

Review

Field Crop Responses and Management Strategies to Mitigate Soil Salinity in Modern Agriculture: A Review

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Abstract: The productivity of cereal crops under salt stress limits sustainable food production and food security. Barley followed by sorghum better adapts to salinity stress, while wheat and maize are moderately adapted. However, rice is a salt-sensitive crop, and its growth and grain yield are significantly impacted by salinity stress. High soil salinity can reduce water uptake, create osmotic stress in plants and, consequently, oxidative stress. Crops have evolved different tolerance mechanisms, particularly cereals, to mitigate the stressful conditions, i.e., effluxing excessive sodium (Na⁺) or compartmentalizing Na⁺ to vacuoles. Likewise, plants activate an antioxidant defense system to detoxify apoplastic cell wall acidification and reactive oxygen species (ROS). Understanding the response of field crops to salinity stress, including their resistance mechanisms, can help breed adapted varieties with high productivity under unfavourable environmental factors. In contrast, the primary stages of seed germination are more critical to osmotic stress than the vegetative stages. However, salinity stress at the reproductive stage can also decrease crop productivity. Biotechnology approaches are being used to accelerate the development of salt-adapted crops. In addition, hormones and osmolytes application can mitigate the toxicity impact of salts in cereal crops. Therefore, we review the salinity on cereal crops physiology and production, the management strategies to cope with the harmful negative effect on cereal crops physiology and production of salt stress.

Keywords: cereal; salinity; Mitigation effects; mechanisms; modern agriculture

1. Introduction

This review aims to focus on how to address the issue of the impact of soil salinity stress on cereal crops growth and yields, the mechanisms of salt stress tolerance, and the management strategies to mitigate these effects. Cereals fulfil more than 50% of the human energy and protein requirement [1]. Among cereals, maize (*Zea mays* L.), rice (*Oryza sativa* L.), bread wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.) and sorghum

(*Sorghum bicolor* (L.) Moench) are the most widely cultivated in the world. Wheat, rice, and maize provide about 48 and 42% of the total calories and protein, respectively [1,2]. Besides their nutritious value, among other uses, there has been an increased interest in the potential use of residues from maize and wheat in the bioenergy industry and wheat as a cover crop [3,4]. Globally, about 66% of the cultivated areas are cultivated with cereal crops [2] since they are adapted to an ample range of climatic conditions. For instance, the temperate climate is suitable for wheat and barley cultivation, while maize is cultivated dominantly in tropical regions [2,5]. In rice, it is mainly cultivated in wet tropic regions of the world, while sorghum is mainly cultivated in dry areas. However, their cultivation in temperate regions is also suitable [6].

As the world's population increases, it is estimated that food production will need to increase between 87% and 100% by 2050 to meet its nutritional needs. Expectations are that a considerable portion of this increase will be provided by increases in the production of cereal crops [7,8]. Different stresses such as heat, salinity, drought, and heavy metal stress severely disturb crop production [9–13]. Among these, salinity stress is perhaps the most critical and pervasive global abiotic stress, affecting 20% of the world's total cultivated area and causing about 20% yield losses [14,15]. On a global scale, soil salinization is accelerated due to climate change, intensive farming, poor cultivated land drainage, and contaminated or low-quality irrigation water [6,14,16]. Cereals are an essential food source to the world population, with a global production of 2719 million tones [8,17]. At present, however, complete global food security has not been achieved, with estimations of more than 800 million people still facing chronic hunger [18]. The detrimental impacts of climate change and different biotic and abiotic stresses on crop productivity, alongside the fast-growing population, and arable land degradation, increase the current global food shortage [19–21]. Thus, without a significant improvement in cereals production, the gap between production and demand will increase.

Salinity can significantly decrease crops' growth and yield due to the osmotic, ionic and oxidative stresses [22]. High sodium (Na^+) in the soil can cause nutrient deficiencies such as potassium (K^+) by decreasing the K^+ uptake and increasing its exclusion from the cells [23]. Salt stress can also damage cellular homeostasis, denature protein and nucleic acids, induce lipid peroxidation, and increase reactive oxygen species (ROS) [15,24,25]. To reduce these adverse effects, plants should utilize adaptive strategies such as reducing the Na^+ ion uptake and maintaining the internal osmotic balance, enhancing the accumulation of osmolytes, and scavenging ROS antioxidant defense system [25].

Management approaches are commonly proposed to mitigate the salinity conditions, including saline-resistant genotypes, nanoparticles application, hormones, and osmoprotectants. This review aims to summarize the question; how the impact of salinity stress on cereal crops growth and yield, the mechanisms of salt stress tolerance, and the management strategies to mitigate these effects.

2. Seed Germination, Vegetative Growth, Yield and Yield Quality under Salt Stress Condition

Unfavourable environmental conditions adversely affect plants' physiological functions, decrease crop yields and quality (Figure 1). Reactive oxygen species generation can induce oxidative stress in plants, determine a cascade of plant responses that negatively affect plant photosynthesis, CO_2 uptake, and relative water content (RWC) and increase plant photorespiration pollen sterility, lipid, and electrolyte leakage. Therefore, the whole plant growth, crop yield and quality are negatively affected. The salt sensitivity of plants varies during their lifecycle, but the seedling and reproductive stages are the most sensitive. In that case, the impacts on crop yields and quality can be drastic, as the reproductive stage is the most susceptible for crop yield and grain quality in cereal crops.

When the electrical conductivity of a soil extract from a saturated paste (ECe) is higher than 4 dS m^{-1} , the soil is considered saline soil [26]. In most cases, sodium (Na^+), chloride (Cl^-), sulphate (SO_4^{2-}), bicarbonate (HCO_3^-), potassium (K^+), magnesium (Mg^{2+}),

and nitrate (NO_3^-) ions are presented in the soil solution. A high concentration of Na^+ ions in the soil solution can create a difference in favour of the monovalent cations over the divalent cations in the soil (i.e., ratio monovalent: divalent cations).

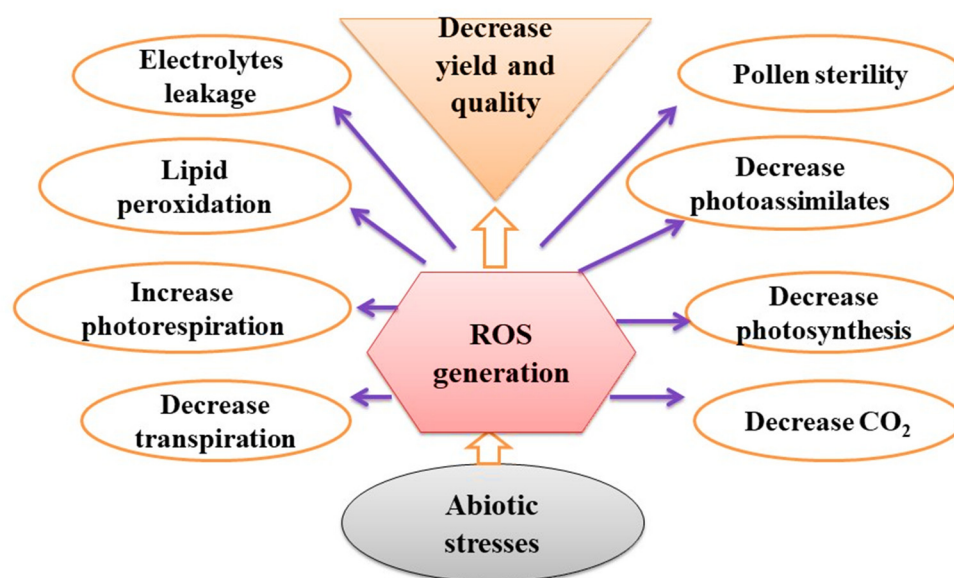


Figure 1. The effect of abiotic stresses on plant's physiological traits, yield and quality.

Other factors, i.e., water shortage, rainfall limitations, and high evapotranspiration, induced soil salinity in various regions of the globe [27,28]. A high concentration of salts in the soil solution can negatively affect the uptake of water and essential nutrients, reduce plant growth and development, and alter the physiochemical processes (Figure 2) [6,28,29]. The first effect of salinity stress on plants is osmotic, while the second effect is ionic. As a result, plants close their stomata, decrease transpiration rate, and lose turgor pressure, which halts root expansion and shoots cells [30]. In response to osmotic stress, plant cells can recover their turgor by increasing the mobility of inorganic ions [31]. However, when Na^+ ions reach a toxic level, they create a metabolic imbalance, triggering oxidative stress [32] and ROS overproduction [14,33]. This oxidative stress can disturb membrane stability, cause lipid peroxidation, damage nucleic acids, ion leakage, disruption, and posterior cellular death [34]. This section describes the effects of salt stress on germination, growth, yield and quality of cereals.

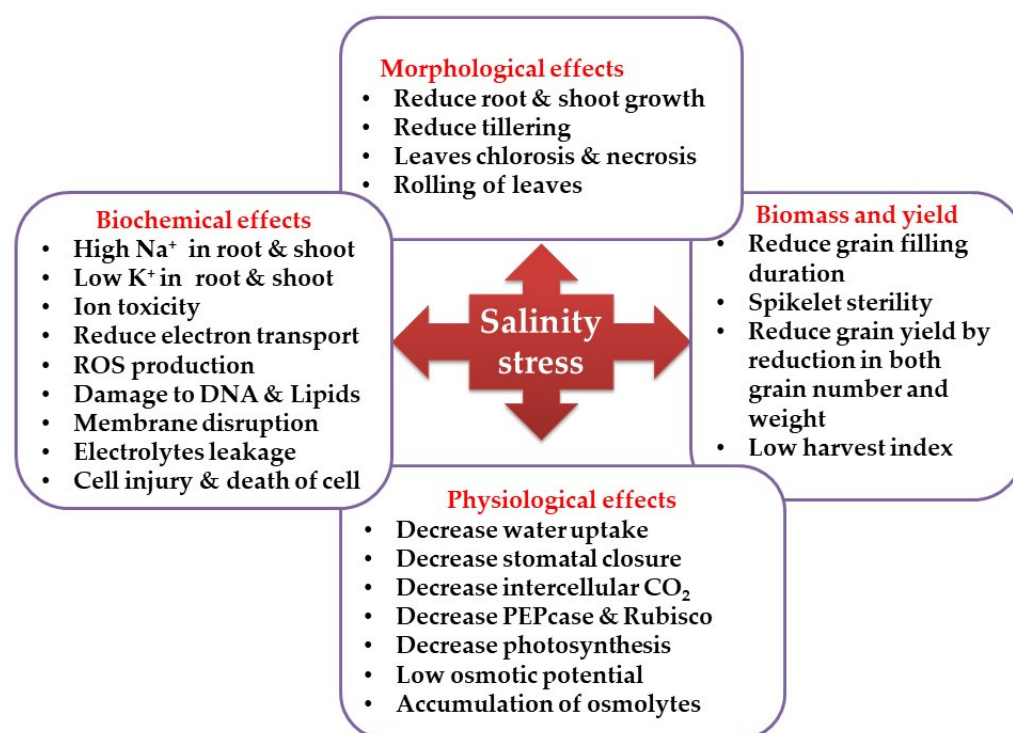


Figure 2. Morpho-physiological effect of salinity stress on cereal crops. PEPcase = Phosphoenolpyruvate carboxylase.

2.1. Seed Germination and Plant Growth under Salt Conditions

The primary germination stage is the most critical process in the seedling establishment [6]. Soil salinity usually delays or even prevents seed germination [29]. Seed imbibition is affected by a high concentration of salts in the soil, reducing the water uptake by decreasing soil osmotic potential [35,36]. Moreover, the excess of NaCl can cause Na⁺ and Cl⁻ toxicity to the seed embryos and alter protein synthesis, energy production, and respiration [35]. Thus, salinity stress can alter the seed's hormonal and nutrient balance during germination, resulting in delays in the germination time [37]. Changes in the hormonal status result from the changes in the activity of enzymes exposed to toxic ions. In salt-sensitive wheat cultivars, a decreased activity of α -amylase during seed germination has been documented compared to salt-tolerant cultivars. Reducing the α -amylase activity can reduce the sugars translocation into the developing embryo [38]. For example, when wheat and barley seeds were exposed to salt stress, between 40 and 120 nM, germination was reduced by 20 to 40%, while seeds were not germinated with salinity levels of 160–200 nM (Table 1) [27].

Similarly, seed germination was reduced in wheat seeds exposed to salt stress (150 mM) by 12.7% as average for 20 wheat genotypes compared to the control treatment [39]. In another study, germination of three genotypes of peanut (*Arachis hypogaea* L.) seeds sown with 200 mM was reduced by 43.29, 42.70, 39.56 and 6.77% compared to those sown at 0, 50, 100 and 150 mM, respectively [40]. The reduction in the percentage of germination observed in other studies with maize, rice, wheat, sorghum and barley is presented in Table 1.

Salinity stress significantly negatively impacts plant growth and development (Table 1); however, plants' responses can differ according to the extent of the plant's stress and the plant's growth stage. Overall, salinity affects plant growth in two phases [41]. The first phase of a decrease in plant growth occurs within minutes, where a high concentration of salts reduces the water uptake and growth rate due to the osmotic effects. The osmotic stress triggers numerous aspects in plant tissues. At the macroscopic level, expansion of both root and shoot cells is immediately obstructed due to a decreased turgor pressure

[42,43]. To cope with this issue, the plant must adjust osmotically. Most of the turgor of the cell in the root is regained within 40–60 min by increasing the uptake of inorganic ions, and the growth is resumed [30,44]. Osmotic stress also causes quick stomatal closure, and the plant reduces CO₂ assimilation, which results in a rapid decrease in the xylem pressure up to 0.05 MPa in maize roots exposed to 100 mM NaCl [45]. Such a decrease in the xylem pressure occurs within minutes upon stress onset, and the hydraulic signals are sensed quickly by the roots. They are transduced almost instantaneously to the shoot, decoded and altering shoot metabolism [46,47]. Because stomatal guard cells possess a range of mechano-sensitive ion channels, they could potentially transduce a change in the xylem pressure caused by salinity into altered stomatal apertures [48,49]. Furthermore, plants grown under salt stress suffer physiological and metabolic changes such as reduced enzyme activity, CO₂ assimilation, protein biosynthesis, leaves water relations, and photo-system II (PS II) [41,50].

In the second phase of growth reduction, salts accumulate in plant leaves, reaching threshold levels and causing toxicity. This phase is longer and can take a few days up to weeks or even months to complete [41]. During the second phase of growth reduction, higher Na⁺ accumulation in the intracellular spaces can inhibit the enzymatic activities. For instance, the cytosolic compartment possesses different enzymes, which have a vital role in the starch synthesis, glycolysis, polyamine, phenylpropanoid pathway and Calvin cycle. The activity of these enzymes is mainly controlled by the K⁺ concentration in the cytosolic space [51]. Due to the close similarity between K⁺ and Na⁺, Na⁺ replaces the K⁺ in these enzymatic reactions but with much less efficiency [44,52]. Moreover, since Na⁺ cations have a smaller “naked” radius than K⁺, they accumulate in regions of greater density, while K⁺ ions tend to accumulate in less dense regions. This difference in the intracellular ions can impact cell operations, water relations and biosynthesis of proteins [53]. Bio-macromolecules with charged 3D structures occupy about 20–30% of the cytoplasmic volume [53]. Studies showed that the functions of the bio-macromolecules are significantly influenced by the ionic strength and the electrostatic interactions of the cytoplasmic solution [54]. As a result, plants under the second phase of growth reduction show chlorosis, necrosis, premature leaf senescence and reduced leaf area due to the reduction in the photosynthetic activity and the overall cell metabolism [41]. The threshold level of ion toxicity varies for plant species and even among cultivars and hybrids. For example, the magnitude of grain yield reduction was lower (41%) in an adapted wheat cultivar, while the maximum reduction (68%) was observed for a susceptible cultivar at 120 mM. Based on their salt tolerance, plants are divided into halophytes and glycophytes. Halophytes are salt-tolerant plants, while glycophytes are very sensitive to salinity stress. Generally, cereals are typically glycophytes among cereals crops, sorghum and barley (70–90 mM NaCl) [55] are more tolerant than wheat, which is more tolerant than rice and maize. When salinity concentrations reach 100 mM NaCl, rice usually does not reach maturity at the field conditions [56].

In contrast, wheat and barley can reach maturity, although the decreases in the grain yields are commonly more significant for wheat than barley. However, with salinity concentrations higher than 250 mM NaCl, barley plants can die after extended periods of exposure [56]. In maize and rice, grain yields start to decline at much lower salt concentrations, 17 mM NaCl and 30 mM NaCl, respectively, while yield decline in wheat occurs at higher concentrations (60–80 mM NaCl) [57].

Table 1. Morphological effects on cereal crops under salt stress.

Salinity Stress Level	Crop	Effects	Reference
40 to 120 mM	Wheat	20–40% reduction in germination	[27]
160 to 200 mM		No germination	[27]
100–300 mM		27–30% reduction in germination	[58]
100–250 mM		15–31% reduction in germination	[59]

30–120 mM		20–38% reduction in germination; 41–67% reduction in yield	[60]
100–150 mM		decreased the dry weights and chlorophyll contents	[61]
100–300 mM		77–86% reduction in dry weight	[58]
100–200 mM		37–58% reduction in germination	[62]
100–200 mM	Sorghum	26–28% reduction in shoot and root growth, respectively	[62]
30–60 mM		Reduced growth and dry matter	[63]
43.8 mM		50% grain yield reduction	[64]
25–100 mM		15–20% reduction in germination while >10% yield reduction	[65]
60–130 mM		Reduced Germination	[66]
100 mM	Maize	Shoot and root growth reduced	[67]
100–200 mM		Germination, fresh and dry weight reduced	[68]
75–150 mM		Reduction in root dry weight and leaves	[69]
100–200 mM		Severe reduction in growth	[70]
80 mM		Plant height, tiller and yield reduced	[71]
60 mM	Rice	50% reduction in yield	[72]
1.16–2.89 g NaCl/kg of soil		36% reduction in grain yield	[73]
18–66 mM		Reduction in shoot and dry root weight	[71]
		Grain yield reduced from 7812 to 997 kg/ha ⁻¹	[74]
100–200 mM	Barley	shoot dry weight, shoot and root length reduced	[75]
100–150 mM		15–25% reduction in germination	[76]

2.2. Effect of Salinity on Grain Yield and Quality

Studies showed that soil salinity could reduce tillers numbers, grains number, and harvest indexes in cereal crops [77]. For instance, salinity (4 dS m⁻²) reduced the number of grains and 1000-grain weight in rice cultivars [78]. However, the salt sensitivity of plants varies during their lifecycle, with the seedling and reproductive stages being the most salt-sensitive stages in cereals. At the crop's reproductive stage, soil salinity reduces grain filling duration and grain yield. Wheat plants produced lower grain yield when exposed to salinity stress at the reproductive stage [79], since plants have fewer compensatory mechanisms to cope with salts in sensitive reproductive tissues, resulting in enhanced floret sterility, a higher percentage of unfilled or partially filled grain, and reduced grain weight and yield [78]. Moreover, salinity stress down-regulates the expression of different genes involved in forming branch and spikelet meristems and reduces the number of grains. Zheng et al. [77] reported that salinity down-regulated Lax panicle 1,2 (LAX1, LAX2), Ideal plant architecture (IPA1), and Dense and erect panicle 1 (DEP1) genes in rice reduced the number of grains per panicle.

In cereals, carbohydrates are the central reserve of grains (50–70%) followed by proteins (5–12%) [78], which determine grain textural, nutritional and taste attributes. Studies showed that high salt concentrations could reduce amylose and starch contents and modulate grain texture [66,67,74,80]. These functional changes might be due to the starch-to-storage protein ratio of grains, distribution of the amylopectin chain, amylose content, the crystallinity of starch granules and particle size [78]. In maize, for example, grain protein content increased while carbohydrate decreased with increasing salt contents in irrigation water [80]. Salinity (0.62–1.16 mS cm⁻¹) decreased grain yield by 36% in rice but did not influence grain texture compared to the control treatment [73]. In barley, salinity reduced grain size and carbohydrate content but increased protein. Contrary to barley [74], the salinity stress decreased the protein content in wheat grains [81].

3. Mechanisms for Salt Stress Responses, Avoidance and Tolerance

Most crops are glycophytes (salt-sensitive) and, thus, are significantly influenced by salt stress. Soil salinity induces three types of stress: osmotic stress, ionic stress, and secondary stress [82,83]. Osmotic stress reduces the plant ability to water uptake from the soil solution, which results in a water deficit in the plant. However, ionic stress is associated with a high concentration of Na^+ and Cl^- ions in the metabolically active cell components and affects enzymatic activities [30]. The osmotic and ionic stresses cause secondary stresses such as nutrient imbalance, accumulation of toxic compounds, and ROS production. In response to these stresses, plants develop the tolerance mechanism to survive their growth (Figure 3). Here, we discuss the mechanisms of plants for salt stress responses, avoidance and tolerance.

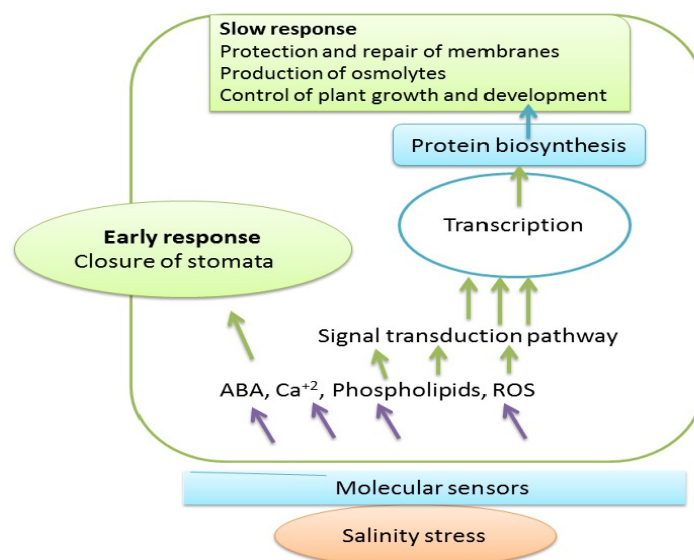


Figure 3. A simple representation of plant signal transduction pathways in response to salinity stress. Different phytohormones and molecular sensors are activated in response to salinity stress. For instance, phytohormones, i.e., ABA, are signal molecules in plants, transducing the quick response to salt stress and closing plant stomata. Biosynthesis of molecules through transcription, on the other hand, is a slow, much slower process.

3.1. Sensing Salt Stress

To avoid or reduce the damages caused by an excessive concentration of salts in the soil, plants must sense the salts stress, adjust cellular traits, and send signals to the interior of the cell (Figure 4). Studies showed that Na^+ could enter the cytoplasm through different cation exchange channels (Figure 4), such as NSCC (i.e., nonselective cation channel), the high-affinity K^+ channel (HKT1) and the low-affinity K^+ channel [82]. Excessive salinity increases the Ca^{2+} concentration in the cytosol of cells within seconds to minutes, induces Ca^{2+} signal, and initiates the Na^+ efflux pathway [84]. The Ca^{2+} binding proteins such as salt overly sensitive (SOS3 and SOS3-Like calcium-binding protein 8 (SCaBP8)) perceives the calcium signal. Then, the SOS3 and SOS2 proteins activate the SOS1, a Na^+/H^+ exchanger, to exclude the cytosolic Na^+ into the apoplast [82]. Osmotic stress triggers the signals that enhance the biosynthesis and concentration of compatible osmolytes such as polyols, glycine betaine, and sugars. The increased concentrations of these compatible osmolytes in cytosol decrease the water losses and increase cell turgor pressure and expansion under salt stress conditions [82,83].

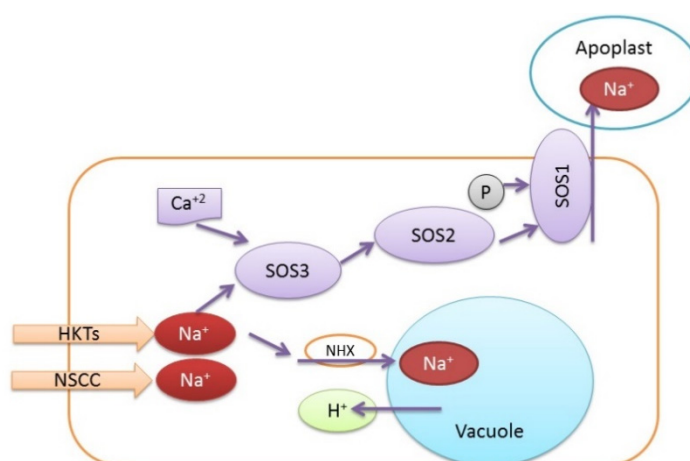


Figure 4. Simple illustration of Na^+ transport across cellular compartments.

3.2. Tolerance Mechanisms

To identify the strategies of stress-resistant crops for enhancing their resistance to individual and combined abiotic stresses (Figure 5), we reviewed a handful of sustainable strategies of crop management under abiotic stress. Salt tolerance mechanisms are complex processes that involve adaptations such as osmoregulation, hormonal regulation, osmotic adjustment, ion homeostasis, and activation of the antioxidant defence system.

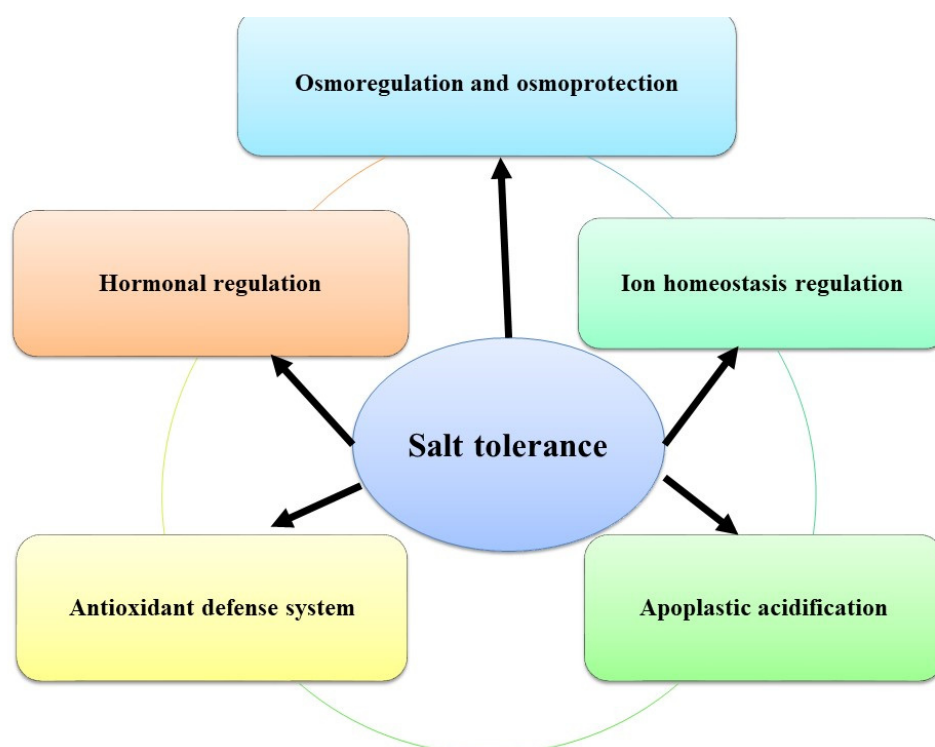


Figure 5. Mechanisms of Salt Tolerance in Plant.

3.2.1. Osmoregulation and Osmoprotectant

Salinity can cause osmotic stress during the first phase of the salinity-induced growth reduction process. At this stage, plants adopt a strategy to minimize the adverse impact of osmotic stress through a mechanism known as osmoregulation [8]. To ameliorate the decrease in both cell water potential and stabilize their protein structures under stressful conditions, plants osmoregulate their water potential by either increasing the biosynthesis

of organic solutes (polyols, sugars, amino acids, and other low molecular weight metabolites) or the inorganic solutes uptake (K^+ , Ca^{2+} , and Cl^-) [30,82]. The organic solutes and inorganic ions are involved in the osmotic adjustment, reducing the loss of water and increasing cell turgor and expansion. To do this, plants synthesize various types of compatible solutes such as glycine betaine, β -alanine betaine, proline, trehalose, and polyols under salt stress (Figure 6). In addition to regulating plant water relations and osmotic adjustment, these osmolytes help the enzymes to activate the plant's antioxidant defense system. Therefore, compatible solutes are called osmoprotectants [8,79].

Salt-tolerant species achieves the osmotic adjustment via Na^+ distribution between cytoplasm and vacuole [85]. Thus, plants maintain their cytoplasmic osmotic pool to stabilize cellular metabolism and growth under salinity. For instance, salt-tolerant wheat cultivars exhibited higher glycine betaine, proline, soluble sugars and phenols, and maintained higher K^+ content by reducing the uptake of Na^+ under salinity stress. Likewise, barley and maize crops accumulated higher glycine betaine concentrations under salt stress than the control treatment [86].

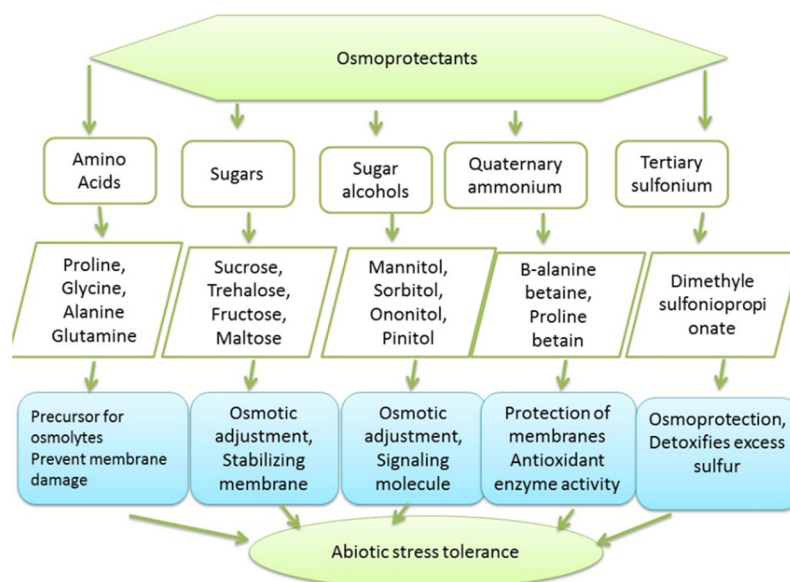


Figure 6. The role of osmoprotectants in abiotic stress tolerance. Under abiotic stress, plants accumulate different types of osmoprotectants. These have different roles, including stabilization and maintenance of cell membrane composition and structure, molecular signalling, and cell detoxification.

3.2.2. Ion Homeostasis Regulation

Ion homeostasis is an essential mechanism for plants to be adapted during salt stress to mitigate the salinity's toxic effects. Keeping a high K^+/Na^+ ratio in the cytosol can prevent cellular damage and increase the plant's ability to tolerate the salinity [82,87]. The plant can eliminate the absorbed Na^+ from the cells or compartmentalise it in less active cells such as vacuoles to maintain ion homeostasis. With this, plants can maintain ion homeostasis and equilibrium. Sodium-ion (Na^+) enters the plant roots and reach the cytoplasm, and then through the support of various Na^+/H^+ antiporters, it gets moved to the vacuole [88]. The primary type of H^+ -pumps present on the tonoplast is H^+ -ATPase, followed by V-phase [89]. Na^+/H^+ antiporters (NHXs) such as NHX1 and NHX2 control Na^+ accumulation in vacuoles through tonoplast Na^+/H^+ exchanger [90]. Another signalling pathway that plays an essential role in reducing Na^+ toxicity is the salt overly sensitive (SOS). Na^+/H^+ antiporter (encoded by SOS1) regulates the Na^+ efflux from the cytosol and increases toxic ions' transportation from roots to shoots. SOS2 and SOS3 participate in Ca^{2+} mechanisms, which deal with Na^+ efflux.

Selective transporters of Na^+ maintain the equilibrium of K^+ and Na^+ in plant cells by excluding Na^+ ions from the cytosol to cell vacuoles [88]. Other studies indicated that maize, wheat and rice could exclude the Na^+ from leaves through the HKT1 channel [91–93]. Although plant cells can efficiently exclude excessive Na^+ from the cell or compartmentalise it in the vacuoles to avoid toxic effects in the cytoplasm [94], there is a wide variation between different cereals and among different genotypes for the same species for ion distribution within the cytosol. For instance, salt-tolerant cultivars of maize, wheat and rice exhibited distinctive transporters (HKT1) to retain a lower concentration of Na^+ in the cytosol [91,93]. In barley, *H. maritimum* plants maintained a lower concentration of Na^+ and Cl and a higher concentration of K^+ in leaves than *H. Vulgare* [95].

3.2.3. Apoplastic Acidification

Salinity stress indirectly affects the cell wall property by causing an alteration in the gene expression; however, Na^+ physically interacts with different cell wall components directly and changes their chemical properties [96]. Excessive soil salinity can lead to a high concentration of Na^+ in the apoplast, increasing the interaction between Na^+ and negatively charged sites in the cell wall and influencing the apoplast's pH. According to the acid growth theory, salinity can cause apoplast's temporary alkalization, limiting the cell wall growth [97]. Under the usual conditions, auxin triggers the plasma membrane H^+ -ATPases, and protons are exuded into the apoplast, decreasing its pH. The acidification of the apoplast activates the expansins and several other enzymes, resulting in the loosening of the cell wall [96]. Poor cell wall acidification can reduce cell wall expansion, and with this, overall plant growth. For example, maize seedlings showed impaired growth under salinity stress because of plasma membrane H^+ -pumping's inefficiency. In contrast, salt-tolerant maize cultivars exhibited a growth rate due to efficient H^+ -pumping, which reduced the pH of apoplast under salt stress [98]. In short, acidification of apoplast under salinity stress is required for cell wall loosening, an indicator of salt resistance.

3.2.4. Antioxidant Defense System

Soil salinity can cause nutrient imbalance, disrupt the plant metabolic functions and increase the production of ROS. These ROS influence cellular functions and damage the structure of membrane lipids, DNA, resulting in leakage of cell solutes. ROS is produced at different cell sites such as chloroplast, plasma membrane, apoplast, mitochondria, endoplasmic reticulum, and cell wall [8]. Plants increase the production of ROS-scavenging enzymes and non-enzymes [99]. Antioxidant enzymes work as scavengers to detoxify ROS in plants and improve the resistance of plants under stress (Figure 7). For example, superoxide dismutase (SOD) is a scavenger of superoxide (O_2^-). It converts it to H_2O_2 , while catalase (CAT) scavengers of H_2O_2 are converted into H_2O and O_2 [100]. Increasing antioxidant enzymes' activities and developing antioxidant metabolism is vital to enhance salts tolerance. For example, wheat plants enhanced SOD, GR, APX and glutathione peroxidase (GPX) under NaCl stress (100 mM) for 30 days [99]. Barley plants had high CAT activities, SOD, APX while lower MDA content under salinity stress after application of Se-nanoparticles [75,101]. However, Habibi and Aleyasin [75] reported that excessive salts stress reduced the activity of SOD but increased the activity of malondialdehyde (MDA) in barley plants. Sorghum plants could increase antioxidant enzymes' activities to adapt to salinity stresses [100]. Studies showed that different non-enzymatic antioxidants such as glutathione, phenols, flavonoids and free proline catalysed redox reactions [102]. Ascorbic acid (ASA) stimulates vegetative growth by increasing cell division and elongation under salinity stress because ASA can detoxify and neutralize the ROS [103]. Similarly, an exogenous spray of thiamin enhanced the antioxidative defense system in maize plants exposed to salt stress [104]. This enhancement in maize growth was attributed to the reaction between thiamin and adenosine triphosphate (ATP) to form thiamin diphosphate (ThDP), which could work as an active co-enzyme for carbohydrate metabolism

and transmetalation (a reaction involving the transfer of a ketole group) reaction of pentose phosphate in the Calvin cycle [105]. Similarly, plant enhances the biosynthesis of phenolic compounds, which act as scavengers and donate a hydrogen atom to the ROS, thus stabilizing free radical reactions [106]. Flavonoids, secondary metabolites phenolic compounds with low molecular weight, also have antioxidant potential against ROS [107]. Thus, increased enzymatic and non-enzymatic antioxidants in plants is essential in plants exposed to salinity stress [91].

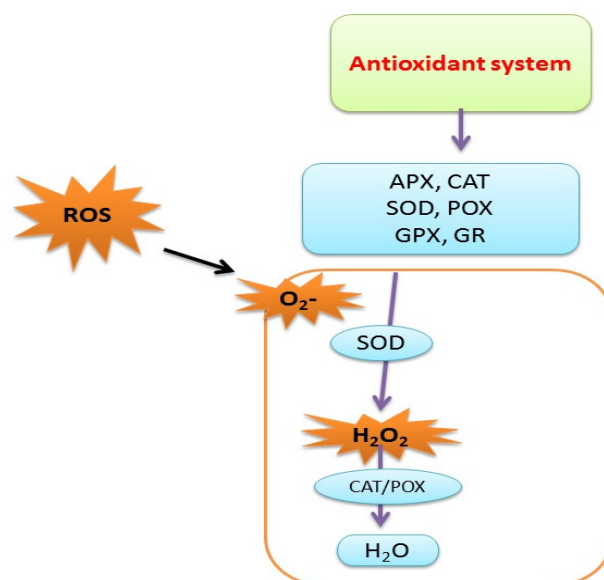


Figure 7. Simple illustration of detoxification of ROS through antioxidants. A plant cell has various antioxidant enzymes which detoxify the ROS. They work in a series. For instance, O_2^- is scavenged by SOD, which converts O_2^- into H_2O_2 , whereas CAT converts H_2O_2 into H_2O and O_2 .

3.2.5. Hormonal Regulation

Phytohormones are biosynthesized in plants in minimal quantities, but they play fundamental roles in plants' growth and development. Among different phytohormones, abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA) and ethylene are known as stress response hormones. While auxin, cytokinins (CKs), gibberellin (GA), strigolactones (SLs) and brassinosteroids (BRs) are regarded as growth-promoting hormones [108]. These hormones generate and transmit a specific defense signal, while synergistic or antagonistic cross-talks among hormones emerge as pivotal for resistance outcomes. Plants have complex cellular and molecular mechanisms to adapt and ensure survival under unfavourable environmental conditions.

The adaptation of plant responses to abiotic stress is controlled by the hormonal signalling cascades that regulate stress responses under unfavourable growth conditions. In response to water stress, several phytohormones such as ABA, GA, JA, SA, and ET acted together and up-regulated 859 genes in *A. thaliana* [109]. Similarly, JA and ABA show synergistic effects in signalling pathways to regulate each other responses against salinity, drought and cold stress [110]. Alike, ethylene (ET) and JAs play an essential role in plants subjected to drought, cold stress, and salinity stress in a synergistic and antagonistic manner [111,112]. Studies showed that the external application of JA and SA could improve drought stress tolerance in wheat. Similarly, the ABA and JA showed an antagonistic effect in plant growth during signalling pathways while operating synergistically in response to environmental stress [110].

Furthermore, each plant hormone does not perform a single role in plants, but it plays different roles in different tissues at various plant stages under different environmental

stresses [113,114]. For example, endogenous ABA concentration increases rapidly, activating sucrose nonfermenting 1-related protein kinases (SnRK2s). SnRK2s further regulate the stomatal closure in plants osmotic stress [115]. Plant root tip first senses the reduced water availability due to osmotic stress and sends the signal to plants' aerial parts (shoots) through ABA. The salt-tolerant plant has higher ABA accumulation under salt stress than salt-sensitive [116]. Recent studies showed shoot ABA synthesis, while root ABA biosynthesis is minimal and scarcely influences the shoot physiology. McAdam et al. [117] reported that exceedingly rapid de novo biosynthesis of ABA as exogenous application, throughout the up-regulation of a single gene in the pathway of ABA-biosynthetic, initiates ABA-mediated stomatal reactions to vapour pressure deficit in angiosperms.

In contrast, GA is a phytohormone that induces salt tolerance in plants. For example, rice plants regulated the GA to tolerate salt stress [23]. Wheat plants with an elevated JA level exhibited salt tolerance [118], while low biosynthesis of JA in rice caused hypersensitivity to salinity [119]. These studies indicate that elevated phytohormones levels in plants under salt stress help reduce water loss and even promote the growth of cereal crops.

4. Management Strategies to Alleviate the Adverse Effects of Salt Stress

The production of salt-tolerant genotypes is essential to sustain crop production in salt-prone areas. Recent developments in physiology, biotechnology, genomics, and breeding approaches can produce cereals cultivars suitable for salt-affected areas. Here we describe the feasible and cost-effective strategies to overcome salt stress in cereal.

4.1. Alleviation of Salt Stress by Nanoparticle Elements

Nanoparticles (NPs; 1–100 nm in size) have enormous potential to help different scientific fields such as biological science, medical, industrial, and agricultural sciences [120,121]. Nanoparticles are applied as nano fertilizers and nano pesticides in agriculture to increase crop yield and productivity under normal and stressful conditions [9,122]. The application of nanoparticles or nano fertilizers could be a helpful technique to overcome soil salinity (Table 2). Nanoparticles have been reported to enter plant cells to adjust osmotic imbalance for enhancing water uptake [123]. During seed germination, the nano-materials penetrate the seed tissues through intercellular spaces or create new pores primarily through the up-regulation of aquaporin production [124,125] and up-regulate the genes involved in various processes, including cell divisions [126]. The application of ZnO and TiO₂ nanoparticles successfully revived embryonic differentiation by helping the enzymes break the seed dormancy [124]. Multi-walled carbon nanotubes used in tomato seed treatment caused an up-regulation of genes such as *CycB*, *NtLRX1*, *extensin* and *NtPIP1* involved in cell divisions, cell wall formation and water transport, respectively. They increased the final germination of tomatoes [126]. In other cases, nanoparticles have been shown to enhance the transcription of genes that confer the cell with an increased antioxidant capacity. Under abiotic stress, nanocarbon tubes increased the germination of seeds and growth of seedlings by decreasing lipid peroxidation and H₂O₂ production by enhancing sodium oxide dismutase (SOD), catalase (CAT), peroxidase (POD) activities and ascorbic acid (ASA) [127]. However, higher concentrations of NPS can promote ROS production and increase cellular damage, disrupt protein function and DNA, interfere with signalling function and gene transcription modulation [128].

Salt stress damages cell membranes and other cellular compounds such as lipids and proteins. A recent study showed that ZnO-NPs triggered the anti-stress enzymes, which significantly reduced malondialdehyde (MDA) levels (72%) and lipid peroxidation in coriander (*Coriandrum sativum* L.) leaves [129]. Alike, acidic ribosomal phosphoproteins contain phosphorylated residues and perform a vital role in protein synthesis and regulation. Moreover, while NaCl stress reduces Acidic ribosomal phosphoprotein (ARP) gene expression, there is evidence that the application of ZnO-NPs can enhance the ARP gene expression under salinity stress [130]. Myelocytomatosis oncogenes (MYCs) proteins are

also negatively impacted under saline stress. These proteins are involved in different processes, including stomatal differentiation, biosynthesis of anthocyanins, root hair formation, embryonic epidermis seed germination, endosperm breakdown, signalling pathways of abscisic acid (ABA), jasmonate, and increased tolerance to biotic and abiotic stresses. ZnO-NPs triggered the MYCs proteins under salinity stress in rapeseed (*Brassica napus* L.), although the mechanism behind this response is not yet clear [130]. Several other studies showed different beneficial effects of NPs. For example, applying silver nanoparticles (Ag-NPs) to rice under salinity stress conditions increased the germination rates and reduced the toxic effects of salts. The increase in seed germination under salt stress after applying nanoparticles might be due to better penetrability of nanoparticles into the seed pores, which increased the water uptake and maintained enzymatic activities of seeds [99]. Combine application of ZnO-NPs (0.8 g/L), and biofertilizers increased the grain yield of Triticale (*X Triticosecale* Wittm. ex A. Camus.) by 39% under high salt-stressed soils (55.5 mM) [131]. Similarly, ZnO-NPs (25–50 mg L⁻¹) increased rice plants' fresh and dry weight exposed to salinity stress, improved water relations, and final paddy yield. Application of nano-Fe (2 g/L) increased the plant growth and grain yield of wheat exposed to salt stress and increased the grain protein and iron contents [132].

Salt stress significantly decreases plant photosynthetic efficiency due to Na⁺ and Cl⁻ ions [133,134]. High Na⁺ concentrations in the cytosol decreased the activity of photosynthetic machinery, particularly photosystem-II (PSII), by disturbing the oxygen-evolving complex (OEC), PSII reaction centres and also by reducing the activity of quinine acceptors and the quantum yield of PSII [135]. As a result, the quantity of absorbed light exceeds the demand for photosynthesis, leading to ROS formation in green tissues [136]. High salinity also decreases the utilization of nicotinamide adenine dinucleotide phosphate (NADPH) via the C3-cycle, decreases rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) activity and consequently decreases CO₂ carboxylation [137]. Wang et al. [138] reported that high salinity levels decreased mesophyll conductance by decreasing carboxylation, reducing total chlorophyll content, degraded chloroplast structure, and disrupting the electron transport chain [139]. In the case of chloroplasts, a vital photosynthetic organelle in plants that contributes to the biosynthesis of vitamins, amino acids, fatty acids, lipids and isoprenoids, salt stress affects vital associated organelles such as the thylakoid membrane, increases oxidative stress, and impairs the osmotic and ionic homeostasis [140]. Several studies showed that nanoparticles application could reduce the adverse toxic effects of Na⁺ and Cl⁻ on photosynthesis. For example, Ag-NPs application in wheat increased photosynthesis due to stimulatory effects by an unknown mechanism and biomass accumulation under saline conditions by reducing Na⁺ translocation from roots to shoots and decreasing H₂O₂ and MDA content [61]. Application of ZnO-NPs increases the production of carbonic anhydrase, a zinc metalloenzyme that facilitates CO₂ utilization in plants and, consequently, increases photosynthesis. Applying SiO₂-NPs increased leaf dry weight and the proline, chlorophyll, and antioxidant contents in salt-stressed sweet basil (*Ocimum basilicum* L.) plants [141]. Silver nanoparticles decreased ROS production and lipid peroxidation in wheat plants under salt-stressed conditions [99]. The reduced ROS and lipid peroxidation production under salinity stress might be due to scavenging system activation through ascorbate-glutathione cycle-mediated, which inhibited lipid peroxidation and modulated the K⁺ efflux [99,142]. Application of nanoparticles increased K⁺ ions in wheat leaves, resulting in enhanced plant growth by decreasing uptake of Na⁺ and Cl⁻ in roots and posterior translocation to shoots [143]. The possible mechanism is that Zn ions accumulate in the apoplast, and the released Zn ions are absorbed by mesophyll cells.

Further, ZnO-NPs triggered the anti-stress enzymes, which are helpful to reduce salt effects [144]. Similarly, the application of Ag-NPs increased the chlorophyll content in wheat by enhancing the PS-II quantum efficiency and photosynthesis-related enzymes activity [143,145]. Studies showed that Ag-NPs (300 ppm) increased the activity of super-

oxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), and glutathione peroxidase (GPX) up to 44, 82, 89, and 20%, respectively in wheat plants that grown under salt conditions [99].

Table 2. Effect of nanoparticles on growth and development under salt-stressed conditions.

Crop	Nanoparticles/Elements	Effects	References
Barley	Nano-TiO ₂ (500–2000 mg kg ⁻¹)	n-TiO ₂ increased the growth and photosynthesis rate of barley. Increased activities CAT, SOD, and APX while decreasing malondialdehyde (MDA) content	[101]
Barley	nano chitosan (0.1–0.3%)	Increased plant height, fresh and dry weight, and leaf area	[76]
Barley	Se nanoparticles	Increased total phenolic contents and reduced MDA activity	[75]
Wheat	Ag-NPs (2–10 mM)	Increased fresh and dry weights and chlorophyll contents	[61]
Wheat	Nano-Fe ₂ O ₃ and ZnO	Increased shoot dry weight, plant height and leaf area	[146]
Wheat	Ag NPs	Increased growth, chlorophyll contents	[61]
Wheat	AgNPs	Increased chlorophyll, ascorbate content up to 26%	[99]
Maize	ZnO-NPs	Increased antioxidant enzymes	[61]
Maize	nano chitosan	Increased chlorophyll content, PS II activity, and an overall improvement in maize growth	[77]
Maize	Nano-ZnO and Fe ₂ O ₃	Increased root growth (17%), net CO ₂ assimilation rate (8%), leaf Fe (22%)	[146]
Maize	Metal NPs	Reduced ROS production by increasing antioxidants enzymes	[147]
Rice	ZnO-NPs	Improved SOD production	[148]

4.2. Alleviation of Salt Stress by Agronomic Practices

The efficient and sustainable management of farm resources can mitigate and overcome salinity adverse effects [15]. Soil salinity can be reclaimed through salt leaching from the rhizosphere, alteration in agronomic practices at the farm level, and introduction of salt-tolerant crops [149]. Some agronomic practices that can halt salinity and mitigate its adverse effects on crops are discussed below:

Chemical amendments: Certain soil chemical amendments, i.e., adding sulphuric acid, sulphur and gypsum, can be used to ameliorate the adverse effects of soil salinity stress [14]. Although, this needs special care in their application due to the corrosive nature of the acid. Likewise, through gypsum amendments, calcium replacement with sodium ions can decrease salinity adverse effects [149,150]. With gypsum application, the sodium ions move downward in the soil through drainage with irrigation water. The addition of H₂SO₄ and elemental sulphur can also reduce the soil pH due to the increment of H₃O⁺ in the soil solution [151].

Fertilization: Soil salinity can also be enhanced by fertilizer application to crops. To alleviate the adverse effects of the fertilizers, application method, timing, fertilizers characteristics, and composition should be kept in mind while applying fertilizers to the field [152]. Less frequent fertilizer application with high purity, low saline and chloride-free contents should be applied. Fertigation is also considered as a best practice that can decrease soil salinization and mitigate salinity stress. Sulphuric acid and nitric acid fertigation can reduce soil pH and increase Ca²⁺ ions in clay soil, decreasing the salinity stress injury and reducing the chloride salinity in the rhizosphere [153]. Soil with high CaCO₃ may be reclaimed through H₂SO₄ fertigation. For optimum Fe availability, its application in chelated form is recommended. In addition, NO₃⁻, Ca²⁺, K, P, silicon and salicylic acid application can enhance the salinity tolerance in different crops [154–157]. On the other hand, the humic acid application can also halt salinity stress by enhancing salt tolerances in crops.

Salt tolerant crops: The most crucial strategy for salinity problems is salt-tolerant crops. Different crops can tolerate the salinity in general, i.e., sugar beet, cotton, and barley. Among cereals, paddy rice, sugarcane, rye, and pearl millet can grow on saline soils. **Leaching maintenance:** For salinity maintenance on arable fields, leaching maintenance is necessary. Irrigation water applied with known volume must accompany the volume of water drained out from the rhizosphere, which is extra water required for regular irrigation. For successful long-term irrigation, leaching is necessary, and the frequency of leaching is dependent on evaporation demand, soil salinization, and crops sensitivity to salinity [154]. This leaching washes the salts from the root zone and enables the plants to thrive [158].

Cover crops and mulching: The incidence of high evapotranspiration brings the soil surface more saline. Salinity in the soil is dependent on water table depth and irrigation water salinity concentrations [159]. Certain practices that flux the water table downward and reduce evapotranspiration through mulching reduce the soil salinity in the root zone [160].

Grafting: Grafting is considered an essential practice that reduces yield losses due to salinity in cucurbits. It prevents salinity stress by inhibiting the plants' Na and Cl uptake, which are the main sources of salinity in the soil [154,161]. **Microbial remediation:** the microorganisms colonize the root zones and enhance plant growth under different circumstances through direct and indirect mechanisms [162]. For salinity stress alleviation, the use of plant growth-promoting bacteria (PGPB) is beneficial and gaining the interest of the researchers. Plant growth-promoting rhizobacteria (PGPR) enhances plant growth by indirectly reducing the incidence of pathogens and diseases or enhancing nutrient uptake with the production of phytohormones. Literature also showed that arbuscular mycorrhizal fungi improve plant growth under salinity stress [163]. The inoculation of PGPR and other microbes is a potential strategy for salinity stress alleviation in salinity susceptible crops [164]. Different genera of salt-tolerant PGPR have been isolated for extreme saline, sodic and alkaline soils.

5. Future Research

Cereal crops are the primary source of food for millions of people around the world. Many efforts are required to increase cereal crops' production to meet the growing population's increasing food demand. Various abiotic stress such as drought, high temperature, heat stress, heavy metal, and salinity stress negatively affects cereal crops' growth and productivity. Among these stresses, the negative effect of medium and high soil salinity concentrations is likely the most critical and pervasive globally. Soil salinity reduces seed germination, growth, yield and quality. However, few studies are available regarding the effect of salinity on the grain quality of cereals.

Under salt stress, plants adopt different tolerance mechanisms to maintain their growth. However, the sensitivity of cereals significantly differs among species.

The use of salt-tolerant genotypes obtained through conventional and biotechnological approaches and the application of nanoparticles, osmolytes and hormones have been among the most efficient approaches to cope against the adverse effects of medium and high salinity concentrations in agricultural soils. Although some success has been recorded in releasing the salt-tolerant cereals lines or cultivars, most of the work has been done on wheat, rice, and maize, while few reports are available on barley and sorghum. Thus, there is a need to develop more salt-tolerant sorghum and barley cultivars for salt-stressed areas worldwide.

Finally, while most studies regarding salt stress have only focused on the negative effect of NaCl in soil, other types of salts are also present in the soil and water and may induce salinity in soils. Thus, future research should consider studying the behaviour in the soil and the agronomic impact of other salts in crop growth and productivity.

6. Conclusions and Recommendations

Soil salinity is a significant threat to crop production and food security. The development of salt adapted crops is the most effective way to overcome this abiotic stress. Soil salinity affects plant physicochemical properties and causes osmotic and oxidative stress, severely decreasing cereals' growth, yield and quality. Salt tolerance by plants is governed by multi-physiological and molecular mechanisms such as ionic, tissue and osmotic stress. Therefore, significant progress has been made, and many studies have been conducted to understand salt stress mechanisms in plants. However, much more studies are needed to develop salt adapted crops. Besides, the development of salt adapted crops through conventional breeding is prolonged. Understanding both sensing and signalling metabolic pathways of plants under abiotic stress is essential to understand the role of other nutrients such as K^+ for salt induction and the salt tolerance genes in different crops to mitigate the salinity. Furthermore, with the advancements in biotechnology, genetic engineering, and genomics, we expect more salt adapted genotypes to become more extensively available for different edaphoclimatic conditions.

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