

Review

ROS Homeostasis and Plant Salt Tolerance: Plant Nanobiotechnology Updates

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Abstract: Salinity is an issue impairing crop production across the globe. Under salinity stress, besides the osmotic stress and Na⁺ toxicity, ROS (reactive oxygen species) overaccumulation is a secondary stress which further impairs plant performance. Chloroplasts, mitochondria, the apoplast, and peroxisomes are the main ROS generation sites in salt-stressed plants. In this review, we summarize ROS generation, enzymatic and non-enzymatic antioxidant systems in salt-stressed plants, and the potential for plant biotechnology to maintain ROS homeostasis. Overall, this review summarizes the current understanding of ROS homeostasis of salt-stressed plants and highlights potential applications of plant nanobiotechnology to enhance plant tolerance to stresses.

Keywords: salt stress; ROS homeostasis; chloroplasts; mitochondria; the apoplast; plant nanobiotechnology



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1. Introduction

According to the Food and Agriculture organization (FAO) report, billions of people are still facing food shortages [1]. It is estimated that, compared to the yield of 2011, the demand for food will increase 40% in 2030 [1]. Agricultural production is affected by many environment stresses, including salinity stress. Salt stress is one of the major abiotic factors which negatively affect crop yield. Almost 7% of the Earth's land and 20% of the total arable area is affected by salinity [2]. Salinity induces the accumulation of ROS (reactive oxygen species) in plant cells. ROS in plant cells mainly include •O₂[−] (superoxide anion radical), H₂O₂ (hydrogen oxide), •OH (hydroxyl radical), and ¹O₂ (singlet oxygen), which are mainly generated from chloroplasts, mitochondria, peroxisomes, and the cell apoplast [3,4]. Compared with the ROS generated in mitochondria under light conditions, the level of ROS produced by chloroplasts is ten times higher [5].

ROS in plant cells is a double edged sword, which damages cells at higher concentrations, while acting as a signal molecule at lower concentrations. ROS have very important roles in plant cell cycle regulation [6] and programmed cell death [7], and may interact with other signaling molecules, including salicylic acid [8], jasmonic acid, ethylene [9], NO [10], and Ca²⁺ [11]. The interaction of ROS and ethylene has been reported in rice under salt stress [12]. ROS can also regulate the redox state in chloroplast stroma. Excessive accumulation of ROS leads to toxic effects on plants under stress. A high level of ROS (especially H₂O₂) damages DNA [13]. ROS induces crosslinks, base modification or deletion, and distorts genomic stability [14,15]. In this case, plants have a set of antioxidant mechanisms, including enzymatic [16] and non-enzymatic [17] systems to protect cells from the toxicity of reactive oxygen species. Enzymatic systems are composed of a set of SOD (antioxidant enzymes including superoxide dismutase), POD (peroxidase), CAT (catalase), and APX (ascorbate peroxidase), etc. Non-enzymatic systems, for example, include small organic molecules such as glutathione [18], mannitol [19], and melatonin [20,21], and can effectively scavenge ROS in plant cells. However, the energy cost of the synthesis of such compounds

and compatible solutes is high. New approaches such as using plant nanobiotechnology to modulate ROS homeostasis to improve plant salt tolerance could be an alternative way. Nanomaterials with ROS scavenging ability could directly modulate ROS homeostasis in plants. For example, cerium oxide nanoparticles with ROS scavenging ability enabled plant tolerance to salinity [22], high light [23], temperature stress [23], and drought [24]. Alternatively, some nanomaterials could modulate the gene expression level of antioxidant enzymes to maintain plant ROS homeostasis under stresses such as salinity. Details will be discussed in the following sections.

In this review, we discuss the main ROS generation sites in plants under salt stress, the importance of the homeostasis between ROS production and scavenging, and its relationship with plant salt tolerance. More importantly, a plant nanobiotechnology approach for modulating stress tolerance under hostile environments such as salinity is discussed in this review.

2. ROS Generation in Plants under Salt Stress

2.1. ROS in Mitochondria

Mitochondria are one of the generation sites of ROS. A previous study showed that about 1–5% of oxygen consumption is due to H_2O_2 generation [25]. At the RETC (respiratory electron transport chain), complexes I and III are considered as directly related to ROS production (Figure 1). Interestingly, it seems that the complexes in mitochondria are very sensitive to salt stress, suggesting that protection of these sites might be able to reduce ROS generation [26]. The mitochondria-located NAD^+ channel, NDT2, is considered the regulator of mitochondrial ROS production. NAD^+ , the electron acceptor of the RETC, plays an important role in ROS generation [27]. UCP (uncoupling protein) could also decrease ROS accumulation through a negative-feedback mechanism which uncouples electron transport and ATP production [28]. UCP-related improvement of tobacco plant salt tolerance was enhanced through decreasing ROS production and improving photosynthesis rate [29]. Mitochondria-located ABC1K10a was reported as an atypical kinase that could regulate ROS accumulation and plant salt stress tolerance. ABC1K10a was induced by salt treatment, and the lack of this gene leads to sensitivity to salt stress and oxidative damage [30]. Plant salt tolerance is considered to be associated with the function of mitochondria, since the ROS generated in mitochondria enhanced the expression of antioxidant enzyme in salt-stressed *Arabidopsis* [26,31,32]. A trojan peptoid (pepto Q) was reported to modulate retrograde signaling to the nucleus to enable strong expression of mitochondrial Mn-SOD, thus alleviating salinity stress in tobacco plants [33].

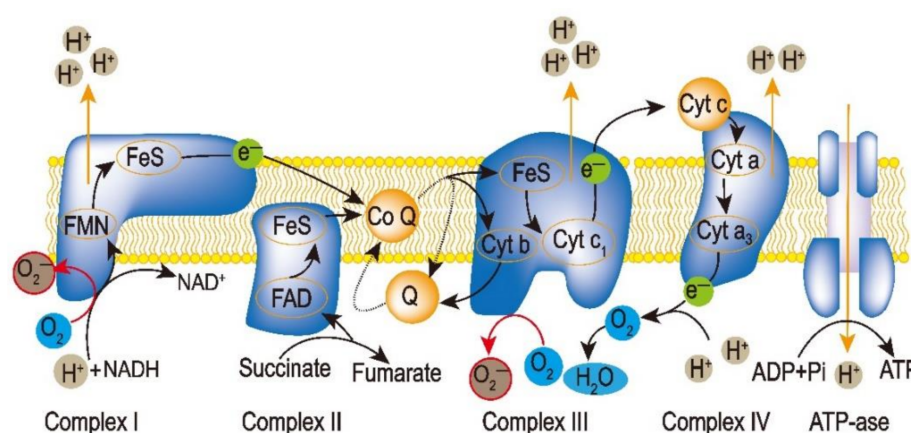


Figure 1. ROS generation along the RETC pathway. Complex I and III in the RETC are the major sites of $\bullet\text{O}_2^-$ production. The black arrows show the electron pathway, and the red arrows represent $\bullet\text{O}_2^-$ generation.

GABA (aminobutyric acid), a shunt pathway, starts with glutamate decarboxylase (GAD) decarboxylating 2-oxoglutarate into GABA. Consequently, GABA takes part in respiration as a substrate. Recently, the effect of salt stress on the respiratory metabolism of wheat plants was reported [34]. The results reveal that the seedlings accumulated sodium while photosynthesis and biomass were reduced, suggesting that wheat mitochondrial respiration alters its source under salt stress. Salinity decreases the capacity for cyclic operation of the TCA cycle. The results provide evidence for the activation of the GABA shunt pathway during salt exposure. Through succinate production, the increased GABA shunt activity would provide an alternative carbon supply into the TCA cycle [35]. In this shunt, plants may reduce ROS generation.

The NADH (nicotinamide adenine dinucleotide) dehydrogenase complex (complex I) is the main electron entry site of the electron transport chain. Carbonic anhydrases CA1 and CA2 constitute the plant-specific “carbonic anhydrase domain” of mitochondrial complex I. It was reported that the mutation of the complex I subunit of the respiratory chain leads to the decrease in or loss of the activity of complex I [36]. The dysfunction of complex I is related to the increase in the level of superoxide $\bullet\text{O}_2^-$ [37]. Additionally, cells with pathogenic mutations in mitochondrial DNA (mtDNA) produce excess ROS, especially when complex I is damaged [38].

2.2. ROS in Chloroplasts

Chloroplasts are very important organelles in plants, since the photosynthetic electron transport chain on thylakoid membranes is crucial for plant photosynthesis. Chloroplasts act not only as organelles responsible for photosynthesis, but also as sensors of environmental stresses such as high light, UV radiation, heat, cold, or drought. They are also the main source of ROS generation in plants under stress, particularly light stress. Through the photosynthetic electron transport chain (PETC), both PSI (photosystem I) and PSII (photosystem II) produce ROS. PSII oxidizes O_2 to $^1\text{O}_2$. Under stress conditions, electron transport relies on a different pathway—the Mehler reaction [39]. In this pathway, electrons are transported from Fd to O_2 , rather than NADP^+ (nicotinamide adenine dinucleotide phosphate), and produce $^1\text{O}_2$ which may be converted to other kinds of ROS, including hydroxyl radicals, hydrogen peroxide, and singlet oxygen. Furthermore, there are also some other ways to produce ROS in chloroplasts (Figure 2). Excited chlorophyll jumps to the ground state in chloroplasts, where it transports energy to oxygen and produces singlet oxygen [40].

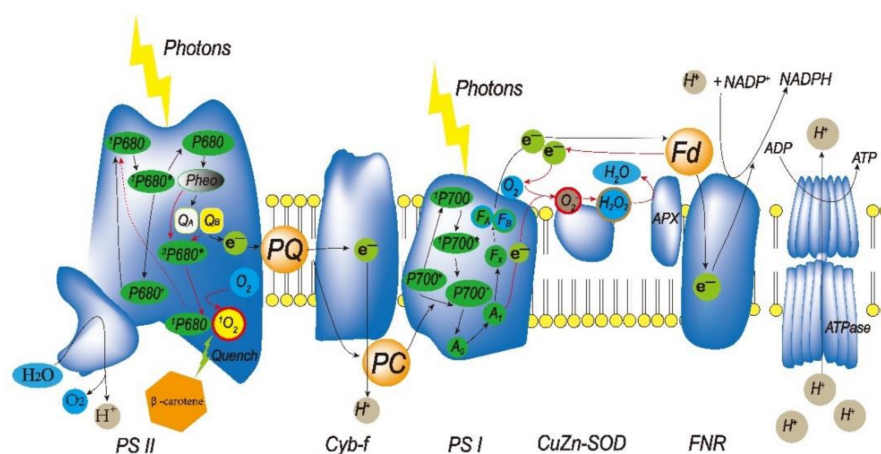
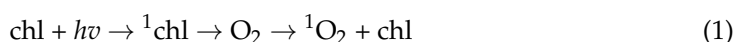


Figure 2. ROS generation in chloroplast thylakoids. At the photosynthetic electron transport chain, singlet oxygen is generated in PSII and $\bullet\text{O}_2^-$ is generated in PSI. Fd, ferredoxin; FNR, ferredoxin-NADP reductase; PC, plastocyanin; and PQ, plastoquinone.

Our previous study demonstrated that salinity stress induces ROS generation in chloroplasts and is a light-dependent mechanism [41], suggesting the importance of chloroplast ROS in modulating K^+ homeostasis, and thus, plant salt tolerance. After stress imposition, many electron acceptors were destroyed in the chloroplasts; however, import rate was limited [42]. Physiological processes in chloroplasts were closely related to the ROS generation in mitochondria. It was evident that PSII had a more efficient recovery rate after damage compared to PSI [43]. Furthermore, reducing elongation factor G (EF-G) may alleviate the high ROS level produced by the catalase/peroxidase double knockout mutant. Under strong light, EF-G and EF-Tu inhibit the *de novo* synthesis of proteins required for PSII repair. These reactions may prevent excessive oxidation caused by light and electron transport and promote redox homeostasis [44]. Soybean plants with GmEF4 overexpression showed significantly higher biomass and lower H_2O_2 and $\bullet O_2^-$ content than the control plants with empty vectors under salinity stress [45], suggesting a possible link between elongation factor and the redox states of the chloroplasts in salinity-stressed plants. The role of elongation factors in modulating chloroplast ROS homeostasis in plants under salt stress may be an interesting topic for further study.

A previous study showed that chloroplast ROS induced K^+ efflux by regulating non-selective cation channels (NSCC) in wheat leaf mesophyll cells under salinity [46]. Interestingly, researchers found that flavodoxin may decrease salt-induced ROS accumulation while having no beneficial effect on plant salt tolerance [47], suggesting a possible confounding effect within the plants. The Trx (thioredoxin) system has been demonstrated to target the enzymes, including sAPX (stroma ascorbate peroxidase), Prx (peroxiredoxin), MDHAR (monodehydroascorbate reductase), DHAR (dehydroascorbate reductase), and GST (glutathione-S-transferase), by regulating their redox state and activity to maintain the ROS homeostasis in the chloroplast [48].

Studies have shown that the production of mitochondrial ROS may be triggered by signal molecules, such as malate, transmitted from chloroplasts [49]. MOD 1 (MOSAIC DEATH 1) encodes the ACP (chloroplast enzyme enoyl-acyl carrier protein) reductase. In MOD1 mutants, mutations in the coding gene suppressors of MOD1 (SOM) associated with mitochondrial complex I or excessively enlarged mitochondria reduce the production of mitochondrial ROS (mROS) oxidase AOXs (alternative oxidases) and inhibit the phenotype of MOD1 and mROS production. This evidence indicates that there seems to be a pathway related to ROS between chloroplasts and mitochondria. Plastidial NAD-dependent malate dehydrogenase (pNAD-MDH), DiT1 (chloroplast dicarboxylate transporter 1), and mNAD-MDH1 (mitochondrial NAD-dependent malate dehydrogenase 1) are three key genes that encode malic acid to shuttle between chloroplasts and mitochondria. As mentioned above, the MOD1 mutant has a high ROS accumulation tendency. Excess NADH in the chloroplast can be oxidized by pNAD-MDH to produce malate. Then, the produced malate can be exchanged for OAA (oxaloacetate) through the DiT1 transporter and be introduced into the mitochondria. Furthermore, malate is oxidized in mNAD-MDH1 to produce NADH as a substrate of complex I, to produce mROS. This redistribution of reducing equivalents is called the malate cycle, which mediates energy homeostasis in cells [50]. Furthermore, malate could be oxidized by mNAD-MDH1 to produce NADH, which can serve as the RETC substrate to generate mROS. Overall, these results call for more fundamental research to understand the role of chloroplast ROS and the possible network with other signaling events in plant salt tolerance.

2.3. ROS in the Apoplast

Apoplast refers to a system composed of cell walls, interstitial spaces, and ducts on the periphery of plant cell protoplasts. The apoplast represents the first barrier between cells and the surrounding environment [51]. Many physiological and biochemical reactions occur in the apoplast, such as signal transduction and water transport [52]. Upon the onset of stress, the signal molecules involved in the early stages of stress response are mostly Ca^{2+} and ROS such as 1O_2 , O_2^- , H_2O_2 , and $\bullet OH$. Ca^{2+} outside the cytoplasm activates

NADPH oxidase to generate H_2O_2 in the apoplast. Hydrogen peroxide acts as a second messenger to activate calcium-dependent protein kinase (CDPK) and mitogen-activated protein kinase (MAPK) pathways. In addition, extracellular Ca^{2+} flows from the apoplast into the cytoplasm, activating CDPK to trigger ROS signal transduction and regulate Ca^{2+} , thereby developing tolerance to abiotic stress [53].

Besides the mitochondria and chloroplasts, the apoplast is also one of the ROS generation sites [54]. Extraplasmic active ROS are produced by several types of enzymes, such as oxalate oxidase, lipoxygenase, and amine oxidase, among which cell wall peroxidase and plasma membrane NADPH oxidase are the most recognized [55]. Extraplasmic peroxidase belongs more to the class III peroxidases, which are responsible for the formation and degradation of ROS induced by stress [56]. Although a relatively small amount of ROS is located in the apoplast, these ROS play a very important role in plant growth and development, and its response to external stress [57].

Under abiotic stress, not only ROS but also certain proteins, peptides, and hormones are produced and accumulated in the apoplast [58]. For example, the accumulation of H_2O_2 leads to a tolerance response or programmed cell death, which also depends on the level of polyamines in the cell [59]. Under salt stress, plants secrete spermidine into the apoplast, which can be further oxidized by apoplast polyamine oxidase to produce H_2O_2 . Under salt stress, the accumulation of extracellular H_2O_2 and $\bullet\text{O}_2^-$ produced by NADPH oxidase increased the activity of peroxidase (POD) and catalase (CAT) in wheat [60]. An h-type thioredoxin (*OsTRXh1*) in rice was shown to be induced and expressed by salt stress to regulate the redox state of the apoplast in rice. Compared with wild-type plants, the plants exhibiting both the knockout and overexpression of *OsTRXh1* produced more hydrogen peroxide in the apoplast, while plants with *OsTRXh1* overexpression produced less hydrogen peroxide under salt stress. More efforts are needed for better understanding of the relationship between apoplastic ROS and the matrix in the apoplast, including proteins and hormones in the apoplast in plants under salt stress, and its role in plant salt tolerance [29].

2.4. ROS in Peroxisomes

Peroxisomes are an organelle widely found in higher plant cells and are an important site for producing different signaling molecules, including H_2O_2 , $^1\text{O}_2$, O_2^- , and $\bullet\text{OH}$. Peroxisomes are one of the main locations where plant cells produce H_2O_2 , and have different pathways [61,62]. Photorespiration is the most efficient pathway to produce H_2O_2 , which mainly occurs in peroxisomes. GO (glycolate oxidase) is one of the key enzymes in the photorespiratory cycle. In this cycle, H_2O_2 production rate is one-fold greater than in chloroplasts, and 50-fold greater than in mitochondria [63]. NADH/NADPH and xanthine oxidase can catalyze O_2 produced in peroxisome membranes and the peroxisomal matrix, respectively. $\bullet\text{OH}$ can be produced in peroxisomes through the Fenton reaction [64]. The Fenton reaction can also cause the production of $^1\text{O}_2$ in peroxisomes [52].

An enzyme system in peroxisomes is used to scavenge ROS [65]. The ASA—GSH (ascorbate-glutathione) cycle also maintains H_2O_2 concentration in peroxisomes [66]. SOD is a large peptide chain metal enzyme involved in the scavenging of superoxide free radicals, and it can be divided into three categories: Cu/Zn-SOD, Mn-SOD, and Fe-SOD. Glutathione transferase in the peroxisomes can not only remove H_2O_2 , but also relieve the toxicity of reactive oxygen species [67].

A previous study showed that MAP KINASE17 (MPK17), as a negative regulator of peroxisome division, plays a role in peroxisome division when *Arabidopsis* is under salt stress [68]. At the same time, the author also found that peroxisome cleavage factor, PEROXISOME AND MITOCHONDRIAL DIVISION FACTOR 1 (PMD1), is a regulator of peroxisome division under the induction of salt and binds to actin [69]. Peroxisomes are known to respond to salt stress by varying degrees, which is related to the ascorbate glutathione cycle [70]. A previous study [71] also revealed that the activities of catalase (CAT), peroxidase (POD), and ascorbic peroxidase (VC) are all increased with the increase

in salt concentration. Furthermore, studies have shown that the peroxisome membrane protein from the PEX11 family is involved in regulating the number and size of peroxisomes in plant cells [72]. Although the overexpression of peroxin 11e (PEX11e) increases the number of peroxisomes [73], it does not increase the activity of peroxisomes, nor plants' tolerance to salinity stress. In peroxisomes, obtaining information on the key proteins modulating ROS level to tune plant salt response, especially the tolerance, deserves more effort [74].

3. ROS Scavenging in Plants

3.1. Enzymatic Scavenging System

Protection of chloroplasts from ROS accumulation is very important for stress tolerance in plants. Superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) constitute an efficient ascorbate–glutathione cycle (ASA–GSH, Figure 3), which is a part of the enzymatic antioxidant system of plants [75–79]. In chloroplasts, a major ROS-scavenging pathway in plants is the water–water cycle (WWC). WWC can protect enzymes in chloroplasts and PSI from ROS and dissipate excess light energy in plant cells [80].

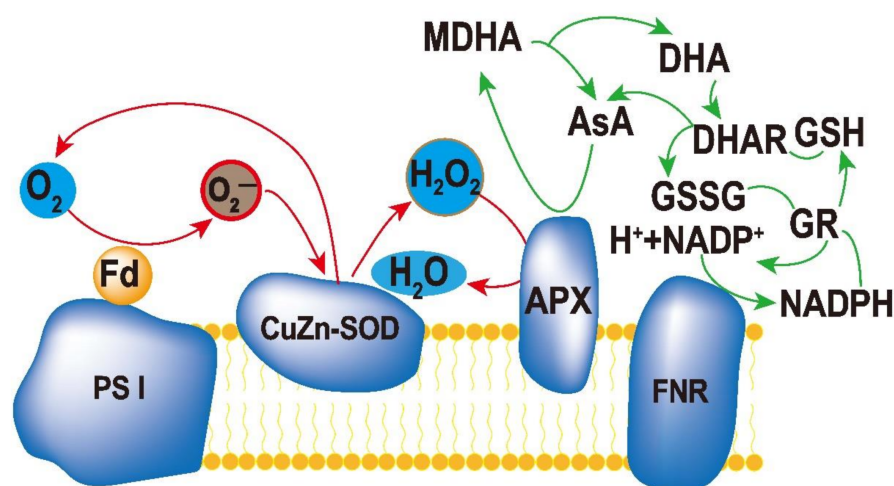


Figure 3. Ascorbate–glutathione cycle in plant cells. The reduced form of ascorbate (Asc) is oxidized to monodehydroascorbate (MDHA), which can either be reduced by monodehydroascorbate reductase (MDHAR) to Asc, or react to dehydroascorbate (DHA). DHA can be reduced by dehydroascorbate reductase (DHAR) to Asc. The reduced form of glutathione (GSH) is oxidized to glutathione disulfide (GSSG), which is reduced by glutathione reductase (GR) to GSH. During the reduction of MDHA and GSSG, the electron acceptor NADP is regenerated.

- (1) $2\text{H}_2\text{O} \rightarrow 4[\text{e}^-] + 4\text{H}^+ + \text{O}_2$ (The photolysis of H_2O in PSII);
 - (2) $2\text{O}_2 + 2[\text{e}^-] \rightarrow 2\text{O}_2^-$ (Photoreduction of O_2 in PSI);
 - (3) $2\text{O}_2^- + 2\text{H}^+ \rightarrow \text{H}_2\text{O}_2 + \text{O}_2$ (SOD catalyzes O_2^- disproportionation);
 - (4) $\text{H}_2\text{O}_2 + 2\text{AsA} \rightarrow 2\text{H}_2\text{O} + 2\text{MDA}$ (APX catalyzes ASA reduction H_2O_2);
 - (5) $2\text{MDA} + 2[\text{e}^-] + 2\text{H}^+ \rightarrow 2\text{AsA}$.
- Total: $2\text{H}_2\text{O} + \text{O}_2^- \rightarrow \text{O}_2 + 2\text{H}_2\text{O}$.

A previous study indicated that optimum exogenous selenium enhanced the activity of POD and APX, which ultimately protected chloroplasts from auto-pepsia and resulted in a higher photosynthesis rate in maize crop grown under salt stress [81]. Transcriptomic and metabolomic analyses revealed that genes encoding LEA (late-embryogenesis-abundant) proteins are up-regulated under salt stress. It is evident that LEA proteins could enhance the antioxidant enzyme activities [82]. It is evident that halophytes have a stronger enzymatic antioxidant system (CAT and SOD), and this capability has been used as a selection criterion for salt-tolerant varieties [83–85]. A previous study reported that SOD converted salt-induced ROS into H_2O_2 , and APX maintained H_2O_2 at an optimum level

as a signal molecule [86]. The study also revealed the importance of PaSOD (superoxide dismutase) and RaAPX (ascorbate peroxidase) gene in plant salt tolerance, which could enhance the biosynthesis of compatible solutes and lignin. Overexpression of mitochondria-located protein 4-hydroxybenzoate polyprenyl diphosphate transferase (PPT) increased the ubiquinone content and enhanced the plant's salt-tolerance. Glutathione peroxidase (GPX) is an important component of the ASA–GSH cycle. The ASC (ascorbate)/GSH cycle is also an important antioxidant system in plants. A study on the glycophyte *Brassica juncea* and the halophyte *Sesuvium portulacastrum* indicated that the ASC/DHA (dehydroascorbate) and GSH/GSSG (glutathione disulfide) ratios were maintained in *B. juncea* but increased in *S. portulacastrum* [85]. By using OsGPX3-RNAi silenced plants, researchers found that GPX had an important role in plant CO₂ assimilation, biomass accumulation, and PS II protection under salt stress [87]. Interestingly, OsGPX3-RNAi silenced plants displayed no observable difference with untransformed plants in ROS accumulation, suggesting a complex role for GPX in plant response to salt tolerance [88]. In addition, the gene related to alternative oxidase (AOX) located in the inner membrane of mitochondria has been reported, and is believed to be involved in the response to abiotic stress [89].

3.2. Non-Enzyme Scavenging System

Several highly toxic ROS, such as ¹O₂ and •OH, cannot be scavenged by enzymatic antioxidant systems. Thus, plants depend solely on non-enzymatic means to scavenge those ROS. Generally, ROS lead to lipid peroxidation [90,91] and an increase in monodehydroascorbate (MDA) content [92]. Overexpression of IbWRKY2 induced MDA accumulation in plant cells, coupled with ROS-scavenging genes up-regulation, resulting in improved salt tolerance [18]. Carotenoids and α-tocopherol, as components of non-enzymatic antioxidant systems, can also scavenge ROS. For example, carotenoids are distributed in the thylakoid pigment–protein complexes in close proximity to chlorophylls near the potential sites of ¹O₂ formation. Furthermore, melatonin is considered a small molecule that may scavenge ROS, and the “manager” in plants under salinity stress. For example, a previous study found that the gene related to the melatonin synthesis enzyme *N*-acetylserotonin *O*-methyltransferase (MzASMT9), which is localized in the chloroplast, is upregulated by salt stress [93]. Additionally, MTs (metallothioneins) interact with AtV-DAC3 (mitochondrial membrane voltage-dependent anion channels) and regulate ROS homeostasis [45]. Flavodoxin is known as an electron transfer shuttle, and can drive reducing equivalents away from oxygen, preventing ROS generation [94]. However, interestingly, compared with the enhanced tolerance to drought, excess irradiation, temperature stress, and iron starvation, overexpression of the plastid-targeted cyanobacterial flavodoxin in tobacco plants failed to result in increased salt resistance [95].

4. Plant Nanobiotechnology Approach to Modulating ROS Homeostasis and Plant Salt Tolerance

In recent years, researchers have begun to focus on the relationship between nanomaterials and plants, including its existence in the food chain and its application to crops as pesticides or growth regulators. Natural soil contains a small number of nanoscale particles, which have been shown to be accumulated by plants and show different characteristics from that of other metal ions [95]. Nanomaterials with different surface characteristics have different effects on plants, and researchers change the properties of nanomaterials by coating them with different materials. Nanoenzymes are defined as a class of inorganic nanomaterials with antioxidant enzyme activity [96]. In recent years, polyacrylic-coated cerium oxide nanoparticles (nanoceria) as a kind of nanoenzymes have been found to be effective in scavenging •OH. As mentioned above, •OH is the most harmful ROS, and has strong oxidative ability and a short lifetime. Currently, no known enzyme system can effectively scavenge •OH. Nanoceria have a large number of surface oxygen vacancies which are the function center of scavenging ROS. The mechanisms of nanoceria ROS scavenging were described by Boghossian [97]. Briefly, because of the dynamic defect sites with dangling Ce³⁺ bonds formed, PNC (poly acrylic acid coated nanoceria) can catalyze the

scavenging of ROS. The Ce^{3+} gives an electron (e^-) to the $\bullet\text{OH}$ to form Ce^{4+} , and Ce^{4+} takes an electron from the $\bullet\text{O}_2^-$ to form Ce^{3+} . The lattice strain ensures that the oxygen vacancies formed by Ce^{3+} and Ce^{4+} can be formed by redox cycles at nanoscale [97]. Researchers reported that nanoceria could effectively scavenge ROS such as $\bullet\text{OH}$ to maintain mesophyll K^+ homeostasis and thus to enhance plant photosynthesis and its salt tolerance [98,99]. Some NPs (nanoparticles) with no-enzyme-like activities also enhance the stress tolerance of plants. Environmentally friendly metal-based nanomaterials have attracted much attention. For example, Zn (zinc) is an essential element for plants. ZnO nanoparticles have been reported to up-regulate the genes related to SOD and GPX in tomato under salt stress [100]. Additionally, TiO_2 and SiO_2 have also been reported to increase the expression of antioxidant enzymes and the photosynthetic performance of plants under stress [101].

Creating plants with a higher ROS scavenging ability to gain better salt stress tolerance is always a hot topic. Nevertheless, the molecular breeding progress so far is slow. Nowadays, using nanomaterials with ROS scavenging ability is also an emerging approach for tuning plant ROS homeostasis under stress conditions [102–105]. ROS overaccumulation is a known secondary stress in plants under stress. Thus, interfacing plants with nanomaterials which have the ability to directly (scavenge ROS) or indirectly (modulate antioxidant enzyme activities) maintain ROS homeostasis could possibly improve their stress tolerance. Many nanomaterials are known to have the ability to scavenge ROS and to help plants manage stresses. Cerium oxide nanoparticles (nanoceria) are a known potent ROS scavenger and can improve plant tolerance to salinity, drought, cold, and heat. With their ROS scavenging ability, Mn_3O_4 nanoparticles alleviated oxidative stress and improved cucumber salt tolerance [106]. Using biomass *Salvia miltiorrhiza* as the precursor, the derived fluorescence carbon dots (CDs) showed strong scavenging ability of $\bullet\text{O}_2^-$ and $\bullet\text{OH}$, and improved salt tolerance in lettuce [107]. Nanomaterials help to improve plant salt tolerance. Other nanoparticles, e.g., SeNP, TiO_2 , and AgNP, could alleviate oxidative stress to improve salinity stress tolerance in plants, including barley [108], potato [109], tomato [110], and broccoli [111]. Overall, plant nanobiotechnology could be a good approach to tuning plant ROS homeostasis to allow the improvement of plant tolerance to stresses.

Besides improving plant salt tolerance, nanomaterials can be also used as tool to deliver agrochemicals, such as nano-fertilizer, nano-pesticides, and nano-enabled chemicals. Nano-fertilizers can provide nutrients needed for plant growth, or improve fertilizer utilization efficiency [112]. For example, iron (Fe) is an essential nutrient, which is involved in chlorophyll biosynthesis. However, the solubility of iron oxide (Fe_3O_4) in water is low, which limits its uptake in plants. Studies showed that Fe-based NPs could enhance photosynthesis and chlorophyll content in maize [113], soybeans [114], and rice [115]. Besides the direct release of elements as nutrients, nanomaterials could also indirectly improve plant performance. For example, cobalt ferrite ($\text{Co-Fe}_2\text{O}_4$) nanoenzyme as an antioxidant is not directly used as nutrient by plants, but it can regulate ROS homeostasis and protect nitrogenase, thereby improving the efficiency of biological nitrogen fixation [116]. Besides nano-fertilizer, nano-pesticide is also a hot topic for agricultural production. Excess use of pesticides not only increases the agricultural production cost, but also causes serious environmental pollution. Nano-pesticides may solve some problems by improving post rate and decreasing pesticide usage [117]. Nano-pesticides such as Ag, Cu, and Zn based nanomaterials present a better broad-spectrum application and low pollution [118]. Nanomaterials also could act as carriers. For example, Zhang et al. [119] reported that the star polymer nanomaterials, which are responsive to temperature and pH, can act as a carrier for fertilizer or pesticide application. Mesoporous silica nanoparticles were used to deliver pesticides in cucumber, with increased utilization efficiency, better deposition performance, and lower residue levels [120]. Recently, targeted delivery of cargoes to plants has been shown. By using a guiding peptide-coated quantum dots-cyclodextrin complex, researchers enabled targeted delivery of methyl viologen and ascorbic acid to a chloroplast to tune its redox status [121]. Overall, plant nanobiotechnology has strong

potential to help to maintain ROS homeostasis in plants under stress and thus to enable sustainable agriculture.

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