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Salt Stress and its Implications in Vegetable Crops with Special Reference to the Cucurbitaceae Family

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Abstract: Salt stress is a significant abiotic factor that constrains agricultural productivity by impairing plant growth, particularly in arid and semi-arid regions. Vegetables, ranging from sensitive to moderately tolerant to salinity, experience adverse effects such as disruptions in seed germination, growth, flowering, and fruit development. Salinity hampers water uptake from the soil, as higher salt concentrations in the root zone increase the energy required by plants to absorb water. Sodium salts, in particular, interfere with the uptake of essential nutrients like nitrogen, phosphorus, and potassium, leading to nutritional imbalances. Furthermore, salinity induces oxidative and osmotic stress, ion toxicity, and hormonal disturbances, while also heightening plants' susceptibility to diseases. Crops in the Cucurbitaceae family, such as *Cucumis sativus* (cucumber) and *Citrullus lanatus* (watermelon), are known to exhibit diverse physiological and biochemical strategies to cope with salinity, including efficient ion transport regulation, osmolyte production, and antioxidant activity. Crops in the Cucurbitaceae family, such as *Cucumis sativus* (cucumber) and *Citrullus lanatus* (watermelon), exhibit diverse physiological strategies to cope with salinity. These traits are critical due to their economic significance in global agriculture. Understanding these mechanisms is crucial due to the economic significance of this family in global agriculture. This review examines the effects of salt stress on plant growth and development, explores tolerance mechanisms, and highlights the potential of crops from the Cucurbitaceae family to contribute to sustainable agricultural practices.

Key words: Salt stress, salinity tolerance, abiotic stress.

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Plants encounter numerous biotic and abiotic stressors at different stages of their life cycle (Liang *et al*., 2018). Soil salinity primarily arises from the buildup of soluble salts due to various natural and anthropogenic factors. This problem is particularly prevalent in arid and semi-arid regions with poor drainage and low-quality irrigation water (Kiremit *et al*., 2017). Globally, this issue impacts over 800 mha of land,

which constitutes nearly 6% of the Earth's total land surface (Yang and Guo, 2018a and 2018b). Soil salinity is assessed by evaluating the electrical conductivity of the soil solution. Currently, soils with an electrical conductivity of 4 dS m^{-1} (approximately 40 mM) or higher are classified as „saline soils (Acosta-Motos *et al*., 2017). The rising salt concentration in soils inhibits the uptake of water and essential nutrients by plants, progressively reducing their ability to adapt and resulting in increased salt stress over time (Isayenkov, 2012). Salt stress is a multifaceted abiotic factor that adversely impacts plant metabolism across nearly all growth and development phases, such as germination, seedling growth, vegetative, and maturity stages. It affects plants at the cellular, organ, and whole-plant levels by inducing osmotic stress in the short term, limiting water availability, and ionic stress in the long term, leading to toxic ion accumulation (Muchate *et al*., 2016). High salinity indirectly impacts plants by triggering oxidative stress, which arises from the combined effects of ionic and osmotic stress (Liang *et al*., 2018). Osmotic stress, an early response to salt stress, manifests within a few hours or days after salt exposure. It leads to reduced water and nutrient absorption, impaired root growth, hindered cell elongation, slower leaf development, and a decline in the formation of new leaves (Carillo *et al*., 2011). High salt concentrations impair the selectivity of cell membranes in plant roots, restricting the absorption of water and nutrients from the soil and leading to nutrient imbalances. This condition results in dehydration and turgor loss in plant leaves, causing yellowing, and eventually leading to the death of leaf cells and tissues (Isayenkov, 2012). This process holds significant importance, as stomatal closure reduces carbon assimilation and diminishes photosynthetic electron transport efficiency. The decline in carbon assimilation due to salinity stress often leads to long-term consequences, including inhibited photosynthesis and enzyme activity. These effects primarily result from sodium (Na^+) and chloride (Cl^-) toxicity, which occurs when these ions accumulate in plant tissues under high salt conditions (Muchate *et al*., 2016). In response to salt stress, plants activate various biochemical and molecular level adaptive mechanisms to mitigate or eliminate its harmful effects. These adaptations enable them to build tolerance to salt stress and sustain their vital functions (Acosta-Motos *et al*., 2017). Salt tolerance is defined as the ability of plants to thrive and complete their life cycles in conditions with elevated concentrations of soluble salts (Parida and Das, 2005). Salt tolerance represents a plant's ability to withstand salt stress, varying significantly across species, their native habitats, and the surrounding environmental conditions (Gürel and Avcıoğlu, 2001). When exposed to salt stress, plants initiate specific biochemical and molecular responses (Parida and Das, 2005). Plants growing in saline soils encounter two major challenges: (i) reduced soil water potential due to increased osmotic pressure from elevated salt levels in the soil solution, and (ii) the accumulation and imbalance of harmful ions like Na^+ and Cl^-. The simultaneous presence of these ions leads to Na^+ and Cl^- toxicity while causing deficiencies in essential nutrients such as K and Ca (Greenway and Munns, 1980). As highlighted earlier, research has demonstrated significant variation in salt tolerance among plant species and even among genotypes within the same species. Efforts to develop salt-tolerant plants are ongoing both in Türkiye and globally.

The accumulation of soluble salts, driven by both natural processes and human activities, is the primary cause of soil salinity. This issue is especially severe in arid and semi-arid regions where inadequate drainage and the use of saline irrigation water are common (Qadir *et al*., 2014). Inefficient irrigation systems, poor drainage, and reliance on water with high salinity levels accelerate the gradual salinization of fertile lands. Yield reductions due to salinity are especially pronounced in essential crops like wheat, rice, and maize, where production may drop by as much as 50% or more under moderate to high saline conditions (Munns *et al*., 2002).

Some studies focus on selecting individuals from existing populations, while others emphasize molecular research aimed at identifying genes responsible for salt tolerance mechanisms and transferring them to target plants (Koç, 2011). The impact of salt stress on plants varies depending on factors such as plant species, the source and intensity of salinity, and the duration of exposure. Plants in saline environments exhibit differing responses based on their genetic characteristics, leading

to significant variation in salt tolerance both within a single genotype and among different genotypes of the same species (Wang *et al*., 2023; Munns *et al*., 2002).

The Cucurbitaceae family, encompassing species like cucumbers, melons, and squashes, has been integral to human diets since ancient times, with many of its edible fruit-bearing members among the earliest domesticated crops globally. This family is distinguished by a significant number of species cultivated for human consumption (Schaefer *et al*., 2022). Cucurbitaceae species have moderate salt tolerance due to their ability to accumulate ions in vacuoles and are therefore suitable for cultivation in moderate saline areas. However, excessive NaCl levels can seriously affect their growth and fruit production (Kumar *et al*., 2023). Some crops in this family, such as melons (*Cucumis melo*), exhibit greater salinity tolerance owing to their effective stress-resistance mechanisms, making them viable for cultivation in saline soils. Salt-tolerant cucurbits require genome-wide studies to enhance the genetic adaptability of other cucurbit species. Recent research has highlighted the crucial role of the multidrug and toxic compound extrusion (MATE) gene family in improving salt tolerance (Ali, 2021).

Impact of salt stress on plant growth and development

salt stress hampers plant growth by limiting water absorption and disturbing ion homeostasis, resulting in osmotic and ionic stress. This stress can trigger physiological drought, reducing germination rates and stunting root and shoot development (Munns *et al*., 2008). In leaves, excess salt causes chlorosis and necrosis, disrupting photosynthetic processes and reducing the efficiency of carbon assimilation due to stomatal closure (Zhao *et al*., 2020). The accumulation of reactive oxygen species (ROS) further exacerbates cellular damage, leading to reduced biomass and plant productivity (Ahmad *et al*., 2019). Addressing these challenges requires exploring salt tolerance mechanisms to develop resilient crop varieties.

***Osmotic Stress and Plant-Water Relationships*:** Excessive accumulation of Na^+ and Cl^- ions decreases the water potential of the soil solution, limiting the plant's ability to absorb water. This condition also disrupts root membrane permeability by inducing hyperosmotic stress in plants. This condition reduces the osmotic potential of the plant, leading to a decline in the water available for plant cells, as well as a decrease in leaf water potential and turgor. Consequently, cell division is adversely affected, resulting in a reduced plant growth rate. The osmotic potential and water potential of the plant show an inverse correlation with salt stress, and a decrease in both potentials is observed with increasing salinity. Under salt stress, leaf water potential, osmotic potential, turgor pressure and transpiration rate decrease in plants. Osmotic stress caused by salinity also causes plant stomata to close, preventing CO_2 diffusion, which disrupts the photosynthesis mechanism and causes an increase in ROS (Munns *et al*., 2002; Shahzad *et al*., 2019).

***Ion Toxicity and Nutrient Imbalance*:** Salt stress disrupts cellular ion balance, also known as ion homeostasis, negatively impacting crucial biological processes such as photosynthesis, cell division, and growth, ultimately hindering plant development (Hao *et al*., 2021). Excessive amounts of soluble salts like Na^+ and Cl^- are absorbed by plants, accumulating in tissues and organs, and causing "specific ion toxicity" (Shahzad *et al*., 2019). This ion accumulation leads to various issues in plant tissues, with shoots, particularly leaves, being more sensitive to sodium than roots. Elevated Na^+ and Cl^- concentrations are commonly observed in these regions. These ions are transported from roots to shoots primarily through the xylem and the transpiration stream. Over time, increased Na^+ levels in leaves and shoots result in osmotic and metabolic disturbances, which become more severe in aging leaves, potentially leading to necrosis and cell or tissue death (Tester and Davenport, 2003; Munns, 2005). Cl^- toxicity in leaves initially manifests as chlorotic discoloration, which may progress to necrotic lesions. With further accumulation, leaves turn pale, and high cytosolic Cl^- levels disrupt chloroplast homeostasis, inhibiting photosynthesis and triggering the production of toxic radicals. Reactive oxygen species (ROS) generated under these conditions can oxidize vital components such as chlorophyll and other pigments, causing depigmentation and the development of chlorotic or necrotic lesions

(Geilfus, 2018). Accumulated salt ions like Na^+ and Cl^- compete with essential nutrients such as K, Ca, N, P and Mg, limiting their uptake and leading to nutrient deficiencies or imbalances in plants (Muchate *et al*., 2016; Parihar *et al*., 2015). For instance, while the cytosolic Na^+ concentration should ideally remain around 10 mM, the optimal K^+ level is 100 - 200 mM. Excessive Na^+ hampers K^+ uptake and transport, disrupting enzymatic activities critical to cellular metabolism. Na^+ toxicity in plants under salt stress impedes the acquisition of K^+, a nutrient vital for maintaining cell turgor, membrane potential, and enzymatic functions, leading to K^+ deficiencies and metabolic disruptions. Excess cytosolic Na^+ also competes with K^+ for cellular binding sites, inhibiting over 50 enzyme activities. A high cytosolic K^+/Na^+ ratio is considered a marker of a plant's salinity resistance (Kader and Lindberg, 2010; Park *et al*., 2016; Wu, 2018). Calcium, another essential nutrient, plays a pivotal role in plant growth, membrane stability, osmotic balance, and intracellular signaling. It acts as a secondary messenger in stress responses, including salinity (Kader and Lindberg, 2010; Park *et al*., 2016). High Na^+ concentrations in the root zone inhibit Ca^{2+} uptake and transport, resulting in lower Ca^{2+}/Na^+ ratios, which negatively affect plant growth and cause morphological and anatomical alterations. Furthermore, excessive cytosolic Na^+ disrupts membrane integrity by replacing Ca^{2+} ions in the membrane (Hadi and Karimi, 2012).

Calcium enhances salinity resistance through two mechanisms (i) it serves as a signaling molecule in adaptive responses to salt stress, and (ii) when present at higher concentrations it alters plasma membrane permeability or cell wall properties, reducing Na^+ entry via passive flow and directly inhibiting Na^+ accumulation. Supplementary calcium can also promote plant growth by mitigating Na^+ uptake in salt-stressed plants (Hadi and Karimi, 2012; Yokoi *et al*., 2002). Salinity influences the concentrations of various micronutrients required by plants, with effects varying depending on plant species, salinity levels, and specific plant organs (Parihar *et al*., 2015). Severity of salt stress factors on plants is presented in Figure 1.

***Germination and Growth*:** Plants exhibit heightened sensitivity to salt stress, particularly during germination and early seedling stages, which are critical for establishing healthy growth. Salinity reduces germination percentage, delays germination, and hinders root and shoot elongation, primarily due to osmotic stress and the toxic effects of specific ions (Ibrahim, 2016). Research on various plant species has shown that salt stress delays or inhibits seed germination, resulting in a marked decline in germination rates (Bybordi and Tabatabaei, 2009; Wu *et al*., 2015; Ahmed *et al*., 2017). Additionally, salt stress significantly impacts plant growth and productivity (Parida and Das, 2005). The inhibition of plant growth under salinity occurs for two main reasons. Firstly, the accumulation of salt in the soil solution creates an osmotic effect, limiting the plant's water uptake and reducing its growth rate. Secondly, the ion toxicity associated with high salt concentrations causes excessive salt ions absorbed by the roots to be transported to the shoots via the transpiration stream, where they accumulate in the leaves, further impairing plant growth. This causes damage to leaf cells and further reduces plant growth (Parihar *et al*., 2015; Munns and Tester, 2008).

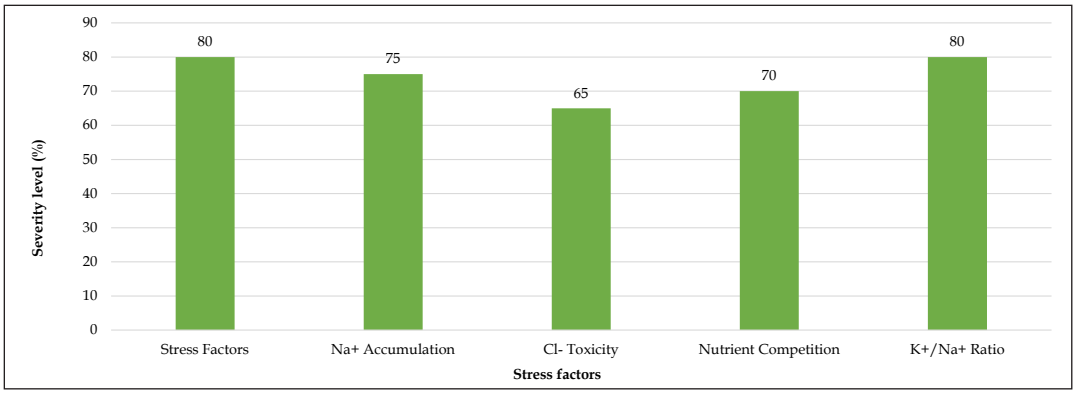


Fig. 1. Severity of salt stress factors on plants.

Salt stress also affects the fresh and dry weights of various organs in plants, causing a decrease in biomass accumulation in plants and slowing down growth. Salt stress has negative effects on plants by reducing growth parameters such as plant height, leaf area and biomass accumulation (Saleh, 2012).

***Photosynthesis, Chloroplast and Photosynthetic Pigments*:** Plant chloroplasts are among the most vulnerable organelles under salt stress, with structural changes often leading to a reduction in photosynthetic efficiency (Hameed *et al*., 2021). Salt stress adversely impacts essential components such as photosynthetic pigments, thylakoid membrane proteins, membrane lipids, and various photosynthesis-related enzymes (Hao *et al*., 2021). High salt levels in plants typically reduce the quantity of photosynthetic pigments like chlorophyll and carotenoids (Zahedi *et al*., 2021). Photosystems I (PSI) and II (PSII) in chloroplast thylakoids are major sites of reactive oxygen species (ROS) production. Salinity severely damages these structures. Elevated salt concentrations disrupt electron transport within the thylakoid membranes, producing ROS such as hydroxyl radicals (OH) and hydrogen peroxide (H_2O_2), which cause thylakoid swelling (Bejaoui *et al*., 2016; Miyake *et al*., 2006).

Osmotic imbalances between the stroma and cytoplasm, along with structural disruptions in chloroplast outer membranes, swelling of thylakoid membranes and grana lamellae in mesophyll tissues, and the disintegration of grana and thylakoids under high salinity conditions, are notable effects of salt stress (Bejaoui *et al*., 2016). The decline in photosynthesis in salt-stressed plants is mainly attributed to reduced water potential and restricted CO_2 diffusion, which results from stomatal closure and decreased mesophyll conductance (Flexas *et al*., 2006). Factors such as the accumulation of ROS (especially H_2O_2), a sudden increase in abscisic acid (ABA) synthesis, and reduced K^+ levels due to elevated Na^+ and Cl^- concentrations in shoots trigger stomatal closure (Hedrich and Shabala, 2018). This stomatal response limits the diffusion of external CO_2 into chloroplasts, reducing intercellular CO_2 levels and subsequently lowering the photosynthesis rate (Hao *et al*., 2021).

While reduced stomatal conductance minimizes CO_2 availability to chloroplasts, it is also an adaptive response to osmotic stress, reducing transpiration and helping the plant retain water (Munns and Tester, 2008; Chaves *et al*., 2009). Salt stress may further impair photosynthesis by altering the activity of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase), the enzyme responsible for CO_2 fixation. In addition to stomatal limitations, non-stomatal factors, such as enzyme activity changes in photosynthesis, also restrict CO_2 utilization and reduce photosynthetic efficiency (Karimi *et al*., 2015). Moreover, secondary oxidative stress induced by salt stress can disrupt photosynthetic metabolism, leading to a decline in net photosynthesis (Flexas *et al*., 2006; Haves *et al*., 2009). Distrubution of salt stress impacts on photosynthesis is shown in Figure 2.

***Effect On Oxidative Stress, Membrane Damage and Antioxidants*:** Salt stress induces the production of highly reactive oxygen species (ROS), which interfere with normal plant metabolism by oxidizing substrates. This overproduction of ROS creates oxidative stress by disrupting the balance between antioxidant defense systems (Shahzad *et al*., 2019). To counteract the effects of ROS generated under salt stress, plants activate antioxidant defense mechanisms that detoxify these reactive species through antioxidant production (Ahmad *et al*., 2019). While low levels of ROS are natural byproducts of cellular metabolism and play roles as signaling molecules in various biological processes, including growth, development, and stress responses, their levels must be tightly regulated (Zhao *et al*., 2020; Hossain and Dietz, 2016). Under normal

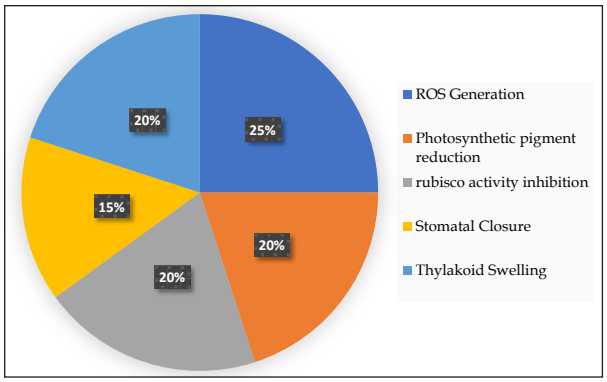


Fig. 2. Mechanism of distrubution of photosynthesis by salt stress.

conditions, ROS production and removal are balanced through antioxidant defense systems, maintaining cellular redox homeostasis (Pang and Wang, 2008; Hasanuzzaman *et al.*, 2021). This balance, achieved by harmonizing ROS generation during redox reactions with their detoxification by antioxidants, is crucial for plant adaptation to stress (Zhao *et al.*, 2020). However, stress factors like salinity disrupt this equilibrium, leading to excess ROS production, oxidative stress, and molecular and cellular damage, ultimately causing cell death (Pang and Wang, 2008; (Hasanuzzaman *et al.*, 2021).

ROS, consisting of oxygen radicals and derivatives such as O_2^-, H_2O_2, OH^-, and $^1O_2$ are primarily generated in chloroplasts, mitochondria, apoplasts, peroxisomes, and plasma membranes, with chloroplasts being the main production site (Hasanuzzaman *et al.*, 2021). In light-exposed green tissues, chloroplasts and peroxisomes are major sources of ROS, particularly O_2^- and $^1O_2$, which are produced at the reaction centers of PSI and PSII in the chloroplast thylakoids (Pang and Wang, 2008; Møller *et al.*, 2007). Reduced photosynthetic rates further amplify ROS production. In the absence of light or in non-green tissues, mitochondria serve as the primary ROS production sites, where O_2^- is generated in complexes I and III as a metabolic byproduct (Choudhury *et al.*, 2017). Peroxisomes, through metabolic reactions, produce O_2^- and H_2O_2, while plasma membrane NADPH oxidases also contribute to ROS generation in the apoplast by producing O_2^- (Pang and Wang, 2008; Møller *et al.*, 2007).

Each ROS type has unique reactivity and half-life. For instance, H_2O_2 is relatively stable and has a longer half-life compared to other ROS. O_2^- reacts primarily with Fe-S protein centers, leading to protein denaturation (Hasanuzzaman *et al.*, 2021; Gill and Tuteja, 2010). O_2^- formed through the Mehler reaction can be converted into H_2O_2 by superoxide dismutase (SOD), and H_2O_2 may further react with Fe^{2+} via the Fenton reaction to produce highly toxic OH^- radicals, which damage cellular components (Ahanger *et al.*, 2017). The destructive effects of ROS include lipid peroxidation in membranes, nucleic acid damage, protein denaturation, carbohydrate oxidation, pigment destruction, enzyme inhibition, and activation of programmed cell death (Zhao *et al.*, 2020; Tuteja, 2007). Among these, OH^- is the most reactive, causing severe damage by oxidizing carbohydrates, lipids, proteins, and DNA, often leading to cell death when excessively accumulated (Huang *et al.*, 2019; Bhattacharjee, 2019).

The overproduction of ROS under salt stress disrupts the plant's antioxidant defense system. However, plants respond by enhancing antioxidant production to detoxify ROS, thereby restoring redox homeostasis (Hasanuzzaman *et al.*, 2021; Paciolla *et al.*, 2016). Key members of the antioxidant defense system include enzymatic antioxidants such as SOD, CAT, POX/POD, GPX, GR, GST, APX, MDHAR, and DHAR, as well as non-enzymatic antioxidants like ascorbic acid (AA), glutathione (GSH), phenolic compounds, alkaloids, carotenoids, flavonoids, α-tocopherols, proline, and free amino acids (Gill and Tuteja, 2010; Ahanger *et al.*, 2017). Impact of salt stress and antioxidant response in plants is presented in Figure 3. Research indicates that salinity stress frequently alters the activities of these antioxidant enzymes.

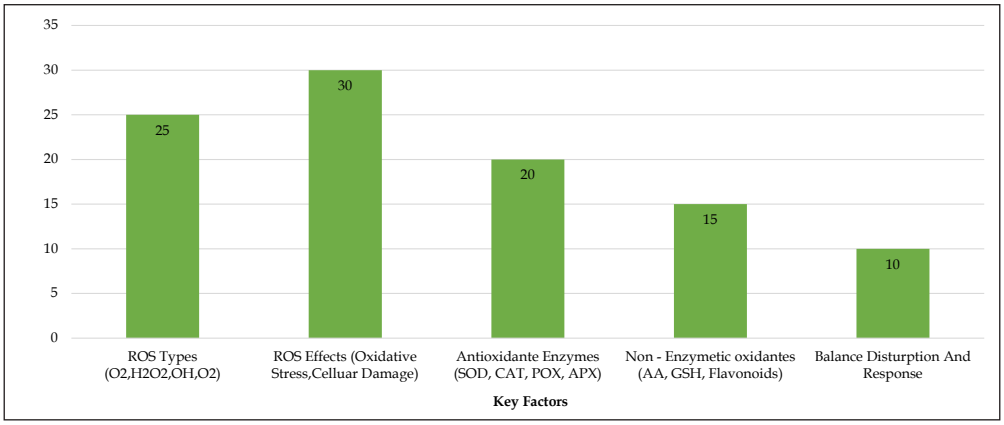


Fig. 3. Impact of salt stress and antioxidant response in plants.

Effect of Salt Stress on Cucurbits

The Cucurbitaceae family originates from Africa and America. Globally, it is cultivated over 1.5 million hectares, yielding approximately 20 mt annually, while in Türkiye, it is grown on 21 thousand hectares with an annual production of 350 thousand tons, contributing significantly to agricultural economic development (Shannon and Francois, 1978). Pumpkin species within this family are primarily grown for their fruits, but in some countries, including Türkiye, they are also cultivated for their seeds (John *et al*., 2023). Cucurbit seeds are rich in vitamins A and E and are a source of unsaturated fats, making them valuable for oil production in many countries. Additionally, these seeds are commonly consumed as snacks (Shannon and Francois, 1978).

Proline plays a crucial role when addressing salt stress in cucurbits. As an important osmoregulator, proline helps maintain protein stability and activate enzymes in plants experiencing salt stress (Shannon and Francois, 1978). Stress conditions lead to an increase in internal proline levels, and external proline applications have been shown to enhance salt stress tolerance (John *et al*., 2023). In cucurbit plants, the application of external proline significantly improves salt tolerance, partly by stimulating the antioxidative enzyme system (Shannon and Francois, 1978). For instance, *Cucumis sativus* (cucumber) has demonstrated increased proline accumulation under salt stress, which correlates with enhanced photosynthetic efficiency and membrane stability (Kumar *et al*., 2019). Salt stress in cucurbits leads to a significant reduction in the fresh weight of aerial parts, with initial symptoms such as leaf chlorosis and necrosis, followed by the abscission of older leaves, ultimately resulting in stunted growth and potential plant mortality (Shannon and Francois, 1978). In *Citrullus lanatus* (watermelon), studies have shown that salt stress disrupts ion homeostasis, leading to Na toxicity and K deficiency, which adversely affects root growth and water uptake (Zhao *et al*., 2020). Furthermore, *Lagenaria siceraria* (bottle gourd), often used as a rootstock for cucurbits, exhibits better salt tolerance due to its ability to compartmentalize Na^+ into vacuoles, reducing their toxicity in the cytoplasm (Yousfi *et al*., 2020). Salt stress also impacts fruit quality in cucurbits. In *Cucumis melo* (melon), salinity reduces fruit size and sugar content while increasing fruit firmness due to osmotic adjustments and changes in carbohydrate metabolism (El-Beltagi *et al*., 2021). Understanding these effects and tolerance mechanisms is critical for developing salt-resistant varieties and sustainable agricultural practices in salinity-affected areas.

Salt Tolerance Mechanisms

Plants employ numerous physiological and biochemical strategies to cope with environmental stresses (Pastori and Foyer, 2002). When stress signals reach plant cells, they activate secondary signaling pathways, leading to a rapid increase in intracellular Ca^{2+} levels. This surge can initiate phosphorylation cascades, influencing defense-related proteins or transcription factors. These transcription factors then regulate stress-responsive genes, enabling plants to adapt to adverse conditions gradually. Under salt stress, responses such as stomatal closure, osmolyte accumulation, and enhanced Na^+/H^+ antiporter activity are commonly observed.

Efforts to enhance salt tolerance in crops using traditional breeding methods have met with limited success, as salt tolerance is governed by complex genetic and physiological factors (Flowers, 2004). While plants have evolved intricate mechanisms to mitigate salt damage, halophytes plants that naturally thrive in saline conditions offer a unique perspective. In contrast to glycophytes, which are salt-sensitive and struggle in saline environments, halophytes exhibit specialized traits that allow them to complete their life cycle under high salinity. These traits include efficient salt exclusion, osmotic balance, and the accumulation of compatible solutes. Investigating these adaptations provides critical insights into improving crop salt tolerance, addressing the significant threat that salinity poses to global agriculture.

***Halophytes and Glycophytes*:** The primary distinction between halophytes and glycophytes lies in their response to salinity. Halophytes are salt-tolerant plants capable of thriving in high-salinity soils or water, while glycophytes are salt-sensitive plants unable to grow in such conditions. Salt-tolerant species, including halophytes such as *Salicornia halimus* (glasswort), *Atriplex halimus* (saltbush), *Sueda*

maritima, and *Tamarix* species (salt cedar), are able to grow and complete their life cycle under salt stress. In contrast, glycophytes lack this capacity and are unable to survive in saline environments (Urao *et al*., 1999). Understanding the mechanisms of salt tolerance in halophytes provides valuable knowledge for enhancing crop resilience. Traits such as osmotic adjustment, ion compartmentalization, and antioxidative responses can be utilized in breeding programs or genetic engineering efforts to improve the salt tolerance of crop plants exposed to saline conditions.

***On Homeostasis and Compartmentalization*:** Salt ions enter plants primarily through passive transport mechanisms, including non-selective cation channels (NSCCs) such as cyclic nucleotide-gated ion channels (CNGCs) and glutamate-like receptor proteins (GLRs), as well as high-affinity K^+ transporters (HKTs) (Shah *et al*., 2021). These ions interfere with the uptake of vital nutrients like K^+ in root cells, and excessive Na^+ accumulation in the cytosol exerts toxic effects on enzymes. Both halophytes and glycophytes struggle with high cytosolic salt levels (Gupta and Huang, 2014). Halophytes mitigate the ion toxicity caused by excessive Na^+ by compartmentalizing the ions into vacuoles. In contrast, glycophytes minimize ion absorption and redirect the absorbed salt ions to older tissues, protecting younger tissues from damage. To maintain growth and prevent cell death, plants either sequester excess salt ions into vacuoles or store them in older tissues, thus maintaining cellular ion homeostasis and balance (Gupta and Huang, 2014).

A key aspect of maintaining this balance is achieving an appropriate K^+/Na^+ ratio in the cytoplasm. By reducing cytosolic Na^+ and increasing K^+ levels, plants prevent cellular damage and nutrient deficiencies, ensuring proper growth (Yamaguchi and Blumwald 2005). The Salt Overly Sensitive (SOS) signaling pathway is integral to ion homeostasis and salt tolerance in plants. The SOS pathway, comprising key proteins such as SOS1, SOS2, and SOS3, protects plant cells from the detrimental effects of excessive ion accumulation (Park *et al*., 2016). Loss of function in SOS-related genes results in heightened sensitivity to NaCl, indicating that the expression levels of these genes are crucial. Enhanced expression of SOS genes is directly associated with improved NaCl tolerance (Ji *et al*., 2013; Zhang and Shi, 2013).

***Biosynthesis of Osmolytes and Osmotic Adjustment*:** Plants exposed to high salinity make the necessary osmotic adjustments by synthesizing compounds with osmotic protective functions such as proline, soluble sugars, glycine betaine, etc., in response to the osmotic stress induced by salt stress (Liang *et al*., 2018). Stabilization of cell turgor pressure and these osmotic adjustments, which are of critical importance in maintaining plant growth and development, require the synthesis of compatible components in plants, called osmolytes or osmo-protectants (Liang *et al*., 2018; Zulfiqar *et al*., 2020). Osmolytes include nitrogen-containing compounds (proline, glycine betaine), soluble proteins (LEA proteins and dehydrins), polyols (mannitol, sorbitol, D-ononitol, D pinitol, Myoinositol), soluble sugars (trehalose, glucose, sucrose/sucrose, fructose) and organic acids (oxalate, malate) (Ashraf, 2004; Pirasteh-Anosheh *et al*., 2016). Among these osmolytes, proline, glycine betaine and mannitol are quite common in plants (Saxena *et al*., 2013). These low molecular weight organic compounds, which do not harm cell metabolism and do not cause toxic effects at high concentrations, try to maintain the necessary osmotic balance at the cellular level by protecting plant cells against dehydration (Singh *et al*., 2015).

***Changes in Signal Transmission and Gene Expression Level During Salt Stress*:** To mitigate or eliminate the adverse effects of salt stress, plants have evolved various tolerance strategies, facilitated by signal transduction pathways activated during stress and the expression of stress-responsive genes (Huang *et al*., 2012). Signal transmission, which begins with the perception of stress by proteins and receptors in the plasma membrane of plant stem cells, continues through the transduction pathway that enables the activation of secondary messengers such as calcium, ROS, inositol phosphate, and this results in the change of Ca^{+2} levels in the extracellular tonoplast and intracellular cytosol (Sathee *et al*., 2015). Increased cytosolic Ca^{+2} level is triggered by calcium sensor proteins such as CaM (calmodulin), CML (calmodulin-like protein), CDPK (calcium-dependent protein kinase), CBL/CIPK (calcineurin-B-like protein/

calcineurin-B-like protein interacting protein kinase). It is detected and signal transmission spreads through the protein phosphorylation mechanism in the cell. In this way, a response to stress is created by increasing the expression of stress response genes responsible for the protection of the cell and by ensuring the phosphorylation of transcription factors that control these genes (Kaleem *et al*., 2018; Lan *et al*., 2017; Nikalje *et al*., 2017).

Salt stress signal transduction in plants involves a complex network of pathways, with the SOS pathway playing a central role. This pathway, comprising SOS3, SCaBP8, SOS2, and SOS1, is crucial for interpreting calcium signals induced by salt stress and maintaining ionic balance in plant cells. Proteins such as 14-3-3, GIGANTEA (GI), ABI2, and BIN2 negatively regulate SOS2 by directly interacting with it and suppressing its kinase activity. Under normal conditions, PKS5-mediated phosphorylation enhances the binding of SOS2 to 14-3-3, keeping its activity at basal levels. SCaBP8 suppresses the activity of Arabidopsis K^+ TRANSPORTER 1 (AKT1). Additionally, GIPCs are proposed to act as cation sensors, binding Na^+ to trigger calcium influx and activate the SOS pathway. AtANN4, a calcium-permeable transporter, may also facilitate calcium influx, initiating the SOS response during salt stress. OSCA1 functions as an osmosensor, producing osmotic calcium signals under osmotic stress.

Regulation of AtANN4 by the SOS pathway fine-tunes the timing and intensity of salt-induced calcium influx for long-term stress adaptation. Phosphatidylinositol (PI) binds to the C-terminal region of the plasma membrane H^+-ATPase AHA2, suppressing its activity under normal conditions. During salt stress, PI is converted into phosphatidylinositol 4-phosphate (PI4P), which releases the inhibition and activates AHA2. PI4P also activates the Na^+/H^+ antiporter SOS1. PIP3 and RLK7 accumulate under salt stress, and their interaction activates RLK7, triggering MPK3/6 to relay stress signals. MAP kinase cascades regulate salt stress signaling, while RAFs phosphorylate and activate SnRK2s in response to osmotic stress. SnRK2 activity is amplified through auto-phosphorylation.

In the nucleus, transcription factors downstream of MPKs and SnRK2s bind to promoters of salt-responsive genes, enhancing their expression. In the vacuole, proteins such as NHXs, CAX1, the Ca^{2+}/H^+ antiporter, and vacuolar H^+-ATPase (VHA) help exclude Na^+ from the cell. Dashed lines represent regulatory interactions under normal conditions.

Conclusion

Salinity, which poses a growing challenge to global agricultural productivity, especially in arid and semi-arid regions, continues to intensify. This increasing salinity makes it progressively harder for plants to adapt and survive, posing a serious threat to their growth. Predictions indicate that rising salinity in cultivable lands could lead to the loss of nearly 50% of agricultural areas in the near future. While natural factors like volcanic eruptions, rainfall, and rock erosion contribute to soil salinization, human activities such as deforestation, overgrazing, accumulation of salts from water and air, and chemical pollution also play significant roles. Furthermore, global warming and climate change exacerbate the issue by increasing soil water loss, thereby concentrating soil solutions and elevating salinity levels. Recent studies on Cucurbitaceae crops, such as *Cucumis melo* (melon) and *Citrullus lanatus* (watermelon), have shown that salinity tolerance can be improved by integrating halophyte-like traits, including enhanced ion compartmentalization and the upregulation of antioxidant enzymes.

Excessive Na and other salts accumulate in the soil, disrupting its structure, reducing porosity, and aggravating issues like poor aeration and low water conductivity. Elevated salinity in soils harms plant growth and development by inducing hyperionic and hyperosmotic stress. Additionally, persistent salt buildup creates a condition known as physiological drought, where plants struggle to absorb water from the soil. Osmotic stress caused by salinity and drought disrupts ionic balance and homeostasis in plant cells, adversely affecting their physiological, biochemical, and molecular processes. This leads to ionic imbalances, inefficient nutrient uptake, and reduced productivity due to disruptions in the redox state of cells and the excessive production of reactive oxygen species (ROS). Future research should focus on the discovery of genotypes with enhanced tolerance to salinity and assess

their adaptability in real-world agricultural settings. Moreover, combining conventional breeding methods with advanced molecular tools like CRISPR-Cas9 gene editing could significantly expedite the creation of cucurbit varieties that can withstand high salinity. Crops in the Cucurbitaceae family, such as cucumber, melon, watermelon, and pumpkin, display varying levels of adaptation to saline conditions. Melon species, for instance, can tolerate moderate salinity by isolating Na^+ within vacuoles, thereby minimizing cytoplasmic toxicity. Watermelon demonstrates resilience under salt stress by maintaining a favorable balance between K^+ and Na^+, which is essential for cellular processes and osmotic regulation. Additionally, bottle gourd, often used as a rootstock, helps cucurbits grow in saline soils by restricting sodium transport and promoting overall plant health. Cucumber, on the other hand, increases proline accumulation under salt stress, which strengthens cell membranes and reduces damage caused by reactive oxygen species. These physiological and biochemical mechanisms underline the potential of *Cucurbitaceae* crops for cultivation in regions affected by salinity.

Plant responses to salinity vary depending on genotype, adaptability, and other traits, reflecting differences in growth, development, and tolerance to saline conditions. These variations highlight the significance of salt tolerance mechanisms developed by plants and emphasize the need for advanced transgenic studies to enhance tolerance in salt-sensitive glycophytes. Halophytes, which thrive under extremely high salinity, serve as valuable models for gene discovery. By altering the expression of genes responsible for ion transporters, osmolytes, and antioxidant enzymes, as well as through transcriptional modifications, researchers aim to develop salinity-resistant transgenic plants. However, achieving salt tolerance in plants is a complex task due to variations in responses to different salt levels and durations across species, and even among genotypes within the same species.

Further research is essential to understand whether salt tolerance mechanisms are sufficient on their own and to explore their contributions and interactions. Addressing salinity stress requires comprehensive studies integrating ecological, physiological, and molecular insights. Advanced molecular methods, modern technologies, and omic techniques are critical for devising strategies to mitigate salinity issues. Ongoing research plays a crucial role in providing the necessary knowledge to develop salt-tolerant plant genotypes.

In conclusion, salt stress remains a significant obstacle for global agriculture, particularly for glycophytes that cannot thrive in saline environments. However, halophytes, with their specialized salt tolerance strategies, offer valuable insights for enhancing crop resilience. For instance, the Cucurbitaceae family, which includes important crops like cucumbers, melons, and squashes, demonstrates varying degrees of salt tolerance. By adopting halophyte-inspired adaptation strategies, the resilience of Cucurbitaceae crops against salinity can be improved. This approach presents a sustainable pathway to address the challenges posed by soil and water salinization, safeguarding food security in affected regions.

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