Chapter 13
Soil Salinity and Climate Change: Microbiome-Based Strategies for Mitigation of Salt Stress to Sustainable Agriculture

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Abstract Global climate change, environmental stresses, intensification of cropping practices, changed precipitation cycles, depleted water resources and reduction in soil fertility are the major constraints limiting crop productivity. Among various environmental (abiotic) stresses, soil salinity is one of the serious climate change impact, which affects about 20 and 33% of the total cultivated and irrigated agricultural lands, respectively. In recent years, soil salinization of agricultural land, along with water and environmental pollution; have emerged as significant threats to worldwide food security and agricultural sustainability. Salt stress results from excessive accumulation of salts in the soil that significantly affects soil fertility, stability, biodiversity, and consequently affects crop productivity. These problems necessitated the search of sustainable and eco-friendly agri-technologies to ameliorate the adverse effects of salt stress on plant growth and crop yield. In this context, some microorganisms inhabiting either the plant rhizosphere in extreme environments, or within halophytic plant roots, also possessing other plant growth-promoting traits, showed enormous potential in enhancing the adaptation ability of stressed plants to salinity stress conditions. These plant-associated beneficial microbes play key role in salt stress mitigation by producing osmoprotectants, antioxidants, ACC deaminase enzyme, hormones, exopolysaccharides, organic acids, nitric oxide and siderophores along with increased nutrient availability. Subsequent inoculations of crop plants with such salt–tolerant plant growth–promoting bacteria (PGPB) were found to increase the plant growth and crop yield of different plants grown in saline soils. This review briefly summarizes the different biochemical and molecular mechanisms employed by rhizospheric microbial communities for alleviation of salinity stress. Further, in-depth knowledge related to beneficial interactions of salt-tolerant microbes with the native crop plants is needed to facilitate plant growth and crop productivity under saline agro-ecosystems.

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Introduction

Increasing crop production to fulfill world food demand is a key agricultural challenge for sustaining 70% of food sources in order to feed 9 billion people by 2050 [1]. Changing agro-climatic factors, using integrated management techniques, as well as current intensive cropping systems are the limiting constraints for increasing crop yield in agricultural systems [2, 3]. Climate change, declining water sources, soil salinization, water pollution and limited availability of cultivated land are the other major constraints to twenty-first century agriculture [4–7]. Moreover, crop yield is hampered by high winds, dryness, soil salinity, high temperatures, and flooding. Among all these constraints, soil salinity is a worst environmental stress that reduces area of productive land, plant growth, crop yield as well as quality of agri-produce [8–10]. In addition, farmers use excessive amount of nitrogenous and phosphatic fertilizers in intensive farming system for increasing food production [11, 12]. The injudicious use of chemical fertilizers in modern agriculture has further degraded soil and water quality, rendering soils biologically inert and often excessively saline, and it has even polluted surface and ground water [13]. It is estimated that between 20 and 33% of the world's agricultural lands have been damaged as a result of soil salinity, which has led to losses of $27.3 billion worldwide [3, 14].

Due to increasing problem of soil salinity, alternative strategies are needed to sustain agriculture production in salt-stressed soil and to increase crop yield in an eco-friendly and sustainable manner [15, 16]. The major strategies include plant genetic engineering, conventional breeding, and the use of salt-tolerant plant growth promoting rhizobacteria (ST-PGPR) as bio-inoculants in order to alleviate deleterious effects of high salt stress on plant growth and development [17–19]. In addition, increased salinity levels have also been reported to adversely affect microbial population and their plant-growth-promoting (PGP) properties [20]. These observations suggested the isolation and utilization of salt-tolerant plant-growth-promoting bacteria (PGPR) to protect crops from salinization and climate change. Therefore, different laboratories worldwide are currently involved in screening of salt-tolerant microorganisms obtained from different habitats and agroclimatic zones, and from various plant parts and regions i.e., phyllosphere, rhizosphere, and endorhizosphere, for their tolerance to high salt concentrations to cope up with high soil salinity levels. These halo-tolerant microorganisms are subsequently tested for mitigation of salinity stress on plants, for increasing nutrient uptake [21] and to enhance plant growth [22, 23]. Thus, application of selected salt-tolerant microbes in the form of bio-enhancers/bioprotectants may lead to increased survivability of crop plants under extreme saline conditions through alteration in various physiological, biochemical, and molecular pathways, resulting in enhancement of crop productivity [24–26].

Several microorganisms belonging to different genera, such as *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Enterococcus*, *Pantoea*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Stenotrophomonas* and *Variovorax* have been found to induce stress tolerance in different crops and positively influence plant growth under adverse saline conditions [19, 26–30]. For instance, salt-tolerant indigenous species of *Pseudomonas*, *Agrobacterium*, *Klebsiella*, *Bacillus*, and *Ochrobactrum* isolated from the halophytic plant, *Arthrocnemum indicum*, showed tolerance to 4–8% NaCl and improved productivity of groundnut in saline soil over uninoculated control plants [31]. Many salt-tolerant strains of *Bacillus* also possessed other plant growth promoting (PGP) traits along with high tolerance to excess of salt (4% NaCl) [32]. Some of the bacterial isolates showed salt tolerance even upto 10% NaCl along with excellent PGP attributes including solubilization of P, K and Zn, and production of indole-3-acetic acid (IAA), cell wall degrading enzymes, exopolysaccharides, biofilm, antibiotics, and siderophores [33–35].

Salt-tolerant bacteria employ several direct and indirect mechanisms to survive and proliferate under salt-stressed conditions in soil, and subsequently contribute towards amelioration of salt stress and stimulation of plant growth resulting into increased crop yield. Some of these salt-tolerant bacteria are currently being developed as biofertilizers; as a cost-effective environmental-friendly agri-technology to increase food production [36–39]. This chapter summarizes the characterization of salt-tolerant microbes and discusses various mechanisms involved in amelioration of salt stress. The use of salt-tolerant PGPR as bio-inoculants to improve crop production under salt stress conditions is also documented. Information provided in this chapter will help in understanding of plant-microbe interactions under saline environments to improve saline soil-based agriculture.

Climate Change and Soil Salinization

Agriculture is the most vulnerable sector that is often exposed to plethora of climate changes. Global warming, changes in precipitation patterns and recent abrupt changes in climatic conditions has increased incidence of abiotic and biotic stresses [6, 40]. The exposure of plants to stressed environments has been accounted for as major cause for stagnation of productivity in agriculture and horticulture crops [40, 41]. Recent climate changes accompanied by altered precipitation cycles and depleted water resources are further expected to exacerbate crop stresses [42]. Several abiotic stresses such as extreme temperatures (heat stress, cold and frost), drought, flooding, soil salinity and nutrient stress have been found to adversely affect crop cultivation, plant development and production of cereal as well as legume crops under field conditions [43, 44]. Besides, intensive utilization of agricultural lands for growth of exhaustive crops has further declined soil fertility and environmental degradation.

Inter-seasonal climatic variability is a major concern among abiotic stress factors, which is normally reflected from year-to-year fluctuations in crop yields. The abiotic stresses, for example, extreme temperatures, dry season, flooding, salinity, metal stress and nutrient stress are the results of climate change and global warming, which causes alteration in precipitation patterns [6]. Abiotic stresses also cause land degradation, which make soil nutrient deficient and more stress prone [43]. Abiotic stresses are blended and associated with each other. For instance, increase or reduction in rainfall, rise or fall in temperature brings dry spell stress. Dry spell stress at last gives rise to salinity stress, which causes alkalization of soil. The nutrients stay inaccessible to the plants developed in alkaline saline soil and it leads to nutrient-deprived circumstances or nutrient stress. Humidity in environment is another climatic variability. In moist regions, pace of precipitation is high and soil leaching decreases soil pH because of decrease of basic cations. Hence, decline in soil pH results in acidification stress. Because of acidification stress, nutrient become inaccessible to plants and further leads to nutrient stress in the soil. Accordingly, abiotic stresses appear to be interconnected with each other and function as a chain because of variations in climatic environments [44].

The probability of occurrence of extreme climatic changes has increased in the last couple of decades and has reshaped the Earth's ecosystems [43, 45]. Climate change has accelerated tenfold in the last century and green house gas (GHG) emissions have caused a rise of 0.9 °C in average temperature in the nineteenth century. Warming could reach 1.5 °C by 2050 due to deforestation, GHG emissions, and pollution of soil, water, and air. The enormous temperature rise has exacerbated droughts, food shortages, unexpected precipitation, and heat waves. On the other hand, farmers lack the appropriate management technologies to sustain agricultural productivity under forced abiotic stress conditions, which adversely influence plant growth and yield [43]. The climate change has also far-reaching effects on survival and functioning of beneficial microorganisms and climate-smart agricultural practices, which is vital to food supply and the global economy [45]. Climate change models have anticipated that warmer temperatures and increase in the frequency and term of dry spells during twenty-first century will have net negative consequences for productivity of agricultural and horticultural crops. Natural disaster damages have topped $200 billion annually since 2016, and 95% of these losses are due to climate-related weather events like cyclones, floods, and droughts. The world's population is predicted to top 9 billion by 2050, straining agricultural areas, which are already impacted by climate change. Thus, rapid climate change has threatened global food security due to its adverse effects on crop productivity [43].

Global Distribution of Saline Soils

Human activities have disrupted the natural hydrological equilibrium in many agro-climatic regions since the beginning of industrialization. These operations disrupt the natural distribution of salt in various landscapes and deteriorated the natural and agricultural environments. Soil salinization is a major threat to global food supply with changes in climatic conditions [46]. Poor drainage, brackish water irrigation, and long-term agricultural irrigation increase the salinity in soil [47]. The primary salinization area is less than one billion acres, where as secondary salinization has covered an area of 77 million hectares (with 58% occurring in irrigated areas and 20% of all irrigated lands) [48, 49]. About 5.2 billion hectares of agricultural land worldwide are salt-affected and are unsuitable for crop cultivation [50]. Low rainfall, erosion of native rocks, excessively surface evaporation, use of inorganic fertiliser, irrigation with salty water, and unsustainable farming techniques all lead to soil salinization [51, 52]. By 2050, half of all arable land may be salt-affected. More than 7×10^6 hectares of soil in India are salt-affected [53, 54].

Excessive accumulation of salts in the soil limits uptake of plant nutrients and water absorption, thereby disrupting plant growth and development processes [55]. Excess calcium, magnesium, sodium, sulphate, and chloride ions limit plant development by causing soil salinization. Farmland salinization is increasing by 0.3–1.5 million hectares per year, resulting in agricultural production losses of more than 20%. The salinization of arable land will have an impact on agricultural revenue and economic development, along with global food supply; and crop productivity losses may cost about 12–27.3 billion dollars per year [14, 56]. Chemical or physical methods used for salt extraction from salt affected soils may contribute towards restoration of saline soils [14] (Fig. 13.1). For example, lime and gypsum are two chemical neutralizers [57], whereas, leaching, scraping and flushing are physical methods for salinity management [58]. In addition, crops that are tolerant to salt, such as barley, rice, wheat, mung bean, cotton, and canola, are being developed [59]. Only a small number of salt-tolerating genes have been investigated for their potential to enhance crop production in both normal and saline soil [60]. It is common to increase agricultural output by employing environment-friendly methods and upgrading irrigated land. Biotic and abiotic factors have an effect on the current agricultural system, making it more efficient and sustainable is a major challenge for agriculture scientists [61].

Recently, use of salt-tolerant plant growth-promoting rhizobacteria as biofertilizers has emerged as novel agri-technology for improving soil health and crop yield under salt stress conditions [7, 44, 62–65]. These salt-tolerant rhizobacteria produce osmo-regulators, antioxidants, exopolysaccharides, ACC deaminase, nitric oxide, phytohormones, siderophores and transporter proteins, which act as promising bio-enhancer for increasing crop productivity and phytopathogen resistance, thereby sustaining soil health under salt stress conditions [3, 18, 39, 56, 64].

Salinity Stress and Impact on Plants and Microbes

Soil salinity has emerged as a major environmental issue due to disastrous consequences of salt deposition in soils and its detrimental influence on agriculture production [4, 6, 14]. Plants acquire an array of protective genetic and metabolic mechanisms during the course of evolution to combat adverse environmental fluctuations and stresses. Many a times, the burden of abiotic stresses is reduced with the contribution of associated microbes. Various studies on plant-microbe interactions established that salinity has profound effect on the survival and activity of soil-inhabiting microorganisms as well as on the growth of plants.

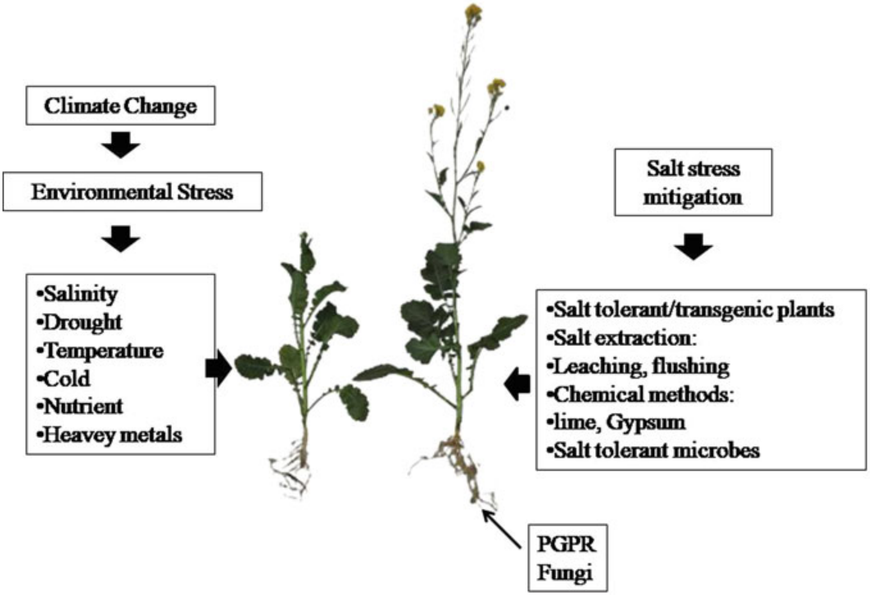

Fig. 13.1 Environmental stresses induced by climate change and mechanisms involved in salt stress mitigation

Effect of Salinity Stress on Plants

Presence of excess salt in soil is detrimental to plant health. Many stages of plant development, from germination through maturity, are known to be influenced by salinity. However, agricultural crops respond differentially to salinized soil conditions. Usually, salinity reduces the agricultural output of most cereals, legumes, forages, and horticultural crops. In addition, salinity also alters the ecological balance and physicochemical properties of the soil. Salt stress leads in low agricultural yield, significant soil erosion, and limited socio-economic returns [66]. Additionally, salt stress has an effect on the morphological, biochemical, and physiological processes of the plant. These processes include germination of seeds, plant health, photosynthetic activity, protein synthesis, lipid metabolism, water holding capacity and absorption of nutrients [67–69]. For instance, the accumulation of sodium ions in leaf laminae hindered flowering in chickpea (*Cicer arietinum* L.) plants [70]. The buildup of sodium ions in plant tissues leads to the formation of different reactive oxygen species (ROS), which impede photosynthesis [71]. ROS are known to damage DNA and further induce lipid peroxidation, protein oxidation, enzyme inactivation, and chlorophyll degradation [72].

Under these saline conditions, plants use the salt overload sensitive (SOS) pathway, which is an essential protective mechanism used for sodium ion extrusion, potassium/sodium ion levels retention, and ion homeostasis [3, 73]. The negative effects on the SOS system under salt stress include a reduction in germination of seeds, leaf area, and pigmentation; an increase in defoliation and senescence; and a reduction in reproductive capability. In addition, salt stress causes ion toxicity, restricts water transfer from soil solutions, limits nutrient absorption, and causes osmotic and oxidative stress. Thus, it affects the overall plant health [56, 74–77]. Additionally, salt stress suppresses the plant growth and development, including enzyme activity [78], DNA, RNA, and protein synthesis, and mitosis during the reproductive stage of the plant [19, 79]. Salinity also impairs reproductive development in plants by retarding sporogenesis and stamen filament elongation, triggering ovule abortion and fertilized embryo senescence, and promoting programmed cell death in plant tissues. The survival and development of plants are monitored to determine their resistance to salt stress because they include the up- and down-regulation of physiological systems, such as osmotic balance [80]. Failure to attain equilibrium between these systems results in cell dehydration, loss of turgidity, and ultimately plant death [76]. Some studies have linked salt stress to stunted plant development and symbiosis in field peas, causing a decrease in biomass and production [81]. Even nutrient-rich weeds, such as *Portulaca oleracea* L., are significantly affected by salt, as seen by alterations in physiology and root architecture, as well as decreases in biomass and yield [82]. Thus, salt stress is hazardous at various stages of cereal and legume cropping systems, producing 15–100% loss in legumes and endangering food security [3, 83, 84].

The drastic effect of salt stress can be observed in terms of crop yield losses. The primary effects related to crop yield can be in terms of germination which either decreases or sometimes ceases under extreme saline conditions. Ali Khan et al. [85] showed that under saline conditions growth, yield, and biomass of pearl millet is adversely affected in terms of germination percentage, plant height, leaf area, total biomass and grain yield plant^{-1}. Impact of salinity on pea was also found to adversely affect growth, yield and biomass [81]. Farooq et al. [83] also reviewed the effects of salt stress on grain legumes, and they described that in different legumes salinity may reduce crop yield by 12–100%. Salt tolerance of black cumin (*Nigella sativa* L.) and its effect on seed emergence and germination, and yield were studied by Faravani et al. [86]. They showed that an increase in salinity level from 0.3 to 9 dS m^{-1} reduced the average seed and biological yield. Similarly, the effect of different levels of salinity on a weed plant *Portulaca oleracea* showed a reduction in biomass and yield, changes in physiological attributes, and alteration in stem and root structure [87]. Salinity has thus a wide level of impacts on seed germination, plant growth and crop yield of different crops.

It was observed that chickpea crop is extremely susceptible to salt stress and salinity is main restrictive factor bringing about low production. Salinity additionally brought about poor plant growth, low nitrogen fixing ability, reduced nodule numbers and decreased percentage of tissue nitrogen in arid and semiarid regions, in this manner, bringing about 8–10% losses in chickpea yield [17, 88]. To distinguish tolerant genotypes from sensitive genotypes of chickpea, a concentration of 40 mmol L^{-1} NaCl was accounted for as optimum level of salinity [89]. Reduction in salinity levels was found to cause excellent recovery with substantial new shoot growth. The critical point of salinity level for seed yield reduction of chickpea was reported as low as 3 dS m^{-1} in field soils [90]. Rhizobial isolates also showed different growth rate at higher NaCl concentrations. Maximum growth rate was seen at 1% (w/v) NaCl and minimum growth rate was seen at 4% (w/v) NaCl [91]. Only 11.1% of isolates tolerated 5% NaCl concentration [91, 92].

Effects of Salinity on Soil Microorganisms

In dry and semiarid locations, where precipitation is scarce and often insufficient to eliminate salts from the plant root zone, soil salinity is a significant constraint on agricultural output [93, 94]. Both microorganisms and plants are negatively impacted by high salt concentrations [95]. However, the metabolic burden imposed by these stress tolerance systems might be deleterious to sensitive bacteria, reducing the activity of the cells that survive the stress [96–98]. Various reports on naturally saline soils have indicated that salinity has negative effects on microbial soil communities and their activity [95, 99–101]. The impact is usually more prominent in the rhizosphere due to enhanced consumption of water absorption by the plants as a result of transpiration. Accordingly, osmoadaptation necessitates a significant amount of energy [102, 103].

Omar et al. [104] reported that higher salt concentration upto 5% significantly decreased the entire microbiota. Other biotic and abiotic stresses (including soil salinity) have been reported to affect rhizosphere microbial composition, biodiversity, microbial metabolic activity and functioning, agricultural residue decomposition and nutrient availability, soil health and plant development [19, 76, 105, 106]. There is genetic variation in salt tolerance among rhizobia, which can have a substantial impact on the productivity of legume crops. The capacity for growth and survival of different chickpea rhizobial strains in salt conditions varies greatly [107, 108]. It also has been found that rapid rhizobia growth is associated with greater salt tolerance. Changes in cell shape and size or abnormalities in the pattern of extracellular polysaccharides (EPS) and lipopolysaccharides (LPS) have been seen in rhizobia that have been exposed to salt stress [108–110]. The symbiosis is more vulnerable to salt stress than free-living rhizobia because legume plants are more sensitive to salinity stress in general. Many strains of *Rhizobium* spp. have had their inoculum viability, nodulation, and nitrogen-fixing abilities reported to be negatively impacted by salt stress [109].

Only 33% of bacterial isolates were able to survive in solutions containing more than 8% NaCl (w/v), and of those, only 19% displayed PGP characteristics at these concentrations, as reported by Upadhyay et al. [111]. Isolate SU8 had the highest proline content and synthesis, with 2.73 and 11.95 g mg protein at 0% and 10% NaCl (w/v), respectively. The synthesis of reducing sugars (RS) and total soluble sugars (TSS) in rhizobacterial isolates was inversely related to the concentration of salt (NaCl), which had the potential to lower salinity levels and promote the development of agricultural crops grown in salty conditions. All of the rhizobacterial-isolated strains were able to grow up to a concentration of 4% NaCl, but their capacity to tolerate salt decreased with rising salt concentrations. The experiment involved screening of 40 rhizobacterial isolates for different concentrations of sodium chloride, ranging from 2 to 8% [20]. Garg and Sharma [112] identified and tested 10 rhizobia from *Trigonella foenumgraecum* for stress tolerance. To evaluate the growth of the isolates, a yeast mannitol medium with a wide pH range (4–10) and varying NaCl concentrations (0.05–5%) was used. Increasing salt concentrations inhibited the development of *Rhizobium* strains. Shultana et al. [113] also isolated salt tolerant rhizospheric bacteria from rice roots grown in saline conditions (0.41–17.64 dS m^{-1}). Salt tolerant rhizobacterial isolates were grown on Tryptic Soy Agar media plates with different NaCl concentration (0, 0.5, 1, 1.5, 2.0M) to check their salt tolerant capacity. Five highly salt tolerant strains were found to grow upto 2.0M NaCl, however increasing salt concentrations inhibited the growth of isolated rhizobacteria.

Mechanisms of Salinity Stress Tolerance in Microbes and Plants

The rhizosphere is the most favourable environment for microbial populations [114]. Numerous microorganisms, such as bacteria, fungi, actinomycetes, and archaea, populate the rhizosphere of different plants. These soil or rhizosphere-inhabiting bacteria influence the ecosystem function, plant health, and pollutant degradation [115, 116]. These microbial communities act as a catalyst for the transformation, decomposition, and recycling of soil nutrients and organic matter in the soil. Thus, microbial populations have been found to affect crop development both directly and indirectly. Some of these soil- or rhizosphere-inhabiting microorganisms have acquired the ability to survive high salt (NaCl) concentrations. These salt-tolerant microbes have the potential to boost productivity of both grains and legumes in arid and semi-arid regions for sustainable agriculture [117]. It has been demonstrated that various bacterial genera such as *Klebsiella, Streptomyces, Pseudomonas, Agrobacterium, Bacillus, Enterobacter, Stenotrophomonas, Rhizobium* and *Ochromobacter* enhance grain and legume production in saline circumstances [31, 118, 119]. As salinity increased in the rhizosphere, it affects root exudation, microbial population and degradation of organic materials [120]. A negative correlation was observed between EC of soil and microbial biomass, indicating that soil salinity has a negative effect on microbial biomass [121]. In similar studies, Nelson and Mele [122] observed that NaCl has an indirect influence on rhizospheric microbial diversity through root exudates and plant quantity/quality, as well as a direct effect via microbial toxicity. Under salt soil conditions, molecular signaling among microorganisms and plants play a substantial effect on their rhizospheric microbiota [123].

When rhizospheric bacteria are exposed to a highly osmosis conditions, fast turgor loss and dehydration occur to compensate for the outflow of water. Ionic instability is caused by elevated ion concentrations, which maintains K^+ osmotic balance, activates osmotic responses, and up-regulates genes involved in adaptation, metabolism, defensive, and amino acid transport pathways in the cytoplasm. Furthermore, the production of organic solutes increases intracellular osmotic strength, which helps to stabilise biomolecules under salt stress conditions [124, 125]. The second mechanism of salt tolerant rhizospheric bacteria is exopolysaccharide (EPS) production, which alters membrane compositions such as periplasmic glucans, proteins, fatty acids, shorter peptidoglycans, and interpeptide bridges, and capsule content for accelerated water retention, regulating carbon source usage in microbial cells, and protecting microbiota from osmotic stress [126–128]. Flexible surface appendages surrounding the microbial cell also act as a protective barrier at low electrolyte concentrations, decreasing osmotic stress and minimizing the damaging effects of ionic strength changes [129].

Various microorganisms, inhabiting the phyllosphere, rhizosphere, and endorhizosphere, have been found to help plants in adaptation during salt stress by absorbtion of nutrients from soil leading to improvement in plant growth and development [21]. Besides this, metabolic activity and functioning of microbial enzymes under salt stress may improve seed germination, root architecture, chlorophyll content, biomass, and disease resistance. In brief, salt mitigation strategies include direct and indirect mechanisms leading to promotion of plant growth and increases in crop yield in saline soils (Fig. 13.2). Direct mechanisms include enhanced accumulation of osmoprotectants such as glycine, betaine, trehalose, and proline [130, 131], upregulating production of antioxidant enzymes, such as SOD, CAT, APX, and GR, to provide protection against oxidative stress [72, 132], maintaining high K^+/Na^+ ratio (ion homeostasis) and regulating the expression of ion transporters to protect against ion toxicity [72, 133, 134], lowering of stress-induced hormone (ethylene) level with expression of ACC deaminase activity [37, 135], synthesizing of exopolysaccharides and biofilm formation to reduce Na^+ ion accumulation in plant roots by binding to excessive Na^+ ions and preventing their translocation to plant leaves via xylems [132, 136], and maintaining high levels of photosynthetic activity and stomatal conductance [137]. Other indirect mechanisms employed for salt stress amelioration by PGPR include enhancing nutrient availability and uptake, siderophore production for iron uptake, phosphate solubilization [136, 138], modulating plant growth hormones for root and shoot development, and by conferring disease resistance through inducing systemic tolerance, production of organic acids and nitric oxide [139], and secretion of extracellular polymeric substances for increased soil aggregation to improve plant growth under salt stress [76, 140–142].

Under salinity stress, *Pseudomonas* sp. and *Novosphingobium* sp. from citrus and *Distichlis spicata* rhizobacterial strains reduced salicylic acid (SA), abscisic acid (ABA), and ethylene, as well as root proline and chloride accumulation and photosystem II activity [143]. He et al. [144] identified a novel salt-tolerant *Pseudomonas* sp. in the rhizosphere of the desert shrub *Haloxylon ammodendron*, which caused perennial ryegrass to become salt-tolerant. Proteomic, genomics and transcriptomics studies characterized various transcription factors, gene expression, protein expression and microbial interactions in plant cells and microbes in response to salt tolerance [145]. For instance, *Burkholderia phytofirmans* strain induced long-term metabolic and transcriptional changes in *Arabidopsis thaliana* involving expression

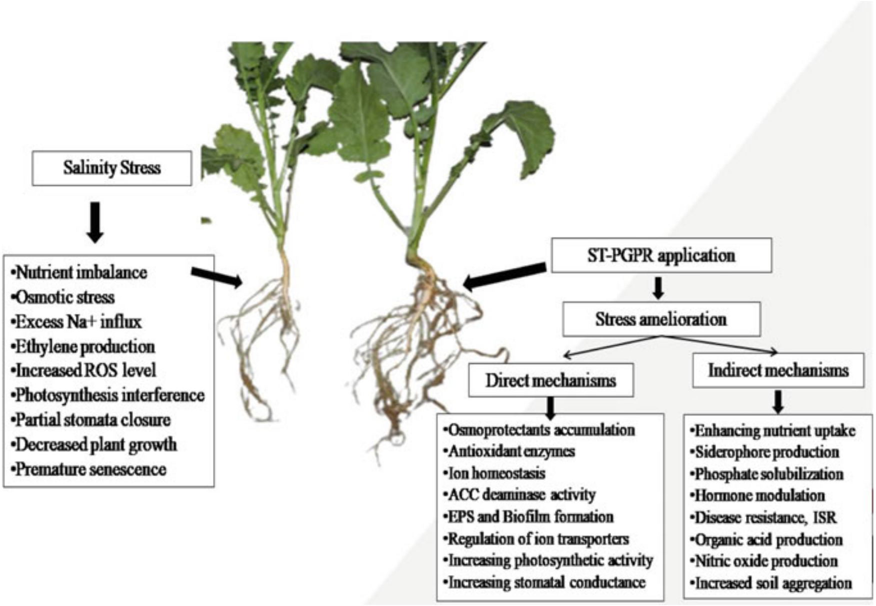

Fig. 13.2 Rhizobacteria-mediated adaptive responses of plants to salinity stress to promote plant growth

of genes related to ROS scavenging (APX2), lipoxygenase-2 reduction, and detoxifying (Glyoxalase 7) under salt stress [146]. Some of the salt-tolerating PGPR strains regulated the expression of dehydroascorbate reductase, catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR) genes under salt stress conditions [147]. Functional metagenomics was used to find numerous salt-tolerant genes in PGPR and some of the salt-tolerant PGPR strains alleviated salt stress along with biological control of phytopathogens [3, 84, 148–150]. Several PGPR strains synthesized phytohormones [e.g., IAA, cytokinins (CK), and gibberellins] as well as having ACC deaminase activity [64, 119, 135, 151].

Production and Accumulation of Osmoprotectants

Stressed plants produce osmoprotectants like quaternary ammonium compounds such as betaine, proline, polyamines, glycine and other amino acids that improve water intake and reduce water losses, and dilute the concentrations of toxic ion [152, 153]. Various plant growth promoting strains have been characterized, which possess the capacity to tolerate osmotic stress from K^+ ions and osmolytes in the cytoplasm [154, 155]. At 2.5 mol L^{-1} NaCl, upregulation of the *pro*A, *pro*H, and *pro*J genes was observed in salt tolerant PGPR strains [156]. During salt stress, *Halomonas* sp.

SBS 10 and *Azospirillum* spp. were found to accumulate proline, ectoine, glycine, betaine and trehalose, making maize plants resistant to salt stress [157, 158]. Inoculation of salt-stressed tomato plants with *Pseudomonas extremorientalis* TSAU20 reported to have increased proline levels [159]. Similarly, increase in glycine and betaine levels conferring salt tolerance under osmotic stress, was observed in rice and sugarcane, when inoculated with *B. pumilus*, *Pseudomonas pseudoalcaligenes*, and *Enterobacter* sp. EN-21 [160, 161]. In wheat crop, inoculation with *Dietzia natronolimnaea* STR1 exhibited strong antioxidants activity and accumulation of proline under salt stress conditions [162]. Inoculating salt-stressed *Acacia gerrardii* with *B. subtilis* strain was reported to enhance proline levels and enhanced salt tolerance by maintaining water balance [150]. Trehalose, an osmoprotectant sugar, was found to confer salinity resistance, and many genes involved in biosynthesis of trehalose were identified in halo-tolerant PGPR strains [3, 163–165].

Antioxidant Enzyme Activity

Salt-stressed plants produce different reactive oxygen species (ROS) that damage various proteins, lipids, and DNA [166]. The level of ROS-scavenging enzymes such as superoxide dismutase (SOD), APX and CAT was reduced on exposure of plants to abiotic stress i.e., salt and drought, and increased the lipid peroxidation [84, 167]. A wide range of antioxidant enzymes, such as superoxide dismutases, nitrate reductase (NR), catalase (CAT), peroxidase (POD) and glutathione reductase (GR) were produced by salt-tolerant PGPR strains under salinity stress [3, 145, 168]. Interestingly, inoculation of chickpea plants with *Azospirillum lipoferum* strain FK1 caused enhanced expression of the anti-oxidant genes and also improved nutrient absorption, non-enzymatic metabolites and flavonoids leading to improvement in symbiotic efficiency [169]. Wheat plants co-inoculated with *Azospirillum brasilense* DSM1690 and *Pseudomonas fluorescens* Ms-01 showed higher POD levels than uninoculated control plants [170]. Salt-tolerant *Bacillus cereus* strain Pb25 enhanced the level of antioxidant enzymes catalase and peroxidase in mungbean (*Vigna radiata*), when grown at 9 dS m^{-1} saline conditions [72]. After PGPR inoculation, salt-stressed plants may stimulate the expression of antioxidant enzyme-related genes, resulting in enhanced ROS-scavenging enzyme activity [171].

During salinity stress, peroxidation of lipids has been reported to increase malondialdehyde (MDA) concentration, indicating damage to structural integrity of cell membrane and inoculation with salt tolerant PGPR strains reduced MDA accumulation and thus, helped plants to combat salinity stress [172]. Similarly, the decreased levels of MDA were observed in rice seedlings after inoculation with *Enterobacter* sp. P23 even during salt stress [119]. Inoculation of PGPR strains viz. *Serratia* sp. SL-12 in wheat [118], and *Klebsiella* sp. IG3 in oat plants [173], were found to reduce MDA level. Thus, inoculation of plants with PGPR was found to increase biomass and nutrient efficiency in stressed plants by altering the level of antioxidants and stomatal conductance [174]. Therefore, use of salt-tolerant rhizobacteria as bio-inoculants causes enhancement of plant growth under salinity stress conditions through modulation of osmoprotectants levels, upregulation of the stress-related genes, and by enhanced production of enzymatic and non-enzymatic antioxidants in stressed plants.

Reduced Uptake of Salt Ions by Microbes and Plants

Another strategy for PGPR tolerance to high salt concentration is minimization of salt absorption by ion affinity transporter control, root structure alteration via broad rhizosheath, and cation trapping in exopolysaccharides. Microbes maintain ion homeostasis by boosting the K^+/Na^+ ratio and decreasing Na^+ and Cl^- in the shoot and leaves, respectively. Salt stress changes the expression of genes such as KT1, NHX2, SOS1, and HKT1, and these molecular alterations result in salt tolerance [146]. Niu et al. [175] reported that *Pucciniella tenuiflora* infected with *Bacillus subtilis* GB30 caused lower Na^+ buildup, which was corroborated by the down-regulation of ptHKT2 and up-regulation of ptHKT1 and ptSOS1 genes in roots exposed to high NaCl concentrations (200 mmol L^{-1}).

Volatile organic compounds (VOCs) have been reported to play crucial role in many cases of PGPR interaction with plants especially antibiosis and biocontrol of plant pathogens, and regulation of auxins [176, 177]. During salt stress, VOCs down-regulate the expression of high affinity K^+ transporter (HKT1), but it is upregulated in shoots, which results in lower accumulation of Na^+ inside the plant [178].

ACC Deaminase Activity and Lowering of Ethylene Formation

Ethylene, a stress hormone, is synthesized under stressed conditions and affects a number of metabolic activities within plants [136]. In addition, plants release 1-aminocyclopropane-1-carboxylic acid (ACC) in root exudates, which is converted to the stress hormone ethylene (C_2H_4) by the enzyme ACC oxidase. Ethylene has been demonstrated to play fundamental roles in root branching, root hair formation, nodule development and for amelioration of biotic as well as biotic stresses [33]. On the other hand, many plant growth-promoting bacteria possess the enzyme ACC deaminase; which scavenges the exuded ACC and thereby down-regulates ethylene production by cleaving ACC into α-ketobutyrate and ammonia [135, 179–182]. Low levels of ethylene acts in plant defence against different abiotic stresses [183], but excessive levels of ethylene can cause ethylene stress, which slows growth and development in plants [184, 185]. Under stress conditions, plants produce ethylene, which subsequently affects legume nodule formation [186, 187]. Under salt stress, PGPR can convert ACC into ammonia and α-ketobutyrate, providing nitrogen to the plants [33, 76]. Rhizobacteria with ACC deaminase activity were reported to reduce salt stress and enhanced plant growth of tomato and rice [188].

ACC deaminase activity has been reported in various salt–tolerant bacterial genera belonging to *Arthrobacter*, *Acidovorax, Bacillus, Brevibacterium, Enterobacter, Exiguobacterium, Gracilibacillus, Klebsiella, Methylobacterium, Planococcus, Pseudomonas, Rhizobium, Salinicoccus, Stenotrophomonas, Variovorax* and *Virgibacillus* [189]. Inoculation of ACC deaminase-containing halotolerant bacteria was found to ameliorate salt stress in plants and improved crop productivity under salinity stress [151, 190–192]. For instance, inoculation of salt-tolerant ACC deaminase activity containing *Enterobacter cloacae* strain KBPD improved nodulation and symbiotic efficiency in *Vigna radiata* at 50, 100, and 150 mmol L^{-1} NaCl concentrations [64]. Similarly, Tiwari et al. [193] found that ACC deaminase-producing salt tolerant PGPR strains improved plant cell biochemical characteristics such as bio-compatible solute formation, membrane permeability, stability, and photosynthetic pigment production under salt and drought stress. Ali et al. [194] reported that inoculation with endophytc strains i.e., *Pseudomonas migulae* and *Pseudomonas fluorescens* containing ACC deaminase activity improved physiological indices in plants under stress conditions.

In another study, inoculation of oat (*Avena sativa*) with *Klebsiella* sp. strain IG 3 enhanced shoot and root lengths, plant biomass, and relative water contents under NaCl stress (100 mmol L^{-1}) [173]. The concomitant higher expression of *acds* genes (encoding ACC deaminase) and *ipdc* genes (encoding IAA) was observed under stress conditions. Expression of ACC deaminase in ST-PGPR strains was demonstrated to enhance the infection thread persistence during nodulation in legume crops, which is adversely affected by ethylene under salt stress conditions [187]. Shaharoona et al. [195] reported that the coinoculation of an ACC deaminase-possessing PGPR and *Bradyrhizobium* in mungbean (*Vigna radiata* L.) improved nodulation and other symbiotic traits by reducing ethylene as compared with the single *Bradyrhizobium* treatment. The ACC deaminase-producing halo-tolerant bacterial strains *Brevibacterium iodinum* RS16, *Zimmermannella alba* RS11, and *Bacillus licheniformis* RS56 have been reported to reduce the secondary ethylene peak in red pepper plants at 150 mmol L^{-1} NaCl [196]. The inoculation of lentils with ACC deaminase-producing PGPR led to higher plant growth, nodulation, and grain yield under oxidative stress conditions [197]. *Arthrobacter* sp. and *Bacillus* sp. producing IAA and ACC deaminase increased proline content under salt stress in sweet pepper and chickpea [198, 199]. Chandra et al. [200] reported that three ACC deaminase-producing bacterial strains viz. *Pseudomonas palleroniana* DPB16, *Pseudomonas* sp. UW4, and *V. paradoxus* RAA3, enhanced growth, nutrient uptake, osmolyte production, antioxidant enzyme activities, and grain yield of wheat under salt and drought stress conditions in contrast to the uninoculated control treatment. Thus, various inoculation studies in different crops suggested that ACC^{+} bacteria could be used as an eco-friendly inoculant to improve growth of salinity-sensitive crop plants [29, 192, 201].

Hussein et al. [202] evaluated eight yeast strains i.e., *Yarrowia lipolytica* YEAST-1, *Candida diddensiae* YEAST-2, *Trichosporon gamsii* YEAST-5, *T. ovoides* YEAST-6, *Y. lipolytica* YEAST-16, *C. subhashii* YEAST-17, *Saccharomyces cerevisiae* YEAST-30, and *S. cerevisiae* YEAST-34) for plant growth-promotion (PGP) traits, biofilm formation, seed germination and for alleviation of salinity stress in wheat (*Triticum aestivum* L.). *Y. lipolytica* YEAST-1 strain was found to enhance the plumule length of *T. aestivum* seedling by more than 4.0, 3.0, and 2.0 cm at salinity stress of 50, 100, and 200 mM NaCl, respectively, after 96 h of treatment. Highest expression of amino-cyclopropane-1-carboxylate deaminase (ACCD) genes was observed in *S. cerevisiae* YEAST-34, at 5 mM ACC. Inoculation of *Y. lipolytica* YEAST-1 enhanced the radicle length of *T. aestivum* seedling significantly by 0.8 cm at 50 mM NaCl, 0.7 at 100 mM NaCl, and 0.06 cm at 200 mM NaCl stress.

Exopolysaccharide Production and Biofilm Formation

Salt-tolerant PGPR strains were found to form exopolysaccharides (EPSs), which promote biofilm formation and root colonization leading to better plant-microbe interactions. Root colonization by exoploysaccharide producing salt tolerant rhizospheric strains improves uptake of nutrients (i.e., potassium and phosphorus), disease resistance, plant development and growth [203]. EPSs improve soil particle aggregation, promote cation exchange, water and nutrient retention, environmental changes, and root colonization [204, 205]. Inoculation of *Bacillus subtilis* in salt-stressed *Arabidopsis* plants suppressed the upregulation of HKT1 (high-affinity potassium ion transporters), prevented excessive Na^+ ion absorption by plant tissues and sustained ion homeostasis [132]. Similarly, salt resistance in oilseeds crops such as *Brassica napus* increased K^+ retention and decreased K^+ ion-permeable channel by activating H^+-ATPase activity and maintaining a negative membrane potential [206]. Increased plasma membrane sodium/hydrogen ions or potassium/sodium ions exchange activity also increased ROS-mediated Na^+ extrusion from plant roots [206]. Microorganisms and host plants, such as *Triticum aestivum*, *Brassica* sp., and *Hordeum vulgare*, were discovered to have a close link with salt tolerance [206–208].

Bacterization with salt-tolerant EPS-producing rhizobacteria was found to improve germination of seeds [203]. The development of biofilm, which was helped along by the synthesis of EPS, contributed to an increase in PGPR's resilience to both abiotic or biotic stresses [209]. EPS-producing *Enterobacter* sp. P23 reduced Na^+ ion concentration in rice seedlings by binding excess Na^+ ions [119]. Similarly, co-inoculation of salt-tolerant *Halomonas variabilis* HT1 and *Planococcus rifietoensis* RT4 at 200 mmol L^{-1} NaCl concentration was found to increase plant growth and soil aggregation by EPS, and biofilm development in chickpea [141]. Treatment with *Enterobacter* sp. MN17 and *Bacillus* sp. MN54 was reported to improve plant water condition and growth of *Chenopodium quinoa* at 400 mmol L^{-1} NaCl irrigation conditions [210]. Salt-tolerant EPS and biofilm-producing *Marinobacter lipolyticus* strain SM19, and *B. subtilis* sub sp. *inaquosorum* alleviated the deleterious effects of drought and salinity stress in *Triticum aestivum* [211]. Recently, Chu et al. [212] demonstrated the essential role of EPS-producing halo-tolerant *Pseudomonas* PS01 in the regulation of the *LOX2* gene related to salt stress tolerance in *Arabidopsis thaliana.*

Siderophore Production

Iron is the fourth most prevalent metal in the Earth and it also acts as a cofactor in 140 enzymes in plants. It is generally present as Fe^{3+} (ferric), insoluble (OH) hydroxides, and oxyhydroxides O (OH) under abundant O_2 availability [213]. Soil- or rhizosphere-inhabiting microorganisms produce low-molecular-weight, iron chelators termed as siderophores [214]. Plants assimilate iron from bacteria-produced siderophores either via ligand exchange, direct absorption of siderophore-Fe complexes, or iron uptake [215, 216]. Numbers of studies have demonstrated that inoculations with siderophore-producing rhizobacteria enhance plant development through increased siderophore-mediated Fe-uptake [213]. Crowley and Kraemer [217] found a siderophore-mediated iron transport system in oat plants. They concluded that siderophores synthesized by rhizospheric bacteria transport the iron to oat plants, which has capabilities for absorbing Fe-siderophore complexes even when there is a scarcity of iron in the soil. In a similar manner, the Fe-pyoverdine complex that was produced by *Pseudomonas fluorescens* C7 was absorbed by *Arabidopsis thaliana* plants, which resulted in an increase of iron within the plant tissues as well as an improvement in plant development [218].

Sadeghi et al. [219] reported that siderophore production in *Streptomyces* increase wheat growth under saline conditions. Tank and Saraf [220] also found PGPR promotes growth of tomato plants grown under 2% NaCl conditions; and PGPR were demonstrated to solubilize insoluble P and produced siderophores. Similarly, bacterial strains viz. *Halobacillus* SL3 and *Bacillus halodenitrificans* PU62 were found to produce siderophores in saline conditions [23]. Siderophore-producing *Pseudomonas* sp. GRP-3 improved iron nutrition in *Vigna radiata* by reducing chlorosis and increasing chlorophyll content. Siderophore-producing rhizobacteria increased plant height and improved nitrogen uptake [221]. Rajkumar et al. [213] also found siderophore-producing *Ensifer meliloti* strains that suppressed groundnut charcoal rot. Siderophore-producing salt-tolerant *Bacillus aryabhattai* MS3 strain was isolated from the root area of salt-prone rice fields and highest siderophore production was observed, which estimated at 60% and 43% under non-saline and saline (200 mM NaCl) conditions, respectively [222]. The expression of the *ent*D gene (involved in the biosynthesis of siderophore) was evidenced irrespective of saline states. The salt-tolerant *Bacillus aryabhattai* MS3 strain may enhance plant growth in saline soils with iron limitation.

Phosphate Solubilization

Phosphorous is the second most important vital macronutrient for plant growth and crop production [223, 224]. It plays a key role in the development of the root stem, the formation of seeds and flowers, nitrogen fixation, and disease resistance. Phosphorous exists in a bound and insoluble form with calcium in neutral soils [as tricalcium phosphate ($Ca_3PO_4)^2$], or with iron and aluminium in acidic soils [as aluminium phosphate (Al_3PO_4) or iron phosphate (Fe_3PO_4) in soil [225]. Thus, the concentration of soluble or inorganic available phosphorus i.e., orthophosphate is very low in the soil [226]. Phosphate-solubilizing microorganisms (PSMs) possess the capability to transform insoluble form of phosphate into inorganic utilizable form mainly through organic acids production [227–230]. Various soil microbes including *Azotobacter*, *Bacillus, Bradyrhizobium*, *Pseudomonas, Erwinia* sp., *Flavobacterium* sp., *Micrococcus* sp., *Corynebacterium, Nostoc, Serratia phosphaticum, Calothrix brauna, Burkholderia, Sarcina* sp., *Scytonema* and *Advenella kashmirensis* have been found to solubilize phosphorous in soil [231–234].

Salt stress in soil has been reported to affect population of phosphorus solublizing microbes and their P-solubilization capability [235]. Alkaline soils containing high level of calcium-phosphate were found to increase P-solubilization [236]. High salt-tolerating rhizobacteria may solubilize phosphate, Zn and K, fix nitrogen, and produce ACC deaminase activity and phytohormones, making more nutrients available to plants even under abiotic (drought and salt) stress conditions [84]. For instance, *Alteromonas* sp. and *Pseudomonas* sp. solubilize phosphate at 2 mol L^{-1} NaCl concentrations [237]. Some bacteria mineralize P by producing phosphatases and phytases enzymes. Mahdi et al. [238] reported that phosphate-solubilizing bacteria produce phosphatase enzyme, which releases P from minerals by replacing phosphate cations with H^+. Potassium (K) is another most important nutrient for growth of plants after nitrogen and phosphorous [239]. Therefore, inoculation of halotolerant K solubilizing bacterial strains i.e., *Acinetobacter pitti* strain L1/4, *A. pitti* strain L3/3, *Rhizobium pusense* strain L3/4, *Caprivadus oxalaticus* strain L4/12 and *Ochrobactrum ciceri* strain L5/1 caused significant increases in the shoot length, fresh weight, dry weight and chlorophyll contents of rice plants under saline conditions [240].

Production of Phytohormones

Auxins (indole acetic acid; IAA), cytokinins, gibberellins (GA), ethylene, and abscisic acid (ABA) constitute up the five major groups of phytohormones [241–244]. These plant and bacterial hormones, known as phytohormones, regulate a wide variety of physiological processes, including as cell division, development, gene expression, and stress responses, as well as the rate and form of root and shoot growth [245–247]. Phytohormones have been shown to improve a plant's nutrient availability, water absorption capacity, and resistance to salt stress by increasing root hair length and root surface area [248–252]. The capability of plants to acclimatize to salinity stress depends on their interaction with beneficial potent microbes that have the ability to produce IAA, CK, and gibberellic acids (GAs) [145, 253]. Therefore, attempts are being made to identify PGPR strains that can help plants to overcome and mitigate salt stress by producing phytohormones. For instance, auxin-producing salt-tolerant *Leclercia adecarboxylata* strain MO1 enhanced carbohydrate synthesis, chlorophyll fluorescence, *ipd*c gene expression, and organic acid production in tomato [254]. IAA-producing PGPR strains were demonstrated to enhance ACC deaminase activity via a signalling cascade that hydrolyzed ACC into ammonia and α-ketobutyrate [33], allowing the plant to proliferate even under salt stress by lowering ethylene levels.

Application of *Enterobacter* sp. found to enhance seed germination (48%) of rice at 150 mmol L^{-1} salt concentration [119]. *Bacillus amyloliquefaciens* SQR9 strain improved maize seedling development, antioxidant enzyme activities (CAT, POD, and GR), total sugar content, and K^+/Na^+ ratio, under salt stress conditions. PGPR-inoculated plants retain K^+ ions to minimise Na^+ toxicity under salt stress [255]. *Streptomyces* lowers salt stress in wheat by producing auxins, according to Sadeghi et al. [219]. Auxins and GAs were found to lower the inhibitory effects of salt's on wheat seedlings [23]. *Enterobacter* sp. EJ01 obtained from halophyte *Dianthus* increased salt tolerance (200 mmol L^{-1}) in tomato plants by boosting desiccation, embryogenesis, proline biosynthesis, and stress-inducing and priming activities [256]. *Ensifer meliloti* genetically modified for enhanced production of IAA conferred the ability to tolerate 0.3 mol L^{-1} salt in *Medicago truncatula* [257]. Zahir et al. [258] found that inoculating a beneficial rhizospheric microbiome increased mungbean (*Vigna radiata*) growth and yield in saline environments via better IAA production. Thus, PGPR's phytohormone synthesis is an exploitable trait; more research is needed to use these rhizosphere bacteria to lessen salinity's effects. *Pantoea agglomerans* strain lma2 can produce 161 g mL^{-1} IAA at 200 mmol L^{-1} of NaCl, making it a potential PGPR under salt stress [259]. Numan et al. [78] showed extensive IAA production in durum wheat with osmotolerant PGPR *Azospirillum brasilense* NH at high salt concentrations, underlining IAA's role in salt tolerance. *Micrococcus luteus* also increase maize growth by producing IAA [78]. As potential auxin makers, many rhizobia and rhizobacteria strains also found to withstand salt and osmotic stress in mung bean [260, 261]. Kuzmina et al. [234] reported that IAA production and phosphate-mobilizing activity of *Advenella kashmirensis* strain IB-K1 showed plant growth-promoting effects on wheat seedlings. Additionally, the presowing treatment of wheat (*Triticum durum* Desf.) seeds with *A. kashmirensis* strain IB-K1 effectively relieved the deleterious effect of salt stress on plant growth under moderate salinization level of cultured soil, which ultimately resulted in higher plant output.

Gibberellin-producing bacterial isolates, such as *Azospirillum* sp., *Bacillus pumilus*, *Bacillus licheniformis*, and *P. fluorescens*, were reported by Bottini et al. [262]. Salinity stress reduces GA synthesis in plants, while PGPR inoculation increases endogenous GA [263], inducing salinity tolerance and preventing tissue damage [264]. For instance, increased endogenous GA levels in *Promicromonospora* sp. SE188, *Burkholderia cepacia* SE4, and *Acinetobacter calcoaceticus* SE370 improved cucumber plant growth under salt stress, with increased proteins and antioxidant enzymes, and decreased sugars and ribonuclease [84, 265]. Attia et al. [266] showed that seed priming with gibberellic acid (GA3, 3 μM) partially attenuated the salt stress effect and efficiently reduced polyamines (PA; putrescine, spermidine and spermine) levels in salt-stressed seedlings of fennel (*Foeniculum vulgare* Mill.) as compared to the control. Organ and treatment-specific reduction in peroxidase and catalase activities were observed. In a similar manner, the responses of PA genes to salinity were found to be varied. In hypocotyls and cotyledons (H+C), up-regulation was observed for SPMS1, ODC1, and ADC1, whereas down-regulation was shown for SAMDC1 in the radicle.

Another phytohormone abscisic acid (ABA) is produced by salt-tolerant strains of *Achromobacter xylosoxidans*, *B. licheniformis*, *Proteus mirabilis*, *P. fluorescens*, *Stenotrophomonas maltophilia*, and *Bacillus megaterium* produce [3, 243]. Recent reports suggested that ABA-mediated signalling increases salt tolerance in different crops. For instance, inoculation of *Dietzia natronolimnaea* STR1 and *Bacillus amyloliquefaciens* RWL-1 in wheat and rice altered auxin and ABA signalling cascades, resulting in increase of salinity tolerance [162, 267]. The mechanism involved in lowering the inhibitory effect of salt on plant development by abscisic acid is through increasing K^+ and Ca^{2+} ions, reducing sugar and proline in the root, and neutralizing Na^+ and chloride (Cl^-) ions concentrations [268, 269]. Patel and Saraf [270] also identified salt-tolerant *Pseudomonas putida*, *Pseudomonas stutzeri*, and *Stenotrophomonas maltophilia* in *Coleus* rhizospheres with elevated CK, gibberellins, and IAA level under salt stress conditions.

Cytokinins (CK) are involved in tissue differentiation and cell proliferation function, and act as master regulators in mitigating salinity stress in plants [271]. Many salt-tolerant species of *Bacillus*, *Arthrobacter*, *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Arthrobacter*, *Halomonas*, and *Stenotrophomonas* were reported to produce cytokinins [272]. Increased cytokinin production decreased ethylene, reducing leaf senescence in cereals and legumes, hence boosting plant growth [273, 274]. Sita and Kumar [275] provided a more in-depth explanation of the function of gamma-aminobutyric acid (GABA) in the resistance of legumes to abiotic stress. Another phytohormone 5-aminolevulinic acid (ALA) has recently received wide applications due to its potential use as herbicide, insecticide, antimicrobial, alleviation of abiotic stress and plant growth stimulator under different stress conditions [276]. Growth rate of root and shoot, and leaf water relations of canola (*Brassica napus*) plants were improved by ALA application under different NaCl (100, 200 mM) concentrations [277]. Bacterial inoculation of mustard plants with ALA producing and salt tolerant (8% NaCl) isolate JMM15 showed 190.89% (at 0 dS m^{-1} EC), 123.18% (at 8 dS m^{-1} EC) and 230.86% (at 12 dS m^{-1} EC) increase in shoot dry weight at 80 days of growth under controlled greenhouse conditions [10].

Organic Acids Role in Amelioration of Salt Stress

One of the most severe abiotic stressors that plants can experience is salinity stress, which can cause disruptions in their physiological, biochemical, and metabolic processes. The application of natural metabolites to the plant is a viable technique for mitigating the deleterious effects of stresses on plants. It has been observed that the use of salicylic acid (SA) has tremendous agronomic potential in terms of enhancing the stress response of a variety of agronomically valuable crops, such as barley, maize, sunflower, wheat, bean, strawberry, and chamomile, amongst others [278]. Under salt stress conditions, SA application has been reported to provide several beneficial effects for plants i.e., the mitigation or reduction of photosynthetic pigments and photosynthetic performance, preservation of membrane integrity, stimulation of ABA and proline accumulation, reduction in lipid peroxidation and membrane permeability, lowering Na^+ content and higher K^+ concentration, etc. [278]. Treatment of wheat seedlings with sinapic acid, caffeic acid, ferulic acid, and p-coumaric acid, in addition to SA, resulted in enhanced growth of the plants despite the presence of salt stress [279]. Caffeic acid protected cucumber from chilling stress [280], and application with ellagic acid expedited the germination and seedling growth of chickpea under osmotic stress conditions. In addition, the treatment with vanillic acid lowered the deleterious effects of salt stress in tomato plants [280–282]. It has been also observed that all of these phenolic acids enhance the antioxidant capacity of plants by improving the activity of antioxidant enzymes and the accumulation of nonenzymatic antioxidants.

When comparing three different *Brassica* crops (kale, white cabbage, and Chinese cabbage), Lini'c et al. [283] found a positive correlation between phenolic acid levels and salinity tolerance, with kale being the most tolerant, white cabbage being moderately tolerant, and Chinese cabbage being the most sensitive species. Salicylic acid (SA) and ferulic acid (FA) were applied topically to plants and their effects on Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis* (Lour.) Hanelt cv. Cantonner Witkrop) that had been exposed to short-term salt stress (150 mM NaCl, 72 h) were assessed [284]. Under salt stress conditions, rise in SA and proline concentration was reported whereas a decline in phenolic compounds, antioxidant activity, and photosynthetic performance (particularly owing to the degradation of PSI function) was observed.

Both proline and SA levels dropped when salt-stressed plants were treated with SA and FA (10 mM). Interestingly, in FA and SA treatments, the content of polyphenolic chemicals, notably FA, sinapic acid (SiA), kaempferol (KAE), and quercetin (QUE), enhanced in salt-stressed plants. As a result, there was an increase in antioxidant activities and a rise in photosynthetic efficiency. When comparing FA and SA, the latter was found to have a more beneficial alleviating impact on salt stress. Gholamnia et al. [285] also examined the effects of three different salt levels and two different temperatures on peppermint (*Mentha piperita* L.) by comparing the expression profiles of genes encoding proteins involved in the rosmarinic acid production pathway and various physiological responses. The upregulation of C4H and HPPR genes indicates the functions of these genes in defence mechanisms as well as the impacts of phenolic chemicals on oxidative stress inhibition.

Nitric Oxide Production and Mitigation of Salt Stress

Nitric oxide (NO) is a gaseous and highly reactive nitrogen species, which is produced under normal as well as environmental stress conditions in living cells. NO has been reported to regulate various developmental processes during plant growth such as seed germination, root growth, stomata closure, flowering, stress response, and cell death [286, 287]. NO also modulates production of reactive oxygen species (ROS) in plants after exposure to various abiotic stresses and subsequently, activate defence mechanisms through enhanced production of antioxidants [288, 289]. Production of nitric oxide also leads to altered gene expression and activation of various redox regulated genes encoding antioxidant enzymes such as glutathione peroxidase (GPx), superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX) and chloramphenicol acetyltransferase (CAT), and may result in suppression of lipid peroxidation or malondialdehyde (MDA) synthesis [290–292]. The exogenous application of NO enhanced the production of ascorbate, glutathione, total phenolic content, proline, and flavonoids in NaCl-treated spinach [293] and tomato plants [294]. In addition, NO acts as an endogenous modulator of several plant hormones resulting in the inhibition of the induced programmed cell death and aid in stomatal function in *Arabidopsis*, wheat and pea plants [295, 296].

Salt stress normally has a negative effect on ion homeostasis and osmotic balance of plant cells [94]. Intracellular ion imbalance inhibits soil nutrient uptake leading to nutrition deficiencies. Furthermore, salt stress provokes membrane disintegration, loss of metabolic function ion leakage, DNA defragmentation, and subsequent cell death [297]. Plants have evolved various protective mechanisms to ameliorate the negative effects of salt stress. NO mediated mitigation of stress and the underlying mechanisms have been extensively studied using different approaches [298–301]. For instance, regulation of Na^+/K^+ ratio and H^+-ATPase of the plasma membrane is caused by NO, which confers salt tolerance in axenically grown cucumber plant [302]. Similarly, NO was demonstrated to activate the synthesis of H^+-ATPase in maize seedlings, resulting in production of H^+ gradient, which force the exchange of Na^+/H^+ and causes homeostasis of Na^+ and K^+ [303]. In another similar study, Zhao et al. [290] showed that NO acted as a signal in salt resistance in the calluses from two ecotypes of reed and induced the expression of the plasma membrane H^+-ATPase, which provided protection by making a balance in K^+:Na^+ ion ratio. NO mediated protection against salt stress in vivo has been shown in *Arabidopsis Atnoa1* mutants with impaired endogenous NO levels as these plants show enhanced sensitivity to salt stress, as well as reduced survival rates compared to wild type plants. Additionally, these mutants exhibited a greater Na^+/K^+ ratio in the shoots than the wild type plants [304, 305].

Besides this, NO donor sodium nitroprusside (SNP) has been found to alleviate osmotic stress tolerance and enhances seedling growth under salt stress in several plant species including rice, lupin, and cucumber [306, 307]. Increases in dry weights have been reported in maize, and seashore mallow seedlings after NO application under salt stress [303, 308]. In addition, the release of the nanoparticle known as chitosan nanoparticles (CS NPs) by NO treatment has been found to mitigate the toxic effects of salinity in maize plants [309]. The induction of polyamines is known to be closely associated with NO production or exogenous application of NO donors [308]. Therefore, NO-polyamine interaction may cause adaptive responses in plants for stress tolerance [310]. The increased levels of H_2O_2 in soybean due to the long-term salinity stress treatment, were reduced to the basal levels with exogenously-applied NO donor [311]. Adamu et al. [312] observed that treatment of salt-susceptible rice seedlings with SNP (NO donor) under salt stress caused a significant increase in the expression of *OsHIPP38*, *OsGR1*, and *OsP5CS2* and provided a resistant response to salt stress. On the other hand, untreated control plants (lacking NO donor treatment) succumbed to salt-stress. Furthermore, SNP-treated plants produced more plant biomass under salt stress conditions.

Inoculation Effects of Salt-Tolerant Bacteria in Improving Plant Growth of Different Crops

The deleterious effects of salinity have been observed on plant growth and yield in various crops including mungbean, soybean, groundnut, pigeon pea, common bean, chickpea, groundnut, maize, tomato and cucumber. The main problem in the agriculture sector is to find an alternate solution for salt-stressed soil that ensures agricultural sustainability while increasing yield production in an environment friendly manner [15, 16].

The capacity of halo-tolerant rhizobacteria to deal with high soil salinity problem is well acknowledged and bacterization with salt-tolerant rhizobacterial strains has been found to mitigate the deleterious effects of salts on plants [9, 313–317]. Thus, use of salt-tolerant microbes as bio-enhancers/bioprotectants not only increases agricultural yield but also ensures plant survival in extreme salty conditions via physiological, biochemical, and molecular routes [24]. Besides salt tolerance, other PGP traits of salt-tolerant rhizobacteria contributes towards improvement of plant growth and increases in crop yield of different crops including cereals, legumes, oil seeds, and vegetables (Table 13.1). Thus, development of microbial consortia consisting of different bacteria or bacteria with mycorrhizal fungi has emerged as another feasible approach for improved amelioration of plant abiotic and biotic stresses [26, 318–320].

When pepper plants were inoculated with *Bacillus* sp. TW4, they showed a decrease in osmotic stress, which is often seen in the form of salt (and/or drought) stress. Under the influence of abiotic stress, the expression of genes associated with ethylene metabolism was found to be suppressed in these pepper plant [198]. *Bacillus* sp. TW4 exhibited ACC deaminase activity, which may be associated to the lowered expression of these genes. It has also been found that salt stress also affects nodulation during *Phaseolus-Rhizobium* interactions. However, in contrast to application of *Rhizobium* strain, *Azospirillum* inoculation of salt-stressed plants resulted in a longer exudation of plant flavonoids, suggesting an upregulation of flavonoid genes [313]. In barley seedlings, inoculation with *Azospirillum* seemed to alleviate NaCl stress, exhibiting the response to salt stress [321]. Salinity reduced the dry mass of the roots and shoots of lettuce plants compared to the control plants growing in non-saline environments [322]. At both medium and high salt conditions, the plants inoculated with *Pseudomonas mendocina* exhibited significantly higher shoot biomass than the control plants. Reduced chlorosis, necrosis, and drying were also seen in salt-stressed Mt-RD64 plants in comparison to salt-stressed Mt-1021 plants [322]. The antioxidant enzymes such as superoxide dismutase, ascorbic peroxidase, glutathione reductase, and proline oxidase were also associated to mitigate the salt stress.

Misra et al. [323] revealed the occurrence of most prominent group of ACC deaminase-producing salt tolerant *Bacillus* sp., which caused salt stress mitigation and improved grain yield of rice in different agro-ecological zones. Similarly, inoculation with *Pseudomonas* strain 002 [314] and *Staphylococcus sciuri* strain SAT-17 [324], which were able to tolerate 75 and 150 mmol L^{-1} NaCl, respectively, were found to improve plant growth and biomass under salinity treatments. The inoculation with saline-adapted *Azospirillum* strains was found to improve grain productivity in wheat [22]. Nadeem et al. [325] documented significantly improved plant height, root length, chlorophyll content, and grain yield in maize under salt stress conditions using ACC deaminase-producing PGPR. Similarly, significant stimulation of growth and seed germination was observed in cotton under saline conditions with the inoculation of *P. putida* strain RS 198 [21]. Likewise, Upadhyay et al. [111] demonstrated that combined inoculation of *B. subtilis* and *Arthrobacter* sp. was found to mitigate soil salinity effects in wheat and caused improvement in plant biomass, total soluble sugars, and proline content. Inoculation of *Halobacillus* sp. and *B. halodenitrificans* also enhanced the growth parameters of wheat in salt-affected soils as compared with the uninoculated control at 320 mmol L^{-1} NaCl [23]. In similar studies, inoculation of wheat (*Triticum aestivum* L.) var. WH157 with salinity-tolerant *Azotobacter* strains i.e., ST3, ST6, ST9, ST17 and ST24 caused significant increase in total nitrogen, biomass and grain yield in earthern pots containing saline soil under pot house conditions [326]. Maximum increase in plant growth parameters were obtained after inoculation with *Azotobacter* strain ST24 at fertilization dose of 120 kg N ha^{-1} and its inoculation resulted in attaining 89.9 cm plant height, 6.1 g seed yield, 12.0 g shoot dry weight and 0.7% total nitrogen.

Significant increases in seed germination and enhancement in plant growth have been reported by several workers due to osmoprotectant accumulation, modulation of gene expression associated with salt stress, and by induction of antioxidative enzymes against the ROS pathway [119, 327, 328]. Recently, Damodaran et al. [329] demonstrated enhanced grain yield in rice and wheat by using *Lysinibacillus* sp. that mitigated the harmful effects caused by high salt stress. Similarly, bacterization of soybean with *Bacillus firmus* SW5 resulted in significant improvement in nutrient uptake, photosynthesis, gas exchange, flavonoid and phenolic contents, osmoprotectants, and antioxidant enzymes under salt stress conditions [330]. Treatment of sunflower (*Helianthus annus*) with fluorescent *Pseudomonas* was found to positively affect plant biomass in salt stress conditions [331] whereas other bacterial genera belonging to species of *Pseudomonas*, *Ochrobactrum*, *Agrobacterium*, and *Klebsiella* induced salt tolerance in groundnut [31]. Similarly, inoculation of a *Pseudomonas* strain isolated from halophilic grass *Distichlis spicata* was observed to improve the growth of different crops under salt stress [332].

Table 13.1 PGPRs conferring salt tolerance in plants

PGPR strains	Crop	PGPR attributes	References
Aeromonas sp.	Wheat (*Triticum aestivum*)	EPS production	[80]
Acinetobacter johnsonii	Maize (*Zea mays* L.)	Enzymatic activities, nutrient uptake and antioxidant defence	[335]
Azotobacter chroococcum	Maize	Improved K^+/Na^+ ratio, polyphenol content and proline	[336]
Bacillus amyloliquefaciens	Rice (*Oryza sativa*)	Betaine, sucrose and trehalose	[327]
Bacillus amyloliquefaciens	Rice	Proline content	[337]
Glutamicibacter sp	Rice	Production of ACC deaminase	[338]
Micrococcus sp.	*Arabidopsis thaliana* and rice	Production of IAA and siderophore	[339]
Klebsiella oxytoca and *Bacillus* sp.	Cotton seeds	Antioxidative enzymes and photosynthetic pigment	[340]
Klebsiella sp.	Oat (*Avena sativa*)	Proline content, malondialdehyde content, antioxidant enzymes	[173]
*Curtobacterium*sp.	Barley (*Hordeum vulgare* L.), soybean (*Glycine max* L.)	Production of proline and IAA	[341]
Bacillus baekryungensis DPM17	okra (*Abelmoschus esculentus*)	Phosphate solubilization, nitrogen fixation, production of ammonia, IAA and gibberellins	[342]
Arthrobacter woluwensis AK1	Soybean (*Glycine max* L.)	Production of IAA and ABA	[343]
Mesorhizobium sp.	Chick pea (*Cicer arietinum*)	ACC deaminase activity	[344]
Bacillus licheniformis, Pseudomonas plecoglossicida	Sunflower	Production of IAA, biofilm formation, phosphate solubilization, and ACC deaminase activity	[345]

(continued)

Table 13.1 (continued)

PGPR strains	Crop	PGPR attributes	References
Bacillus marisflavi sp., *Bacillus cereus*	*Pisum sativum*	Production of ACC deaminase	[346]
Orchbactrum sp	Groundnut (*Arachis hypogaea* L.)	Production of IAA and ACC deaminase	[347]
Pseudomonas sp.	Tomato	Production of IAA, ACC deminase and EPS	[164]
Pantoea sp.	Mungbean (*Vigna radiata* L.)	ACC deaminase activity	[348]
Tsukamurella tyrosinosolvens, Burkholderia pyrrocinia	Peanuts	Increased catalase, superoxide dismutase and peroxidase activities	[349]
Streptomyces sp. and *Bacillus* sp.	Ice-plant (*Mesembryanthemum crystallinum* L.)	IAA, phosphorus solubilization, ACC deaminase, siderophore production	[350]

Saravanakumar and Samiyappan [333] showed that ACC deaminase-producing *P. fluorescens* strain TDK-1 significantly enhanced the growth of groundnut seedlings under salt stress conditions as compared with inoculation of strain lacking ACC deaminase activity. Inoculation of wheat with *Chryseobacterium gleum* sp. strain SUK possessing ACC deaminase activity showed significant stimulation of plant growth and enhancement in grain yield under salt stress conditions [64]. In another experiment, combined application of rhizobia and ACC deaminase-producing *Pseudomonas* on mungbean (*Vigna radiata*) showed superior growth, nodulation, and yield under salt stress conditions [261]. Similarly, coinoculation of soybean with salt-tolerating *P. putida* TSAU1 and ACC deaminase-producing *Bacillus japonicum* USDA 110 improved plant growth, macro- and micro-nutrient acquisitions, and seed protein content by modulating root architecture under salt stress conditions [159]. The combined inoculation of *Variovorax paradoxus* 5C-2 and *Mesorhizobium loti* strains possessing ACC deaminase activity had additive and synergistic effects on nodulation, root growth, and uptake of elements (e.g., N, P, Mg, Ca, Na, and Zn) in *Lotus ornithopodioides* and *L. edulis* [334]. Separate inoculation with the two bacterial strains viz. *Rhizobium* sp. LSMR-32 and *Enterococcus mundtii* LSMRS-3, possessing multifunctional growth promoting traits, ameliorated salinity stress effects and increased seed germination, grain yield, plant height, biomass, chlorophyll content, and nutrient uptake compared to uninoculated plants under salt stress conditions [319]. Inoculation with both the strains increased nodule number, nodule biomass, and leghaemoglobin amount in spring mungbean along with increase in soil phosphatase and dehydrogenase levels.

Ullah et al. [351] inoculated wheat cv. Inqlab-91 seeds with cultures of *Pseudomonas mendocina* Khsr2, *Pseudomonas putida* Khsr4, *Pseudomonas stutzeri* Khsr3 and *Azotobacter vinelandii* Khsr1. The applied PGPR strains significantly improved the transfer of K, Ca, Mg and Zn from soil to plant shoots and reduced the transfer of Cr in inoculated plants over that of uninoculated soil. The maximum K^+/Na^+ ratio of rhizosphere soil and wheat leaves was recorded in *Pseudomonas putida* Khsr4 inoculation. The applied PGPR helped in selective uptake of K over Na and enhanced transfer of nutrients resulting in higher yield. Yield of ridge sown plot was 3.59% higher than drill sown plot, and 10.87% higher than broadcast sown plot respectively. Oliveira Lopes et al. [352] reported that synergistic interactions between five different rhizobia (*B. elkanii* BR 2003, *B. pachyrhizi* BR 3262, *B. yuanmingense* BR 3267, *B. paxllaeri* BR 10,398, and *B. icense* BR 10,399) and *Azospirillum baldaniorum* strain (Sp245), alone or in combination, attenuated the deleterious effects of salt stress (75 mM NaCl) on lima bean. Plants coinoculated with rhizobia and *A. baldaniorum* showed the highest value for root length, plant biomass (shoot, root, and nodules), number of nodules, and photosynthetic pigments. Coinoculated plants under salt stress showed a minor increase in sodium and the highest potassium content values, and nitrogen fixation efficiency than plants inoculated with rhizobia.

Three isolates e.g., E-2, T-2, and T-1 (identified as *Klebsiella* sp. strain BAB-6433, *Citrobacter freundii* strain R2A5, and *Citrobacter* sp. DY1981, respectively) showed salt (NaCl) tolerance at concentrations of 7%, 6%, and 6%, respectively [353]. Inoculation of these salt-tolerant isolates significantly improved plant growth of paddy plants in a hydroponic study, ensuring nutrient availability to the plants grown under a nutrient (nitrate or phosphate) deprived growth matrix. Naseri et al. [354] reported that highest saline stress, 10 dS m^{-1}, reduced shoot and root dry weight and root volume of tomato up to 51.3, 41.5, and 51.8%, respectively. In addition, it also increased stomatal resistance and proline content 2.01- and 3.66-folds and decreased K^+/Na^+ ratio 4.16-folds, respectively. Inoculation of *Bacillus megaterium* P2 on tomato plants was found to modulate salt tolerance mechanisms, improved plant growth factors, soil biological indicators and also balanced K^+/Na^+ uptake even at 10 dS m^{-1} salinity level. However, the efficiency of strains was dependent on the magnitude of salt stress. In similar studies, Gritli et al. [26] evaluated the effect of different microbial inocula consisting of nodule-forming and nitrogen-fixing *Rhizobium laguerreae* and arbuscular mycorrhizal fungus (AMF) *Rhizophagus irregularis*, along with various plant growth-promoting bacteria (PGPB) including *Bacillus subtilus*, *Bacillus simplex* and *Bacillus megaterium* on alleviating salt stress in *Lathyrus cicera* under pot trial studies. Exposure of plants to salinity (100 mM NaCl) significantly reduced growth of *L. cicera.* On the other hand, inoculation with different inocula enhanced plant growth and markedly promoted various biochemical traits, and resulted in mitigating deleterious effects of salinity stress on *L. cicera.* Coinoculation also upregulated the expression of two marker genes (*LcHKT1* and *LcNHX7*) related to salinity tolerance.

Genetic Engineering of Plants and Microbes for Efficient Alleviation of Salinity Stress

In response to a wide range of environmental challenges, plants have evolved a wide range of strategies for modulating their rhizosphere. A deeper knowledge of the inter-kingdom signaling and biological processes occurring between microbes and plants may provide insights as to how the rhizosphere might be controlled to enhance plant health and production [355–358]. In the long term, rhizosphere engineering might lessen our need for herbicides and pesticides by substituting beneficient microbiota, biostimulants, or transgenic plants for agrochemicals [359]. Rhizosphere engineering is possible through the appropriate selection of crop species and cultivars, by application of stress-tolerant microbes as soil/seed treatments [360, 361]. Microorganisms can be developed to enhance nutritional availability in addition to resistance to abiotic or biotic stresses, inhibition of harmful bacteria, or that can support the survival of beneficial microorganisms. Crops can be chosen by breeders to have beneficial attributes, or beneficial microorganisms can be developed [5, 59, 362, 363]. The development of genetic techniques and the growing field of metagenomics will speed up research on the rhizosphere's microbial diversity, and rhizosphere engineering will lead to efficient modification of microorganisms for ecologically sustainable farming practices [315, 364, 365].

Various genetic engineering techniques and molecular biology approaches are being employed recently to improve the beneficial traits in plants and microorganisms to improve soil health resulting into increased plant growth and crop yield [361, 366]. In addition, identification of novel effective microbial inoculants, detecting particular bacterial gene sequences, analyzing population density with copy number of particular functional genes and the persistence of microbial inoculants in soil is a never-ending process to achieve desirable impacts on crop productivity [367–370]. The genetic diversity of rhizobacterial isolates is shown by DNA finger printing [371]. For instance, two efficient bacterial isolates i.e., *Bacillus cereus* (P31) and *Achromobacter xylosoxidans* (P35) were identified by 16S rDNA analysis out of seven bacterial strains isolated from surface-sterilized sweet potato roots and these strains were recommended to decrease chemical fertilizer consumption in sustainable agriculture [372]. *Enterobacter* spp. exhibiting PGP features and isolated from maize roots was phylogenetically described using the MicroSeqTM 16S rDNA technology, and it showed the closest similarity (99.4%) with *Enterobacter asburiae* [373]. *Bacillus*, *Delftia, Methylobacterium, Microbacterium, Paenibacillus, Staphylococcus*, and *Stenotrophomonas* were identified in common bean based on 16S rDNA sequences [374]. The inoculation of *Dianthus caryophyllus* roots with *Klebsiella* SGM 81 having *ipd*C gene significantly altered plant development in both laboratory and field environments, and caused an increase in root hair formation suggesting increased synthesis of auxins [375]. The presence of the *acd*S gene was detected in nine strains using PCR amplification and *Microbacterium* sp. ECI-12A showed the highest ACC deaminase activity (539.1 nmol α-ketobutyrate mg^{-1}

protein h^{-1}) [19]. Amplification of the *pqq* gene (involved in phosphate solubilization) revealed similarities between the indigenous and previously sequenced *Bacillus licheniformis* strains in this gene and its surrounding regions [376].

Multiple strategies are utilized by halotolerant PGPR in order to overcome the effects of salinity stress. In saline agroecosystems, salt-tolerant rhizobacteria boost plant performance under abiotic stress, which leads to higher crop output [377]. There is still a paucity of knowledge on the salt tolerance mechanisms of halotolerant PGPR. This lack of knowledge includes bacterial genes and proteogenomics in osmotolerance as well as plant-microbial interactions in saline soil. In spite of this, numerous studies on salt-resistant rhizobacteria have been carried out in the last ten years in order to investigate the molecular processes of gene expression when salt is present in the environment [378]. Ma et al. [379] have proposed that understanding the regulation networks of salt-tolerant rhizobacteria during abiotic stress could be a critical way of combating such stressors and promoting global food production in an environmentally acceptable manner. This method might be used to develop either specific microbes or beneficent microbial consortium to boost plant development in a variety of soil conditions. Thus, plant/soil-optimized microorganisms may be employed as inoculum for various crops in various soils. Various reports indicated that crop-specific soil microbiomes improve plant-microbe interactions over time [380].

Recently, functional metagenomics provided a magnificent way of identification of various genes responsible for salt resistance in microorganisms. Liu et al. [381] carried out whole genome analysis of a halotolerant PGPR *Klebsiella* sp. D5A and it revealed the presence of salt tolerance genes with a wide range of pH adaptability and PGP traits including phosphate solubilization, IAA biosynthesis, acetoin, and 2,3-butanediol synthesis, siderophore production, and N_2 fixation. The salt-stress induced damage in citrus plants was reduced by treatment with *Pseudomonas putida* and *Novosphingobium* sp., which resulted in lowering the level of abscisic acid (ABA) and salicylic acid (SA), reducing the efficiency of photosystem II (Fv/Fm), increasing accumulation of IAA in the leaf and inhibiting accumulation of root chloride and proline during salt stress [382]. A salt-tolerant *Enterobacter* sp. UPMR18 strain containing ACC deaminase showed plant growth-promoting effects through induction of reactive oxygen species scavenging enzymes including superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT) and upregulating to ROS pathway genes [143]. In similar studies, a novel salt-tolerant bacterial strain *Pseudomonas* sp. M30-35 was obtained from the rhizosphere of succulent xerohalophyte shrub *Haloxylon ammodendron*, which showed salt and drought tolerance capabilities. *Pseudomonas* sp. M30-35 was found to contain 34 genes possessing homology with certain genes associated with PGP traits and abiotic stress tolerance [144]. *Bacillus safensis* VK strain showed salt tolerance up to 14% NaCl and pH ranging from 4 to 8 [383]. Several genes were characterized by genomic studies of *B. safensis* strain, which were associated with functioning of PGP traits under conditions of high salt concentrations, drought, heavy metals, and polyaromatic hydrocarbons contamination. Sapre et al. [173] isolated *Klebsiella* sp. IG 3 from the rhizosphere of wheat and it showed salt tolerance up to 20%. This strain positively modulated the expression profile of *rbc*L (codes for the ribulose-1,5-bisphosphate carboxylase/oxygenase RuBisCo) and WRKY1 (transcription factor dealing with plants reaction to biotic stress) genes under salt-stress conditions.

An integrated strategy that included already identified genetic variants, using diversified and new sources to produce novel variations. Moreover, instead of focusing on a single attribute or characterstics during breeding, it may be more productive to look for combinations of characteristics (Table 13.2). A variety of genes involved in various pathways that increase plant tolerance to abiotic stresses have been used in the development of transgenic plants in recent years. Genes encoding different enzymes involved in promoting tolerance to multiple abiotic stresses through modifications in membrane phospholipids, production of osmoprotectants, and late embryogenesis proteins can be introduced into cereal or legume plants using single-gene transformation [384]. In legumes, mass screening is being used to identify salt-tolerant germplasm for enhancement of legume genotype. Sehrawat et al. [385] assessed 117 mungbean genotypes for salt tolerance and observed significant diversity in their efficiency under salt treatment, and classifying them as highly tolerant, moderately tolerant, sensitive, and extremely susceptible genotypes. Characteristics such as germination and seedling growth, proline content, photosynthetic efficiency, osmoregulation, crop yield, nodule formation, and ion homeostasis were used to screen genotypes for salt stress resistance.

Various reports on the salt tolerant transgenic plants have shown that activating a stress-response signal transduction pathway is an effective and potential method for increasing plant tolerance to biotic stresses [406–408]. Co-activation of various stress-response pathways, with either synergistic or antagonistic effects, may emerge from simultaneous exposure of a plant to multiple abiotic stress conditions. To deal with abiotic stresses, numerous distinct stress hormones, including ethylene, jasmonic acid, and abscisic acid or reactive oxygen species activation, receptors and signaling complexes, and networks of transcription factors and mitogen-activated protein kinase (MAPK) cascades are likely to communicate with one another. It was recently discovered that ethylene plays a fundamental role in the response of *Arabidopsis* to heat and osmotic stress. It was also observed that the expression of the transcriptional co-activator MBF1c in *Arabidopsis* enhances the tolerance of transgenic plants to these stresses by activating the ethylene-response signal transduction pathway [409].

ERF1 genes in various species have been frequently reported to participate in abiotic and biotic stress responses. The overexpression of *ERF1* gene in *Arabidopsis* enhanced the defense of transgenic plants against *P. cucumerina* [410], as well as their resistance against drought and salt stress [411]. The overexpression of *ERF1* gene in wheat strengthened the responses of the transgenic plants to pathogen stress and several abiotic stresses [412]. In *Arabidopsis*, *AtERF1* gene played a positive role in salt, drought, and heat stress tolerance by regulating stress-specific gene, and by integrating jasmonic acid, ethylene, and abscisic acid signals [413]. Overexpression of the pepper *CaERF5* gene in tobacco plants enhanced the resistance to *Ralstonia solanacearum* infection under the influence of salicylic acid, methyl jasmonate, and

Table 13.2 Transgenic plants having improved salt tolerance

Crops	Transferred gene	Observations	References
Wheat	Mt1 D	Turgor maintenance	[386]
Brassica	SOS1	Plasma membrane Na^+/K^+ antiporter	[387]
	h-type Trx proteins, AtTrx-*h*2	Improved antioxidant enzyme activity	[388]
Tomato	BADH1	Improves salt tolerance; accumulation of betaine	[389]
	SIMYB 102	Salt tolerance by regulating Na^+-K^+ homeostasis and ROS balance	[390]
Arabidopsis thaliana	JcDREB	Transcription factor	[391]
Soybean	WRKY11	Improves salt tolerance	[392]
Chickpea	P5CS	Synthesis and accumulation of proline	[393]
Mungbean	codA	Improve abiotic stress tolerance	[394]
	VrWRKY	Enhance abiotic stress tolerance	[395]
Common bean	Asr1, Asr2	ABA signaling pathway	[396]
Alfalfa	CsALDH12A1	Improves salt tolerance	[397]
	GmDREB1	Conferred salt tolerance	[398]
	IbOr	Increased tolerance to multiple abiotic stresses	[399]
Faba bean	PR10a	Synthesis and accumulation of osmolytes	[400]
Populus	*OsCYP714D1*	Improved the salt tolerance	[401]
Pigeon pea	OsRuvB	Improve salt tolerance through increases in chlorophyll content, relative water content, peroxidase and catalase activity	[402]
Peanut	AhWRKY75	Increased antioxidant activity	[403]
Potato	StCYS1	High proline and chlorophyll content	[404]
Birch	BpERF1.1	Improved tolerance to cold, salt and drought stress	[405]

ethylene [410]. In similar studies, overexpression of the soybean *GmERF3* gene, an AP2/ERF type transcription factor improved the tolerance of transgenic tobacco against drought, salinity, and even mosaic disease [411]. Zhang et al. [405] overexpressed *BpERF1.1* gene in birch (*Betula platyphylla* Suk.) using *Agrobacterium*-mediated infection method and obtained 11 transgenic lines with improved tolerance against multiple abiotic stresses. RNA-seq analysis identified 689 differentially expressed genes (DEGs) in the transgenic birch compared with WT, including 228 up-regulated genes and 461 down-regulated genes. Gene ontology enrichment analysis showed that among these DEGs, 273 genes were involved in various plant biological processes, and 83% of them were involved in cellular processes, metabolic processes, biological regulation and response to stimulus (11%). Thus, *BpERF*1.1 gene was found to improve the tolerance and resistance of birch against cold, salt and drought stress, probably by interconnecting with other genes involved in plant response to abiotic stresses.

Conclusions and Future Perspectives

Extensive studies have been carried out to analyze various environmental factors, which affect soil fertility and cause agricultural yield losses due to salt stress [6, 45, 414]. The study of ecological and evolutionary responses to salt stress in agroecosystems could benefit from the identification and examination of significant local microorganisms that are found in salty environments [415]. It is impossible to exaggerate the significance of using metagenomic, proteogenomic, and metabolomic approaches in order to harness and discover new PGPR, as well as specific metabolites and upregulated gene expression for the salt tolerance [145]. Given the effects of climate change, screening of sufficient salt-resistant PGPR strains is needed that may provide tolerance to abiotic stresses in order to maintain crop quality [416–418]. For developing novel and effective bio-enhancers, bioinoculants, and bio-protectants, characterization of essential metabolites, such as osmoprotectants, anti-oxidant enzymes, biosurfactants, phytohormone precursors and nutrients are needed. In agriculture, microbial consortia have become increasingly popular that may provide tolerance not only to abiotic stress, but also give resistance against phytopathogens [419].

Abiotic stresses are one of the most serious barriers to agricultural production on a global scale. Salt-tolerant microorganisms that are associated with rhizoplane, rhizosphere, and endophytic bacteria can play an important role in conferring abiotic stress resistance to plants. Currently, a lot of efforts are being made to improve the field efficacy of ACC deaminase-producing halo-tolerant bacteria. For instance, significant efforts are invested in development of improved biofertilizer formulations and bioinoculants to resist salt stress in wheat and cucumber such as chitosan-immobilized aggregated *Methylobacterium oryzae* strain CBMB20 [420], super absorbent polymer [421], and *Paenibacillus beijingensis* BJ-18 and *Bacillus* sp. L-56 [422]. Inoculations of effective salt-tolerant bioinoculants will assist in the mitigation of the adverse effects of climate change and help in enhancing crop productivity in salt-stressed soils contributing to an expanded global food supply for ever-growing global population. These salt-tolerant biofertilizers will provide phytohormones and nutrients, lower ethylene levels, induce novel plant genes to accelerate osmolyte accumulation, increase K^+ concentration, reduce Na^+ uptake, and ultimately maintaining a high K^+ ions. Numerous plant species have demonstrated salt tolerance as a result of bacterization with PGPR.

The production of stress-tolerant cultivars through conventional breeding and genetic engineering is essential, but the process is time-consuming and expensive. In comparison, the utilization of microorganisms to alleviate the negative effects of abiotic stresses is less expensive, friendlier to the environment, and requires less time. To maximize the benefits of microbial inoculants and enhance plant development and tolerance to a variety of biotic and abiotic stressors, new strategies will be developed once it is understood how the various microbial populations and plant systems are connected to one another. In the future, more in-depth research focusing on the gene expression level and multi-functional PGP features of salt-tolerating rhizobacteria needs to be carried out in order to build tailor-made bioformulations that may mitigate the effects of salinity stress under changing climate conditions and may boost plant growth under abiotic stresses in saline soil [423, 424].

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