detected in plants at distinctive cell loci: electron-transport chains in mitochondria and chloroplast, a few oxidases and peroxidases (lipoxygenase, NADH oxidase, xanthine oxidase, amine oxidase, glycolate oxidase, and NADPH oxidase), and photosensitizers consisting of chlorophyll molecules [30].

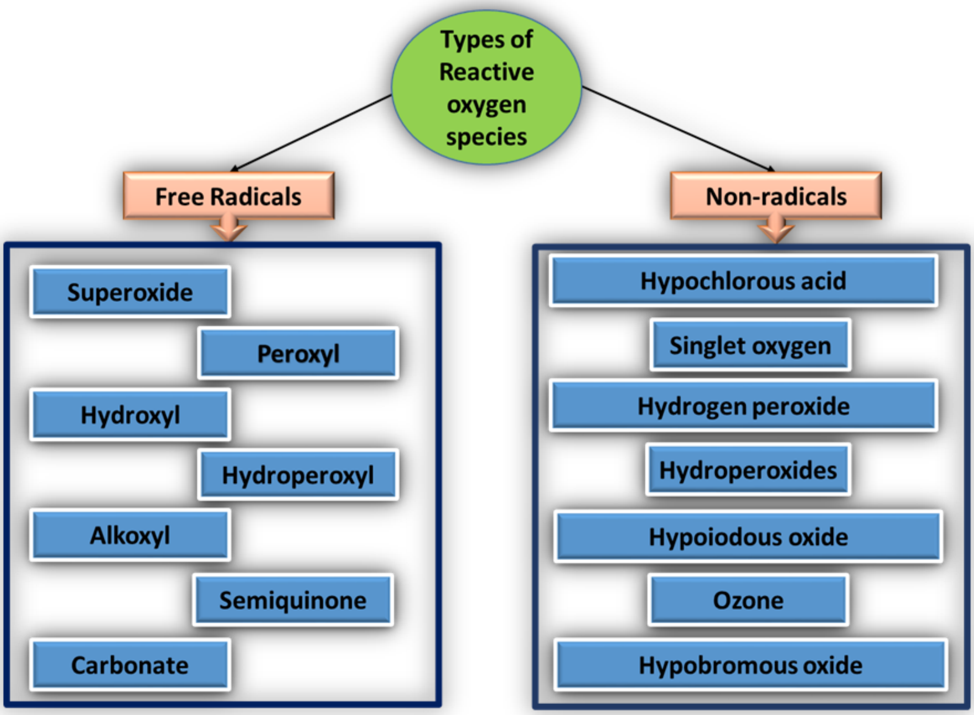

Figure 1 Forms of reactive oxygen species, the free radicals, and nonradical types.

1.2 ROS Production in Plants Under Abiotic Stress

Under abiotic stresses, ROS is synthesized in two ways: ROS generated as a result of metabolic activity interruptions (metabolic ROS) and ROS generated as a result of signaling, as ROS play a role in the abiotic stress signaling pathways (signaling ROS). Metabolic ROS alter the redox status of rate-limiting enzymes and control metabolic fluxes in the cell; this is known as flux manipulation. Therefore, ROS alters a type of metabolic reaction to oppose the outcome of stress [22]. Moreover, flux manipulation disturbs transcription and/or translation by changing the features of crucial regulatory proteins through ROS-induced redox modifications [31, 32]. However, signaling ROS is produced as a reaction to stress sensitivity by using stress sensors, e.g., cyclic nucleotide-gated channels triggered by heat stress [33]. It is mediated by calcium-stimulated and/or phosphorylation-stimulated respiratory burst oxidase homolog (RBOH) on the plasma membrane [34, 35]. Signaling ROS regulates the oxidation and reduction conditions of modulating proteins without delay, apart from regulating translation and transcription, ensuing in the initiation of an acclimation reaction that could lessen the effects of stress on metabolic rate and decrease the extent of metabolically formed ROS. Signaling and metabolic ROS may be formed at distinct subcellular parts (e.g., metabolic ROS inside the chloroplast and signaling ROS inside the apoplast). For example, H_2O_2 can be transported by aquaporins localized in the cell membrane, leading to long-distance oxidative damage and cell signaling regulation [36]. During abiotic stress, ROS is majorly produced at different cellular compartments [37-39]; the ROS production methods are described in Figure 2.

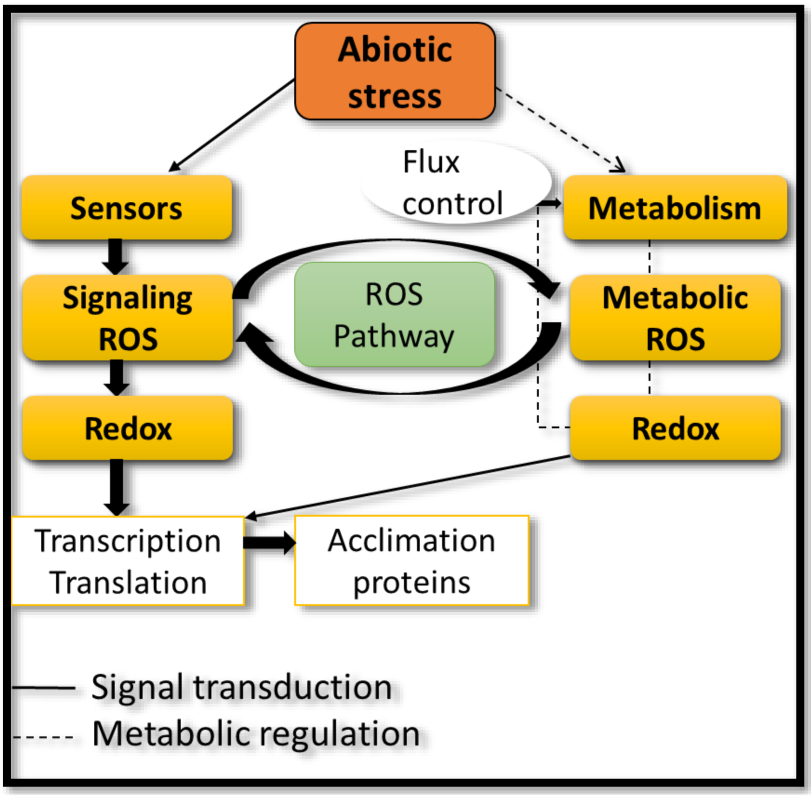

Figure 2 Two major methods of ROS production during abiotic stress in plants.

1.3 ROS-Induced Protein and Enzyme Modifications in Response to Abiotic Stresses in Plants

In addition to the regulation of transcriptional networks, ROS initiate irreversible or reversible adjustments of proteins and inflict flip changes for switch and control of plant metabolic rate. Proteins induced by ROS are essential for the alteration of the metabolic rate and gene expression under abiotic stresses. The post-translational adjustments induced by ROS are carbonylation, S-nitrosylation, sulfonylation, and glutathionylation [6].

Tryptophan (Trp) is oxidized to Trp hydroperoxide. This harmful product is quickly degraded into N-formylkynurenine and kynurenine (NFK), a method of protein alteration by ROS. This type of protein oxidation performs a critical role in photosynthesis regulation. Therefore, Trp365 oxidized to NFK inside the CP43 unit of PSII is related to excessive mild stress and elevated photo-inhibition [40, 41]. Tryptophan oxidation is additionally involved in glycine decarboxylase (essential enzymes in the photorespiration method involved in glycine deamination and oxidative decarboxylation) [42].

Carbonylation is an irreversible process and oxidizes residues, such as proline, arginine, threonine, histidine, and lysine [43]. Protein carbonylation can also be facilitated by subsidiary reactions of lipoperoxidation reactants with Cys and His residues [44]. Numerous mitochondrial enzymes, such as glycine decarboxylase, aconitase, and pyruvate dehydrogenase, are susceptible to deactivation by carbonylation and oxidation; therefore, inhibition of these enzymes by increased ROS production may inhibit the flow to the TCA cycle and reduce the cellular energy [45, 46]. In Arabidopsis, several chloroplast proteins, such as Rubisco, Cys synthase, and Asp kinase, are the targets of carbonylation in light-induced stress because of oxidation [47].

S-nitrosylation, a post-translational adaptation, is the covalent bonding of nitric oxide to the Cys thiol groups that can control certain proteins under stress. A study indicated that several enzymes involved in antioxidation, photorespiration, and respiration were S-nitrosylated under salt stress [48]. In plants exposed to low temperatures, the major S-nitrosylated proteins were linked to carbon breakdown [49]. Protein nitrosylation is vital for metabolic rate reprogramming, which is essential to maintain homeostasis in stress situations. For instance, nitrosylation can act as a negative controller, which is a crucial regulator under abiotic stress conditions [50].

1.4 ROS Scavenging: An Antioxidant Defense Mechanism

The antioxidant mechanism mitigates the aforementioned oxidative damage induced by ROS and is of two types: enzymatic and nonenzymatic antioxidants [51]. The antioxidant enzymes are localized in different subcellular compartments and include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and guaiacol peroxidase (GPX) (Table 1). In plants, naturally occurring phytohormones maintain the metabolic pathway under abiotic stresses. Melatonin is a phytohormone whose metabolite 4-hydroxymelatonin plays a pivotal role in the maintenance of polyamine levels in plant cells. A study reported that 4-hydroxymelatonin regulated ROS in eggplants exposed to nickel toxicity by maintaining polyamine levels; moreover, it improved the plants' physiology [52]. The endogenous activation of phytohormone translocation and breakdown may lead to homeostasis in plants. Brassinosteroids, a phytohormone, are steroidal, have polyhydroxylated sterol structure, and were first recovered from the flowers of *Brassica napus*. These hormones play a major role in several physiological and biochemical processes in plants, such as cellular development leading to seed germination, root and shoot growth, reproduction, and stress tolerance [53].

Table 1 List of the antioxidant families and their features.

Enzymatic antioxidants	**Location**	**Type**
Superoxide dismutase (SOD)	Peroxisomes, chloroplast, cytosol, Mitochondria	Direct-acting enzyme
Catalase (CAT)	Mitochondria, Peroxisomes, cytosol	Direct-acting enzyme
Xanthine oxidase	Mitochondria, cytoplasm, chloroplast, peroxisomes	Supporting enzyme
Glutathione peroxidase (GPx)	Mitochondria, cytoplasm, chloroplast	Direct-acting enzyme
Glutathione reductase (GR)	Mitochondria, cytoplasm, chloroplast, Endoplasmic reticulum	Direct-acting enzyme
Non-Enzymatic antioxidants	**Location**	**Type**
Carotenoids	Chloroplasts and other non-green plants	Large-molecule, Exogenous
Reduced Glutathione	Peroxisomes, chloroplast, cytosol,	Water-soluble,

	Mitochondria, vacuoles, apoplast	Endogenous
Vitamin C	Peroxisomes, chloroplast, cytosol, Mitochondria, vacuoles, apoplast	Water-soluble, Exogenous
Vitamin E	Mostly in membranes	Small-molecule, Exogenous

[51]

The nonenzymatic antioxidants comprise amino acids (AA), glutathione (GSH), α-tocopherol, carotenoids, phenolics, flavonoids, and proline (amino acid cum osmolyte) (Table 1). They not only protect cell components from damage but also play a vital role in plant growth and development by tweaking cellular processes like mitosis, cell elongation, senescence, and cell death [54]. For example, hydrogen sulfide (H_2S) strengthens the plant's defense mechanism by linking it with other signaling molecules, such as polyamines. Therefore, it enhances photosynthesis, limits the absorption of metals, such as cadmium, and inhibits ROS accumulation in Fenugreek plant cells [55].

1.5 ROS in Rapid and Widespread Systemic Signaling

The ROS wave is a cell-to-cell self-propagating handle of ROS generation facilitated by respiratory burst oxidase homolog D (RBOHD) [56, 57]. The activation of this protein increases ROS production in cells, leading to ROS buildup till the apoplast level. This is detected by nearby cells, leading to increased ROS production through their RBOHD proteins. This, in turn, activates neighboring cells, leading to increased ROS generation throughout the plant [34].

Although the ROS wave is activated by numerous abiotic and biotic stresses and is vital for acclimatization to different abiotic stresses [58-60], it does not contribute to the systemic response. The ROS wave is a basic signal that alarms cells and tissues of upcoming stress and functions together with other signals that carry specific information [35, 61, 62].

One of the newly discovered functions of the ROS wave is to facilitate the stomatal response of the plant to different stresses [62, 63]. In reaction to light stress influencing a single leaf, the ROS wave coordinates a closure reaction from the whole plant stomata [59]. In reaction to heat stress on a single leaf, the ROS wave induces a stomatal opening reaction from the whole plant [64]. The extensive control of stomatal opening not only influences water shortage, leaf cooling (through transpiration), and CO_2 trade rates (required for photosynthesis) but may also influence hydraulic waves and their assembly. Therefore, the control of stomatal opening in plants to different medications highlights the crucial role of the ROS wave in activating and planning plant acclimatization. A study revealed that the inhibition of the ROS wave and systemic stomatal reactions avoids the acclimatization of plants to light stress [59].

Metal stress, such as cadmium (Cd), causes ROS overproduction, leading to the inhibition of plant growth. The use of new technology, plant smoke water (PSW), has been reported in the seedlings of carrots [65], *coriandrum sativum* [66], *Triticum aestivum*, and *Isatis indigotica* [67], as well as in the plants of *Tulbaghia ludwigiana* [68] growing under abiotic stresses. It consists of a specific type of lactone known as butanolide, 3-methyl-2H-furo [2,3-c] pyran-2-one, fused with a pyran ring and acts in association with karrikinolide (KARs). The KARs (KAR1 to KAR6) are produced by the ignition of plant materials and released in nature as organic compounds. KAR1 promotes the production of enzymatic antioxidants, which ultimately activate compounds, such as proline, CAT, and SOD, thereby improving the plants' tolerance under abiotic stresses. The use of PSW restricts the accumulation and activity of ROS to plant metabolism [66].

1.6 Molecular Roles of Ca^{2+}-Dependent Protein Kinase During Abiotic Stress Conditions

In plants, the Ca^{2+}-dependent protein kinase (CDPK) mechanism is involved in a variety of intracellular signaling pathways that control stomatal activity and plant adjustment to different environmental stresses, such as drought, salt, and cold. A study reported that the CDPK mechanism could be involved in signal transduction that uses calcium as a second messenger [26]. Certain CDPKs involved in abiotic stresses have been studied using Arabidopsis as a plant model [69]. Of the CDPKs, CPK3, and CPK6 act as positive controllers of the abiotic stress reaction. The salt-sensitive phenotype, CPK3 mutant, is linked with the vacuole and the plasma membrane. CPK3 controls the abiotic stress signaling pathway independent of the MAPK-mediated signaling pathway [70]. Moreover, plants that overexpress CPK6 have a higher tolerance to drought and salt stresses, while CPK6 mutants lack evident phenotypes. Although CPK6 acts as a positive controller of salt and water stress tolerance, it is practically unnecessary in abiotic stress indication in Arabidopsis [71]. Moreover, in Arabidopsis, CPK10 is intricate in tolerance to drought stress.

Several CDPKs are involved in tolerance to abiotic stresses in different plant species, such as *Brassica napus* [72], Betula platyphylla [73], Fenugreek [55], and rice [74]; all these CDPKs have already been studied in Arabidopsis, which is a model plant species in particular. Because of their participation in ROS detoxification, CDPKs perform a substantial role in modulating abiotic stress tolerance. These findings suggest that CDPKs increase abiotic stress tolerance through distinct processes. In addition, opposing functions have been reported for CPK21 and CPK23 in abiotic stress signaling. This implies that the system that controls CDPK-mediated abiotic response to stress is complicated. The settlement of the complex regulatory systems participating in CDPK-mediated signaling to environmental stresses may be assisted by abiotic stress signaling pathways.

1.7 Abiotic Stresses Are Arbitrated by Overlapping Arrays of MAPKs

The MAPK cascade is a major signaling pathway associated with abiotic stresses in plants. This cascade links external stimuli to a variety of cellular responses. Different abiotic stresses cause both common and specific impacts on plant development and advancement. Therefore, plants may possess more stress insights and signal transduction trails, which might meet at diverse stages. Moreover, these kinases act as key regulators in the transduction of various types of stress signals. A study indicated that the MAPK cascade is involved in the cross-talk between the abiotic stress pathways in plants [75], thereby protecting against oxidative stress. Initiation of ROS-induced MAPK proved that ROS acts upstream of MAPK [76].

In numerous species, MAPK cascades are involved in signaling pathways initiated by abiotic stresses, such as osmotic shock, cold, touch, UV, wounding, salt, heat, and heavy metals [75]. Most studies evaluating the role of MAPKs in abiotic stress signaling pathways have used Arabidopsis and indicated that MPK6 and MPK4 are triggered by cold, dryness, external touch, damage, and salt [77]. Moreover, MPK3 is induced by osmotic stress [78], whereas MEKK1 is transcriptionally activated by stresses, such as salt, dry spell, cold, and harm; it also intervenes in flagellin (protein of flagellum) signaling through the activation of MKK4 and MKK5. A functional study in yeast proposed that MEKK1 is the upstream regulator of MKK1 and MKK2 and the downstream regulator of MPK4. This MAPK cascade composed of MEKK1, MKK2, and MPK4/MPK6 is involved in cold and salt stress [76]. After the confirmation of MKK2 in yeasts as the activators of MPK4 and MPK6, it was concluded that MKK2 could be stimulated by cold and salt stress in transitory protoplast tests [79]. Therefore, MKK2null mutant plants are not affected phenotypically under natural circumstances but are affected by cold and salt stress.

Plants with overexpression of MKK2 are more tolerant to cold and salt stress, with alterations in 152 qualities. In MKK2 subordinate mode, MEKK1 can actuate MPK4 and MPK6; moreover, MKK1 may be included in abiotic stress signaling because MKK1 is triggered by damages caused by cold, dry spell, and salt stress and can phosphorylate MPK4 [80]. Plants' self-resistance against pathogens is the best tool to maintain their growth at the molecular level [72]. In a study, the resistant lines of *Brassica* exhibited a stable and elevated gene expression and downregulated the brassinosteroids (BR) pathway and relevant genes, i.e., *WRKY22* and pathogen responsive gene1 (*PR1*). The invading pathogens were restricted with the upregulation of the calcium ion chain. The transcription factors MEKK2 and MKS1 of MAPK activate the plant defense machinery against pathogens in Brassica. Therefore, the PR genes regulate the defense against pathogens in Brassica.

2. Conclusions

Abiotic stresses affect the development and growth of plants worldwide. A major impact of abiotic stress is the imbalance between ROS production and antioxidant defense mechanism, leading to an increased accumulation of ROS and oxidative stress in plants. Scientific research has elucidated the cellular, physiological, metabolic, and molecular processes of abiotic stress responses and adaptation to improve long-term agricultural production. This study summarized the findings related to ROS sources, mechanisms of ROS production, and ROS accumulation in various plant parts. The pathways involved in ROS removal from plant parts and the key enzymatic and nonenzymatic antioxidant molecules in ROS scavenging have also been discussed.

3. Future Aspects

The recent advancements in genetic and molecular tools have paved the way for improvement in plant stress tolerance. The emergence and development of transgenic plants expressing genes encoding antioxidant enzymes have improved abiotic stress reactions and antioxidant enzyme potential. The identification of candidate genes that can substantially improve transgenic plants' tolerance and yield in stressful environments is crucial. Furthermore, to achieve similar goals, chemical priming is a viable alternative to genetic engineering because it often involves the regulation of the antioxidant defense system. Synthetic biology initiatives, such as genomics, transcriptomics, and metaproteomics, may assist in the development of new methods for stress tolerance. For example, RNAseq is the latest technology with a deeper insight into the molecular interactions at the transcriptomic level and unravels the functional genes or gene expression profile of an organism under differential conditions. To define critical and stress-related regulatory bodies, genes, proteins, and metabolites, as well as the combination of these strategies should be used. Furthermore, stress-tolerant genotypes can be improved by the identification and manipulation of ROS-detoxifying regulators. Cutting-edge genome-editing tools, such as CRISPR/Cas could aid in the modification of the genome by growing mutant plants with one or more genes for appropriate plant growth, as well as by improving the antioxidant defense monitoring system. Speed breeding is a relatively new technique for boosting plant growth in controlled environments. Therefore, genetic engineering could be coupled with speed breeding to develop transgenic plants with improved antioxidant apparatus. Such an apparatus enhances stress tolerance in plants, which would lead to increased agricultural production and food security.

Author Contributions

The idea of manuscript was planned by BR. The basic literature was collected and first draft was prepared by AM and UA edited the draft. FA and FB collected and compiled the information in the tabulated and pictorial forms. SH edited the final draft and BR approved the final version of the manuscript. All the authors have read and approved the submission of manuscript.

Competing Interests

The authors have declared that no competing interests exist.

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