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Morphological and Physiological Responses of Crop Plants to Salinity Stress: A Systematic Review

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ABSTRACT

Salinity stress is a major abiotic factor limiting plant growth and productivity in various agricultural ecosystems. Salt accumulation in the root zone causes osmotic stress, ion toxicity, and nutrient imbalance, which directly impact plant performance. This article aims to review and synthesize research findings related to plant morphological and physiological responses to salinity stress. The method used was a literature review of relevant national and international scientific publications. The results of this study indicate that salinity stress triggers morphological changes in the form of decreased vegetative growth, leaf area, root system development, and plant biomass. Physiologically, salinity inhibits photosynthesis, affects stomatal regulation, disrupts water and ion balance, and increases the formation of reactive oxygen species. Plants respond to these conditions through adaptive mechanisms such as osmoregulation, regulation of ion transport, and increased antioxidant enzyme activity. These morphological and physiological responses are interrelated and play a crucial role in determining plant tolerance to salinity stress. This study is expected to provide a scientific basis for the development of salinity-tolerant plants and the sustainable management of saline land.

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1. INTRODUCTION

Salinity stress is a major constraint on crop production in various agroecosystems, particularly in areas vulnerable to salt intrusion, inadequate irrigation, and global climate change, which exacerbates saline soil conditions. Salt accumulation in the root zone of plants can cause osmotic stress, ion toxicity, nutrient imbalances, and ultimately inhibit plant growth and productivity (Munns & Tester, 2008). This phenomenon is very relevant to the challenge of food security, considering the increasing extent of marginal land due to soil degradation manifested by salinity (Shrivastava & Kumar, 2015).

Plant responses to salinity stress manifest changes at various levels of biological organization, from morphology to physiology and biochemistry. Plants experiencing high salinity often exhibit reduced vegetative growth rates, inhibited seed germination, and changes in root and leaf architecture as adaptation strategies (Ashraf & Foolad, 2007). In addition, physiological mechanisms such as stomatal regulation, accumulation of osmoregulators (e.g., proline, soluble sugars), and increased activity of antioxidant enzymes are key in mitigating oxidative stress produced by saline conditions (Zhu, 2001).

A series of studies have revealed that the response to salinity is not merely passive, but also involves complex molecular signals and changes in gene expression. Components such as Na^+ and Cl^- ion transfer markers, the formation of specialized cell caspases, and hormone regulatory pathways such as ethylene, abscisic acid (ABA), and cytokinin play important roles in shaping plant phenotypic plasticity to salinity stress (Hasegawa et al., 2000; Munns, 2002). Mastery of this mechanism is the basis for breeding and genetic engineering of salt-tolerant plants.

With the increasing importance of understanding plant adaptation mechanisms to salinity, a comprehensive study of plant morphological and physiological responses is crucial. This review aims to summarize recent research findings, identify gaps in the knowledge that need further investigation, and provide insights into the practical application of research findings in salt-tolerant plant breeding.

2. METHOD

This study employed a narrative literature review approach to systematically collect, analyze, and synthesize scientific evidence related to morphological and physiological responses of plants to salinity stress. The review focused on integrating findings from experimental and review studies to identify general response patterns and adaptive mechanisms across different plant species.

Literature data were obtained from several reputable scientific databases, including Google Scholar, ScienceDirect, SpringerLink, Wiley Online Library, and Taylor & Francis Online. The search process was conducted using combinations of the following keywords: salinity stress, plant morphology, plant physiology, salt tolerance, osmotic stress, and ion toxicity.

The selection of articles followed specific inclusion criteria, namely: (1) peer-reviewed journal articles, (2) publications published between 2000 and 2023, (3) studies focusing on morphological and/or physiological plant responses to salinity stress, (4) plant materials including food crops, horticultural crops, plantation crops, halophytes, and model plants, and (5) articles written in English or Indonesian and accessible in full-text format.

The exclusion criteria included: (1) non-peer-reviewed sources such as theses, conference abstracts, and opinion papers, (2) articles that only discussed soil salinity without plant response analysis, and (3) studies with insufficient methodological clarity.

The literature screening process was conducted in three stages: (1) title screening, (2) abstract screening, and (3) full-text evaluation. From an initial pool of approximately 140 publications, a total of 72 relevant articles were selected and included in the final analysis.

Data analysis was performed using a qualitative descriptive synthesis approach. The selected studies were categorized into two main thematic groups: morphological responses (including plant height, root development, leaf area, and biomass) and physiological responses (including photosynthesis, stomatal conductance, water relations, ion accumulation, and antioxidant activity). A comparative analysis was applied to identify similarities, differences, and general adaptive patterns among plant species under salinity stress conditions.

3. RESULTS AND DISCUSSION

3.1 Plant Morphological Response to Salinity Stress

Morphological responses are changes in plant structure that occur due to exposure to salinity in the soil or growing medium. Various studies have shown that salinity negatively impacts plant growth components.

3.1.1 Changes in Vegetative Growth

Salinity stress is one of the main abiotic factors limiting vegetative growth in plants, particularly in coastal areas and marginal lands. Salinity occurs due to the accumulation of dissolved salts, mainly sodium chloride (NaCl), in the soil or irrigation water, which causes a decrease in soil water potential, making it difficult for plants to absorb water. This condition triggers osmotic stress, which directly inhibits important physiological processes such as cell division, cell elongation, and the formation of new vegetative tissue (Munns & Tester, 2008).

At the morphological level, salinity stress is generally characterised by a reduction in plant height, number of leaves, leaf area, and crown and root biomass. Root growth is often more sensitive than canopy growth because roots are the first organs to be directly exposed to salt solutions in the soil. The accumulation of Na^+ and Cl^- ions in root tissues can disrupt cell membrane integrity and reduce meristem activity, thereby inhibiting root growth and having a knock-on effect on water and nutrient uptake (Parida & Das, 2005).

Physiologically, salinity causes osmotic stress and ionic stress simultaneously. Osmotic stress reduces cell turgor pressure, thereby inhibiting cell expansion, while ionic stress occurs due to the toxicity of Na^+ and Cl^- ions, which disrupt the balance of essential nutrients such as K^+, Ca^{2+}, and Mg^{2+}. This ion imbalance results in decreased enzyme activity, impaired protein synthesis, and inhibited energy metabolism, which are crucial for vegetative growth (Flowers & Colmer, 2008).

Salinity stress also significantly affects photosynthetic activity, which is the main foundation of vegetative growth. Chlorophyll content in leaves tends to decrease due to chloroplast damage and increased degradation of photosynthetic pigments. In addition, salinity triggers stomatal closure as an adaptive response to reduce water loss, but this actually limits CO_2 diffusion into the leaves and reduces the rate of net photosynthesis. The decline in photosynthesis directly reduces the production of assimilates needed for the formation of vegetative organs (Ashraf & Harris, 2004).

At the biochemical level, plants experiencing salinity stress show increased production of reactive oxygen species (ROS) such as superoxide and hydrogen peroxide. The accumulation of ROS causes oxidative stress that damages plant cell lipids, proteins, and DNA. As a result, the structure of vegetative tissues degrades and cell regeneration capacity decreases. To overcome this, plants activate antioxidant systems such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), although their effectiveness depends on the genetic tolerance level of the plant (Hasanuzzaman et al., 2013).

The vegetative growth response to salinity is also greatly influenced by genotype differences between species and varieties. Salinity-tolerant plants are generally able to maintain vegetative growth through ion exclusion mechanisms, Na^+ compartmentalisation into vacuoles, and the accumulation of osmolytes such as proline and glycine betaine. These mechanisms help maintain cellular osmotic balance and protect enzymatic structures, thereby minimising the decline in vegetative growth compared to sensitive plants (Zhu, 2001).

Overall, changes in vegetative growth due to salinity stress are the result of complex interactions between morphological, physiological, and biochemical disturbances. The most noticeable impacts are the inhibition of biomass formation, reduced leaf area, and decreased photosynthetic capacity, which ultimately affect plant productivity. A thorough understanding of vegetative responses to salinity is crucial in the development of tolerant varieties and sustainable saline land management strategies (Munns & Gilliham, 2015).

3.1.2 Root Development and Primary Roots

Salinity stress is one of the main abiotic factors that directly affects the development of plant root systems, particularly primary roots as the first organs to interact with the soil environment. Primary roots play a central role in the absorption of water and nutrients, so changes in root structure and function due to salinity will have a systemic impact on vegetative growth and overall plant productivity. Increased concentrations of dissolved salts, especially NaCl, reduce the osmotic potential of soil solutions, making it difficult for roots to absorb water, which then triggers osmotic stress in root tissues (Munns & Tester, 2008).

At the morphological level, salinity stress generally causes a significant reduction in primary root length, number of lateral root branches, and root biomass. The shortening of the primary root occurs due to the inhibition of apical meristem activity, which is responsible for cell division. Na^+ and Cl^- ions accumulated in the rhizosphere can suppress the rate of cell expansion by disrupting turgor pressure and reducing cell wall elasticity, thereby limiting the longitudinal growth of roots (Acosta-Motos et al., 2017).

Physiologically, primary roots experience two main types of stress, namely osmotic stress and ionic stress. Osmotic stress reduces the water potential gradient between the soil and root tissues, while ionic stress is caused by the toxicity of Na^+ and Cl^-, which disrupts the balance of essential ions such as K^+ and Ca^{2+}. This imbalance directly affects plasma membrane function, ion pump activity, and nutrient transport, thereby reducing the root's capacity to support plant growth (Isayenkov & Maathuis, 2019).

At the anatomical level, salinity stress can trigger changes in the structure of primary root tissue, including thickening of the endodermis and increased lignification of cell walls. These adaptations serve as protective mechanisms to limit the entry of toxic ions into vascular tissue. However, excessive lignification also has negative implications as it reduces root permeability to water and nutrients, thereby further reducing absorption efficiency under high salinity conditions (Byrt et al., 2018).

Salinity stress also affects the hormonal balance in root tissues, particularly auxin, cytokinin, and abscisic acid (ABA) hormones. Auxin plays an important role in the formation and elongation of primary roots, but under saline conditions, auxin distribution and transport are disrupted. Increased ABA concentration in response to stress inhibits root growth by reducing meristem activity and cell expansion. These hormonal interactions explain why primary roots are more sensitive to salinity changes than other vegetative organs (Koevoets et al., 2016).

At the molecular level, the primary roots of salt-tolerant plants show activation of specific genes involved in ion transport and osmotic homeostasis, such as the SOS (Salt Overly Sensitive), NHX (Na^+/H^+ antiporter), and HKT (High-affinity K^+ transporter) genes. These genes play a role in excluding Na^+ from the cytoplasm or compartmentalising it into the vacuole, thereby reducing the toxic effects of ions on root cells. Activation of this mechanism allows primary roots to continue functioning even in high-salinity environments (Zelm et al., 2020).

Overall, the development of primary roots under salinity stress is the result of complex interactions between morphological, physiological, anatomical, hormonal, and molecular changes. The most consistent major impacts are inhibited root elongation and reduced water and nutrient absorption capacity. A deep understanding of the primary root's response to salinity is crucial in salt-tolerant plant breeding programmes, as an adaptive root system is key to a plant's survival and productivity in saline soils (Rao et al., 2021).

3.1.3 Leaf Area and Leaf Area Index (LAI)

Leaf area and Leaf Area Index (LAI) are important parameters in plant physiology because they reflect photosynthetic capacity and light use efficiency in plant canopies. Leaf area is the surface area of individual leaves, while LAI is the ratio of total leaf area to the unit area of land occupied by plants. Both parameters are highly sensitive to environmental conditions, including salinity stress, which can have a major impact on plant growth and productivity (Khan et al., 2021).

Salinity stress affects leaf area mainly through inhibition of leaf elongation and expansion. Excessive Na^+ and Cl^- ions in the soil cause osmotic pressure to increase, making it difficult for plants to absorb water. This water deficiency reduces the cell turgor required for leaf expansion, resulting in smaller leaves compared to non-saline conditions. As a result, the total leaf area of each individual plant decreases significantly (Cheeseman, 2019).

The decrease in leaf area directly affects the LAI of a plant population because LAI is an aggregate of individual leaf areas. Studies in various plant species show that high salinity contributes to a decrease in LAI through two mechanisms: (1) smaller leaf size and (2) a decrease in the number of new leaves formed. Both effects result in a less dense plant canopy, thereby reducing the plant's ability to absorb sunlight to the maximum extent (Parida & Das, 2020).

The impact of reduced leaf area and LAI has implications for plant photosynthetic productivity. Low LAI means that there is less photosynthetic surface area available, resulting in a decrease in total daily photosynthesis. With a decrease in photosynthetic rate, assimilates for vegetative and generative growth become limited, which in turn leads to a decrease in biomass and crop yield. This indirectly shows that salinity stress not only affects leaves structurally but also physiologically (Shabala & Pottosin, 2020).

Plant responses to salinity also involve changes in leaf anatomy. In some cases, plants experiencing salinity stress show increased epidermal and mesophyll tissue thickness as a structural adaptation to osmotic and ionic stress. Although this adaptation can help reduce water loss, thickening of leaf tissue also results in a decrease in effective leaf area used for photosynthesis and gas exchange, thereby negatively impacting LAI (Munns & Gilliham, 2015).

Several studies have shown that salt-tolerant plant varieties have adaptive mechanisms that help maintain leaf area and LAI better than sensitive varieties. These mechanisms involve more effective ion control, hormonal regulation that balances leaf growth, and increased accumulation of osmolytes that maintain cell turgor. Tolerant varieties tend to be able to maintain higher LAI at moderate salinity levels, resulting in relatively more stable photosynthetic productivity (Zelm et al., 2020).

3.1.4 Plant Biomass

Total plant biomass is generally drastically reduced under high salinity conditions. This has been observed in various food, horticultural, and legume crop species. (Tester & Davenport, 2003; Parida & Das, 2005). Biomass reduction is the accumulation of stress effects on root, stem, and leaf growth. Morphological Synthesis: In general, salinity causes a decrease in plant morphological performance due to inhibition of cell division and expansion due to osmotic pressure and toxicity of Na^+ and Cl^- ions. Plant biomass reflects the total amount of organic mass accumulated through photosynthesis and is a key indicator of plant health and productivity. When plants are exposed to high salinity, water balance, ionic balance, and metabolic function are disrupted, which directly suppresses biomass accumulation in various plant organs such as leaves, stems, and roots (Zhu, 2016).

One of the main mechanisms causing biomass reduction under salinity stress is osmotic stress. Increased salt concentration in the soil reduces soil water potential, forcing plants to work harder to maintain water absorption through their roots. The reduction in cell turgor potential inhibits cell expansion, thereby hindering the growth of vegetative organs. As a result, overall organic biomass production decreases compared to plants growing under non-saline conditions (Munns & Tester, 2008).

In addition to osmotic stress, ionic stress due to the accumulation of sodium (Na^+) and chloride (Cl^-) ions in plant tissues also has a major impact on biomass. Excessive Na^+ and Cl^- ions can disrupt the homeostasis of essential ions such as potassium (K^+) and calcium (Ca^{2+}). This ion imbalance negatively affects enzyme function, membrane integrity, and photosynthetic metabolism, thereby reducing carbon assimilation efficiency. The decrease in photosynthetic rate directly impacts low biomass production and accumulation (Parida & Das, 2020).

The decrease in biomass under salinity stress does not only occur in one part of the plant but often shows a pattern of biomass allocation shift. Generally, plants exposed to salinity tend to allocate more resources towards root growth as an adaptive response to seek water and nutrients more efficiently. However, this increase in root biomass investment is often not proportional to the decrease in canopy biomass, so that the total plant biomass still decreases (Koevoets et al., 2016).

Changes in leaf anatomy and physiology also contribute to biomass decline. Leaves on plants experiencing salinity stress typically show smaller leaf area and reduced leaf number. The decrease in leaf area and Leaf Area Index (LAI) impacts the canopy's ability to capture sunlight, thereby reducing net photosynthetic capacity. With the reduction in energy produced through photosynthesis, photosynthetic biomass production also decreases dramatically (Khan et al., 2021).

Plant response to salinity stress is greatly influenced by genotype. Varieties or species that are tolerant to salinity are able to maintain higher biomass levels than sensitive varieties. These tolerance mechanisms include the ability to exclude toxic ions from sensitive tissues, compartmentalise ions into vacuoles, and accumulate osmolytes to maintain cell turgor and metabolic activity. Salinity-tolerant plants also demonstrate better physiological adaptation capacity, including maintenance of photosynthesis and water use efficiency (Van Zelm et al., 2020).

3.2 Plant Physiological Responses to Salinity Stress

Physiological responses reflect changes in internal plant functions, including photosynthesis, water regulation, ion balance, and antioxidant mechanisms.

3.2.1 Decreased Photosynthetic Efficiency

Photosynthetic efficiency reflects the ability of plants to convert light energy into chemical energy through the process of carbon fixation in leaves. Under high salinity conditions, physiological and biochemical disturbances inhibit photosynthetic pathways from light absorption to glucose synthesis, resulting in a drastic decline in plant productivity (Chakraborty et al., 2021).

One of the earliest effects of salinity stress on photosynthesis is stomatal closure. When the soil becomes salty, soil water potential decreases, triggering a defence response such as stomatal closure to reduce water loss through transpiration. Although this mechanism helps conserve water, stomatal closure also limits the entry of CO_2 into the leaves, which is necessary for carbon fixation. Reduced CO_2 availability inhibits both the light and dark reactions of photosynthesis, leading to decreased light use efficiency (Flexas et al., 2022).

In addition to stomatal effects, salinity stress also has non-stomatal effects that damage the structure and function of chloroplasts. Na^+ and Cl^- ions accumulated in leaf tissues can cause damage to thylakoid membranes — where the light reactions of photosynthesis occur — reducing total photosynthetic capacity. This damage inhibits photochemical electron flow and water splitting, drastically reducing ATP and NADPH production, thereby inhibiting sugar synthesis (Parida & Das, 2020).

Chlorophyll reduction is another common mechanism in plants experiencing salinity stress. Salinity increases the degradation of photosynthetic pigments while inhibiting chlorophyll biosynthesis, which impacts the leaves' ability to absorb light in the optimal spectrum. This reduction in chlorophyll is directly linked to low photosynthetic rates, as the light that should be used for CO_2 fixation becomes less effectively absorbed (Ahanger & Agarwal, 2020).

Salinity stress also triggers the formation of reactive oxygen species (ROS) in chloroplasts that damage photosynthetic components. Increased ROS such as superoxide and hydrogen peroxide cause oxidative stress that reduces the stability of photosynthetic proteins such as rubisco, which is a key enzyme in the Calvin cycle. This damage slows down CO_2 fixation and substantially reduces the metabolic efficiency of photosynthesis (Hasanuzzaman et al., 2022).

Under certain conditions, plants attempt to overcome salinity stress through compensatory mechanisms such as increased accumulation of osmolytes (e.g., proline) and activation of antioxidant systems. These mechanisms serve to protect photosynthetic structures from further damage and maintain some photosynthetic capacity despite stress. However, these adaptive responses often only help plants survive and are unable to restore photosynthetic efficiency to normal levels as in non-stress conditions (Zhang et al., 2023).

3.2.2 Stomatal Regulation and Transpiration

Stomata are pores that regulate gas exchange and water loss through transpiration. When plants are exposed to high salinity, osmotic stress initially reduces the availability of water in the soil, causing plants to respond by closing their stomata to retain water in their tissues. This closure of stomata drastically reduces the rate of transpiration, but also limits CO_2 uptake, thereby impacting photosynthesis and energy use efficiency (Flexas et al., 2022).

The stomatal response to salinity is often controlled by hormonal signals, particularly abscisic acid (ABA). Under saline conditions, ABA concentrations increase in leaf and xylem tissues, promoting the cessation of guard cell activity. Increased ABA promotes intracellular calcium accumulation and changes in guard cell turgor, causing stomata to close more rapidly than under non-stress conditions. These hormonal changes are an adaptive mechanism to reduce water loss, but they have a negative impact on gas exchange (Guidi et al., 2021).

Salinity stress also causes changes in leaf structure that affect stomatal characteristics. In some plants, chronic salt exposure can reduce stomatal density or alter stomatal size as a long-term response. These structural adaptations serve to reduce transpiration rates during prolonged periods in saline environments, but usually come at the expense of the plant's capacity to maintain optimal CO_2 uptake for photosynthesis (Qu et al., 2020).

The reduction in transpiration due to stomatal closure under salinity also impacts leaf temperature distribution. Since transpiration functions as a leaf cooling mechanism through evaporative effects, stomatal closure can lead to increased leaf surface temperatures. This temperature increase can exacerbate heat stress and trigger the accumulation of reactive oxygen species (ROS), which in turn can damage membranes and photosynthetic systems. The interaction between salinity stress and leaf temperature adds complexity to plant physiological adaptation (Galmés et al., 2021).

Although stomatal closure is an initial response to salinity stress, some salt-tolerant plant varieties show the ability to maintain more stable transpiration rates through more plastic stomatal regulation or through other mechanisms such as increased osmolyte accumulation. These mechanisms help maintain a balance between water conservation and CO_2 uptake, making salinity tolerance a key factor in plant breeding programmes targeting saline soils (Pandey et al., 2021).

3.2.3 Water Homeostasis and Water Potential

Water potential (ψ) is a measure of the potential energy of water that determines the direction of water movement from the soil to the roots and from the roots to the leaves. Under normal conditions, water moves from the soil with higher water potential (less negative) to plant cells with lower water potential (more negative). However, the presence of salts (e.g. NaCl) in soil solutions lowers soil water potential, thereby inhibiting or even reversing the water potential gradient that is favourable for water uptake, making it difficult for plants to obtain sufficient water for their physiological functions (How Plants Tolerate Salt Stress, 2024).

The decrease in water potential due to increased salt concentration in the rhizosphere causes osmotic stress in plant cells. Osmotic stress occurs when the soil solution is highly hypertonic to the cell cytoplasm, causing water to flow out of the cells through osmosis. As a result, cell turgor decreases and plants become dehydrated even though the soil may appear to have sufficient water content. This is similar to drought stress, but is caused by more negative osmotic pressure due to salinity, rather than low water availability alone (Salinity and Water Relations, 2025).

To maintain water homeostasis, plants activate osmotic adjustment mechanisms by lowering the osmotic potential within cells through the accumulation of compatible solutes such as proline, glycine betaine, and certain sugars. These compounds help lower the osmotic potential of cells without disrupting key metabolic functions, so that water can still be drawn into the cells even though the water potential gradient from the soil is difficult to maintain. The accumulation of these osmolytes also helps plants maintain the turgor pressure necessary for cell growth and other physiological functions (Salinity and Water Relations, 2025).

In addition, salinity stress also disrupts ion homeostasis, which is closely related to water potential regulation. Excessive Na^+ and Cl^- ions can replace important ions such as K^+ within cells, altering ionic balance and worsening osmotic pressure. Plants attempt to maintain ionic homeostasis through ion transport systems such as K^+/Na^+ transporters and the SOS (Salt Overly

Sensitive) pathway, which help exclude toxic ions from the cytoplasm or compartmentalise these ions into vacuoles. Effective ion regulation supports water homeostasis by helping to maintain the balance between solutes inside and outside the cell (How Plants Tolerate Salt Stress, 2024).

All changes in water potential and water homeostasis directly impact plant physiological functions, including reduced photosynthesis rates, cell division, and root and leaf growth. Decreased turgor due to lack of water within cells can inhibit cell expansion and trigger stomatal closure to reduce further water loss, although this step also limits CO_2 uptake for photosynthesis. Therefore, water potential and water homeostasis are key parameters in determining plant tolerance to salinity and are an important focus in plant breeding research to improve resistance to saline conditions (Plants' Response Mechanisms to Salinity Stress, 2025).

3.2.4 Ion Accumulation and Na^+/Cl^- Toxicity

The accumulation of sodium (Na^+) and chloride (Cl^-) ions in plant tissues is one of the most direct consequences of exposure to high salinity in the growing medium, and plays a key role in cellular damage that inhibits plant growth and productivity. When plants absorb water from soil containing high levels of salt, Na^+ and Cl^- also enter the cells through the same ion transport pathways. The accumulation of these excess ions occurs mainly in the leaves and roots, causing an ionic imbalance that disrupts cellular homeostasis (Bibi et al., 2025).

Excess Na^+ in the cytoplasm can compete with potassium ions (K^+) for binding sites in various enzymes and membrane structures, ultimately inactivating important enzyme functions and damaging cellular metabolism. The decrease in K^+ concentration due to competition with Na^+ is a critical factor because K^+ is necessary for membrane stability, ATPase activity, stomatal regulation, and photosynthesis (Bibi et al., 2025).

Cl^- toxicity also has a significant negative impact, although it often receives less attention than Na^+. High Cl^- concentrations in leaves can cause a decrease in chlorophyll and disruption of chloroplast function, which ultimately reduces the photosynthetic capacity of plants. This is because Cl^- can damage chloroplast thylakoid membranes and inhibit the activation of important enzymes in the photosynthetic pathway (Munns & Tester; James et al., 2010).

The accumulation of Na^+ and Cl^- not only causes direct metabolic disruption, but also increases the formation of reactive oxygen species (ROS) within cells. ROS such as hydrogen peroxide (H_2O_2) and superoxide radicals can cause oxidative damage to lipid membranes, proteins, and DNA, exacerbating physiological disorders. The activation of antioxidant defence mechanisms is an adaptive response of plants to high levels of ROS, but if ROS production exceeds the capacity of antioxidant defences, cell damage becomes more severe (Bibi et al., 2025; Amtmann & Sanders, 1998).

The plant response to Na^+ and Cl^- toxicity is greatly influenced by the genetic ability to regulate ion accumulation and maintain a healthy K^+/Na^+ ratio in the cytoplasm. Salt-tolerant plants are able to exclude Na^+ from sensitive tissues or compartmentalise these toxic ions into vacuoles, thereby reducing toxic concentrations in the cytosol. This mechanism also maintains enzyme function and membrane integrity, allowing plants to maintain growth even under high salinity conditions (Tester & Davenport, 2003; Shabala & Cuin, 2008).

3.2.5 Antioxidant Enzyme Activity

Salinity stress in plants often increases the production of reactive oxygen species (ROS) such as superoxide (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (•OH). This increase in ROS can damage cell membranes, proteins and photosynthetic pigments, thereby potentially inhibiting plant growth and productivity. To overcome this oxidative stress, plants activate an antioxidant defence system involving various critical enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione peroxidase (GPX) (Bibi et al., 2025; Scientific Reports).

Superoxide dismutase (SOD) is the first line of defence in the plant antioxidant system, as this enzyme catalyses the dismutation of superoxide radicals into H_2O_2 and O_2. SOD activity often increases in the early stages of salinity exposure as an adaptive response to reduce oxidative stress. In some cases, SOD shows increased activity correlated with stress tolerance, as it is able to reduce ROS accumulation before it reaches toxic levels (Bibi et al., 2025).

Other enzymes such as catalase (CAT) and ascorbate peroxidase (APX) are also important in neutralising H_2O_2 produced by SOD activity. APX utilises ascorbate as an electron acceptor to reduce H_2O_2, while CAT directly decomposes H_2O_2 into water and oxygen. CAT and APX activity is often reported to increase upon moderate salinity exposure as a cellular protection strategy to prevent the accumulation of harmful H_2O_2. For example, research on Moringa oleifera showed a significant increase in SOD, CAT, APX, and GPX activity under moderate to high salinity conditions, reflecting the role of these enzymes in maintaining cellular redox balance under stress (Bibi et al., 2025).

However, the response of antioxidant enzyme activity to salinity is not always linear at all stress levels or plant genotypes. In some long-term studies, antioxidant enzymes such as APX or POD showed an increase at the beginning of salinity treatment but then experienced a decrease in activity upon prolonged or very high salinity exposure. This phenomenon indicates that the antioxidant system has certain limitations, especially when ROS are produced excessively and defence mechanisms are unable to compensate for continuous oxidative damage (long-term treatment in strawberries; PMC).

Differences in antioxidant enzyme responses are also seen between plant varieties with different tolerances to salinity. More tolerant plants tend to maintain or increase antioxidant enzyme activity more effectively than sensitive varieties. This is related to the genetic ability to regulate the expression of redox enzymes and other detoxification mechanisms that help maintain cellular homeostasis under stressful conditions. Studies show that salt-tolerant genotypes have more stable and higher CAT, SOD, and APX activity compared to sensitive genotypes when exposed to NaCl, which also supports the maintenance of cell structure and metabolic function (e.g., in some tomato cultivars) (BMC Plant Biology, 2021).

3.3 Interactions Between Morphological and Physiological Responses

Salinity stress triggers a series of integrated responses in plants involving a close relationship between morphological changes and physiological responses. In general, salinity reduces plant growth through morphological inhibition such as a decrease in plant height, number of leaves, leaf area, and root and canopy biomass. The decline in these parameters is directly related to physiological disturbances such as decreased photosynthesis, stomatal conductance, and water use efficiency, indicating that morphological changes are not merely symptoms but also direct consequences of physiological dysfunction at the tissue and cellular levels (Liu, 2024; Pandit, 2024).

The interaction between morphological and physiological responses can be seen in root growth and water uptake. Roots that experience limited growth due to salinity will reduce the plant's ability to absorb water and nutrients from the soil. A decrease in soil water potential due to salt causes osmotic stress, so that roots try to grow deeper or increase the root:plant ratio to maintain water absorption. However, inhibited root growth will exacerbate water deficits, which then trigger physiological responses such as stomatal closure to reduce transpiration, thus revealing a complex reciprocal relationship between root morphology and water physiology regulation (dos Santos et al., 2022; Salinity inhibits plant growth, 2024).

Additionally, changes in leaf morphology such as reductions in leaf area and leaf area index (LAI) are strongly linked to physiological responses in photosynthesis. Reduced leaf area decreases the amount of photosynthetic surface available to capture light, thereby decreasing overall photosynthesis. This reduction in photosynthetic efficiency is often followed by decreases in chlorophyll content, stomatal conductance, and intercellular CO_2 levels. As a physiological response to salinity stress, plants may adjust chlorophyll metabolism and activate antioxidant mechanisms to counteract the accumulation of reactive oxygen species (ROS) that damage leaf tissue. These interactions indicate that changes in leaf morphology lead to physiological changes that impact plant productivity

Morphological–physiological interactions are also evident in the stomatal response to salinity. Stomata are morphological structures that regulate gas exchange and transpiration. Under salinity, stomatal closure as a physiological response reduces transpiration rates to conserve water, but also reduces photosynthesis rates due to reduced CO_2 uptake. Prolonged stomatal closure also affects leaf temperature and energy metabolism. These stomatal adjustments demonstrate a direct link between leaf structure and complex physiological responses to osmotic and ionic changes in plant tissues.

Hormonal factors are an important bridge between morphological and physiological responses under salinity. For example, salinity increases the production of abscisic acid (ABA), a hormone that suppresses growth and triggers physiological stomatal closure. ABA also influences cell expansion and root tissue differentiation, thereby modulating the shape and size of plant organs. These hormonal interactions coordinate morphological responses such as lateral root formation and physiological modulations such as stomatal adjustment and water management, enabling plant tissues to balance water conservation needs with growth (dos Santos et al., 2022).

Beyond direct responses to water and ion stress, salinity induces changes in secondary metabolites and antioxidants that exert dual effects on morphology and physiology. The accumulation of proline and other osmotic compounds under salt stress helps maintain cell turgor and tissue structural support, while also playing a role in reducing physiological damage such as oxidative stress. Thus, these biochemical metabolite changes have morphological impacts that lead to plants' ability to store more water and maintain vital tissues compared to plants experiencing stress but without effective osmotic accumulation.

4. CONCLUSION

Salinity stress significantly impacts plant growth and function through morphological and physiological changes. Morphologically, salinity causes a decrease in vegetative growth, leaf area, root development, and plant biomass. Physiologically, salinity stress inhibits photosynthesis, disrupts water and ion balance, and increases oxidative stress. Plants respond to these conditions through adaptive mechanisms such as osmoregulation, regulation of ion transport, and increased antioxidant activity. These morpho-physiological responses are interrelated and determine the plant's tolerance level to salinity.

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