

Chapter

Wild and Cultivated Soybean: Mechanisms of Salt Tolerance and Agricultural Applications

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Abstract

Soil salinity poses a major challenge to global soybean productivity by inducing osmotic imbalance, ion toxicity, and oxidative stress. Cultivated soybean (*Glycine max*), a glycophytic crop, is particularly salt sensitive, whereas its wild progenitor (*Glycine soja*) exhibits remarkable tolerance through diverse structural and molecular adaptations. This chapter provides a comparative overview of the morphological, physiological, biochemical, and genetic mechanisms underlying salt tolerance in *G. max* and *G. soja*. Under saline conditions, wild soybean maintains superior root architecture, efficient ion exclusion, and sustained photosynthetic performance compared with the cultivated species. Enhanced accumulation of osmolytes and antioxidant enzymes enables *G. soja* to mitigate oxidative damage and preserve cellular homeostasis. At the molecular level, key genes such as *GmSALT3*, *GmNHX5*, *GsCLC-c2*, *GsWRKY40*, *GmFDL19*, and *GsCBRLK* play central roles in ion regulation, ROS detoxification, and ABA-mediated signaling pathways. Transgenic studies confirm that overexpression of these genes improves stress resilience and yield stability under saline conditions. The integration of wild genetic resources with modern molecular breeding and genome-editing tools offers new opportunities to enhance salt tolerance in soybean. Insights from this comparative analysis contribute to developing sustainable strategies for improving crop performance and productivity in salt-affected agroecosystems.

Keywords: soybean, salt tolerance, wild relatives, *Glycine max*, *Glycine soja*, transgenic development, molecular breeding

1. Introduction

Soybean (*Glycine max* (L.) Merr.) is one of the important oil-yielding legumes globally and belonging to the Fabaceae family. It holds immense significance as economic value not only as a multipurpose crop, serving as a key source of edible oil, protein, and raw material for various food products such as soya milk, tofu, and soya sauce. Owing to its high protein content, soybean forms an essential dietary component for both humans and livestock and also serves as a sustainable feedstock

for biodiesel production [1]. Soybean has also been extensively used in biodiesel production. Its demand continues to rise due to its versatility and widespread industrial applications. Currently, soybean contributes nearly two-thirds of globally produced plant protein and ranks among the leading oilseed crops. In response to growing demand, its global production has reached approximately 350 million in recent decades [2]. Rapid climatic fluctuations and environmental degradation have intensified both biotic and abiotic stresses on agriculture. Among the abiotic stresses, drought, cold, and salinity are detrimental to crop productivity. These stresses pose serious threats to global food security by causing progressive decline in yield [1]. To meet future food demands, agricultural production must increase by nearly 70% [3]. Among the various abiotic stresses, salinity is particularly destructive, reducing crop yields and degrading arable lands worldwide. It is projected that by 2050, approximately 50% of the world's arable land could become salinized due to continued soil mismanagement and climate change [2, 4]. Currently, around 1.4 billion hectares—or about 10% of the global land—are affected by salinity, with an additional one billion hectares at risk [5]. Anthropogenic activities—such as excessive fertilizer use, poor irrigation management, and seawater intrusion—further aggravate salinity in both rain-fed and irrigated systems [6, 7].

Salinity imposes osmotic imbalance and ion toxicity in plants, disrupting growth, metabolism, and nutrient homeostasis [8, 9]. Initially, high soil Na^+ concentration reduces water uptake, causing osmotic stress; later, ion accumulation in shoots impairs photosynthesis and cellular metabolism [10]. The dominant salts include Na^+ and Cl^- ions, which account for 50–80% of the total soluble salts in saline soils [11, 12]. These ions limit the nutrient uptake—especially of Ca^{2+} , K^+ , and NO_3^- and cause oxidative damage to plant tissues.

Soybean, a glycophytic crop, is highly sensitive to elevated soil salinity [13]. Salt accumulation in soil and irrigation water negatively affects plant growth, yield, and physiological attributes. Therefore, developing stress-resilient soybean cultivars has become a global priority. Several soybean genotypes show moderate variation in salt tolerance [1, 2, 13], but progress in breeding salt-resistant varieties has been constrained by the crop's narrow genetic base [14]. Wild relatives of cultivated crops often exhibit greater stress tolerance than domesticated lines. *Glycine soja*, the wild progenitor of *G. max*, demonstrates superior salt tolerance through diverse adaptive mechanisms [2, 15, 16]. Its rich genetic diversity offers valuable traits for breeding salt-tolerant cultivars. Despite several reports describing individual physiological and molecular responses, comprehensive comparative analyses integrating morphological, biochemical, and genetic mechanisms remain limited. This chapter aims to synthesize current understanding of the salt-tolerance mechanisms in cultivated and wild soybean species, identify key adaptive traits and genes contributing to tolerance, and highlight their potential use in breeding and transgenic improvement programs for developing salt-resilient cultivars.

2. Habit and Habitat

Soybean (*Glycine max* (L.) Merr.) is an erect, fast-growing, herbaceous leguminous plant that can reach a height of up to 1 m [17]. Native to Asia, soybean is now cultivated globally under diverse agro-climatic conditions [18]. The genus *Glycine* comprises one wild species, one semi-wild species [19], and one cultivated species, along with two polyploid species [20]. Among them, *Glycine max* represents the cultivated soybean,

while *Glycine soja* is its wild progenitor. Soybean is one of the most extensively studied oilseed crops, owing to its agronomic and nutritional significance [7]. The wild soybean (*Glycine soja*) shares the same diploid chromosome number ($2n = 40$) as the cultivated *G. max* and is a rich source of genetic diversity for improving stress resilience and other agronomic traits [17]. Recent studies have reported the existence of polyploid *Glycine* species, such as *G. tabacina* ($2n = 80$) and *G. tomentella*, which shows variation in chromosome number ($2n = 38, 78, \text{ or } 80$) [20, 21]. Wild soybean is native to East Asia, particularly China, Japan, Korea, and Russia, and is typically found in varied habitats such as riverbanks, roadsides, moist areas, and warm climates with fertile, well-drained soils. Globally, the leading producers of soybeans are the United States, Brazil, and Argentina. In India, the major soybean-producing states include Madhya Pradesh, Maharashtra, Rajasthan, Karnataka, and Telangana [22, 23].

3. Morphology and anatomy under salt stress

Salt stress significantly influences the morphology and anatomy of soybean plants, affecting growth, vigor, and productivity. The impact varies considerably between cultivated soybean (*Glycine max*) and its wild relative (*Glycine soja*), reflecting differences in their adaptive strategies and genetic makeup.

3.1 Cultivated soybean (*Glycine max*)

In cultivated soybean, salinity causes significant reductions in plant height, number of leaves, stem thickness, and both root and shoot biomass [7, 24]. Growth suppression is often associated with inhibited cell expansion, reduced water uptake, and impaired photosynthesis. For example, salt-treated soybean plants generally exhibit shorter hypocotyls, fewer leaves, and lower fresh and dry weights compared to controls, particularly at higher salt concentrations [7, 13].

Anatomically, high salinity leads to notable alterations in the vascular system of soybean roots and stems. Studies have shown a decline in metaxylem vessel number and diameter, restricted cell enlargement, and thickening of the cortex and pith under elevated salt levels [25, 26]. The formation of aerenchyma and thicker epidermal and endodermal layers in roots are adaptive responses that restrict sodium entry and mitigate oxidative damage [27]. Additionally, increased cuticle thickness and reduced stomatal density in leaves act as protective barriers to minimize water loss and ion toxicity. These structural modifications, although beneficial for stress tolerance, often come at the cost of reduced growth and productivity.

3.2 Wild soybean (*Glycine soja*)

Wild soybean exhibits more stable growth and structural integrity under salinity compared to its cultivated counterpart. In salt-tolerant lines such as *G. soja* ‘Tongyu06311’, root length and biomass remain largely unaffected even under high salt concentrations, while sensitive lines like ‘Huinan06116’ show significant reductions [28]. This resilience is attributed to better root architecture, enhanced vascular organization, and efficient ion compartmentalization.

Anatomical observations indicate that *G. soja* maintains larger cortical and vascular regions with intact xylem structure under salt stress, supporting improved water and nutrient transport. The presence of well-developed aerenchyma and thicker root

Sr. No.	Trait/response	Cultivated soybean (<i>Glycine max</i>)	Wild soybean (<i>Glycine soja</i>)	References
1	Growth	Reduced plant height, leaf number, shoot, and root biomass	Stable growth and biomass under moderate to high salinity	[7, 28]
2	Root structure	Reduced radicle diameter, and fewer and narrower metaxylem vessels	Well-developed cortex and vascular system, intact metaxylem	[25, 26]
3	Leaf anatomy	Reduced stomatal density, thicker cuticle, smaller leaf area	Maintains leaf area and stomatal function	[19, 29]
4	Aerenchyma formation	Present but limited; primarily in high-salt conditions	Prominent and efficient formation across gradients	[27, 28]
5	Vascular tissue	Collapsed or reduced vessel diameter under high NaCl	Stable and well-differentiated xylem vessels	[26]
6	Adaptation	Structural restriction and growth inhibition	Sustained growth and ion regulation efficiency	[2, 15]

Table 1.

Comparative morphological and anatomical responses of cultivated and wild soybean under salt stress.

cortex enhances its ability to withstand ionic and osmotic imbalances. Comparative studies among *Glycine soja*, *G. tomentella*, and *G. tabacina* further suggest that wild species maintain leaf area and biomass more effectively than cultivated soybean even under increasing salinity levels [29].

A comparison of both species (**Table 1**) highlights that *G. soja* demonstrates special structural adaptations—optimized root architecture, sustained vascular integrity, and efficient ion exclusion—whereas *G. max* primarily responds through growth restriction and tissue thickening. These anatomical and morphological traits collectively contribute to the superior salt tolerance of wild soybean by maintaining ion balance and physiological functionality. Integrating these traits into cultivated genotypes through conventional and molecular breeding could enhance resilience in salt-affected environments.

4. Physiological response and salt tolerance

Salt stress exerts profound effects on soybean physiology, influencing photosynthesis, water relations, ion balance, and metabolic activity. The severity of these responses varies across genotypes, salinity levels, and experimental conditions, with cultivated soybean (*Glycine max*) generally exhibiting greater sensitivity compared to its wild relatives (*Glycine soja*), which reveals the adaptive capacities to maintain cellular homeostasis under saline conditions (**Figure 1; Table 2**).

4.1 Physiological alterations

Salinity reduces the efficiency of photosynthetic processes by disturbing both stomatal and non-stomatal components. Controlled greenhouse and growth chamber

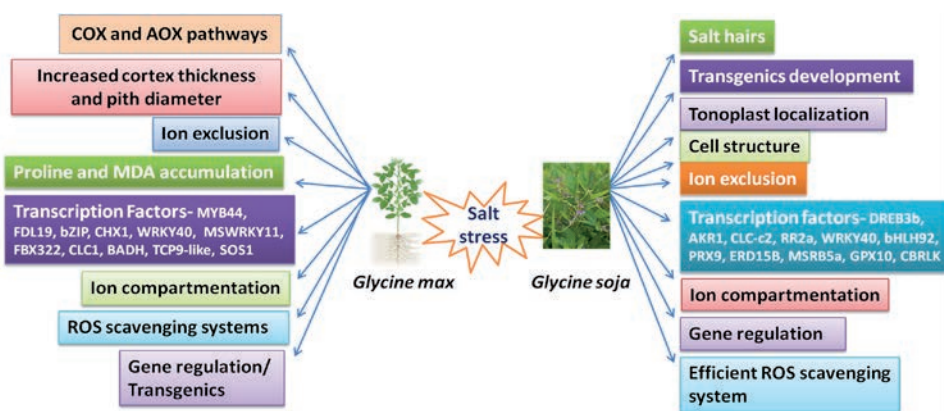


Figure 1. Strategies involved in the salt tolerance mechanism of cultivated soybean *Glycine max* and wild soybean *Glycine soja*. (AOX—alternative oxidase; COX—cyclooxygenase; ROS—reactive oxygen species; MDA—malondialdehyde; MYB44—myeloblastosis 44; bZIP—basic leucine zipper; CHX1—cation/proton exchanger 1; WRKY40—DNA binding protein 40; FBX322—F-box protein 322, CLC1—chloride voltage-gated channel 1; BADH—betaine aldehyde dehydrogenase; TCP9-like—teosinte branched/cycloidea/proliferating cell factor; SOS1—salt overly sensitive 1; DREB3b—dehydration-responsive element binding; AKR1—Aldo-keto reductase 1; CLC2—chloride voltage-gated channel 2; RR2a, WRKY40—DNA-binding protein 40; bHLH92—basic helix-loop-helix 92; PRX9—peroxidase 9; ERD15—early responsive to dehydration 15; MSRB5a—methionine sulfoxide reductase B; GPX10—glutathione peroxidase 10; CBRLK—calmodulin-binding receptor-like kinase).

Sr. No.	Trait/parameter	Cultivated soybean (<i>Glycine max</i>)	Wild soybean (<i>Glycine soja</i>)	Type of study	References
1	Photosynthetic rate and gas exchange	Strong decline in photosynthetic rate, stomatal conductance, and transpiration under salinity	Maintains higher photosynthetic efficiency and PSI/PSII stability	Controlled pot and growth-chamber studies	[13, 30]
2	Relative water content (RWC)	Substantial reduction, indicating poor osmotic adjustment	Higher RWC maintained even under moderate salinity	Pot experiments	[31]
3	Ion regulation (Na^+ , K^+)	High Na^+ accumulation, low K^+/Na^+ ratio	Efficient Na^+ exclusion, maintains higher K^+/Na^+ ratio	Controlled and hydroponic assays	[19, 32]
4	Chlorophyll and pigments	Significant loss of chlorophyll a, b, and carotenoids	Smaller reductions; maintains chlorophyll stability	Greenhouse trials	[33, 34]
5	Osmolyte accumulation (proline, glycine betaine)	Increases under stress but insufficient to prevent injury	Higher accumulation contributes to osmotic balance	Controlled pot studies	[24]
6	Antioxidant enzymes (SOD, CAT, POX)	Moderate or inconsistent induction	Strong and sustained up-regulation under salinity	Pot and transgenic studies	[19, 35]

Sr. No.	Trait/parameter	Cultivated soybean (<i>Glycine max</i>)	Wild soybean (<i>Glycine soja</i>)	Type of study	References
7	Oxidative markers (MDA, H ₂ O ₂)	High accumulation indicating lipid peroxidation	Low accumulation due to better ROS detoxification	Controlled assays	[30]
8	Membrane stability/electrolyte leakage	Elevated leakage and structural damage	Lower leakage; improved membrane integrity	Controlled irrigation trials	[31]
9	Genetic/transgenic validation	Overexpression of salt-responsive genes improves tolerance modestly	Wild-derived genes (e.g., <i>GsWRKY40</i> , <i>GsMYB15</i>) confer strong protection	Transgenic lines (greenhouse and field tests)	[35, 36]

Table 2.

Comparative physiological and biochemical responses of cultivated and wild soybean under salt stress.

studies have demonstrated that increased leaf sodium (Na⁺) accumulation correlates strongly with declines in photosynthetic rate, stomatal conductance, transpiration rate, and water use efficiency [13, 37]. The decrease in carbon assimilation is partly due to stomatal closure caused by osmotic stress and impaired chloroplast function under ion toxicity. Saline irrigation also elevates the electrolyte leakage and reduces relative water content (RWC), indicating membrane damage and reduced water retention capacity. In a pot-based study, the cultivar Giza-111 maintained higher RWC and K⁺/Na⁺ ratio than Giza-35 and Giza-82, suggesting better osmotic adjustment and ion regulation [31]. Similarly, increased NaCl concentrations significantly reduced chlorophyll a, chlorophyll b, and carotenoids in soybean leaves, as observed under controlled experiments using salt-treated irrigation water [33, 34].

Salinity reduces photosynthetic efficiency through both stomatal and non-stomatal limitations. In *G. max*, increased Na⁺ accumulation leads to stomatal closure, reduced transpiration, and impaired CO₂ assimilation. In contrast, *G. soja* sustains higher photosystem stability (PSI/PSII) and maintains a more favorable K⁺/Na⁺ ratio, enabling better osmotic adjustment and chlorophyll retention [30]. The wild species also exhibits lower electrolyte leakage and higher relative water content, indicating improved membrane integrity and water conservation [19]. These physiological responses collectively allow *G. soja* to preserve the photosynthetic performance under saline conditions.

4.2 Biochemical adjustments

Soybean plants counteract salt-induced osmotic and oxidative stress through a suite of biochemical responses. Controlled pot experiments and hydroponic assays have shown that salt exposure significantly increases levels of compatible solutes such as proline and glycine betaine, which stabilize cellular proteins and membranes [24]. Concurrently, the accumulation of reactive oxygen species (ROS) triggers enhanced activity of antioxidant enzymes including superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT), helping to scavenge ROS and maintain redox balance.

Increased MDA content under salinity serves as an indicator of lipid peroxidation, reflecting membrane injury. However, wild soybean exhibits lower MDA and H₂O₂

accumulation compared to cultivated varieties [30], consistent with its enhanced antioxidant defense. This trend is further supported by biochemical analyses of salt-tolerant lines such as *NARC-1* and *NARC-2*, which showed higher biological yield and antioxidant activity under 150 mM NaCl stress [37]. These experiments demonstrate that targeted gene manipulation can strengthen intrinsic stress-mitigating biochemical pathways.

4.3 Interlinked physiological and biochemical mechanisms

Physiological and biochemical adaptations are closely interconnected in determining overall plant tolerance. In soybean, reduced stomatal conductance limits water loss but also affects CO₂ assimilation, which is partly offset by biochemical mechanisms that preserve photosystem efficiency and membrane stability. Osmolyte accumulation (e.g., proline, sugars, glycine betaine) contributes to osmotic balance and protects enzymes, while antioxidant enzymes mitigate ROS-induced damage in chloroplasts and mitochondria. Together, these processes sustain photosynthetic function and cellular homeostasis under salinity stress. The superior salt tolerance observed in wild soybean arises from the synergistic regulation of these physiological and biochemical responses—efficient ion exclusion, enhanced osmotic adjustment, and robust ROS-scavenging mechanisms—making it a valuable genetic resource for improving cultivated soybean resilience through breeding and transgenic approaches [7, 13].

5. Gene regulation and salt tolerance

Salt stress in soybean triggers a complex network of molecular responses involving ion transporters, transcription factors, and signaling proteins that collectively maintain ionic balance, osmotic stability, and redox homeostasis. Studies using transcriptomic, quantitative trait loci (QTL), and single-nucleotide polymorphism (SNP) analyses have identified numerous genes contributing to salinity tolerance. These can be broadly classified into four functional categories: (1) ion homeostasis, (2) transcriptional regulation, (3) reactive oxygen species (ROS) detoxification, and (4) abscisic acid (ABA)-mediated signaling pathways. The key salt responsive genes with their primary function and localization are given in **Table 3**.

5.1 Ion homeostasis and transport regulation

Maintaining intracellular ionic balance is essential under salinity stress. Soybean achieves this through the coordinated activity of Na⁺/H⁺ exchangers, chloride channels, and potassium transporters. The comparative transcriptomic studies in soybean revealed that genes such as *GmHAK5*, *GmKUP6*, and *GmCHX20a* are upregulated under saline conditions to regulate K⁺ transport and maintain a favorable K⁺/Na⁺ ratio [46]. The *GmNHX5* gene, localized to the Golgi apparatus, enhances K⁺ retention and contributes to Na⁺ sequestration in vacuoles [38]. Quantitative trait loci (QTL) mapping has identified *GmSALT3* and *GmSALT18* as the major salt tolerance genes derived from *Glycine soja*, both involved in long-distance Na⁺ and Cl⁻ exclusion from leaves [39]. Similarly, chloride channel genes (*GmCLC1*, *GsCLC-c2*, and *CLC-b* family members) facilitate Cl⁻ compartmentalization, preventing toxic accumulation in shoots [40, 49]. Collectively, these transport-related genes play central roles in sustaining ion homeostasis and minimizing ionic toxicity under saline conditions.

Sr. No.	Functional category	Gene(s)	Source/localization	Primary function	Experimental evidence	References
1	Ion homeostasis	<i>GmNHX5</i> , <i>GmSALT3</i> , <i>GmSALT18</i> , <i>GmCLC1</i> , <i>GsCLC-c2</i>	Golgi, tonoplast, plasma membrane	Na ⁺ /H ⁺ exchange, Cl ⁻ sequestration, ion balance	QTL mapping, transcriptomics	[38–40]
2	Transcriptional regulation	<i>GmFDL19</i> , <i>GsWRKY40</i> , <i>GsbHLH92</i> ,	Nucleus	Activation of stress genes, ABA signaling, ROS regulation	Transgenic & controlled studies	[35, 36, 41, 42]
3	ROS detoxification	<i>GsPRX9</i> , <i>GsMSRB5a</i> , <i>GsoGPX10.1</i>	Cytosol, chloroplast, mitochondria	ROS scavenging, lipid peroxidation reduction	Gene overexpression, biochemical assays	[43–45]
4	ABA and signaling pathways	<i>GmOST1/SnRK2.6</i> , <i>GmERF98</i> , <i>GsCBRLK</i> , <i>GsRR2a</i>	Plasma membrane, cytoplasm	ABA signaling, Ca ²⁺ -mediated stress sensing	Transcriptomic & functional assays	[46–48]

Table 3.
Summary of functional category, localization, primary function, and experimental evidences of key salt-responsive genes in soybean.

5.2 Transcriptional regulation

Transcription factors (TFs) serve as master regulators that activate stress-responsive genes. Members of the *WRKY*, *DREB*, *MYB*, and *bZIP* families have been extensively characterized in soybean. For instance, *GmFDL19*, a basic leucine zipper (*bZIP*) transcription factor, enhances tolerance to drought and salinity through ABA-mediated pathways and promotes early flowering [35]. The *DREB3b* allele from *G. soja* confers greater salt tolerance than the reference *DREB3* gene in cultivated soybean [41]. The *WRKY* family is particularly important in oxidative stress and hormonal regulation. Co-overexpression of *GsWRKY40* and *GsbHLH92* from *G. soja* significantly enhances salt tolerance while reducing ROS accumulation, demonstrating the synergistic regulation of stress-responsive networks [35]. Similarly, overexpression of *AtWRKY11* in transgenic soybean lines improved survival and growth under saline conditions [42].

5.3 ROS detoxification and antioxidant defense

Salt stress leads to oxidative damage through the overproduction of reactive oxygen species (ROS), including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl ions (OH^-). Soybean counteracts this *via* genes encoding antioxidant enzymes and ROS-regulating proteins.

Key examples include *GsPRX9* (peroxidase) and *GsMSRB5a* (methionine sulfoxide reductase), both isolated from *G. soja*, which enhance enzymatic detoxification and regulate ROS signaling [43, 44]. The *GsoGPX10.1* gene, encoding glutathione peroxidase, shows continuous upregulation under salt exposure, highlighting its function in maintaining redox balance [45].

5.4 ABA signaling and stress perception pathways

The abscisic acid (ABA) pathway plays a pivotal role in integrating external salt signals with internal physiological responses. Genes such as *GmOST1/SnRK2.6* and *GmERF98* are upregulated under salinity, participating in ABA-dependent stomatal regulation and downstream stress signaling [46]. In wild soybean, *GsCBRLK* (a calcium/calmodulin-binding receptor-like kinase) positively regulates tolerance to both salt and ABA stress by mediating Ca^{2+} -dependent signaling cascades [47]. Likewise, *GsRR2a*, a cytokinin response regulator, shows dual responsiveness to salt and alkali stress, suggesting its involvement in multiple hormonal pathways [48].

In summary, the gene regulation in soybean under salinity stress represents a tightly coordinated molecular system. Wild soybean (*G. soja*) contributes to unique alleles and transcription factors that enhance tolerance by fine-tuning ion balance, maintaining ROS homeostasis, and activating ABA-linked signaling networks. The integration of QTL mapping, transcriptomic analysis, and transgenic validation provides valuable insights for molecular breeding and the development of salt-resilient soybean cultivars.

6. Development of transgenics for improved salt tolerance

The development of transgenic soybean lines represents a promising strategy to enhance salt tolerance beyond the limits of conventional breeding. Traditional

breeding efforts are often constrained by the narrow genetic base of cultivated *G. max*, whereas transgenic approaches allow direct incorporation of stress-responsive genes from wild soybean (*G. soja*), halophytes, and other plant species [39, 41, 43]. Advances in *Agrobacterium*-mediated transformation, genome editing, and transcriptomic analyses have greatly accelerated gene discovery and functional validation.

Several successful transgenic interventions in soybean have focused on maintaining ionic balance under saline conditions. Overexpression of *GmCHX1*, a cation/H⁺ antiporter, confers enhanced Na⁺ exclusion and Cl⁻ sequestration by coordinating root and shoot ion transport [50]. Similarly, *GmNHX5*, localized in the Golgi apparatus, increases intracellular K⁺ retention and improves the K⁺/Na⁺ ratio in transgenic plants [38]. The introduction of the *BADH* (betaine aldehyde dehydrogenase) gene from *Atriplex hortensis* (*AhBADH*) via *Agrobacterium*-mediated transformation led to stable enhancement of salt tolerance in soybean. Transgenic lines (e.g., TL7) demonstrated better growth, higher chlorophyll content, and reduced ROS accumulation under 300 mM NaCl compared to controls [51]. These greenhouse and field studies confirmed *AhBADH*-expressing lines as the strong candidates for commercial breeding programs.

Transcription factors derived from *Glycine soja* and other species have proven effective in enhancing tolerance by activating multiple downstream stress-response pathways. Overexpression of *GsMYB15* in transgenic *Arabidopsis* enhanced resistance to both salinity and insect stress, highlighting its dual role in defense regulation [52]. Similarly, *GsWRKY40* and *GsbHLH92* co-overexpression in *G. soja* led to greater salt tolerance through suppression of ROS accumulation and stimulation of antioxidant enzyme activities [36]. Transgenic soybean plants expressing *GmFDL19* (a bZIP transcription factor) showed improved drought and salt tolerance through ABA-dependent signaling and early flowering [35]. In addition, *AtMYB44* expression in soybean enhanced drought and salinity tolerance without negative effects on yield [53]. These examples demonstrate that transcription factor engineering provides broad-spectrum stress resilience.

Manipulation of ROS-scavenging systems offers another effective strategy for developing salt-tolerant soybean. Overexpression of *GsPRX9* (peroxidase) and *GsERD15B* (early responsive to dehydration gene) from wild soybean improved the oxidative stress tolerance by maintaining membrane integrity and reducing MDA accumulation [43, 54]. Similarly, *GsMSRB5a*, encoding methionine sulfoxide reductase, enhanced salt and alkali tolerance by regulating ROS signaling [44].

Recent genome-wide studies in *G. soja* identified multiple glutathione peroxidase genes (*GsoGPX10.1*, *GsoGPX4.2*, *GsoGPX7.1*), among which *GsoGPX10.1* was most responsive under 250 mM NaCl, highlighting its regulatory role in ROS homeostasis [45]. These transgenic findings, primarily validated under controlled greenhouse conditions, collectively emphasize the potential of ROS-related genes in mitigating oxidative damage during salinity stress.

Several signaling-related genes have been exploited to enhance stress perception and response. The *GsCBRLK* gene, encoding a calcium/calmodulin-binding receptor-like kinase from *G. soja*, improved salt and ABA tolerance when overexpressed in *Medicago sativa* [47]. This gene functions as a positive regulator of Ca²⁺-mediated signaling pathways. Similarly, *GmNFYA13*, encoding a nuclear factor Y subunit, increased salt and drought tolerance in transgenic soybean by enhancing ABA-responsive gene expression [55]. Incorporating multiple genes within ABA and calcium pathways, such as *AtAVP1* (vacuolar H⁺-pyrophosphatase) and *AtNHX1* (Na⁺/H⁺ antiporter) in co-expression systems, has also produced the additive benefits for salt tolerance by improving ion compartmentalization and osmotic adjustment [56].

Sr. No.	Gene(s)	Source species	Mechanism of action	Effect in transgenic soybean	Reference
1	<i>AhBADH</i> , <i>GmNHX5</i> , <i>GmCHX1</i>	<i>Atriplex hortensis</i> , <i>G. max</i>	Osmolyte synthesis, Na ⁺ sequestration, K ⁺ retention	Improved growth, higher chlorophyll, better K ⁺ /Na ⁺ ratio	[38, 50, 51]
2	<i>GsWRKY40</i> , <i>GsbHLH92</i> , <i>GmFDL19</i> , <i>GsMYB15</i> , <i>AtMYB44</i>	<i>G. soja</i> , <i>A. thaliana</i>	Activation of salt-responsive genes, ABA regulation	Enhanced tolerance, reduced ROS, stable yield	[35, 36, 52, 53]
3	<i>GsPRX9</i> , <i>GsERD15B</i> , <i>GsMSRB5a</i> , <i>GsoGPX10.1</i>	<i>G. soja</i>	ROS scavenging, membrane protection	Lower MDA and H ₂ O ₂ , improved survival	[43–45, 54]
4	<i>GsCBRLK</i> , <i>GmNFYA13</i> , <i>AtAVP1</i> , <i>AtNHX1</i>	<i>G. soja</i> , <i>G. max</i> , <i>A. thaliana</i>	ABA-responsive regulation, Ca ²⁺ -mediated signaling	Enhanced salt and drought resilience	[47, 55, 56]
5	<i>SpRAB18</i>	<i>Sesuvium portulacastrum</i>	Stress-induced protein expression, osmoprotection	Increased biomass, photosynthetic stability	[57, 58]

Table 4.
Key transgenic developments in soybean.

Beyond soybean relatives, genes from halophytic species have provided promising tools for engineering salinity tolerance. For instance, overexpression of the *SpRAB18* gene from the halophyte *Sesuvium portulacastrum* enhanced growth, chlorophyll content, and antioxidative defense in transgenic soybean under saline conditions [57]. Such cross-species gene transfers expand the genetic toolkit for crop improvement. The key transgenic soybean development studies are enlisted in **Table 4**.

7. Conclusion and future prospects

Salt stress remains a major constraint on global soybean productivity, particularly due to the crop's classification as a moderately salt-sensitive glycophyte. Traditional breeding has made limited progress owing to the narrow genetic base of cultivated soybean (*G. max*). In contrast, its wild relative, *G. soja*, exhibits remarkable salt tolerance owing to a wide array of adaptive morphological, physiological, biochemical, and molecular traits. This genetic diversity has emerged as a vital resource for developing stress-resilient cultivars. Significant progress has been made in identifying and functionally characterizing salt-responsive genes from *G. soja*. Several transcription factors (*GsMYB15*, *GsWRKY40*, *GsERD15B*, *GsCBRLK*, *GmFDL19*), antioxidant-related genes (*GsPRX9*, *GsoGPX10.1*, *GsMSRB5a*), and ion transporters (*GmCHX1*, *GsCLC-c2*, *GmCLC1*, *GmNHX5*, *GmSALT3*) have been found to enhance salt tolerance through diverse mechanisms including ROS detoxification, ion homeostasis, and hormone signaling. Many of these genes have been successfully

overexpressed in model and crop plants, leading to improved physiological responses and yield stability under saline conditions. Transgenic approaches using genes from *G. soja* and other halophytes (e.g., *AhBADH* from *Atriplex hortensis*) have demonstrated considerable success in greenhouse and early field trials. Notably, lines such as TL7 expressing *AhBADH* have shown stable salt tolerance and promising agronomic traits, highlighting the translational potential of these genes in crop improvement programs. Furthermore, the co-expression of multiple stress-related genes has been more effective than single-gene strategies in enhancing salt tolerance. Despite these advances, large-scale field validation, regulatory clearance, and public acceptance remain critical bottlenecks in the commercial deployment of transgenic salt-tolerant soybean varieties. Continued research into the genetic mechanisms of salt tolerance in *G. soja*, coupled with modern genome-editing and gene-stacking technologies, holds great promise for developing robust soybean cultivars suitable for saline environments. This integrated approach is essential for ensuring future food and energy security under increasing soil salinization and climate variability.

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Conflicts of interests

All authors have no conflict of interest.

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