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The Role of Calcium in Salinity Stress Alleviation: Mechanisms and Implications

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Abstract

Soil salinity is one of the most severe abiotic stresses limiting agricultural productivity worldwide by adversely affecting plant growth, development, and yield. Excessive salt accumulation disrupts ion homeostasis, induces osmotic and oxidative stress, impairs photosynthesis, and alters essential metabolic processes. Calcium (Ca^{2+}) plays a pivotal role in enhancing plant tolerance to salinity by functioning as both a structural component and a critical secondary messenger in stress signaling pathways. This review comprehensively examines the mechanisms through which Ca^{2+} mitigates salinity stress, including its role in maintaining membrane integrity, regulating ion transport, preserving Na^+/K^+ homeostasis, and activating the Salt Overly Sensitive (SOS) signaling pathway. Particular emphasis is placed on calcium-mediated regulation of antioxidant defense systems, osmo-protectant accumulation (such as proline, glycine betaine, and soluble sugars), and the biosynthesis of secondary metabolites including phenolics and flavonoids that contribute to stress adaptation. Furthermore, the review highlights the intricate crosstalk between Ca^{2+} signaling and phytohormones, including abscisic acid, salicylic acid, jasmonic acid, ethylene, and auxin, which collectively coordinate plant responses to saline environments. Recent advances in understanding calcium-dependent signaling networks, transcriptional regulation, and reactive oxygen species (ROS) interactions are also discussed. In addition, the practical applications of calcium-based amendments, foliar sprays, and nutrient management strategies for improving crop performance under saline conditions are evaluated. Despite significant progress, challenges related to signaling specificity, ion interactions, and field-level implementation remain. A deeper understanding of calcium-mediated stress responses will facilitate the development of innovative strategies to enhance crop resilience and sustain agricultural productivity in salt-affected ecosystems.

Keywords: Calcium signaling; salinity stress; ion homeostasis; osmo-protectants; secondary metabolites; phytohormones; antioxidant defense; crop improvement

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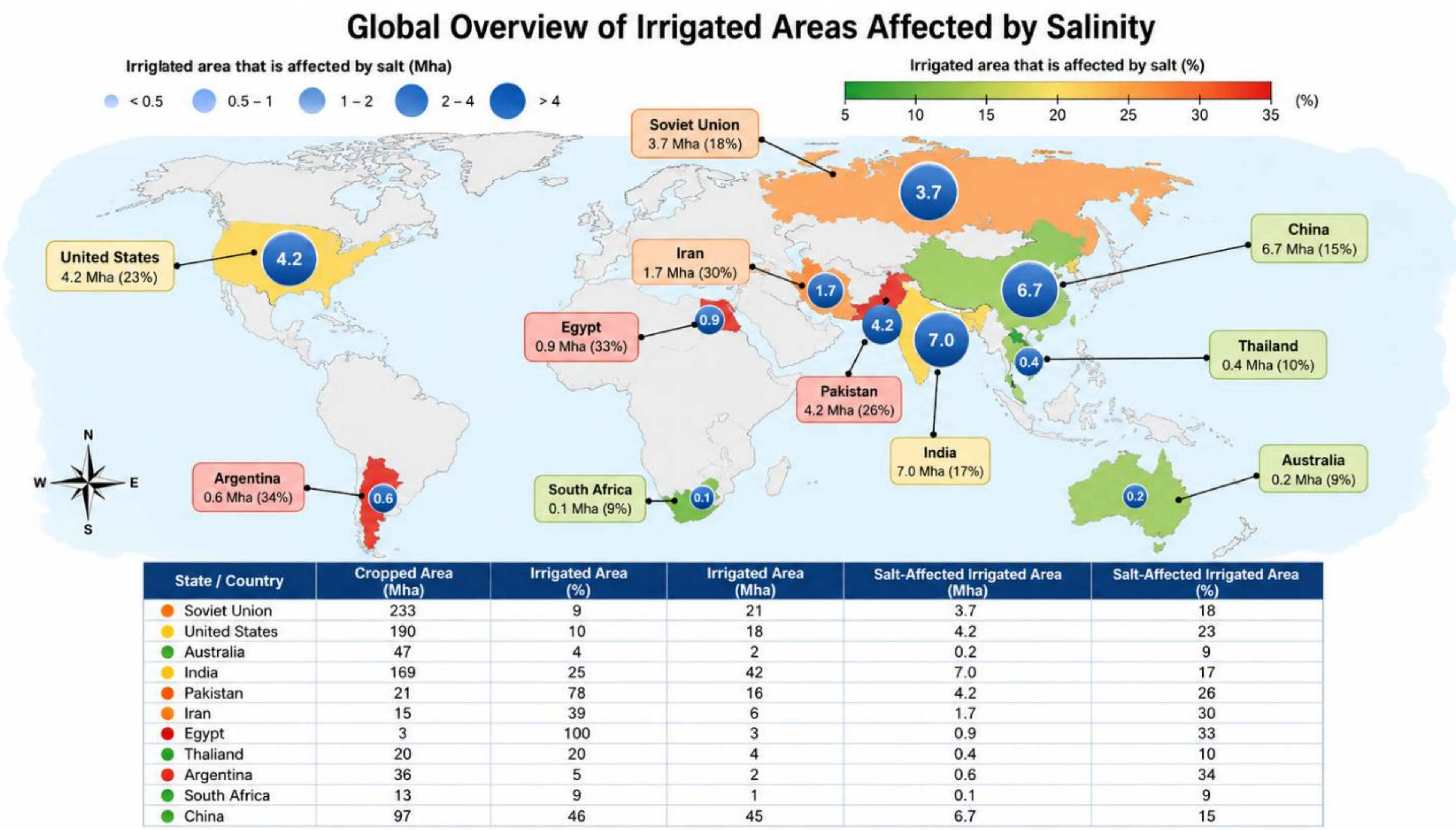
Introduction

Stress is any outside abiotic (salinity, temperature, water, etc.) or biotic (herbivores) force that slows down photosynthesis and makes it harder for plants to crack energy in to biomass [1]. There are many problems in world agriculture, such as the need to produce 70% more food to feed a growing population while crop yields are not rising at the same rate as food demand. Most of the time, the lower output is due to different abiotic pressures [2]. To encounter the growing request for food, one of the most important things that needs to be done is to stop crop losses caused by different natural factors. High salt levels, drought, cold, and heat are some of the main abiotic stresses that hurt the life, biomass production, and output of key food crops by up to 70%. Salt stress is what plants go through when they have too many chemicals like Na^+ and/or Cl^-. It has been shown that soil salt existed before people and farming. However, farming methods like drainage have made the situation worse. There are two main types of soils based on the structure, traits, and plant growth connections in saline soils. (1) Saline soils are distinguished by an abundance Na_2SO_4 and NaCl, along with trace quantities of Cl^- and SO_4^- derived from Ca^{2+} and Mg^{2+} ions. These soils have sufficient quantities of soluble salts to hurt the growth of most crops, and (2) sodic soils, which have a lot of soluble salts like Na_2CO_3 that can be broken down by alkaline water [3]. Salinity is a major problem that keeps crops from producing as much as they could. It hurts seedlings, plants, and food output. A lot of watered places get salinized because they use salty water [4]. Salt has ruined more than 45 million (hac) of wet land around the world. Also, every year, high amounts of salt in the soil keep 1.5 million hectares from being used for farming [5].

Natural or primary salinity

The main cause of primary salinity is salts building up over time in soil through natural processes. Mainly caused by two natural things. First is the aging of source materials that have salts and dissolve in water. Rocks are broken down by weathering, which releases different kinds of liquid salts, mostly sodium chloride, magnesium and calcium, but also sulfates and carbonates to a smaller level. The salt that dissolves the best is sodium chloride [6]. The second is the buildup of salty water caused by rain and wind. "Cyclic salts" are salts from the ocean that break off and fall back into the ocean when it rains. Most of them are sodium chloride [7].



State / Country	Cropped Area (Mha)	Irrigated Area (%)	Irrigated Area (Mha)	Salt-Affected Irrigated Area (Mha)	Salt-Affected Irrigated Area (%)
🟠 Soviet Union	233	9	21	3.7	18
🟡 United States	190	10	18	4.2	23
🟢 Australia	47	4	2	0.2	9
🟡 India	169	25	42	7.0	17
🟠 Pakistan	21	78	16	4.2	26
🟠 Iran	15	39	6	1.7	30
🔴 Egypt	3	100	3	0.9	33
🟢 Thailand	20	20	4	0.4	10
🔴 Argentina	36	5	2	0.6	34
🟢 South Africa	13	9	1	0.1	9
🟢 China	97	46	45	6.7	15

Figure 1. Global distribution of irrigated agricultural land affected by salinity in selected countries. The map illustrates the extent of irrigated areas affected by salt accumulation (Mha) and the percentage of irrigated land impacted by salinity across major agricultural regions worldwide. Bubble size represents the area of salt-affected irrigated land (Mha), while country colors indicate the percentage of irrigated land affected by salinity. The accompanying table summarizes cropped area, irrigated area, and salinity-affected irrigated area for each country. Data were compiled from published reports and national assessments for the former Soviet Union [15], United States [16], Australia[17], India[18], Pakistan [19], Iran [20], Egypt [21], Thailand [22], Argentina [23], South Africa [24], and China [25].

Secondary or human-induced salinity

People change the water balance of the land by doing things like watering crops or applying water through irrigation. This can lead to secondary salinization [8]. The most common reasons are (a) clearing land and planting yearly crops instead of permanent ones, and (b) irrigation systems that use salty water or don't let enough water run away [9]. The increasing salinity of the soil is causing significant strain on more than 831 million hectares of farmland worldwide [10]. Soil salt has hurt about 30% of the flooded land and 6% land area of entire world. This has cost agriculture 12 billion US dollars in lost production [11]. Salt affects 32 million of the 1,500 million hectares of arid land agriculture and 45 million of the 230 million hectares of irrigated land (19.5% and 2.1%, respectively) [12]. Table 1 explain that the amount of salty watered land in different states runs from 9% to 34%, with 20% being the average around the world. There is only 15% watered land that is farmed, provide one-third of the world's sustenance, because it is at least twice as productive as land that is fed by rain [13]. More and more fertile land is becoming salty, which means we need to learn more about how plants can handle it so we can keep crops growing well by changing the conditions of growth as much as possible (Figure 1) [14].

Lack of water, ion toxicity, nutrient problems, oxidative stress, changes in biological processes, membrane disruption, lower cell division and growth, and damage to DNA are some of the ways that high salt can hurt plants [26]. All of these effects make it harder for plants to grow, develop, and stay alive. Major processes of plant are slowed down or stopped when it is under salt stress, including photosynthesis, protein production, energy and fat processing [27]. If plants get subjected to salt for the first time, they suffer water stress, which makes leaves less likely to grow [28]. Osmotic consequences of salinity stress can be seen right away after salt is added and are thought to last as long as the plant is bare to it. These effects stop cells from growing and dividing and also close stomata [29]. When plants are bare to salt for longtime, they go through ionic stress, which can cause grown leaves to die before they should, reducing the amount of green area that can support growth [30].

Halophytes

It is well known that higher plants can handle high salt levels by either excluding salt or incorporating salt. Salt excluders can keep salts out of the plant as a whole or just from certain parts of it [31]. In this case, membrane selection makes it more likely for K^+ to be taken up than Na^+. This is why excluder products have low amounts of Na^+ and Cl^-. On the other hand, salt accumulators can handle taking in high salt levels in one of two ways. There are plants called halophytes that can grow in areas with a lot of salt and also take salts from the soil's surface. Halophytes are plants from more than 80 groups that have evolved to be able to handle the high salt levels in the water they drink. Salt glands are special leaf cells on some halophytes that let out salt [32]. Some plants have salt hairs on the stem that release salt. The sodium ion makes the stomatal guard cells in some plants work [33]. These plants change how much water they lose through transpiration based on how much salt is in the air. It is now easier and more useful to use these kinds of plants to fix grounds that have been damaged by salt than to use chemicals [11]. The first way halophytes are able to survive is by having cell walls that can handle high amounts of intercellular salts. In this case, it is clear that the tissue Na$^+$ to K$^+$ ratio is high [34]. The second approach is to stop too much salt from getting into the plant. Salt ions can be taken up by the roots without hurting them [35].

Glycophytes

It is mostly made up of glycophytes, which include many important food and business items. Salt stress is too much for glycophytes to handle, but they can learn how to deal with it [36]. These plants are very sensitive to salt levels 100–200 mM salt can kill or stunt them. Fruit trees, like avocado and orange trees, need dirt with less than a few millimoles per litter of NaCl [37]. Salinity can stop seeds from sprouting and stop plants from doing usual things as they grow. You could not say that glycophytes can handle salt; instead, they have ways to fight off salt [38]. Glycophytes can handle some things by actively moving ions around and making the K$^+$/Na$^+$ ratio high. This changes the ionic and electrochemical gradients so that they are better for cytoplasmic processes [39]. The sexual parts and leaves get salty, and the plant stops caring about growth or reproduction and just tries to stay alive [40]. Glycophytes can't do much to adapt to salty conditions, though. Scientists are looking into transgenic plants that use genes from halophytes to make glycophytes more tolerant of salt [41]. Soil saltiness needs to go down or glycophytes need to slowly change through natural processes, human-made breeding, or genetic modification in order to fight against salt [42] as shown in figure 2.

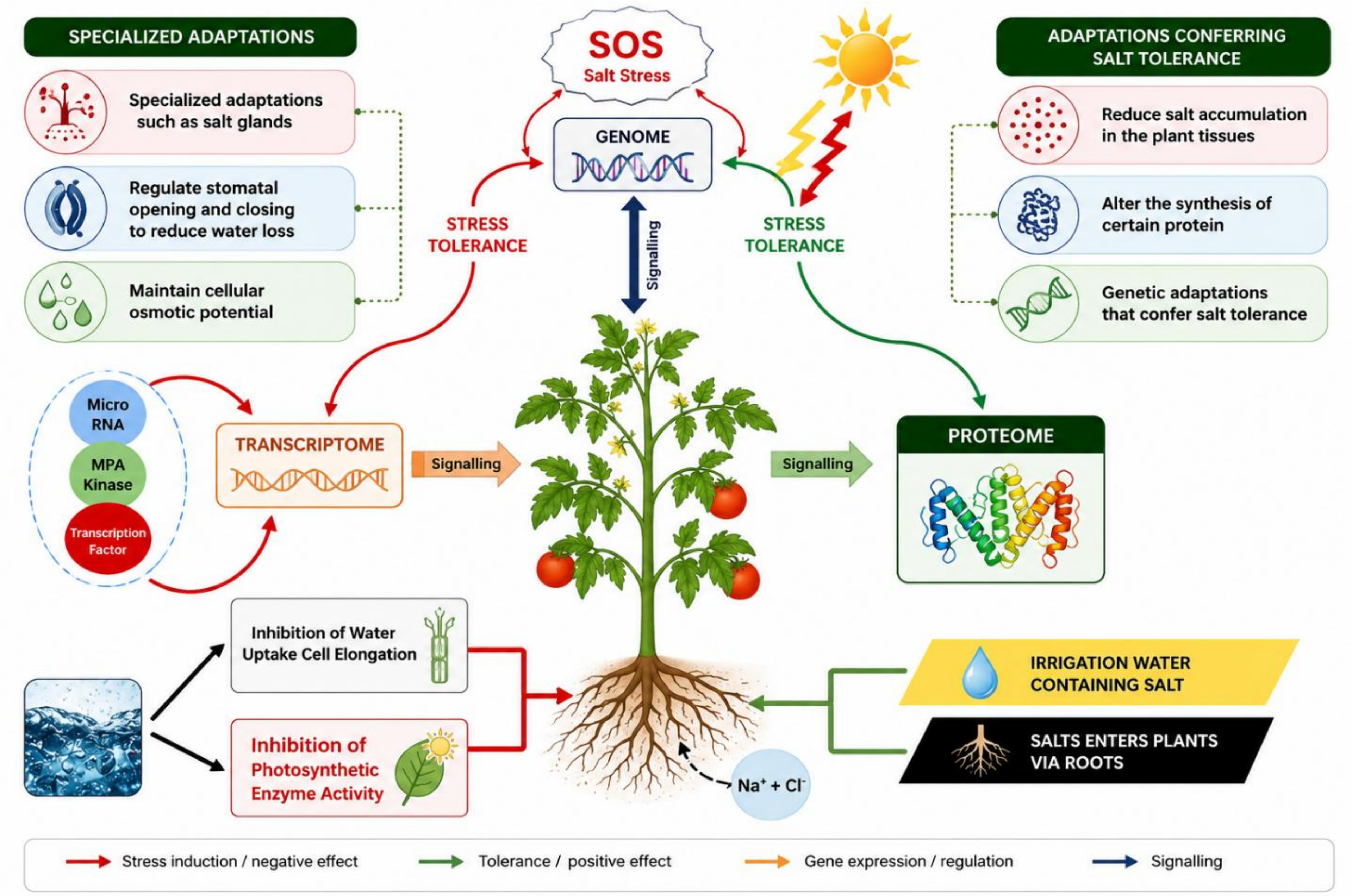


Figure 2. Plant mechanisms of salt stress tolerance. Salinity stress caused by Na$^+$ and Cl$^-$ accumulation negatively affects plant growth by reducing water uptake, inhibiting cell elongation, and impairing photosynthesis. In response, plants activate genomic, transcriptomic, and proteomic pathways through complex signaling networks involving transcription factors, microRNAs, and MAPK cascades. Salt tolerance is achieved through osmotic adjustment, regulation of stomatal activity, ion homeostasis, reduced salt accumulation in tissues, and the expression of stress-responsive genes and proteins. Together, these physiological, biochemical, and molecular adaptations enhance plant survival and productivity under saline conditions. Red arrows indicate negative effects, green arrows indicate tolerance responses, orange arrows represent gene regulation, and blue arrows denote signaling pathways.

Physiological Responses to Salinity Stress

Overarching influence on development and growth

Severe duress conditions possess the capacity to hinder the growth and development of plants, reduce their yield, and potentially lead to their demise [43]. Salinity hinders plant growth by dropping the osmotic potential of the soil solution and causing a nutritional imbalance. As the outcome of the hyperosmotic effect of salt stress, secondary stresses, including oxidative damage, frequently manifest as a consequence of its primary effects [44]. Globally, increased salinity is a significant constraint on agricultural production and a severe problem [45]. On average, each litter of water on earth typically covers around 30 g of NaCl. This may result in an extremely saline planet [11]. Germination and development of seedlings can be substantially impeded by elevated soil salinity levels, owing to the synergistic influence of elevated osmotic potential and specific ion toxicity [46]. The detrimental impacts of salt stress on plant metabolism and functionality significantly impede crop productivity. The presence of salt in the soil reduces the availability of water to the roots. For instance, Kodikara*, et al.* [47] observed that *Rhizophora mucronata* plants grew optimally in 50% seawater and experienced a decline in weight as salinity increased. In contrast, *Alhagi pseudoalhagi*, a leguminous plant, exhibited an increase in total plant weight at low salinity levels (50 mM NaCl) but a decrease at high salinity levels (200 and 100 mM NaCl). At 200 mM NaCl, leaf area and the fresh and dry biomass of leaves and roots were significantly reduced in sugar beet, while leaf number remained relatively unchanged. Karimi*, et al.* [48] stated that a greater reduction in dry matter accumulation was observed in the shoots of sultana vines compared to the roots, especially when bare to high concentrations of NaCl. This suggests that photo-assimilates are partitioned in favor of roots. They hypothesized that the outcomes might be attributable to a greater capacity for osmoregulation when the roots are under stress (Figure 3).

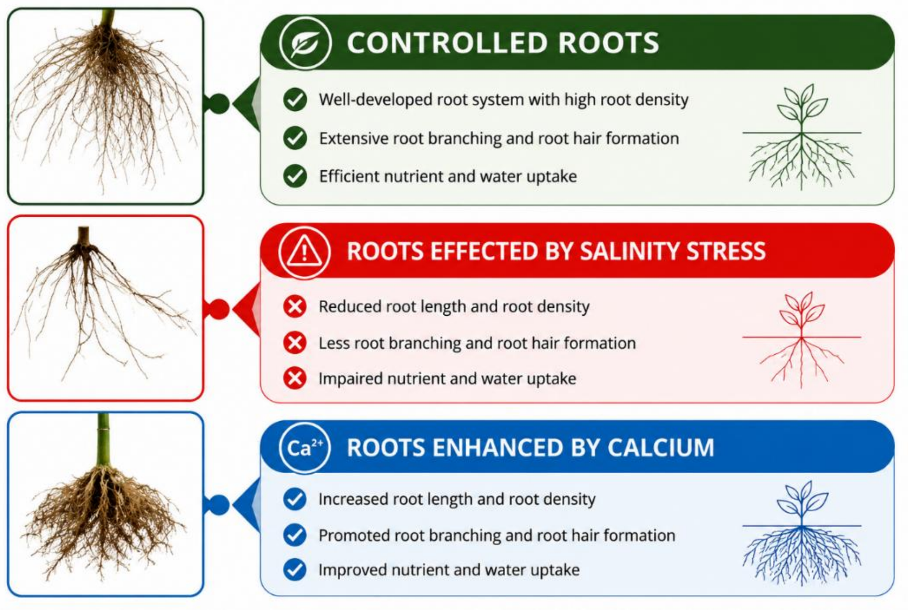


Figure 3. Effect of calcium on maize root growth under salinity stress. Calcium treatment enhanced root development compared with untreated salt-stressed plants. Salinity stress significantly inhibited root growth and development in maize seedlings, resulting in reduced root length, biomass, and overall root system architecture. Application of calcium mitigated the adverse effects of salt stress by promoting root elongation, enhancing lateral root formation, and improving root vigor compared with untreated salt-stressed plants. Calcium-mediated improvements in root growth are associated with its role in maintaining membrane stability, regulating ion homeostasis, reducing sodium toxicity, and enhancing water and nutrient uptake.

Effects of salinity on photosynthesis

Photosynthesis is necessary for plants to grow, so natural stresses that hurt growth also hurt photosynthesis. Recent study showed that saltiness reduced the aptitude of plants to make food through photosynthesis. Different crops, like *Gossypium hirsutum* and Asparagus officinal, have shown a link between photosynthetic rate and output when the soil is salty. Yildiz*, et al.* [49] found that plants that were bare to salt had a lot less photosynthesis when their vegetative growth was stopped. On the other hand, many studies show that there is little to no link between growth and photosynthetic ability, like the one on *Triticum repens*.

Cell walls lose water, which makes them less permeable to CO_2. When there is a lot of salt in the water and soil, the potential for osmosis is high. This makes it harder for plants to get water. Osmotic stress is caused by a drop in water potential, which stops photosynthetic electron transport by making the space between cells smaller. Because of Na^+ and Cl^- ions, salt is poisonous. Dubey*, et al.* [50] analyze that Cl slows down the rate of photosynthesis by stopping the roots from taking in NO_3-N. Al-Tawaha*, et al.* [51] stated that NO3-N levels dropped a lot in sultana plants that were stressed by salt, and this drop was linked to a drop in photosynthesis. The fact that less NO_3-N is taken in and osmotic stress may explain why salt stops photosynthesis. Less CO_2 entering the plant because stomata close. Because stomatal leakage is lower, there is less CO_2 available for carboxylation processes. Closing the stomata reduces the amount of water lost through evaporation. This changes the way chloroplasts collect light and use energy, which changes how active chloroplasts are. It is known that plants with higher stomatal leakage let more CO_2 into their leaves, which helps them make more food.

Effect on ion homeostasis and plant water

Ionic stress and toxins are the two main effects that salt has on plants. Both of these have an impact on all the important processes that plants do [52]. Plants can take in water and minerals because, in normal conditions, they have more water flow than the dirt [53]. Salt stress is characterized by an upsurge in osmotic pressure within the sediment relative to the pressure within the plant cells. The plant can't get enough water because of this [41]. In order to save water, the stomata will close and cell lose turgidity. When stomata close, plants may fix less carbon and make more reactive oxygen species (ROS) [54]. Viral outgrowth is caused by ROS, which inflicts harm on lipids, proteins, and nucleic acids. Ionic toxicity is characterized by an imbalance of sodium concentrations within cells, which obstructs cellular processes and metabolism [55]. Potassium, a similar cation, is nutritionally disrupted at the root surface by sodium ions, which inhibit both potassium uptake and cellular enzymatic processes. Potassium is an essential nutrient for plants, as it controls more than fifty enzymes [56]. Potassium must be maintained in the cytosol at 100-200mM for functions including constructing membrane potential, modulating enzymatic activities, and maintaining cell turgor pressure. However, sodium induces stress in the cytosol at concentrations exceeding 10mM. Similar to K^+, the cation Na^+ traverses the cell membrane with relative ease [57]. It inhibits a multitude of enzymes, thereby interfering with metabolic processes [58]. On the contrary, certain plant species are safeguarded by calcium cations via signaling pathways that control potassium sodium transporters. Calcium concentrations in the cytosol increase when transmembrane proteins or enzymes within a plant detect salt duress [59]. As an essential second mediator in numerous biochemical pathways, calcium can assist plants in coping with salt duress. Osmotic and ionic stress from salinity can impede the growth of plants, which redirect their energy towards water conservation and ionic balance improvement [60]. For plants to resume regular photosynthesis and functionality, they must support their own detoxification process (Table 1) [61].

Table 1. The effect of Calcium on different aspects of plant physiology under salinity stress.

Species	Calcium Treatment	Effects on Physiology	Reference
Tomato	Calcium nitrate soil application	Improved water uptake, reduced oxidative stress	Yang, *et al.* [62]
Arabidopsis	Genetic modification for enhanced calcium signaling	Improved growth under salinity	Yun, *et al.* [63]
Wheat	Calcium foliar application	Increased photosynthetic efficiency, reduced lipid peroxidation	Gao, *et al.* [64]
Barley	Calcium-enriched irrigation water	Enhanced root growth, reduced sodium uptake	Shaddam, *et al.* [65]
Maize	Calcium signaling activator treatment	Improved stomatal regulation, increased salt tolerance	Mahmood, *et al.* [66]
Soybean	Calcium supplementation in nutrient solution	Increased osmolyte accumulation, maintained cell turgor	Lin, *et al.* [67]
Pepper	Calcium foliar spray + gypsum soil amendment	Enhanced membrane stability, reduced ion accumulation	Pal, *et al.* [68]
Cotton	Calcium-enriched hydrogel application	Improved root morphology, increased water use efficiency	Sedek, *et al.* [69]

Molecular Mechanisms of Calcium-Mediated Stress Alleviation

Mechanism of salt stress perception

Vegetation that experiences salinity stress have strong growth reduction in different parts [70]. The HKT (High-Affinity Potassium Transporter) controls the flow of Na^+ into the cell. But because Na^+ and K^+ have very similar hydrated ionic radii, PM (Plasma Membrane) ion transporters usually can't tell the difference between their entry. This makes Na^+ poisonous when it comes into contact with high salt amounts. Several enzymes are thrown off by this one-way flow, and since a high amount of Na^+ isn't needed, it happens at the same time as osmotic pressure damage [71]. When plant growth is slowed down, especially in the leaves, plant biomass drops sharply because less leaf area means less photosynthesis [72]. Researchers have found that corn plants that can handle salt have cells that can stretch more when they are stressed by salt [73]. On the other hand, hypersensitive *Arabidopsis* mutants have problems with how their cell walls are put together. It's not fully clear how cell walls expand during osmotic shock, but the FERONIA (FER) receptor kinase activity has been linked to maintaining cell wall stability during salt stress [74]. FERONIA is a PM localized receptor kinase that is very important for keeping the shape of plant cell walls when they are bare to salt shock [75]. This is mostly linked to the Ca^{2+} signaling chain. When plants are under salt stress, Na^+ damages the cell wall structure [76]. It notices this damage and opens a Ca^{2+} channel through an unknown route. This causes a short-lived Ca^{2+} signaling in the root cells [77] as shown in Figure 3. Salt-sensitive receptors, which include histidine kinases, AHK1/ATHK1, nonselective cation channels, SOS1, Na^+ H^+ antiporters, and NSCCs (Non-Selective Cation Channels), detect Na^+. The Elevation of the sodium ion concentration in the surrounding environment induces a transcellular uptake of Na^+ via NSCCs [78]. Some of the most important types of NSCCs in A. thaliana are (cyclic nucleotide gated channels) CNGCs (Cyclic Nucleotide-Gated Channels) and GLRs (glutamate-activated channels). Research has revealed that CNGCs help keep ions in balance, which is related to Arabidopsis plants' ability to handle salt [79]. It has also been suggested that CNGCs play a role in Ca^{2+} entry and communication. It connects with calmodulin (CaM), a protein that changes depending on calcium levels, in the IQ-motif and controls communication further down the line (Figure 4).

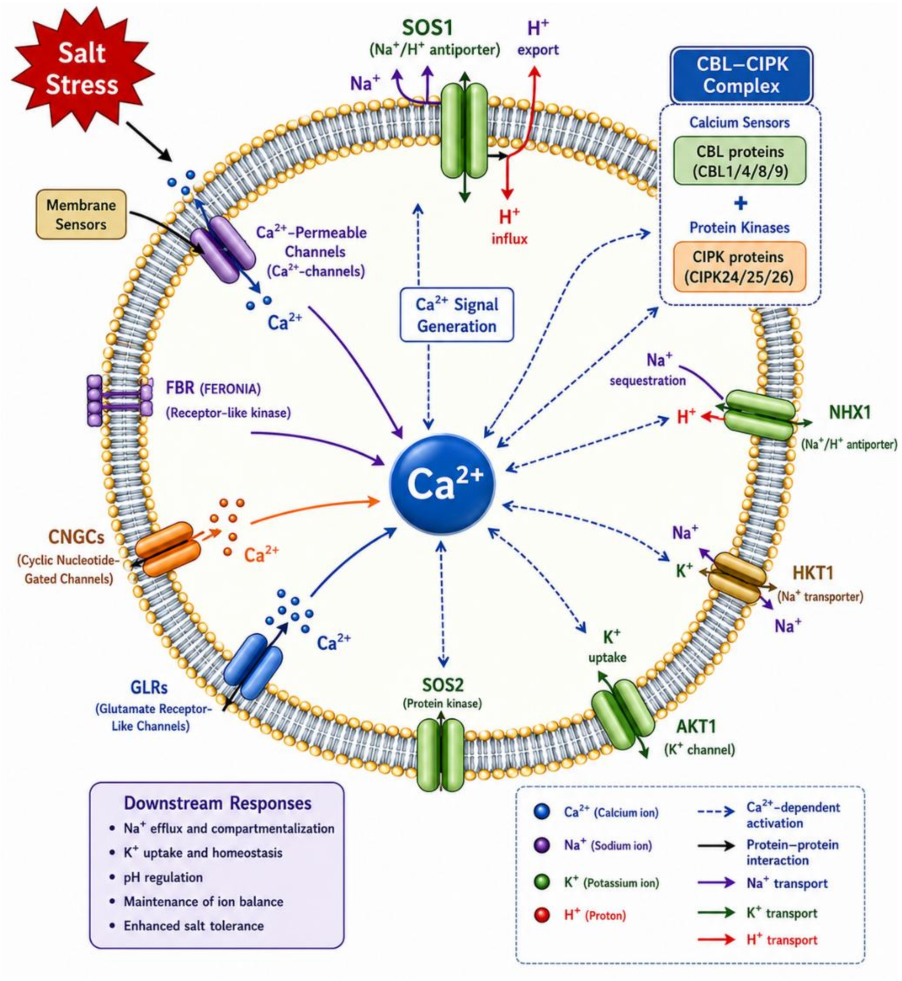


Figure 4. Calcium (Ca^{2+})-mediated signaling pathway involved in plant responses to salinity stress. Elevated cytosolic Ca^{2+} activates CaM and CBL–CIPK signaling modules, which regulate ion

transporters including SOS1, NHX1, HKT1, and AKT1 to maintain ion homeostasis and enhance salt tolerance.

Under salt stress, Considerable research has been dedicated to investigating the possible roles of the SOS signaling system in excluding Na^+ and keeping the balance of ions [80]. Studies in the past have shown that plants can be protected from Na^+ poisoning by having high amounts of Ca^{2+} [81]. When the root senses Na^+, it starts the SOS signal transmission intracellular cascade via Ca^{2+} oscillation. This stops the buildup of too many ions that is triggered by salt stress [82]. High levels of Ca^{2+} are caused by Na^+ constantly entering the cell. This activates SOS proteins, which bind to Ca^{2+} [83]. In turn, SOS antiporters (like SOS1) help remove Na^+ and keep the balance of ions (Na^+/K^+) in the cell [84] illustrated in Figure 3. This backwards-controlling system, which is controlled by Ca^{2+} signals, keeps the Na^+ level in root cells balanced when the soil is salty. In *sos2* and *sos3* mutants, ethylene production and signaling control salt stress signaling. Salt stress induces modifications in the expression of ethylene response genes (ERF) [85]. This causes expression of ethylene and salt-inducible ERF1 (ESE1). The protoplast of roots of maize (*Zea mays* L.) plants quickly increased intracellular Ca^{2+} after being bare to saline shock. This was the first time that this had been recorded [86]. Also, aequorin-based fluorescence imaging of a Ca^{2+} reporter protein shows that osmotic and salt pressures can cause Ca^{2+} signals to be sent [87].

Osmotic and ionic stresses induce comparable Ca^{2+} oscillations in Arabidopsis, indicating that both stress events induce a distinct Ca^{2+} readout [88]. The activity of endomembrane localized Ca^{2+}-ATPases and the vacuolar membrane H^+/ Ca^{2+} antiporter (Vcx1p) governs the duration and magnitude of the Ca^{2+} transient [89]. Additionally, Ca^{2+} transients contribute to the compartmentalization of divalent cations by activating energy-dependent transport systems and channels responsible for ion influx. ACA Ca^{2+} -ATPases (ACAs; plasma membrane and organellar Ca^{2+} pumps), CAX1, and ECA (ATP-driven Ca^{2+} pump) are responsible for regulating the increase in cytosolic Ca^{2+} caused by salt stress [90].

Salt stress-induced Ca^{+2} signaling and ion channel modulation

Salt stress-induced Ca^{2+} signaling activates SOS3 and induces its interaction with SOS2. The SOS3/SOS2 complex turns on SOS1 via direct phosphorylation induced by SOS2, which leads to Na^+ efflux. In an alternative manner, SOS2 maintains equilibrium in Na^+ vacuole sequestration and regulates vacuole channels (CAX and NHX) (Figure 5).

Gene expression regulation

A variety of genes, including MYB and CAMTA (CaM binding transcription activator), have been demonstrated to be turned on by Ca^{2+} CaM in *Aegilops tauschii* in retort to salt stress; this suggests that the Ca^{2+} signaling pathway may play a role in salt stress responses in plants [91]. Using microarrays, a transcriptome analysis of *myb59* mutant of *A. thaliana* and wild-type identified 45 transcripts that were differentially regulated, with 33 and 12 genes, respectively, being upregulated and downregulated [92]. 25% of the upregulated transcripts encode Ca^{2+} -binding proteins, while the remaining transcripts are involved in signal transduction pathways, transport, or Ca^{2+} homeostasis [93]. The confirmation of the genes' involvement in Ca^{2+} signaling has been achieved through the utilization of DAVID enrichment analysis [94]. A comparative analysis of wild-type, myb59, and overexpressed (OE) lines revealed that the Ca^{2+} signaling genes (*CML24, CML35, CML47, KIC,* and *PILS4*) were expressed constitutively. Reportedly, calcium signaling is involved in the stomatal motility regulation. Similarly, Ca^{2+} has no effect on the stomata of *myb59*, whereas stomatal motility was observed in the wild type and OE [95]. This indicates that *MYB59* is likely to be involved in stomatal function via Ca^{2+} signaling during salt stress, given that salt stress-induced *MYB59* countenance can inhibit CAX1 and induce stomatal closure [96]. Salt stress induces an upregulation of *MtCML40*, a *Medicago truncatula* CML, as has been well documented. Surprisingly, increasing *MtCML40* has a negative effect on the expression levels of *MtHKT1;1* and *MtHKT1;2* [97]. These genes encode proteins that are very important for lowering too much Na^+ in shoots [98]. This may establish an indirect correlation between the regulatory function of *MtCML40* and Ca^{2+} signaling via a Na^+ accumulation process dependent on *MtHKT* in plants experiencing osmotic stress [99].

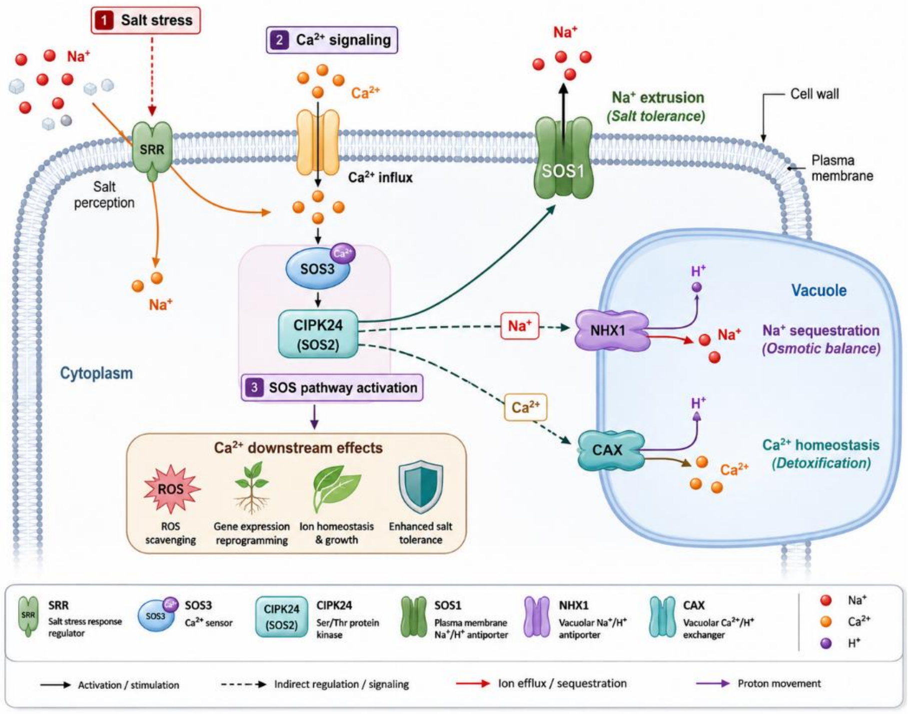


Figure 5. Schematic representation of the Ca^{2+} regulated SOS pathway during saline shock.

Duplication of genes is regarded as a significant adaptive mechanism that plants have progressed in response to unanticipated environmental incentives [100]. An investigation was conducted into the impact of duplicated *CBL10* alleles on the salt tolerance of *Eutrema salsugineum*, a plant known for its lenience to salt [101]. The findings recommended that the growth of plants was significantly impacted by salinity when the expression levels of duplicated *CBL10* genes (*EsCBL10a* and *EsCBL10b*) were downregulated [102]. However, a more pronounced decrease in growth was observed when the expression levels of each gene were reduced individually, suggesting that both genes serve a unique purpose in salt stress [103]. An investigation using a cross-species complementation assay revealed that *EsCBL10b* may serve as a stimulus for the SOS pathway, whereas *EsCBL10a* performs an entirely distinct role. Notably, modifications to the N-terminus of *EsCBL10* homologue proteins result in distinct functionalities for each protein [104]. The duplication of *EsCBL10a* and *EsCBL10b* enhances the Ca^{2+} mediated signaling capacity of *Eutrema salsugineum*, notwithstanding their distinct functionalities [105]. Furthermore, an increased quantity of operational Ca^{2+} sensors is hypothesized to induce salt tolerance and adaptation [106]. *EsCBL10a, EsCBL10b,* and *EsSOS3* are the three Ca^{2+} sensors found in *Eutrema penlandii*. These sensors have both individual and combined functions. Co-expression of *EsCBL10a* and *EsSOS3* in *Atsos3* mutant has been shown to promote root growth, indicating that these genes have an additive effect on salt tolerance and, consequently, root development [107].

Involvement of transcription factors

A crucial part of how plants respond to abiotic stresses is the regulation of transcription [108]. So far, many transcription factors (TFs) that change the activity of genes further down the line in reaction to stress have been found and described in terms of how they work. The main TF families that regulate salt tolerance for rice have been extensively deliberated [109]. NAC (NAM, ATAF1/2, CUC2), ABA-responsive element (ABRE) binding protein/factor (AREB/ABF), and dehydration-responsive element (DRE) binding protein (DREB) are some examples [110]. Transcription elements DRE (dehydration-responsive element)/CRT (C-Repeat) element, A *cis*-acting element that influence the gene expression in Arabidopsis in reaction to cold, drought and salt was found to bind to DREBs. An analysis of conserved sequences across the entire rice genome has identified a number of DREBs, of which a subset is susceptible to salinity stress [111]. Nevertheless, the precise mechanism by which DREB controls stress-responsive gene expression in rice remains unknown [112]. Five DREB homologs were isolated in rice by [113] *OsDREB1A, OsDREB1B, OsDREB1C, OsDREB2A,* and *OsDREB1D*. In response to salt stress, *OsDREB1 (OsDREB1A, OsDREB1B, OsDREB1F,* and *OsDREB1G)* and *OsDREB2* (*OsDREB2A* and *OsDREB2B*) exhibit comparable functionalities to *AtDREB1* (*AtDREB1C*, *AtDREB1B*, and *AtDREB1A*), thus demonstrating the functional conservation of *DREB1*. High salt was observed to induce *OsDREB4-1*, a member of the DREB4 subgroup, alongside *DREB1s* and *DREB2* [114]. It was hypothesized that OsDREB4-1 functions as a trans-acting factor in the stress-responsive pathway regulated by DRE/DREB [115]. It was hypothesized that *OsDREB6*, an A-6 subtype of DREB, would be involved in stress responses via signal transduction pathways that are both ABA-independent and ABA-dependent [116]. It was reported that *SERF1*, a member of the DREB subfamily's group IIc ERFs, positively regulates the tolerance of rice to long-term and short-term salt stress [110]. SeRF1 can also increase the ROS-activated MAPK cascade signal in roots when plants are under salt stress. ABA is a vital signal molecule in plants' reactions to both living and nonliving stresses. It is needed for full activity of ABF TFs/AREB [117]. One type of transcription factor is AREB/ABF, which is an elementary leucine zipper. It is capable of binding to cis-acting elements that respond to ABA. A lot of AREB/ABF-homologous genes are said to be controlled by salt stress [118]. It was found that both *OsABF1* and *OsABF2* helped control how rice responded to abiotic stress and how ABA-dependent signaling pathways worked [119]. Other bZIP TFs, like *OsbZIP23*, *OsbZIP46*, and *OsbZIP72*, can bind to ABRE and are thought to play a role in ABA signaling and responding to abiotic stress [120]. It is very important for plants to have the AREB/ABF-SnRK2 pathway for ABRE-mediated transcription when they are under osmotic stress [121]. *OsSAPK8*, *OsSAPK9*, and *OsSAPK10* are member of rice subclass III SnRK2 protein kinases family. They can be set off by ABA signals and high salt levels, and in response to ABA signals and high salt levels, they can directly phosphorylate *OsTRAB1*, a rice AREB/ABF. By working with *OsSGT1* and *OsSAPK9* controls how well plants can handle salt stress and how resistant they are to bacterial blight [122].

ROS and calcium interaction during the response to salt stress

Reactive oxygen species are extremely unstable compounds composed of O_2, which is produced by nearly all biochemical processes within cells [123]. They are integral to the growth and development of organisms and are regarded as significant indicators of abiotic and biotic stresses [124]. A high concentration of Na^+ under salinity stress can induce oxidative stress by promoting the excessive generation of ROS, including superoxide radicals (O_2^-) and H_2O_2. The overaccumulation of ROS disrupts cellular redox homeostasis and overwhelms the plant antioxidant defense system. In addition to causing oxidative damage, ROS also function as important signaling molecules that initiate local and systemic signaling cascades, enabling the transmission of long-distance stress signals throughout the plant and triggering adaptive responses to salinity stress [125]. ROS and Ca^{2+} are widely acknowledged as crucial signaling molecules in plants, influencing a multitude of processes, such as reading hormones, dealing with salt stress, and drought. It is widely recognized that ROS and Ca^{2+} signaling can talk to each other in plant cells, which suggests that they are connected [126].

During the initial phases of salt stress, increased secondary ROS production was directly associated with the Ca^{2+} wave induced by stress [127]. High $[Ca^{2+}]$ cyt (cytosolic calcium concentration) turns on *CBL9*, which sets off a chain reaction that increases the production of ROS. Nox potentially serves as a Ca_2^+ sensor, as evidenced by the activation of two EF-hand motifs located in the hydrophilic N-terminal regions of plant RBOH proteins upon exposure to ionomycin, a Ca_2^+ ionophore that induces ROS production [128]. In addition, Ca^{2+} binding to EF-hand domains and membrane-localized NOX activation by CDPKs demonstrate the enzyme's synergistic effect, indicating that ROS-generating enzymes are dependent on Ca^{2+} [129]. Recent research has unveiled that the Ca^{2+} plant systemic signaling system in Arabidopsis is supported by a calcium-release mechanism that is aided by ROS and the vacuolar ion channel TWO PORE CHANNEL1 (TPC1). This calcium-release mechanism involves Ca^{2+} release [130]. But we don't fully understand the ROS-controlled channels that are involved in this signaling process [131]. It has been shown that different abiotic and biotic triggers can cause a rise in Ca^{2+} in tobacco plants [132]. This is sensed by the Ca^{2+} CaM complex (calmodulin), which then activates a NAD kinase. This increases NADPH, which in turn increases ROS production [133].

Guard cells of Arabidopsis and *Vicia faba* exhibited hyperpolarization-activated Ca_2^+ channels in response to ROS that were regulated by ABA. [134]. This closed the stomata, which reduced salt stress. More [Ca_2^+] cyt and ROS were found to make ABA build up [135]. This then turned on the ABA-dependent SnRK2 class 3, which led to more ROS being made by targeting respiratory burst oxidase homologue F (RbohF) (Figure 6)[136].

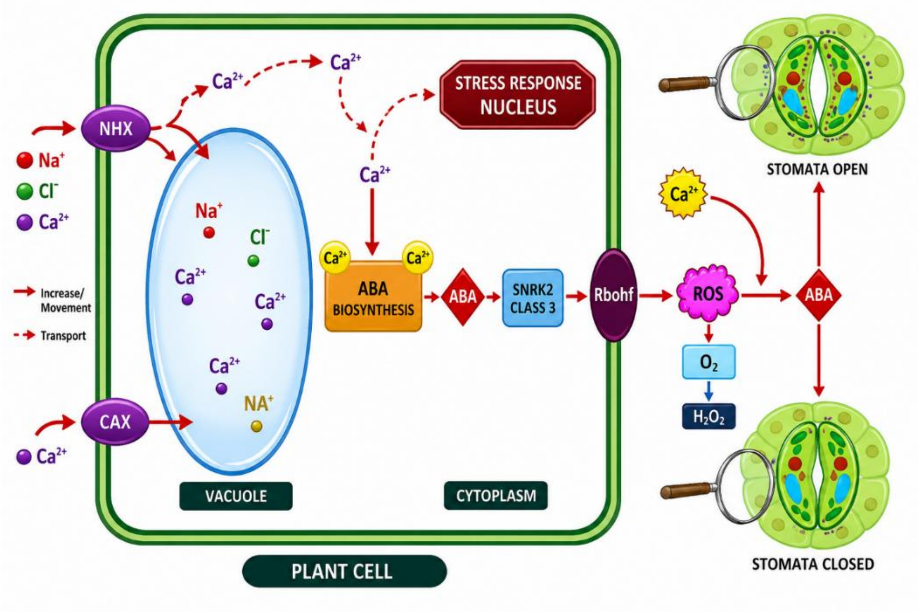


Figure 6: Interaction of ROS, Ca^{2+}, and ABA signaling pathways in regulating stomatal closure during salt stress. Under salt stress, excess Na^+ and Cl^- ions trigger cytosolic Ca^{2+} influx and signaling. NHX antiporters sequester Na^+ into vacuoles, while CAX transporters regulate Ca^{2+} homeostasis. Elevated Ca^{2+} activates ABA biosynthesis and signaling through SnRK2 class III kinases. At the same time, Ca^{2+} activates RBOH enzymes, leading to ROS (O_2^- and H_2O_2) production. ROS and Ca^{2+} act as secondary messengers and amplify each other's signaling. ABA, ROS, and Ca^{2+} together regulate ion channel activity in guard cells, causing efflux of K^+ and anions, loss of turgor pressure, and ultimately stomatal closure under salt stress.

Calcium-Mediated Regulation

Salinity stress disrupts cellular homeostasis by causing osmotic, ionic, and oxidative stress. To mitigate these effects, plants accumulate osmo-protectants such as proline, glycine betaine, and soluble sugars, which help maintain osmotic balance, stabilize cellular structures, and protect metabolic processes. Calcium (Ca^{2+}) plays a key role in regulating the synthesis and accumulation of these compounds, thereby enhancing plant tolerance to saline conditions. Calcium also promotes the production of secondary metabolites, including phenolics, flavonoids, and alkaloids, which function as non-enzymatic antioxidants. These metabolites help scavenge ROS, reduce oxidative damage, and improve cellular protection under stress. Increased accumulation of these compounds has been associated with improved stress tolerance in several plant species exposed to salinity. In addition, Ca^{2+} acts as an important signaling molecule that interacts with phytohormone pathways to coordinate stress responses. Calcium signaling is closely linked with ABA-mediated regulation of stomatal closure, ion homeostasis, and antioxidant defense. Furthermore, interactions between Ca^{2+} and salicylic acid (SA), jasmonic acid (JA), ethylene, and auxin contribute to the regulation of growth, stress signaling, and adaptive responses under saline conditions.
Biochemical Changes Induced by Calcium

Calcium-Dependent Protein Kinases (CDPKs)

Frequently, calcium signaling requires the stimulation of PLC. It is cleaved by PLC into IP3 and DAG. Calcium is released from intracellular stores in response to IP3, thereby amplifying the calcium signal [137]. As a result of this mechanism, calcium concentrations remain elevated in response to salinity stress. CDPKs endure conformational alterations upon binding to calcium, which initiate the activation of their kinase activity [138]. Target proteins, such as TFs and other enzymes occupied in stress responses, are phosphorylated by activated CDPKs [139]. Phosphorylation events have the ability to regulate both gene expression and enzymatic activities. Activation of calcium-responsive transcription factors occurs when calcium concentrations are increased [140]. Translocation to the cell's nucleus and binding to specific DNA sequences are mechanisms by which these transcription factors regulate the expression of genes involved in stress responses [141]. Calcium-activated protein phosphatases inhibit the activity of protein kinases. The intricate interaction between phosphatases and kinases regulates the cellular reaction to salinity stress [142]. Calcium sensors, including calmodulin, endure conformational alterations upon binding to calcium ions [143]. Osmo-protectants function as compatible solutes, aiding plants in the regulation of cellular turgor and safeguarding cellular structures when bare to salinity-induced osmotic stress [144]. The action of enzymes implicated in osmoprotectant synthesis, including proline and soluble carbohydrates, is susceptible to calcium signaling [145]. Calcium-calmodulin complexes engage in interactions with a diverse array of target proteins, such as TFs and enzymes [146]. In calcium signaling, calmodulin functions as a pivotal node, transmitting the calcium signal to effectors located downstream [147]. Calcium-dependent signaling pathways aid in the regulation of ion transporters, thereby contributing to the maintenance of intracellular ion balance [148]. Ion transporter activity is significantly impacted by calcium signaling, specifically those that govern the movement of sodium (Na^+) and potassium (K^+) ions [98]. Ion homeostasis maintenance is vital for cellular function in the existence of salinity stress. Plant cells generate ROS in response to salinity stress [149]. Owing to the activation of antioxidative enzymes by elevated calcium levels, ROS are neutralized. Superoxide dismutase (SOD), for instance, facilitates the dismutation of superoxide radicals, whereas catalase decomposes hydrogen peroxide into oxygen and water [150]. By acting collectively, these enzymes safeguard cellular components from oxidative injury [151].

Case studies

Case I

Calcium-fortified composted manure from animals (Ca-FCM) was applied at three different levels, 1%, 2%, and 3%, to saline soil. This improved plant growth and yield metrics such total biomass, shoot length, root dry weight, root length, straw weight, number of pods per plant, grain amount per pod, 1000-grain weight, and net grains weight [152]. But when Ca-FCM was used at a 3% amount, all of the measures showed the most growth. Among the tested treatments, 3% Ca-FCM exhibited the strongest growth-promoting effect, increasing total plant biomass by 117%, 132%, and 155% at EC 1.5, 5, and 10 dS m^{-1}, respectively, compared with the control [153]. Likewise, shoot length was enhanced by 37%, 43%, and 47% under the respective salinity levels, demonstrating the effectiveness of Ca-FCM in mitigating salt stress-induced growth inhibition [154]. Also, adding two different amounts of humic acid made all of the above growth characteristics much better compared to control plants and plants that were stressed by salt. When Ca1 and two concentrations of humic acid were mixed, the plants grew faster than normal plants and plants that were stressed by salt. When Ca^{+2} was mixed with the two concentrations of humic acid, the plants grew faster than salt-stressed plants [155]. Pepper plant leaves bare to salt stress had much lower concentrations of total photosynthetic pigments, chlorophyll a and b, carotenoids, and chlorophyll a, compared to unstressed leaves [156]. Consistent with the observed improvements in plant growth, the application of Ca1, HA1, HA2, and their combinations (Ca1 + HA1, Ca1 + HA2, and Ca2 + HA2) significantly increased photosynthetic pigment concentrations relative to untreated and salt-stressed plants [157]. Notably, HA2 (1500 mg kg^{-1} soil), Ca1 (120 mg kg^{-1} soil), and especially their combined treatment (Ca1 + HA2) exhibited the greatest efficacy, highlighting their potential role in alleviating salinity-induced reductions in photosynthetic [158].

Case II

When treated with salt, there was a clear drop in the amount of protein present. In comparison to the control, the amount of protein decreased by 1.52 times [159]. Adding potassium and calcium, on the other hand, caused a rise of 1.24 and 1.08 times compared to the salt-stressed state. The biggest rise was seen when both potassium and calcium were used together (1.29 times). Calcium treatment made a lot more proline, an important amino acid that helps with osmotic adjustment, protein stability, and other stress responses. It was much higher in the treated group than in the control group. T4 had the highest levels (15.71 ± 2.55), then T2 (13.14 ± 2.13), T3 (12.19 ± 1.98) and finally T1 (11.96 ± 1.94) for each group. Here, T1 represents the control, T2 represents low salt stress, T3 represents moderate salt stress, and T4 represents high salt stress. But there wasn't a big difference between T1 and T2 [160]. The treatments made the MDA content of the leaves go up a lot; the biggest increase (3.16 times) was seen in T1, and the smallest (0.872 times) was seen in T4. Under the treatment settings, there were big changes in SOD function. There was a big increase in SOD activities in the leaf tissue after different treatments, with the biggest increase (1.88 times) happening in T4 [161].

Case III

Akladious and Mohamed [162] demonstrated that When Ca^{2+} treatments, especially Ca1 (60 mg kg soil), were used on stressed plants, their growth factors got better. There are several possible reasons for this, such as the fact that Ca^{2+} is part of the structure of the cell wall and cell membrane. As a result, it retains the balance and safety of membranes by interacting with different types of proteins and lipids on the membrane's surface. It also changes the pH inside the cell, which stops the fluid from leaving the cytoplasm, and it works to make the shoot longer [163]. Concerning the influence of calcium on yield components, adding Ca^{2+} helped pepper plants recover due to the adverse repercussions of salt stress by improving their yield characteristics. The same kinds of results have been described before by [164] who said that giving tomato plants calcium while they were in a salty environment made the fruit weigh more per plant than giving stressed plants calcium without calcium. When compared to control plants, peeper plants that were stressed by salt had less photosynthetic pigments. Photosynthesis pigments were stimulated by humic acid. This could be because it lowered the pH level and made soil organisms more active, which released more nutrients from the soil, such as iron. The amount of chlorophyll a, b, and pigments in faba bean stems went up when amino acids and humic acid were added. If pepper plants are stressed by salt, elements like Mg and Fe levels drop and chlorophyll enzyme activity goes up. This can cause the colors that help the plants make food to go down [165]. Adding Ca^{2+} to plants made the flowers of those plants weigh more. It also increased the concentration of chlorophyll in plants that had been stressed. The lower amount of calcium (Ca1; 60 mg kg^{-1} soil) made the levels of chlorophyll higher in both stressed and un-stressed plants, which suggests that they can repair pigments that have been damaged by salt. This rise might be because calcium is an important part of making cytokinin, which is part of the chlorophyll production process and helps protect the chloroplast wall and photosynthesis enzymes work [166].

Implications for Agriculture and Crop Improvement

Enhanced salt tolerance in calcium-treated plants

In the end, we can say that Ca^{2+} is a part of the control systems that allow plants to respond to bad salt stress situations for the reasons given below. Next, giving rice plants more Ca_2^+ improved the FGP and GRI, as well as the length and weight of the shoots and roots, the RWC, and the SES. This happened in both resistant (Binadhan-10) and sensitive (Binadhan-7) plants. In the second place, Ca^{2+} increased the ability to make food by recovering the colors needed for photosynthesis. Third, Ca^{2+} controlled the production of proline, which makes up for the energy needed for growth and life and assist the plant deal with stress. Fourth, Ca^{2+} lowered oxidative damage by controlling the antioxidant defense and ROS purification system and increasing the activity of antioxidant enzymes.

Practical applications for agriculture

Using calcium-based soil management techniques to reduce salt stress in soil is a complex process that aims to solve the many problems that salinity causes [167]. Using gypsum, for example, not only helps get rid of dangerous sodium ions, but it also improves the structure of the soil, which makes it easier for water to get in and roots to grow [4]. This is very important because salty soils often have bad structure, are compacted, and can't let water through easily. All of these problems make plants more stressed out by salt stress[168]. Along with gypsum, calcium-rich fertilizers and liming materials are also used to keep the soil environmentally healthy. Calcium products give plants a straight source of this important nutrient, which helps their bodies work better and makes them more resistant to salt stress [169]. Liming materials, on the other hand, raise the pH of the earth, which makes it less likely for sodium to build up and more likely for calcium to be available. This double action helps heal the soil and encourages healthy plant growth even in salty circumstances [170]. Foliar sprays of calcium solutions are also a quick way to get calcium directly to plant cells, without having to go through the root walls that salt stress creates [171]. Calcium foliar sprays make plants more resistant to osmotic stress and ion poisoning, two main types of salt stress [172]. They do this by strengthening cell walls and stabilizing cellular membranes. In salty soils, adding organic matter that is high in calcium can help in many ways [173]. They not only help make calcium available, but they also improve the structure of the soil, encourage microbial activity, and speed up the cycle of nutrients [174]. This all-around method helps the soil heal and become more resilient, which slowly lessens the negative effects of salt on food growth [175]. Adding soil amendments that raise calcium levels and using efficient watering methods like drip irrigation and controlled shortage irrigation are also important for long-term management of salt stress [176]. Long-term, these methods help keep water and salt from building up in the root zone, which makes salinity less harmful to plant health and output [177]. Using a wide range of calcium-based soil management techniques, farmers can successfully reduce salt stress, improve soil health, and keep food growth high in areas that are susceptible by salt stress [170]. This method not only solves the problems that salt causes right now, but it also makes farming systems more resilient and long-lasting [178].

Challenges and Future Directions

Soil variability is a big problem because salt levels can change a lot from field to field [179]. This means that calcium-based treatments have to be carefully applied to make sure they work well and cover the whole area evenly [180]. Using calcium-based soil management techniques to reduce salt stress means figuring out how to deal with a lot of difficult academic and practical issues [181]. Because the soil is so different, it needs advanced maps and application tools to make sure that solutions are properly matched to each soil state [182]. Soil amendments or management techniques that improve soil structure and porosity to make it easier for ions to move are needed to make calcium move around more easily [183]. Also, calcium ions are not very mobile in soil, especially in heavy or clayey soils, which makes it harder to get them to plant roots, where they are needed most [184]. When soils are salty, calcium has to compete with sodium and other cations for binding sites on the root surfaces. This makes it harder for plants to take in calcium [185]. Additionally, calcium loss through leaching from heavy rain or too much watering can make it less effective over time at reducing salt stress [186]. Using water management methods that reduce leaking, like drip irrigation or planning watering times to meet plant water needs, can help solve this problem [187]. To get around this problem, you might need to choose calcium sources that are easier for roots to take up or add things to the soil that move sodium ions around to make room for calcium. To keep calcium-based soil management plans working for a long time, they need to be carefully watched and changed as soil and weather conditions change [188]. Conservation of soil techniques, such as cover crops, crop rotation, and cover cropping, may be implemented to sustain soil health and fertility in the long run [189]. Lastly, in order to prevent unintended consequences, potential environmental impacts, such as soil alkalinity or nutrient discharge, must be meticulously managed [190]. In order to achieve this, a comprehensive strategy is necessary, taking into account the wider ecosystem and incorporating methods that reduce adverse environmental impacts while optimizing the advantages of calcium-based soil management [191].

Conclusion

Calcium (Ca^{2+}) plays a central role in enhancing plant tolerance to salinity stress by regulating ion homeostasis, maintaining membrane stability, modulating antioxidant defense systems, and activating stress-responsive signaling pathways. Through its interactions with the SOS pathway, ROS, phytohormones, and calcium-dependent signaling networks, Ca^{2+} contributes significantly to plant adaptation under saline conditions. In addition, calcium promotes osmotic adjustment through the accumulation of compatible solutes and supports the synthesis of protective secondary metabolites, thereby improving overall stress resilience. The growing body of evidence highlights the potential of calcium-based approaches, including soil amendments, foliar applications, and integrated nutrient management strategies, for improving crop performance in salt-affected environments. However, the complexity of calcium signaling, its interaction with other ions, and the variability of field conditions remain important challenges. Future research should focus on elucidating the molecular mechanisms underlying calcium-mediated stress responses, identifying key regulatory genes and signaling components, and integrating omics-based approaches to enhance salinity tolerance in crops. A deeper understanding of these processes will facilitate the development of innovative breeding and management strategies, contributing to sustainable agriculture and food security in increasingly saline environments.

Data availability

Not applicable

Acknowledgments

Not applicable

Conflict of interest

The authors declare that they have no conflict of interest.

Author Contribution

The authors confirm contribution to the paper as follows: U.T, A.A and R. K: writing-original draft, conceptualization, writing, review, and editing. A.A, B.A, F.S, K.R, and A.R.: review and editing, conceptualization and reviewing. U.T and A.A: Supervision, reviewing, editing and manuscript polishing. All authors discussed the content, reviewed the results and approved the final version of the manuscript.

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