

Review

Salinity Stress in Maize: Consequences, Tolerance Mechanisms, and Management Strategies

Mohammad Sohedul Islam ^{1, *}, Md. Rafiqul Islam ², Md. Kamrul Hasan ¹, ASM Golam Hafeez ³, Md. Kaium Chowdhury ⁴, Moaz Hosen Pramanik ⁵, Muhammad Aamir Iqbal ⁶, Murat Erman ⁷, Celaledin Barutcular ⁸, Ömer Konuşkan ⁹, Anamika Dubey ¹⁰, Ashwani Kumar ¹⁰, Ayman El Sabagh ^{11, 12, *}

1. Department of Agronomy, Hajee Mohammad Danesh Science and Technology University, Dinajpur, Bangladesh; E-Mails: islam.agn@hstu.ac.bd; kbdkhasan@gmail.com
2. Agronomy Division, Regional Agricultural Research Station, Bangladesh Agricultural Research Institute, Ishwardi, Pabna, Bangladesh; E-Mail: rafiq_bari2@yahoo.com
3. Department of Agricultural Finance and Banking, Faculty of Agricultural Economics & Rural Sociology, Bangladesh Agricultural University, Mymensingh, Bangladesh; E-Mail: ghkennedy01@yahoo.com
4. Department of Agricultural Extension, Agricultural Training Institute, Gaibandha, Bangladesh; E-Mail: kaium34bcs@gmail.com
5. Department of Agricultural Chemistry, Hajee Mohammad Danesh Science and Technology University, Dinajpur, Bangladesh; E-Mail: moazhosen42@gmail.com
6. Department of Chemical Engineering, Louisiana Technical University, USA; E-Mail: aamir1801@yahoo.com
7. Department of Field Crops, Faculty of Agriculture, Bursa Uludağ University, Bursa, Turkey; E-Mail: Merman56@hotmail.com
8. Department of Field Crops, Faculty of Agriculture, Çukurova University, Adana, Turkey; E-Mail: cbarutcular@gmail.com
9. Department of Field Crops, Faculty of Agriculture, Mustafa Kemal University, Hatay, Turkey; E-Mail: okonuskan@mku.edu.tr
10. Metagenomics and Secretomics Research Laboratory, Department of Botany, Dr. Harisingh Gour Central University, Sagar, MP 470003, India; E-Mails: anamikadubey909@gmail.com; ashwaniitd@hotmail.com
11. Department of Field Crops, Faculty of Agriculture, Siirt University, Siirt, Turkey; E-Mail: ayman.elsabagh@agr.kfs.edu.eg
12. Department of Agronomy, Faculty of Agriculture, Kafrelsheikh University, Kafrelsheikh, Egypt



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* **Correspondences:** Mohammad Sohiful Islam and Ayman El Sabagh; E-Mails: islam.agn@hstu.ac.bd; ayman.elsabagh@agr.kfs.edu.eg

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Abstract

Maize, along with rice and wheat, is a popular staple food crop worldwide, and the most widely produced cereal crop. It is a versatile crop that may be utilized as a source of raw materials for human and animal fodders. Low agricultural yield and rapid population expansion significantly threaten future food security. Maize production is hampered by biotic and abiotic causes, with abiotic factors being the most critical limitation to agricultural output worldwide. Soil salinity is a key abiotic factor that reduces agricultural production by imposing negative impacts at several life cycle phases, including germination, seedling, vegetative, and reproductive development. Maize plants experience many physiological changes due to osmotic stress, toxicity of particular ions, and nutritional imbalance induced by salt stress. The degree and duration of stress, crop growth phases, genetic characteristics, and soil conditions influence yield reduction. Maize plants can tolerate salt stress involving a complex mechanism by changing their physiological, biochemical, and metabolic activities like stomatal functioning, photosynthesis, respiration, transpiration, hormone regulation, enzymes, metabolite generation, etc. After studying the salt tolerance mechanisms of maize plants under stress, integrated management techniques should be developed for maize agriculture in saline settings. Therefore, the study of plant responses to salt stress, stress tolerance mechanisms, and management strategies is one of the most imperative research fields in plant biology, and the study will focus on the effects of salt stress in different growth stages, plant tolerance mechanisms, and agronomic management practices for successful maize production all over the world.

Keywords

Salt stress; physiological changes; mitigation techniques; management practices; maize

1. Introduction

Globally, maize (*Zea mays* L.) ranks top position among cereals in terms of total cultivated area [1] as well as grain and fodder production [2]. Over 1147.7 million MT of maize is produced on 193.7 million hectares of land in 170 countries, with an average productivity of 5.75 t ha⁻¹ [3]. Over 50 maize varieties are cultivated worldwide, and they can be divided into five broad groups based on their food, feed, and production needs, like popcorn, sweet corn, flour corn, flint corn, and field

corn or dent corn [4]. Among them, dent corn accounts for around 99% of the corn grown in the United States, and is mainly used for livestock feed and industrial items. Due to its higher starch content than sweet corn, dent corn has a bland flavor and a mealy texture [4]. Maize is the highest-yielding cereal crop, and holds a prominent position as one of the major crops in most countries. It occupies 24% of the farmlands worldwide [5, 6]. It is one of the most important cereals in the world, with a wide range of commercial and economic uses [1, 2, 7]. Cereals, such as maize, account for 52% of global human nourishment [8], and maize-derived products have been used in various aspects of our daily life due to their high-value nutrients [9, 10].

Maize is a major cereal in Southern and Eastern Africa, Central America and Mexico, and is a staple in Sub-Saharan Africa [11], where maize accounts for nearly a quarter of total calorie consumption. Maize is a staple food for 1.2 billion people worldwide, accounting for more than 20% of total calories in 21 countries [12]. The use of maize as food is expected to increase mainly in developing countries (72%) where growing populations and maize are becoming increasingly crucial in diets. Hence, the rising demand for animal-based protein sources will likely drive the trade and the market for maize globally. Maize is also used to produce ethanol fuel (ethyl alcohol) in alcoholic beverages, and is most often used as a motor fuel, mainly as a biofuel additive for gasoline. From a global perspective, the USA has been the leading consumer, followed by China, accounting for about 32% and 23%, respectively. However, the highest per capita consumption is noticed in southern Africa, such as Lesotho (120 kg/year) and Malawi (107 kg/year) [10]. From 2018 to 2027, maize output and area are predicted to expand by 1.2 billion MT and 3.2 percent due to rising demand [11].

Global food insecurity has become one of the most significant concerns, and land degradation due to abiotic pressures (environmental stresses) is causing poorer agricultural output, exacerbating the problem [13]. Moreover, high population growth puts pressure on increasing productivity to ensure food security and meet future needs [8]. Land degradation occurs mainly due to abiotic factors like salinity, drought, and pollution. Soil salinity is severe abiotic stress to agriculture worldwide [13-15], with considerable economic consequences due to the loss of arable area and lower agricultural production. Therefore, increasing food production per unit of cultivated land area with more sustainable production systems is a great challenge, given the exponential population growth [16] and adverse environmental conditions due to changing climate [17]. This chapter will delve into the intricacies of how maize responds to salt stress, examining its underlying causes, the effects it has on the plant, its ability to tolerate such stress, and the adaptive mechanisms it employs.

2. Maize and Salt Stress Effects

2.1 Germination & Seedling Growth Stages

The ability of a seed to germinate in saline soil is critical for many plant species' survival, and better crop production on salt-affected soils depends on successful seed germination. Since the seed and the soil surface are close together, seeds are more susceptible to salt stress [18]. Germination and seedling growth traits are the most critical factors for selecting salinity tolerance species/cultivars. Because the effective establishment of healthy seedlings depends on seed germination, the germination stage is susceptible to salinity compared to other vegetative stages [19]. Germination rate had the most critical effect on the stand establishment and plant density. The main harmful effects of salinity are reduced germination and emergence, stand, and

establishment of seedlings [20, 21]. Salinity stress mainly reduces the seed germination and seedling growth characteristics. It delays the onset of germination, and environmental factors like temperature and light interact with the germination and seedling growth properties [22, 23]. It has been reported that high salt concentration in soils limits seed germination and root proliferation, and impedes plant water and nutrient uptake, further reducing plant vegetative growth [24, 25]. Soil salinity amasses the toxic ions in plants, which imbalances essential ions following interference with the normal physiological functions of the plant. Sodium (Na^+) and chloride (Cl^-) ions induce hyperosmotic stress and toxic effects on germinating seeds under a saline environment, which may delay or reduce the speed of seed germination [26, 27]. Excess salinity slows the seed germination, while lower salinity provokes seed dormancy [28]. Seeds, on the other hand, develop a method for maintaining reduced water potential and dealing with the restrictions of nutritional imbalance [29], or they evolve other particular tolerance mechanisms for avoiding salt stress damage [30].

Imbibition of water is the first stage of seed germination, and salinity interrupts seed germination by decreasing the soil's osmotic potential, inhibiting the imbibition of water by seeds [28]. Salinity creates ionic toxicity that alters the enzymatic activity needed for nucleic acid metabolism. Salinity stress reduces seed germination rate by changing the metabolism of protein [21, 31]. Ionic pressure due to NaCl accumulation to a toxic level in soil decreases the germination rate [32, 33]. Water absorption by the seed is reduced because of lower water potential caused by salt stress, thus posing toxic effects on the developing embryo and delaying the germination process [34]. The reduction of seed germination due to salinity stress was noted by lowering the osmotic potential of the germinating media, increasing Na^+ and Cl^- toxicity to the embryo, or modifying protein synthesis. For example, salinity delays germination in maize [21, 33] and other crops such as soybean [27] and black gram [35]. Priming seeds with NaCl significantly improved germination and early seedling growth of maize under saline conditions [36]. However, the seed's mean germination time (MGT) depends on the strengths of salinity stresses and species/genotypes. The germination rate consistently decreases with increasing the trend of salinity stress [21, 37]. The imposition of salt stress reduced the germination index of maize cultivars [38, 39]. Salinity had a very distinct negative effect on germination, vigor index, seedling growth, and water uptake in maize [40]. A high value of germination index is recorded in small-sized seeds compared to large-sized seeds under saline conditions. Salinity stress reduced the germination percentage, index, germination speed, MGT, and seedling growth of maize genotypes [41]. Salinity stress reduced *Zea mays*' germination rate, plumule length, shoot length, root length, and seed vigor by 32, 78, 78, 80, and 95%, respectively [42].

2.2 Vegetative Stage

Maize vegetative development was greatly hampered by salinity. Soil salinity inhibited leaf initiation, expansion, and internode growth, reducing maize plant growth and enhancing leaf abscission [43, 44]. The reduction of growth caused by salinity is predominantly responsible for acidification in the apoplast and enzyme activity. Salt stress diminished cell division, the number of elongating cells, and cell elongation rate, resulting in rapidly reduced leaf growth and plant growth of maize. It has been reported in many studies that salt stress primarily reduces the shoot growth of maize [45-48]. Salinity remarkably reduces the leaf and stem biomass [49, 50], leaf area, shoot, and root dry weights of maize [51]. The activities of various enzymes that take part in nitrogen

metabolism in plants are reduced by salt stress; hence, plant nitrogen status is reduced in cereal crops [52].

The shoots of maize are more responsive to salt stress than roots [53]. Salinity reduces the shoot growth by suppressing the initiation and expansion of leaves, and retards the internodes growth resulting from the reduction of the shoot growth [54]. Salt stress causes membrane leakage as a primary cellular response through displacing Ca^{2+} from the binding sites of the plasma membrane [55]. The integration of the plasma membrane and cell wall acidification process, which is partially dependent on adenosine triphosphate-driven outward pumping of protons across the intact plasma membrane in maize, is seriously affected by salinity stress [56]. The growth extension mainly depends on the apoplast's acidification, resulting in the enlargement of cells [57].

Chlorophyll is a raw material of photosynthesis, and salinity stress inflicted maize plants results in a notable reduction in leaf chlorophyll content [58-64] and carotenoid content [65, 66]. Salinity decreased maize seedlings' chlorophyll fluorescence ratio (Fv/Fm) [60]. Plants exposed to salinity stress higher than 10 dSm^{-1} severely declined the Fv/Fm of maize [67]. The photosynthesis of maize is decreased due to inhibition of growth and development of leaves and early abscission. At the same time, prolonged salt stress augmented ion toxicity, membrane disruption, and stomatal closure, which are responsible for severely reducing photosynthesis [68]. Salt stress harshly influenced the carbon fixation in maize [68]. Generally, the carbon fixation capacity of maize plants mostly depends on enzymes, stomatal conductance, photosynthetic pigments, and photosynthetic apparatus, which are severely reduced by salinity stress [44, 69]. Na^+ concentrations in the stems and leaves of maize genotypes increased under saline stress [50, 70-72]. A higher Cl^- concentration was recorded than Na^+ concentration in maize shoots [59]. On the other hand, the translocation of potassium (K) from root to shoot tissues in maize is disturbed by salinity, causing fewer K contents in the shoot than in the root [73]. Na^+ and Cl^- concentrations in maize varied due to genotype variations, experimental duration, growth stages, and fertility.

Salt stress conditions affect plants' physiology by changing plant cells' water and ionic balance, nitrogen and carbon dioxide assimilation rates, and protein biosynthesis mechanisms [21, 27, 74]. Reduced plant growth due to salt-stressed conditions depends upon the amount of salt in the soil, the type of specific salt, and salt-affected plant tissues [75]. Primarily, excess salt concentration species (Na^+ and Cl^-) damage plant root membranes, affecting the selectivity mechanism of the membrane, followed by an adverse effect on K balance, decrease in nitrogen assimilation enzyme activity (nitrate reductase), inhibition of photosystem II [76], and chlorophyll breakdown [26, 64, 77].

2.3 Reproductive Stage

Salinity significantly reduced the growth and productivity of crops throughout the globe [78-80]. Salinity stress considerably reduced the grain yield of maize by decreasing the number of grains and grain weight during the reproductive growth stage [81]. Reduced photosynthesis and photo-assimilates under saline stress are the major causes of poor grain formation, decreasing grains and grain weight [82], and poor biomass production [83]. Poor grain setting and filling at the reproductive stage owing to reduced translocation of assimilates from source to developing grains (sink) under salt stress ultimately reduced grain yield [84]. It has been accounted that salinity stress reduced the grain yield of maize by 22% when salinity increased to 20 dSm^{-1} [85], by 34% when soil

salinity increased from 3.8 to 7.4 dSm⁻¹ [86] depending on the nature of variety, growing seasons, growth stages, etc.

3. Maize - Salt Stress Mechanisms

It has been judged earlier [87] that maize is moderately sensitive to salt stress. A crop species that maintains average growth and development in saline soils ranging the ECe of 3-6 dSm⁻¹ is treated as a moderately tolerant crop [88]. Plants countenance saline stress in two phases: the osmotic stress phase and the specific ion toxicity phase [89]. Therefore, plant tolerance mechanisms are practically fragmented in those two phases. Proline and other compatible solutes contribute to establishing osmotic-stress tolerance in the plant by lowering tissue water potential [90]. On the other hand, stress tolerance mechanisms through the ionic phase comprise ion exclusion and tissue tolerance [75] and transportation of Na⁺ ions from the shoot to the root via the phloem [91]. However, the use of each tolerance mechanism broadly varied by individual factors in salt-sensitive and salt-tolerant plants [75].

Maize plants develop various mechanisms to survive in saline soils. The principles mechanisms are: i) Ion homeostasis and compartmentalization (exclusion of toxic ions), ii) Biosynthesis of osmoprotectants and compatible solutes (activation of the antioxidant defense system), iii) Activation of enzymes and synthesis of antioxidant compounds, iv) Regulation of hormones (changes in hormonal balance), v) Apoplastic acidification, vi) Synthesis of polyamines, and vii) Generation of nitric oxide (NO) (Figure 1).

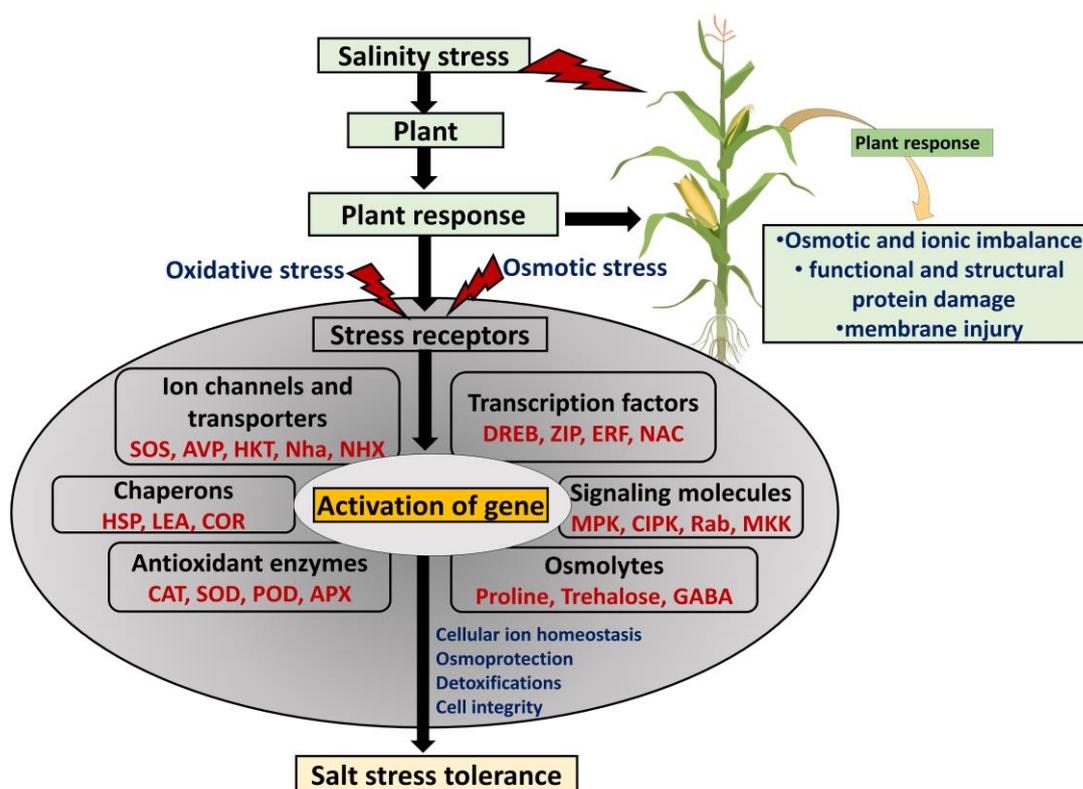


Figure 1 Mechanisms adopted by maize plants to survive in saline soils.

3.1 Ion Homeostasis and Compartmentalization

Excess accumulation of Na⁺ is highly toxic to maize plants [92]. Therefore, excluding excessive Na⁺ is an adaptive trait of plants to acquire salt resistance. Ion homeostasis through ion uptake and compartmentalization is an essential adaptive strategy for plants under salt stress [93-95]. Excess Na⁺ is either transported to the vacuole through tonoplast Na⁺/H⁺ antiporters driven by the proton gradient or sequestered in older tissues, protecting the plant from salinity stress [96, 97]. Two types of H⁺ pumps, viz., vacuolar-type H⁺-ATPase (V-ATPase) and vacuolar pyrophosphatase (V-PPase), are present in the vacuolar membrane [98-100], and V-ATPase is more dominant H⁺ pump present within the plant cell. Maize plants escape the cytosol from the toxic Na⁺ in this way, and reduce the osmotic potential [101]. The salt tolerance of maize is connected with higher K⁺, lower Na⁺, and Cl⁻ fluxes [102], and is associated with a higher K⁺/Na⁺ ratio [103]. The salt-resistant maize plants excluded Na⁺ more efficiently from leaf cell cytoplasm than the salt-sensitive maize plants [104]. Increasing K⁺ uptake and preventing Na⁺ entry by maintaining desirable K⁺/Na⁺ ratios in the cytosol are common adoption strategies of plants under salt stress [105]. Salt-tolerant maize genotypes have higher K⁺/Na⁺ ratios than sensitive ones [106].

3.2 Biosynthesis of Osmoprotectants and Compatible Solutes

Osmoregulation is a fundamental plant adaptation for reducing the impacts of salt stress, and it reduces the effect of salinity-induced osmotic stress by lowering osmotic potential due to the accumulation of some suitable solutes [26]. Compatible solutes (osmolytes) are a group of chemically diverse organic compounds that are uncharged, polar and soluble, and do not interfere with cellular metabolism, even at high concentrations. Proline, glycine betaine, soluble sugars, sugar alcohols, organic acids, and trehalose are the major compatible solutes, and the key osmolytes responsible for osmoregulation in maize under salt stress are proline and glycine betaine amid them. It has been reported that salt stress-induced maize plants accumulated more proline [73, 104, 107] and glycine betaine [108]. Salt-stressed plants produce more proline for osmotic adjustments and curtail saline toxicity [109, 110]. It provides tolerance towards stress, and serves as an organic nitrogen reserve during stress recovery. Salt-stressed plants also produce a sufficient amount of glycine betaine, which defends the plant cell from osmotic stress, improves salinity tolerance [76, 111], protects the photosynthetic pigments [112], and reduces the activity of reactive oxygen species (ROS) [109, 113]. It is evidenced that a strong positive correlation between increased proline and glycine betaine levels and stress tolerance index exists in plants under saline habitats. Salinity significantly reduced the total soluble sugar contents in maize leaves [107, 114] due to the inhibition of photosynthetic activity and increased partial utilization of carbohydrates into other metabolic pathways under salt stress. Higher accumulation of sugars and starch under salt stress [115] mitigates stress involving osmoprotection, carbon storage, and scavenging of ROS. The tolerant maize genotype accumulated more carbohydrates (122%) than the salt-sensitive genotype [104], indicating salt tolerance levels depend on the overproduction of carbohydrates.

3.3 Activation of Enzymes and Synthesis of Antioxidant Compounds

Plants under stress (abiotic and biotic stresses) conditions interrupt the electron transport chains (ETC) in chloroplasts and mitochondria, and molecular oxygen (O₂) acts as an electron acceptor under these conditions, leading to an increase in the accumulation of ROS. Moreover, plants' metabolic processes and enzymatic activities are changed due to salt-induced osmotic stress,

leading to the overproduction of ROS, which causes oxidative stress [116]. Overproduction of ROS like singlet oxygen ($^1\text{O}_2$), the hydroxyl radical (OH^-), the superoxide radical (O_2^-), and hydrogen peroxide (H_2O_2) are strongly oxidizing compounds (highly toxic) and damages proteins, lipids, carbohydrates, and deoxyribonucleic acid [117]. In chloroplasts, photosystems I and II and complex I, ubiquinone, and complex III of the ETC in mitochondria are essential sites for ROS formation [118]. For example, overproduction of H_2O_2 under salt stress collapses the leaf veins of maize due to leakage of adjacent cells [116]. Antioxidant metabolism, including antioxidant enzymes and nonenzymatic compounds, is critical in detoxifying ROS induced by salinity stress. Plants under salt stress show multigenic responses, including osmotic and ionic homeostasis and cell detoxification for antioxidant defense systems [119-121]. Salt tolerance of maize is associated with higher antioxidant activity (such as an enormous accumulation of polyphenols) under saline conditions [122]. Under saline conditions, higher antioxidant activity with higher polyphenol accumulation confirmed better leaf water content, leaf growth, membrane stability index, and plant growth in salt-tolerant maize [73]. Salinity tolerance in plants is directly linked with the activities of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR), and nonenzymatic antioxidant compounds [123, 124]. Enhanced enzyme activities are more pronounced in salt-tolerant maize plants than in salt-sensitive ones [125]. For example, CAT, GPX, and APX enzymes combined with SOD have superior H_2O_2 scavenging activity in the leaves and roots of salt-tolerant maize plants to salt-sensitive genotypes under salt stress [125].

3.4 Regulation of Hormones

Plant growth hormones influence the growth and development of plants [126]. The most essential phytohormones are auxins, gibberellins, cytokinins, ethylene, and abscisic acid, which help to promote plant growth. Salt-stressed maize plants synthesize endogenous growth hormones like abscisic acid (ABA) levels at the expense of indole acetic acid (auxins), which may escort stomatal closure for lessening water loss as a consequence of salinity-induced osmotic stress [127]. The root tips of maize get the gesture of impaired water availability under saline-induced osmotic effect and send a signal to shoots for regulating the whole-plant metabolism [128]. In this connection, salt-tolerant maize accumulates more ABA than salt-sensitive maize hybrid under salt stress [128, 129]. An increased concentration of ABA under salt stress enhanced leaf growth (reduced leaf sensitivity) of maize, possibly which could be allied to a growth-promoting function at the first phase of salt stress [130]. Salinity stress enhances osmotic stress and water deficit, increasing the endogenous ABA levels in the shoots and roots of maize [131], and this endogenous ABA in maize plants mitigates the inhibitory effect of salinity on photosynthesis, growth, and translocation of assimilates [131] and improves salt tolerance [132]. The accumulation of ABA in maize plants under salt stress increased the levels of K^+ , Ca^{2+} , and compatible solutes such as proline, glycine betaine, total soluble sugars Na^+/K^+ and $\text{Na}^+/\text{Ca}^{2+}$ ratios, which work against the uptake of Na^+ and Cl^- , and enhanced salt tolerance [133].

3.5 Apoplastic Acidification

Apoplastic acidification under salt stress is an essential indicator of salt tolerance. Cell-wall-loosening enzymes are activated due to lower apoplastic pH, which expands the cells [134]. Less

acidification reduces the seedling growth in maize during the first phase of salt stress owing to inefficient plasma membrane H⁺ pumping by ATPase [135]. Reduced apoplastic pH maintained higher H⁺-pumping in the salt-tolerant maize genotype by loosening the cell wall, which promoted more plant growth under salt stress than in the salt-sensitive genotype [47, 136]. In another study, it was reported that the growth of the salt-tolerant maize genotype dropped off throughout the first phase of salt stress despite sufficient cell wall acidification, indicating that other factors are responsible for limiting plant growth than apoplastic pH [137]. Therefore, apoplastic acidification under salt stress is not always an essential consideration for recovering the growth of maize plants [138].

3.6 Synthesis of Polyamines

In plants, polyamines (PA) are small, low molecular weight, ubiquitous, polycationic aliphatic molecules. Polyamines extensively recovered the growth and development of plants under stress [139, 140] and non-stress conditions [141, 142]. Plants under salt stress increased the endogenous PA levels. They played a significant task in abiotic stress tolerance, including salinity, owing to the positive correlation between increased polyamine levels and plant stress tolerance [143-146]. The PA catabolism regulates the intracellular polyamine level, and produces copper-binding diamine oxidases and FAD (flavin adenine dinucleotide) binding polyamine oxidases. It has been proved that these enzymes are involved in abiotic stress tolerance in plants [147, 148]. It has been noted the positive effects of PA through the maintenance of membrane integrity, regulation of gene expression for the synthesis of osmotically active solutes, reduction in ROS production, and inhibition of Na⁺ and Cl⁻ ions accumulation in different plant organs [149-152]. The most common PA that are found within the plant system are diamine putrescine (PUT), triamine spermidine (SPD), and tetra-amine spermine (SPM) [153-156]. For example, SPM improves the growth and development of sorghum plants by increasing the activity of peroxidase and glutathione reductase enzymes with decreasing membrane lipid peroxidation levels under salt stress [157]. SPD increased the salt stress tolerance of cucumber seedlings by changing proteomic functions and metabolic pathways [158]. Overproduction of PUT in rice enhanced the salt tolerance [159]. Moreover, SPM and SPD are considered potent inducers of nitric oxide, another essential signaling molecule [160], and have been discussed in a separate title underneath. It has been reported that salt stress regulates PA biosynthesis and catabolism by acting as a cellular signal in hormonal pathways, thereby regulating ABA in response to stress [161].

3.7 Generation of Nitric Oxide

Nitric oxide (NO) is assumed to play a crucial role in salt stress tolerance in crop plants. NO is a small volatile gaseous molecule that contributes to various plant growth and developmental processes under stress and non-stress conditions, such as seed germination, root development, respiration, stomatal closure, flowering, cell death, and stress responses, as well as a stress signaling molecule [162-164]. It has been reported that NO protects against salinity stress in maize plants [165, 166]. NO triggers the activity of antioxidant enzymes (SOD, CAT, GPX, APX, and GR) in crop plants [165, 167]. NO mitigates the salt-induced oxidative damage in maize plants by enhancing the activities of antioxidant enzymes (SOD, POD, and CAT) and lowering MDA and H₂O₂ [166]. NO reacts with lipid radicals, thus preventing lipid oxidation, exerting a protective effect by scavenging

superoxide radicals and forming peroxyxynitrite that other cellular processes can neutralize. NO increases the salinity tolerance in maize plants due to enhanced antioxidant activities and modulation of the ROS detoxification system [168].

Plant salinity tolerance is also related to regulating plasma membrane (PM) H⁺-ATPase and Na⁺/K⁺ ratio [163]. NO increases PM H⁺-ATPase (H⁺-PPase) activity [169], creating an H⁺ gradient that stimulates the exchange of Na⁺/H⁺. An increment of Na⁺/H⁺ exchange may contribute to K⁺ and Na⁺ homeostasis, and increase the Na⁺/K⁺ ratio, leading to salt stress tolerance in maize inbred line seedlings [170].

4. Management Strategies

No doubt, salinity reduces crops' growth and productivity; hence, different methods are practiced to alleviate the salinity problem and increase the relative salt tolerance of crops. Various strategies are used to mitigate salt stress's negative impact on crop plants, like exogenous application of phytohormones, amino acids, sugars, osmolytes, and other plant growth regulators (Figure 2).

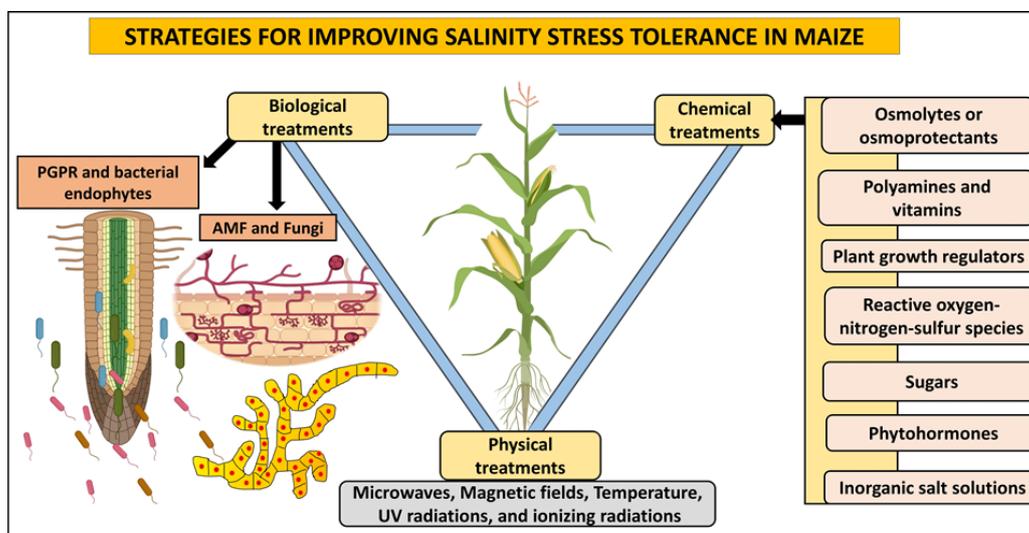


Figure 2 Different strategies for alleviating the effect of salt stress in maize.

4.1 Selection of Salt-Tolerant Genotypes

Introduction and selection of salt-tolerant maize genotypes in conjunction with suitable production technology are required to increase productivity in salt-affected regions. Maize genotypes have different levels of tolerance against salinity [43, 171, 172], and relative salt-tolerant genotypes that can enhance crop yield should be selected. Therefore, choosing tolerant genotypes would be an essential retrieval method to grow in saline-prone areas [173].

4.2 Seed Priming

Successful crop production depends on the optimum crop stands determined by the ideal level of seed germination. Salt stress extensively delays and reduces seed germination of maize because of osmotic stress induced by salinity on germinating seeds [26, 27, 174], and seed priming has the

potential role in overcoming these problems (Table 1). It has been reported in many studies that hydropriming of maize seed under saline conditions significantly increased germination rate [175], germination percentage, germination index, seedling vigor index, and seedling length [33]. Priming with sodium chloride, potassium chloride, and calcium chloride alleviates the adverse effects of salt stress and increases maize's germination and seedling growth traits [175-177]. Hormonal priming also alleviates the adverse effects of salt stress. It improves germination and seedling growth properties, as priming of maize seed with chloroethyl phosphonic acid augmented the biomass of seedlings under salt conditions [178], with 28-homobrassinolide increased seedling growth by enhancing the activities of antioxidative enzymes in addition to lowering lipid peroxidation and increasing protein concentration [179], with salicylic acid enhanced growth and development [180], with hydrogen peroxide improved seed germination percentage by increasing the activities of APX, CAT, and GPX [181], with ascorbic acid, thiamin, and pyridoxine improved growth or seed yield under [182]. Seed priming with 24-epibrassinolide (EBL) on maize grown with different levels of saline stress under semi-controlled conditions positively influenced the root length, root surface area, stem diameter, relative leaf water contents, total chlorophyll, photochemical activity of PSII (Fv/Fm), net rate of photosynthesis and transpiration, and nutrients (Zn, K) uptake in roots and shoots of maize, while it resulted in the lowest Na⁺ and Na⁺/K⁺ ratio [183].

Table 1 Role of seed priming reclaims the salt tolerance.

Priming techniques	Priming agents	Improvement	References
Hydropriming	Water	Germination	[33]
		Germination and seedling growth characteristics	[175]
	Ascorbic acid, thiamin, & pyridoxine	Growth, grain yield	[182]
Hormonal priming	Salicylic acid	Growth and physiology (photosynthesis and carbohydrate metabolism)	[180]
	Ethylene	Biomass	[178]
	28-homobrassinolide	Protein content, antioxidative enzyme activities (decreased lipid peroxidation)	[179]
	Hydrogen peroxide	Germination percentage, activities of ascorbate peroxidase, catalase, and guaiacol peroxidase	[181]
Halopriming	NaCl	Emergence and germination rate, plant height, and yield;	[176]
		Shoot length, dry weight, leaf number and area, and chlorophyll content	[177]
Osmopriming	CaCl ₂	Germination rate, number of cobs, shoot & root lengths, yield	[184]

Osmopriming (Organic)	<i>Moringa</i> leaf extracts	Crop growth & net assimilation rates, leaf area index, maintain more extended green leaf area.	[185]
Chemipriming	Phenylalanine	Germination, leaf area, root & shoot fresh & dry weights, lengths, chlorophylls and carotenoids	[186]

4.3 Organic Matter Management

An organic amendment has been proved as a practical approach to attenuate the salinity stress in soil. Modifications of soil through organic matter improve soil's physical and chemical properties. However, applying organic matter effectively combats salinity's adverse effect and increases salt-stressed maize's growth and yield. Using organic substances, such as solid waste, compost, vermicompost, manure, and cow dung, decreases soil salinity. It increases total nitrogen, available phosphorus, exchangeable potassium, calcium, and magnesium concentrations, and soil organic carbon and cation exchange capacity (CEC) by decreasing Na⁺ concentration in maize crops.

Application of solid waste, vermicompost, and cow dung alleviates the adverse effects of soil salinity. It improves the shoot and root growth of maize plants by improving the physicochemical properties of soil and by reducing the electrical conductivity (EC) in soil [187]. Compost and vermicompost application in salt-stressed maize plants increased plant height and dry matter production by lowering soil pH and EC [188]. Manure application significantly released the salt-induced osmotic stress, decreased the electrolyte leakage in maize plants, and increased plant growth and grain yield [189]. Biochar is also an essential organic amendment of abiotic stresses, which enhances soil physicochemical properties such as soil structure, surface area, water holding capacity, CEC, and pH [190]. Salinity significantly decreased the growth of maize, whereas biochar mitigated the adverse effects of salt stress and enhanced the growth by lowering the uptake of xylem Na⁺ concentration or maintaining nutrient balance within the plant [191]. The utilization of biochar has been demonstrated to enhance the growth and productivity of salt-stressed maize plants by augmenting K uptake while reducing Na uptake, as evidenced by studies [192-194]. Similar positive effects of biochar under salt-stressed-plants have been observed in other cereal crops such as wheat [195, 196] and rice [197, 198]. Compost manure and crop straw-derived biochar application in salt-stressed maize plants decreased saline toxicity by reducing the accumulation of Na⁺ and Cl⁻ accumulation, increasing K concentration, CEC, water holding capacity, and pH, and improving maize growth and productivity [199]. Application of cow manure-made biochar significantly increased net water uptake efficiency (WUE), hydraulic conductivity, total N, P, exchangeable cations, CEC, total C, and pH, resulting in increased productivity of maize [200].

Additionally, using rice straw-derived biochar reduced the additional chemical fertilizers (NPK) rate by 25% in cowpeas under saline conditions [201]. Exogenous application of organic matter is an efficient and feasible way to mitigate saline toxicity and improve soil health and plant growth. Therefore, organic matter amendment could be an efficient approach for sustaining maize production in salt-affected soils.

4.4 Nutrients Management

Salinity stress reduces the growth and development of maize plants by reducing the uptake of essential plant nutrients such as N, K, Ca, Mg, Fe, and Zn [44, 59, 73, 202, 203]. Salt-stressed plants suffer nutrient deficiency by reducing their uptake due to over-competition of Na^+ with cationic ions (NH_4^+ , K^+ , Ca^{2+} , Mg^{2+} , Zn^{2+} , etc.) and Cl^- with anionic ions (NO_3^- , PO_4^{3-} , SO_4^{2-} , Fe^{2+} , etc.) [204, 205]. Hence, more significant reductions of K^+ , Ca^{2+} , and Mg^{2+} contents were recorded in leaves and roots of maize owing to combined stresses rather than with only the salt stress or only K^+ , Ca^{2+} , and Mg^{2+} deficiency [44, 204]. Na^+ and Cl^- accumulation is increased in leaves and roots of maize under saline stress, while their accumulation is also aggravated due to K deficiency. Likewise, K^+/Na^+ , $\text{Ca}^{2+}/\text{Na}^+$, and $\text{Mg}^{2+}/\text{Na}^+$ ratios are reduced rigorously in maize leaves and roots under saline and K stresses compared to their stress [44]. Therefore, applying essential nutrient elements in any form (through elemental/fertilizers) quickly rescued the adverse effects of salinity stress in maize plants.

The growth and productivity of maize are also affected by N deficiency due to the antagonistic effects of Cl^- and NO_3^- under salinity stress [204]. Therefore, nitrogen (N) application significantly ameliorated the adverse effects of salt stress and conspicuously increased the growth, yield, and N uptake in salt-stressed maize plants [206]. Application of N in salt-stressed maize plants increased the leaf area index, crop growth rate, net assimilation rate, and yield to a large extent [207]. In earlier studies, it has been acknowledged that the application of N extensively increased the antioxidant enzymes like such as CAT, GR, and glutathione-S-transferase activities in maize while decreasing the peroxide dismutase (POD) and SOD activities [54]. So, the N source is also an essential factor.

Potassium application enhanced the yield contributing characteristics and increased the yield of maize under saline conditions [208]. Similarly, K application in saline-affected maize plants significantly increased the grain yield by enhancing water uptake and turgor maintenance, mineral nutrition, leaf area index, and crop growth rate and reducing Na uptake through osmoregulation [209]. Na^+ concentration increased in saline soils, showing a higher value of Na^+/K^+ ratio. Conversely, K application exogenously decreased this ratio and alleviated the nasty effects of Na in maize [210, 211]. Recently, Hussain *et al.* [211] claimed that applying K sulfate and diammonium phosphate (DAP) as a mixture in saline soil increased the growth and productivity of maize. Foliar application of KCl and thidiazuron on maize plants remarkably increased growth by alleviating the adverse effects of saline stress [212]. They also concluded that thidiazuron more efficiently alleviated the adverse effects of salt stress than K fertilization due to considerable improvement of K, chlorophyll content, total carbohydrate, and total soluble sugar.

Among the micronutrients, boron (B) has a significant role in the plant cell wall and membrane constancy [212-214] and the growth and productivity of crops [215]. Applying B in salt-induced maize plants increased the membrane integrity of plants by increasing the concentration of K. It increased the growth by alleviating the negative effect of Na^+ and Cl^- [216].

Applying flue gas desulfurization gypsum (FGDG) reduces the deadly effects of Na^+ due to the swapping of Na^+ with Ca^{2+} at the cation exchange site. Consequently, it increases clay particle flocculation near the soil surface [217]. Adding furfural residue (FR) has been shown to increase soil organic carbon (SOC) content while reducing soil bulk density, particularly under saline conditions, attributed to its ability to lower soil pH [218]. The combined application of FGDG and FR in saline

soils recovered the soil properties by increasing SOC and mineral nutrients, decreasing soil pH and sodium content, and increasing maize [219].

Applying silicon (Si) increases the photosynthetic paraphernalia of salt-stressed maize plants by triggering the electron transport chain [220]. It has been proved that Si increased the salinity tolerance of the maize crop; the application of Si enhanced the salt tolerance of maize plants by reducing the oxidative and osmotic stress [221] by increasing biochemical and physiological activities like water-use efficiency, photosynthetic pigments, etc. [222]. Combined B and Si application helps enhance salinity-induced maize plants' growth and physiological functions. It alleviates the adverse effects of salt stress by increasing the concentration of total soluble sugars and proline [223]. It has been reported that the nutritional status of stress-stressed maize seedlings increased with the foliar application of iron [224]. Foliar application of H₂O₂ enhanced the salt tolerance of maize plants by increasing antioxidant enzymes like APX, GPX, SOD, and CAT [225].

4.5 Fresh Water Irrigation

Applying fresh water in saline habitats reduced salinity stress and increased the growth and yield of crops. Irrigation with fresh water at jointing, heading, and grain filling stages of maize increased the grain yield by 81.16% as compared to saline water irrigation of those stages, not only that two times saline water and one-time freshwater application increased yield by 35.39% [226]. It has been evidenced that alternating irrigation times of salt water and fresh water had a significant effect in lowering soil salinity and increasing grain yield of maize [227], irrigation of fresh water at the seedling stage promoted salt leaching and enhanced maize yield [228], freshwater irrigation at the heading stage recovered the earlier stress and improved the WUE and growth of maize [229]. Alternating fresh and saline water irrigation enhanced plant growth [230]. Applying fresh water during the sensitive stages and saline water during the non-sensitive stages of plant growth increased the irrigation utilization rate of saline water [231]. Alternate irrigation of fresh and saline water at 80:20 produced a similar yield of tomatoes with irrigation with fresh water alone [232]. Alternate irrigation of fresh water and saline water produced a higher yield of wheat and mustard than mixed irrigation at the same level of salt [233]. Freshwater can be substituted with saline water up to high values of EC (9 dSm⁻¹) without any loss in wheat and barley production where there is deficit irrigation [234]. An effective irrigation system and strategy control soil salinity and reduce soil's high saline toxicity. Alternate fresh and saline water irrigation (at seedling, jointing, and tasseling, and after tasseling) alleviates the salt stress and increases the yield of maize [235, 236].

The application of brackish water in salt-induced maize plants alleviated the stress effects. Brackish water irrigation in saline conditions increased the uptake of K while retarded the uptake of Na in some maize genotypes. Irrigation frequency affected soil salinity accumulation when using brackish water [237]. Generally, saline water irrigation alters the soil environment [238], affects the soil capillary action, and changes soil permeability and water retention [239], leading to accumulating salts in the soil and restricting crop growth [240, 241]. Applying three times irrigation with fresh and brackish water (80 mm of freshwater + 80 mm brackish water + 80 mm of salty water) increased the yield of winter wheat by reducing the soil salinity [242]. Applying high saline water with high frequency (one-day interval) enhanced the growth and yield of tomatoes [243].

Exogenous application of hydrogen-rich water (HRW) mitigated the effects of salt stress on the growth of maize roots. H⁺-transporters are closely associated with transporting ions and small

molecules, essential for maintaining osmotic balance, ion homeostasis, and nutrition absorption. Application of HRW remarkably increased the activities of PM H⁺-ATPase, tonoplast H⁺-ATPase, and H⁺-PPase, and increased the relative water content biomass, maintained ionic balance in maize seedlings, and finally increased salt tolerance [242].

4.6 Exogenous Application of Phytohormones

Phytohormones are chemical substances that play a significant role in plants' physiological and biochemical processes. Five classical phytohormones, viz., auxins, gibberellins, cytokinins, ethylene, and abscisic acid, significantly affect abiotic stress tolerance. Other well-known phytohormones are brassinosteroids, methyl jasmonates, salicylic acid, strigolactones, etc., which also alleviate environmental stresses. Applying phytohormones exogenously under salt stress conditions overcomes the adversative properties of salt stress and increases the growth and productivity of maize plants.

Indole-3-acetic acid (IAA), popularly known as auxin, significantly regulates plant growth. Salinity stress influences IAA homeostasis due to the alterations in IAA metabolism and distribution [244], and endogenous IAA level is decreased under salt stress [245, 246]. At the same time, the exogenous application of IAA alleviates the adverse effects of salt stress and enhances plant growth [247, 248]. However, foliar application of IAA increased the growth and yield of salt-stressed maize plants by improving the CAT and SOD activities [249]. It has also been reported that exogenous application of IAA enhanced the growth and yield of a salt-stressed maize plant by increasing the uptake of essential plant nutrients and decreasing the uptake of Na⁺ remarkably [250]. Applying inorganic nutrients and IAA exogenously as pooled in maize plants grown in saline conditions increased P, Ca, and Mg while decreasing Na contents. Enhancement of plant growth by IAA and nutrient application is linked with an improved concentration of photosynthetic pigments, more K⁺/Na⁺ ratio, enhanced activities of antioxidant enzymes like CAT and SOD, and reduced membrane permeability under saline conditions. In another study, it has also been postulated that IAA enhanced the maize plant growth at the earlier stages to a variable extent by reducing the Na⁺ and Cl⁻, increasing K⁺ and Ca²⁺ concentrations, and maintaining higher membrane permeability [73]. Likewise, exogenous IAA in wheat increased germination, growth, yield, and seed quality by alleviating the adverse effects of salt stress [251, 252].

Gibberellic acid (GA₃) generally involves improving the growth, yield, and quality of crops [126, 253], and salt stress reduces the endogenous level of GA₃ in crops, including maize [254]. It has been proved that salinity-induced oxidative stress and ionic toxicity usually inhibit plant growth by changing physiological and biochemical functions. At the same time, GA₃ overcame the harmful effects of NaCl-induced stress and enhanced physiological and biochemical traits macro and micro-nutrient concentration. Exogenous application of GA₃ on maize plants grown in NaCl-induced saline stress curtailed the adverse effects of Na⁺ and Cl⁻ and enhanced the growth and nutritional status by increasing the concentration of proline that sustained membrane permeability and salt tolerance [255]. Foliar application of GA₃ in salt-induced maize plants enhanced plant growth by increasing the uptake of nutrients and decreasing Na⁺ and Cl⁻ concentrations [256]. GA₃ is more efficient in tolerating the salinity of maize plants than salicylic acid (SA). Under the saline condition, GA₃ also ameliorated the saline toxicity in different crops and enhanced the seed germination of wheat [257-259], growth and yield of wheat grain [260, 261], rice [262], and tomato [263].

Cytokinin (Ck) is a vital phytohormone that plays a significant role in the growth and development of plants [264]. Generally, the application of Ck regulates the metabolism of the maize plant [265], and any alteration affecting the synthesis and homeostasis of Ck leads to the death of the plant tissue. Ck is reported to control plant adaptation to stress and increase plant salt tolerance [266-268]. However, exogenous application Ck is involved in numerous vital plant growth and development processes. Foliar application of Ck in maize plants considerably ameliorated the harmful effect of salt stress and increased growth, yield traits, and grain yield [248]. Exogenous application of Ck increases yield and quality (starch concentration) in rice cultivars under salt stress [269-271]. Ck interacts with auxins and ABA and increases the salt resistance in wheat plants [272]. Salama and Awadalla [273] stated earlier that kinetin is one of the cytokinins responsible for increasing plant growth in saline conditions. Kinetin application conquered the effects of salinity stress and increased the growth of wheat seedlings [274]. Kinetin enhances salt tolerance by modulating shoot chloride exclusion in maize [275]. Foliar spraying of Kinetin and IAA overcame the adversative effects of NaCl-induced stress in maize plants by increasing membrane permeability, K^+ , and Ca^{2+} and reducing Na^+ concentrations [73].

Ethylene (ET) also plays a pivotal role in plant growth and metabolism as a phytohormone. Ethylene has been shown to enhance plant salt tolerance by promoting the homeostasis of Na^+/K^+ , nutrients, and ROS [276]. Salinity stress induces ET production, which helps maintain the Na^+/K^+ homeostasis, resulting in enhanced salt tolerance [277]. In a recent study, it has been reported that ET triggers salinity tolerance in maize genotypes by modulating polyamine catabolism enzymes [278]. Foliar application of ET alleviates the adverse effects of salt stress in tomatoes and increases salt tolerance by improving chlorophyll content, stomatal conductance, and ion homeostasis [279]. Application of ET exogenously enhances salt tolerance in plants by increasing chlorophyll a/b, photosystem II function (Fv/Fm), redox state, and retention of K^+ in shoots and roots of arabidopsis [280]. Salinity stress inhibits seed germination through elevation of the H_2O_2 , and exogenous ethylene treatment has been shown to regulate ROS homeostasis to induce the seed germination of arabidopsis [281]. They also concluded that ET with NO enhances seed germination by decreasing the H_2O_2 levels and modulation of ROS production induced by salinity stress.

Abscisic acid (ABA) is also a critical phytohormone that ameliorates stress-induced damage to crop plants. ABA facilitates signals to the plants to stay alive under salt stress [282]. Endogenous ABA level is increased due to plants being exposed to salt stress or water deficit conditions [283]. The concentration of ABA significantly increases in salt-resistant maize genotypes [284]. ABA weakened the harmful effect of NaCl and improved the tolerance of ionic stress in sorghum [285]. ABA amplifies xylem water potential and water uptake capacity in barley plants in the presence of salt stress [286].

Nonetheless, the exogenous application of ABA-induced rice salt tolerance [287]. Salt stress stimulates the synthesis of ABA in roots, which transports from root to shoot through xylem sap, and the concentration is correlated to the stomatal reactions. Exogenous application ABA reduces ethylene release and leaf abscission under salt stress in rice, probably by decreasing the accumulation of toxic Na^+ ions in leaves and roots [288]. Salt-induced ABA mediated the inhibition of leaf expansion and limited the accumulation of Na and Cl in the leaves of maize [289]. Soil salinity up-regulates the generic stress hormone like ABA that induces genes to alleviate salt stress in *Iris hexagona* [245].

Brassinosteroids (BRs) are a novel phytohormonal group of steroids distributed throughout the plant kingdom [290, 291]. The most critical BRs are brassinolide (BL), 24-epibrassinolide (24-EpiBL), 28-homobrassinolide (28-HomoBL), castasterone (CS), and 24-epicastasterone (24-EpiCS), which are commonly used for biotic stress tolerance of plants. BRs ameliorate plants under environmental stress, such as oxidative damage [292]. Under salt stress, the effects of BRs were mainly focused on plant growth and antioxidant systems [179, 293-295]. BRs are prominent in various physiological processes, like cell division and expansion, xylem differentiation, stem elongation, and root growth [292, 296]. BRs application enabled maize seedling growth to recover from the effects of salinity [297]. BRs boost seed germination, development, and the ability of maize seedlings to withstand salt stress by enhancing oxidative responses [298]. Exogenous application of BRs ameliorates the salt stress. It increases the yield in many crops by altering physiological activities like rice [299, 300], oilseed rape [301], berseem (*Trifolium alexandrinum* L.) [302], cowpea (*Vigna sinensis*) [303], and cucumber [304].

2-hydroxybenzoic acid is known as salicylic acid (SA) and is considered a plant phenolic phytohormone. It plays crucial regulatory functions to protect plants against biotic and abiotic stresses. It encourages plants against salinity by adjusting physiological and biochemical processes. NaCl-induced salinity stress reduced the growth, photosynthetic pigments, water status, electrolyte leakage, and antioxidant enzymes of maize, while exogenous SA improved those traits and increased salt tolerance [107]. SA increased the uptake of nutrients in maize plants under saline conditions by considerably reducing Na⁺ and Cl⁻ accumulation [203]. Salinity stress decreased maize's dry weight and leaf area. At the same time, foliar application of SA alleviated the lethal effects of salinity and enhanced those traits by increasing lysine, arginine, glutamic acid, and serine [305]. SA application significantly increased photosynthetic pigments by preventing the degradation of the nucleus and chloroplast and overcame the toxicity generated by NaCl-stressed maize plants, which delays leaf senescence/abscission [306]. Khodary [180] postulated that the photosynthetic rate and carboxylating enzyme activities are increased in salt-induced maize plants with SA. Exogenous application of SA increased plant growth under saline conditions by increasing mineral nutrition and, decreasing oxidative stress in maize [203] and inducing hormonal status in wheat seedlings [307]. Many studies support that the exogenous application of SA increased the tolerance of maize to salinity and osmotic stress [308, 309].

Methyl jasmonate (MeJA) and its free-acid, jasmonic acid (JA), collectively referred to as jasmonates, are important lipid-based phytohormones that enhance the growth of plants under stress [245, 310, 311]. It has been reported that the JA level increases under salt stress, and salt-tolerant cultivars accumulate higher JA than salt-sensitive cultivars such as rice [312, 313], tomato [314], etc. No specific study was found regarding the exogenous application of JA on maize crops. However, application of JA exogenously alleviated the salinity stress in other cereal crops like rice seedlings by decreasing Na concentration and inducing ABA activity [313], enhanced the growth and photosynthesis of barley by reducing the inhibitory effect of high salt concentrations [315].

Strigolactones (SLs) are isolated from cotton root exudates and used as seed germination stimulants for plants in the Orobanchaceae family that parasitize plant roots (*Striga*, *Phelipanche*, and *Orobanche* spp.) [316]. The biosynthesis and signaling of SLs are regulated by various abiotic stress factors [317], including salinity stress [318, 319]. SLs interact with other phytohormones, especially auxin and ABA. SLs and H₂O₂ signaling alleviate the salt stress induced by arbuscular mycorrhizal fungus in *Sesbania cannabina* seedlings [320]. Arbuscular mycorrhizal (AM) colonization

alters the ABA catabolism, and higher ABA protects plants from the harmful effects of salt stress by encouraging the production of SLs via H₂O₂ signaling [321]. AM symbiosis boosts the strigolactone levels in plants, thereby alleviating salt stress in maize plants through enhanced stomatal conductance and photosystem II efficiency [322]. Applying stigmasterol in maize plants mitigated the adverse impacts of salt stress and enhanced growth and yield [323]. SLs are also involved in the interaction of plant roots with nitrogen-fixing bacteria (Rhizobium) and increased the nodulation of alfalfa inoculated with *Sinorhizobium meliloti* following SL (GR24) treatment [324].

Therefore, exogenous application of phytohormones helps to improve maize performance under salt stress, as manifested by increasing nutrient uptake, osmotic adjustment, and the antioxidant defense system.

4.7 Exogenous Application of Osmoprotectants

Compatible osmolytes mitigate the harmful effects of salt stress and improve plant growth. Proline is the main osmolyte produced by the hydrolysis of proteins in the plant under abiotic stress, reducing osmotic stress. However, proline is usually made and accumulated in plants under salt stress and plays a multifunctional role in regulating cytosolic acidity, maintaining protein and ROS, and aiding osmotic adjustments [325]. Applying proline led to elevated proline levels in plants experiencing salt stress, which correlated with enhanced salt tolerance [326]. Kaur and Asthir [327] mentioned the functions of proline as scavenging ROS, stabilizing DNA, proteins, and membranes, and reducing denaturation of NaCl-induced enzymes. It has been found in many studies [104, 328] that salt stress decreases the growth and yield of maize plants by reducing the total nutrient uptake and excess accumulation of Na⁺ and Cl⁻ ions. Exogenous application of proline has been shown to increase nutrient uptake and reduce the adverse effects of salt stress in maize [328, 329]. Total nutrient uptake in maize plants decreases under saline stress, but the exogenous application of proline increases nutrient uptake and salt tolerance [330]. Exogenous proline also improves the salinity tolerance of maize by increasing the uptake of nutrients and decreasing Na accumulation in plants [331, 332].

Glycine betaine (GB) is a vital osmolyte curtailing abiotic stresses. It has been proved earlier that exogenous application of GB improved the growth, water status, net photosynthesis, and yield in salt-stressed maize plants by improving stomatal conductance and actual photosystem II efficiency [333]. They also noted that GB promoted plant growth under salinity by reducing Na and increasing K concentrations in shoots. The application of osmoprotectants exogenously improves the overall performance of maize through osmotic adjustment and antioxidant defense system under salt stress. Exogenous application of GB in plants under stressed environments plays a critical role in regulating enzyme activity, ROS homeostasis, etc., and improves stress tolerance [334-336].

Hydrogen peroxide (H₂O₂) application exogenously effectively curtailed salinity-induced stress by increasing the activities of CAT, GPX, APX, and SOD [225]. H₂O₂ pretreatment increased the salt resistance during subsequent exposure to salt-persuaded plants, and H₂O₂ metabolism is involved as a signal in the process of salt acclimation in maize plants [337]. El Sayed [46] mentioned another piece of information regarding hydrogel polymers: it improved maize plants' growth and morphophysiological traits under salt stress by enhancing soil properties.

4.8 Exogenous Application of Polyamines

Exogenous application of polyamines enhanced the membrane integrity. It regulated the expression of genes for the synthesis of osmotically active solutes, as well as reduced ROS production and Na⁺ and Cl⁻ ions accumulation in different organs of crops [151, 152, 338]. Exogenous application of polyamines alleviated the salt-induced reduction of photosynthetic efficiency [339]. Polyamines (SPM) application increased sorghum seedlings' growth and salt tolerance by increasing the activity of POX and GR enzymes and decreasing the level of membrane lipid peroxidation [157]. Exogenous SPD significantly enhanced enzymatic activities (SOD, POD, CAT and APX), soluble sugar, soluble protein, and free proline levels while reducing O₂ production rate, H₂O₂ and MDA accumulation, thereby aiding in maintaining osmotic balance and increased salt stress tolerance in oat seedlings [340]. They also urged that SPD contributes to higher expressions of proteins and defense mechanisms on antioxidant and detoxification and inhibits proteolysis, which might play essential roles in salt tolerance.

4.9 Exogenous Application of Nitric Oxide

Nitric oxide (NO) has a promoting effect on seed germination and plant growth under saline stress. Exogenous application of NO remarkably mitigates abiotic stress in crop plants [341-343]. Application of NO significantly improved plant growth under salinity stress by increasing the activities of antioxidant enzymes, for example, SOD, CAT, GPX, APX, and GR [344], and decreasing lipid peroxidation or MDA production [345]. Sodium nitroprusside (SNP) is well known as a donor of NO, and exogenous application of SNP on salt-induced *Lupinus luteus* seedlings heightened the seed germination and root growth by reducing the detrimental effect of the abiotic stress [346]. Foliar application of SNP increased the shoot dry weight of sweet corn under salinity stress [347].

4.10 Uses of Arbuscular Mycorrhizal Fungi

Arbuscular mycorrhizal fungi (AMF) improve stress tolerance and increase plant growth by mitigating abiotic stresses. AMF improved the photosynthesis and water use efficiencies in maize plants subjected to saline conditions [348]. AMF quickly penetrates the cortical cells of plant roots and forms arbuscular and vesicles. These unique structures in roots might contribute to the uptake of macro- and micro-nutrients from the soil and improve plant tolerance against stress. *F. mosseae*, an AM fungus, enhanced maize's resilience to salt by bolstering tissue density, expelling Na⁺ from leaves, distributing Na⁺ within plant organs, upholding K⁺: Na⁺ equilibrium, and safeguarding organelle structural integrity and functionality. [349]. Accumulation of soluble sugars in salt-stressed maize plants is increased by AMF colonization in the root, which improves salt tolerance [350]. This improvement is correlated with the nutrition of the host plant, improved K⁺/Na⁺ ratios, and superior osmotic adjustment. It has been reported earlier [351] that arbuscular mycorrhizal symbiosis regulates the expression of plant genes involved in proline biosynthesis, genes encoding aquaporins, and genes encoding late embryogenesis abundant proteins with chaperone activity. More than 30 different aquaporin genes are encoded in maize [352], and mycorrhizal plants maintain better water status in their tissues by regulating these genes. Although salt stress reduced the formation and colonization of AMF in maize roots [348], mycorrhizal plants are less affected by salt stress than non-mycorrhizal plants [351, 353-355].

4.11 Application of Plant Growth-Promoting Rhizobacteria

Soil microorganisms are used to lessen many abiotic stresses in crop plants [356]. Several microorganisms of different groups, like bacteria, fungi, and archaea, are available in soil [357, 358]. Among them, bacteria are extensively used for promoting plant growth under abiotic stresses, and these bacteria are known as plant growth-promoting rhizobacteria (PGPR). These bacteria (rhizospheric or endophytic) relieve abiotic stresses and enhance tolerance to host plants. The most critical bacterial genera are *Achromobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Methylobacterium*, *Microbacterium*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Rhizobium*, *Variovorax*, etc. [357, 358]. PGPR produces a key enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which mitigates the inhibitory effects of salt stress by lowering the ethylene concentration in maize plants and increasing production [359]. ACC deaminase containing PGPR eliminates the adverse effects of salt-induced ethylene in plants [360]. Inoculation of plants with PGPR strains, particularly *Pseudomonas* and *Enterobacter* spp., stimulated the growth and yield of maize expressively under salt stress [361]. PGPR (*Azospirillum*) inoculation enhanced salt resistance in maize plants by reducing the Na concentration, increasing the K⁺/Na⁺ ratio and calcium level in tissues, enhancing water flow and more dry matter production, and decreasing proline concentration [362] (Table 2). Maize seeds inoculation with PGPR detoxifies the salinity levels and increases the salt tolerance. PGPR inoculation in maize seeds improves plant growth by increasing proline levels and helps in osmotic adjustments under salt stress, which has been well documented. For example, inoculation of *Geobacillus* sp. increased the photosynthetic rate [363], *Pseudomonas* spp. Improved plant growth [325], *Arthrobacter pascens* decreased the Na accumulation. They increased plant growth [364], *Azotobacter chroococcum* improved nutrition [365], *Rhizobium* spp., *Rhizobium tropici* strain CIAT, *Azotobacter brasilense* strains Ab-V5 and Ab-V6 [366], and *A. faecalis* [367] enhanced the photosynthetic pigments and photosynthetic rate by the overproduction of proline in maize plants.

Table 2 Role of PGPR on salt tolerance of maize.

PGPR strains	Mechanisms	Improvement	References
<i>Pseudomonas syringae</i> , <i>P. chlororaphis</i> , <i>P. bathycetes</i> , <i>Enterobacter aerogenes</i> , <i>P. fluorescence</i>	ACC deaminase	Plant growth, RWC, chlorophyll content, and K ⁺ /Na ⁺ ratio	[361]
<i>P. aeruginosa</i>	IAA production, ACC deaminase, phosphate solubilization, and biofilm formation	Growth, yield, and nutrition	[368]
<i>Pseudomonas</i> spp.	IAA production, ACC deaminase, phosphate solubilization, and biofilm formation	Water status, nutrition, and growth	[369]
<i>Pseudomonas</i> spp.	Osmotic regulation, EPS	Root and shoot growth	[367]
<i>Pseudomonas putida</i> biotype A, <i>P. fluorescens</i> biotype A	Osmotic regulation	Root-shoot length under gnotobiotic conditions	[370]

<i>Azotobacter chroococcum</i> strains C5 and C9.	Osmotic regulation	Exclusion of Na ⁺ , uptake of K ⁺ in maize, K ⁺ /Na ⁺ ratio, polyphenol, and chlorophyll contents	[365]
<i>Azospirillum lipoferum</i> strain Z4/1	Osmotic regulation	Markedly alter Na, K, & Ca selectivity; Decrease Na uptake, enhance K & Ca uptake; stimulate nitrate reductase and nitrogenase activity.	[362]
<i>Bacillus megaterium</i>	Osmotic regulation	Increase root hydraulic conductance that correlates with more plasma membrane-type two (PIP2) aquaporin in roots; More <i>ZmPIP1;1</i> protein in leaves.	[371]
<i>B. amyloliquefaciens</i>	Soluble sugar content and antioxidant enzymes	Plant growth and photosynthetic rate	[372]
<i>Rhizobium</i> strain Thal-8 chickpea modulating	Osmotic regulation	Reduce electrolyte leakage and osmotic potential, increase proline, LRWC, and K and Ca uptake.	[325]

4.12 Adaption with Molecular Strategies

Molecular studies on salt tolerance in maize have revealed crucial insights. These include the identification of critical genes involved in salt tolerance mechanisms [373], the exploration of physiological, biochemical, and molecular responses in contrasting maize lines under salt stress [374], the use of genome-wide association studies to uncover the genetic basis for salt tolerance traits [375], and the classification of maize genotypes based on morphological characteristics to determine salt tolerance levels [376]. Research has identified essential genes like *ZmPIF3*, *ZmHAK1*, *ZmNHX1*, *ZmSTG1*, and *Zm00001d053925* that play pivotal roles in enhancing salt tolerance in maize [375-379]. Luo et al. [380] used genome-wide association analysis to identify salt tolerance markers in maize. They predicted candidate genes and confirmed their roles with CRISPR/Cas9, advancing our understanding and offering avenues for genetic manipulation to enhance crop resilience to salinity stress. These genes involve various mechanisms, such as regulating stress responses, ion transport, osmotic balance, and photosystem activity under salt stress conditions. Maize utilizes defense mechanisms such as osmolyte production, activation of antioxidant enzymes, and regulation of ion transport to counteract salt stress [133]. Research endeavors to unravel salt tolerance mechanisms have resulted in the discovery of salt-tolerance QTL and the breeding of salt-tolerant maize varieties [381]. Additionally, studies have highlighted the importance of hormone signaling, Ca²⁺ signaling, and transcription factors in mediating salt stress responses in maize. The

findings underscore the significance of understanding the molecular basis of salt tolerance in maize for developing salt-resistant varieties and improving crop productivity in saline environments.

5. Conclusion

Salinity stress is a severe threat to agriculture, considerably reducing the growth, physiological functions, and yield of maize by negatively affecting different growth stages, such as seed germination and vegetative and reproductive stages. Salinity adversely affects photosynthetic apparatus, photosynthesis, respiration, transpiration, stomatal and hormonal regulation, water status, and enzymatic activities, which distress the growth performance of plants and consequently reduce yield. Plants cope with saline stress in various mechanisms like homeostasis of toxic ions, synthesis of compatible solutes, antioxidant compounds, and other substances (polyamines, NO), regulation of hormonal balance, apoplastic acidification, etc. It has been proved that different agronomic management practices can effectively eliminate/alleviate the phytotoxic effects of salt stress like the selection of salt-tolerant genotypes, priming of seeds and seedlings, the addition of organic matters, management of nutrients, application of freshwater, exogenous application of hormones, osmoprotectants, polyamines, and NO, and uses of arbuscular mycorrhizal fungi and PGPR. Plant scientists are focusing on developing a complete profile of genes, proteins, and metabolites responsible for different mechanisms of salinity tolerance in different crops. Recent molecular studies on salt tolerance in maize have identified essential genes, such as *ZmPIF3*, *ZmHAK1*, *ZmNHX1*, *ZmSTG1*, and *Zm00001d053925*, and utilized genome-wide association analysis and CRISPR/Cas9 technology to uncover genetic markers and mechanisms, offering the potential for enhancing crop resilience to salinity stress. However, there is a lack of information integration from genomic, transcriptomic, proteomic, and metabolomics studies. Therefore, a combined approach is essential for determining the key pathways or processes controlling salinity tolerance in maize/crops in the future. This chapter displays the tolerance mechanisms and mitigation strategies of maize under salinity stress that will be helpful for other maize improvement strategies.

Author Contributions

Conceptualization, Manuscript Development, writing—original draft preparation: Mohammad Sohedul Islam, Md. Rafiqul Islam, Md. Kamrul Hasan, ASM Golam Hafeez, Md. Kaium Chowdhury, Moaz Hosen Pramanik ; writing—review and editing, Muhammad Aamir Iqbal, Murat Erman, Celaleddin Barutcular, Ömer Konuşkan, Anamika Dubey, Ashwani Kumar, Ayman El Sabagh. All authors have read and agreed to the published version of the manuscript.

Competing Interests

The authors declare no conflicts of interest.

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