

# Research Progress on Crop Root Morphology, Ion Transport and Rhizosphere Microbial Responses Under Combined Salt–Alkali Stress

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## Abstract:

There exists a vicious feedback loop between crop yield decline and land degradation. Combined salt–alkali stress is not merely the superposition of salt and alkali injuries, but synergistically aggravates ion toxicity and high pH-induced damage at cellular and tissue levels. This paper systematically reviews three core contents: morphological adaptation of crop root systems, regulatory mechanisms of ion homeostasis, and response characteristics of rhizosphere microbial communities. It analyzes existing gaps in current research and offers perspectives on future studies into crop salt-alkali tolerance mechanisms and the remediation of saline-alkali soils. Soil salinization and alkalization have become critical threats to food security in China; ongoing secondary salinization and alkalization further create a vicious feedback cycle.

## Keywords:

Combined Salt–alkali Stress, Root Architecture, Ion Homeostasis, Rhizosphere Microorganisms, Stress Resistance Mechanisms

## 1. Introduction

Soil salinization and alkalization are getting worse. It reduces crop productivity and threatens national agricultural security [1]. Saline-alkali lands are common in China. The total area of saline-alkali land expands year by year. Excessive soluble salts and elevated soil pH inhibit the normal growth of most crops. This restricts land utilization efficiency and severely hinders the construction of high-standard farmland [12].

Salt stress originates from elevated soil osmotic potential and excessive Na<sup>+</sup> accumulation, which triggers osmotic injury and ion toxicity in plants. Alkali stress is induced by high soil pH, which destroys soil colloidal structures, reduces nutrient bioavailability, and impairs cell membrane integrity. When salt and alkali stresses occur simultaneously, their damage adds up. They hurt crop growth in many ways. These include changes in form, physiology, molecules, and microbes. It also impairs seed germination, root elongation, photosynthesis and final crop yield [16]. Studies

show that the combined effect of salt and alkalinity stress is much stronger than either one alone. So this combined stress is a main factor that limits farming in saline-alkali areas [13].

Currently, extensive research has been conducted both domestically and internationally on the mechanisms of plant salt and alkali tolerance; However, most existing studies only focus on plant physiological responses under single stress or analyze individual regulatory pathways [3]. Based on relevant domestic and international research findings, this paper systematically reviews the multilevel response mechanisms of crops to combined salt and alkali stress and summarizes the shortcomings of current research, with the aim of providing a reference for the biological remediation of saline-alkali lands, the breeding of salt- and alkali-tolerant crops, and in-depth studies on the molecular mechanisms of stress resistance.

## **2. Mechanisms of Synergistic Damage to Crops Caused by Combined Salinity and Alkalinity Stress**

Salinity and alkalinity stress happen together. They harm crop physiology in many ways. These include osmotic imbalance, ion toxicity, and oxidative damage from high pH. These different types of stress are linked. They also make each other worse. So they have a strong combined inhibitory effect.

### ***2.1. Osmotic Stress Inhibits Plant Growth and Development***

Saline-alkali soils have high soluble salt content. This raises soil solution osmotic pressure. Therefore, the water potential of the crop root system is higher than the soil's. This stops the roots from taking up water and causes physiological drought [12]. To deal with this osmotic damage, plants use a lot of photosynthetic products. They use these to make osmotic regulators like soluble sugars and proline. These regulators help keep cell turgor pressure up and reduce water imbalance [18]. This process uses many carbohydrates, thus fewer nutrients go to plant height growth and biomass buildup. This leads to slow crop growth and weak plants. With increasing stress intensity, stomatal closure is aggravated and photosynthetic capacity declines sharply. Under severe salt – alkali stress, seed germination and seedling establishment are significantly suppressed. This seriously limits early crop growth [16].

### ***2.2. Sodium Ion Accumulation Induces Cellular Ion Toxicity***

Saline-alkali soils have high  $\text{Na}^+$ . Massive  $\text{Na}^+$  enters cells through non-selective ion channels in the plasma membrane. It competes with  $\text{K}^+$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  for absorption sites. Thus the ion ratios inside the plant become unbalanced [4].  $\text{K}^+$  is a key ion in plants. It works with enzyme reactions, stomatal movement, and osmotic pressure. When the  $\text{Na}^+/\text{K}^+$  ratio inside cells is off, many metabolic enzymes lose activity. This disrupts protein synthesis and energy metabolism. Too much sodium also damages chloroplasts and mitochondria. These organelles lose their structure. This damage causes reactive oxygen species to build up. The accumulation exacerbates oxidative injury and disturbs normal plant metabolism [6].

### ***2.3. High pH Stress Disrupts the Rhizosphere Soil Environment and Cell Membrane Structure***

High pH from alkali stress changes how soil nutrients like phosphorus, iron, zinc, and manganese exist. These nutrients are transformed into insoluble forms unavailable

for plant absorption, thus crops do not get enough nutrients. This causes yellow leaves and slow growth [11]. High pH also impairs root cell membranes and destroys their lipid bilayer structure, thus membranes lose their ability to pick and choose what goes through. Massive intracellular soluble substances leak out, reducing enzyme activity and weakening root vitality. To deal with high pH in the root zone, crops must keep putting out organic acids. These acids help bring pH down. Nevertheless, the synthesis of organic acids consumes plant carbon reserves, further suppressing plant growth [15].

#### ***2.4. Synergistic Cumulative Damage Effects of Combined Salinity and Alkalinity Stress***

Single salt or alkali stress exerts relatively independent adverse effects on crops. However, when they happen together, they create much stronger damage [16]. High pH makes cell membranes more open, thus more sodium ions come in from the soil. This makes ion toxicity worse. Too much sodium then slows down the making of antioxidant enzymes; therefore the plant cannot clear away reactive oxygen species well. This makes the oxidative damage from high pH even worse. These stresses make each other stronger. They form a vicious cycle; thus, the combined damage is far severer than the additive effect of single stress. This is why yields are low in saline-alkali soils [13].

### **3. Morphological and Physiological Adaptive Responses of Crop Root Systems Under Saline-Alkali Stress**

The root system is the primary organ through which crops perceive soil stress; the plastic adjustments in its morphological structure, physiological characteristics, and antioxidant systems form the crucial foundation for crops to withstand saline-alkali stress [15].

#### ***3.1. Effects of Saline-Alkali Stress on Root Morphological Characteristics***

Studies show that salt and alkali stress together stop taproots from growing long. It also inhibits the initiation of lateral and fibrous roots, thereby significantly reducing total root length, surface area and volume. As stress gets stronger, these effects get worse [8]. Under mild stress, crops develop thicker fine roots and adjust root spatial distribution to enhance nutrient absorption. However, severe stress completely arrests root growth, accelerates senescence and rot of old roots, and only a small number of new roots remain viable.

There are significant genotypic differences in stress tolerance among crops. Stress-tolerant crops such as sweet sorghum and sunflower exhibit a significantly lower degree of inhibition in root parameters compared to sensitive crops like wheat and rice, and they demonstrate a stronger ability to maintain root vitality; this trait has become an important morphological indicator for screening salt-alkali-tolerant germplasm [13].

#### ***3.2. Changes in Root Cell Structural Plasticity Under Salt-Alkali Stress***

Salt and alkali stress make root epidermal cell walls thicker. It also promotes cell wall lignification and suberization, thus reducing passive  $\text{Na}^+$  influx. This helps the root defend itself [15]. Intercellular spaces emerge in cortical tissues and form aerenchyma to adapt to waterlogged saline-alkali soil. This helps roots survive when

saline-alkali soil has too much water. At the cellular organelle level, mitochondria proliferate and expand to supply energy for osmotic adjustment and stress defense. Under severe stress, intracellular organelles degrade, accompanied by endoplasmic reticulum swelling and chloroplast disintegration. Salt-tolerant crops can achieve the compartmentalized storage of sodium ions by increasing the volume of their vacuoles, significantly reducing the ionic toxicity within the cytoplasm [4].

### ***3.3. Stress Defense Mechanisms of the Root Antioxidant System***

Combined salinity and alkalinity stress induces plants to produce large amounts of reactive oxygen species (ROS), such as superoxide anions and hydrogen peroxide, leading to membrane lipid peroxidation damage and disrupting cell membrane stability [18]. Crops can synergistically resist oxidative damage by activating both enzymatic and non-enzymatic antioxidant systems: on the one hand, they enhance the activity of antioxidant enzymes such as SOD, POD, and CAT to rapidly scavenge excess ROS; on the other hand, they accumulate antioxidant substances such as proline, glutathione, and flavonoids to alleviate oxidative stress, reduce malondialdehyde accumulation, and maintain the structural stability of cell membranes.

Salt- and alkali-tolerant varieties typically exhibit higher basal antioxidant enzyme activity and a more significant upregulation following stress, resulting in lower levels of cellular oxidative damage; this is a key physiological characteristic of their stress tolerance [16].

## **4. Molecular Mechanisms of Ion Transport and Homeostasis Regulation in Crops Under Salinity and Alkalinity Stress**

Maintaining the intracellular  $\text{Na}^+$  and  $\text{K}^+$  homeostasis is the core molecular mechanism by which crops resist the toxic effects of saline and alkaline ions. This is mainly achieved through the coordinated regulation of the three major transporter protein families: SOS, HKT, and NHX.

### ***4.1. Genotypic Differences in Ion Uptake and Distribution in Crops***

Under saline-alkali stress, sensitive crops have a weaker ability to block sodium ions. A large amount of sodium ions are transported to the aboveground parts and accumulate in the leaves. This hurts the photosynthetic structures and slows down metabolism. However, salt-tolerant crops have a strong ability to selectively absorb ions, and they preferentially absorb and retain  $\text{K}^+$ . At the same time, excess  $\text{Na}^+$  is fixed in the roots and senescent tissues, reducing the ion accumulation in functional leaves, effectively protecting the normal operation of the photosynthetic system [5].

### ***4.2. Key Transport Proteins Regulate Ion Efflux and Segregation***

The SOS signaling pathway is the key mechanism for sodium excretion in plants. It has three parts: SOS1, SOS2, and SOS3 [4]. When stress happens, calcium levels go up inside the cell. SOS3 senses this calcium change. Then it binds with SOS2. They form a complex that turns on SOS1. SOS1 sits on the cell membrane and pumps sodium out of the cell. This lowers ion toxicity [6].

HKT transporters move sodium in the xylem. They take extra sodium from the shoots and stop it from going up, thus they keep the right ion balance in leaves and stems [5]. NHX transporters work on the vacuole membrane. The NHX vacuolar

membrane transporter transports excess  $\text{Na}^+$  in the cytoplasm to the vacuole for storage, thereby achieving ion compartmentalization. At the same time, they release potassium from the vacuole back into the cytoplasm. This keeps the sodium and potassium levels balanced [3]. In salt and alkali stress, tolerant crops show higher expression of these three gene families, thus their ability to control ions gets much stronger.

#### ***4.3. Adverse Effects of Ion Imbalance on Crop Metabolism and Photosynthesis***

Ion homeostasis imbalances directly slow down photosynthesis and carbon-nitrogen metabolism in crops. Too much  $\text{Na}^+$  can lower the activity of key photosynthetic enzymes like Rubisco. It also cuts down chlorophyll synthesis, thus the photosynthetic rate drops a lot. At the same time, it upsets stomatal rhythm. This lowers  $\text{CO}_2$  assimilation, and dry matter accumulation goes down a lot [16]. Furthermore, ion imbalance also inhibits the synthesis of osmotic regulatory substances, weakening the plant's stress-resistance reserve capacity. Eventually, this leads to stunted plant growth, reduced yield, and in severe cases, plant death [13].

### **5. Responses of Rhizosphere Microorganisms and Growth-Promoting Mechanisms in Crops Under Salinity and Alkalinity Stress**

Rhizosphere microorganisms are important microecological factors that regulate crop adaptability to soil stress. Salinity and alkalinity stress can reshape the structure of the rhizosphere microbial community, while salt- and alkali-tolerant growth-promoting bacteria can improve the rhizosphere environment and enhance crop stress resistance through multiple pathways [2].

#### ***5.1. Effects of Salinity and Alkalinity Stress on Rhizosphere Microbial Community Structure***

Extreme soil environments have high salinity and high pH. These conditions drastically reduce rhizosphere microbial diversity and eliminate salt-alkali sensitive microbial taxa. They also push the community to change in a clear direction [8]. Under saline-alkali stress, stress-tolerant bacterial groups like *Bacillus*, *Pseudomonas*, *Aspergillus*, and *Penicillium* become much more common. They slowly turn into the main groups. Soil pH and soluble sodium ion content are the key factors that drive microbial community differences [17]. Crops can selectively recruit beneficial bacterial communities through the secretions of their root systems. In this way, they build a special rhizosphere microecosystem that fits saline-alkali stress [2].

#### ***5.2. Regulatory Mechanisms by Which Plant-Growth-Promoting Rhizosphere Bacteria (PGPR) Enhance Crop Tolerance to Saline-Alkali Stress***

Plant-growth-promoting bacteria (PGPR) can help crops in many ways. They secrete organic acids and extracellular polysaccharides to regulate the pH of the rhizosphere microenvironment and activate the fixed nutrients in the soil. They produce plant hormones such as auxin and gibberellin, which promote root development and expand the absorption area. They synthesize ACC deaminase to degrade the stress-induced ethylene and alleviate the growth inhibition. They use extracellular polysaccharides to coat the surface of the root system, preventing sodium

ions from invading. At the same time, it activates the antioxidant enzyme activity of the plant and reduces oxidative damage [7]. These microorganisms can improve the soil microenvironment without increasing the cost of improvement, and they are an important resource for the green improvement of saline-alkali land [10].

### ***5.3. Synergistic Stress Resistance Effects of Microbe-Plant Symbiotic Systems***

Arbuscular mycorrhizal fungi (AMF) can form an efficient symbiotic system with crop roots. Through the fungal network, they expand the absorption area of the roots and regulate the expression of genes related to ion transport in the host. This reduces the sodium ion accumulation in the plants [9]. Studies show that using PGPR and AMF together works better than using just one type [10]. However, at present, the functional strains generally have problems such as weak field colonization ability and poor environmental stability. These restricts the large-scale application of microbial agents [7].

## **6. Research Gaps and Outlook**

### ***6.1. Current Research Gaps***

From a review of recent studies, we still have some gaps in knowing how crops respond to salt and alkali stress. First, most studies use lab systems like hydroponics or pots with soil. They lack verification of the combined adverse conditions of salt and alkalinity in the field, and there is a deviation between the indoor conclusions and the actual situation in the field [13]. Second, research usually looks at only one pathway or one gene family at a time. The regulatory network among root morphological characteristics, ion transport processes and rhizosphere microorganisms remains unclear [3]. Third, for microbes that can tolerate salt and alkali, most work is still in the lab. The adaptability and stability in the field are insufficient, and the industrialization application system is not yet mature [7]. Fourth, Salt-tolerant and alkali-tolerant breeding still mainly relies on phenotypic screening. The development of key stress-resistant molecular markers is lagging behind, and the application of molecular-assisted breeding is thus restricted [14].

### ***6.2. Future Research Prospects***

To fill the gaps in current research, future work should focus on these areas:

(1) Put together different omics studies, like transcriptomics, metabolomics, and microbiomics. Use them to look at how roots change, how ions stay balanced, and how microbes act under salt and alkali stress. Find out how these three things affect each other. Then find the key genes and pathways that help plants resist stress [3].

(2) Strengthen the screening and evaluation of indigenous, highly salt-tolerant, and highly active rhizosphere microbial resources; optimize the preparation processes and field application protocols for composite microbial preparations; improve strain colonization efficiency; and establish a low-cost, scalable biological remediation technology system for saline-alkali lands [10].

(3) Use molecular markers to track traits like root shape and ion movement. This helps breeders select new varieties that have both stress tolerance and high yields [13].

(4) Put together different methods like microbial improvement, water and fertilizer control, straw return, and tolerant cultivar cultivation. Through the synergy of

agronomic and biological approaches, build a complete system for improving saline and alkaline land, so that these resources can be used efficiently and sustainably over the long term [14].

## Conflicts of Interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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