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Chapter

Introductory Chapter: Making Plant Life Easier and Productive under Salinity – Updates and Prospects

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1. Introduction

1.1 Human, food and plants

Almost all life forms on the Earth fundamentally depend on plants and/or plant-based (food and non-food) resources. Human being, in particular, are indebted (directly or indirectly) to the diversity of plants for oxygen, food, fuel, fiber, medicines, and even for shelter. Being sessile by nature, plants have to closely interact with the immediate environment (growing conditions comprising air, water, soil, energy/light) to sustain their own lives and accomplish the aforementioned notable contributions to human life. As an enigmatic, heterogeneous, multiphasic and porous system, soil acts as a natural growth environment/medium for diverse land plants. The health of soil is closely linked with the health of plants and that of their immediate and long-term consumers. Interestingly, 80% of average calorie consumption comes from crop plants grown directly in soil. Hence, healthy soil has been widely argued vital both as a resource for feeding the burgeoning global population via agriculture, and also for realizing most of the United Nations Sustainable Development Goals [1–5].

1.2 Soil salinization: concept and types

The health of soil is being significantly impacted by increased salinization due to excess accumulation of varied salts (e.g., cations: Na^+, Ca^{2+} and Mg^{2+}; anions: Cl^-, SO_4^{2-}, CO_3^{2-} and HCO_3^-). Based mainly on the soil properties, namely electrical conductivity (EC), pH, exchangeable sodium (Na^+) percent (ESP), Na^+ adsorption ratio (SAR), total soluble salts (TSS), and total dissolved solids (TDS), soils can be categorized in three major types: saline, sodic and saline-sodic. EC of the saturation paste extract (EC_e) is the measure of salinity, whereas the measure of sodicity is the exchangeable sodium (Na^+) percentage (ESP) or the sodium adsorption ratio (SAR). Soils can be saline ($ECe > 4$ $dS\,m^{-1}$ (decisiemens per meter)) at 25°C and ESP < 15 (high soluble salts and low exchangeable Na^+; pH 7.0–8.5), sodic ($Ece < 4\ dS\,m^{-1}$ and ESP > 15; with a high amount

of exchangeable Na$^+$ ions on the cation-exchange sites; weak bond between soil particles; pH > 8.5) or saline-sodic (Ece > 4 dS m^{-1} and ESP > 15; both salts and exchangeable sodium are high). According to the first ever country-driven global map of salt-affected soils (GSASmap, V1.0.0), which comprised over 118 countries with 257 and 419 locations (covering 85% of global land area), 85% of salt-affected top-soils are saline, 10% are sodic and 5% are saline-sodic, 62% of salt-affected subsoils are saline, 24% are sodic and 14% are saline-sodic (FAO-GloSIS 2023 [6]; **Figure 1**). Major consequences of sodicity and salinity on soil health are summarized in **Figure 2**.

The building-up of elevated level of varied salts (e.g., cations: Na$^+$, Ca^{2+} and Mg^{2+}; anions: Cl$^-$, SO$_4^{2-}$, CO$_3^{2-}$ and HCO$_3^-$) in the soils may be caused naturally (*leading to primary salinity*) or human-induced (or anthropogenic activities) (*leading to secondary salinity*). Interestingly, the natural climate conditions; different geological, hydrological and pedological processes; wind; rainfall; parent rock weathering; long-term natural accumulation of salts (including Cl$^-$ of Na$^+$, Ca^{2+} and Mg^{2+} and sometimes SO$_4^{2-}$ and CO$_3^{2-}$); and higher evapotranspiration (versus precipitation) largely contribute to the primary or natural salinity in the soil or surface water. On the other hand, the human-induced (or anthropogenic) activities done in agricultural management practices are largely inappropriate, which cause poor drainage and arbitrary irrigation, disrupt the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration), leading ultimately to the secondary salinization, the major cause of the loss of agricultural soils (**Figure 3**) [6, 8]. Both primary and secondary
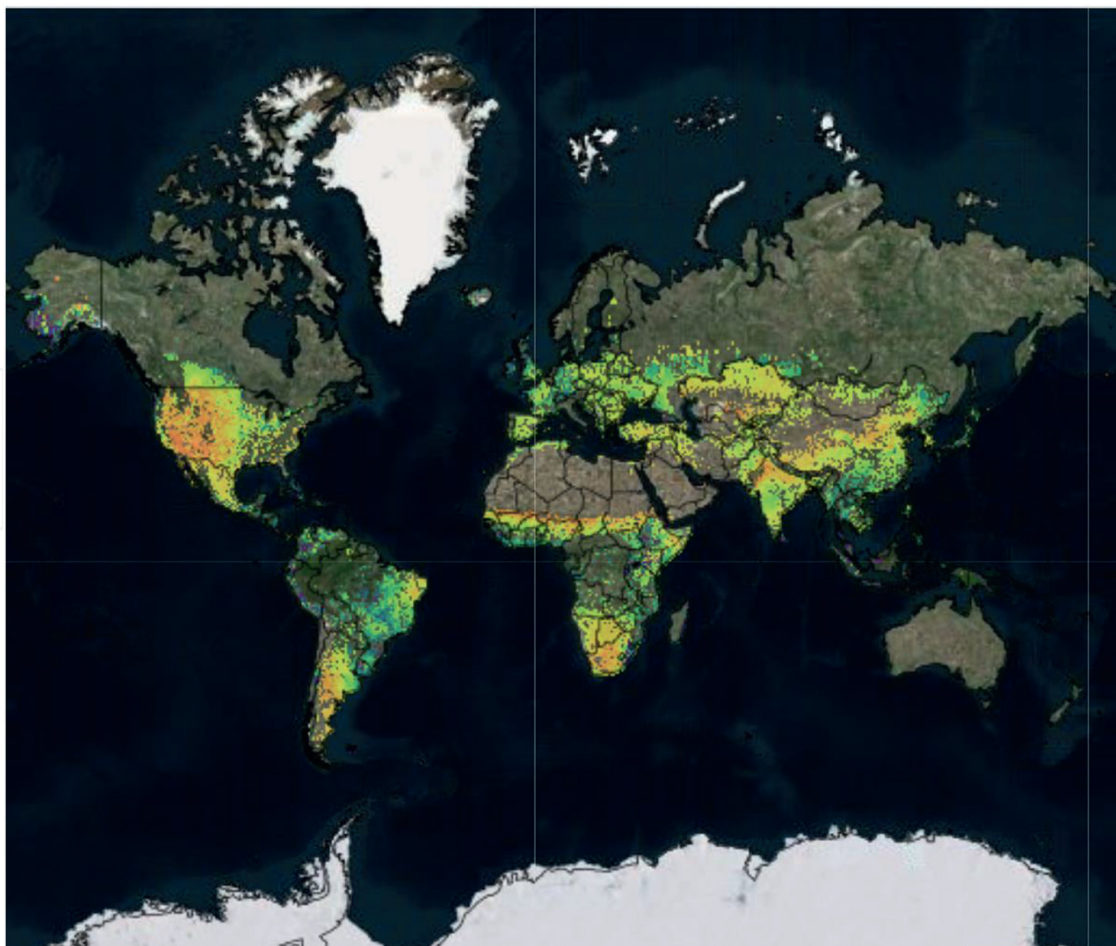

Figure 1.
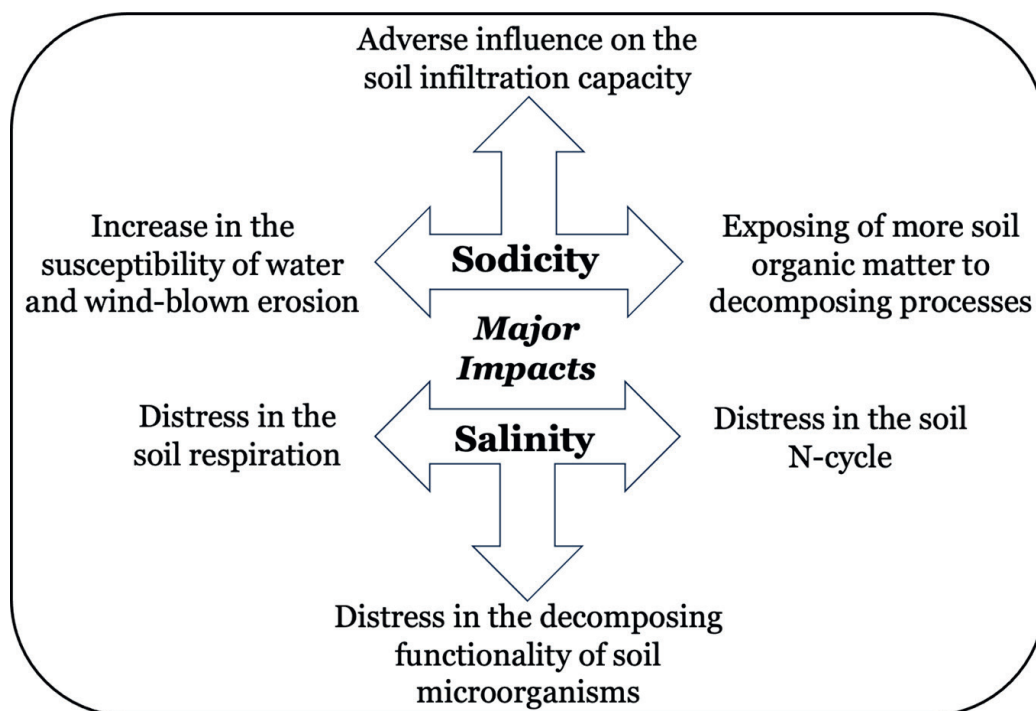*Global map of salt-affected soils (GSASmap) [6].*

Figure 2.
Schematic representation of the major impacts of sodicity and salinity on soil health [7].
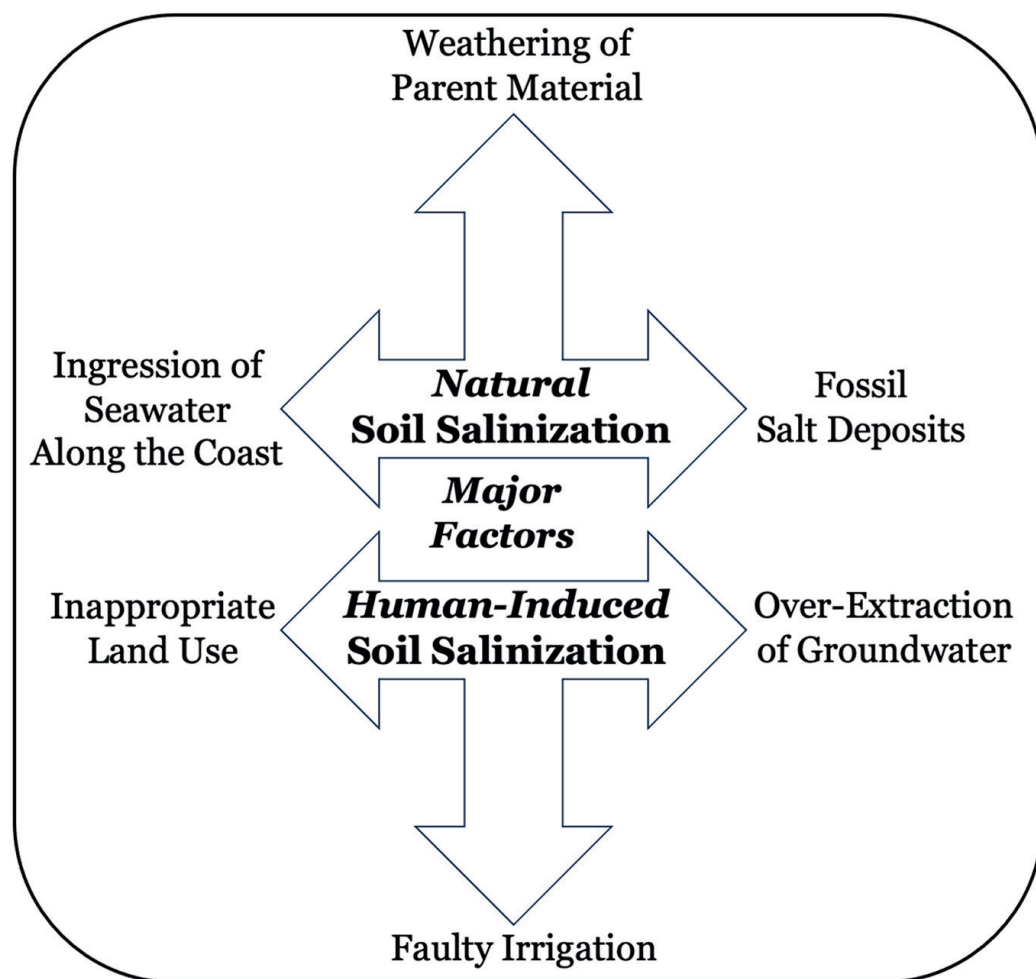

Figure 3.
Schematic representation of the major factor contributing to natural and human-induced soil salinization [7].

salinization of soils mainly occurs in arid and semi-arid regions, where precipitation to evapotranspiration ratio is low. Notably, climate change is among the major factors known to influence the global distribution of salt-affected soils [9–13].

Notably, soil salinization is at the top among the major climate change-influenced abiotic stress factors and is also known to bring severe consequences at both agricultural soil and agricultural crop plant levels. It significantly changes the major physiochemical and biological characteristics (including soil structure, soil microbial activity, etc.). These soil-level changes culminate in the inhibition of absorption of water and nutrients by plants and severely impairing the physiological/biochemical, molecular and yield (≈50% reduction) attributes of crop plants. On the other hand, agriculture, in particular, is under pressure to accelerate crop plant yield (by >70%) in order to feed the burgeoning world population that is projected to stabilize at around 9.7 billion by the year 2050 [14].

Given above, efforts must be made to make crop plant life easier and more productive under rapidly increasing soil salinity. It is required to consider a multi-level approach comprising monitoring, assessment, and the management of soil salinization; getting insights into the crop plant physiological/biochemical and molecular-genetic responses to soil salinity; and dissecting the strategies for strengthening plant/crop salinity-tolerance mechanisms.

2. Salinity-impacts in plants

Three major physiological stresses encountered by salinity-exposed plants include ion (Na^+ and Cl^-) toxicity; physiological drought due to low osmotic potential; and nutrient imbalance in plants (**Figure 4**) [15–17]. Salinity-accrued decrease in plant growth and photosynthesis and related variables may also be possible as a result of hyperionic and hyperosmotic stress [18]. Plant tolerance to salinity of the soils of the root zone greatly varies with plant types and their age, and the salinity concentration and exposure duration. However, exhibition of yield reduction was noted in most crop plants at the electrical conductivity (EC) of the saturation extract (Ece) in the root zone >4.0 dS m^{-1} (≈40 mM NaCl; exchangeable sodium of 15%) at 25°C [19–21]. Taking into account representative studies, the major impacts of salinity on plant growth, photosynthesis, yield, nutrient uptake and metabolism, water status, oxidative stress, and antioxidant metabolism are briefly overviewed hereunder.

2.1 Growth, photosynthesis and yield

Soil salinization impacts almost every stage of plant growth and development. Salinity impact on germination has been extensively reported in several test plants [22, 23]. Contingent to salinity concentration, type of salt present, type of plant species, age of test plant, and time of exposure were reported to control the extent of salinity impacts. The major growth traits, namely the rate, percentage and index of germination; leaf area; length, fresh and dry weights of root and shoot; and plant dry mass, were varyingly decreased in salinity-exposed plants [23–25]. Salt stress impacts on photosynthesis and involved several mechanisms. Salinity-accrued impediment in photosynthesis is caused by decreased leaf area and stomatal conductance, declined CO_2 availability and assimilation; Cl^--led inactivity of RuBisCO; degraded D1 and D2 proteins of PSII reaction center; diminished activity of enzymes involved in photosynthetic pigment synthesis; low uptake of Mg^{2+}, and destruction of pigment-protein
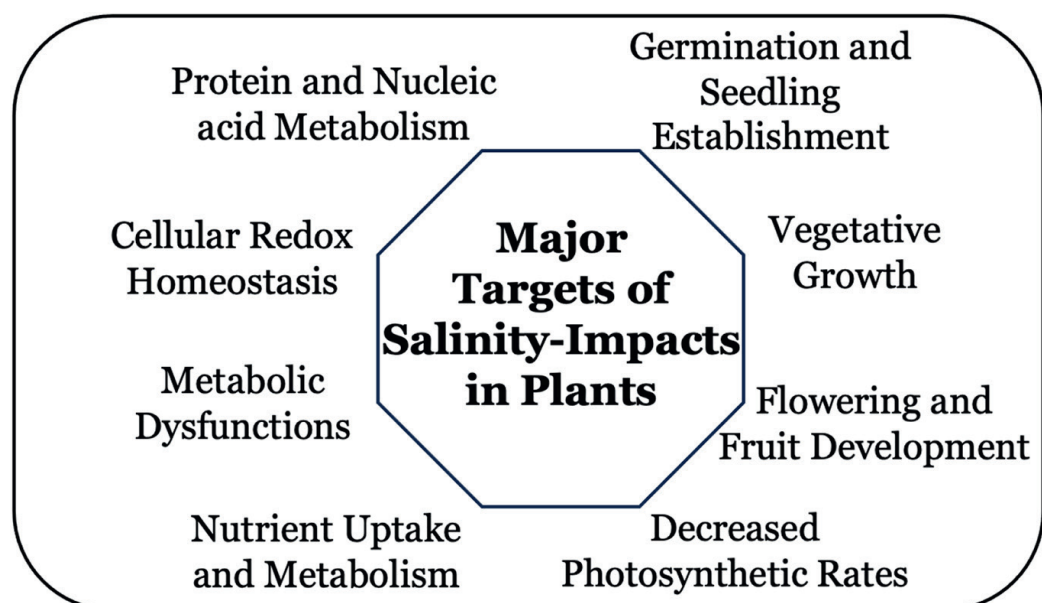
Major Targets of Salinity-Impacts in Plants

- Protein and Nucleic acid Metabolism
- Germination and Seedling Establishment
- Cellular Redox Homeostasis
- Vegetative Growth
- Metabolic Dysfunctions
- Flowering and Fruit Development
- Nutrient Uptake and Metabolism
- Decreased Photosynthetic Rates

Figure 4.
Schematic representation of the major targets of salinity impacts in plants.

complexes [26, 27]. Elevation in the soluble salts in the rhizosphere is bound to result in brutal yield losses in most crops, which was widely argued to involve salinity impact on different yield components [28, 29].

2.2 Nutrients uptake and metabolism, and water status

Elevated soil salinity significantly impacts the acquisition of most mineral nutrients including Ca, Cu, Fe, N, P, K, S and Zn. Decreased solubility and mobility of Cu and Fe were earlier noted in plants under salinity stress [30, 31]. In fact, salinity conditions tend to immobilize nitrate (NO_3^{2-}; by Cl^-) and ammonium (NH_4^+; by Na^+) ions, the major plant-absorbed N forms [32]. Unavailability of soil-P to plants, its deficiency therein are caused by salinity [33]. Impaired uptake and metabolism of Ca, K, P, N and S were observed in salinity-treated plants, which mainly involved salinity-accrued changes in soil solution's osmotic potential and/or the activity of K^+-selective ion channels [22, 34]. Salt-affected plants exhibit significantly decreased uptake and use efficiency of B, K and P due mainly to the negative interactions with higher concentrations of cations and anions. Salinity-exposed plants also exhibited inhibited K^+ uptake and decreased K^+/ Na^+ ratio, which were argued to involve salinity-mediated depolarization of the plasma membrane potential, activation of voltage-gated guard cell outward rectifying K^+ channels and eventual K^+ efflux [35, 36]. Salinity-caused reduced uptake and deficiency of Mn, and decreased solubility and P uptake were also observed in plants under salinity exposure [37, 38]. In several instances, elevated salinity also impacted the assimilation of both N and S via impacting the major N-S assimilatory enzymes [39–41]. Notably, high salinity was reported to affect the major genes involved in the uptake and transport of N, and assimilation can also be affected by high salinity [42]. Salt stress can also impact nitrification and ammonification [43]. The proportion of N-transport amino acids (such as asparagine, glutamate, aspartate and glutamine) decreased in several salinity-exposed test plants [44, 45]. Notably, physiological drought in plants has been reported due to the imposition of high salt concentration in the rhizosphere, and eventual salt-accrued immobilization of water and its unavailability to the plants [46].
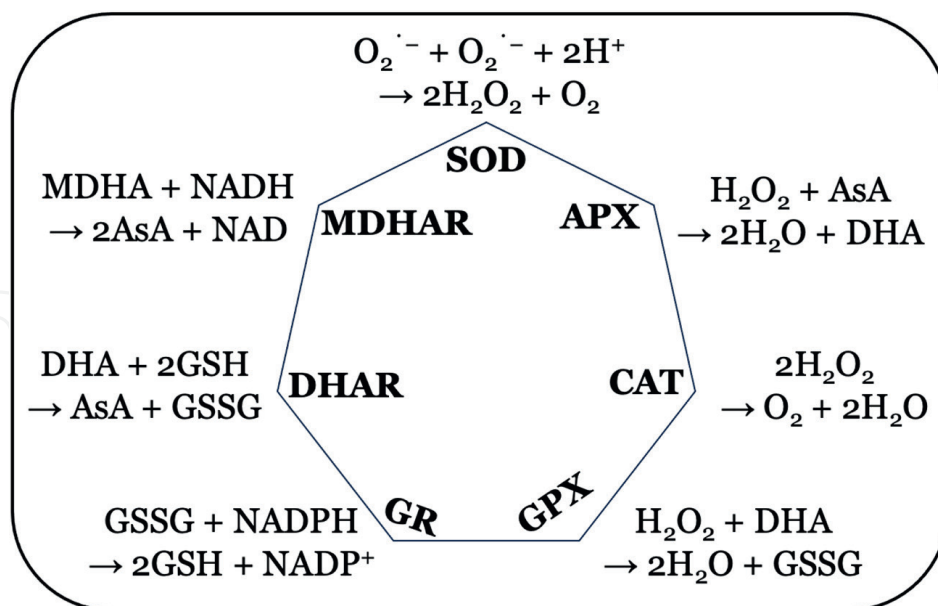
Figure 5.
Schematic representation of the main reactions performed by selected enzymatic antioxidants involved in the scavenging of varied reactive oxygen species (ROS). Abbreviations: DHA, reduced dehydroascorbate; GSSG, oxidized glutathione/GSH disulfide; MDHA, monodehydroascorbate; NADH, nicotinamide adenine dinucleotide; NAD, nicotinamide adenine dinucleotide; NADPH, nicotinamide adenine dinucleotide phosphate; NADP$^+$, oxidized form of nicotinamide adenine dinucleotide phosphate [49–52].

2.3 Oxidative stress and antioxidant metabolism

Elevated soil salinity is widely known to accelerate the accumulation of reactive oxygen species (ROS; such as O_2^-, H_2O_2, •OH, and $^1O_2$) leading to oxidative stress, a physiological condition of imbalance between generation of ROS and their scavenging [22, 47, 48]. Elevated or non-metabolized ROS cause lipid peroxidation and damage macromolecules including DNA and protein. Interestingly, plants possess inherent capacity to activate ROS-scavenging system in order to counteract potential ROS-accrued consequences. Interestingly, plant antioxidant defense system is comprised of enzymatic (superoxide dismutase, SOD; peroxidase, POD; catalase, CAT; ascorbate peroxidase, APX; glutathione peroxidase, GPX; glutathione reductase, GR; monode-hydro ascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR); and non-enzymatic (reduced ascorbate, AsA; reduced glutathione, GSH; phenolic, vitamin E, carotenoids and mannitol etc.) components (**Figure 5**) [49–51].

Extensive reports are available on the salinity-mediated elevation in the levels of varied (such as O_2^-, H_2O_2, •OH, and $^1O_2$), and their impact on membrane lipids and leakage of electrolytes have been reported. Salinity stress was also found to induce different components of antioxidant defense system in salinity-exposed plants. Significant enhancements in the activity of enzymes involved in the dismutation of O_2^- (SOD); H_2O_2-metabolism (CAT; APX) and GSH-regeneration (GR) [22, 47, 48].

3. Salinity impacts-minimization in plants

The life of plants under salinity can be made easier considering both plant- and soil-focused strategies, namely adopting approaches aimed at improving plant growth, metabolism, and productivity and employing the management approaches for managing the health (physico-chemical and biological traits) of saline soils.

3.1 Plant health-improving approaches

Plants are endowed with inherent mechanisms for salt stress-impact mitigation, which include hormonal stimulation, ion exchange, antioxidant enzymes and non-enzymes (metabolites) and activation of signaling cascades. However, efficiency of most of these inherent mechanisms can be further improved by employing approaches comprising the optimum and timely supply of mineral nutrients, compatible solutes, bio-stimulants, nanomaterials, phytohormones, phenolic compounds, microorganisms and considering mineral nutrients-phytohormones crosstalk and molecular-genetic approaches.

3.1.1 Mineral nutrients

The role of different mineral nutrients (such as N, P, K and S) in both minimization of salinity impacts and strengthening plant salinity tolerance has been widely studied. The major mechanism involved in the improved health of salinity-treated and N-supplied plants included diminished accumulation of Na^+, efficient N-uptake and assimilation processes, controlled K^+/Na^+ homeostasis, and improved plant-K status [53–55]. S-supply improved plant health and salinity tolerance via maintaining the improved status of S and S-containing compounds (including cysteine, Cys; glutathione, GSH); improved cellular redox homeostasis; efficient ROS-metabolism; decreased oxidative stress; decreased Na^+/K^+ ratio and Na^+ accumulation, increased K^+ and Ca^{2+}; improved uptake of K and P; and reduced electrolyte leakage [22, 48, 56, 57].

3.1.2 Phytohormones

Sustainable improvement of plant growth, metabolism, photosynthesis and productivity (yield) under salinity-affected soils can be possible with the judicious and timely use of various phytohormones and signaling molecules, and thereby minimizing increasing strain on the global food security. The major role (and underlying basic mechanisms) of phytohormones (namely abscisic acid, ABA: a sesquiterpenoid, 15-C compound; auxins: endogenous plant growth regulators; brassinosteroids, BRs: polyhydroxy steroidal phytohormones; cytokinins, CKs: derivatives of adenine or that of phenylurea; ethylene: an unsaturated hydrocarbon gas; and gaseous hormone; gibberellins, gibberellic acid (GA): a large family of tetracyclic di-terpenoid compounds; jasmonic acid, JA: a cyclopentane fatty acid; nitric oxide, NO: a highly versatile gaseous, free-radical, redox-signaling molecule; salicylic acid, SA: a phenolic plant hormone; and strigolactones, SLs: carotenoid derived phytohormone) in improving plant salinity tolerance are briefly highlighted hereunder.

Under saline condition, ABA supply improved plant health by modulating ABA signaling components; reducing Na^+ content, increasing K^+, Mg^{2+} and Ca^{2+} content; improving coordination among antioxidant defense system components; improving cellular level of AsA and GSH; significant reduction in Na^+ content, increasing the contents of hormones such as 1-aminocclopropane carboxylic acid, trans-zeatin, N6-isopentyladenosine, indole-3-acetic acid (IAA); reduction of transpiration flow, regulation of Na^+ ion homeostasis; involving calmodulin signaling cascade; and induction of osmolytes accumulation [58–60]. The supply of auxins has been widely reported to improve plant salinity tolerance involving various mechanisms [61–63]. BRs-mediated improvements in plant salinity tolerance and growth and development mainly involved BRs-supply-induced activity of ROS-metabolizing enzymatic antioxidants (including

APX and CAT), and the cellular levels of non-enzymatic antioxidants (such as AsA and GSH); and decreased electrolyte leakage and membrane lipid peroxidation [24, 64, 65]. Cytokinins-supply can improve plant salinity tolerance via modulating shoot Cl^- exclusion and enhancing antioxidant system and photosynthetic efficiency [66, 67].

Ethylene-induced plant salinity tolerance was argued earlier as a result of ethylene-mediated maintenance of the homeostasis of ions; up-regulation of antioxidant enzymes; improved endogenous ethylene-overproduction; increased activity of seed α-amylase; decreased H_2O_2 and lipid peroxidation; decrease in osmotic stress; PSI cyclic electron flow-mediated controlled non-photochemical quenching [68–70]. Gibberellins (GA)-mediated improvement in plant health involved decreased ion leakage; improved osmolyte accumulation and proline content; elevated Ca^{2+} and K^+ concentrations, and transpiration rates; modulated antioxidants and secondary metabolites; and improved redox homeostasis and coordination among antioxidant enzymes [71–73]. Jasmonic acid (JA)-supply can mediate the salinity-impact mitigation in plants involving increased endogenous levels of cytokinins and auxins, increased α-tocopherol, phenolics, and flavonoids levels; enhanced activity of SOD and APX; increased K^+ and Ca^{2+}; declined Na^+ content; and crosstalk on JA and ABA [74, 75]. Nitric oxide (NO) is the smallest diatomic gas and a gaseous signaling molecule in plants [76, 77]. NO-supply protected plants against salinity impacts by enhancing mineral absorption, maintaining hormone equilibrium, improving osmolyte accumulation, strengthening antioxidative defense systems, mitigating H^+-ATPase inhibition, and maintaining oxidative homeostasis in plants under salt stress [78, 79]. Alleviation of salinity stress in plants has also been achieved through crosstalk of NO with other signaling compounds and phytohormone signaling pathways [80, 81]. In salinity-exposed plants, salicylic acid (SA)-supply reduced Na^+ and Cl^- ions; maintained high GSH level; improved cellular redox environment; regulated AsA-GSH cycle, elevated osmolyte accumulation; and involved characteristic changes in the expression pattern of major GST-gene family members [82–84]. Strigolactones (SLs)-mediated improved salinity tolerance in plants was argued to involve enhanced antioxidant enzyme activity; improved ROS-metabolism, decreased lipid peroxidation and cellular damage; and SLs-ABA-arbuscular mycorrhizal fungi crosstalk [85–88].

3.1.3 Mineral nutrients-phytohormones crosstalk

The major outcomes of the crosstalk of most mineral nutrients with phytohormones have improved plant salinity tolerance. To this end, in several instances, the crosstalk between the major phytohormones (such as indole-3-acetic acid (IAA), gibberellic acid (GA), kinetin (CK), ethylene, 24-epibrassinolide, SA, ABA, brassinosteroid (BR)), with N and S resulted in differential decreasing the content of Na^+ and Cl^- ions; modulation of key enzymes of N and S metabolism; cellular homeostasis, photosynthesis; lowering oxidative damage, improving photosynthetic efficiency, assimilation of N and S, proline content and antioxidant defense system and decreased generation of oxidative stress markers; maintain osmotic balance via controlling cellular osmolytes; modulating the photosynthetic N-use-efficiency and antioxidant metabolism; increased levels of free amino acids and soluble proteins [22, 44, 60, 68].

3.1.4 Osmolytes

Exhibition of almost ceased water flow from soil into roots and cellular dehydration as a result of decreased cellular turgor pressure are common in plants under

salinity stress. To counter this, plants employ the mechanism of osmoregulation, which involves the accumulation of varied small water-soluble organic non-toxic solutes (osmolytes/compatible solutes). Osmolytes/compatible solutes such as polyamines (PAs), glycine betaine, b-alanine betaine, dimethyl-sulfonio propionate, and choline-O-sulfate are 'ammonium compounds'; whereas fructan, trehalose, mannitol, D-ononitol and sorbitol are grouped as the 'sugars and sugar alcohols'. On the other, the list of major amino acids acting as osmolytes includes proline and ectoine. The accumulation of most of these solutes in the cytoplasm largely leads to the maintenance of low cytosolic and cytosolic concentrations within narrow limits (100–150 mM) across a broad range of external and vacuolar concentrations of NaCl [89–91]. In addition to performing cytoplasmic osmoregulation/osmotic adjustment, osmolytes have been considered as efficient oxidative stress-busters in plants under varied abiotic stresses (**Figure 6**) [92].
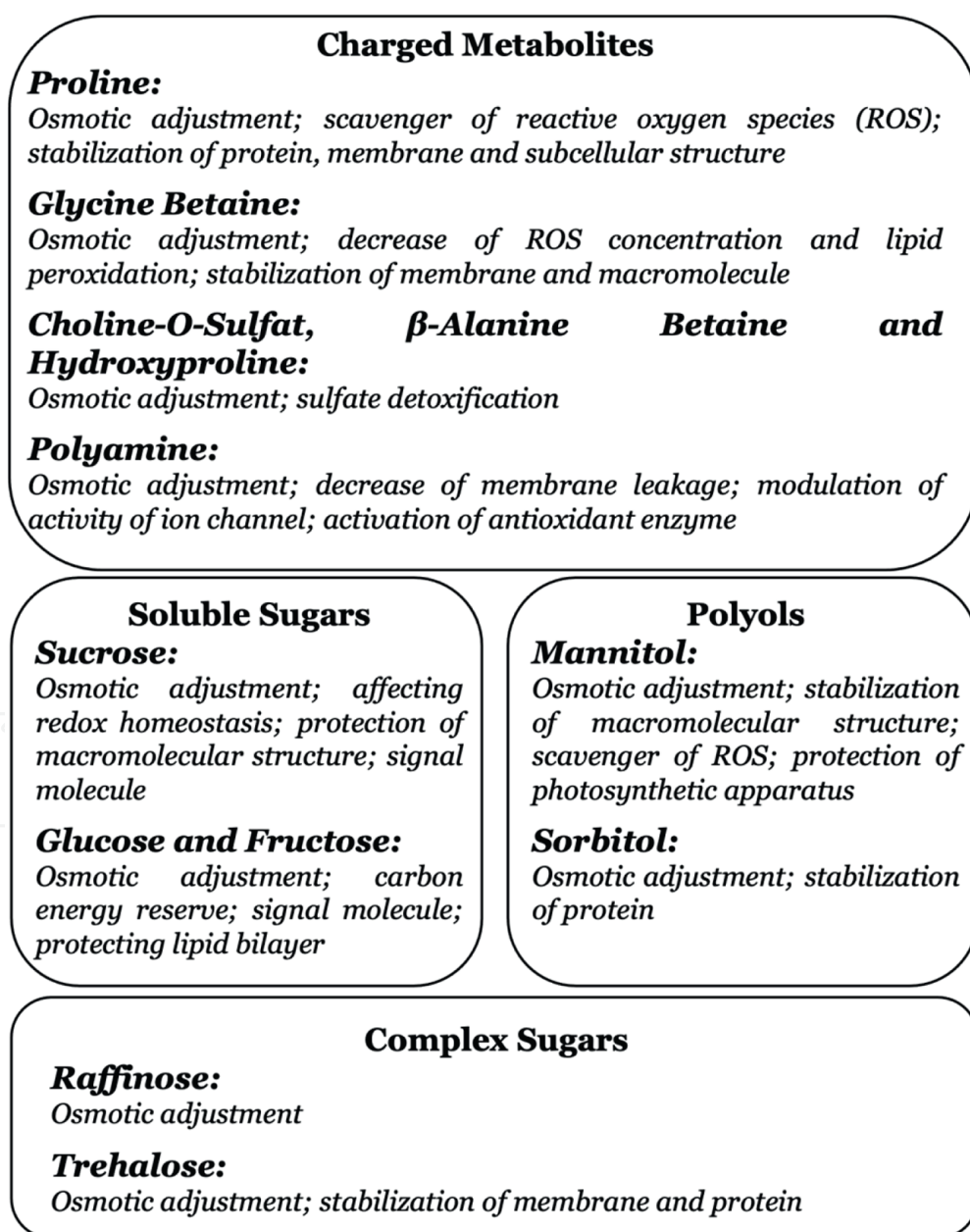

Charged Metabolites

Proline:
Osmotic adjustment; scavenger of reactive oxygen species (ROS); stabilization of protein, membrane and subcellular structure

Glycine Betaine:
Osmotic adjustment; decrease of ROS concentration and lipid peroxidation; stabilization of membrane and macromolecule

Choline-O-Sulfat, β-Alanine Betaine and Hydroxyproline:
Osmotic adjustment; sulfate detoxification

Polyamine:
Osmotic adjustment; decrease of membrane leakage; modulation of activity of ion channel; activation of antioxidant enzyme

Soluble Sugars

Sucrose:
Osmotic adjustment; affecting redox homeostasis; protection of macromolecular structure; signal molecule

Glucose and Fructose:
Osmotic adjustment; carbon energy reserve; signal molecule; protecting lipid bilayer

Polyols

Mannitol:
Osmotic adjustment; stabilization of macromolecular structure; scavenger of ROS; protection of photosynthetic apparatus

Sorbitol:
Osmotic adjustment; stabilization of protein

Complex Sugars

Raffinose:
Osmotic adjustment

Trehalose:
Osmotic adjustment; stabilization of membrane and protein

Figure 6.
Schematic representation of the major osmolytes involved in osmotic adjustment in plants under salinity stress [52].

Salinity-exposed plants have been extensively reported to accumulate polyamines (PAs) which are low-molecular-weight aliphatic amines/polycations [91, 93, 94]. Notably, the list of most common natural PAs present in plants includes Spermidine (Spd), spermine (Spm) and putrescine (Put). These PAs are known to act as signaling molecules in plant-environmental stresses [95]. PAs-supply mediated strengthening of antioxidant defense system has been reported in plants [36, 96]. The synergistic effect of PAs (Put + Spd) was reported to confer salinity tolerance in foxtail millet (*Setaria italica*), by inducing antioxidant enzymes and osmoprotectants, and maintaining coordination among the complex physiological and biochemical processes [97]. Elevation in the cellular level of proline is involved plant salt stress tolerance mechanisms. Beside delivering C, N, and energy during stress condition, proline scavenges varied ROS and also stabilizes DNA, proteins and membranes, and reduces NaCl-induced enzyme denaturation [91, 98]. Osmotic adjustment in salinity-impacted plants can also be accomplished with the accumulation of total soluble sugars, namely glucose, sucrose, dextrins, and maltose, where these sugars provide osmoprotection and also act as C-storage [99]. A non-reducing storage disaccharide, trehalose is mainly involved in the regulation of carbohydrate metabolism [100]. Interestingly, trehalose-mediated improvement in plant salinity tolerance involves the maintenance of $K^+:Na^+$ ratio, ROS-scavenging ROS, and increased soluble sugar concentration [101–103]. Mainly acting as important osmolytes in plant vacuoles, organic acids can also significantly contribute in plant tolerance to salt stress [104].

3.1.5 Microorganisms

Numerous plant growth-promoting microorganisms have been identified, which have become a useful tool for achieving sustainable agricultural production [105, 106]. Interestingly, rhizosphere is the home to numerous plant growth-promoting bacteria (PGPB) (or plant growth-promoting rhizobacteria; PGPR) (**Figure** 7). Most of these PGPB/PGPR are cheap and easily available resources; hence, they are generally used as an inoculant for bio-stimulation, biocontrol and biofertilization for the mitigation of salinity impacts in plants. Therefore, PGPB/PGPR has been argued as an alternative strategy for salt tolerance in plants [106–108]. The role of plant growth-promoting rhizobacteria (PGPR) in plant salinity tolerance and immunity is worth mentioning, where most PGPR protect plants by colonizing within the rhizosphere and producing antimicrobial metabolites (antagonistic) and producing regulatory hormones [109]. Plant inoculation with selected PGPRs (including *Bacillus pumilus* and *Pseudomonas pseudoalcaligenes*) under saline conditions resulted in increased uptake of N, P, K, decreased uptake of Na and Ca; and improved growth traits [110]. Thus, the use of selected PGPR makes the solubility and bioavailability of major mineral nutrients (such as soil-P) feasible under saline condition. PGPR strain-mediated induction of antioxidant enzymes can also be promising in improving plant salinity tolerance.

The role of arbuscular mycorrhizal fungi (AMF), a unique group of root obligate endophytic fungal symbionts (reported in about 90% of terrestrial plants), in plant salinity tolerance has also been found significant [17, 91]. AMF-mediated improvements in plant health involved enhanced ability of plants to replace K^+ with Na^+ using various transporters [111]; maintenance of high K^+ in roots and shoots [112, 113]; efficient regulation of K^+/Na^+ ratio required for cytoplasmic ion-balance maintenance [18]; strengthening of antioxidant defense mechanism [114]; improving water-use-efficiency, and compartmentalization of Na^+ within plant tissues
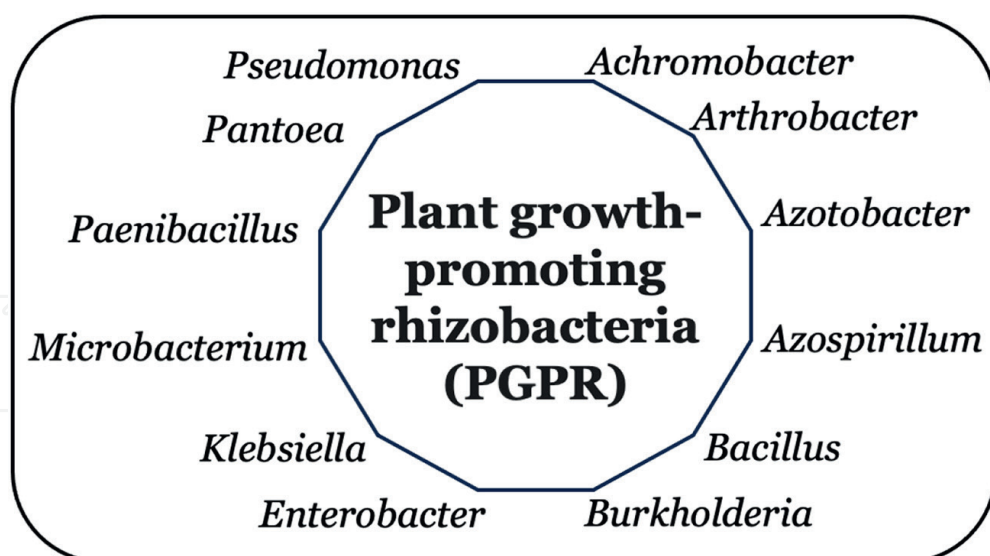
Figure 7.
Schematic representation of the major plant growth-promoting rhizobacteria inhabiting the plant rhizosphere [106–108].

[115, 116]; and inducing the osmolytic solutes (including proline, glycine betaine, or soluble sugars) [117].

3.1.6 Phenolic compounds

Elevated accumulation of phenolic compounds has been reported in salinity-impacted plants [118–120]. Considered significant among the most widely distributed secondary metabolites in the plant kingdom, phenolic compounds (including polyphenols and flavonoids) are the low-molecular-weight non-enzymatic antioxidants generated in plant cells. Most phenolic compounds act as signaling molecules and mediate auxin transport [121]. These phenolic compounds improve plant salinity tolerance via acting as reactive oxygen species (ROS)-scavengers, thereby maintaining a fine cellular redox homeostasis [118, 119].

3.1.7 Bio-stimulants

Bio-stimulants (also termed as bio-effectors) are viable microorganisms or active natural compounds, and can fall within four prime groups: acids (*humic acid*, *fulvic acid*, *humins*, *amino acids*, *fatty acids*, and *organic acids*), microbes (*plant growth-promoting rhizobacteria*, *PGPR*; *arbuscular mycorrhizal fungi*, *AMF*; *Trichoderma* spp.), plant-derived bioactive substances (*polyphenols* and *allelochemicals, etc.*), and others (*beneficial elements: Al*, *Si*, *Na*, *Se*, *Co*, etc.). Most bio-stimulants are considered as the regulators of both ROS-metabolism and also stress metabolites involved in enhancing plant tolerance to major stresses (including salinity) [122, 123]. Bio-stimulants-mediated improved salinity tolerance in plants involved bio-stimulants-induced maintenance of reduced non-enzymatic antioxidants (such as GSH and AsA); improved tissue water status, ionic and nutrient homeostasis, and osmotic tolerance; stabilized membrane properties; maintenance of a fine-tuning among antioxidant enzymes; and decreased ROS generation electrolyte leakage and lipid peroxidation) [7, 124–126].

3.1.8 Nanomaterials

Nanomaterials (NMs) are materials with a basic structure of 1–100 nm in at least one dimension. Nanomaterials (in terms of nano-fertilizer and nano-pesticides, and other plant protection nano-agents) have shown great potential in agriculture [127]. The major mechanisms underlying NMs-mediated improved plant salinity tolerance included NMs-mediated alleviation of osmotic and ionic stress, enabling the better ability to maintain cytosolic K^+/Na^+ ratio; enhancing leaf mesophyll K^+ retention; efficient scavenging of ROS; maintaining a fine-tuning among the components of antioxidant defense system; and protection of photosynthesis [128–131]. The role of nanozymes in salinity-exposed plants has also been reported, where the supplied nanozymes with ROS-scavenging ability in plants helped to improve plant salt tolerance via maintaining ROS homeostasis and alleviating ROS-accumulation in plant organs [132, 133].

3.1.9 Molecular-genetic approach

Deep understanding of molecular insights into plant salinity stress tolerance has come to light mainly due to exhaustive studies on omics techniques. The list of the mentioned techniques comprises transcriptomics, genomics, proteomics, and metabolomics, where crucial cell signaling compounds crosstalk and integrative multi-omics techniques could be employed for improving salinity tolerance in plants [134, 135]. Notably, plants are of multi-genetic nature, which makes actual understanding of their responses to salinity very difficult. To this end, genomics (studies on a certain genome aimed at unveiling insights into organism's biology) has greatly helped identify and characterize the salinity stress response gene [135, 136]. Notably, understanding plants' salinity tolerance and also the development of salinity tolerant plants have been enabled to a great extent by employing high-throughput approaches including forward genetics, serial analysis of gene expression, expression sequence tag, next-generation sequencing), targeting-induced local lesion in genomes, RNA interference, and genome-wide association study [135, 137–139]. Additionally, plant salinity tolerance mechanisms are very complicated and involve polygenic traits [15]. To this end, dealing mainly with the RNA expression profile of organisms at temporal and spatial bases, transcriptomics has helped in the identification of transcripts/genes essential in controlling transcription and translation machinery in several studies on plants under salinity stress [20, 140–142].

Critical studies on the protein profiles (*which is actually the expression-reflection of the salinity-caused genes*) employing the proteomics approach have helped to identify proteins, and get their expression profile, post-translational modifications, and protein-protein interactions in both agricultural [143–145] and non-agricultural [146, 147] plants under salinity stress. Clear and reliable information about the major metabolites (such as most organic acids, hormones, amino acids, ketones, vitamins, and steroids) in salinity-exposed plants has been obtained employing metabolomics [47, 148, 149]. The collection of minerals and elements of an organism is considered as 'ionome', which has helped in understanding the role of adoption of controlled ion uptake, distribution system (homeostasis), and detoxification as plant's major strategy for adjusting high salinity [142, 143, 150]. The major impacts of salt stress on photosynthesis and related variables, ionic relationships, plant senescence, and yield can be assessed well by employing high-throughput phenotyping [151, 152].

The manipulation of N-dynamics through genetic engineering has great potential to improve plant life under salinity stress [153]. As also mentioned above that, ethylene is an important gaseous phytohormone involved in the regulation of plants growth, development, and senescence [154]. Among the small transcription factor gene families in higher plants, ethylene-insensitive 3 (EIN3)/ethylene-insensitive 3-like (EIL) gene family is very important. All members of the EIN3/EIL gene family are key genes in the ethylene signaling pathway [155–157]. Ethylene-mediated downstream transcriptional cascade has been reported to involve EIN3/EILs as the major key elements and positive factors [158]. Ethylene-mediated enhanced salt tolerance in *Arabidopsis* involved EIN3/EIL1, which promoted EBF1/EBF2 proteasomal degradation and modulated several EIN3/EIL1-regulated genes. Further, overexpression of EIN3 target genes (e.g., ERFs and SALT INDUCED EIN3/EIL1-DEPENDENT1 (SIED1)) can also improve plant salinity tolerance [159].

3.2 Saline soil health-management approaches

Appropriate, effective, cheap and environment-friendly management/amelioration approaches can be applied to improve the health (physicochemical and biological traits) of saline soils, and thereby providing the soil conditions favorable for establishment, and optimum growth and development of plants, which in turn can contribute in securing foods for future generations [160, 161]. Reclamation (salt removal from the plant-root zone) stands at the top of the saline soil health-management approaches, which is mainly comprised of reducing salinity by leaching; salt scraping; and phytoremediation of accumulated salt. Approaches such as the addition of organic amendments as ameliorant (such as crop residue, compost, farm yard manure, cattle manure, poultry manure, clover hay and wheat straw; aimed at improving soil physical conditions; stabilization of soil aggregates and improving water holding capacity); addition of chemical amendments (flushing out of the Na^+ from the root zone; can be done using gypsum, $CaSO_4$; lime, $CaCO_3$; sulfuric acid, H_2SO_4; hydrochloric acid, HCl; nitric acid, HNO_3); and soil ripping (reduce the compaction and assist with salt leaching; normally considered in sodic soils with compaction problem) may be adopted to reduce salt leaching from the upper layers of the soil. Salt scraping approach involves the physical removal of the salt crust, followed by leaching for salts (including Na^+) removal from the root zone [162, 163].

Phytoremediation is a plant-assisted approach alternative and efficient technique that has the potential to replace the abovementioned costly physical and chemical methods for reclaiming sodic and saline-sodic soils. Interestingly, the phytoremediation approach is based on the ability of plant roots to enhance the dissolution rate of native calcite and the removal of Na^+ [161, 164]. Plant species exhibiting hyperaccumulation of elevated soil salts and strong salinity tolerance can be considered in the phytoremediation-based management of saline soils. In particular, halophytes are the plants reported to exhibit salt resistance or salt tolerance to soils with >200 mM NaCl [165]. Notably, most halophytes (including grasses, shrubs, and trees) exhibit their extraordinary capacity of salt exclusion, excretion or salt accumulating at cellular, organelle and whole body levels. Given this, several halophytes have been considered a panacea in the remediation of salt-affected problematic soils (**Figure 8**). The use of phytoremediation approach
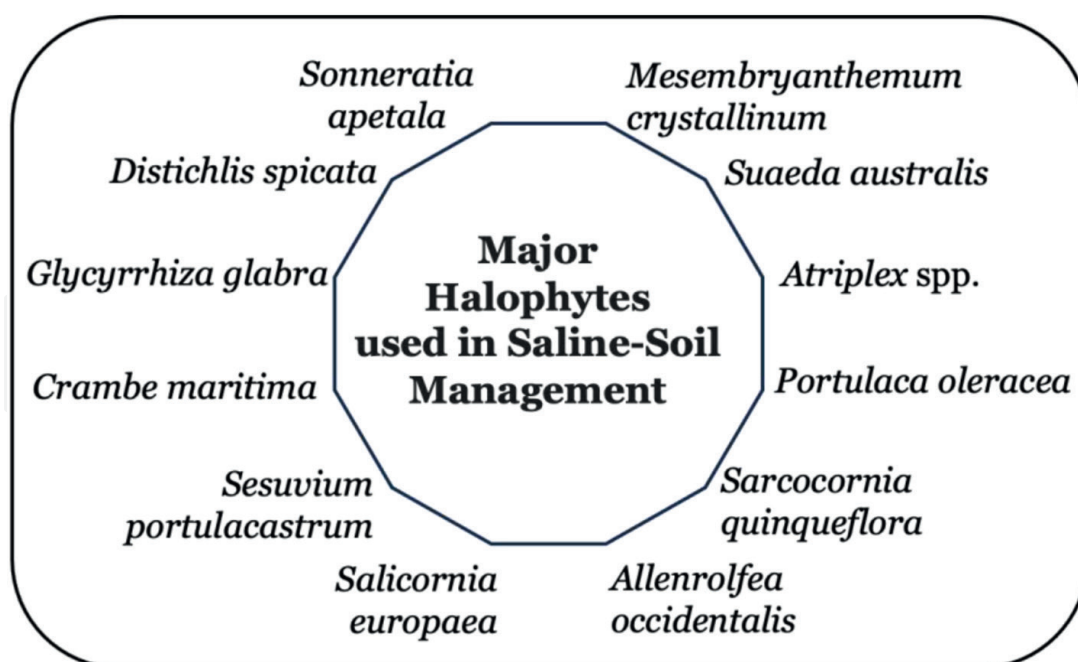
Figure 8.
Schematic representation of the major halophytes used in saline soil management [161, 164].

in salinity-loaded soils helped in improving physical, chemical, and microbiological properties; increasing soil fertility, organic matter accumulation, erodibility reduction, and increasing soil water retention [166–168].

4. Conclusions and prospects

This chapter overviewed the concept and the global status of soil salinization; highlighted the major mechanisms underlying salinity impacts in plants, and critically discussed in detail the potential approaches for making plant life easier under salinity. Notably, salinity-accrued decrease in plant-water status led to salinity-mediated impairments in growth and development; ionic imbalance, impaired nutrient uptake and assimilation were argued as a result of elevated accumulation of Na^+ and Cl^-; and impact on the tuning among the components of antioxidant defense system (causing oxidative stress) was cumulative resulted in severely hampered plant growth, metabolism, development and productivity. Notably, despite the fact of a very complex nature of plant salinity responses, the major approaches considered so far, have mainly focused on physiological/biochemical and agronomical (and molecular) aspects of salinity-exposed plants. Integrating these aspects with more molecular-genetic aspects, a critical crosstalk on gasotransmitters, phytohormones and mineral nutrients; intricacies therein of potential synergism and antagonism may help in understanding and getting insights into the complexity of signaling pathways. Evaluating how AMF influence the cell wall; and lipid metabolism under saline conditions will also be important.

Little success has been achieved in the field of breeding and genetic engineering of plants for their improved salinity tolerance. Exhaustive studies on the PGPR-colonization within the rhizosphere and the production of antimicrobial metabolites may also yield promising outcomes in plant salinity response and tolerance research. The use of varied plant bio-stimulants (bio-effectors) can also be employed to

stimulate growth, nutrient uptake and crop plant salinity tolerance. Most mechanisms underlying the control of ion homeostasis, cell activity responses, and epigenetic regulation have been extensively unveiled in salinity-exposed. However, further insights into the identification of Na^+ sensor or receptor, ontogenic variation in the salt-induced signaling, and salt-tolerance markers for crop breeding can also be promising in future research on plant salinity stress tolerance. Additionally, further dissection and use of the outcomes of the crucial cell signaling compounds crosstalk and integrative multi-omics techniques will help further understand plants salinity responses and develop salinity tolerant plants.

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