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Review

Breeding for Salt-Resilient Soybean: Integrating Physiological Traits and Molecular Mechanisms

Cui He [†], **Deshuai Shao** [†], **Jiahui Yao, Shu Yao, Guoji Wang, Xiaoyu Hu, Zhuofan Xia, Bingcan Wu, Xiaobo Wang** [*], **Jiajia Li** [*]

School of Agronomy, Anhui Agricultural University, Hefei 230036, China
*** Corresponding author:** wxbphd@163.com (X.W.), lijia6862@163.com (J.L.)
[†] These authors contributed equally to this article.

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Abstract: As soil salinization becomes increasingly severe, most crops face significant challenges, with soybean being particularly sensitive to salt stress. In saline environments, soybean yields frequently exhibit substantial declines. In recent years, considerable efforts have been devoted to achieving high and stable soybean production in such adverse conditions. Significant progress has been achieved in the breeding of salt-tolerant varieties and in elucidating the signaling pathways and molecular mechanisms underlying soybean salt tolerance. This review systematically outlines the major mechanisms by which plants respond to salt stress, including the Salt Overly Sensitive (SOS) signaling pathway and hormonal regulation of ion homeostasis, with a particular focus on soybean-specific adaptive responses. It summarizes the regulatory roles of over 30 functional genes associated with salt tolerance. Furthermore, it proposes effective strategies to enhance soybean productivity in saline soils, such as improving soil fertility through rhizobial nitrogen fixation, optimizing carbon allocation, and employing seed coating and other pre-sowing treatments to improve plant stress resilience. Additionally, the article discusses the potential applications of cutting-edge technologies, including single-cell omics and gene editing, in accelerating the development of salt-tolerant soybean cultivars. These advances are expected to facilitate the development of more efficient breeding strategies and promote the sustainable development of the soybean industry.

Keywords: soybean; saline stress; breed cultivation; yield improving

1. Introduction

Soil salinization represents one of the most significant constraints on global agricultural production and economic growth. As global climate change intensifies, the annual mean temperature is progressively increasing, exacerbating the issue of secondary soil salinization. The ongoing expansion of saline land areas poses a substantial threat to agricultural productivity, including reductions in arable land area, alterations in crop yields and soil microbial communities [1–4]. According to Food and Agriculture Organization of the United Nations (FAO) statistics, by 2025 the global area of saline land had reached 1.381 billion hectares, representing 10.7% of the total global land area. Moreover, given the ongoing trend of rising temperatures, the affected area could potentially expand to between 24% and 32% of the total land area. Currently, soil salinization is especially pronounced in regions such as North Africa, East Asia, and South Asia (including countries like China, Tunisia, Bangladesh, and India) [5–8]. These salt-affected soils have resulted in a marked decrease in arable land area and a considerable drop in crop yields, thus posing a severe threat to global food security and the sustainability of agricultural development while also undermining biodiversity [9–11].

Soybean (*Glycine max* (L.) Merr.), which originated in China, is among the world's most important oilseed and grain crops [12,13]. It is rich in nutrients such as protein and oil, conferring high economic and nutritional value. Soybean serves as a primary source of plant-based protein for human consumption and animal feed for protein production. Additionally, it plays a critical role in food processing and soybean oil production [14–16]. However, soybean exhibits extreme sensitivity to salt stress. Under such conditions, photosynthesis is inhibited, resulting in stomatal closure and a subsequent reduction in photosynthetic efficiency. This ultimately leads to slower growth and reproductive disorders. Studies indicate that soil salinization can significantly reduce seven quantitative traits of soybean, including germination rate and seedling fresh weight. Furthermore, salt tolerance varies significantly among soybean varieties, across geographic origins, and at different developmental stages [17,18]. Additionally, salt stress adversely affects nodulation in soybean, decreasing nodule number and impairing nitrogen fixation efficiency, which consequently reduces yield and protein content [19,20]. To enhance the rational utilization of saline land resources, ensure agricultural sustainability, and boost global soybean production, it is crucial to expand soybean cultivation on saline soils. The key lies in deeply analyzing the mechanisms underlying soybean tolerance to saline stress, developing high-quality salt-resistant varieties, and consequently enhancing soybean salt tolerance.

The question of how soybean fortifies its salt resistance, thereby elevating both quality and yield, stands as a pivotal challenge in modern agronomy. In recent years, the global scientific community has achieved remarkable strides in unraveling the intricate mechanisms behind soybean salt tolerance, encompassing ion homeostasis regulation, antioxidant defense systems, root adaptability, and photosynthetic metabolism. This review summarizes recent advances in the molecular and physiological underpinnings of soybean salt tolerance, pinpoints critical genes and regulatory networks essential for cultivating high-quality salt-resistant soybean, and illuminates future directions for enhancing soybean resilience through the integration of gene-metabolism-phenotype and organ/tissue-specific responses.

2. The Salt Tolerance Mechanisms in Plants

2.1. Physiological Damages Induced by Salt Stress in Plants

Salt stress impairs plant physiological development mainly via ionic stress, oxidative stress, and osmotic stress [21]. Excessive soil Na^+ disrupts intracellular ion homeostasis, disturbs nutrient uptake, impairs enzyme activity and osmotic balance, and even induces plant reproductive abnormality. As an indispensable macronutrient, K^+ participates in osmotic regulation, enzyme activation, protein synthesis and membrane transport [22]. High external Na^+ competes with root K^+ absorption, lowering K^+ availability and further disabling core cellular physiological functions [23]. Salt stress also triggers massive accumulation of reactive oxygen species (ROS), including O_2^-, H_2O_2 and $^1O_2$, caused largely by damaged chloroplast electron transport chains and aggravated electron leakage [24,25]. Excess ROS induces membrane lipid peroxidation, protein oxidation and DNA damage, disrupting normal plant physiology [24,26]. Plants activate antioxidant defense systems to scavenge ROS by upregulating antioxidant enzymes (Superoxide Dismutase (SOD), Catalase (CAT), Ascorbate Peroxidase (APX)) and non-enzymatic antioxidants (Glutathione (GSH), Ascorbic Acid (AsA)) [27]. Nevertheless, once ROS burst exceeds the scavenging capacity of the antioxidant system, membrane integrity collapses, enzyme activity declines, and plant growth and yield are severely inhibited.

2.2. Molecular and Hormonal Signaling Networks in Salt Stress Response

Through long-term natural selection, plants have evolved sophisticated, multilayered mechanisms to withstand salinity. Central to this adaptive capacity are two well-characterized signaling systems: the Salt Overly Sensitive (SOS) pathway and hormone-mediated regulatory networks. Over the past several decades, a substantial body of research has elucidated the underlying mechanisms. The SOS pathway comprises three core components: SOS3 (a calcineurin B-like (CBL) family Ca^{2+}-binding protein), SOS2 (a CBL interacting protein kinase (CIPK) family kinase), and SOS1 (a plasma membrane-localised NHX family Na^+/H^+ antiporter). Under salt stress conditions, an increase in extracellular Na^+ triggers a rapid rise in cytosolic calcium (Ca^{2+}) levels. SOS3 and SCaBP8/CBL10 function as calcium sensors that detect this change, bind to SOS2, and activate its kinase activity. The activated SOS2 kinase then phosphorylates SOS1, thereby enhancing the activity of Na^+/H^+ antiporters in the plasma membrane and facilitating the efflux of excess Na^+ from the cytoplasm to the extracellular space [25,28] (**Figure 1**).

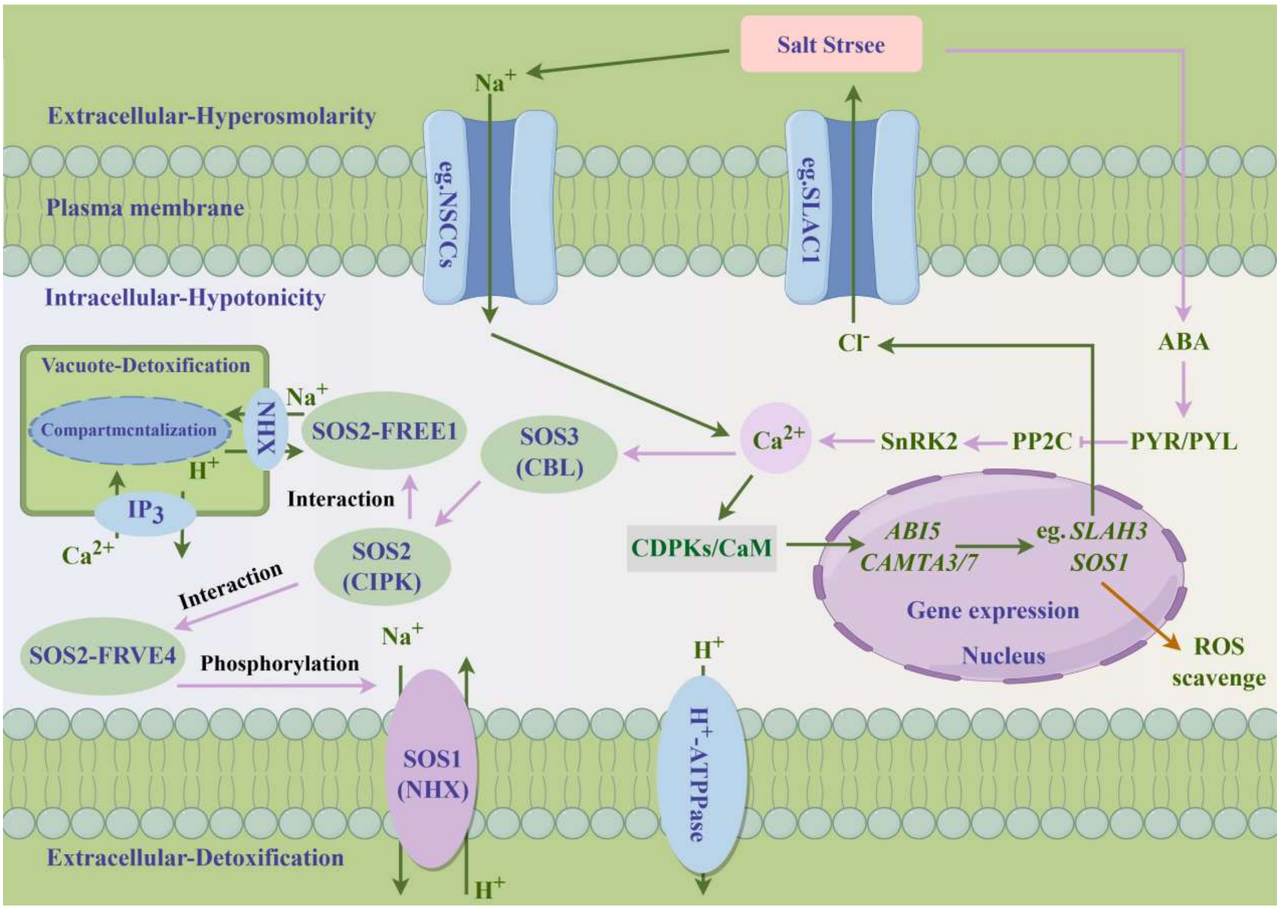

Figure 1. Overview of plant metabolic and signaling pathways under salt stress. Note: Green arrows indicate ion metabolic pathways, purple arrows denote ABA and SOS signaling pathways, and yellow highlights ROS scavenging mechanisms.

Beyond its canonical function in cytoplasmic Na^+ extrusion, SOS1 also participates in regulating sodium redistribution among subcellular compartments to achieve vacuolar sodium sequestration under high salinity. In the model plant *Arabidopsis thaliana*, recent cryo-imaging studies have refined this classical view by revealing stress-dependent, SOS1-mediated redistribution of Na^+ across subcellular compartments [29]. Under mild salt stress (2.5 mM NaCl), Na^+ predominantly accumulates in the cell wall. There is a notable increase in Na^+ levels in the cytoplasm of the *Arabidopsis thaliana sos1* mutant, suggesting that SOS1 plays a role in Na^+ efflux across the plasma membrane. When salt concentrations are elevated (25～100 mM NaCl), a significant relocalization of Na^+ occurs in wild-type (WT) root tip cells: Na^+ shifts from the cell wall to the vacuole, where it accumulates extensively. In contrast, the *sos1* mutant exhibits a marked reduction in vacuolar Na^+, a sharp increase in Na^+ concentration in the cytoplasm, and a concomitant loss of potassium. These observations indicate that the plants primarily detoxify Na^+ through vacuolar sequestration rather than plasma membrane extrusion under high-salt conditions, underscoring the essential role of SOS1 in facilitating vacuolar Na^+ accumulation [29]. Furthermore, the SOS2-FREE1 module enhances Na^+ compartmentalization through the coordinated regulation of multi-layered processes, including ion transport (mediated by SOS1 activity), endomembrane trafficking (characterized by SOS1 relocalization due to ESCRT inhibition), and organelle morphology (marked by increased vacuolar fragmentation that expands membrane surface area). These mechanisms collectively reduce cytoplasmic Na^+ toxicity and enable the utilization of Na^+ for osmotic adjustment [30,31]. Additionally, the plant-specific ESCRT-III component FYVE4 interacts with SOS2 under salt stress conditions, thereby promoting SOS1 phosphorylation and modulating the plant's response to salt stress [25]. Collectively, these findings demonstrated that the SOS pathway not only mediates salt excretion but also contributes to the regulation of plant salt homeostasis through additional mechanisms.

Hormonal regulation plays a pivotal role in plant responses to salt stress **(Table 1)**. Abscisic acid (ABA) modulates germination, root and shoot growth, and controls salt exclusion mechanisms, osmotic balance, and ROS homeostasis under salinity [32–34]. ABA signaling intensifies during later stages of salt stress, mitigating root cell swelling and membrane damage; its absence leads to prolonged Na^+-responsive gene expression and shoot Na^+ accumulation [34]. ABA also activates the ABI5-ZAT10-SLAH3 module to promote chloride efflux from roots, and accumulates in the root cap to trigger Ca^{2+} signals that delay root cap shedding and enhance salt adaptation [35]. Beyond ABA-dependent pathways, plants employ ABA-independent mechanisms involving jasmonic acid, ethylene, and salicylic acid to coordinate comprehensive stress responses [35,36]. Strigolactone (SL) improves leaf structure, enhances antioxidant enzyme activity, and reduces malondialdehyde (MDA) levels under salt stress [37,38]. Ethylene alleviates salt-induced inhibition of seed germination by suppressing ABI5 expression through EIN3-mediated COP1-dependent degradation of HY5, thereby activating antioxidant and hormone synergistic pathways [39,40].

Table 1. Plant hormones involved in the regulation of salt stress in crops.

Hormone	**Regulation Direction**	**Key Functions under Salt Stress**	**Key Molecular Components / Pathways**	**References**
Abscisic Acid (ABA)	Positive	Modulates development (germination, root/shoot growth); controls salt exclusion; maintains osmotic balance; regulates ROS homeostasis.	ABI5-ZAT10-SLAH3 module (Cl- efflux); CPK10/30/32 kinases (root cap)	[32–36]
Jasmonic Acid (JA)	Positive	Part of ABA-independent pathways; interacts with other hormones (ETH, SA) to coordinate a comprehensive stress response.	COI1-JAZ-MYC2/3/4 core module	[35,36,41]
Strigolactone (SL)	Positive	Improves leaf structure; enhances antioxidant enzyme activity (SOD, POD, CAT); reduces MDA levels.	D14-MAX2-mediated SCFMAX2 ubiquitin-degradation module	[37,38]
Ethylene (ETH)	Positive	Alleviates inhibition of seed germination; activates antioxidant and hormone synergistic pathways.	EIN3-mediated pathway; COP1-dependent degradation of HY5; suppresses ABI5	[39,40]

Salicylic Acid (SA)	Positive	Part of ABA-independent pathways; interacts with other hormones (JA, ETH) to coordinate a comprehensive stress response.	NPR1-TGA3/TF pathway	[35,36]

3. Research Progress on Salt Tolerance of Soybean

3.1. Physiological and Cellular Responses to Salt Stress in Soybean

Soybean, as a salt-sensitive crop, exhibits a range of physiological and cellular adaptations critical for survival under saline conditions. The primary challenges include ionic toxicity, osmotic stress, and secondary oxidative damage. To maintain ion homeostasis, soybean plants actively limit Na$^+$ uptake and translocation to shoots while preserving K$^+$ acquisition, ensuring a favorable Na$^+$/K$^+$ ratio. This is achieved through enhanced Na$^+$ exclusion at the root surface and vacuolar sequestration in root cells [42,43]. Concurrently, osmotic adjustment is facilitated by the accumulation of compatible osmolytes such as proline and soluble sugars [44,45]. At the cellular level, the antioxidant defense system is upregulated, with increased activities of enzymes like SOD, CAT, and APX, along with elevated levels of non-enzymatic antioxidants such as GSH, to scavenge excess ROS and prevent oxidative damage to membranes and proteins [46,47]. Photosynthesis is protected through the stabilization of chlorophyll content and photosystem II (PSII) efficiency, though overall carbon assimilation is often compromised [24,25]. Furthermore, salt stress significantly influences root architecture, frequently promoting deeper root growth to avoid saline surface layers, while adversely affecting nodulation and nitrogen fixation efficiency due to the combined ionic and osmotic stresses, which is a particular vulnerability for soybean's nitrogen metabolism [19,20].

Beyond these conserved physiological responses, soybeans have evolved specific molecular strategies to fine-tune their adaptation. For instance, *MiR4359b* is significantly upregulated under salt stress and targets the mRNA of *GmFBX193* for cleavage. Suppressing this F-box protein allows for the accumulation of positive regulators like the Na$^+$/H$^+$ transporter *GmNHX1*, thereby promoting Na$^+$ compartmentalization and enhancing tolerance [48]. Similarly, salt-induced *miR160a* cleaves *GmARF16* mRNA, alleviating its repression on *GmMYC2*, which subsequently activates P5CS and ROS scavenging genes to boost proline biosynthesis and mitigate oxidative damage [45]. The transcription factor GmCOL1a further directly binds to the promoters of *GmDREB2A* and *GmP5CS* to activate their expression and promote proline accumulation [44]. Moreover, *Gm5PTase8* plays a key role by hydrolyzing inositol 1,4,5-trisphosphate (IP$_3$), which negatively regulates the Ca^{2+}/CBL10-SOS2 signaling cascade, reduces Na$^+$ influx via *GmSOS1*, maintains cytoplasmic Ca^{2+} homeostasis, and enhances antioxidant system activity [49]. The introduction of the betaine aldehyde dehydrogenase (BADH) gene from *Atriplex hortensis* L. into soybean enables the synthesis of the osmoprotectant betaine, which stabilizes protein and membrane structures and upregulates antioxidant enzyme activities, collectively improving salt tolerance [50].

3.2. Salt Tolerance Characteristics during Soybean Flowering and Podding Stages

The flowering and pod-setting stages represent two physiologically decisive phases in soybean development. Relative to the vegetative stage, reproductive organs, including flowers, pods, and developing seeds, exhibit significantly greater sensitivity to abiotic stresses. Consequently, salt stress during these stages inflicts more severe damage to grain yield [51–53].

Salt stress imposed during the flowering stage can result in excessive Na^+ accumulation in leaves and consequent ionic toxicity and osmotic stress. These stresses cause significant declines in chlorophyll content index and leaf relative water content, coupled with accelerated chlorophyll degradation [54]. At the subcellular level, chloroplast ultrastructure is disrupted, as evidenced by thylakoid disorganization and starch grain accumulation, leading to impaired PSII photochemical efficiency and suppressed carbon assimilation [55]. In response, soybean upregulates betaine and proline; however, this compensatory mechanism is inadequate to restore cellular homeostasis, thereby causing marked reductions in seed yield [54]. Concurrently, salt stress triggers a pronounced burst of ROS, particularly O_2^- and H_2O_2, which overwhelms endogenous antioxidant capacity, intensifies membrane lipid peroxidation, and elevates MDA concentrations. While plants partially counteract oxidative damage through coordinated induction of antioxidant enzymes. including SOD, CAT, and APX, and accumulation of osmoprotectants, such responses are often insufficient in magnitude. This redox imbalance may contribute directly to pollen abortion, defective microsporogenesis, and failure of double fertilization, culminating in markedly elevated flower and pod abscission rates. Moreover, salt stress suppresses nodule initiation, and nitrogenase activity, thereby compromising biological nitrogen fixation and disrupting nitrogen allocation to developing pods during the critical pod-setting stage [20]. Collectively, these interconnected physiological, biochemical, and symbiotic impairments synergistically constrain reproductive output and drive substantial yield loss in soybean.

3.3. Molecular Mechanisms and Functional Genomics of Salt Tolerance

Building upon the physiological foundations, soybean employs a sophisticated molecular network for salt tolerance, characterized by the coordinated regulation of numerous functional genes. Significant progress has been made in identifying and characterizing these genes and their roles in key pathways, including ion homeostasis, ROS scavenging, hormonal signaling, and root system architecture optimization (**Table 2, Figure 2**). The identification and characterization of salt-tolerant genes in soybean are of great significance for molecular breeding and crop improvement in saline environments. In terms of ion homeostasis regulation, salt stress triggers an increase in intracellular calcium signals, which are perceived by *GmCBL9* and subsequently interact with *GmCIPK6* to form a functional complex [56–58]. This complex phosphorylates and activates the Shaker-type potassium channel gene *GmAKT1*, thereby enhancing K^+ uptake and maintaining the Na^+/K^+ balance [56,57]. Meanwhile, *GmCHX1* (also known as *GmSALT3*), a Na^+/H^+ antiporter, sequesters Na^+ into vacuoles or extrudes it from root cells, thereby limiting Na^+ translocation to the shoot. Additionally, it facilitates Cl^- reabsorption in the phloem, contributing to leaf ion compartmentalization via a dual mechanism of "root Na^+ exclusion + stem Cl^- retrieval" [42,43,59]. *SST1* regulates ROS homeostasis and mitochondrial function through modulation of mitochondrial RNA editing. The loss-of-function allele, *SST1*HapT, reduces RNA editing efficiency but improves ROS regulation, thereby negatively modulating salt tolerance. This allele was selectively fixed during soybean domestication and acts synergistically with *GmCHX1* to enhance salt tolerance in cultivated soybeans [60]. Under salt stress, *GmNTL1* undergoes oxidative modification and activates *GmRbohBs* to amplify ROS signaling, which in turn positively regulates the expression of *GmNHX1* and *GmCHX1*, further reducing Na^+ accumulation in roots [61,62]. In contrast, *GmCHYR16* mediates the ubiquitin-dependent degradation of GmERF71, thereby suppressing its transcriptional activation of *GmNHX1* and negatively modulating salt tolerance [63,64]. Regarding ROS scavenging mechanisms, *GmFER1* enhances Fe^{3+} accumulation, which boosts the activities of SOD and CAT, effectively eliminating ROS and upregulating *GmSOS1* to promote Na^+ efflux [46]. *GmMDH2* utilizes excess NADPH through NADP-dependent malate synthesis, thereby maintaining redox homeostasis, suppressing ROS overproduction, and enhancing the activities of antioxidant enzymes such as APX, POD, and SOD [47]. Similarly, *GmAHP10* reduces H_2O_2 and MDA levels, alleviates membrane lipid peroxidation, and promotes root development [65]. In addition, a T/C single-nucleotide variant in the coding region of *GmPM30* gives rise to the HapT haplotype, which enhances the interaction of *GmPM30* with GmLEA1 and GmLEC1 proteins. This enhanced protein interaction alleviates cell membrane damage and reduces ROS accumulation under salt stress, thereby improving stress tolerance and significantly increasing soybean yield and salt tolerance in saline-alkali soils [52]. *GmbZIP131* interacts with flavonoid biosynthesis-related genes, leading to the accumulation of quercetin and kaempferol [66]. These flavonoids not only scavenge ROS but also suppress Na^+ influx and synergistically enhance Na^+ compartmentalization mediated by *GmNHX1* [66,67]. Root morphogenesis is another critical aspect of salt tolerance. *GmHSL1b* promotes root elongation by activating cytokinin signaling components (e.g., CKX3) and cell wall-loosening enzymes (e.g., EXP), while mitigating ROS-induced damage through MAPK-hormone signaling crosstalk [68]. In contrast, *GmERF13* interacts with *GmLBD16a* under the regulation of the ABA-*GmABI5* signaling cascade, which inhibits the expression of *GmEXP17c* and suppresses nodule formation, thus actively sacrificing nitrogen-fixing capacity for short-term survival [20]. Moreover, the jasmonic acid (JA) signaling pathway contributes to salt tolerance by activating *GmAOC3/4* through the interaction between *GmPRL1b* and *GmST2*, thereby promoting JA biosynthesis. JA signaling enhances the expression of antioxidant enzymes and ion transporters, synergistically reducing ROS and Na^+ accumulation [41]. Notably, *GmCDF1* negatively regulates salt tolerance during seed germination by maintaining Na^+/K^+ homeostasis, and its overexpression results in salt-sensitive phenotypes [69].

Table 2. Functional genes related to salt tolerance of soybean.

Gene Name	**Types of Saline Stress**	**Tolerance**	**Function Description**	**Reference**
GmCBL9	NaCl	+	Perceives salt-induced Ca^{2+} signals and forms a functional complex with *GmCIPK6* to phosphorylate and activate *GmAKT1*, promoting K^+ uptake and maintaining Na^+/K^+ homeostasis.	[56–58]
GmCIPK6	NaCl	+	Interacts with *GmCBL9* to phosphorylate and activate the K^+ channel *GmAKT1*, enhancing K^+ influx and stabilizing the Na^+/K^+ ratio.	[56–58]
GmAKT1	NaCl	+	Shaker-type K^+ channels, when phosphorylated by the *GmCBL9–GmCIPK6* complex, facilitate increased K^+ influx and mitigate Na^+ toxicity.	[56–58]
GmCHX1/ SALT3	NaCl, $NaHCO_3$	+	Vacuolar/plasma-membrane Na^+/H^+ antiporter that sequesters Na^+ into vacuoles or exports it from root cells and retrieves Cl^- in phloem, achieving "root Na^+ exclusion + stem Cl^- retrieval".	[42,43,59]
SST1	NaCl	-	The *SST1* gene, through a natural loss-of-function variant, reduces mitochondrial RNA editing efficiency, thereby negatively regulating salt tolerance in soybeans. This allele has been selectively fixed during domestication, contributing to enhanced adaptation to salt stress.	[60]
GmNTL1	NaCl	+	Undergoes oxidative modification, activates *GmRbohBs* to amplify ROS signalling, up-regulates *GmNHX1* and *GmCHX1*, and reduces root Na^+ accumulation.	[61,62]
GmRbohBs	NaCl	+	NADPH oxidase that amplifies ROS signalling and positively regulates Na^+ efflux/compartmentalization genes.	[61,62]
GmNHX1	NaCl	+	Tonoplast Na^+/H^+ antiporter that compartmentalizes Na^+ into vacuoles, lowering cytosolic Na^+ concentration.	[66,67]
GmCHYR16	NaCl	-	E3 ubiquitin ligase that mediates degradation of *GmERF71*, suppressing its activation of *GmNHX1* and thereby negatively regulating salt tolerance.	[63,64]
GmERF71	NaCl, $NaHCO_3$	+	*AP2/ERF* transcription factor that activates *GmNHX1* expression and promotes Na^+ compartmentalization; degraded by *GmCHYR16*.	[63,64]
GmFER1	NaCl	+	Enhances Fe^{3+} accumulation, increases SOD and CAT activities to scavenge ROS, and up-regulates *GmSOS1* to drive Na^+ efflux.	[47]
GmSOS1	NaCl	+	Plasma-membrane Na^+/H^+ antiporter that exports Na^+ out of cells, decreasing Na^+ load.	[47]
GmMDH2	NaCl	+	NADP-dependent malate dehydrogenase that consumes excess NADPH to maintain redox balance, restrains ROS over-production and boosts APX, POD and SOD activities.	[47]
GmAHP10	NaCl	+	Reduces H_2O_2 and MDA levels, alleviates membrane lipid peroxidation and promotes root development.	[65]
GmPM30	NaCl	+	The non-synonymous mutation (Val→Ile) strengthens protein stability and membrane	[52]

			localization, thereby enhancing the activation of ion transport and osmoprotective genes by the *GmLEA1-GmPM30-GmLEC1* module.	
GmbZIP131	NaCl	+	bZIP transcription factor that activates flavonoid-biosynthesis genes; accumulated quercetin and kaempferol scavenge ROS and suppress Na$^+$ influx while enhancing *GmNHX1*-mediated Na$^+$ compartmentalization.	[66]
GmHSL1b	NaCl	+	Promotes root elongation by activating cytokinin signalling (CKX3) and cell-wall-loosening enzymes (EXPs), and mitigates ROS damage via MAPK–hormone crosstalk.	[66,67]
GmERF13	NaCl	-	Acts downstream of the ABA–*GmABI5* cascade; interacts with *GmLBD16a* to repress *GmEXP17c* and nodule formation, shifting resources to salt acclimation.	[20]
GmLBD16a	NaCl	-	Interacts with *GmERF13* to jointly suppress nodule initiation, negatively affecting symbiotic salt tolerance.	[20]
GmABI5	NaCl	-	Core ABA-responsive transcription factor that activates the *GmERF13–GmLBD16a* module and inhibits nodulation, negatively regulating symbiosis-dependent salt tolerance.	[20]
GmEXP17c	NaCl	+	Expansin that loosens cell walls; its repression by *GmERF13* blocks nodule formation, while normal expression supports nodule development and indirectly influences salt tolerance.	[20]
GmAOC3	NaCl	+	Allene-oxide cyclase and key jasmonic-acid (JA) biosynthetic enzyme; activated by the *GmPRL1b–GmST2* interaction, and JA signalling enhances antioxidant enzymes and ion transporters.	[41]
GmAOC4	NaCl	+	Functions together with *GmAOC3* to promote JA biosynthesis, improving ROS scavenging and Na$^+$ homeostasis.	[41]
GmPRL1b	NaCl	+	Interacts with *GmST2* to activate *GmAOC3/4*, initiates JA signalling and cooperatively reduces ROS and Na$^+$ accumulation.	[41]
GmST2	NaCl	+	Partners with *GmPRL1b* to activate the JA pathway and positively modulates salt tolerance.	[41]
GmCDF1	NaCl	-	Maintains Na$^+$/K$^+$ homeostasis during seed germination; over-expression causes salt-sensitive phenotypes, thus acting as a negative regulator.	[69]

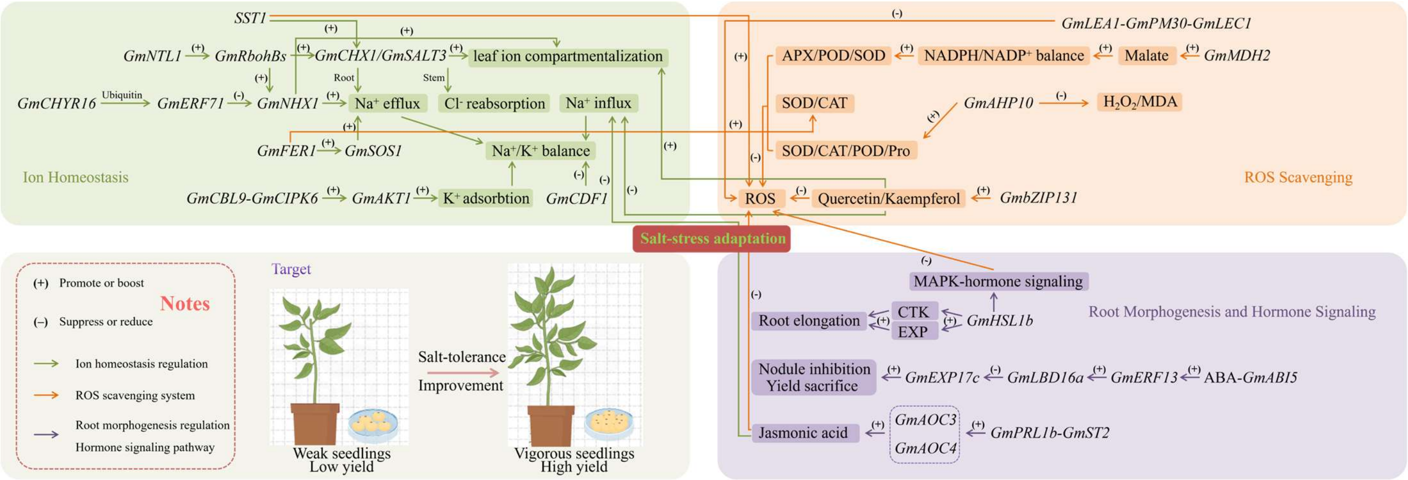

Figure 2. Functional gene regulation of soybean response to salt stress.

4. Strategies for Enhancing Soybean Yield in Saline Soils

4.1. Enhance and Optimize the Soil Environment

Based on extensive literature retrieval and a systematic summary of published results, this section elaborates rhizosphere regulation strategies to improve soybean yield in saline soils. Nodulation and nitrogen fixation substantially influence soybean yield. The root nodules formed by the symbiosis of rhizobia and soybeans can convert atmospheric nitrogen into nitrogen available to soybeans, effectively improving fertilizer utilization and soybean stress resistance. In soybean rhizosphere management, the nitrogen input per unit area can be increased without additional fertilization by optimizing the carbon source and inoculating efficient rhizobia, thereby increasing soybean yield in saline land [70]. Co-inoculation of a mixed bacterial consortium comprising Enterobacter and Klebsiella with rhizobia (Bradyrhizobium) rapidly establishes a "trilateral symbiotic network" within the rhizosphere. Specifically, Enterobacter synthesizes indole-3-acetic acid (IAA) and siderophores, while Klebsiella secretes organic acids and extracellular polysaccharides. Collectively, these activities regulate rhizosphere pH, solubilize phosphorus and iron, and promote root hair elongation [71]. It is speculated that the combined application of these microbes may enhance rhizobial attachment and infection capacity. Meanwhile, the mixed bacteria may potentially upregulate the expression of soybean nodulation factor receptor *GmNFR5* and nitrogen transporter *GmNRT1.1B*.When rhizobia (Bradyrhizobium) are co-inoculated with arbuscular mycorrhizal fungi (AMF, Rhizophagus irregularis), a "dual symbiotic system" can be established in the rhizosphere [72,73]. Rhizobia perform biological nitrogen fixation, and the extraradical hyphae of AMF transport soil water and nutrients such as phosphorus, zinc, and iron to the root surface. This symbiotic combination can elevate the content of available phosphorus in soil and slow down the decline in leaf water potential under salt stress. The improved rhizosphere microenvironment is presumed to activate the expression of *GmNIN*, *GmP5CS*, and *GmDREB2A*. Under soda salt stress, arbuscular mycorrhizal fungi (Rhizophagus intraradices) can effectively improve the salt adaptability of soybeans [51,74]. The extraradical hyphae of this fungus assist plants in regulating ion balance by facilitating Na^+ excretion and K^+ uptake. From the perspective of molecular regulation, it is hypothesized that this ion homeostasis adjustment may be associated with the functional changes of salt-responsive genes, including *GmNHX1*, *GmAKT1*, and *GmSOS1*. In addition, inoculation with Rhizophagus intraradices increases the content of photosynthetic pigments and Rubisco, enhancing the actual quantum efficiency of photosystem II (ΦPSII) and net photosynthetic rate (Pn), and reducing ROS, thereby significantly improving soybean salt tolerance and yield during the critical period of soda salt stress [51,74]. In addition, studies have shown that inoculating *GmHSP17.9* overexpression strains (or gene-edited symbiotic systems) into the roots of soybean seedlings can rapidly accumulate small molecular heat shock protein GmHSP17.9 in root nodules [75]. This protein stabilizes the nitrogenase complex and protects root nodule cells from ROS and high temperature stress, significantly extending the active period of root nodules. We infer that this treatment can improve nitrogen fixation capacity and nitrogen supply to roots, and further promote pod development and increase the 100-grain weight of soybean.

4.2. Seed Priming and Pre-sowing Enhancement

Combining literature data and a comprehensive summary of existing experiments, we discuss the effects and application prospects of soybean seed pre-sowing treatments under salt stress. For soybeans, the growth stages of seed germination and seedling emergence are critical for yield establishment and exhibit the highest sensitivity to salt stress. Seed germination and early seedling development are also pivotal for successful plant establishment and are particularly vulnerable to saline conditions. Therefore, appropriate seed pretreatment is of great significance in mitigating the adverse effects of salt stress. Seed priming is a controlled hydration process, followed by redrying, that activates a range of physiological mechanisms associated with the early stages of germination and prepares the seed for radicle emergence [76–78]. Furthermore, it can reduce the physical resistance of the endosperm during imbibition, facilitate membrane repair, and promote the development of immature embryos by leaching out germination inhibitors.

Following seed coating with Azospirillum brasilense enables the strain to colonize root surfaces rapidly. This plant growth-promoting bacterium secretes indole-3-acetic acid (IAA) and gibberellic acid (GA3), promotes root growth, enhances nutrient availability and optimizes rhizospheric microbial community [79]. This microbial treatment can effectively relieve salt-induced yield reduction in soybeans. Soybean seeds were pretreated by soaking in 24-epibrassinolide (EBR, 0.1 μM) for 12 hours, which can activate brassinosteroid (BR) signaling at root apices, promote the development of lateral roots and root hairs, and thereby expand the rhizosphere absorption surface. Concurrently, it enhances the activity of the nitrogen transport systems and nitrogenase [80]. It is speculated that EBR treatment may induce the expression of *GmSOS1* to accelerate Na^+ exclusion in root cells, lower MDA content and boost proline production. In addition, vacuum-assisted seed soaking facilitates the rapid penetration of growth-promoting nanoparticles through the seed coat, enhancing germination vigor and stimulating the proliferation of lateral roots and root hairs. This leads to improved rhizospheric nitrogen fixation and nutrient uptake, ultimately contributing to increased soybean yield [81]. Soaking seeds in a 0.5% chitosan solution for 12 hours significantly enhances seed germination rate, α-amylase activity, and soluble protein content. This pretreatment elevates proline and soluble sugar levels, as well as antioxidant enzyme activities in seedlings under salt stress, which in turn improves plant height, root length, and dry weight [82]. Soaking corn seeds in 10 $mg \cdot L^{-1}$ indole-3-acetic acid (IAA) for 12 hours synchronously upregulates SOD-CAT-GPX enzymatic activities and soluble sugar synthesis under salt stress [83]. Although demonstrated in maize, similar auxin priming strategies maybe also enhance soybean germination under saline conditions. This method offers a promising strategy for improving salt tolerance in soybean seeds as well.

5. Molecular Breeding and Biotechnological Strategies for Salt-Tolerant Soybean Improvement

Molecular marker-assisted selection (MAS) is now a well-established and highly efficient strategy for salt-tolerant soybean germplasm development and cultivar breeding. The elite soybean variety ZH357 harboring the functional allele *GmSALT3*/*GmCHX1* achieves stable yields exceeding 3750 $kg \cdot hm^{-2}$ under field conditions of coastal saline soils [84]. Similarly, near-isogenic lines (NILs) carrying *GmCHX1*, developed via MAS, consistently outperform recurrent parents in grain yield under both controlled salinity treatments and natural saline field environments [84]. Concurrently, CRISPR/Cas9-mediated genome editing has emerged as a powerful tool for precise genetic enhancement of salt tolerance in soybean. Targeted knockout of *GmeIF2b5* markedly mitigates salt-induced leaf wilting, suppresses electrolyte leakage and pathological ROS accumulation, and robustly elevates the activity of key antioxidant enzymes, including SOD, CAT, and APX [85]. The *GmST2* overexpression line enhances JA biosynthesis by upregulating expression of core genes such as *AOS, OPR3,* and *JAR1*, thereby increasing endogenous JA levels and activating JA dependent defense signaling cascades that confer enhanced salt resilience [41]. Furthermore, *gm-mir396a* knockout lines exhibit broad-spectrum tolerance to combined salt stress across critical developmental stages (seedling, flowering, and full vegetative reproductive growth), coupled with optimized architectural traits—including moderate plant height reduction, increased branch and pod numbers, and concomitant gains in seed weight per plant and final grain yield [86]. Integrated multi-omics approaches spanning transcriptomics, metabolomics, and proteomics have become indispensable for reconstructing the hierarchical molecular regulatory network governing soybean salt responses. Salt stress robustly induces central stress-responsive pathways, notably flavonoid biosynthesis, glutathione metabolism, and ABC transporter–mediated ion homeostasis. Comparative physiological profiling reveals that the salt-tolerant cultivar Qihuang 34 sustains significantly lower growth inhibition, maintains superior antioxidant capacity, and accumulates markedly less MDA than the salt-sensitive cultivar Dongnong 50 under equivalent salinity exposure, collectively reflecting a more coordinated, systemic adaptation mechanism [87].

6. Future Insights into Salinity Adaptation and Variety Improvement

6.1. Multi-Technology Integrated Strategies for Precision Salt-Tolerant Soybean Breeding

Despite substantial advances in elucidating salt tolerance physiology, cloning and functional characterization of key genes, optimizing agronomic management practices, and implementing molecular breeding strategies in soybean, several critical bottlenecks continue to impede translational progress. First, the molecular regulatory architecture governing salt resilience specifically during the reproductive phase, encompassing flowering, fertilization, pod initiation, and pod set, remains largely uncharacterized; consequently, the mechanistic basis for salt-induced flower and pod abscission, impaired fertilization, and diminished pod-setting rate is still inadequately resolved. Second, the low genetic transformation efficiency and pronounced genotype dependency in soybean constrain both the throughput and broad applicability of genome editing and transgenic approaches for trait improvement. Third, the majority of edited and transgenic lines are evaluated only under controlled environments (e.g., growth chambers or pot trials), with scarce empirical evidence from multi-year, multi-site field trials conducted on naturally saline-alkali soils, thus limiting robust assessment of their agronomic performance, yield stability, and adaptive fitness under realistic production conditions. Finally, the physiological and genetic trade-offs among salt tolerance, symbiotic nitrogen fixation capacity, and sink strength for yield formation remain poorly quantified and mechanistically undefined, hindering the rational design of elite cultivars that concurrently achieve high salinity resilience, superior grain yield, and efficient biological nitrogen fixation.

Some modern technologies can be applied to address the corresponding issues. Single-cell omics technologies enable the classification of cell populations, facilitating the investigation of stress-tolerance modules across distinct cell types and uncovering tissue- and cell-specific molecular responses in roots, nodules, and leaves under salt stress [88–91]. Haplotype-based pangenome studies allow for the precise identification and tracking of structural variations specific to particular haplotypes, revealing long-term accumulated salt-tolerance alleles that are often missed in reference genomes, thus offering novel strategies for crop improvement [92–94]. The *AT1* gene encodes an atypical G protein γ subunit that suppresses the phosphorylation of PIP2 (plasma membrane intrinsic protein 2) aquaporins, thereby reducing H_2O_2 efflux under alkaline stress. Gene editing-mediated knockout of *AT1* has been shown to significantly enhance the survival and yield of sorghum, rice, maize, and millet in saline soils [95]. Furthermore, advances in synthetic biology have opened new frontiers in the design and breeding of salt-tolerant crops. By modular assembly of signaling components (e.g., Ca^{2+} sensing modules, SOS activation modules, ROS scavenging modules), artificial optimization of metabolic pathways (e.g., osmoprotectant synthesis), and engineering of controllable ion transport systems, precise trait construction and regulation can be achieved, thereby improving the accuracy and efficiency of salt-tolerance breeding [96,97].

6.2. Concluding Remarks

These findings collectively validate the potential of integrated approaches in enhancing crop resilience and provide a solid foundation for designing next-generation soybean breeding strategies tailored to saline environments. Further exploration and functional validation of salt-tolerance genes in soybean are essential to achieve high and stable yields in saline soils. Ideally, future salt-tolerant soybean varieties should exhibit a combination of efficient salt exclusion, restricted internal salt translocation, and effective salt compartmentalization, alongside robust antioxidant capacity and maintained symbiotic nitrogen fixation. The rapid development of agricultural science and technology, the emergence of innovative breeding tools, and the integration of cross-disciplinary technologies are collectively providing efficient and precise pathways for the selection and breeding of high-yield, salt-tolerant soybean varieties. With sustained efforts, soybean has the potential to be developed into a more salt-resilient crop, thereby contributing significantly to the sustainable development and food security goals of the global soybean industry.

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