ISSN: 3007-9640 DOI: https://doi.org/10.70114/acmsr.2026.7.1.P29

Mechanisms of Plant Tolerance to Salt-Alkali Stress: A Functional Trait-Based Perspective

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Abstract. Soil salinization and alkalization are major abiotic stresses limiting global crop productivity. Salt-alkali stress imposes combined effects of osmotic stress, ion toxicity, oxidative stress, and high pH on plants, disrupting membrane integrity, inhibiting photosynthesis, and impairing nutrient uptake. Plant tolerance to such stresses is a complex quantitative trait controlled by multiple genes, involving various physiological and morphological adaptation mechanisms. Functional traits play critical roles in plant adaptation to saline-alkaline environments. This review synthesizes current knowledge on the physiological mechanisms of plant responses to salt-alkali stress, emphasizing functional trait-based adaptation strategies, and analyzes the effects of salt-alkali stress on plant growth, biomass allocation, nutrient uptake, and photosynthesis through specific case studies. Research indicates that a single indicator cannot accurately reflect plant adaptability to salt-alkali stress; instead, multiple functional traits should be integrated for scientific evaluation. Understanding these mechanisms provides a theoretical basis for breeding stress-tolerant crops and managing agricultural ecosystems under changing environmental conditions.

Keywords: Salt-alkali stress; functional traits; osmotic adjustment; ion toxicity; photosynthetic inhibition; stress tolerance mechanisms.

1. Introduction

Soil salinization is one of the most severe abiotic stresses affecting agricultural productivity worldwide [1]. Salt stress primarily impacts plants through osmotic stress, ion toxicity, oxidative stress at the subcellular level, and secondary stresses, which compromise membrane integrity and enzyme activity, ultimately inhibiting water and nutrient uptake [2]. Plant salt tolerance is a complex trait controlled by multiple genes [3], a single indicator is insufficient for assessing plant salt tolerance, and a comprehensive evaluation integrating multiple indicators is required [4-6].

Both salt stress and drought stress inhibit water uptake by creating osmotic stress at the root-soil interface [7-8], however, in addition to osmotic stress, salt stress also causes Na^+ toxicity [8]. Plants respond rapidly to osmotic stress but exhibit a slower response to the toxic effects of Na^+ accumulation [9], and the ionic phase largely determines plant salt tolerance [8]. Furthermore, alkaline salts such as Na_2CO_3 not only produce harmful Na^+ but also increase soil pH, imposing combined salt and alkali stress on plants [10].

In recent years, plant functional trait-based ecological research methods have been widely applied across various levels of ecological research [11]. Plant functional traits encompass a range of morphological, biochemical, physiological, structural, and phenological characteristics that influence plant performance or adaptability [12], and can objectively express plant adaptability to external environments [13]. Studies have shown that variation in plant functional traits reflects plant feedback to various environmental factors [14], exhibiting significant plastic responses under salt stress [15]. This review systematically summarizes the physiological mechanisms of plant responses to salt-alkali stress, with emphasis on functional trait-based adaptation strategies, aiming to provide

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a theoretical foundation for breeding salt-alkali tolerant crops and managing agricultural ecosystems in saline-alkaline regions.

2. Physiological Mechanisms of Plant Response to Salt-Alkali Stress

2.1 Osmotic Regulation and Ion Homeostasis

Under salt stress, plants first experience osmotic stress [8]. Osmotic stress leads to water deficiency, prompting plants to synthesize osmoregulatory substances to maintain cellular osmotic potential, similar to water stress. However, unlike water stress, osmoregulatory substances under salt stress include not only organic compounds but also inorganic osmoregulators such as Na^+ and K^+ [9].

Accumulation of metal ions such as Na^+ and K^+ in the cytoplasm disrupts osmotic balance, inhibits physiological and biochemical metabolic processes, impairs photosynthetic capacity, and ultimately leads to starvation and death [16]. Excessive Na^+ in plants also inhibits the uptake of other beneficial metal ions, affecting plant growth [17].

Under NaCl stress, plant roots are the first to respond to stress conditions, subsequently affecting aboveground growth [18]. Regardless of salt concentration, plant growth and development are affected, harming seed germination and causing a series of adverse consequences for seedling and root development, organic matter accumulation, and leaf area [19]. Salt stress also affects nucleic acid synthesis by influencing nuclease activity, which shows a negative correlation with salt concentration [20], leading to reduced nucleic acid content in plant cells [21].

Alkaline salts such as Na_2CO_3 cause more severe damage to plants and soil. In addition to producing harmful Na^+, Na_2CO_3 increases soil pH, creating an alkaline environment that imposes combined salt and alkali stress on plants [10]. Increasing salt stress raises Na^+ content in plants while reducing K^+ content. While NaCl does not significantly affect Na^+ content, Na_2CO_3 stress reduces K^+ content in various plant organs, disrupting osmotic balance and adversely affecting plant growth and development [10].

2.2 Oxidative Stress and Antioxidant Defense

Osmotic stress causes water deficiency, inducing the production of large amounts of reactive oxygen species within cells. Reactive oxygen species can disrupt normal plant metabolism by oxidizing lipids, proteins, and nucleic acids, leading to membrane damage and increased permeability. Malondialdehyde is a key end product of membrane lipid peroxidation, and its content is an important indicator of membrane damage. To counteract reactive oxygen species, plants enhance activities of antioxidant enzymes such as superoxide dismutase and peroxidase, which are commonly used as physiological indicators of salt tolerance [22-23].

2.3 Inhibition of Photosynthesis

Salt stress reduces photosynthetic rates in plants. Lin et al. (2006) studied photosynthetic responses of Kosteletzkya virginica to salt stress and found that photosynthetic rates initially decreased under salt treatment, with higher salt concentrations causing more pronounced declines. After reaching a minimum, rates partially recovered before further declining with prolonged stress [24]. The mechanisms underlying salt-induced photosynthetic decline remain debated. Considerable research indicates that initial photosynthetic decline results from stomatal limitation due to stomatal closure, while later declines are primarily attributed to non-stomatal limitation caused by reduced mesophyll cell photosynthetic activity. Zhao et al. (2000) studied photosynthetic gas exchange characteristics of different reed ecotypes and found that photosynthetic rates decreased with increasing habitat salinity, with stomatal limitation being one contributing factor [25].

Additionally, salt-induced reduction in chlorophyll content significantly contributes to decreased photosynthetic rates. Guan et al. (2011) studied the effects of water and salt stress on Suaeda salsa seedling growth and antioxidant enzyme activities in the Yellow River Delta coastal wetlands and

ISSN: 3007-9640 DOI: https://doi.org/10.70114/acmsr.2026.7.1.P29
found that under constant water conditions, chlorophyll a and b contents decreased with increasing salinity [26]. Salt stress-induced physiological effects lead to decreased leaf chlorophyll content and photosynthetic enzyme activity, ultimately reducing photosynthesis and transpiration rates [27].

3. Functional Trait-Based Adaptation Strategies to Salt-Alkali Stress

3.1 Concept and Connotation of Functional Traits

Through evolution and development, plants form internal physiological and external morphological adaptation strategies to minimize adverse environmental effects; these adaptive strategies manifest as plant traits. Plant traits objectively express plant adaptability to external environments [13], and the presence or absence and quantitative characteristics of certain traits reflect ecosystem functional characteristics, thus termed plant functional traits [28]. Examples include plant height, seed size, leaf carbon, nitrogen, and phosphorus content and ratios, potential photosynthetic rate, and specific leaf area [29-30].

Plant functional traits encompass a range of morphological, biochemical, physiological, structural, and phenological characteristics that influence plant performance or adaptability [12], and reflect plant nutrient trade-offs and survival and adaptation strategies [31]. Plant height determines competitive ability for light, with taller species affecting light availability for shorter neighboring plants [32]. Leaf morphological characteristics indicate strategies for water use efficiency, growth patterns, and nutrient utilization, Leaf carbon and nitrogen concentrations reflect leaf structure and photosynthetic capacity, correlating with photosynthetic rate, leaf lifespan, and decomposition rate [33]. Roots are primary organs for competing for substrate resources [34]. Comas and Eissenstat found that faster-growing species exhibit higher specific root length and finer root diameters [35].

Due to plant adaptability and plasticity along environmental gradients, functional traits vary significantly among species. Species can adjust morphological and physiological characteristics to mitigate environmental stress, increase acquisition of limited resources, enhance environmental adaptability, and improve fitness [36]. Variation in plant functional traits reflects plant feedback to various environmental factors [14].

3.2 Morphological Adaptations

Under salt stress, plants exhibit various morphological adaptations. Leaves become smaller or absent, leaf epidermis becomes cutinized, and mechanical tissues form in or outside leaves. Epidermal thickness, mesophyll thickness, spongy tissue cell diameter, and palisade tissue cell size increase [37]. Dense trichomes and bristles of various shapes, fewer stomata on the upper epidermis, sunken bulliform cells, and more stomata on the lower epidermis reduce water loss [38]. Leaf succulence allows water storage, enabling dilution of absorbed salts to non-toxic levels [39]. During the day, stomatal closure reduces transpiration, limiting salt entry into aboveground parts via transpiration streams, or isolation cells form in leaf cells to exclude salt, enhancing salt tolerance [40]. Some plants possess salt glands on leaves that secrete salt under salt stress, or secrete salt through epidermal wax formation, demonstrating adaptation to high salt stress [38].

Salt-alkali content is a critical environmental factor affecting wetland plant survival, growth, distribution, and reproduction [41]. Moderate salt-alkali content can promote plant growth, but exceeding tolerance thresholds leads to significant growth inhibition. Zhang et al. (2008) studied the effects of different salt concentrations in irrigation water on reed growth and found that with increasing salt concentration, aboveground biomass, plant height, fresh weight, and dry weight significantly decreased ($P<0.01$). However, irrigation with saline water below 3 g/kg did not affect reed biomass, yield, or quality [42].

Excessively high soil salt-alkali content reduces plant height, halts leaf growth, inhibits root development [43], affects nutrient concentrations, and alters biomass allocation between aboveground and belowground parts [44]. Cui et al. (2008) studied Suaeda salsa and found that salt stress significantly inhibited leaf area, dry matter mass, and plant height [45].

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3.3 Physiological and Biochemical Trait Adjustments

Variation in plant functional traits reflects plant feedback to environmental factors [14]. Grewell et al., in experiments on Spartina alterniflora under salt stress, found that 15 of 21 measured leaf chemical, pigment, morphological, and physiological traits exhibited plastic responses to salinity [15].

Sobrado (2005) studied Laguncularia racemosa and found no significant relationship between specific leaf weight and soil salinity, but leaf nitrogen content increased with salt concentration [46]. Shi and Chang (1990) studied nutrient uptake in Puccinellia tenuiflora and found that nitrogen and phosphorus uptake showed significant positive correlations with soil salt concentration [47]. Wang and Cao (2004) studied Taxodium distichum seedlings and found that soil salt concentration increased total nitrogen and phosphorus content in leaves, while decreasing these contents in roots and stems [48].

4. Summary

Salt-alkali stress adversely affects plant growth through multiple pathways including osmotic stress, ion toxicity, oxidative stress, and high pH damage. Plants have developed complex adaptation mechanisms during evolution, including accumulation of osmoregulatory substances, activation of antioxidant enzyme systems, regulation of photosynthesis, and morphological modifications. Functional traits play critical roles in plant adaptation to salt-alkali environments.

As plant salt-alkali tolerance is a complex trait controlled by multiple genes, a single indicator cannot accurately reflect plant adaptability. Therefore, evaluating plant salt-alkali tolerance should integrate multiple functional traits, including morphological, physiological, biochemical, and photosynthetic characteristics. These findings provide theoretical foundations for breeding salt-alkali tolerant crop varieties and managing agricultural ecosystems in saline-alkaline regions.

Acknowledgements

This work was funded by the Special Funds Projects of the China Institute of Water Resources and Hydropower Research and and Special Funds Projects of the China Institute of Water Resources and Hydropower Research (MKST2024JK018).

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