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Review Article

IMPACT OF SALT STRESS ON PLANT GROWTH AND APPROACHES FOR ENHANCED TOLERANCE

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Abstract *Salt stress is a major environmental factor that limits plant growth and productivity, particularly in regions with high soil salinity. As salt accumulation disrupts cellular functions, plants face challenges in water uptake, nutrient absorption, and maintaining metabolic processes, leading to reduced yield and crop quality. Plants have developed several mechanisms of salt tolerance, including ion homeostasis, osmotic adjustment, and antioxidant defense, which help plants adapt to saline conditions. Soil management techniques, such as leaching and the use of amendments, alongside plant growth regulators and microbial inoculants, can enhance plant resilience to salinity. There is a dire need for interdisciplinary research to understand the complex interactions between plants, soil, and microorganisms, as well as the need to develop salt-tolerant crop varieties through genetic engineering. Rising temperatures and sea levels due to climate change have exacerbated salinity issues. Long-term solutions, such as soil reclamation and sustainable water management, are crucial to ensuring the future of agriculture in saline-prone regions.*

Keywords: *salt stress; tolerance mechanisms; soil management; sustainable water management*

Introduction

Agriculture forms the backbone of global food security, supporting the livelihoods of millions and meeting the nutritional needs of an ever-growing population (Junaid and Gokce, 2024; Sharma & Singh, 2017). It is essential for economic development, especially in regions where a large portion of the population depends on farming. The demand for agricultural productivity continues to rise as the global population increases, making it crucial to address challenges that threaten crop yields. Among these challenges, environmental stresses, particularly salt stress, pose significant hurdles to sustainable agricultural production (Abbas et al., 2024ab; Irfan et al., 2024; Msangi, 2014). Salt stress is a major abiotic stress that affects crop growth and productivity, especially in arid and semi-arid regions where irrigation is extensively used (Haroon et al., 2024; Hussain et al., 2019). Excessive salt accumulation in the soil disrupts plant physiological processes, reducing water uptake and causing ionic toxicity. The increasing prevalence of saline soils has become a significant threat to global agricultural sustainability. It is estimated that more than 20% of irrigated lands are affected by salinity, leading to reduced crop yields and a substantial economic burden. For countries relying heavily on agriculture, combating salt stress is critical to ensuring food security and supporting rural economies (El Sabagh et al., 2020). Understanding salt stress and its impact on plant growth is vital for developing effective solutions (Ondrasek et al., 2022). Salt stress affects plants by hindering their ability to absorb water and causing the accumulation of toxic ions, such as sodium and chloride. These effects result in physiological changes, such as stunted growth, reduced photosynthetic efficiency, and compromised

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reproductive success (Chatta et al., 2024; Chauhan et al., 2023; Sami et al., 2023). Over time, these stresses lead to poor crop yields, threatening the stability of food supplies and increasing the vulnerability of farming communities to economic and social challenges (Bhat et al., 2020).

Causes of salt stress

Salt stress is an abiotic stress condition in plants caused by the accumulation of soluble salts, such as sodium chloride (NaCl), in the soil or irrigation water (Yadav et al., 2011). This excess salinity interferes with plant growth and development, affecting both their physiological and metabolic functions. Salt stress primarily disrupts water uptake by creating an osmotic imbalance in the soil and introduces toxic ions like sodium (Na^+) and chloride (Cl^-), which impair cellular processes. These combined effects result in reduced plant growth, lower yields, and in severe cases, plant death (Rasool et al., 2013). Salt stress arises from the accumulation of high concentrations of salts in the root zone, primarily in arid and semi-arid regions where water evaporation exceeds precipitation. It is caused by both natural and human-induced factors. Salinity can occur due to the weathering of rocks and the deposition of salts by wind or rain over time (Carillo et al., 2011). In coastal areas, seawater intrusion is a significant source of salt accumulation in soils. Irrigation with saline water, poor drainage systems, and excessive use of fertilizers contribute to increased soil salinity. Inappropriate irrigation practices can lead to salt build-up as water evaporates, leaving salts behind in the root zone. Climate change further exacerbates the problem by reducing freshwater availability and increasing soil evaporation rates (Ullah et al., 2021).

Salt affected areas

Salt stress is a global issue, affecting agricultural productivity in many regions. Approximately 20% of irrigated lands, which produce about one-third of the world's food, are impacted by salinity (Hussain et al., 2019). Countries in the Middle East, North Africa, and South Asia face significant challenges due to limited rainfall and high reliance on irrigation. In areas prone to seawater intrusion, such as parts of Bangladesh, India, and Southeast Asia, salt stress is a persistent problem for agriculture. Poor irrigation management has led to salinization in productive agricultural lands, such as parts of Pakistan, China, and the southwestern United States (El Sabagh et al., 2020).

Types of Salt Stress

Salt stress can be categorized into two main types based on its effects on plants:

Osmotic Stress

This occurs when high salt concentrations in the soil reduce the water potential, making it difficult for plants to absorb water from the soil. Osmotic stress leads to dehydration symptoms in plants, such as wilting and reduced leaf expansion. It is the initial effect of salt stress and impacts the plant's ability to maintain normal growth (Rasool et al., 2013).

Ionic Stress

Over time, salt stress causes an accumulation of toxic ions, particularly sodium and chloride, in plant tissues. These ions disrupt cellular functions by interfering with essential nutrient uptake, enzyme activity, and membrane stability. Ionic stress often results in leaf chlorosis (yellowing), necrosis (tissue death), and premature leaf drop, further reducing the plant's photosynthetic capacity (Yildiz et al., 2020).

Impact of salt stress on plant growth and development

Salt stress significantly affects plants, disrupting their growth, physiological processes, and reproductive success (figure 1). These impacts ultimately reduce agricultural productivity, posing a major challenge to global food security. High salinity creates osmotic stress, making it difficult for plants to absorb water from the soil. This leads to stunted growth, with noticeable reductions in plant height, leaf area, and root length. The roots, which are the first point of contact with saline soil, often exhibit inhibited elongation and branching. This hampers the plant's ability to access nutrients and water, further limiting growth (Shahid et al., 2020).

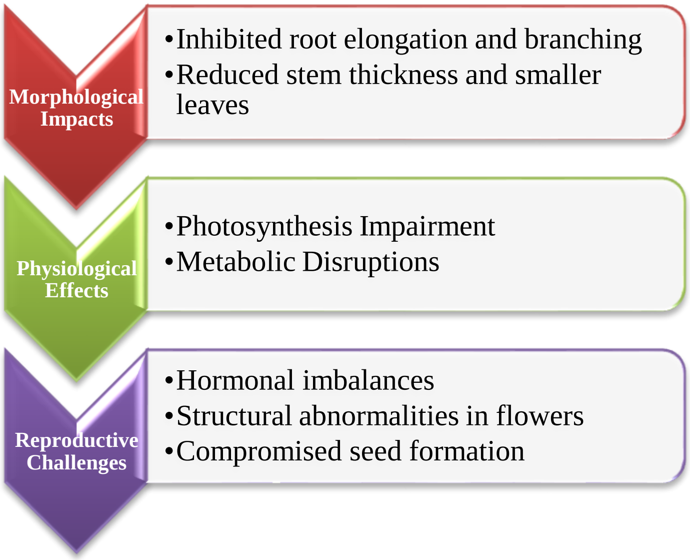

Figure 1: Impact of salt stress on growth and development of plants

Shoot development is also affected, with symptoms such as reduced stem thickness and smaller leaves. The accumulation of toxic ions like sodium (Na^+) and chloride (Cl^-) in plant tissues disrupts cellular structure, causing damage to cell walls and membranes. This structural damage manifests as leaf wilting, chlorosis (yellowing), and necrosis (tissue death). Over time, these morphological changes weaken the plant and diminish its overall

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productivity (Zhao et al., 2020). Photosynthesis, the process by which plants convert sunlight into energy, is highly sensitive to salt stress. Salinity affects photosynthesis by reducing the efficiency of the photosynthetic machinery. Sodium and chloride ions accumulate in chloroplasts, interfering with the functioning of enzymes and proteins involved in photosynthesis. Additionally, salt stress reduces stomatal conductance—the opening and closing of stomata—leading to limited carbon dioxide (CO_2) uptake. This restricts the photosynthetic process and lowers the energy available for plant growth (Van Zelm et al., 2020).

Metabolic processes are also disrupted under salt stress. Osmotic stress alters the production of vital organic compounds like amino acids, sugars, and proteins. Plants often accumulate osmolytes, such as proline and glycine betaine, to combat osmotic stress, but this adaptation diverts energy and resources away from growth and development (Arsahd et al., 2024; Fu & Yang, 2023; Rehman et al., 2024). Furthermore, salt stress increases the production of reactive oxygen species (ROS), which causes oxidative damage to lipids, proteins, and DNA. Although plants activate antioxidant defense systems to mitigate ROS damage, prolonged exposure to high salinity overwhelms these protective mechanisms. Reproductive development is one of the most sensitive stages of plant growth, and salt stress poses significant challenges to successful reproduction (Trușcă et al., 2023). High salinity affects flowering, pollination, and seed development, leading to reduced reproductive success. Plants under salt stress often exhibit delayed or incomplete flowering due to hormonal imbalances and energy deficits. Pollination is negatively impacted as salt stress causes structural abnormalities in flowers, such as smaller anthers and reduced pollen viability. Even if pollination occurs, seed formation may be compromised. Seeds often develop poorly or exhibit lower viability, further reducing the plant's ability to reproduce effectively. In crops, this translates to lower yields, smaller fruits, and poor-quality seeds, directly affecting agricultural productivity (Mbarki et al., 2018).

Mechanisms of Salt Tolerance in Plants

Plants have evolved several mechanisms to tolerate salt stress and maintain growth under adverse conditions (Joshi et al., 2022). These mechanisms enable plants to manage ionic toxicity, maintain water balance, and mitigate oxidative damage caused by high salinity (figure 2). Understanding these strategies is crucial for developing salt-tolerant crops (Hao et al., 2021).

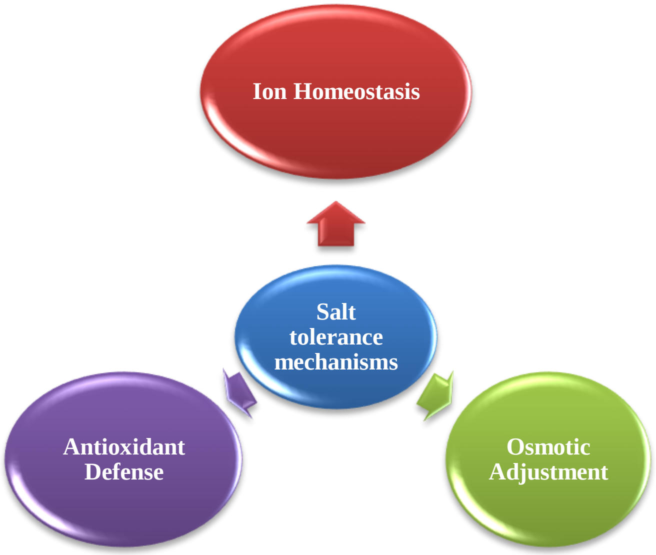

Figure 2: Major mechanisms in plants to cope with salt stress

Ion Homeostasis

Ion homeostasis refers to a plant's ability to regulate the uptake, transport, and compartmentalization of ions like sodium (Na^+) and chloride ($Cl^−$) under saline conditions. Excessive accumulation of these ions in the cytoplasm is toxic to plant cells, disrupting enzymatic functions and membrane integrity (Van Zelm et al., 2020). Plants restrict the entry of Na^+ and $Cl^−$ into root cells while maintaining the uptake of essential nutrients like potassium (K^+). Potassium is particularly important as it plays a vital role in enzymatic activities, osmotic regulation, and photosynthesis. High salinity can disrupt the K^+/Na^+ ratio, so plants use specialized ion channels and transporters, such as HKT1 and SOS1, to maintain this balance (Joshi et al., 2022).

To prevent toxic ion accumulation in the cytoplasm, plants compartmentalize excess Na^+ and $Cl^−$ into vacuoles. This process is facilitated by vacuolar antiporters, such as NHX transporters, which use the proton gradient created by H^+-ATPases to pump ions into vacuoles(Joshi et al., 2022). This sequestration protects vital cellular processes while maintaining ionic equilibrium. Plants actively transport ions to leaves and other tissues while ensuring that toxic levels do not accumulate in sensitive parts like growing tips. This regulation is achieved through long-distance transport systems in the xylem and phloem (Balasubramaniam et al., 2023).

Osmotic Adjustment

Salt stress creates an osmotic imbalance in the soil, reducing water availability for plant roots. To counter this, plants undergo osmotic adjustment by accumulating compatible solutes, also known as osmolytes (Zhao et al., 2020). These solutes help maintain cell turgor and water uptake without

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interfering with cellular functions. Plants synthesize and accumulate small organic molecules such as proline, glycine betaine, and sugars like trehalose and sorbitol (Balasubramaniam et al., 2023). These osmolytes act as osmoprotectants, stabilizing proteins and membranes while reducing the effects of osmotic stress. The accumulation of osmolytes lowers the osmotic potential inside cells, enabling plants to draw water from the surrounding environment. This process is crucial for sustaining metabolic activities and maintaining cell expansion during salt stress. Aquaporins are membrane proteins that facilitate water transport across cell membranes. During salt stress, plants regulate aquaporin activity to optimize water uptake and distribution throughout the plant body (Rahman et al., 2021).

Antioxidant Defense

Salt stress induces the production of reactive oxygen species (ROS), such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals, which cause oxidative damage to lipids, proteins, and DNA. Plants activate their antioxidant defense system to neutralize ROS and protect cellular components. Plants produce enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD) to scavenge ROS (Singh, 2022). These enzymes convert harmful ROS into less toxic molecules, such as water and oxygen. In addition to enzymatic mechanisms, plants synthesize non-enzymatic antioxidants like ascorbic acid (vitamin C), glutathione, and flavonoids. These compounds act as free radical scavengers, preventing oxidative damage. The production of ROS also acts as a signal to activate stress-responsive genes. These genes regulate the synthesis of protective proteins and molecules that enhance the plant's overall stress tolerance (Hasanuzzaman et al., 2021).

Management strategies

To mitigate the adverse effects of salt stress on plants, various physiological and agronomic practices can be employed. These practices aim to improve soil health, enhance plant stress tolerance, and maintain agricultural productivity in saline environments. By combining scientific knowledge with practical strategies, farmers can better manage the challenges posed by salt stress (Paz et al., 2023).

Soil Management Techniques

Proper soil management is essential to reduce salinity levels and create favorable growing conditions for plants. Several techniques can be employed to manage saline soils effectively. Irrigating fields with high-quality water to leach salts below the root zone is a common practice. However, it requires proper drainage systems to prevent waterlogging and secondary salinization. Adding soil amendments, such as gypsum (calcium sulfate), helps displace sodium ions from soil particles (Paz et al., 2023; Sahab et al., 2021). This improves soil structure, enhances water infiltration, and reduces soil salinity. Organic or inorganic mulches can reduce soil evaporation, minimizing salt accumulation on the surface. Conservation tillage practices help retain soil moisture and prevent the upward movement of salts. Growing salt-tolerant crops or including deep-rooted plants in rotation can improve soil conditions by reducing salt build-up and enhancing nutrient cycling (Sahab et al., 2021).

Use of Plant Growth Regulators

Plant growth regulators (PGRs) are chemical compounds that influence plant growth and development. Under salt stress, PGRs can enhance plant tolerance by regulating physiological and biochemical processes (Quamruzzaman et al., 2021). Cytokinin hormones promote cell division, delay leaf senescence, and improve chlorophyll content under stress conditions. Cytokinin also enhances root growth, helping plants access water and nutrients more effectively. ABA plays a crucial role in stress signaling. Under salt stress, it helps regulate stomatal closure, reducing water loss through transpiration. ABA also activates stress-responsive genes, enhancing the plant's ability to cope with salinity. Salicylic Acid and Jasmonic Acid modulate plant defense mechanisms. They help reduce oxidative damage by enhancing the production of antioxidants and protecting cellular structures from stress-induced injuries. Gibberellins and Brassinosteroids promote growth and alleviate stress-induced damage by improving photosynthetic efficiency and stabilizing cellular membranes (Khan et al., 2020).

Development of salt-tolerant varieties

Genomics-driven approaches, such as genome-wide association studies (GWAS) and genomic selection, can identify genes and markers associated with salt tolerance. These insights can accelerate the breeding of salt-tolerant crop varieties (Qin et al., 2020). CRISPR/Cas9 and other gene-editing technologies also hold promise for introducing precise genetic modifications to enhance tolerance (Han et al., 2022). Combining data from genomics, transcriptomics, proteomics, and metabolomics can provide a holistic view of how plants respond to salinity (Ashraf & Munns, 2022). These insights can inform the development of integrated solutions to improve salt tolerance.

Conclusion

Salt stress poses a significant challenge to global agriculture, threatening food security and sustainable farming. Salt stress has negative impacts on plants, including growth inhibition, disrupted metabolism, and reduced productivity. Strategies such as ion homeostasis, osmotic adjustment, and antioxidant defense play crucial roles in plant tolerance. Future research should focus on interdisciplinary collaboration, climate-resilient approaches, and long-term strategies for combating salinity.

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Consent for Publication

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All authors contribute equally.

Conflict of interest

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