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Review

Plant Responses and Adaptations to Salt Stress: A Review

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Abstract: Salinity poses a significant environmental challenge, limiting plant growth and development. To cultivate salt-tolerant plants, it is crucial to understand the physiological, biochemical, and molecular responses and adaptations to salt stress, as well as to explore natural genetic resources linked to salt tolerance. In this review, we provide a detailed overview of the mechanisms behind morphological and physiological responses triggered by salt stress, including salt damage to plants, the disturbance of cell osmotic potentials and ion homeostasis, lipid peroxidation, and the suppression of photosynthesis and growth. We also describe the physiological mechanisms that confer salt tolerance in plants, such as osmotic adjustments, reactive oxygen species (ROS) scavenging, photosynthetic responses, phytohormone regulation, and ion regulation. Additionally, we summarize the salt-stress sensing and signaling pathways, gene regulatory networks, as well as salt-tolerance mechanisms in plants. The key pathways involved in salt-stress signal perception and transduction, including Ca^{2+}-dependent protein kinase (CDPK) cascades, the salt overly sensitive (SOS) pathway, and the abscisic acid (ABA) pathway, are discussed, along with relevant salt-stress-responsive genes and transcription factors. In the end, the important issues and challenges related to salt tolerance for future research are addressed. Overall, this review aims to provide essential insights for the future cultivation and breeding of crops and fruits.

Keywords: salt stress; physiological responses; adaptive mechanisms; signaling pathways; gene co-regulatory networks

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1. Introduction

As salinization spreads, it increasingly threatens crop growth and yield and jeopardizes agricultural and environmental sustainability. According to the FAO, the total area of global salt-affected soils is more than 833 million hectares, and more than two thirds of this is found in arid and semi-arid climatic zones. The salinization rate of cultivable lands is increasing by 10%, annually [1]. Generally, saline soils have a saturated hydraulic conductivity exceeding 4.0 $dS \cdot m^{-1}$ (≈40 mM NaCl), which significantly impacts plant growth and development [2]. Researchers have categorized plants as salt-tolerant or salt-sensitive, based on their growth statuses under salt stress, which not only depend on species, genotype, and age but also on the duration and intensity of stress [3,4].

In saline conditions, plants first experience a water deficit caused by an elevated salt ion concentration and high osmotic potential around the roots [5]. This initial response occurs rapidly, within minutes. Over time, the water uptake may recover partially or fully, and intracellular metabolism gradually readjusts [6]. Subsequently, toxic ions enter plant cells through membrane transporters and slowly accumulate in shoots and leaves, disrupting the normal metabolism of plants [2,7,8]. This cumulative process may lead to visible symptoms, such as leaf curling, etiolation, wilting, or even plant death over weeks or months [9]. In summary, plants may suffer from osmotic stress, ion toxicity, nutrient

deficiency, and the combined effects under salt stress, resulting in a range of morphological, physiological, biochemical, metabolic, and gene-expression changes [10,11].

Therefore, it is essential to revel the mechanisms behind plant responses and adaptations to salt stress. This review synthesizes the information on plant salt tolerance at the morphological, physiological, biochemical, and molecular levels. These mechanisms include the effects of salinity on specific organs, physiological responses, hormonal regulation, ion homeostasis, sensing and signaling pathways, and gene expressions in plants. This knowledge will be valuable for future crop and fruit cultivation and breeding efforts.

2. Morphological Responses and Adaptations to Salt Stress

Salt stress negatively impacts plant growth, leading to stunted development, delayed organ formation, shorter vegetative phases, early flowering and fruiting, and accelerated aging or death [2,11,12]. Previous studies show that high salinity inhibits the growth of roots, shoots, and leaves, as well as flowering and yields (Table 1). In soybean (*Glycine max*), an increased salinity reduces the root number and length, restricting plant roots' access to water and nutrients and diminishing their ability to transport essential resources [13]. In wheat (*Triticum aestivum*), the total root length, total surface area, total root volume, tips, and lateral root decrease with increasing saline water, which are the primary root traits that contribute the most to salt-tolerant genotypes [6]. The shoot length, internode length and number, and cap/root ratio of 'Taishanhong', 'Malas Torsh', and 'Alak Torsh' pomegranate (*Punica granatum*) significantly decrease under high salinity [14]. For leaves, salt stress mainly reduces the number and area of young leaves, while accelerating the senescence of mature leaves [5]. Toxic ions highly accumulate in the basal zone of the leaf blade, contributing to the reduction in leaf elongation and growth [15]. In Arabidopsis, salt stress results in the abortion of flower buds and inhibits the development of anthers, pistils, and petals, especially pollen grains and ovules [16]. Also, the fruit yield, number of fruiting branches, seed number, and seed yield in plants decrease with increasing salt levels [17,18]. In total, salt stress can inhibit plant growth and development, resulting in dwarfing, smaller and senescence leaves, early flowering and fruiting, and lower yield phenotypes.

Table 1. The morphological responses to salt stress in plants.

Organs	Phenotypes	Species
Root	Fewer main roots and lateral roots and reduced root length, surface area, total root volume, tips, etc.	*Glycine max* [13], *Triticum aestivum* [6], and *Arabidopsis thaliana* [19]
Shoot	Shorter shoots and internodes and decreased number of internodes and fruiting branches	*Punica granatum* [14] and *Oryza sativa* [4]
Leaf	Etiolated, curled, and wilted leaf margins, smaller and senescence leaves, increased stomatal density, and thicker cuticle on leaf surface	*Triticum aestivum* [6], *Sorghum bicolor* [15], and *Spartina* [20]
Flower	Early flowering; abortion of flower buds; and inhibited development of anthers, pistils, and petals	*Arabidopsis thaliana* [16] and *Populus alba* [21]
Fruit	Lower fruit weight and yield, poor fruit color, and increased fruit firmness	*Solanum lycopersicum* [22]
Seed	Decreased seed number and yield and lower seed germination	*Helianthus annuus* [18] and *Halostachys capsica* [23]

Plants exhibit tissue-specific sensitivity to salinity, with aerial parts being more affected than roots [3,13]. Previous studies found that some plants thrive in saline environments, suggesting that sodium may serve as a 'functional nutrient' for plant growth [24,25]. For example, certain halophytes, such as *Atriplex halimus* and *Nitraria retusa*, grow, bloom, and fruit normally in high NaCl concentrations exceeding 400 mM [26]. Conversely, glycophytes like lucerne (*Medicago arborea*) and tomato (*Solanum lycopersicum*) can grow in a low NaCl concentration environment but fail to complete their life cycle at high salinity levels (>200 mM) [22,26]. Salt stress also changes the microstructure and ultra-

microstructure of plants, including enhancing palisade tissues; increasing vascular bundle numbers; thickening cuticles, epidermides, and mechanical tissues; and disintegrating or damaging nuclei, chloroplasts, and mitochondria [27,28]. The main salt-induced changes in the chloroplast ultrastructure include reduced grana stacks, less distinct thylakoid membranes, and increased starch and plastoglobuli [29,30]. In several important crops, a diminished starch content indicates its remobilization to provide energy, sugars, and metabolites to alleviate salt stress [30]. After a long evolution process, some halophytes have evolved structural adaptations to saline environments, such as *Spartina* [20] and *Limonium bicolor* [31], developing salt glands to expel excess ions and improve salt tolerance.

3. Physiological and Biochemical Responses and Adaptations to Salt Stress

Salinity results in the accumulation of toxic ions, the production of reactive oxygen species (ROS), a decrease in the photosynthetic rate, the peroxidation of membranes, and a disorder of organic osmolytes in plant cells. In the long-term process of evolution, plants have developed various strategies to cope with high salinity, including osmoregulation; ROS scavenging; photosynthesis responses; phytohormone regulation; and ion uptake, exclusion, and compartmentation (Figure 1) [4,31].

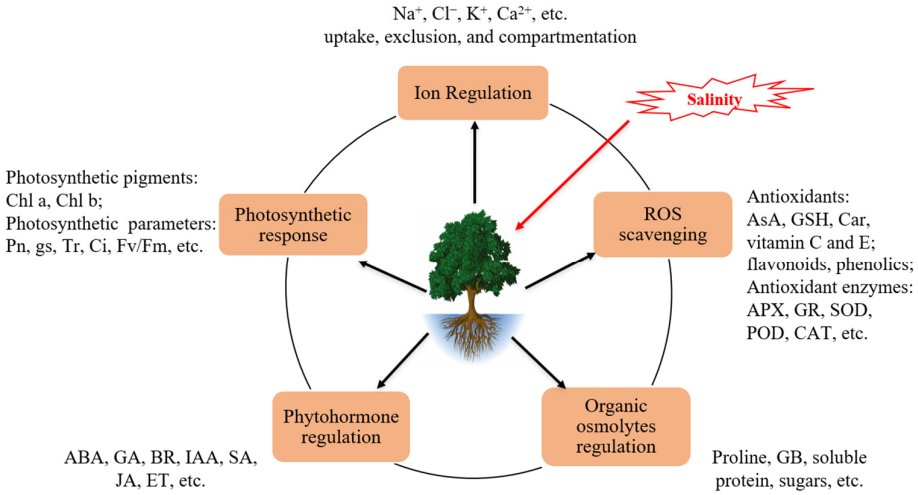


Figure 1. Plant physiological and biochemical responses and adaptations to salt stress. ROS: reactive oxygen species, SOD: superoxide dismutase, POD: peroxidase, CAT: catalase, APX: ascorbate peroxidase, GR: glutathione reductase, AsA: ascorbic acid, GSH: glutathione, Car: carotenoids, GB: glycine betaine, ABA: abscisic acid, SA: salicylic acid, JA: jasmonic acid, IAA: auxin, GA: gibberellin, CK: cytokinin, BR: brassinosteroids, ET: ethylene, Chl a: chlorophyll a, Chl b: chlorophyll b, Pn: photosynthesis rate, gs: stomatal conductance, Tr: transpiration rate, Ci: CO_2 concentration, Fv/Fm: optimal/maximal photochemical efficiency of PSII in the dark.

3.1. Osmoregulation by Organic Osmolytes

Soluble amino acids (proline, glycine betaine, glutamine, and serine) and sugars (sucrose, hexoses, and sugar alcohols) serve as compatible osmolytes to alleviate the adverse effects of salt stress on plants [32–34]. Proline, which primarily exists in its free form, helps to manage cell dehydration, stabilize subcellular structures, scavenge free radicals, and lower redox potentials [35]. The rapid breakdown of proline supplies reductants for oxidative phosphorylation and adenosine triphosphate (ATP) production in mitochondria, aiding in osmotic balance restoration and cellular repair from salt damage [36]. The proline content is closely linked to plant salt tolerance, emphasizing its critical role in osmoregulation under salt stress [37].

Glycine betaine (GB) is an active compatible osmolyte of plants, which essentially contributes to salt tolerance. Many research studies show that the foliar application of GB facilitates the growth of plants, including their total height, shoot length, leaf weight,

number of branches, number of pods, and seed weight under salt stress [38,39]. Also, the application of GB significantly increases the chlorophyll, protein, and proline contents, while decreasing the malondialdehyde (MDA) content and the activities of catalase (CAT) and superoxide dismutase (SOD) under salt stress [38]. Notably, the potential role of GB in ameliorating salt tolerance is mainly found through its reduction in the entry of deleterious ions (Na^+ and Cl^-) and boost in the accumulation of Ca^{2+} and K^+ in plant tissues [38,40].

Many studies show that the contents of soluble protein and soluble sugar significantly increase with increasing salinity [14,31,41], However, some studies argue that the buildup of organic osmolytes, such as proline, soluble protein, and soluble sugar, is a stress response rather than a measure of plant tolerance [36].

3.2. Oxidative Stress and ROS Scavenging

Plants generate various ROS, including hydrogen peroxide (H_2O_2), superoxide anion (O_2^-), and hydroxyl (OH^-), during aerobic metabolism. In general, the production and elimination of ROS maintain a dynamic balance in plant cells. However, salt stress consistently breaks this dynamic balance, causing ROS accumulation. The excess ROS inflicts oxidative damage on proteins, lipids, DNA, and other cellular components in plant cells [42]. Despite their harmful effects, ROS also serve as signaling molecules in response to environmental stimuli.

A range of enzymatic and non-enzymatic scavengers helps to alleviate ROS-induced damage under salt stress, including antioxidant enzymes and non-enzymatic antioxidants. The antioxidant enzymes include SOD, peroxidase (POD), CAT, ascorbate peroxidase (APX), and glutathione reductase (GR), which are mainly responsible for the removal of excess ROS in plant cells [43]. The non-enzymatic antioxidants mainly include ascorbic acid (AsA), glutathione (GSH) and carotenoids (Car), vitamin C and E, flavonoids, and other phenolic compounds, which are also involved in scavenging hydroxyl and alkyl peroxyl radicals in membranes of plants [43]. In many plants, such as cauliflower (*Brassica oleracea*) [44], rice (*Oryza sativa*) [4], and pea (*Pisum sativum*) [45], salinity triggers the increased activity of antioxidant enzymes (SOD, CAT, GPX, and APX) and the accumulation of non-enzymatic antioxidants (AsA and GSH), helping to scavenge excess ROS in cells. In fenugreek (*Trigonella foenum-graecum*) and cherry tomato (*Solanum lycopersicum var. cerasiforme*), total phenolics, flavonoids, and antioxidant activities increase under salt stress, contributing to scavenging ROS and defending against oxidative stress [40,46]. Thus, the defense mechanisms of enzymatic and non-enzymatic scavengers represent an efficient strategy for plants to adapt to salt stress [44,47].

3.3. Photosynthesis Responses

Short-term exposure to salinity can affect the photosynthesis of plants by stomatal limitations (the stomatal factor), leading to a decrease in carbon assimilation. In the long term, adverse effects of salinity on plant photosynthesis are mainly due to the salt ions' accumulation in young leaves, which results in the degradation of photosynthetic pigments and the inhibition of Calvin cycle enzymes (non-stomatal factors) [48]. Studies have reported that the net photosynthesis rate (Pn), stomatal conductance (gs), transpiration rate (Tr), maximal efficiency of PSII (Fv/Fm), and variable fluorescence (Fv/Fo) of plants decline under salt stress [49,50]. Overall, salinity typically decreases the Pn and outputs in most plants, primarily due to both stomatal and non-stomatal factors. Studies have suggested that stomatal factors and non-stomatal factors that limit photosynthesis are not independent, and both of these dynamically change with the duration and concentration of stress [51]. Regarding stomatal factors, closed stomata block CO_2 from diffusing to photosynthetic sites in plant leaves, thereby lowering the intercellular CO_2 concentration (Ci) and Pn, ultimately affecting the production of photosynthesis [29]. At the same time, closed stomata also reduce the Tr in plant leaves. Generally, reduced K^+ levels in leaf cells can trigger stomatal closure under salt stress [52].

Non-stomatal factors include a decline in photosynthetic membrane proteins, the disintegration of thylakoid membranes, and a loss of photosynthetic pigments. Salt stress disrupts the structure and function of various components involved in photosynthesis, such as enzymes, pigments, and membrane proteins [29,51]. Photosynthetic pigments like chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoids play vital roles in light absorption and transmission. The Chl a/b ratio is directly related to active light-harvesting antenna complexes and reaction centers, being commonly used as the indicator of an enhancement in the plant photochemical capacity [53]. For many plants, chlorophyll contents always decrease in leaves under salt stress [9,48]. Studies show that while chlorophyll contents decrease in salt-sensitive cotton (*Gossypium hirsutum*), it remains relatively stable in salt-tolerant varieties [54]. For plants subjected to a saline environment, alongside high light and temperature conditions, photoinhibition and limited CO_2 fixation in their leaves are likely to occur. The excess light energy leads to the destruction of the photosynthetic apparatus, like the thylakoid membranes of chloroplasts. Plants display several strategies to protect the photosystems against photoinhibition and photodamage [55]. These photoprotective mechanisms lead to a decrease in the quantum yield of PSII, relying on the energy dissipation process of the lutein cycle and turnover of D1 proteins [56]. The salt-tolerant *Ricinus communis* has higher photorespiratory activity, nitrate assimilation, and electron transport/photophosphorylation, which are closely associated with an efficient photoprotection mechanism [57]. While, in the salt-sensitive *Jatropha curcas*, salinity significantly decreases both the Vcmax (in vivo Rubisco activity) and Jmax (maximum electron transport rate), increases Ci values, and decreases Rubisco activity, leading to biochemical limitations in photosynthesis [57].

3.4. Phytohormones Regulation

Stress-responsive hormones, like abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), as well as growth-related hormones, such as auxin (IAA), gibberellin (GA), cytokinins (CKs), and brassinosteroids (BRs), are crucial in managing salinity stress signals and balancing growth with stress responses. Previous studies report that the accumulation pattern of these phytohormones in plant cells vary among each other under salt stress. For instance, the levels of ABA, SA, and JA increase, whereas that of GA decrease in plants [58]. Additionally, the levels of trans-zeatin (tZ) and IAA first increase and then decrease under salinity [59]. Obviously, some hormones enhance salt tolerance, while others may have inhibitory effects [60]. ABA, a positive regulator of the defensive responses of plants, can target specifically guard cells to induce stomatal closure and avoid water deficits in plants [61]. The exogenous ABA regulates the osmotic balance, ion homeostasis, and ROS levels in green alga (*Chlamydomonas reinhardtii*) cells under salt stress [62]. Auxin promotes the root growth of Arabidopsis to mitigate salt stress [19]. The exogenous GA_3 may compensate for salt-induced growth deficiencies and consequently help tomato plants to adapt to saline conditions [63]. BRs alleviate salt stress by enhancing sugar and GB contents in pepper (*Capsicum annuum*) [64], and the application of CKs and SA mitigate salt damage on the photosynthetic apparatus and gas exchange in *Tropaeolum majus* [65]. A low concentration application of SA and JA could provide tolerance against salt stress by enhancing physiological processes and improving salt tolerance [66]. In Arabidopsis and tomato, ET positively regulates salt tolerance [67,68], whereas in rice and zucchini (*Cucurbita pepo*), it plays a negative role in the response to salt stress [69,70]. Therefore, it can be inferred that the variations in phytohormone levels under manageable salt stress can be used as an indicator of plant salt tolerance.

3.5. Ion Uptake, Exclusion, and Compartmentation

In saline conditions, toxic ions invade root cells and gradually accumulate in plant shoots and leaves, then disrupt the normal metabolic processes. Research studies show that Na^+ and Cl^- extensively accumulate in plant cells, organs, and even in the whole plant under NaCl stress, which affect the absorption and transport of essential nutrients

such as N, P, S, K, Ca, Mg, Fe, Mn, Cu, and Zn [71,72]. Also, plant salt tolerance is closely related to the patterns of ion uptake, transport, and accumulation in tissues [73]. Numerous studies suggest that plants generally cope with excess Na^+ and Cl^- through three strategies (Figure 2): (a) limiting the uptake of Na^+ and Cl^- in roots, (b) sequestering Na^+ and Cl^- into vacuoles, and (c) enhancing Na^+ and Cl^- exclusion from shoots and leaves [74].

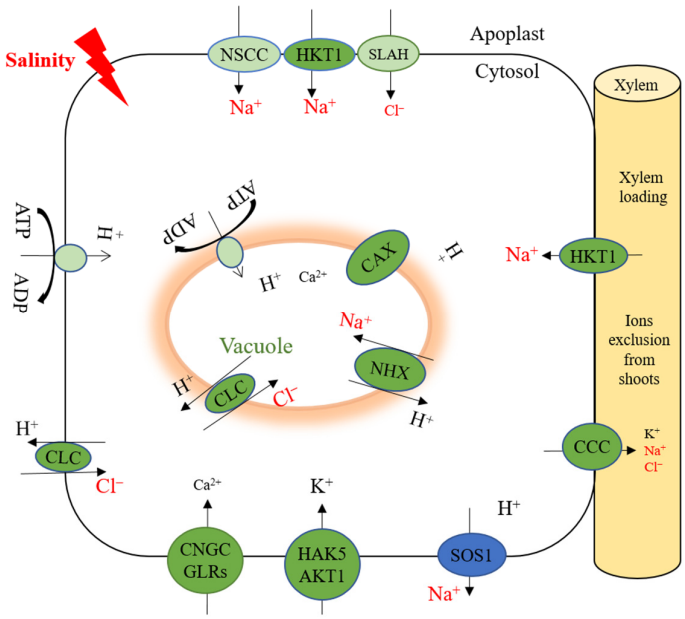


Figure 2. Ion uptake and transport in plant tissues under NaCl stress. ADP: adenosine diphosphate, AKT1: affinity K^+ transporter 1, ATP: adenosine triphosphate, CCC: cation-chloride cotransporter, CHX: Cation/H^+ exchanger, CLC: chloride channel, CNGC: cyclic nucleotide-gated channel, GLR: glutamate receptor-like channel, GR: glutathione reductase, GSH: glutathione, HKT1/HAK5: high-affinity K^+ transporter 1/5, NHX: Na^+/H^+ antiporter, NSCC: non-selective cation channels, SLAH: slow anion channel-associated 1 homolog, SOS1: salt overly sensitive gene 1.

For halophytes, salt tolerance mainly relies on the inclusion of salts rather than their exclusion [75,76]. In pomegranate [13] and barley (*Hordeum vulgare*) [77], toxic Na^+ and Cl^- primarily damage their leaves rather than roots, indicating overall salt tolerance. In contrast, glycophytes such as bean (*Glycine max*) [78], tomato [79], and olive (*Canarium album*) [80] tend to exclude Na^+ and Cl^- from their shoots and retain more toxic ions in their roots. Thus, toxic ion accumulation can aid salt-tolerant plants in osmotic regulation, but only if they are able to compartmentalize these ions into vacuoles.

Na^+ enters plant cells mainly through the high-affinity K^+ transporter (HKT1) and non-selective cation channels (NCSSs), which work together to regulate Na^+ uptake [81]. Cl^- enters cells mainly through the chloride channels (CLCs) [82] and slow anion channel-associated 1 homolog 3 (SLAC1/SLAH) [83]. The cation–chloride cotransporter (CCC) is predicted to improve salt exclusion in shoots by directly catalyzing the retrieval of Na^+ and Cl^- from the root xylem in grape (*Vitis vinifera*) [84]. Ion antiporters, such as the Na^+/H^+ antiporter (NHX1) and the salt overly sensitive protein (SOS1), contribute to managing cytosolic Na^+ levels by either extruding it from the cytoplasm or sequestering it into vacuoles [85–87]. HKT1 also helps to mitigate Na^+ toxicity through unloading Na^+ from xylem ducts into xylem parenchyma cells then recirculating it to roots through phloems and reducing the Na^+ accumulation into leaves [88]. K^+ is crucial for regulating cell osmotic potential, activating enzymes, mitigating oxidative stress, and protecting plants from abiotic stress-induced damages [89]. Halophytes preferentially select and transport K^+ into the aerial parts through affinity K^+ transporters (AKT1 and HAK5), helping to maintain a high K^+/Na^+ ratio in leaves (Figure 2) [81]. A newly identified K^+ channel beta subunit, KSB1, also helps to maintain cellular Na^+ and K^+ homeostasis in tomatoes through the SlHY5-

KSB1-KSL1 module, thus enhancing salt tolerance [90]. Due to the similar properties of Na^+ and K^+, excess Na^+ severely interferes with the K^+ function in cells. On the one hand, there is an antagonistic effect on the uptakes of two ions, and excess Na^+ inhibits the uptake of K^+ in plants [91]. On the other hand, excessive Na^+ in cells binding to enzyme active sites leads to enzyme inactivation and even degradation. The K^+ concentration in plant cells is around 100 to 150 mM, while Na^+ should remain low to support normal metabolic functions [37]. Therefore, a high concentration of K^+ and a low concentration of Na^+ in cells are essential for plant growth and development. Plants like pomegranate [9], oak (*Quercus virginiana*) [92] and chickpea (*Cicer arietinum*) [3] demonstrate a strong capacity to transport K^+ into their shoots and leaves, thereby maintaining an optimal K^+/Na^+ ratio and mitigating ion toxicity in cells.

Ca^{2+}, a major component of cell walls, plays an important role in maintaining membrane stability and responding to various stresses [93]. Meanwhile, Ca^{2+} acts as a second messenger to participate in signal transduction, along with ABA and ROS [94,95]. Ca^{2+} enters plant cells mainly through ion transporters and non-selective cation channels, such as glutamate receptor-like channels (GLRs) and cyclic nucleotide-gated channels (CNGCs). The vacuolar H^+/Ca^{2+} antiporters CAX1/3 contribute to mitigating the potential toxicity from cytosolic Ca^{2+}, thereby heightening a plant's tolerance to salt stress [87,96]. Mg^{2+} is vital for chlorophylls, enzyme catalysis in photosynthesis, and respiration and the activation of DNA and RNA polymerases [97]. Many studies have found that an increased Na^+ impedes the uptakes of Ca^{2+} and Mg^{2+} in roots, with various accumulation patterns across different cultivars under salt stress [14,98,99]. For instance, in pomegranates, the contents of Ca^{2+} and Mg^{2+} in the leaves and stems of 'Taishanhong', 'Kandahar', 'Dwarf Moy', 'Mollar', and 'Wonderful' increase while that of 'Red Angel', 'Pecos', 'Surh-Anor', and 'Sweet' decrease at low salinity (100 mM of NaCl) [9]. These findings indicate that Na^+ may replace Ca^{2+} and Mg^{2+} in roots and facilitate the transport of them to shoots and leaves [92].

Essential nutrients, nitrogen (N), phosphorus (P), sulfur (S), iron (Fe), manganese (Mn), copper (Cu), and zinc (Zn) are critical for plant growth. However, salt stress can reduce the uptake and transport of N, P, and S, which cause vegetative deficiency and adversely affect plant growth and development [71,72]. Studies report that the contents of Fe, Mn, and Cu in the whole plants of soybean [12] and mango (*Mangifera indica*) [100] increase, while the Al, Si, and Zn contents in pomegranate leaves decrease under salt stress [9]. In general, micronutrients affect the catalytic activities of enzymes and metabolites through directly or indirectly alleviating salt stress in plants.

4. Molecular Responses and Adaptations to Salt Stress

Plant salt tolerance is a complex and quantitative trait controlled by multiple genes [2]. According to their functions, these salt-related genes can be divided into two main categories: (1) effectors, which encode proteins that directly participate in physiological and biochemical responses to salt stress, including POD, SOD, APX, HKT, NHX, aquaporin (AQP), late embryogenesis abundant (LEA) proteins, and H^+-ATPase (VHA) [101–103] and (2) regulatory factors, which modulate the expression of downstream genes and signal transduction pathways, such as transcription factors (TFs) and various kinases. The key TFs include the Apetala2/ethylene response factor (AP2/ERF), dehydration-responsive element-binding protein/C-repeat binding factor (DREB/CBF), WRKY, NAC, basic leucine zipper (bZIP), MYB, and basic helix–loop–helix (bHLH) family genes. These well-characterized TFs facilitate plant responses to salinity by regulating the expression of genes that are related to hormone signaling, Ca^{2+}-related pathways, and ion homeostasis [2,58]. In saline environments, plants mitigate salt-induced damage through physiological and biochemical mechanisms, such as ROS scavenging, photosynthetic regulation, and ion exclusion and compartmentation, which are all orchestrated by a complex molecular network composing of effectors and regulators. This molecular regulatory

network encompasses cellular ion influx, signal sensing and transducing, transcriptional regulation, and gene expression within plant cells (Figure 3) [2,53,74].

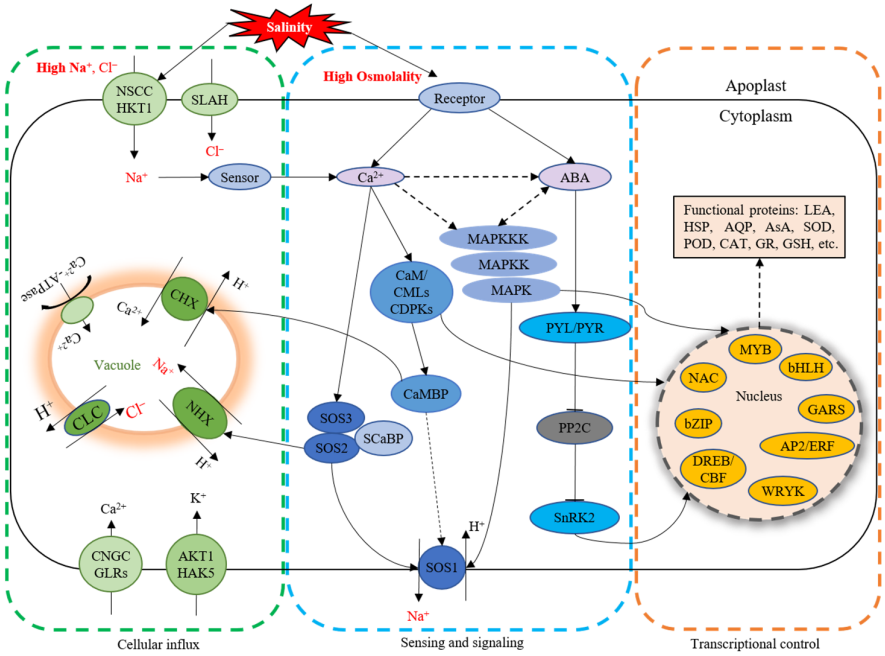


Figure 3. The molecular responses of plants to salt stress. ABA: abscisic acid, AKT1: affinity K^+ transporter 1, AP2/ERF: Apetala2/ethylene response factor, APX: ascorbate peroxidase, AQP: aquaporin, AsA: ascorbic acid, bHLH: basic helix–loop–helix, bZIP: basic leucine zipper, CaM: calmodulin, CaMBP: CaM-like binding protein, CAT: catalase, CDPK: Ca^{2+}-dependent protein kinase, CHX: Cation/H^+ exchanger, CLC: chloride channel, CML: CaM-like, CNGC: cyclic nucleotide-gated channel, DREB/CBF: dehydration-responsive element-binding protein/C-repeat binding factor, GLR: glutamate receptor-like protein, GR: glutathione reductase, GSH: glutathione, HKT1/HAK5: high-affinity K^+ transporter 1/5, HSP: heat shock protein, LEA: late embryogenesis abundant protein, MAPKs: mitogen-activated protein kinases, MAPKK: MAPK kinase, MAPKKK: MAPKK kinase, NHX: Na^+/H^+ antiporter, NSCCs: non-selective cation channels, POD: peroxidase, PP2C: protein phosphatase 2C, PYR/PYL: pyrabactin resistance/pyrabactin resistance 1-like protein, SCaBPs: SOS3-like calcium-binding protein, SnRK2: sucrose non-fermenting-related protein kinase 2, SOD: superoxide dismutase, SOS1/2/3: salt overly sensitive gene 1/2/3.

4.1. Ion Channels and Other Transporters

Ions channels, such as NCSSs, GLRs, andCNGCs, participate in the uptakes of Na^+ and Ca^{2+} ion transporters, including HKT1, HAK5, and AKT1, and monovalent cation proton antiporters (CPAs), including NHX, the K^+ efflux antiporter (KEA), and the Cation/H^+ exchanger (CHX) and regulate monovalent cations (Na^+, Li^+, K^+, and Ca^{2+}) and protons to sustain the intracellular voltage and pH homeostasis [104–106]. Also, anion transporters and anion channels are involved in regulating the ion balance in plant cells. The CLC gene family is responsible for the absorption and transport of anions, such as Cl^-, NO_3^-, HCO_3^-, I^-, and Br^- [82]. The *CLC* genes primarily encode Cl^- channels and Cl^-/H^+ antiporters. Research studies on *Arabidopsis thaliana* have proven that *AtCLCa* [107] and *AtCLCb* [108] encode NO_3^-/H^+ antiporters on the vacuolar membranes to regulate nitrogen accumulation. The upregulation of the *GmCLC1* gene in soybeans leads to higher accumulations of Cl^- and NO_3^- in roots and maintains a lower Cl^-/NO_3^- ratio in the whole plant by restricting Cl^- transport to shoots under NaCl stress [109]. In pomegranates, *PgCLC-B* encodes a NO_3^-/H^+ exchanger, while *PgCLC-C1*, *PgCLC-C2*, *PgCLC-D*, and *PgCLC-G* encode Cl^-/H^+ antiporters, sequestering excess Cl^- into vacuoles to mitigate its toxic effects [110]. The activity of nitrate transporters (NRTs) [111] and sulfate transporters

(Sultrs) [112] are also affected by salt stress, leading to imbalances in intracellular NO_3^- and SO_4^{2-} levels. In other words, these ion channels and transporters are responsible for the uptake and transport of Na^+, K^+, Ca^{2+}, Cl^-, and NO_3^- into or out of cells. Then, the elevated ions ABA and ROS act as signal messengers to transduce stress signals through the ABA signaling pathway, SOS pathway, and Ca^{2+}-dependent protein kinase (CDPK) cascades, and, in turn, the activities of these transporters are regulated by multiple signal transduction pathways.

4.2. Signal Transduction Pathways

Salinity increases the intracellular Ca^{2+} concentration in plants. A portion of this Ca^{2+} acts as a second messenger, directly participating in signal transduction through the SOS pathway and CDPK cascades. Another part of intracellular Ca^{2+} is engaged in the generation of ABA and ROS, collaborating with these molecules to relay stress signals through the ABA signaling pathway and SA signaling pathway, ultimately initiating transcriptional responses in plant cells. These signaling pathways form intricate networks to regulate downstream target gene expressions under salt stress [60].

Ca^{2+}-related cascades participate in ionic, osmotic, and oxidative stress signals' transduction in plants, and these conserved signaling pathways are important for establishing ion homeostasis under salt stress. Calmodulin (CaM) and CaM-like (CML) proteins are vital for the regulation of Ca^{2+} channels and Ca^{2+} pumps, such as CNGC and Ca^{2+}-ATPases [113,114]. CDPKs, belonging to multigene families, serve as essential Ca^{2+} sensors in plant responses to salt stress, likely facilitating crosstalk between signaling pathways to influence the phosphorylation of downstream targets [115]. Also, the Ca^{2+}-independent signal transduction pathway, like mitogen-activated protein kinase (MAPK) cascades, participates in multiple stress signaling, contributing to protect plants from salt stress [116]. MAPKs, with each cascade consisting of an MAPKK kinase (MAPKKK), an MAPK kinase (MAPKK), and an MAPK, have important roles in different biological processes. These kinases act as sequential signal transducers to channel, integrate, and amplify signals from the cellular environment to transcriptional and metabolic response centers via phosphorylation. For example, salt-stress signals are transduced from the heteromeric G-protein to GMK1 via phospholipases in the early response stages of salt stress in soybean [117]. Meanwhile, a *TMPK3* of wheat complements the salt sensitivity of the loss-of-function *mpk3-1* mutant, where its overexpression promotes salt tolerance to transgenic Arabidopsis [118].

4.2.1. SOS Signal Transduction Pathway

The SOS signal transduction pathway is mainly responsible for maintaining the ion balance within plant cells, making it crucial for salt tolerance [119]. The SOS signal transduction pathway under salt stress behaves as follows: A high Na^+ triggers an increase in intracellular Ca^{2+} levels, which then binds to calcineurin B-like proteins (CBLs) and forms a CBL–CIPK complex with CBL-interacting protein kinases (CIPKs) [120,121]. This CBL–CIPK complex phosphorylates and activates SOS1 and NHX1, facilitating the management of cytosolic Na^+ levels by either extruding it from the cytoplasm or sequestering it into vacuoles [85,86].

The *SOS* genes in plants are found to be involved in the signal transduction pathways to regulate the Na^+ balance in cells [120]. The *SOS1* gene encodes a plasma membrane Na^+ antiporter with 12 transmembrane domains at the N-terminus and a long hydrophilic tail at the C-terminus, which mainly express in xylems and root tips under salt stress. The *SOS2* gene encodes a CIPK protein with a catalytic region at the N-terminus and a regulatory region at the C-terminus. The *SOS3* gene encodes a CBL protein with a myristoylation structure and four EF-hands at the N-terminus. The C-terminus of the SOS2 protein can interact with the Ca^{2+} sensor SOS3 to activate the SOS1 protein. An overexpression of *SOS1*, *SOS2*, and *SOS3* can enhance the salt tolerance of transgenic plants, such as sweet potato (*Ipomoea batatas*) [122] and Poplars [123]. Furthermore, SOS2 can self-phosphorylate and activate NHX1 on the tonoplast membrane to transport Na^+ into vacuoles, thus alleviating

Na^+ toxicity, which is a process that may occur independently of SOS3 through the SOS3-like calcium-binding proteins (SCaBPs) [120].

4.2.2. ABA Signal Transduction Pathway

ABA is a growth-inhibiting phytohormone that promotes plant dormancy and leaf abscission and also plays a critical role in plant stress responses. It transmits stress signals and regulates stomatal movement and Na^+ transport [124]. Three protein families are key factors to the ABA signaling pathway: PYR/PYL/RCARs, protein phosphatase 2C (PP2Cs), and SNF1-related protein kinase 2s (SnRK2s). PYR/PYL/RCARs is an ABA receptor, PP2Cs are negative regulators, and SnRK2s are positive regulators of downstream signals [125]. Salt-stress signals can be classified into ABA-dependent and ABA-independent cascades. ABA regulatory components (RCARs), including pyrabactin resistance PYR/PYL genes; SnRK2-type protein kinases; transcription factors (WRKY, NAC, AREB1, and bZIP); ROS; JA; and CK, can all regulate ABA-related gene expressions under salt stress [125,126].

In the ABA-dependent signal transduction pathway, when plants are exposed to salt stress, the ABA level increases and interacts with PYR/RCARs, leading to the inhibition of PP2C phosphatase activity. This inhibition enhances SnRK2 activity and promotes the phosphorylation of downstream targets [127]. SnRK2s, binding to an ABA-responsive element (ABRE), trigger the expression of salt-related genes, which in turn induces a series of physiological and biochemical responses. In the absence of ABA, however, PP2C activity increases, resulting in reduced SnRK2 activity and inhibited downstream signaling [125]. Transcription factors such as ABRE, MYB, NAC, and CBF4 regulate the expression of salt-related genes through an ABA-dependent transduction pathway during salt stress [124]. In contrast, the model of an ABA-independent signal transduction pathway simulates as follows: upon exposure to salinity, the ABA receptor recognizes the stress signal and then transduces it through Ca^{2+} and the ABA-responsive element DREB to elicit physiological and biochemical responses to salt stress [125]. Also, other genes can be transcriptionally regulated through both ABA-dependent and -independent manners to mitigate salt stress, such as *ABAI5* and *RD29A* [128].

4.3. Transcription Factors

Transcription factors play crucial roles in various biological processes of plant growth and development under salt stress. Altering the expression of genes encoding these transcription factors can improve stress tolerance by regulating signaling transduction pathways and salt-related gene expressions [58]. At present, many transcription factors associated with plant stress responses have been isolated and identified from various species, including NAC, MYB, AP2/ERF, WRKY, bZIP, and GRAS [7].

NAC transcription factors are involved in plant secondary cell wall synthesis, apical meristem differentiation, lateral root development, flower bud differentiation, and other growth and development processes [129], and they also respond to various environment stresses such as droughts, high salinity, and high temperature and cold environments [130,131]. The regulation mode of NAC in plants is simulated as follows: upstream factors like *DREBs* and *ABREs* bind to the promoter region of *NAC* genes and activate its transcription under salt stress [132]. The post-transcriptional regulation of NAC proteins is modified and activated by other proteins, allowing them to bind to target gene promoters and regulate their expression [132]. Previous studies have shown that *NAC* genes are induced by salt stress, and their overexpression improves the salt tolerance of transgenic *Populus* and rice plants [130,133,134]. *NAC* genes can improve plant salt tolerance via regulating Na^+/K^+ homeostasis in cells [135].

MYB transcription factors are crucial in plant organ morphogenesis, secondary metabolism, and hormone signaling [136]. Their regulation patterns in response to salt stress vary among different species; some *MYBs* regulate plant salt tolerance through an ABA-dependent pathway [137], while others, like wheat *MYBs* (*TaMYB56-b*), directly activate the downstream stress-related genes of DREB/CBF factors to enhance plant salt tolerance [138].

PtrSSR1, a salt-stress regulator of the R2R3-MYB gene family in poplars (*Populus trichocarpa*), confers salt tolerance to transgenic Arabidopsis plants through regulating lateral root emergence and ABA signaling [139]. Similarly, an overexpression of strawberry (*Fragaria ananassa*) *FaMYB63* enhances salt tolerance by directly binding to the SOS1 promoter in Arabidopsis [140].

AP2/ERF transcription factors play important roles in plant growth and development and responses to various stresses. The AP2/ERF family is typically divided into three subfamilies: the AP2 family, ERF/DREB family, and RAV family. The AP2 subfamily mainly participates in leaf epidermis recognition and flower and ovule development, and the RAV subfamily regulates plant development and stress responses [141]. The ERF/DREB subfamily, including DREB and ERF, which has amplified in large numbers, mainly responds to a series of environmental stresses, such as droughts, salt, cold environments, oxidative stress, heat, and heavy metals [142]. DREBs are unique to plants and include the DREB1/CBF and DREB2 subfamilies. Studies have shown that an overexpression of *DREB* genes can enhance the salt tolerance of transgenic wheat [143] and rice [144].

WRKY transcription factors regulate plant defense responses to droughts, low temperatures, and salt stress by interacting with other families of transcription factors or by recognizing and binding to W-boxes in their own target genes [145]. The wheat WRKY transcription factor *TaWRKY17* enhances salt tolerance in transgenic Arabidopsis and wheat [146]. WRKY transgenic lines have exhibited a high capacity for adapting to saline conditions by scavenging ROS and regulating ABA-responsive and stress-responsive genes [147,148]. An overexpression of soybean *GmWRKY13* improves salt tolerance in Arabidopsis plants, while *GmWRKY54* increases its sensitivity to salt stress [149]. Therefore, the WRKY gene family members employ various mechanisms to manage salt stress.

The bZIP gene family is essential for environmental and developmental signaling in plants. The *SabZIP* gene in *Suaeda australis*, located in the nucleus, positively regulates salt-stress responses [150]. bZIP transcription factors can bind to *ABRE*, a promoter element of ABA-induced genes, to modulate a broad range of stress-related genes through ABA-dependent pathways [150,151].

GRAS transcription factors, unique to plants, regulate plant growth and development, cell detoxification, signal transduction, and stress responses. An overexpression of the GRAS gene *HcSCL13* of *Halostachys caspica* increases salt tolerance in Arabidopsis [152]. Also, an overexpression of the GRAS gene *VaPAT1* of *Vitis amurensis* increases tolerance to cold temperatures, droughts, and high salinity in Arabidopsis [153].

5. Conclusions and Future Perspectives

Salinity is a major environmental stress that restricts plant growth and development. When plants are exposed to a saline condition, they experience osmotic stress in roots due to the short-term water deficit, followed by ion toxicity from nutrient imbalances in the cytosol over longer periods [6]. In the long-term evolution process, plants develop comprehensive and executive mechanisms to cope with salt stress, which depend on the gene regulatory networks of the morphological, biochemical, molecular, and physiological responses of plants [53,74]. Briefly, plants perceive salt-stress signals caused by osmotic stress or toxic ions via receptors or sensors in cells under salt stress, and then, the second messengers Ca^{2+}, ROS, and ABA receive and transmit these signals to cascades, which are involved in secondary and tertiary regulatory networks. These cascades, including Ca^{2+} sensors, MAPK cascades, and transcription factors, are activated to transduce stress signals through SOS, ABA, CDPK, and MAPK signaling pathways. Transcription factors regulate the expression of downstream functional genes, such as *AKT1*, *NHX*, *P5CS*, *HSPs*, *LEAs*, *AQPs*, *SODs*, and *APXs*, in response to salt stress (Figure 4) [2,10]. Consequently, plants exhibit morphological and physiological changes, including alterations in plant phenotypes, microstructures and ultra-microstructures, lipid peroxidation, and ion disequilibrium. They also initiate protective adaptations against salt damage, including osmolyte osmoregulation, ROS scavenging, photosynthesis responses, hormone regulation, ion homeostasis, and

gene regulation (Figure 4) [53]. Obviously, the executive capacity of these mechanisms to cope with salt stress are important determinants to evaluate whether a plant is salt-tolerant or salt-sensitive [8,53,74].

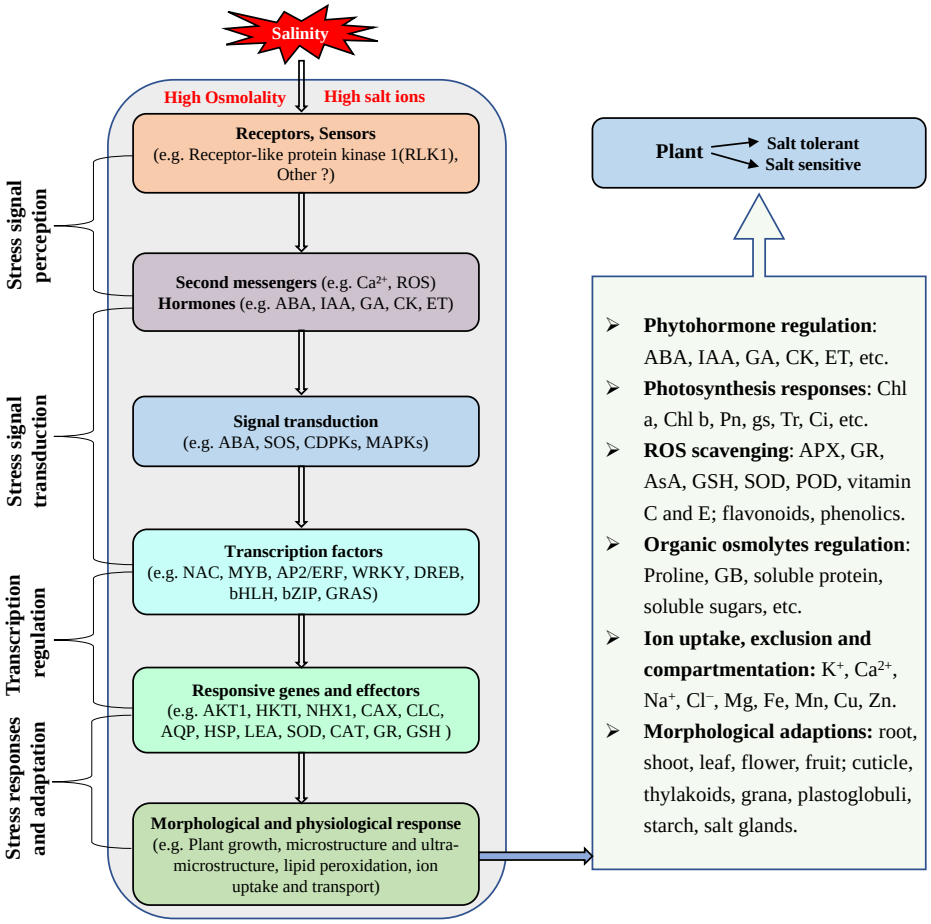


Figure 4. The mechanisms of plant responses and adaptations to salt stress. ABA: abscisic acid, AKT1: affinity K^+ transporter 1, AP2/ERF: Apetala2/ethylene response factor, APX: ascorbate peroxidase, AQP: aquaporin, AsA: ascorbic acid, bHLH: basic helix–loop–helix, BR: brassinosteroids, bZIP: basic leucine zipper, CAT: catalase, CAX: H^+/Ca^{2+} antiporter, CDPK: Ca^{2+}-dependent protein kinase, Chl a: chlorophyll a, Chl b: chlorophyll b, Ci: CO_2 concentration, CK: cytokinin, CLC: chloride channel, DREB/CBF: dehydration-responsive element-binding protein/C-repeat binding factor, ET: ethylene, GA: gibberellin, GB: glycine betaine, GR: glutathione reductase, gs: stomatal conductance, GSH: glutathione, HKT1: high-affinity K^+ transporter 1, HSP: heat shock protein, IAA: auxin, JA: jasmonic acid, LEA: late embryogenesis abundant protein, MAPKs: mitogen-activated protein kinases, NHX1: Na^+/H^+ antiporter 1, Pn: photosynthesis rate, POD: peroxidase, ROS: reactive oxygen species, SA: salicylic acid, SOD: superoxide dismutase, SOS: salt overly sensitive, Tr: transpiration rate.

As mentioned, it is well known that the ability to maintain ion homeostasis is vital for salt tolerance in plants. The toxic ions Na^+ and Cl^- disrupt the uptake and transport of K, Ca, Mg, Fe, Mn, Cu, and Zn, resulting in a nutrient deficiency [9]. Plants exclude or compartmentalize excess toxic ions from cells or into vacuoles through transporters and channels on plasma membranes or tonoplasts, such as AKT1, NHX1, SOS1, CAX, and CLCs [96]. Halophytes readily transport and accumulate toxic ions in shoots and leaves [75,76], whereas glycophytes preserve more salt ions in roots [78]. To adapt to salt stress, amino acids and sugars serve as effective and compatible osmolytes, maintaining osmotic potentials and cell membrane stability, as well as removing ROS [8]. Salt-tolerant

species exhibit stronger antioxidant defenses to scavenge ROS compared to salt-sensitive species, which may show no change or reduced antioxidant activity under salt stress [4,43].

In the past few decades, significant advancements have been made in understanding how plants respond to and adapt to salt stress. Nonetheless, the specific salt-stress sensors and receptors, along with their underlying mechanisms, remain largely unidentified. Unveiling salt-stress sensors or receptors is now a key object in the study of plant responses to salt stress. Moreover, the main determinants and upstream elements of the CDPK and MAPK signaling pathways, as well as their certain details of regulatory mechanisms, are still not fully understood. Thus, future research should focus on the CDPK and MAPK cascades activated by salt-stress signals and the unknown members within these pathways.

Another pressing issue is the breeding of more salt-tolerant varieties of glycophytic crops and fruits. To address this issue, genetic engineering-based alterations of plant genomes via inserting or overexpressing beneficial salt-responsive genes have been extensively researched. However, the potential gene pool from halophytes is far from its full exploration, indicating a need for the identification and application of more stress-related genes from various halophytes to enhance the salt tolerance of crops and fruits.

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