SALINITY STRESS IN CULTIVATED PLANTS: TOXIC IMPACTS, TOLERANCE MECHANISMS AND MITIGATION STRATEGIES

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Abstract. Salinity stress is an ever-present threat to crop productivity and its extent is continuously increasing due to climate change and anthropogenic activities. The accumulation of excessive concentration of salts disturbs photosynthesis, and hormonal balance and causes nutrient imbalance, ionic toxicity, and osmotic stress which in turn reduce the final yield and quality. Further, excessive concentrations of salts also induce reactive oxygen species (ROS) production that damages the cellular membranes, proteins, lipids, and photosynthetic apparatus and cause a reduction in the synthesis of photosynthetic pigments. Therefore, it is mandatory to develop the appropriate measures to mitigate the adverse impacts of salinity tolerance in plants. The development of salt-tolerant crops, exogenous application of hormones and osmoprotectants, nutrient application, plant growth promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), biochar and nano-particles can help to mitigate the adverse impacts of salinity on plants. In the present review, the effects of salt stress on plants, the mechanism of salt tolerance in plants and different strategies that can be used to mitigate adverse effects of salinity are discussed. This review will provide new insights into existing knowledge to ensure better crop production in salt-affected soils.
Keywords: antioxidant, biochar, PGPR, reactive oxygen species, salinity

Introduction

Soil salinity is a serious abiotic stress that negatively affects crop productivity and global food security (Zhang et al., 2023). The increasing soil and water salinity is considered a major threat to crop production particularly in arid and semi-arid areas (Vimal et al., 2023). Globally, over 20% of the irrigated soils are salt-affected and this will increase to 50% by the end of 2050 (Hopmans et al., 2021). Human activities like excessive use of agrochemicals, industrial wastes, and unsustainable agricultural practices

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are important reasons for increasing soil salinity (Aksoy et al., 2022). Soil salinity is also affecting ecosystems, natural balance, bio-diversity, food production, food security, and the socio-economic health of farmers in over 120 countries around the globe (Mokrani et al., 2022). Salinity stress is a vital abiotic stress that significantly damages crop production owing to the accumulation of soluble salts in soil and water (Venâncio et al., 2023). The concentration of salts above 4 dS/m leads to toxic impacts on field crops, however, salt-tolerant crops perform better up to a salinity stress level of 4 dS/m.

Global food security could be strongly linked with salinity owing to its detrimental impacts on physiological, biochemical and morphological traits (Alkharabsheh et al., 2021). Salinity stress induces osmotic and oxidative stresses and leads to the production of reactive oxygen species that damage proteins, lipids and major cellular organelles (Singh et al., 2023). When soil salinity reaches the threshold level, it negatively affects plant growth, development, and yield by inducing osmotic and oxidative stresses (Whitney et al., 2018). The accumulation of salts in the root zone creates negative water potential which restricts the uptake of nutrients and water by root cells (Talat, 2020). The high concentration of Na^+ also disrupts the soil structure, decreases the infiltration rate, and restricts the movement of water and air (Ramos et al., 2020). Further, prolonged exposure to salinity stress causes the building up of Na^+ and Cl^{-1} in plant tissues which leads to ionic toxicity (Ahammed et al., 2020). At the sub-cellular level salinity stress also induces the production of reactive oxygen species (ROS) that damage the cellular membranes, impair cell functioning and disrupt the biosynthesis of photosynthetic pigments (Negacz et al., 2021; Singh, 2022). Besides this salinity-induced water scarcity induces stomata closing which hinders gas exchange and therefore decreases the rate of photosynthesis in plants (Abideen et al., 2020).

It has been documented that soil salinity also impairs metabolic activities, physiological activities, and nutrient uptake and subsequently reduces plant growth and yield. Thus, it is mandatory to develop the appropriate measures to remediate the polluted soils to enhance crop production. Different on-farm practices, genetic modification and salt tolerant crops and application of various natural and synthetic compounds can help to alleviate salinity and enhance crop productivity (Hajihashemi et al., 2020). Nonetheless, lack of skill knowledge, imbalanced ecosystems, environmental hazards and highs are restricting the effective utilization of salinity mitigation practices (Mansour, 2023a). Different approaches like the development of salt-tolerant cultivations, (Yassin et al., 2023), nutrient management, and application of hormones and osmolytes, biochar, and nano-particles can help to mitigate the adverse impacts of salinity in plants (Abdeen and Hefni, 2023). The use of these techniques helped to mitigate the adverse impacts of salinity and substantially improved the production of different crops, like, wheat (*Triticum aestivum),* maize *(Zea mays),* rice *(Oryza sativa),* and sunflower *(Helianthus annuus)* (Vimal et al., 2023).

The agriculture sector is a unique field that provides food and raw materials to humans for energy, construction and textile industries (El-Ramady et al., 2023). Currently, the agriculture sector is facing many problems like increasing climate change, urbanization, decreasing land holding, unsustainable use of resources and increased intensity of abiotic stress (Yadav et al., 2023a). Therefore, there is a dire need to adapt innovative approaches to ensure better productivity in the scenarios of rapidly changing climate and increasing extent of salinity stress (Sharma et al., 2023). Therefore, in the present, we highlighted the effects of salinity stress on field crops and the mechanism of salinity tolerance in crops. This review also discussed the role of

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arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR), externally applied hormones and osmoprotectants, biochar, and nano-particles to mitigate the adverse impacts of salinity on plants. In addition, this manuscript also identified the various research gaps that must be fulfilled to ensure a better crop under saline conditions using different practices.

What is salinity stress?

Salinity stress refers to excessive salt ions (i.e., the sulfate and carbonates of Na^+, Cl^-, Mg^+ and Ca^{+2}) present in the soil solution (Safdar et al., 2019). Among these, sodium and chloride salts caused more than 80% salinity stress (Liang et al., 2018). Salinity reduces water absorption, seed germination, seedling establishment, plant growth and development under less photosynthesis rate that lowers the crop yield (Safdar et al., 2019). Salt stress is of two types; primary salt and secondary salt stress. The primary salt stress is due to the presence of native salt ions whereas, the secondary salinity is due to anthropogenic activities including the use of brackish water for irrigation, overgrazing, high cropping intensity, etc. (Seleiman et al., 2022). Salt stress has severe damage to agriculture in Asian countries. The economy of the agricultural countries relies on land productivity, whereas the 40% crop yield the reduced under salt stress. Therefore, proper management practices should be adopted to cope with the increasing trend of salt stress-related problems (Boorboori and Zhang, 2023).

Effects of salinity stress on plants

Effects on seed germination and growth

Salt stress affects the seed embryo, lowers the water uptake and decreases seed germination and seedling growth (*Table 1*) (Atta et al., 2023). Micea et al. (2023) reported a considerable decrease in radical emergence in saline soil significantly reducing the water absorption and different enzymatic (a-amylase and b- amylase) activities to hydrolysis the food reserves (Li et al., 2019). In addition, starch metabolism is vital for optimum seedling germination (Alam et al., 2022). Contrary, the salinity stress develops osmotic stress that affects the starch percentage, which causes a 60% reduction in seed germination (Gómez-Pando et al., 2010). Less water potential under a saline environment leads to the closure of stomatal openings, affects the photosynthesis rate, and a significant reduction in crop growth and yield (Garg and Bhandari, 2016).

Specific ion toxicity

The severity and longevity of salt stress resulted in a specific ion effect that is mainly due to the excessive salt ions movement from root to other plant tissues (Seleiman et al., 2022). Nutrient absorption and hormonal regulation are significantly affected in plants growing in salt stress due to the effect of specific ion toxicity (Aslam et al., 2023). High Na^+ uptake affects the structure of stomata, and its opening, and lowers the K^+ and Ca^+ ions, while the Cl^- ion degrades the chlorophyll and leads to considerable reduction in photosynthesis (Arif et al., 2020). High sodium chloride (NaCl) concentration decrease the water balance that causes cell dehydration in plants (Mansour, 2023b). However, plant species are specific with the mechanisms of ion exclusion (Aslam et al., 2023). Huang et al. (2022) observed various transporters help plants to exclude Cl^- and Na^+ ions.

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Table 1. *Effect of salinity stress on plant growth, development and physiological traits*

Salinity stress	Plant species	Effects	References
200 mM NaCl	*Triticum aestivum*	Salt stress reduced the relative growth rate of root and shoot length, K^+/Na^+ ratio, stomatal conductance, quantum efficiency of PSII, chlorophyll fluorescence and chlorophyll content	Saddiq et al., 2021
10 dSm^{-1} EC	*Oryza sativa*	Salinity decreased the root and shoot length, K^+ uptake, and increased Na^+ uptake Na^+/K^+ value	Krishnamurthy et al., 2016
100 mM NaCL	*Zea mays*	Germination (%), leaf area, fresh and dry weight of plant biomass, Chl-a, Chl-b, carotenoid, and total chlorophyll contents were significantly reduced under salt stress	Zahra et al., 2020
80 mM NaCl	*Phaseolus vulgaris* L.	Salt stress significantly reduces the growth attributes (plant height, leaf area, root surface area, plant dry biomass), and physiological traits (RWC, WUE, photosynthetic rate, transpiration rate, MSI%) and increases the leaf Na^+	Beykkhormizi et al., 2016
160 mM NaCl	*Triticum aestivum*	Salinity stress significantly decreased the root and shoot dry weights, photosynthesis rate, stomatal conductance, transpiration rate, shoot K^+ content, root K^+/Na^+, shoot K^+/Na^+, root-to-shoot K+ translocation, and increased the Na^+ content in root and shoot	Pour-Aboughadareh et al., 2021
12 dS m^{-1} NaCl	*Triticum aestivum*	Fresh and dry weight of seedlings (root + shoot), leaf water and relative water contents, chlorophyll contents, stomatal conductance, germination percentage and germination index were significantly decreased by increasing salinity level	Ahmed et al., 2022
12 dS m^{-1} NaCl	*Triticum aestivum*	Salt stress reduced spikelet/spike, grains/spike, 1000 grain weight, grain and biological yield), RWC, turgor and osmotic potential, photosynthetic rate, Chl a, b, total Chl contents, and MSI in plants	Yadav et al., 2023b
EC 20 mmho/cm	*Triticum aestivum*	Salinity stress increased electrolyte leakage, MDA and proline contents, and reduced plant height, tiller count, and plant biomass	Amin et al., 2023
15 dSm^{-1} NaCl	*Gossypium herbaceum*	Salinity decreased the plant height, number of bolls/plant, boll weight, lint weight, seed cotton yield/plant, seed index, seeds/boll, seed mass/boll, lint mass/boll, 100 seed volume, strength and length of fiber, lint%, K^+, K^+/Na^+ ratio, CAT, TSP, chlorophyll a, b, and relative water contents	Zafar et al., 2022

RWC: relative water contents, WUE: water use efficiency, MSI: membrane stability, CAT: catalase, TSP: total soluble protein. MDA: malondialdehyde

Mineral uptake and assimilation

The presence of salt ions in soil solution interferes with the different nutrients and develops an imbalance in plant nutrient uptake (Hailu and Mehari, 2021). The nutrient (nitrogen (N), phosphorus (P), potassium (K), boron (B), zinc (Zn), calcium (Ca), and magnesium (Mg) absorption reduced under Na^+ and Cl^- ions in saline soil (Yang et al., 2023a). Likewise, Nitrogen uptake and translocation in legumes decreased due to the antagonistic effect of Cl^- and nitrate (NO_3) (Zayed et al., 2023). Under salinity, free amino acid accumulation decreases the activities of enzymes involved in nitrogen assimilation (Aouz et al., 2023). Further, less activity of nitrogenase enzyme under salinity stress could be the reason for low N assimilation in plants (Dong et al., 2023). Farooq et al. (2022) stated a significant reduction in essential (Ca^{2+}, Mg^{2+}) nutrient uptake in the presence of high salt ions.

Ragab et al. (2022) also noticed less uptake of Ca^{2+} and K^+ ions in faba beans under saline conditions. Boron and magnesium contents also decreased under salinity (Hussain et al., 2019). Less nutrient uptake leads to a significant reduction in assimilation and carbohydrate synthesis that affects plant growth and yield.

Hormonal imbalance

Salinity stress significantly reduced the concentration of hormones including Indole-3-acetic acid (IAA), gibberellic acid (GA), and cytokinins (CK) in the plant tissues and

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therefore leads to considerable reduction in the plant normal functioning under stress conditions (*Fig. 1:* Fahad et al., 2015a). These hormones are responsible for cell growth, cell differentiation, and organelle development, along with the primary and secondary growth of plants. The salt stress imperatively restricts the hormone production in plants leading to the reduction in plant growth and development (Aslam et al., 2023). Likewise, the high uptake of Na^+ ions from saline soil considerably reduced wheat production (Hassan et al., 2022). Zeeshan et al. (2020) reported better crop yield under saline soil due to improved hormonal regulation in salt-tolerant cultivars. However, the exogenous application of hormones regulates the hormonal concentration under salinity stress (Youssef et al., 2023). The exogenously applied jasmonates improve photosystem (PS) II efficiency, leaf anatomy and photosynthetic pigments under salt stress (Amiri et al., 2023). A foliar spray of salicylic acid regulates photosynthesis and protects the photosynthetic apparatus from oxidative damage under salt stress (Nigam et al., 2022). Further, Omidi et al. (2022) reported the membrane permeability and protection from lipid peroxidation under salt stress, which enhances the growth and yield of the crop. In rice, externally applied salicylic acid improves root growth and prevents the chlorophyll structure from oxidative damage that increases crop yield (Urmi et al., 2023). Similarly, the salinity tolerance increased in wheat due to high anti-oxidant production with exogenous application of salicylic acid (El-Hawary et al., 2023).

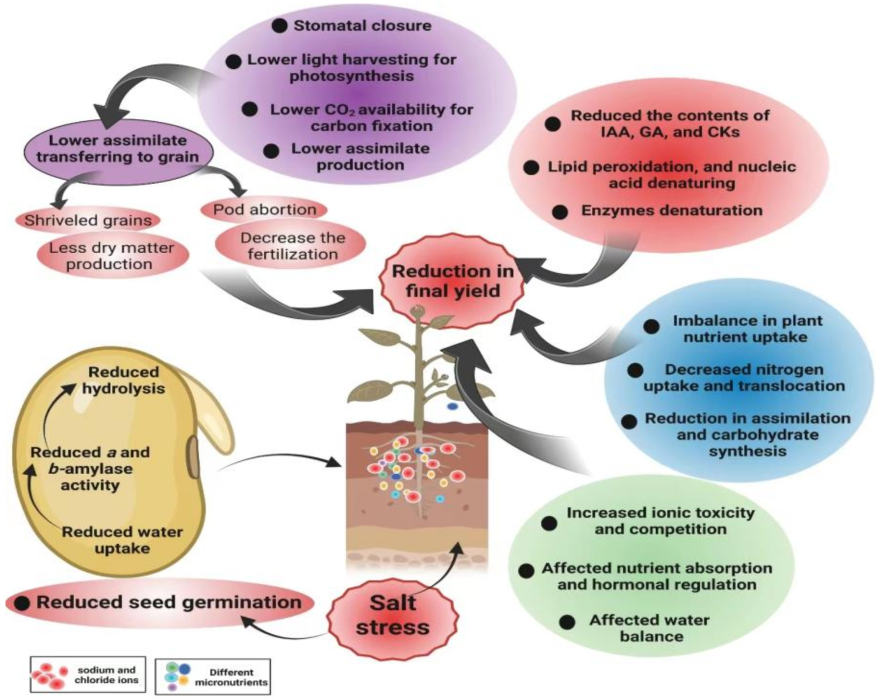

Figure 1. *Salinity stress reduced the seed germination, and nutrient uptake, induce stomata closure, decreases chlorophyll synthesis, assimilate production, electron transport, and cause enzymes denaturation and lipid peroxidation therefore, and leads to reduction plant growth*

Oxidative stress

Reactive oxygen species (ROS) under salt stress lead to the development of oxidative stress that considerably disturbs the plant's metabolic processes (*Fig. 1*). Moreover, lipid peroxidation and nucleic acid denaturing are the most common effects of oxidative

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stress in plants that result in cell death (Ali et al., 2023). Plants adopt the closure of stomata to cope with the stress condition, in resulting, less carbon dioxide (CO_2) availability for carbon fixation reducing the assimilate production and final yield production (Murchie et al., 2022). Plants produce ROS in peroxisomes and mitochondria under salinity (Aziz et al., 2022) whereas Ali et al. (2023) reported a dual role of ROS in the regulation of metabolic processes and signal transduction pathways under salt stress. Conversely, these ROS also damage membranes, chloroplast degradation and denaturation of proteins, hence decreasing plant growth and development (Aslam et al., 2023).

Light harvesting and carbon fixation

The closure of the stomatal opening during salt stress significantly reduced the carbon fixation and light harvesting into photosynthesis (Dourado et al., 2022). Less CO_2 intake causes oxidative damage in plant cells. Oxidative damage to PS-II resulted in a significant reduction in photosynthesis compared to stomatal closure in chickpeas during salt stress (Paul et al., 2023). Similarly, reduced CO_2 fixation leads to damage to the thylakoid membrane and lowers photosynthesis during salt stress (Krausko et al., 2022). Likewise, decreased photosynthetic pigments and poor conductance of the electron transport chain are the main consequences of salt-induced oxidative damage in mungbean (Naz et al., 2022).

Grain development and yield formation

Salt stress has considerable effects on crop growth (*Table 1*) and developmental stages (Maryum et al., 2022). Salinity stress reduced the crop growth rate (CGR), net assimilate rate (NAR), leaf area index (LAI), and plant height (Mohammadi Alagoz et al., 2023). Interestingly, the consequence of salt stress is more prominent in upper plant parts during growth stages (Hasanuzzaman et al., 2013). Salt stress affects crops at the flowering stage and lowers the number of flower production, and pollen integrity following a considerable decrease in the number of pod formations, the number of seeds per pod, and the grain yield of chickpea crops (Maryum et al., 2022). Salt stress affects the pollen viability, and receptivity of stigma and lowers the assimilate transferring to grain causing a significant decrease in grain weight, size and final yield production in cereals (Bhardwaj et al., 2022). Salinity stress decreases fertilization by lowering the length of the pollen tube, substantially leading to decreased grain production in chickpeas (Saini et al., 2022). Other studies reported pod abortion under salt stress (Pushpavalli et al., 2016) that reduces the grain count, and pulse yield (Farooq et al., 2017; Rehman et al., 2022). Sheldon et al. (2017) noted that salt-induced water shortage resulted in less leaf area; reduced light interception, decreased photo-assimilate production, shriveled grains and less dry matter production (Albacete et al., 2014). Similarly, Mubushar et al. (2022) observed a considerable reduction in dry matter production and grain yield due to salt stress. Conclusively, grain filling is the most sensitive stage and salt stress develops shriveled grains that lower the grain weight and cause a serious reduction in final yield (Saini et al., 2022).

Grain quality

The salinity problem has negative impacts on the grain quality (protein, carbohydrate, and starch percentage) attributes of different crops (Zheng et al., 2023).

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Less nitrogen uptake during salinity stress considerably reduced the grain protein contents (Qados, 2011). Amino acid and carbohydrate contents were remarkably decreased with increasing salt stress (Razzaq et al., 2020). Similarly, grain protein, carbohydrate and amino acid production level significantly decreased in wheat growing in saline soil (Alsahli et al., 2019). The oil and protein contents were severely reduced in soybeans under salt stress (Sadak et al., 2020). Aouz et al. (2023) reported the imbalance in essential nutrient uptake from saline soil lowers the carbohydrate and protein levels in grains.

Biological nitrogen fixation (BNF)

Salinity stress has a devastating impact on biological nitrogen fixation (BNF) ability of legume crops (Gupta et al., 2021). Less BNF resulted in a decrease in atmospheric nitrogen fixation in soil that affected grain production. Nodules are imperative for the BNF process whereas salt stress severely damages the nodule formation in legumes However, cultivars are specific in salt tolerance (Elgharably and Benes, 2021). Gupta et al. (2021) reported that the process of symbiosis is sensitive to salt stress reducing the symbiosis relationship between legume roots- and rhizobia (Ramírez and Damo, 2023). Further, salt stress lowers the activity and density of nodules in soil (Ilangumaran et al., 2021). Salt stress resulted in premature nodule senescence and less nodule formation in legumes leads to a significant reduction in soil nitrogen contents and less grain yield (Kaur et al., 2022a).

Mechanism of salinity tolerance

Accumulation and adjustment of osmotic substances

Salt stress has negatively reduced plant growth through specific ion toxicity (SIT), ROS, imbalances in plant nutrition and hormones (Zeng et al., 2015). Osmotic adjustments are crucial to keep cells turgid and help the plants (*Fig. 2*) maintain the optimum metabolic activities which in turn improves the plant growth and final (Abid et al., 2018). Plants produced various kinds of osmotic substances i.e., sugars, proline, glycine betaine (*Table 2*), and other osmolytes within their body to maintain the osmotic balance (Hussain et al., 2021). Proline is an imperative lower molecular weight substance that occurs in the plant body has higher water solubility and has a no-net charge on different pH. It significantly improved the plant performance under salt stress and leads to a significant increase in growth and yield (Butt et al., 2016). The plant accumulates a different kind of osmolytes under salt stress which maintains the osmotic adjustment and therefore ensures the plant's survival under salt stress (Choudhary et al., 2023). Proline is one of the important osmolytes produced by the plant under salt stress and it increased the salt tolerance against the salinity stress (Butt et al., 2016). On the other hand, other sugars like trehalose, glucose, and sucrose, can easily stabilize the cell membrane as well as the protoplast (Guo et al., 2015). Moreover, these sugars also protect the different enzymes from higher concentrations of toxic ions (Sharma et al., 2019).

In salt stress increase in the osmotic potential increases the osmotic stress. Plants accumulate soluble sugars to enhance their osmotic potential (*Fig. 2:* Aslam et al., 2023). Consequently, the concentration of soluble sugar can be used as an indicator of salt tolerance in different plants. Previously it was reported that sugars i.e., betaine

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blocked the transport of Na^+ and Cl^- from plant roots to upper plant parts and promoted the transportation of K^+ (Chakraborty et al., 2022). Moreover, exogenously applied betaine improved the relative water contents and reduced the osmotic potential in maize crops under saline conditions (Hafez et al., 2021). In addition, glycine betaine also increases the concentration of protein and sugars and can also increase the soluble protein and soluble sugar content of maize leaves in low-temperature stress conditions (Gupta et al., 2021).

Table 2. *Effect of salinity stress on osmolytes accumulation, oxidative stress markers and antioxidant activities under salinity stress*

Salinity stress	Plant species	Effects	References
60 mM NaCl	*Triticum aestivum*	Salt stress increased the MDA, and H_2O_2 decreased the antioxidant enzymes (SOD, POD, CAT, NR), and non-enzymatic antioxidants (ascorbate, glutathione, total phenolic content, and total flavonoid content) activity	Sadak et al., 2022
60 mM NaCl	*Thymus vulgaris*	Total phenolic contents, leaf flavonoid, and Cinnamic acid were increased by 20%, 36.6% and 31.4% during salt stress	Bistgani et al., 2019
150 mM NaCl	*Zea mays*	Salinity increased the MDA by 109%, $O_2^{\bullet-}$ and H_2O_2 by 130 and 99%, respectively. Further, LOX activity was also enhanced by 133%. And SOD, POD, CAT, GPX, APX and DHAR were significantly increased	Rohman et al., 2019
150 mM NaCl	*Triticum aestivum*	Salts stress significantly increased the proline (74%), MDA (34.26%), glycine betaine (15.45%), catalase (88.32%) and peroxidase (77.56%) contents in wheat seedlings	Datir et al., 2020
100 mM NaCl	*Solanum lycopersicum*	Salinity increased the H_2O_2, EC, MDA contents, protease (79.64%) and lipoxygenase (180.9%) over control. Further salinity decreased the soluble sugars, proline, glycine betaine, SOD, POD, CAT, APX, and GR concentration	Ahanger et al., 2020
150 mM NaCl	*Phaseolus vulgaris*	Salinity causes oxidative damage by increasing lipid peroxidation, electrolyte leakage, and ROS	Dawood et al., 2022
100 mM NaCl	*Lepidium draba*	EL, MDA, and H_2O_2 increased with increasing NaCl levels. However, APX, SOD, and guaiacol peroxidase activity decreased at severe salinity levels	Jamshidi Goharrizi et al., 2020
100 mM NaCl	*Vicia faba*	Salinity stress reduced enzymatic activities, proline concentration, and protein contents, and increased the MDA and H_2O_2 accumulation	Alzahrani et al., 2019
100 mM NaCl	*Triticum aestivum*	The SOD, APX, GR, and GPX contents were increased up to 95%, 52%, 84%, and 54%, respectively along with significant rise in H_2O_2, EL (%) and TBARS contents in salinity	Wahid et al., 2020

MDA: malondialdehyde, H_2O_2: hydrogen peroxide, CAT: catalase, SOD: superoxide dismutase: POD: peroxidase, NR: nitrate reductase, LOX: lipoxygenases, GPX: glutathione peroxidase, APX: ascorbate peroxidase, DHAR: dehydroascorbate reductase, EC: electrical conductivity, TBARS: thiobarbituric acid reactive substances

Ion-selective absorption and compartmentalization

Salinity stress caused the SIT in plant cells due movement of Na^+ into plant cells. The influx of Na^+ into plant cells disturbed the ion balance. The excessive concentration of Na^+ reduces the K^+ and has negative impacts on enzymatic activities, photosynthesis, and various other plant metabolic activities (Alam et al., 2022). Salt tolerances do not mean that plants only have the tolerance against toxic ions, but they also have the adaptations against the salinity secondary effects i.e., water (Mansour, 2023a). Salt-tolerant plants maintain a higher concentration of K^+ under salt stress which maintains the stomata movements and therefore ensures their survival under salt stress. When plants absorb the Na^+ plants either discharge Na^+ or transport the Na^+ into an inactive region. The anti-porter (Na^+/H^+) is responsible for the portioning of Na^+ into the vacuole and thereby reduces the concentration of Na^+ in the vacuole. The anti-porter (Na^+/H^+) is

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responsible for the translocation of Na^+ from the cell to extracellular regions (Flessner and Orlowski, 2022). Moreover, ani-porter (Na^+/H^+) is also necessary to maintain the cell pH and Na^+/H^+ ratio in the plant cells (Yue et al., 2012). It has been reported that overexpression of anti-porter (Na^+/H^+) significantly increased the salt concentration in the Arabidopsis plants (Yang et al., 2021). Similarly, overexpression of the ant-porter (Na^+/H^+) gene $TaNHX_3$, in wheat crops significantly increased the crop yield under salt stress (Lu et al., 2014). Similarly, the introduction of the wheat antiporter gene $TaNHX_2$ significantly enhanced the salt tolerance in chili plants (Bulle et al., 2016). The optimum availability of zinc improved the expression of anti-porter (Na^+/H^+) under salt stress and therefore improved the salt tolerance in plants (Xu, et al., 2014). In conclusion, anti-porter (Na^+/H^+) can significantly improve the plant's survival under salt stress.

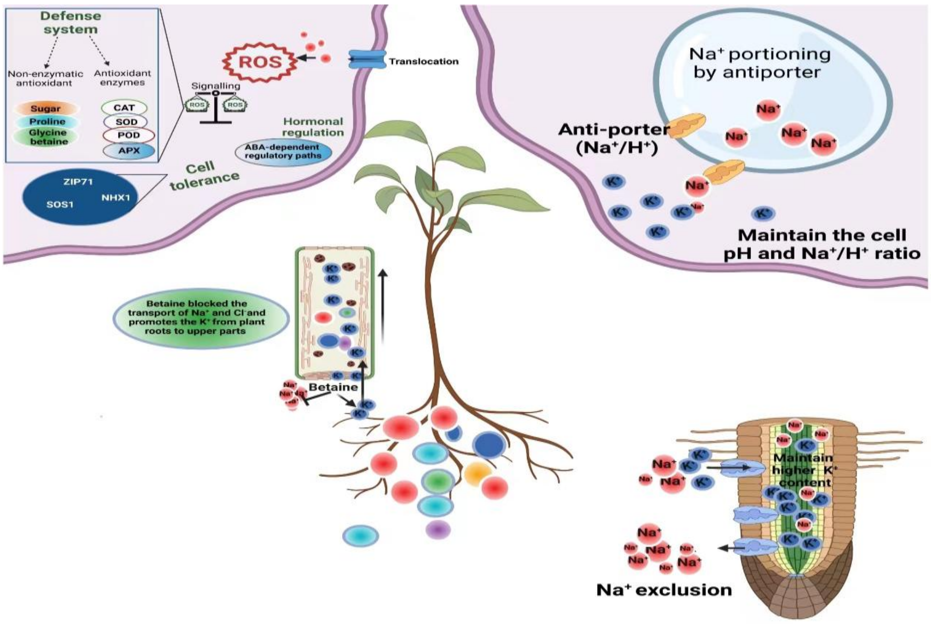

Figure 2. *Mechanism used by plants to counter the toxic effects of salinity*

Scavenging of ROS

Oxygen is essential for plants as it participates in mitochondrial respiration and oxidative phosphorylation to produce energy. However, the oxygen is activated into ROS which reduces the plant growth and leads to a significant reduction in the final yield. ROS damages membrane permeability denatures the protein, lipids and causes irreversible metabolic dysfunctions, and leads to cell death (Hasanuzzaman et al., 2021). ROS also converts the amino acid residues into carbonyl derivatives (Akagawa, 2021). Plants have different enzymatic and non-enzymatic antioxidant defensive systems that they use to cope with the ROS. Superoxide dismutase (SOD) is the first enzymatic defensive system in plants and can remove the toxic ions from cells. SOD also converted the O_2 into the H_2O_2 which prevents the plants from damages of O_2 (Wang et al., 2016). Ascorbate peroxidase (APX) is another important enzymatic defensive system that also plays a significant role in plant survival under salt stress. APX removes the H_2O_2 from the chloroplast and protects it from damage to H_2O_2. The increase in APX significantly increases the plant's tolerance against the ozone. The increase in

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concentration of ROS in plants also leads to lipid peroxidation. Malondialdehyde (MDA) is one of the main enzymes which prevents plants from lipid peroxidation. The extent and concentration of MDA in plants represent the ability of plants against the lipid per peroxidation.

Research of salt-tolerance genes

Salinity stress reduces seed germination, seedling establishment, plant growth, flower development, and fruit setting leading to a significant decline in the crop yield (Mangena, 2023). The selection of tolerant varieties and identification of salt-tolerant genes in crop plants can play a significant role to cope with the problems of salt stress. We can identify the salt tolerant genes and these genes can be used to develop the genotypes with good tolerance against the salt tolerance. Plenty of genes for the salinity tolerance have been identified and they have been studied to understand the mechanisms of salt tolerance. Likewise, the anti-porter (Na^+/H^+) genes SOS_1 and anti-porter (Na^+/H^+) vacuolar gene AtNHX1 remarkably improved the salt tolerance in transgenic (Yang et al., 2023b).

Likewise, the AtSAT32 gene also enhanced the salt tolerance in plants and increased the activities of vacuolar H^+ (Hasanuzzaman, 2022). Moreover, in rice OsbZIP71 gene remarkably improved the salt tolerance in the plants through the ABA-dependent regulatory paths (Liu et al., 2014). The use of genetic engineering approaches can also help us in identifying the different genes and development of transgenic plants having tolerance against salt stress (Singh and Roychoudhury, 2021). Salt tolerance in plants is controlled by thousands of genes and hundreds of physiological mechanisms. Therefore, it is necessary to study the maximum number of genes related to salt stress. Different biological approaches including breeding approaches, marker selection, and genetic engineering can help us to identify the different salt-tolerant genes and development of cultivars with good salt tolerance (Ashraf et al., 2008).

Management strategies

Selection and conventional breeding approaches

Salt tolerance in plants is a multi-gene function and it is a very complex process. The use of conventional breeding techniques has made progress in this area of research (Alam et al., 2022). The development of salt-tolerant genotypes involves the identification of genetic variation, and the exploitation of new resources to create the genetic variations (Sharma et al., 2013; Duc et al., 2015). It has been reported that a strong variation exists among the genotypes for salt tolerance that can used to develop the genotypes with good salt tolerance (Al-Ashkar et al., 2020).

Mass screening is a promising approach that is used to identify the salt-tolerant genotypes and for the development of salt tolerance. Sehrawat et al. (2014) compared the various genotypes for salt tolerance. They reported a considerable reduction in germination and seedling growth of genotypes and they found that genotypes differed significantly for the salinity stress. Moreover, the various plant attributes including, seed germination seedling growth, leaf Na^+/K^+ ratio, plant osmotic adjustments, grain weight and grain yield are considered to develop the genotypes with good salt tolerance abilities have been considered to develop the genotypes (Alam et al., 2022). Tissue ion homeostasis is an imperative character that is considered to develop and identify

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cultivars with good salt tolerance (Munns and Tester, 2008). The accumulation salts like Na and Cl at reproductive stages are the cultivars more sensitive against the salt stress (Samineni et al., 2011). Moreover, there is no correction between the grain yield and quantity of Na^+ present on a percentage dry matter basis (Vadez et al., 2007). It has been reported that chickpea combinations of ion exclusion and tolerance against toxic ions have a significant contribution to the development of salt-tolerant cultivars of chickpeas (Sehrawat et al., 2013). For salt tolerance grain yield is considered as the important trait, therefore, the traits identified for salt tolerance should be co-related with grain yield (Flowers et al., 2010). Moreover, direct selection of cultivars may also be used to develop the genotypes with good salt tolerance abilities (Sharma et al., 2013). In conclusion, conventional breeding can be used to develop cultivars with good salt tolerance capabilities.

Biotechnology and functional genomics

Biotechnological approaches can also help us to cope with salt stress problems. The identification of quantitative trait locus (QTLs) of related traits along with the markers can be used for the introduction of salt-tolerant traits in the un-adapted. The use of molecular markers has gained attention in recent times to develop genotypes with better salt tolerance. Likewise, Sehrawat et al. (2014) developed the 38 micro-satellite markers (SSRs) to determine the genetic variations among the mungbean cultivars against the salt tolerance. They noted that 100 out of 124 genes were polymorphic in wild and cultivated mungbeans. The SSRs can be used to identify the QTLs and the genes having good salt tolerance. Moreover, salt-resistant genes of wild genotypes can also be used for the development of cultivars and hybrids for the salt stress problem (Lee et al., 2004).

The SSRs can be used in breeding programs for the early selection of cultivars rather than the phenotypic screening (Nirmala et al., 2016). It has been reported that mi-RNAs have been accumulated in drought stress and abscisic acid (ABA) applied in drought stress, however, their role under salt stress is not explored yet. Moreover, it was also found that the mi-RNAs expressed and accumulated under salt stress in the soybean nodules (Dong et al., 2013). Salt tolerance in plants is regulated by different mechanisms which are modulated by the various TFs in plants. The TFs are proteins, which regulate the gene's transcription. Sarkar et al. (2014) reported that DREB1A is a prime TF that confers with the salt stress at the seedling stage in the AtDREB1A groundnut plant.

The salt tolerance with DREB1A can be attributed to its expression and upregulation of downstream genes which contributed significantly towards the salt tolerance. In a study, Khatib et al. (2011) inserted transgene (DREB1A) into embryo explants of lentil plants. They reported that the incorporation of transgene in the lentil plants increased the drought and salt tolerance in lentil plants. Mutation breeding is a promising approach that can be used to develop crop plants with more salt tolerance (Kaur et al., 2022b). However, the development of whole genome sequencing (WGS) has made mutation breeding easier because of faster mapping and identification of the genome simultaneously (Ayan et al., 2022). Moreover, the sequencing of the next generation can be used to study the differential response of variables under different environments (Pandey et al., 2016). Therefore, the identification of salinity-tolerant genes by WGS and mutation breeding can help in understanding the molecular mechanism of salt salinity tolerance to develop salt-tolerant cultivars (Kudapa et al., 2013).

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Role of arbuscular mycorrhizal fungi in salt stress

The use of arbuscular mycorrhizal fungi (AMF) for improving crop performance under salt stress has gained attention in recent years (*Fig. 3*). AMF improved crop growth under salt stress owing to improvements in water and nutrient uptakes, nodulation, and improvement in (Parihar et al., 2020). Likewise, it was reported that AMF improved the N uptake in chickpea plants under salt stress and consequently increased the final grain production (Sheteiwy et al., 2022). Moreover, AMF also improved the phosphorus uptake increasing the surface area for P absorption and by solubilizing P through the release of organic acids and different (Etesami, 2020). The salinity reduced the formation and occurrence of nodules, owing to senescence, which resulted in the formation of green pigments and loss of N (Etesami and Adl, 2020). Conversely, the application of AMF mitigates the damaging effects of salinity on nodules and improves the nodule count and N fixation under salt stress (Ben-Laouane et al., 2020). They noted that AMF improved the plant growth and fixation of N under salt stress. Another study reported that AMF protects the plants of faba beans from salinity stress. Similarly, seeds of alfalfa treated with AMF showed better growth under saline conditions as compared to untreated seeds (Shi-Chu et al., 2019).

Figure 3. *Different management practices used to manage salinity stress. The use of conventional breeding and biotechnological approaches, and application of AMF, PGPR, hormones, osmolyte, biochar and nano-particles can be used to mitigate adverse impacts of salinity*

Metwally and Abdelhameed (2018) reported that AMF also increased the proline contents under salt stress and in mungbean plants as compared to seeds without AMF. Likewise in soybeans, AMF-treated plants had more proline concentration as compared to non-AMF-treated plants (Grümberg et al., 2015). Conversely, it was also reported that non-AFM treated plants had more proline concentration as compared to treated

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AMF. Moreover, the soybean seed treated with AMF had no accumulation of sugar under salt stress (Sharifi et al., 2007). Recently it was reported that AMF and Si application together remarkably improved the growth, yield, and nutrient uptake in chickpea plants. However, the application of AMF appreciably improved the growth and N uptake while the application of Si improved the Na^+/K^+ (Garg and Bhandari, 2016). Therefore, the AMF improved the growth under salt stress due to better uptake of nutrient uptake and by improving the osmotic adjustments and maintenance of the Na^+/K^+ ratio.

Role of plant growth promoting rhizobacteria (PGPR) in salt stress

PGPR has an imperative role in plant growth and development. They inhabited plant roots and improved plant growth. Seed inoculation with PGRP reduced the salt-induced effects of ethylene (Nadeem et al., 2013). The use of PGRP improved crop growth under salt stress by improving nutrients and photosynthetic activities (Vejan et al., 2016). Seed inoculation with PGRP in mungbean plants significantly improved plant seedling growth and final yield (Ahmad et al., 2011; Zaheer et al., 2019). Seed inoculation with PGPR improves the root system by regulating the phytohormones and helps in the development of roots and root hairs thereby improving the nutrient uptake crop growth and other signal triggers involved in lateral root branching and root hair development (Grover et al., 2021).

Moreover, seed inoculation with PGRP in leguminous crops improved soil fertility and helped in adding important nutrients to the soil (Chen et al., 2023). Moreover, the symbiotic relationship between the PGRP and legumes is a cost-effective way to increase soil fertility and crop growth under salt (Zandi and Basu, 2016). Soybean seed inoculation with PGRP appreciably improved crop growth, uptake of nutrients, and rate of photosynthesis under salt stress (Han and Lee, 2005). In a study, Nadeem et al. (2013) reported that seed inoculation with the PGRP improved the shoot growth and yield under varying salinity stress levels. In another study, Azadikhah et al. (2019) found that seed inoculation with Pseudomonas improved crop growth, and final yield under salt stress. Similarly, Riviezzi et al. (2020) inoculated the soybean with B. japonicum and found a remarkable increase in root growth, nodule formation, and seed production as compared to no seed inoculation. Likewise, in another study, Ahmad et al. (2021) treated the seed of legume crops with PGPR and found appreciable improvement in crop growth and yield with seed inoculation. In conclusion, PGPR improved plant performance by reducing the effects of salt stress and by increasing phytohormone activities and nutrient uptake (Li et al., 2020).

Role of externally applied hormones and osmoprotectants in salt stress

External application of hormones can mitigate the damaging effects of salt stress in plants (*Fig. 3*). Likewise, the application of 0.5 mM salicylic acid significantly reduced the toxic effects of salinity on soybean plants by increasing the nutrient uptake and activities of antioxidant enzyme systems (Jia et al., 2023). The exogenous application of osmoprotectants improved the plant performance by increasing nutrient uptake, maintaining membrane stability, and by protecting the different enzymes from denaturation (Khalid et al., 2022). Moreover, the application of osmoprotectants also protects the protein, and amino acids from the damaging effects of ROS (Deinlein et al., 2014; Nawaz et al., 2022).

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Exogenous application of proline under saline conditions increased the salt tolerance in crop plants by improving the activities of POD and SOD (Mansour, 2023a). Likewise, the exogenous application of brassinolide improved carbon fixation, enzymatic activities, and dry matter production under saline conditions in mungbean crops (Liu et al., 2022). In another study, Verma et al. (2022) noted that foliar feeding of triacontanol and kinetin overcame the consequences of salinity stress by improving the enzymatic activities. The exogenously applied ABA increased nitrogen fixation and purine metabolism under salt stress (Kaur et al., 2021). Moreover, ABA also helps in gene expression and therefore leads to a reduction in damages of salinity stress (Chowrasia et al., 2023). Thus, hormones and Osmo protectants can be exogenously applied to improve crop performance under salt stress.

Role of seed priming and nutrient management in salt stress

Salinity stress significantly reduced the seed germination and led to poor stand establishment which in turn reduced the outcome. Therefore, proper management considerations should be adopted to mitigate the deleterious impacts of salt stress at the early stages of plant life (Alkharabsheh et al., 2021). Salt stress reduces the germination of seeds by osmotic stress or by toxic effects of higher concentrations of Na^+ and Cl^- ions increasing the (Atta et al., 2023). Seed priming is an important technique that improves the salt tolerance in crop plants by improving seed germination. Likewise, seed priming with mannitol significantly improved crop growth and performance under salt stress as compared to no seed priming (Biswas et al., 2023). Moreover, seed priming also improved seed germination and seedling growth by improving the nutrient uptake, and rate of photosynthesis and by maintaining the osmotic adjustments.

Farooq et al. (2019) soaked the seed for a certain time period in the water and noted that seed soaking with water significantly improved the seed germination and crop growth. Azooz (2009) soaked the seeds of faba bean in SA and noted that seed priming with SA significantly increased the seed germination and crop performance under salt stress. Fatema (2021) conducted a study to determine the impact of seed priming on the chickpea under salt stress. They noted that halo-priming in chickpeas improved the crop performance under salt stress. In another study, Jisha and Puthur (2014) noted that seed priming with SA improved the seed germination and seedling growth by maintaining the osmotic adjustments and by improving the photosynthesis and nutrients uptake. Patil et al. (2020) soaked the seed of a chickpea in the water for a certain period. They noted soaking of seed in water appreciably improved the seed germination, and root and shoot growth as compared to non-soaked seeds.

Likewise, the application of nutrients also improved the crop performance under salt stress. Likewise, Larbi et al. (2020) noted that application of K under salt stress significantly increased the salt tolerance in crop plants. Likewise, application of urea to soils deficient in N under salt stress remarkably improved the chickpea growth and yield under salt stress. Kafi et al. (2012) noted that the application of K and Ca mitigates the negative impacts of salinity stress and increases dry matter production. Murillo-Amador et al. (2007) studied that exogenously applied Si improved the seed germination and seedling growth under salt stress. In another study, Zuccarini (2008) found that exogenously applied Si improved crop growth and final yield by maintaining the osmotic adjustments under salt stress.

Abraha and Gebremedhn (2013) performed an investigation to compare the influence of seed priming with NaCl on maize crops. They noted that seed priming with NaCl

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significantly improved seed germination. They also noted that seed priming with NaCl remarkably improved the root and shoot growth, and root and shoot weights. Dai et al. (2017) Soda saline-alkali soil has double adverse effects on the growth, morphogenesis, and yield of the seed the influence of hydro priming and seed priming with $ZnSO_4$ and $CaCl_2$ on the performance of soybean. They noted a significant reduction in salt stress with seed priming techniques. However, they noted that seed priming with $ZnSO_4$ was more effective, and it resulted in maximum improvement in growth. They also observed that seed priming with $ZnSO_4$ also improved the activities of SOD and POD under salt stress and leads to consideration of reduction in consequences of salt stress.

Theerakulpisut et al. (2017) studied the effect of seed priming with different salts on the performance of rice crops under salt stress. They noted that seed priming with KNO_3 was effective in mitigating the damaging impacts of salt stress. They noted that seed priming with KNO_3 increased the activities of enzymatic defensive systems and led to a significant reduction in salt stress effects. Yohannes and Abraha (2013) treated the seeds of maize with different concentrations of NaCl. They noted that seeds treated with 2 mM NaCl remarkably improved the germination of maize seeds and root and shoot growth. Saed-Moocheshi et al. (2014) primed the seeds of maize with urea and KNO_3 and sown in saline conditions. They observed that seed priming with urea was more effective, and it significantly improved the activities of POD, SOD, and CAT and concentrations of Chlorophyll and other photosynthetic pigments.

Nasri et al. (2011) studied the effect of osmo-priming on the performance of lettuce under salt stress. They observed Osmo priming considerably increased the seedling growth and activities of phosphatase enzyme under salt stress and led to significant reduction in consequences of salt stress. Nakaune et al. (2012) primed the seeds of tomato in NaCl solution and sown them in salt stress conditions. They observed a clear difference in seed germination and seedlings with seed soaked in NaCl as compared to no soaking. Farhoudi et al. (2011) treated the seeds of muskmelon with a NaCl solution. They observed that seed priming with NaCl remarkably increased the concentration of proline and other sugar and decreased the membrane damage. They also noted a significant increase in enzymatic defensive systems with seed priming.

In another study Kardoni et al. (2013) exogenously applied Si improved the seedling growth and crop performance under salt stress as compared to no Si application. Hellal et al. (2012) studied the impact of foliar applied Si on the performance of faba bean under salt stress. They noted that foliar-applied Si significantly improved seedling growth, plant biomass production, and dry matter yield as compared to no Si application. Garg and Bhandari (2016) performed a study to determine the impact of Si on the performance of chickpeas under salt stress. They noted that foliar feeding of Si improved the nutrient uptake, growth, and yield under salt stress. In conclusion, seed priming with different nutrients and external application of nutrients can help to overcome the deleterious impacts of salt stress.

Role of biochar in salinity tolerance

Soil salinity poses a substantial limitation to crop productivity and global food security (Sofy et al., 2020). Dadshani et al. (2019) reveal the increasing trend of soil salinization has deteriorated 20% of cultivated and 33% of irrigated land globally. Biochar (BC) is a carbon-rich substance that ameliorates the harmful effects of salinity on soil characteristics and augments the physiological attributes of plants by enhancing salinity tolerance (Ali et al., 2021). Lashari et al. (2015) found that biochar

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supplementation improved the membrane stability by reducing MDA contents; reducing electrolyte leakage and increasing relative water content (RWC) in leaves. Ndiate et al. (2021) reported protection against oxidative stress and a high amount of unsaturated fatty acid and anti-oxidative enzyme activity in plants under salt stress with BC application (Ran et al., 2020). Owing to this, crops exhibited larger water use efficiency and productivity under saline stress conditions (Shabbir et al., 2021).

Usman et al. (2016) found that BC significantly increased P, K, Fe, Mn, Zn, and Cu concentrations in tomato plants growing under saline soils. Wheat straw-based BC increased P precipitation and reduced P concentration in plants growing under sodic soils (Wu et al., 2023). Hammer et al. (2015) found that ionic homeostasis in plants improved after BC application. Mansoor et al. (2021) noticed the reduced Na^+ absorption and increased plant growth with BC amendments in saline soils. Mehdizadeh et al. (2020) also found that BC application leads to a slight increase in the EC of both normal and sodic soils and caused to release of various nutrients (Ca, K, and Mg). Biochar application improves the K^+/Na^+ ratio, water holding capacity (WHC), and water use efficiency (WUE), while reducing salinity-induced osmotic stress in plants (Wu et al., 2023).

Salinity stress significantly reduces RWC, photosynthesis, and chlorophyll synthesis in plants (Manan et al., 2016). Conversely, BC application improved the stomatal conductance, leaf gas exchange, chlorophyll synthesis, and nitrogen use efficiency under SS (Shabbir, 2021). Further, biochar-mediated development in photosynthetic pigments is associated with improvement in soil physiochemical and biological characteristics as well as nutrients (K, P, Mg, Ca, and S) uptake and availability under salinity stress (Farhangi-Abriz and Torabian, 2018). Kaya et al. (2018) found that plants growing under SS exhibited more damage to photosynthetic pigments. Whereas, BC application significantly enhanced antioxidant activities, which prevented oxidative damage to photosynthetic pigments and photosynthetic apparatus of plants growing under SS (Rasheed et al., 2019).

Moreover, reactive oxygen species produced under salt stress damage the plant membranes, and proteins, and cause lipid peroxidation. While BC application reduces ROS production and restores the normal functioning of plants under salinity stress (Abbas et al., 2022). Biochar supplementation increased the antioxidant (CAT, POD, and SOD) production and lowered the TBARS, and H_2O_2 concentration during oxidative stress in saline sodic soils (Abbas et al., 2022). Kim et al. (2016) reported increased plant growth, grain quality, and yield with the use of biochar in saline soil. Biochar increases root surface area, nutrient acquisition, water intake, leaf area, photosynthesis, plant height, biomass, and grain yield (Akhtar et al., 2015b; Usman et al., 2016). Further, biochar-induced modification in soil properties resulted in better CEC, reduced Na^+ accumulation, high nutrient uptake and assimilation, chlorophyll synthesis, photosynthesis, and stress tolerance in plants (Soliman et al., 2022).

Role of nanoparticles in salinity tolerance

The use of nanoparticles (NPs) is considered the most promising technology to combat the effect of salinity stress on crops (Ahmad and Akhtar, 2019). The nanoparticles comprise smaller-sized particles (less than 100 nm) with large surface areas that influence the soil and properties and plant components at a macro level under salt stress (Das and Das, 2019). Different studies reported the use of nanoparticles (*Table 3*) at various plant growth stages with different (positive or negative) approaches during stress conditions (Zulfiqar and Ashraf, 2021). Mostly, researchers found

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improved morphological, biochemical, physiological, and yield-related attributes using nanoparticles application on plants at stress conditions (Noohpisheh et al., 2021). NPs modify hormonal regulation, activate antioxidants and related gene expression, and boost the salinity tolerance in plants (Zulfiqar and Ashraf, 2021). However, this effect varies depending on the abiotic stress conditions (Wahid et al., 2020).

Photosynthesis is reduced under salinity due to the presence of salt ions (Na^+, Cl^-) in soil solution (Hnilickova et al., 2021). NPs enhance the chlorophyll contents in leaves, light harvesting, and increase the photosynthetic rate under stress conditions (Ali et al., 2021). Other researchers also reported a higher concentration of photosynthetic pigment production during different salinity stress levels (Zulfiqar and Ashraf, 2021). The manganese-based NPs enhance the photosynthetic activity which could be due to the confirmatory role of Mn in chloroplast and electron transport chain strengthening during salt stress (Ye et al., 2020). Further, ribulose bisphosphate carboxylase (RuBisCO) fixes the CO_2 concentration during the Calvin cycle, and the TiO_2-NPs augment the Rubisco production (Xuming et al., 2008), a result, the increased photosynthesis helps in salinity tolerance and high yield achievement in field crops (Ullah et al., 2020).

Table 3. *Influence of nano-particles (NPs) on the performance of different crops under saline conditions*

Salinity stress	Plant species	NP types	Effects	References
100% sea water	*Abelmoschus esculentus*	Zn NPs	Nanoparticles improved the photosynthetic pigments, SOD, and CAT activities, and reduced the accumulation of proline and total soluble sugars	Alabdallah and Alzahrani, 2020
100 mM NaCl	*Sophora alopecuroides*	Cu NPs	The PSII activity, protein contents in root and leaves, and soluble sugar content were significantly increased with the application of NPs. Further, NPs enhanced the unsaturated fatty acids to maintain membrane integrity and improved the carbon/nitrogen metabolism, glycolysis, and TCA cycle for increased ATP production under stress conditions	Wan et al., 2020
150 mM NaCl	*Pennisetum americanum*	Ag NPs	The application of nanoparticles significantly enhanced the RWC and proline contents; and decreased the oxidative damage by enhancing the antioxidant enzymes. NPs also decreased the Na^+ and Na^+/K^+ ratio while increasing K^+ contents.	Khan et al., 2020
50 mM NaCl	*Solanum lycopersicum*	Si NPs	NPs improved the chlorophyll contents, GSH, and PAL activity	Pinedo-Guerrero et al., 2020
100 mM NaCl	*Ocimum basilicum*	Cu NPs	NPs enhanced chlorophyll and carotenoid content enzymatic antioxidants (APX, CAT, and guaiacol peroxidase GP) activity	Gohari et al., 2020
100 mM NaCl	*Dracocephalum moldavica*	Fe NPs	NPs improved the total phenolic, flavonoid and anthocyanin contents as well as the activities of guaiacol peroxidase, APX, CAT and GR	Moradbeygi et al., 2020
12 dS m− 1 NaCl	*Trachyspermum ammi*	Fe NPs	NPs application increased the K+ uptake, K^+/Na^+ ratio, Fe content, endogenous levels of SA, upregulation of antioxidant enzymes (SOD, CAT, POD and polyphenol oxidase), and osmolytes	Abdoli et al., 2020
125 mM NaCl	*Brassica napus*	Cu NPs	NPs maintained redox balance and ion homeostasis to improve salt tolerance	Zhao et al., 2019
100 mM NaCl	*Triticum aestivum*	Si NPs	NPs enhanced the germination and chlorophyll contents and improved the salinity tolerance in plants	Mushtaq et al., 2019

GSH: glutathione, TCA: tricarboxlic acid, ATP: PAL: phenylalanine ammonia-lyase

The nutrient balance in the plant body is affected by salt stress which lowers plant growth and development. Plant nutritional balance can be improved with NPs application under salinity stress (Kopittke et al., 2019). NPs improve the uptake of

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essential mineral nutrients from saline soil and their translocation in plant parts (Kopittke et al., 2019). NPs improved the Na^+/K^+in plants growing under saline conditions (Sytar et al., 2019). The effect of osmotic stress was significantly reduced under high Na^+/K^+ ratio during salinity stress conditions (Tahjib-UI-Arif et al., 2019). In salinity, Nano SiO_2 application increased the K+ concentration in the leaves of soybean crops (Farhangi-Abriz and Torabian, 2018). Similarly, a higher Na+/K+ ratio in tomato plants from saline soil boosted the salinity tolerance with Cu-NPs application (P´erez-Labrada et al., 2019). Similar kind of results were reported with Fe_2O_3 NPs in *Trachyspermum ammi* plants (Abdoli et al., 2020). Further, Ye et al. (2020) reported increased root growth with a significant effect of Mn-NPs on the distribution of Ca, Na, Mn, and K in plant parts during salinity stress. Zn-NPs regulate the ionic concentration in canola plants under salinity stress (Farouk and Al-Amri, 2019). Liu et al. (2021) stated the cerium NPs improved the K^+ uptake from saline soil and boosted the salinity tolerance in plants. Wu et al. (2018) noticed the exclusion of Na^+ ions and more transportation of potassium in plant cells growing in saline soil thus, helps in salinity tolerance in crops (Etesami et al., 2021).

The presence of high salt ions impairs water absorption in plants and develops the osmotic effect that lowers the stomatal opening, leaf turgidity, and surface area, decreases chlorophyll contents, and reduces plant growth (Munns and Tester, 2008). Recent studies revealed that NPs application reduced the osmotic stress by improving water use efficiency during salt stress conditions (Mahmoud et al., 2020). NPs increase salinity tolerance by augmenting the stomatal conductance, transpiration and leaf water contents helps in maintaining the cell turgidity and larger leaf area index during salt stress (Zulfiqar and Ashraf, 2021). NPs boosted the Aquaporin; responsible for hydraulic conductance and therefore water absorption increases during stress conditions (Kapilan et al., 2018). NPs increased the water imbibition and water retention properties of seeds (Ali et al., 2021). Likewise, the use of NPs as seed treatment improved the water content by 19% in seeds (Khodakovskaya et al., 2009). The increased water intake might be due to the creation of microspores in seeds (Sanborn et al., 2018) or because of the increased permeability of the seed coat. Further, Ali et al. (2021) reported the promising role of NPs as Silicon-based NPs improved the aquaporin structure involved in water absorption during salinity stress (Rios et al., 2017).

Salinity stress triggers reactive oxygen species (ROS) production whereas plants deal with the synthesis of antioxidants (You and Chan, 2015), and the use of NPs significantly improved the enzyme involved in antioxidant synthesis during salt stress conditions (Mushtaq et al., 2020). Rico et al. (2015) observed that NPs of Co, Fe, and cesium act as catalase (CAT) enzymes, whereas the NPs of Mn and Cu are similar in function to peroxidase (POD) in stress. Further, cerium oxide nanoparticle helps in ROS scavenging program in Arabidopsis during saline stress conditions (Wu et al., 2018). Ag-NPs used as priming agents improved the antioxidant enzyme (SOD, CAT, GPX) production in pearl millet during stress conditions (Khan et al., 2020). Similarly, silver nanoparticles mitigate the salinity effect by producing more antioxidants that enhance plant growth (Sami et al., 2020). Application of TiO_2-NPs at 100 mg L^{-1} decreased H_2O_2 production in *Dracocephalum moldavica* at 100 mM NaCl level (Gohari et al., 2020a). Similarly, Gohari et al. (2020b) reported that the use of carbon nanotubes with carboxylic acid at 50 mg L^{-1} is effective in enhancing the photosynthetic pigment, and various (enzymatic and non-enzymatic) antioxidant production during salinity. Moreover, plants synthesized more phenolic contents and flavonoid compounds with Fe

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NPs application during salinity stress, in resulting optimum plant growth and yield was reported (Moradbeygi et al., 2020).

Plant adapts the adverse abiotic conditions by modifying their mechanism through phytohormone synthesis (Fahad et al., 2015b). Similarly, these phytohormones help to regulate plant functions during salinity stress (Etesami et al., 2021). Further, the contributed role of NPs in phytohormone generation improved the salinity tolerance in plants (Paramo et al., 2020). A significant effect of silver-NPs on ABA, GA, and ethylene production was noticed in rice crops (Manickavasagam et al., 2019). Zulfiqar and Ashraf (2021) noticed that Ag-NPs significantly decreased ABA levels and increased the production of indole-3-butyric acid (IBA), 1-naphthalene acetic acid (NAA) and 6-benzylaminopurine (BAP) in wheat during salinity stress. Further, Se-NPs mediated salinity tolerance is involved in the production of IAA and ABA concentration in strawberry (Zahedi et al., 2019). Ag-NPs increased the production of different plant hormones (BAP, NAA, and IBA) and decreased the ABA synthesis in wheat growing in saline soil (Abou-Zeid and Ismail, 2018).

Conclusions

Salinity stress imposes ionic toxicity, and osmotic stress and impairs the hormonal balance, nutrient and water uptake, reduces photosynthesis, and chlorophyll synthesis, and induces stomata closing leading to impaired growth, yield, and quality. Nevertheless, plants increase osmolyte accumulation, antioxidant activities, and gene expression and maintain hormonal regulation, and osmotic adjustments to counter the toxic impacts of salinity. Different practices are also being used to improve crop production under saline conditions. The development of salt-tolerant crops is a promising approach to mitigating the adverse impacts of salinity, however, this technique is time-consuming and needs a lot of resources and effort. In this regard, the exogenous application of hormones, nutrients, osmoprotectants, PGPR, seed priming, and nutrient management has emerged as excellent practices to mitigate the adverse impacts of salinity in plants. Recently, biochar and nano-particles also got appreciable attention across the globe to mitigate the adverse impacts of salinity. However, the effectiveness of biochar largely depends on soil properties, biochar application rate, feedstock properties, and the pyrolysis procedure used to prepare the biochar. Future research should focus on optimizing the application of biochar and nano-particles to alleviate salinity stress. The complex understanding of plant responses and interactions between biochar and nano-materials can offer effective solutions to improve crop production under saline conditions. The synergetic impacts of different management practices and genetic engineering can help to improve crop resilience under saline conditions.

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