



Review

A Review on Plant Responses to Salt Stress and Their Mechanisms of Salt Resistance

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Abstract: Nowadays, crop insufficiency resulting from soil salinization is threatening the world. On the basis that soil salinization has become a worldwide problem, studying the mechanisms of plant salt tolerance is of great theoretical and practical significance to improve crop yield, to cultivate new salt-tolerant varieties, and to make full use of saline land. Based on previous studies, this paper reviews the damage of salt stress to plants, including suppression of photosynthesis, disturbance of ion homeostasis, and membrane peroxidation. We have also summarized the physiological mechanisms of salt tolerance, including reactive oxygen species (ROS) scavenging and osmotic adjustment. Four main stress-related signaling pathways, salt overly sensitive (SOS) pathway, calcium-dependent protein kinase (CDPK) pathway, mitogen-activated protein kinase (MAPKs) pathway, and abscisic acid (ABA) pathway, are included. We have also enumerated some salt stress-responsive genes that correspond to physiological mechanisms. In the end, we have outlined the present approaches and techniques to improve salt tolerance of plants. All in all, we reviewed those aspects above, in the hope of providing valuable background knowledge for the future cultivation of agricultural and forestry plants.



Citation: Hao, S.; Wang, Y.; Yan, Y.; Liu, Y.; Wang, J.; Chen, S. A Review on Plant Responses to Salt Stress and Their Mechanisms of Salt Resistance. *Horticulturae* **2021**, *7*, 132. <https://doi.org/10.3390/horticulturae7060132>

Academic Editor: Mercè Llugany

Received: 29 April 2021

Accepted: 30 May 2021

Published: 3 June 2021

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Keywords: salt stress; osmotic stress; antioxidants; reactive oxygen species; signaling; salt-responsive genes

1. Introduction

More than eight million hm^2 of land worldwide is affected by salt, accounting for 6% of the world's total arable land area. It is expected that 30 percent of arable land will be lost in the next 25 years, and 50 percent by the middle of the 21st century [1]. Soil salinity has become one of the most concerning environmental issues in the 21st century. With an increasing population to feed and insufficient arable land to plant, it is of great urgency to solve the problem of soil salinity. So far we have chiefly two ways to alleviate soil salinization, which are using chemical amendments to restore damaged soil; and using biotechnology to cultivate salt-tolerant varieties. When it comes to comparing one from the other, the former way is considered costly and may risk causing secondary salinization. Therefore, cultivating salt-tolerant plants is of great importance, and requires us to put more effort into it.

In nature, some plants are created to be salt-tolerant called halophyte, while almost all kinds of crops humans can utilize are glycophytes, which are sensitive to high concentrations of salt in soil [2]. Researchers have been studying salt tolerance mechanisms in salt-tolerant plants and trying to apply them to plants that are not salt tolerant. Previous studies have figured out a big part of the whole defensive network (Figure 1). Salt stress can be divided into two components. In the short-term, salt stress produced osmotic stress, whereas at long-term ion toxicity occurred due to the accumulation of phytotoxic ions, especially Na^+ and Cl^- . In addition to the osmotic and toxic effects, salt stress also induced oxidative stress; with all these factors contributing to the deleterious effects of salinity in plants [3–5]. Na^+ is sensed by a specific Na^+ -sensing module that has not been

identified yet. After early perception, upstream signaling responses are induced. K^+ , Ca^{2+} , H^+ , phospholipid, ROS, various protein kinases, and plant hormones are involved in the complex signal transduction network. Subsequently, transcription factors that regulate stress-responsive genes are induced. As a result, functional genes like ion transporter genes and antioxidant genes are efficiently expressed. Finally, plants that can survive and gain tolerance under salt stress account for the physiological adaptive responses like ROS scavenging. Every step on the chain is of great importance for plants to develop resistance, and that is where we can come in with modifications in plants on saline soil.

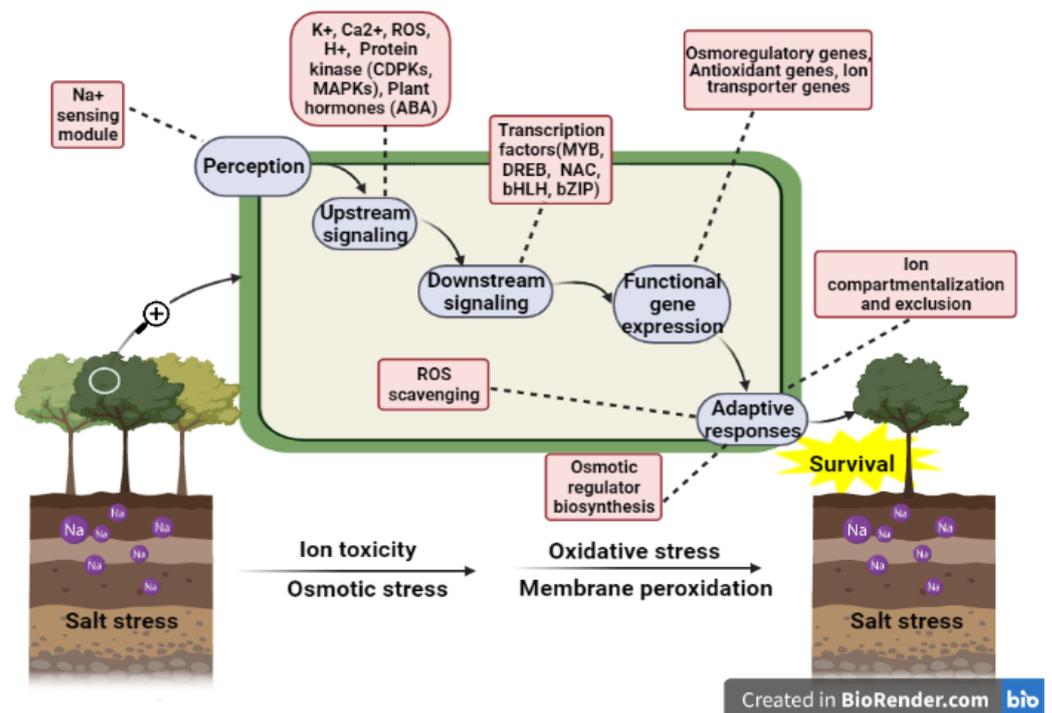


Figure 1. The process of plant salt tolerance development.

However, future works must build on what has already been done. A general understanding of the current research progress about plants under salt stress is always indispensable, which is the reason for writing this review. Different from other reviews on plant salt tolerance, which only focus on one area, our review covered a wider range of topics. In this review, we summarized the mechanism of plant salt injury, the mechanism of salt stress signaling, the mechanism of plant salt tolerance, and modifications we can implement on plants. Through this review, readers can have a more comprehensive and integrated understanding of the background knowledge of plants under salt stress. At the same time, we also put forward our views on the future research direction of this area. Thus, this paper may provide valuable background knowledge and genetic information for revealing plant salt tolerance mechanisms and for future plant cultivation. All abbreviations used in the text are listed in Table 1.

Table 1. Abbreviations and their full titles.

Abbreviation	Full Name	Abbreviation	Full Name
ROS	reactive oxygen species	ABA	abscisic acid
OST1	ABA-activated SnRK2 protein kinase open stomatal	CDPK	calcium-dependent protein kinase
MAPK	mitogen-activated protein kinase	QA/B	plastoquinone A/B
NADPH	reductive coenzyme	RuBP	ribulose-1, 5-bisphosphate
MDA	malondialdehyde	PPI	pyrophosphoric acid

Table 1. Cont.

Abbreviation	Full Name	Abbreviation	Full Name
AsA	ascorbic acid	MDHA	monodehydroascorbic acid
DHA	dehydroascorbic acid	GSH	glutathione
GSSG	oxidized glutathione	CAR	carotenoids
Ve	α -tocopherol	ABRE	ABA response element
P5CS	1 pyrroline—5—carboxylic acid synthetase	NSCC	non-selective cation channel
GDH	glutamate dehydrogenase	CAX	$\text{Ca}^{2+}/\text{H}^{+}$ antiporter
OAT	ornithine aminotransferase	VP	vacuolar H^{+} phosphorylase
ProDH	proline dehydrogenase	SOD	superoxide dismutase
BADH	betaine aldehyde dehydrogenase	POD	peroxidase
CMO	choline monooxygenase	APX	ascorbic peroxidase
TPS	trehalose phosphate synthase	CAT	catalase
FBP	1, 6-diphosphate fructose	GCL	glutamate cysteine ligase
TPP	trehalose phosphate phosphatase	MDHAR	monodehydroascorbic acid reductase
SPS	phosphate sucrose synthase	GS	glutathione synthase
CWIN	cell wall invertase	AspX	ascorbate peroxidase
VIN	vacuolar invertase	DHAR	GSH-dependent dehydroascorbic acid reductase
CIN	cytoplasmic invertase	GR	glutathione reductase
HKT	high-affinity K^{+} transporter	GST	glutathione S-transferase
NHX	$\text{Na}^{+}/\text{H}^{+}$ antiporter	SOS1	salt overly sensitive 1
KT	K^{+} transporter	SOS2	salt overly sensitive 2
SKOR	stelar K^{+} outward rectifier	SOS3	salt overly sensitive 3
GORK	guard cell outward rectifying K^{+} channel	ACA	Ca^{2+} -ATPase isomer
G6PDH	glucose-6-phosphate dehydrogenase	SuSy	sucrose synthase
CAM	calmodulin	Orn	ornithine
Glu	glutamate	PEPCase	phosphoenolpyruvate carboxylase
CAM	crassulacean acid metabolism		

2. Effects of Salt Stress on Plants

The plants suffering from salt stress show symptoms of slow growth, reduced growth of new branches, reduced plant height, reduced germination rate, and withered leaves according to previous studies. Salt stress leads to these results through two successive processes. Firstly, salt stress reduces the water absorption of plants resulting in the inhibition of plant growth, which is called osmotic stress. Then, if excessive salty ions get into the transpiration stream of plants, they will damage plant cells by inhibiting photosynthesis, impairing ion homeostasis, and peroxidating membrane lipids, thus further affecting plant growth, which is called ion toxicity [6,7]. In conclusion, knowing the physiological response mechanism of plants to salt stress is vital for improving the salt tolerance of plants (Figure 2).

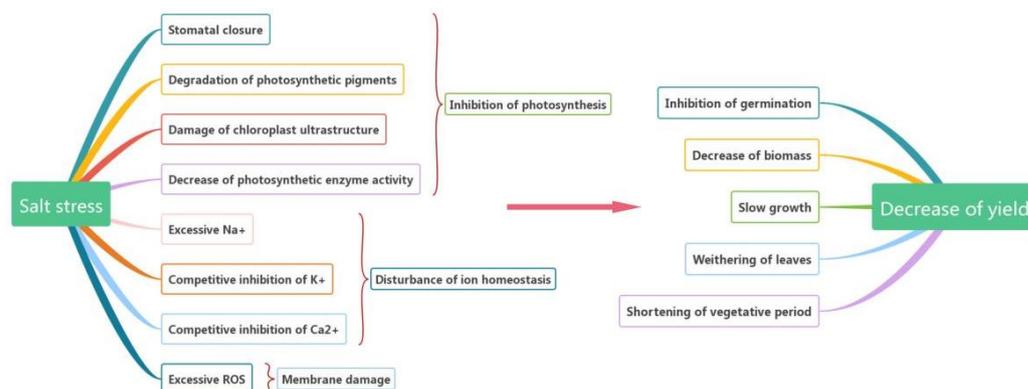


Figure 2. The mechanism of plant salt injury.

2.1. Inhibition of Photosynthesis

Photosynthesis is the main resource of the materials and energy needed for plant growth and development. Studies have shown that plant photosynthetic rate, osmotic potential, water potential, transpiration rate, leaf temperature, and relative water content of plant leaves are significantly affected under salt stress [8]. The components of photosynthetic structures, such as enzymes, photosynthetic pigments, thylakoid membrane proteins, and membrane lipids, are also affected by salt stress [3]. Salt stress adversely affects photosynthesis from two aspects. Firstly, the stoma of plants is closed under salt stress, which in turn decreases intercellular CO₂ concentration. Secondly, salt stress also leads to the damage of the photosynthetic membrane system, reduced CO₂ assimilation capacity [9], impaired photosynthetic pigments [10], and other restrictions unrelated to the stoma.

Stoma, located on the surface of plant leaves, are pores formed by a pair of specialized epidermal cells called guard cells. Stomatal movement controls the absorption of CO₂ in photosynthesis and the transport of H₂O in transpiration. Because of the absence of plasmodesmata, the thickening of cell walls, and the radial arrangement of microfilaments in mature guard cells, they can effectively respond to turgor pressure changes and regulate stomatal aperture [11]. A decrease in osmotic pressure in guard cells will result in water outflow, resulting in guard cell contraction and stoma closure. In most cases, salt stress increases the Na⁺ and Cl⁻ content in leaves, which subsequently reduces K⁺ content and eventually induces stoma closure [12]. The reduction of stoma opening seriously impedes the diffusion of CO₂ from the environment to the chloroplast, which leads to a decrease in intercellular CO₂ concentration and a decrease in photosynthetic rate.

In addition to stomatal restrictions, salt stress adversely affects many parts of photosynthesis without impacting the stoma. In salt-sensitive plants, salt stress often leads to the decrease in chlorophyll which is the most important pigment related to photosynthesis. According to Li et al., long-term moderate salinity, short-term drought, and the combination of these stressors decreased leaf pigment content by 11.4–31.5% in leaves of hybrid *Pennisetum* [13]. Similarly, in pepper [14], soybean [15], and rice [16], chlorophyll content was decreased after salt stress. Salt stress also affects the ultrastructure of chloroplasts. Thylakoid membrane, the most important structure in the chloroplast, is the site of light reaction. When plants are subjected to salt stress, the arrangement of chloroplasts in mesophyll cells is disordered, the connection between granum is loose, the cavity in the thylakoid is enlarged, the bilayer of chloroplast is damaged, and the lipid globules are increased [17]. This is found in most higher plants, such as *Sulla coronaria* [18], *Thellungiella salsuginea* [19], and *Cucumis sativus* [10].

Besides, salt stress affects photosynthesis by affecting related substances, especially enzymes and structural proteins involved in light energy absorption, photosynthetic electron transfer, and CO₂ fixation. Gao et al. found that glucose-6-phosphate dehydrogenase (G6PDH) has a close relationship with the photosynthetic process. They hypothesized that it may provide NADPH for the circulating electron flow around the PSI under salt stress in *Physcomitrella patens* [20]. Salt stress impairs the function of the oxygen-evolving complex [21], hinders electron transfer from plastoquinone A (QA) to plastoquinone B (QB), and impairs the function of the pigment–protein complex on the thylakoid membrane [22], resulting in the decrease in electron transfer efficiency. Rubisco, as a rate-limiting enzyme in photosynthesis, is affected by salt stress too. Salt stress reduces the activity of Rubisco, and restricts the regeneration of ribulose-1, 5-bisphosphate (RuBP), thus reducing the absorption and utilization of CO₂ by plants [23]. In conclusion, previous studies have shown that salt stress impedes photosynthesis of salt-intolerant plants by stomatal restrictions and non-stomatal restrictions.

However, not everyone agrees with views above. Although there have been many reports on the mechanism of salt stress on plant photosynthesis, no unified understanding has been formed so far. Some believe that physiological drought caused by salt stress causes stomatal closure. However, some studies have shown that the decrease in plant

water potential under salt stress is not synchronous with the decrease in photosynthetic rate. It is believed that the decrease in leaf water potential does not seem to cause stomatal closure [24]. Some believe that the increase in sugar concentration in plant tissues inhibits photosynthesis due to the feedback effect when plants grow in saline soils. However, this view cannot account for the very low carbohydrate content in the stems of perennial woody plants under long-term salt stress [25]. Therefore, the mechanism of a salt stress reducing plant photosynthesis needs to be further studied.

2.2. Disturbance of Ion Homeostasis

Mineral elements that usually exist as ions in plant cells are the components of the structural substances of cells. Mineral elements act as components of enzymes and coenzymes to regulate enzyme activity. They also play an electrochemical role in osmotic regulation, colloidal stabilization, and charge neutralization. The balance of ion metabolism plays an important role in maintaining the stability of the cell membrane and ensuring plant growth and development. The main causes of salt damage include excessive accumulation of Na^+ and Cl^- and the consequent deficiency of other vital ions, like Ca^{2+} and K^+ .

The high concentration of Na^+ in the soil leads to the accumulation of Na^+ in plants. Na^+ of a high concentration will reduce the membrane potential and promote the absorption of Cl^- under a chemical gradient. Excessive Na^+ is harmful to cell metabolism and some enzymes [26]. A high concentration of Na^+ leads to osmotic imbalance, membrane dysfunction, increased production of ROS, and thus affects cell division and growth [27]. A high concentration of Cl^- leads to a decrease in chlorophyll content and the destruction of the cell membrane system and organelle structure, which also impedes plant growth [28].

In addition to the toxic effect of Na^+ , it shows obvious competitive inhibition to K^+ on account of its similar ionic radius and hydration energy to K^+ . Most cells maintain a relatively high concentration of K^+ and a relatively low concentration of Na^+ in the cytoplasm to ensure their physiological activity. Therefore, a large amount of external Na^+ influx will hamper K^+ influx, which leads to plant damage caused by K^+ deficiency. As an important element involved in signal transduction of various physiological processes in plants, the Ca^{2+} level in cells is also decreased due to the competitive inhibition of Na^+ . Studies by Zhou et al. demonstrated that the value of $\text{Ca}^{2+}/\text{Na}^+$ reduced as a result of increasing NaCl concentration in flowering *Schizonepeta tenuifolia* [29]. According to Ottow et al., the regulation of osmotic pressure of plants under high concentrations of Na^+ is partly achieved through the compensatory decrease in Ca^{2+} [30]. In addition, the experiment of Song et al. indicated that the uptake of NH_4^+ and NO_3^- by plants would also be inhibited under salt stress [31]. In short, salt stress disrupts ion homeostasis in plant cells, thus affecting plant growth and development.

2.3. Membrane Damage

The cell membrane, as an important protective barrier of plant cells, plays an important role in substance transportation, energy transmission, and signal transduction. The selective permeability of the cell membrane enables it to regulate ion homeostasis and ensure the physiological activities of plants. However, under salt stress, the production of excessive ROS causes great damage to the membrane, increasing the membrane's relative permeability and reducing its fluidity. On the one hand, it affects the selectivity, flow rate, and transportation of ions. On the other hand, it also leads to the exosmosis of a large number of electrolytes, resulting in osmotic stress [32].

As one of the main products of membrane lipid peroxidation, MDA can inactivate proteins and enzymes on the membrane, thus destroying the structure and function of the biofilm. The content of MDA is an important index to reflect the degree of plasma membrane damage. Experiments by Li et al. illustrated that MDA content in *Carex rigescens* increased significantly after salt stress treatment [33]. According to Du et al., the MDA content showed an obvious increase in soybean under salt stress [15]. In addition, the increase of ROS can also destroy the structures of organelles in cells, such as the expansion

of the endoplasmic reticulum, fragmentation of the vacuole membrane. In a word, salt stress leads to excessive ROS production in plant cells, causing oxidative stress and harming plant growth and development.

The destruction of plant cell structure, the accumulation of ROS, and the disruption of ion homeostasis lead to the decrease in protein synthesis rate. Unable to synthesize protein, the accumulation of amino acids leads to the production of many toxic substances. For example, a large number of intermediates in nitrogen metabolism, including NH_3 and certain free amino acids (isoleucine, ornithine, and arginine), are converted to some toxic polyamines (e.g., butane diamine, glutamine, etc.). Those toxic polyamines, especially putrescine, in turn, are oxidized to NH_3 and H_2O_2 . If the concentration of these toxic substances accumulates to a certain level, they may cause harm to plants [34]. In conclusion, the accumulation of these substances will inhibit the synthesis of some important substances in plants, making the growth of plants inhibited.

2.4. Indicators for Salt Stress in Plants

Speaking of morphological indicators, the weight of shoot, root, and leaves, the length of roots and shoots, diameter of shoot are all frequently used in the evaluation of salt stress [35]. However, biomass is an indicator that can thoroughly represent the growth of plants under salt stress. In general, plant biomass decreases under salt stress, but the degree of decrease depends on plants. In tomato [36] and sunflower [37], the biomass decreased on 50 mM NaCl application while in wheat [38], rice [39], maize [40], the decrease of total plant biomass was observed at 100–150 mM NaCl levels. The biomass of halophytes like *salicornia* does not decrease until the NaCl level is above 400 mM [41].

When it comes to physiological indicators, first, measurement of Na^+ or Cl^- concentration in the leaves and roots reflects salinity stress in plants. K^+ content and K^+/Na^+ ratio are also frequently used. K^+ content decreased in *Arabidopsis* on NaCl application of 100 mM for 4 h [42]. In addition, ratios of other ions such as $\text{Na}^+/\text{Ca}^{2+}$, $\text{Ca}^{2+}/\text{Mg}^{2+}$, and $\text{Cl}^-/\text{NO}_3^-$ are usually evaluated as they influence nutrient uptake [43]. Besides, salinity stress decreases the photosynthesis process. Stomatal conductance, chlorophyll fluorescence, and chlorophyll contents are also measured under salt stress [44]. The decrease in chlorophyll content was observed under 100 mM salt application for 3d in wheat [45]. Salt stress is usually accompanied by osmotic stress. This is usually evaluated by the changes in turgor pressure, osmotic pressure, relative water content (RWC), and water potential. For example, water potential in tomatoes decreases upon treatment with 100 mM NaCl for 2 h [46]. RWC in maize decreases with the treatment of 60 mM NaCl for 7 d [47]. The ROS is dramatically increased upon salinity stress. The cell membrane damage is generally due to the enhancement in ROS production during the salt stress. Therefore, another indicator of salt stress is cell membrane injury and this can be determined by electrolyte leakage and water loss. For example, electrolyte leakage of sunflower increases on 100 mM NaCl application for 2d [48]. Moreover, lipid peroxidation indicators such as MDA content increase under salinity stress. Additionally, the instability of the membranes may be visualized by thermography and hyperspectral reflectance technique measurements based on the abilities of plants to reflect and absorb light at different wavelengths [49].

According to transcriptome analysis of plants under salt stress, the expression of some genes was changed under different salt concentrations. These genes can be used as molecular indicators to predict and confirm plant salt stress. Molecular indicators for stress evaluation are rarely used in practical research compared to morphological and physiological measurements, which are less costly and easier to perform. While many morphological and physiological indicators, like RWC, MDA content, and chlorophyll content, are triggered not only by salt stress but also other stresses, many morphological indicators, like plant height and shoot diameter, can only be detected when the plant has already been severely damaged. In contrast, molecular indicators may estimate the degree of salt stress early and more accurately. Still, each stress indicator, either morphological, physiological or molecular changes in plants, have their limitations. The integration of

morphological, physiological, and molecular approaches for plant stress detection requires future study.

3. Physiological Mechanisms of Plant Tolerance under Salt Stress

When plants are subjected to salt stress, there are two ways to reduce the damage caused by salt stress: to reduce the concentration of saline ions to the tolerable range or to enhance plant tolerance to salt stress. There are four ways for plants to avoid salt injury: salt excretion, salt dilution, salt accumulation, and salt exclusion. Salt excretion, common in halophytes, is a strategy by which plants maintain ion homeostasis by excreting excess salt out from their salt glands. Salt dilution is a strategy by which plants dilute the salt in their bodies by absorbing large amounts of water or by increasing the size of their cells. Salt accumulation is a strategy by which plants store excess salt in vacuoles to reduce its damage to other parts of the cell. Salt exclusion is a strategy by which plants prevent salt from entering their bodies with some special structures [50]. In addition to the above four ways to avoid the injury of saline ions, all higher plants can enhance their tolerance to salt stress through the following two physiological regulation processes, namely osmotic adjustment and ROS scavenging.

3.1. Osmotic Adjustment

The osmotic adjustment refers to the process by which plants maintain their ability to absorb water by increasing the concentration of solutes in their cells. There are two mechanisms of osmotic adjustment under osmotic stress. On the one hand, the solute itself acts as an osmolyte. On the other hand, solutes play a protective role by stabilizing the structure of biological macromolecules. A hypothesis may explain the mechanism: the hydrophobic regions on the protein surface are weak in binding to water molecules, especially in hypertonic environments. Cells lose this part of water first in a hypertonic environment [51]. The osmotic regulators can be dissolved in the binding water on the surface of proteins and the surface polarity of proteins can be enhanced by forming hydrogen bonds, to improve their adhesion to water [52]. Osmotic regulators mainly include two categories: (1) Organic substances and (2) Inorganic ions. Under osmotic stress, the content of these substances will increase to different degrees in cells.

3.1.1. Organic Substances

Organic solutes can generally be classified into three categories. (1) Free amino acids, mainly proline. Proline has a strong hydration ability. Its hydrophobic end can bind to proteins, while its hydrophilic end can bind to water molecules. Proteins attached with proline can bind more water, thus preventing protein dehydration and denaturation under osmotic stress. Plants can accumulate proline by increasing proline synthesis and decreasing proline degradation to respond to stress [53]. Furthermore, proline can also act as an antioxidant to remove excessive ROS produced under stress. As a fast compensated nitrogen and carbon source, it can help plants recover from stress. As a signal of stress, it activates multiple responses related to stress [54]. Many experiments have shown that an external application of proline can reduce the damage of salt stress to plants. For example, Wani et al.'s experiment suggested that treatment with proline to two contrasting cultivars of *Brassica juncea* could in some way counteract the adverse effects of salinity on photosynthesis and seed yield [55].

Glycine betaine is also an osmotic regulator. Betaine is obtained by the oxidation of choline by choline monoxygenase (CMO) and betaine aldehyde dehydrogenase (BADH). There are 12 kinds of betaine in plants, the simplest and most studied is glycine betaine. It could help plant cells maintain membrane integrity and enzyme activity under salt stress, thus reducing the damage caused by salt stress. Many higher plants, especially plants of chenopodiaceae and gramineae, have been found to accumulate betaine under salt stress. According to Gao et al., an up-regulation of glycine betaine biosynthesis was found in halophytic seashore paspalum under salt stress induced by choline [56]. Many experiments

also proved the benefit of the external application of betaine on the plant under salt stress. Experiments by Chen et al. showed that exogenous glycine betaine mitigated salt stress in maize seedlings [57]. In addition, betaine is involved in many metabolic processes. For example, methylated betaine is involved in the synthesis of other plant alkaloids according to Byerrem et al. [58] Betaine can also stabilize the peripheral polypeptide of the PS II, which is beneficial to maintain the physiological function of chloroplast at low water potential.

Soluble carbohydrates and polyols can also be used as osmotic regulators. Non-structural carbohydrates (such as glucose, sucrose, fructan, starch, etc.) are important substances involved in plant metabolism. In particular, sucrose production, transportation, storage, and consumption are closely related to plant development and environmental response. When plants are under osmotic stress, sucrose synthesis is increased by increasing the activity of sucrose phosphate synthase (SPS). In Peng et al.'s study, they found that as sucrose and starch contents in the cotton (*Gossypium hirsutum* L.) main-stem leaf and its subtending leaf boll both increased, so did the activities of sucrose phosphate synthase (SPS) and sucrose synthase (SuSy) [59]. A great decrease in starch synthesis could also maintain the content of sucrose in plant cells in *Phaseolus vulgaris*. Although osmotic stress reduced the activity of sucrose phosphate synthase (SPS), it caused a greater reduction of starch synthesis so that the concentration of sucrose could maintain a relatively high level [60]. Therefore, sucrose metabolism in plants is often used to measure the degree of environmental stress and the adaptability of plants to the environment. In addition, trehalose [61] and fructan [62] were also found to accumulate in plants under salt stress. More importantly, soluble sugars are involved as signaling substances in plant response to the environment, and sugar signaling has become a valuable area of research [63]. Polyols, especially mannitol and inositol, also play a role in osmotic adjustment, enhancing the salt tolerance of plants [64].

3.1.2. Inorganic Ions

Inorganic ions, mainly K^+ , Na^+ , and Cl^- , consist of 80% to 95% of the osmotic pressure of cells in dicotyledons [65]. K^+ is an essential element for plant growth and plays an important role in preventing plant cell damage under salt stress. Chakraborty et al. demonstrated that exogenous K^+ application improved the water status of plants, leading to higher biomass and better salt tolerance under stress in peanuts [66]. For halophytes, the absorption of Na^+ is much greater than that of K^+ . Most of the Na^+ absorbed by plant cells does not exist in the cytoplasm but is isolated in vacuoles as an osmotic regulator to maintain cell turgor pressure [67]. For example, the seedlings of a salt-sensitive cabbage cultivar and a salt-tolerant cabbage cultivar were exposed to $NaCl$ for 30 days. The results indicated that separating Na^+ into vacuoles was the main strategy of salt adaptation in Chinese cabbage [68].

In terms of Cl^- , the rapid uptake of Cl^- by plants in the early stage of salt stress promoted osmotic regulation of the root system in non-halophytes. However, Cl^- still relies on Na^+ or K^+ to complete the regulation of osmotic pressure [69]. Ca^{2+} in the cytoplasm is an important component of signal transduction. When plants are subjected to salt stress, Ca^{2+} channels are induced to open. Then Ca^{2+} is released from the vacuole. Ca^{2+} binding with calmodulin or other calcic binding proteins regulates cell metabolism and gene expression, promoting plant adaptation to adversity. In a word, plants maintain their ability to absorb water from the environment by increasing the concentration of inorganic ions like K^+ , and organic substances like proline and betaine under salt stress.

3.2. Scavenging of ROS

In the process of metabolism, oxygen will be activated into free radical ROS and non-radical ROS. Free radicals usually include superoxide radical ($O_2^{\bullet-}$), hydroxyl radical (OH^{\bullet}), and alkoxy radical (RO^{\bullet}), while non-radicals usually include hydrogen peroxide (H_2O_2), and singlet oxygen (1O_2) [70]. As the by-products of aerobic metabolism, ROS are found to generate naturally in plants. Under normal conditions, there is a balance between

the production and scavenging of ROS kept by the action of the antioxidant defense system within the plants. At the same time, ROS are also signals that regulate many important biological processes. In particular, they can be used as injury signaling molecules to induce plant response to stress [71]. However, when exposed to a stressful environment, the over-generation of ROS disrupts the equilibrium between ROS accumulation and scavenging, causing oxidative damage of cells [72]. In the long-term evolution of plants, they have developed a multifaceted antioxidant defense network to reduce ROS overgeneration under different abiotic stresses. The antioxidant defense system consists of two different types of antioxidants, namely enzymatic antioxidants (SOD, superoxide dismutase; CAT, catalase; POD, peroxidases; APX, ascorbate peroxidase; MDHAR, monodehydroascorbate reductase; DHAR, dehydroascorbate reductase; GR, glutathione reductase; GPX, glutathione peroxidase; GST, glutathione S-transferase) and non-enzymatic antioxidants (AsA, ascorbic acid; GSH (Figure 3), glutathione; CAR, carotenoids; α -tocopherol; some alkaloids; some flavonoids) [73].

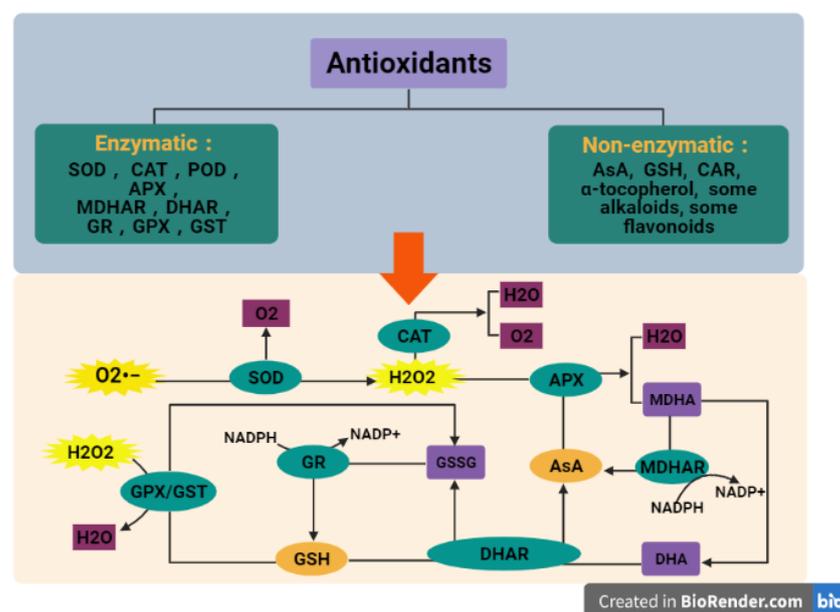


Figure 3. Antioxidant defense mechanisms. Additional details are in the text.

3.2.1. Enzymatic Antioxidants

In the whole antioxidant enzymatic system of plants, SOD forms the first line of defense against oxidative stress in plants. It dismutates $O_2^{\bullet-}$ into H_2O_2 . According to the difference of SOD-binding metal ions, SOD can be classified into CuZn-SODs, Mn-SODs, and Fe-SODs. Fe-SODs are mainly distributed in the chloroplast, Mn-SODs in mitochondria, and CuZn-SODs in chloroplast, cytoplasm, and extracellular space [74]. In Yan et al.'s study, CuZnSOD was transferred into a salt-sensitive sweet potato with the stress-inducible SWPA2 promoter. A significant increase in expression level in the transgenic plants was found under salt stress compared with wild type [75].

The main function of POD is to oxidize phenolic compounds (PhOH) to produce phenoxyl radical (PhO \bullet), where H_2O_2 contributes to this reaction as an electron acceptor, and it is converted to $2H_2O$ [76]. POD widely exists in different tissues of plants. As an adaptive enzyme with high activity, it can reflect the characteristics of plant growth and development, metabolism status in vivo, and adaptability to the external environment. In He et al.'s experiments, POD activity was detected to have increased with the help of AMF (*arbuscular mycorrhizal* fungi) to respond to the ROS damage under NaCl treatment [77].

CAT can rapidly decompose H_2O_2 , producing H_2O and O_2 . In plants, the higher the CAT activity is, the smaller the increase ratio of H_2O_2 is, which shows its ability to alleviate oxidative damage. CAT has been found to have three isoenzymes, CAT1, CAT2, and CAT3,

mainly found in peroxisomes and glyoxysomes [78]. Gondim et al. studied the effect of H_2O_2 pretreatment on maize leaves. CAT showed the strongest response to H_2O_2 and the highest activity at the beginning of treatment, indicating its role in ROS scavenging in plants [79].

APX can catalyze the formation of MDHA from AsA using H_2O_2 as an oxidant. The APX isoenzymes of higher plants are classified into two groups: cytosolic APX (cAPX) and chloroplasts APX (chlAPX). Chloroplasts APX includes stroma APX (sAPX) and thylakoid-bound APX (tAPX). The cytoplasmic types include microsomes (peroxisomes, glyoxysome) isoenzymes, and some isoenzymes whose location in the cytoplasm is still unclear [80]. All isoenzymes can participate in the detoxification of H_2O_2 and the oxidation of AsA to produce MDHA and subsequently DHA. In Shafi et al.'s study, *Arabidopsis thaliana* transgenics overexpressing cytosolic CuZn-superoxide dismutase (PaSOD), cytosolic ascorbate peroxidase (RaAPX), and dual transgenics overexpressing both the genes showed changes in genes related to secondary cell wall cellulose biosynthesis and salt stress response [81].

Other enzymes do not act directly on ROS but are involved in AsA and GSH regeneration in the AsA-GSH cycle (Figure 3). MDHAR is an NADH or NADPH-dependent enzyme involved in the AsA regeneration from MDHA [82]. DHAR catalyzes the oxidation of DHA to achieve AsA regeneration [83]. In the AsA-GSH cycle, GR is another important enzyme that regulates redox homeostasis by reducing GSSG to GSH [84]. Enzyme GPX can use GSH and thioredoxin to reduce H_2O_2 and protect cells from oxidative damage [85] with the help of GST [86]. In the study of Gaafar and Seyam, they found solid evidence to prove the involvement of the AsA-GSH cycle in the salt tolerance mechanism of Egyptian lentil cultivars (*Lens culinaris Medikus*) [87].

3.2.2. Non-Enzymatic Antioxidants

AsA is a strong water-soluble antioxidant that is abundant in active growth sites such as meristem, photosynthetic cells, root tips, flowers, and young fruits [88]. Normally, AsA is significantly involved in scavenging ROS under stress by donating electrons as a co-enzyme. AsA also participates in regenerating α -tocopherol, which is also an important antioxidant [82]. Besides, AsA is also considered to be an important signal substance in regulating cell redox state and plays an important role in the photosynthetic system, mitochondrial electron transport [89]. Many studies have reported the stimulative effect of exogenous AsA on plant growth and the enhancement of plant resistance under salt stress. For example, exogenous AsA significantly improved the growth of wheat seedlings under water shortage [90].

Reduced glutathione (GSH) and oxidized glutathione (GSSG) coexist in plants and can be transformed into each other. GSH plays a critical role in regulating intracellular defense by scavenging ROS. Besides, GSH maintains redox homeostasis as a component of the AsA-GSH cycle [91]. In the first step of the AsA-GSH cycle, H_2O_2 is reduced to water by APX using AsA as the electron donor. The oxidized AsA (MDHA) is regenerated by MDHAR. However, MDHA is a free radical, and if not rapidly reduced it will turn into DHA. DHA is reduced to AsA by DHAR at the expense of GSH, yielding GSSG. Finally, GSSG is reduced to GSH by GR using NADPH as the electron donor. Thus AsA and GSH are not consumed [92]. In Wang et al.'s experiment, exogenous AsA and GSH enhanced the activities of SOD, APX, and GR in the chloroplasts of two rice varieties under salt stress, increased the contents of endogenous AsA and GSH, and decreased the contents of H_2O_2 and MDA, indicating that exogenous AsA and GSH could be useful for ROS scavenging and salt stress resistance [93].

CAR can be used as light-collecting auxiliary pigments in chloroplasts. It can also remove ROS produced by photosynthetic apparatus. CAR protects the photosystem in four ways: they interact with lipid peroxidation products to terminate the chain reaction; remove singlet oxygen and dissipate it in the form of heat energy; react with triplet or activated chlorophyll molecules to prevent the formation of singlet oxygen; dissipate excess energy through the lutein cycle [94].

In addition, tocopherol, especially α -tocopherol (Ve), is also an important ROS scavenger in plants. It captures ROS and free radicals produced by lipid peroxidation to regulate the stabilization of membrane lipid. Flavonoids are active oxygen scavenging agents mainly studied in recent years, but it was found that they can only work at or near the site where ROS are produced, such as vacuole or a cell wall [95]. Osmotic regulatory substances such as proline [96] and mannitol [97] are also found to have the ability to scavenge ROS. All in all, plants scavenge ROS with the help of an enzymatic and non-enzymatic system to alleviate the damage of salinity.

3.3. Other Physiological Regulation under Salt Stress

The presence of ion compartmentation in both halophytes and non-halophytes suggests that ion compartmentation is a universal capability of plants. The ion separation function of halophytes is different from that of non-halophytes. Generally, halophytes collect the absorbed saline ions in vacuoles and separate them from the cytoplasm, so that the cytoplasm is protected from the toxicity of saline ions. Non-halophytes, on the other hand, generally minimize the absorption of harmful saline ions and at the same time transport the absorbed saline ions to old tissues for storage, protecting young tissues at the expense of old tissues [98]. The compartmentation of saline ions depends on the transmembrane proteins like H^+ -ATPase, PPase, Ca^{2+} -ATPase, secondary transporters, and various ion channel proteins. First of all, H^+ -ATPase, and H^+ -PPase on the membrane or vacuolar membrane generate energy by hydrolyzing ATP or pyrophosphate (PPI) to pump H^+ out of the cell, forming a transmembrane potential gradient [99]. The Na^+/H^+ antiporters on the membrane and vacuolar membrane, which are closely associated with proton pumps, then transport Na^+ into the cell along the potential gradient. Likewise, ions can be transported into the vacuole to reduce the osmotic potential in the cytoplasm. Under salt stress, the activity of Na^+/H^+ antiporters is inhibited, but the influence of this hindrance can be eliminated by increasing the content of unsaturated fatty acids on the cell membrane [100]. Na^+/H^+ antiporters, which ensure Na^+ compartmentation in the vacuole, greatly reduce the osmotic potential of the vacuole and reduce the damage of Na^+ to the cytoplasm.

The three carbon assimilation pathways in higher plants are the C3 pathway, C4 pathway, and the crassulacean acid metabolism (CAM) pathway. Compared with C3 plants, C4 and CAM plants maintain a higher photosynthetic rate and water use efficiency, as well as higher stress resistance in drought, salt, and other adverse environments. Meanwhile, C4 or CAM metabolism can be induced from C3 metabolism [101]. A high concentration of Cl^- can activate phosphoenolpyruvate carboxylase (PEPCase) in the C3 pathway, resulting in the conversion of C3 pathway to the CAM pathway [102]. In high salinity soil, C3-CAM plant, *Mesembryanthemum crystallinum*, converted from the C3 mode to the CAM mode to reduce water loss during daytime [103].

Salt vesicle is one of the characteristics of salt resistance in higher plants. It is a kind of large and highly vacuolized cell converted from the trichome. The structure and size of salt vesicles vary from species to species [104]. The salt vesicle of Chenopodiaceae plants consist of epidermal bladder cell (EBC), stalk cell (SC), and epidermal cell (EC), which is called EC-SC-EBC complex. The functions of salt vesicles in plants mainly include storage of excess salt in plants [105]; storage of water to protect plants from short-term osmotic stress [106]; storage of organic osmolytes; storage of ROS scavengers [107]; storage of photosynthetic protein [108], etc. We have revealed a big part of the mechanism of salt vesicle, but only at the cellular level. The mechanism of the whole salt secretion process is not complete and needs to be further supplemented. At the molecular level, there are few studies on the development of salt vesicles. The key genes that control the development of salt vesicles have not been found. Moreover, whether the related genes controlling the development of salt vesicles are related to salt tolerance is also worth paying attention to.

4. Salt Stress Signal Transduction System

Under salt stress, various stress-inducible signals intersect with each other and form a complex network to regulate the physiological response of plants to salt stress. Several signal transduction pathways that respond to salt stress in plants have been studied. According to whether Ca^{2+} is involved in the process, they can be classified into two categories, which are a Ca^{2+} -dependent signal transduction pathway (SOS pathway, ABA pathway, CDPK pathway) and a Ca^{2+} -independent signal transduction pathway (MAPK pathway).

4.1. Ca^{2+} -Dependent Signal Transduction Pathway

Under salt stress, Ca^{2+} concentration in plant cells increases sharply. In addition to being an osmotic regulator, Ca^{2+} has long been considered as a signal molecule involved in salt stress signal transduction. The participation of Ca^{2+} as a second messenger mainly depends on the change of Ca^{2+} concentration in cells. Plant cells control Ca^{2+} influx and efflux by different Ca^{2+} channels, Ca^{2+} pumps, and $\text{H}^+/\text{Ca}^{2+}$ antiporters located on the cell and organelle membranes. Thus, cells can flexibly regulate the changes of Ca^{2+} concentration and intensity, and trigger the cascade of different signaling pathways [109].

4.1.1. SOS Pathway

When plants are exposed to high salinity, a high concentration of Na^+ enters the cytoplasm through non-selective cation channels (NSCC) and high-affinity potassium transporters (HKT). A high concentration of Na^+ in the cytoplasm can cause ion toxicity to cells. Plant cells discharge Na^+ from the cytoplasm or separate Na^+ into vacuoles mainly through the SOS signal transduction pathway. In *Arabidopsis thaliana*, the *SOS1* gene encodes an Na^+/H^+ antiporter located on the plasma membrane. It is involved not only in Na^+ excretion at the cellular level [110] but also in Na^+ transport from root to aboveground [111]. The *SOS2* gene encodes a Ser/Thr protein kinase with a catalytic region at the N-terminal and a regulatory region at the C-terminal [112]. *SOS3* gene encodes a Ca^{2+} binding protein [113]. *SOS3* protein can interact with the regulatory region at the C-terminal of *SOS2* protein to activate the activity of *SOS2* kinase [114]. Activated *SOS2* protein then enhances the transporter activity of *SOS1* by phosphorylating it [115].

Therefore, the SOS signal transduction mode is: high external Na^+ induces internal Ca^{2+} increase. *SOS3* first binds to Ca^{2+} and then to *SOS2*. *SOS3* activates *SOS2* kinase activity by disinhibiting the self-inhibition of *SOS2*. Subsequently, the complex of *SOS3* and *SOS2* phosphorylates the *SOS1* transporter located on the plasma membrane, enhancing its ability to transport Na^+ out of the cell. *NHX1* is also a Na^+/H^+ antiporter located on the vacuole membrane. It can transport not only Na^+ but also K^+ into the vacuole by a proton gradient. In addition to participating in the salt response process, *NHX1* also regulates the pH in the vacuole, K^+ concentration, vesicle transport, and protein localization [116]. *SOS* kinases regulate Na^+ to enter vacuoles by regulating *NHX1*, which is also regulated by ABA [117]. Because *NHX* needs a proton gradient to provide energy during Na^+ transport, there is a lot of H^+ -ATPase and H^+ -PPase on the vacuole membrane to promote Na^+ compartmentation [118]. Qiu et al.'s experiment showed that the process that transports Na^+ into vacuoles is not completely dependent on *SOS3*. The homologous protein ScaBPs of *SOS3* can also play the same role [119].

4.1.2. ABA Pathway

Stress induces the accumulation of ABA in plants, which plays an important role in multiple stress-related signal transduction networks. Salt stress firstly induces ABA synthesis by regulating the expression of the ABA synthase genes through a Ca^{2+} dependent signaling pathway. The ABA synthesized by this method can further promote ABA synthesis through a positive feedback mechanism [120]. Salt stress mainly induces the accumulation of ABA in roots. In addition to participating in the response to salt stress in the rhizosphere, ABA can also be transported to active sites of growth through the xylem. Then ABA will be redistributed in plants according to the pH values of different sites [121].

After redistribution, ABA responds to salt stress mainly by regulating the stomatal opening and inducing the expression of resistance genes.

ABA can regulate the expression of corresponding genes directly without the participation of Ca^{2+} . In the absence of ABA, the phosphatase ABI1-insensitive1 (ABI1) [122] inhibits the action of SNF1-related protein kinases (subfamily 2) (SnRK2s). ABA is perceived by the PYR/PYL/RCAR family proteins. When the PYR/PYL/RCAR family protein binds to ABA induced by abiotic stress, the complex inhibits the action of ABI1. When SnRK2s are released from inhibition, they activate several transcription factors from the ABA-responsive element-binding factor (ABF) family. ABFs then regulate the expression of a large number of stress-related genes [123]. It can also be transformed into a Ca^{2+} signal for indirect regulation. ABA increases the Ca^{2+} concentration of cytoplasm by promoting the activity of selective Ca^{2+} channels on the plasma and vacuole membrane [124]. Then, Ca^{2+} -dependent phosphorylations, in turn, activate the activity of OST1 (ABA-activated SnRK2 protein kinase open stomata 1), which is inhibited by 2C-type protein phosphatases (PP2C). OST1 further regulates the activity of guard cells SLAC1 anion channel (slowly activating anion conductance 1) and K^+ channel KAT1, resulting in stomatal closure (Figure 4) [125].

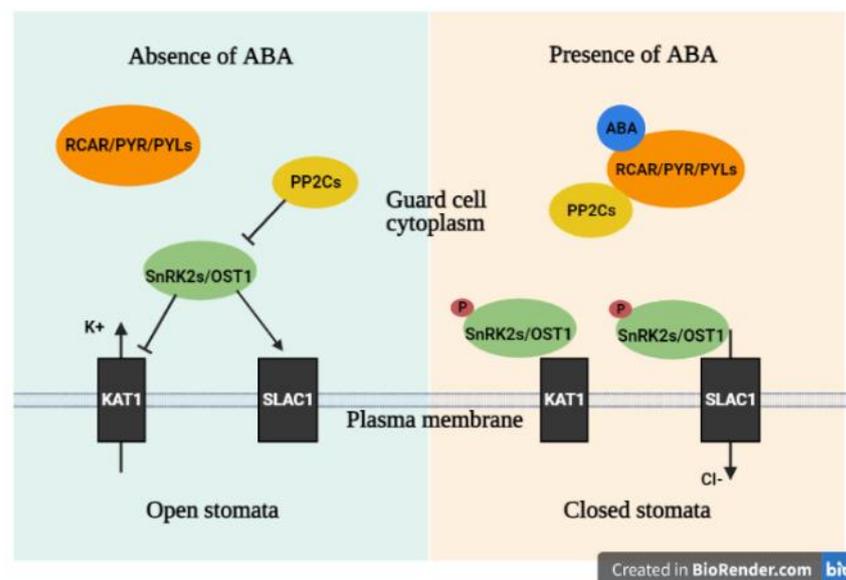


Figure 4. The mode of ABA regulating stomatal closure. Additional details are in the text.

4.1.3. CDPK Pathway

Ca^{2+} -dependent protein kinases (CDPKs) are widely distributed in plants. Subcellular localization shows that CDPKs can exist in either membrane-bound or a membrane-free state in cells. Most of them are located on the plasma membrane and organelle membrane. They are involved in the regulation of the whole process of plant growth and development, and the process to resist abiotic stress [126]. It is generally believed that CDPKs regulate plant tolerance to salt stress mainly through regulating the stomatal opening and the expression of ion channel-related genes. The CDPK genes have been identified in a variety of plants, which decode transcription factors related to signal transduction, thereby increasing the activity of protein kinase and other downstream signaling elements [127]. CDPKs can also regulate the balance of ROS by inducing the expression of antioxidant genes and inhibiting the expression of NADPH oxidase, thus playing a role in the response to oxidative stress and improving the salt tolerance of plants [128].

4.2. Ca^{2+} -Independent Signal Transduction Pathway (MAPKs Cascade)

As one of the most important signal transduction pathways in plants, MAPK cascades can gradually amplify environmental signals through protein phosphorylation catalyzed

by protein kinases. It can communicate a signal from a receptor on the surface of the cell to the DNA in the nucleus of the cell [129]. MAPK cascades consist of three protein kinases MAPKKK (MAP kinase, kinase, kinase), MAPKK (MAP kinase, kinase), and MAPK, which are in turn activated by phosphorylation. MAPKKK is the most upstream protein kinase in the MAPK cascade, which is activated by the signals transduced by receptor kinase on the plasma membrane through phosphorylation. MAPKKK activates MAPKK by phosphorylating the S/T-X₃₋₅-S/T motif in the conserved region of MAPKK (S represents serine, T represents threonine, X represents any amino acid, and 3–5 represents the number of amino acids). MAPKK activates MAPK by phosphorylating the serine/threonine and tyrosine residues between the seventh and eighth subdomains of MAPK. As the most downstream of the whole cascade, MAPK enters the nucleus and activates the activity of specific transcription factors to induce the expression of corresponding functional genes, resulting in plant cells in a series of physiological and biochemical reactions (Figure 5) [130]. The MAPK cascade can transduce many kinds of signals, such as ROS signals [131]. Under osmotic stress, plant cells perceive ROS signals through specific receptors. Once ROS is sensed, it induces Ca²⁺ signaling and activates protein kinase OxI1 (Oxidative signal-induced kinase 1), thus activating the MAPK cascade [132].

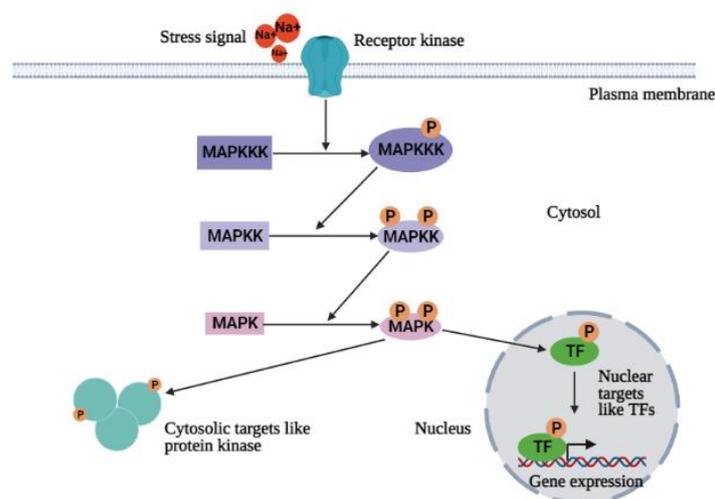


Figure 5. The mode of the MAPK cascade. Additional details are in the text.

All in all, there is a complex network consisting of various stress-inducible signal pathways to regulate the physiological response of plants to salt stress. The SOS pathway, ABA pathway, CDPK pathway, and MAPK pathway are the only four that we know better and that play more important roles. In recent years, more and more components involved in salt stress signal transduction have been identified, but some questions remain to be further studied. The specificity and cross-reactions of the various signal transduction pathways in plants under salt stress are still poorly understood. How signal transduction networks differ in response to different abiotic stresses and how multiple signals interact with each other in the presence of multiple abiotic stresses are also worth investigating in the future.

5. Salt Tolerance Related Genes

The molecular mechanism of plant salt tolerance is the basis of its physiological mechanism. At present, research into salt-responsive genes in higher plants mainly focuses on osmolyte-related genes, antioxidation-related genes, ion transporter genes, signal transduction-related genes, and regulatory genes, as shown in Table 2 and Figure 6.

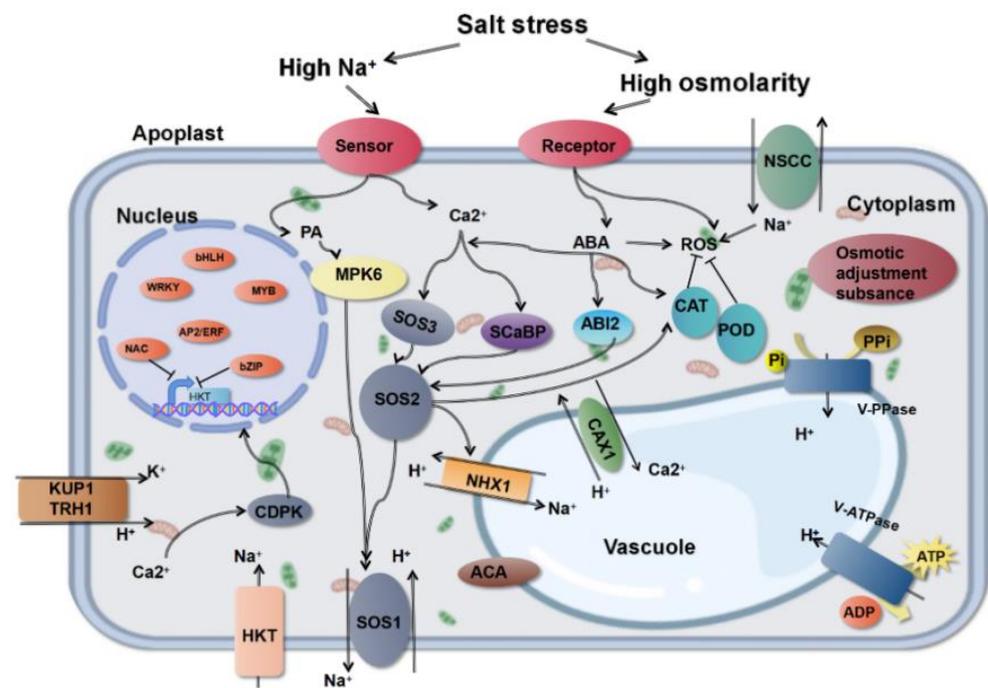


Figure 6. Important regulatory networks in response to salt stress in plants. Additional details are in the text.

5.1. Osmotic Adjustment Related Genes

Plants can accumulate small molecule solutes or other osmotic agents under salt stress. The introduction of osmotic regulator synthase genes enables plants to synthesize more osmotic regulators (such as proline, betaine, trehalose, mannitol, fructan, glycogen, etc.) under water stress. At present, the metabolic pathways of proline in plants are clear. There are two pathways for the synthesis of proline in plants: the Glu pathway and the Orn pathway. The initial substrates are Glu and Orn, respectively. Each pathway is regulated by key rate-limiting enzymes. The key enzymes of the Glu pathway are $\Delta 1$ pyrroline—5—carboxylic acid synthetase (P5CS) and glutamate dehydrogenase (GDH); the key enzymes in the Orn pathway are ornithine aminotransferase (OAT) and arginase. Proline dehydrogenase (ProDH) is the key enzyme of proline degradation [133]. For example, Chen et al.'s [134] experiment indicated that the introduction of *P5CS1* and *P5CS2* cDNA in transgenic *Arabidopsis thaliana* can lead to excessive production of proline and improve salt tolerance. The synthesis of glycine betaine in plants is mainly accomplished by two steps of enzymatic reactions. The first step is the oxidation of choline into betaine aldehyde catalyzed by CMO. The second step is the oxidation of betaine aldehyde to betaine catalyzed by BADH [135]. Liu et al. isolated and characterized a salt stress-responsive BADH, LrAMADH1, in *Lycium ruthenicum* Murr [136]. In Wang et al.'s study, the BADH gene was cloned from *Suaeda liaodongensis* and transformed into tomato (*Solanum lycopersicum*). The expression of *SIBADH* in P5:BADH transgenic plants showed higher salt tolerance [137]. OtsA-OtsB biosynthetic pathway of trehalose in plants consists of two steps: trehalose phosphate synthase (TPS) catalyzes the formation of trehalose-6-phosphate (Tre6P) from uridine diphosphate (UDP) glucose and glucose-6-phosphate. Then trehalose phosphate phosphatase (TPP) catalyzes the dephosphorylation of trehalose-6-phosphate (Tre6P) to form trehalose. Since the enzymes that catalyze the above two reactions in *Escherichia coli* are encoded by *OstA* and *OstB* respectively, the pathway is called the OstA-OstB pathway. Finally, trehalose is degraded by trehalase to yield two molecules of glucose [138]. The experiment of Krasensky et al. proved that plants deficient in *AtTPPD* were hypersensitive to salt, whereas plants overexpressing *AtTPPD* were more tolerant to high salinity, suggesting a role for *AtTPPD* in regulating sugar metabolism under salinity

conditions [139]. Besides, a novel tonoplast intrinsic protein GmTIP2;3 was found in soybean, which may play an important role in osmotic regulation [140].

Sucrose biosynthesis is a complicated process. In the process of sucrose synthesis, the main rate-limiting enzymes are 1, 6-diphosphate fructose (FBP), and sucrose phosphate synthase (SPS). During its degradation, sucrose invertase (including cell wall invertase CWIN, vacuolar invertase VIN and cytoplasmic invertase CIN) irreversibly catalyzes the hydrolysis of sucrose to glucose and fructose. It was found that the expression of the VIN gene and the activity of the VIN enzyme were up-regulated in maize leaves under moderate water shortage, which resulted in the increase of hexose accumulation in vacuoles, the improvement of osmotic potential, and a better water absorption capacity of the plant [141]. Proteomic analysis of mangrove plant *Bruguiera gymnorhiza* was performed by Tada and Kashimura. Three proteins differentially expressed under salt stress were identified by two-dimensional electrophoresis and internal peptide sequence analysis, and one of them was FBP. This result suggests that FBP plays a role in the mechanism of salt tolerance in mangrove plants [142].

5.2. Ion Transporter Related Genes

In the last two decades, dozens of ion transporters connected with salt tolerance have been identified in a variety of plant species. Among them, high-affinity K^+ transporter (HKT) and Na^+/H^+ antiporter (NHX, on the vacuolar membrane) play key roles in the absorption, long-distance transportation, and redistribution of Na^+ and K^+ . In addition, the K^+ transporter (KT) family, Arabidopsis K^+ transporter (AKT) family, stelar K^+ outward rectifier (SKOR) and guard cell outward rectifying K^+ channel (GORK) families, Ca^{2+} -ATPase (ACA, both on the plasma membrane and vacuolar membrane), NSCC, Ca^{2+}/H^+ antiporter (CAX), Vacuolar H^+ phosphorylase (VP), H^+ -PPase and plasma membrane H^+ -ATPase pump, are also involved in maintaining $Na^+/K^+/Ca^{2+}$ homeostasis under salt stress [143].

An HKT is a Na^+ or Na^+-K^+ transporter closely related to plant salt tolerance. It can unload excessive Na^+ from the xylem into surrounding parenchyma cells, reduce the content of Na^+ in shoot and maintain K^+ homeostasis in vivo [143]. According to the different transport of Na^+ and K^+ in the heterologous expression system, HKT proteins can be divided into two types: HKT1 mainly acts on the transport of Na^+ and mediates the absorption of Na^+ when the external K^+ is deficient; HKT2 has the function of K^+-Na^+ cotransporter [144]. Han et al.'s study on wild barley in Tibet showed that the knockout of *HvHKT1;1* caused the accumulation of Na^+ in roots and leaves. Overexpressing *HvHKT1;1* in salt-sensitive Arabidopsis *hkt1-4* and *sos1-12* mutant strains, Na^+ content in root and shoot was significantly decreased, indicating that *HvHKT1;1* plays an important role in the transport of Na^+ in roots [145], while a recent study found that, compared with the wild type, the translocation of Na^+ from root to shoot was significantly reduced and K^+/Na^+ was increased in the *HvHKT1;5* knockdown barley lines. *HvHKT1;5* Negative regulation in salt tolerance makes it different from other *HKT1;5* members, indicating that barley has a unique Na^+ transport system [146]. Kader et al. found that the transporter genes *OsHKT1*, *OsHKT2*, and *OsVHA* in rice were induced to be expressed under salt stress, and could reduce the concentration of Na^+ by regulating the ratio of Na^+/K^+ [147].

On the vacuolar membrane, NHXs, which are driven by a proton gradient formed by H^+ -ATPase and H^+ -pyrophosphatase, participate in the transportation of Na^+ , realizing the compartmentation of Na^+ in the vacuole [148]. The first NHX gene was found in *Arabidopsis thaliana* and was named *AtNHX1* [149]. Since then, such transporters have been found in various plants, for example, *Leptochloa fusca* *LfNHX1* [150], *Iris halophila* *IhNHX1* [151], and *Halostachys caspica* *HcNHX1* [152]. There are also many successful examples of *AtNHX* or other *NHX* genes being overexpressed in plants to make them stress-resistant. For instance, the salt tolerance of transgenic plants was significantly improved when *AtNHX1* was introduced into groundnut (*Arachis hypogaea*) [153] and *Torenia fournieri* [154]. The

same for *Pennisetum alopecuroides* PgNHX1 introduced into *Brassica juncea* [155], and *Vigna radiata* VrNHX1 introduced into *Arabidopsis thaliana* [156].

Since the energy of NHX protein to compartmentalize Na⁺ is mainly provided by the proton gradient produced by H⁺-ATPase and H⁺-PPase, it is speculated that the co-overexpression of VP and NHX or just the overexpression of VP can provide a stronger driving force for NHX to compartmentalize more Na⁺ into the vacuole. This hypothesis has been tested in a variety of plants. For example, Yang et al.'s study indicated that the overexpression of a *Populus trichocarpa* H⁺-pyrophosphatase gene *PtVPP1.1* confers salt tolerance on transgenic poplar [157]. In Brini et al.'s experiment, wheat *TaNHX1* and *TaVPP1* were co-overexpressed in *Arabidopsis thaliana* [158] and *Pennisetum alopecuroides* PgNHX1 and *Arabidopsis thaliana* AVP1 were co-overexpressed in tomato (*Solanum lycopersicum*) in Bhaskaran and Savithramm's experiment [159].

5.3. Antioxidant-Related Genes

Salt stress leads to the production of a large number of ROS. By overexpressing the genes of antioxidant enzymes, such as SOD, CAT, POD, and APX, ROS can be eliminated quickly. In recent years, many plant antioxidant enzyme gene families have been identified and their differential expression under abiotic stress has been analyzed. Verma et al. carried out the genome-wide identification and characterization of the abiotic-stress responsive SOD gene family in *Brassica juncea* and *B. rapa* [160]. Wu et al. carried through the identification and expression analysis of the class III POD gene family in Cassava [161]. Wang et al. conducted the genome-wide characterization and bioinformatics analysis of the CAT gene family in Cotton [162]. Tao et al. implemented the genome-wide investigation and expression profiling of the APX gene family in *Gossypium hirsutum* [163].

In addition to antioxidant enzyme gene families, there are other genes related to antioxidants. AsA and GSH are also important antioxidants in plants. They can achieve synergism and regeneration through the AsA-GSH cycle. By overexpressing key enzymes in this cycle, we can achieve high production of AsA and GSH, thereby enhancing the ability of plants to resist oxidative stress. GSH in plants is synthesized in two steps. First, Glu and Cys are catalyzed to form γ -glutamylcysteine by glutamate cysteine ligase (GCL), and then glutathione synthase (GS) catalyzes glycine and γ -glutamylcysteine to form GSH [164]. APX participates in detoxifying H₂O₂ and oxidizes AsA to produce MDHA. Furthermore, MDHA can be transformed into AsA with the help of MDHAR or can be spontaneously transformed into DHA [165]. DHA is further reduced to AsA by DHAR. Other key enzymes include GR, GSTs, etc. For instance, Horváth et al. reported that *AtGSTF8* and *AtGSTU19* were involved in *Arabidopsis* salt stress resistance by functioning in the root fine-tuning the redox homeostasis [166]. The main role of CAR is to remove ROS produced during photosynthesis. There are many kinds of CAR. Correspondingly, their synthesis pathways are varied, and different enzymes are involved in each step. In Sun et al.'s experiment, overexpression of the *Cerasus humilis* ChVDE gene, encoding a violaxanthin de-epoxidase, improves tolerance to drought and salt stress in transgenic *Arabidopsis* [167].

5.4. Signal Transduction-Related Genes

Previous studies have identified six genes directly or indirectly associated with salt tolerance in the *Arabidopsis* SOS gene family. SOS3 and SOS2 located in the cytoplasm can regulate the ion homeostasis of K⁺ and Na⁺ by regulating SOS1 on the plasma membrane, thus enhancing salt resistance. Among them, SOS1 is a gene directly related to plant salt tolerance in the SOS family [168]. SOS4 enhances salt tolerance by regulating the activity of SOS1 and other ion transporters and the development of root hair under salt stress [169]. The SOS5 protein located outside the plasma membrane plays an important role by promoting cell wall development and enhancing junctions between cells [170]. SOS6 plays an important role in regulating cell osmotic stress and oxidative stress [171]. At the same time, great progress has also been made in the identification of SOS gene families

in other species of plants. Cheng and her team completed the Genome-wide identification and gene expression analysis of SOS family genes in tuber mustard (*Brassica juncea* var. *tumida*) [172]. Zhao et al. carried out the isolation and characterization of SOS family genes in spinach (*Spinacia oleracea*) [173].

In the ABA signaling pathway, ABA regulates plant salt tolerance through signaling to Ca^{2+} and inducing reversible protein phosphorylation. Ca^{2+} activated protein kinases can be involved in regulating the expression of salt stress response genes. ABFs/AREBs (ABRE binding factors) are a class of regulatory factors involved in ABA-dependent gene expression, which regulate the expression of corresponding genes through binding with ABA-responsive elements (ABRE) [174]. ABA does not act directly, but through inducing these AREBs, thus it is believed that overexpressing these AREBs can enhance plants' tolerance to abiotic stress. Li et al. suggested that *PpSARK* (Senescence-associated receptor-like kinase) functions as a positive regulator in salt stress responses through an ABA-related pathway in *Physcomitrella patens* [175]. Zhang and his team found that *OsNAC45* plays a key role in ABA signal responses and salt tolerance in rice [176]. Xu et al. revealed that *OsMADS25* may be an important transcription factor that regulates rice root growth and salt tolerance through ABA-mediated regulatory pathways and ROS scavenging [177].

Protein kinases, especially CDPKs and MAPKs, play an important role in regulating plant response to abiotic stress as an important signal transduction element. CDPK gene families have been identified and analyzed in many species of plants. Among them, 34 CDPK members have been found in *Arabidopsis thaliana* [178], most of which are related to stress signaling. In ion flux analysis, *cpk27-1* mutants that were more sensitive to salt stress had lower capacities for Na^+ excretion and H^+ uptake than wild-type plants after long-term salt treatment, indicating that *AtCDPK27* plays a role in *Arabidopsis* adaptation to salt stress [179]. Under NaCl treatment, the level of Na^+ in the roots of *cpk12-RNAi* plants increased, and was higher than that of wild-type plants, suggesting that *AtCPK12* was required for plants to adapt to salt stress [180]. *AtCPK6* is involved in the positive regulation of methyl jasmonic acid signaling in guard cells under salt and drought stress [181]. *AtCPK8* interacts with *CAT3* and regulates the activity of *CAT3* by phosphorylating the 261st serine residue of *CAT3*, thereby regulating the ability of plants to scavenging ROS [182]. In the past two decades, members of MAPK involved in salt stress response have been found in a variety of plants. In *Arabidopsis*, *AtMEKK1* activates downstream kinases *AtMPK4* and *AtMPK6* by phosphorylating *AtMKK2* and *AtMEK1* in response to high salt stress [183]. According to Yang et al., overexpression of *Populus trichocarpa PtMAPKK4* enhances salt tolerance in tobacco [184]. In Wang et al.'s study, when grape *VvMKK2* and *VvMKK4* genes were overexpressed in transgenic *Arabidopsis thaliana*, the seedling growth was better than that of wild type under stress conditions. Overexpression of *VvMKK2* increased the tolerance of *Arabidopsis* to both salt and drought stress, while overexpression of *VvMKK4* only increased the tolerance to salt stress [185]. Overexpression of maize *ZmMKK4* [186], *ZmMPK5* [187], cotton *GhMAP3K40* [188], *GhMPK2* [189], and other genes can enhance the resistance of transgenic plants to a high concentration of salt and alkali.

5.5. Regulatory Genes

Salt tolerance is a quantitative genetic trait controlled by multiple genes. Under salt stress, transcription factors regulate the expression levels of various genes by changing their expression. Several families of core transcription factors reported include bZIP, WRKY, AP2/ERF, MYB, DREB, bHLH, CBF, NAC, etc. In soybean, the overexpression of *GmbZIP2* in soybean hairy roots could enhance the expression of the stress-responsive genes *GmMYB48*, *GmWD40*, *GmDHN15*, *GmGST1*, and *GmLEA* [190]. Transcription Factors bHLH and WRKY help to confer increased salt tolerance of *Arabidopsis thaliana* by regulating the expression of salt responsive gene *AtKUP2* [191]. *AtMYB20* in *Arabidopsis thaliana* affects plant resistance to salt stress by regulating ABA signaling pathways. The expression of the *AtMYB20* gene is induced by salt and ABA stress. Overexpression of the *AtMYB20* gene can enhance the resistance of transgenic *Arabidopsis* to salt stress, and decrease the expression

levels of *ABI1*, *ABI2*, and *AtPP2CA* (negative regulator of ABA signal) genes under salt stress [192]. ThDREB transcription factor can improve salt tolerance by enhancing the activity of antioxidant enzymes in *Tamarix hispida* [193]. The overexpression of *SIMYB102* in tomato (*Solanum lycopersicum* L.) affected multiple parameters under salinity stress, like a better K^+/Na^+ ratio and a higher activity of ROS scavenging enzymes. The qRT-PCR analysis confirmed that the transcript abundance of many salt stress-related genes (*SISOS1*, *SISOS2*, *SINH3*, *SINH4*, *SIHAK5*, *SICPK1*, and *SICPK3*) was upregulated in two OE lines under salt stress [194]. Over-expression of *VvNAC17* in *Arabidopsis thaliana* enhances plant resistance to drought and salinity while up-regulating the expression of ABA and stress-related genes including *ABI5*, *AREB1*, *COR15A*, *COR47*, and *P5CS* according to Ju et al. [195].

Except for transcription factors, there are other regulatory genes related to plant salt tolerance. In recent years, several small non-coding RNAs, like microRNAs (miRNAs), are important regulators of mRNA desolation, translation inhibition, and chromatin modification. The target genes of miRNA include enzymes in the metabolic pathway, enzymes in the ubiquitination pathway, transcription factors, signal transduction components, and genes involved in RNA processing and protein synthesis. Compared with wild-type controls, transgenic *Osa-miR393a* improved salt stress tolerance associated with increased K^+ uptake [196]. *TaemiR408* targets six genes that encode proteins involved in biochemical metabolism, microtubule organization, and signaling transduction, which mediate plant response to salt stress and Pi starvation in wheat [197].

In recent years, research on salt tolerance genes in plants has made rapid progress, but it still largely remains at the level of identifying and manipulating the homologous genes known for salt tolerance in *Arabidopsis*. There is an attractive way of discovering new salt-responsive genes. We can use comparative genomics or transcriptomics to analyze halophytes and to discover new salt-responsive genes. For example, Guo et al. identified some candidate genes related to salt tolerance in the halophyte *Atriplex canescens* with transcriptomic analysis [198]. Although a comparative genomic and transcriptomic study requires complete genome information, it is believed that more and more genome sequences will be available along with rapid advances in sequencing technologies, which will provide valuable information for molecular breeding in the future.

Table 2. Salt stress-related genes.

Name of Gene	Origin of Gene	Transgenic Plant	Role of Gene	Reference
<i>P5CS1</i>	<i>Phaseolus vulgaris</i>	<i>Arabidopsis thaliana</i>	rate-limiting enzyme in proline biosynthesis	[134]
<i>P5CS2</i>	<i>Phaseolus vulgaris</i>	<i>Arabidopsis thaliana</i>	rate-limiting enzyme in proline biosynthesis	[134]
<i>LrAMADH1</i>	<i>Lycium ruthenicum</i> Murr	null	catalyze betaine aldehyde to betaine	[136]
<i>SIBADH</i>	<i>Suaeda liaodonggensis</i>	<i>Solanum lycopersicum</i>	catalyze betaine aldehyde to betaine	[137]
<i>AtTPPD</i>	<i>Arabidopsis thaliana</i>	<i>Arabidopsis thaliana</i>	catalyze dephosphorylation of trehalose 6-phosphate to form trehalose	[139]
<i>HvHKT1;1</i>	<i>Hordeum vulgare</i>	<i>Arabidopsis thaliana</i>	transport Na^+ and mediates the absorption of Na^+ when the external K^+ is deficient	[145]
<i>HvHKT1;5</i>	<i>Hordeum vulgare</i>	null	negatively transport Na^+ in Barley	[146]
<i>OsHKT1</i>	<i>Oryza sativa</i>	null	transport Na^+	[147]
<i>OsHKT2</i>	<i>Oryza sativa</i>	null	transport Na^+	[147]
<i>OsVHA</i>	<i>Oryza sativa</i>	null	transport Na^+	[147]
<i>AtNHX1</i>	<i>Arabidopsis thaliana</i>	<i>Arachis hypogaea</i> , <i>Torenia fournieri</i>	vacuolar Na^+/H^+ antiporter	[149]
<i>LfNHX1</i>	<i>Leptochloa fusca</i>	null	vacuolar Na^+/H^+ antiporter	[150]
<i>IhNHX1</i>	<i>Iris halophila</i>	null	vacuolar Na^+/H^+ antiporter	[151]
<i>HcNHX1</i>	<i>Halostachys caspica</i>	null	vacuolar Na^+/H^+ antiporter	[152]
<i>PgNHX1</i>	<i>Pennisetum alopecuroides</i>	<i>Brassica juncea</i>	vacuolar Na^+/H^+ antiporter	[155]
<i>VrNHX1</i>	<i>Vigna radiata</i>	<i>Arabidopsis thaliana</i>	vacuolar Na^+/H^+ antiporter	[156]

Table 2. Cont.

Name of Gene	Origin of Gene	Transgenic Plant	Role of Gene	Reference
<i>PtVP1.1</i>	<i>Populus trichocarpa</i>	<i>Populus trichocarpa</i>	vacuolar H ⁺ phosphorylase	[157]
<i>TaTVP1</i>	<i>Triticum aestivum</i>	<i>Arabidopsis thaliana</i>	vacuolar H ⁺ phosphorylase	[158]
<i>AVP1</i>	<i>Arabidopsis thaliana</i>	<i>Solanum lycopersicum</i>	vacuolar H ⁺ phosphorylase	[159]
<i>ChVDE</i>	<i>Cerasus humilis</i>	<i>Arabidopsis thaliana</i>	violax-anthin de-epoxidase that catalyze the transformation of different CAR	[167]
<i>OsNAC45</i>	<i>Oryza sativa</i>	null	transcription factor participate in different stress responses and ABA signal response	[176]
<i>OsMADS25</i>	<i>Oryza sativa</i>	null	transcription factor involved in ABA-mediated regulatory pathways and ROS scavenging	[177]
<i>AtCDPK27</i>	<i>Arabidopsis thaliana</i>	null	membrane-localized protein kinase in CDPKs signaling	[179]
<i>AtCPK12</i>	<i>Arabidopsis thaliana</i>	null	protein kinase in CDPKs signaling	[180]
<i>PtMAPKK4</i>	<i>Populus trichocarpa</i>	<i>Nicotiana tabacum</i>	protein kinase in MAPKs signaling	[184]
<i>VvMKK2</i>	<i>Vitis vinifera</i>	<i>Arabidopsis thaliana</i>	protein kinase in MAPKs signaling	[185]
<i>VvMKK4</i>	<i>Vitis vinifera</i>	<i>Arabidopsis thaliana</i>	protein kinase in MAPKs signaling	[185]
<i>ZmMKK4</i>	<i>Zea mays</i>	<i>Arabidopsis thaliana</i>	protein kinase in MAPKs signaling	[186]
<i>ZmMPK5</i>	<i>Zea mays</i>	<i>Nicotiana tabacum</i>	protein kinase in MAPKs signaling	[187]
<i>GhMAP3K40</i>	<i>Gossypium herbaceum</i>	<i>Nicotiana benthamiana</i>	protein kinase in MAPKs signaling	[188]
<i>GhMPK2</i>	<i>Gossypium herbaceum</i>	<i>Nicotiana tabacum</i>	protein kinase in MAPKs signaling	[189]
<i>GmbZIP2</i>	<i>Glycine max</i>	null	transcription factor involved in salt stress response	[190]
<i>AtbHLH122</i>	<i>Arabidopsis thaliana</i>	null	increased salt tolerance by regulating salt responsive gene AtKUP2	[191]
<i>AtWRKY33</i>	<i>Arabidopsis thaliana</i>	null	increased salt tolerance by regulating salt responsive gene AtKUP2	[191]
<i>AtMYB20</i>	<i>Arabidopsis thaliana</i>	null	negatively regulates type 2C serine/threonine protein phosphatases	[192]
<i>ThDREB</i>	<i>Tamarix hispida</i>	<i>Nicotiana tabacum</i>	transcription factor involved in stress responses	[193]
<i>SlMYB102</i>	<i>Solanum lycopersicum</i>	null	transcription factor involved in stress responses	[194]
<i>AtGSTF8</i>	<i>Arabidopsis thaliana</i>	null	function in the root fine-tuning the redox homeostasis	[196]
<i>AtGSTU19</i>	<i>Arabidopsis thaliana</i>	null	function in the root fine-tuning the redox homeostasis	[196]
<i>PpSARK</i>	<i>Physcomitrella patens</i>	null	senescence-associated receptor-like kinase related to ABA	[175]
<i>GmTIP2;3</i>	<i>Glycine max</i>	null	a tonoplast intrinsic protein related to osmotic regulation	[140]
<i>VvNAC17</i>	<i>Vitis vinifera</i>	<i>Arabidopsis thaliana</i>	up-regulates the expression of ABA and stress-related genes	[195]

6. Improvement Techniques for Increasing Plant Salt Tolerance

So far, many approaches have been reported to improve the salt tolerance of plants, which can be classified into two categories: genetic improvement and non-genetic improvement.

6.1. Non-Genetic Improvement Techniques

Conventional breeding is an effective method to improve the salt tolerance of plants. New salt-tolerant plant varieties can be cultivated through repeated hybridization, artificial selection, cutting, grafting, tissue culture, and other asexual propagation methods. Besides, we can also improve the ability of plants to resist salt stress by applying exogenous substances. Common exogenous substances mainly include the following categories: substances that can activate the activity of antioxidant enzymes in plants, such as NO, silicon, selenium, etc.; betaine, sugar, organic acids, and other substances as osmotic

regulators; naphthalene acetic acid, jasmonic acid, gibberellin, and other plant growth regulator; substances such as salicylic acid, humic acid, and Ca^{2+} that reduce cell membrane permeability [199,200]. For example, plants applied with exogenous melatonin under salt stress, compared with the control group, showed a stronger antioxidant enzyme activity, higher photosynthetic rate, and a lower rate of electrolyte leakage, and lower MDA content, indicating that melatonin may enhance the salt resistance of plants by increasing plant photosynthetic capacity, oxidation resistance and ion homeostasis [201]. Using the interaction of fungi and roots to form symbionts with specific structures and functions to improve the salt tolerance of plants has also been a direction taken in recent years. In Kumkum Azad and Susan Kaminskyj's study, they colonized tomato with systemic fungal endophytes, which were isolated from plants naturally growing in salinized soil, and studied the effect of these strains on plant tolerance to salt. Results showed that endophyte-colonized plants exposed to salt had higher root and shoot biomass, better water-use efficiency, higher photosynthetic efficiency, and lower ROS content than non-colonized plants [202]. Rational fertilization can also effectively alleviate the damage caused by salt stress on plants. For example, phosphorus Fertilizer improved the salt tolerance of *Phaseolus vulgaris* [203].

6.2. Genetic Improvement Techniques

Introducing salt stress-related genes into plants through genetic engineering is the most direct and effective means to improve plant salt tolerance. In addition to the genes listed in the previous section, recently, the tobacco osmotin gene has been widely discussed to alleviate salt stress in plants. Osmotin is a multifunctional stress-responsive protein belonging to the PR-5 family of pathogenesis-related (PR) proteins, which is produced when plants are exposed to various biotic and abiotic stresses. It protects plants by reducing ROS production, limiting lipid peroxidation, initiating programmed cell death (PCD), and increasing proline content and antioxidant enzyme activity [204–206]. According to studies, overexpression of tobacco osmotin protein in transgenic plants protects them from different stresses, like salt stress and fungal infections. In Subramanyam et al.'s experiment, the putative transgenic chili pepper plants overexpressing the osmotin gene were morphologically similar to wild-type plants but enhanced in salt tolerance [207]. The same results were observed in soybean plants with overexpression of the tobacco osmotin gene [208]. Bashir et al. found that improving salt tolerance by overexpressing tobacco osmotin protein in Olive has something to do with the sulfur metabolism of the transgenic plants [209,210]. Though we have found some evidence for the role of tobacco osmotin protein in enhancing plant stress resistance, the complete mechanism of osmotin activity has not been fully elucidated, and is waiting to be revealed.

Salt tolerance in plants is a complex network involving multiple levels and genes. Through transgenic technology, the salt tolerance of plants can be improved by a single strategy, such as increasing the content of a certain osmolyte or the activity of a certain oxidase. However, the improvement degree is limited. Therefore, we need to figure out how to rank the importance of each strategy. Better improvements can be achieved if we select strategies according to their priority when we are trying to improve the salt tolerance of plants.

7. Conclusions

In this review, we have reported what will happen to plants when they are exposed to salt stress and outlined the following physiological response, which mainly involves osmotic adjustment and ROS scavenging but also includes four main signaling pathways, the corresponding salt stress-responsive genes, and some improvement techniques for plant salt tolerance. Great efforts have been made in understanding the mechanism of plant salt tolerance in the past two decades. Nevertheless, there is still plenty of room to explore and discover in the future. Firstly, the mechanism of salt stress reducing plant photosynthesis is still unclear. No unified understanding has been formed so far. Secondly,

the integration of morphological, physiological, and molecular approaches for plant stress detection requires future study. Thirdly, much remains to be discovered about the specific salt-tolerant mechanisms of halophytes, such as salt vesicles. Fourthly, the perception of salt stress is still unidentified and the cross-reactions of the various signal transduction pathways in plants under salt stress are still poorly understood. Fifthly, the discovery of salt stress-responsive genes may rely more on comparative genomic and transcriptomic methods in the future. Finally, we need to figure out how to rank the importance of each improvement strategy, so that better improvements can be achieved. All in all, we still have a long way to go in decoding the mechanism of plant salt tolerance and improving plant salt tolerance.

Author Contributions: This review was mainly organized by S.H., Y.W., Y.Y., Y.L. and J.W. were contributors to the collection of materials and revision of the manuscript. S.C. conceived the study and revised the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This review was funded by the National Natural Science Foundation of China, grant number 31870659, the Fundamental Research Funds for the Central Universities (2572019CG08), and Heilongjiang Touyan Innovation Team Program (Tree Genetics and Breeding Innovation Team).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare that they have no competing interests.

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