PUTTING PLANT GROWTH-PROMOTING MICROBES IN ACTION EFFECTIVE WAY TO MITIGATE SALINITY STRESS IN PLANTS: REVIEW AND FUTURE PERSPECTIVE

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Abstract. Salinity stress is the most pernicious abiotic stress negatively affecting crop productivity around the globe. Soil salinity is significantly decreasing the agricultural lands every year which is posing serious food security threats. The global population is rapidly increasing and it demands the use of every soil for crop production. Salt stress negatively affects plant growth and development by inducing ionic, osmotic, and oxidative stress and it also negatively affects soil biological properties and microbial activities. Using microbial-based techniques is considered an effective, and environmentally friendly way to mitigate stress effects and improve crop production. The application of plant growth-promoting rhizobacteria (PGPR) is an imperious way to improve plant productivity and reclaim salt-affected soils. The use of PGPR can reduce the production of reactive oxygen species (ROS), facilitate nutrient uptake, and regulate gene expression, osmolyte, and hormone synthesis which helps mitigate deleterious impacts of salinity. Besides this, PGPR also improves antioxidant activities, and they produce organic acids, and siderophores which help to counter

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ROS production. Thus, in the present review, we discussed the different mechanisms of PGPR in modulating plant growth under saline conditions. We also identified different research gaps that must be abridged in future studies. This review will provide better insights into the present knowledge and will help to improve crop production in saline soils using PGRP.

Keywords: *antioxidants, microbial activities, PGPR, ROS, soil fertility*

Introduction

Soil salinity is a global threat and its intensity is continuously rising which is a challenge in the context of a rapidly growing population. Globally, soil salinity is affecting 1100 Mha which accounts for 7% of global land surfaces (FAO, 2023). Soil salinity occurs through natural, and anthropogenic activities (Singh et al., 2022). Atmospheric deposition, elevated sea level, and saltwater intrusion are important natural causes of soil salinity (SS), whereas, excessive use of fertilizers, and intensive agricultural practices are important cause anthropogenic causes of SS (Machado and Serralheiro, 2017; Hopmans et al., 2021). The increasing water scarcity and ongoing land degradation cause substantial yield losses, especially in semi-arid areas. Soil salinity occurs owing to soluble salt's accretion which causes osmotic stress and reduces water absorption by plants (Stavi et al., 2021). Salinity-induced osmotic stress occurs due to an increase in salt uptake and a reduction in water potential around the plant roots which reduces plant growth by decreasing water conductivity in plant cells (Abbasi et al., 2016). Further, prolonged SS also increases the accretion of toxic ions like sodium (Na^+), chloride (Cl^-), and sulfate (SO_4^{2-}) which ionic toxicity and impairs nutrient uptake (Isayenkov and Maathuis, 2019). The undesirable effects of SS on plants manifested seed germination, induced chlorosis and stunted growth, inhibited photosynthesis, and increased production of malondialdehyde (MDA), electrolyte leakage (EL), and hydrogen peroxide (H_2O_2) (Hannachi et al., 2022; Rafaliarivony et al., 2022).

Salinity stress is a major problem for field crops particularly in areas with insufficient rain to leach salts from the root zone (Safdar et al., 2019). The reduction in germination is an important cause of SS, which occurs due to restricted water uptake and a reduction in enzymatic activities (Kumar et al., 2020). Besides this, SS also reduces chlorophyll synthesis, damages photosynthetic apparatus, and negatively affects gas exchange properties, thus leading to a reduction in photosynthetic efficiency and finally assimilating production (Kumar et al., 2020). Salinity stress also leads to the overproduction of ROS that damages membranes, proteins, and lipids (Hasanuzzaman et al., 2021). Moreover, SS also alters soil properties reduces microbial diversity and health, and leads to a reduction in plant growth (Cardoso et al., 2013).

To counter the toxic effects of SS, plants activate a complex enzymatic and non-enzymatic antioxidant defense system to scavenge ROS production (Laamari et al., 2023). Besides this, plants also increase the synthesis and accumulation of different lower molecular weight osmolytes which play a critical role in mitigating the toxic effects of salinity (Smiatek et al., 2012; Rai et al., 2023). The increase in accumulation of osmolyte under SS is an important practice to prevent the deficiency of water by decreasing the osmotic potential of cells. This decrease in water potential can be offset by an increase in water uptake, and thus maintenance of cell turgor and water contents (Nemati et al., 2011). The present agriculture techniques and salt-tolerant crops will not be sufficient for future needs (Kumar et al., 2020). Thus, in this context use of biological agents could be an important way to manage crop production under saline soils (Füzy et al., 2019). Sustainable crop production can be ensured by using microbes that don't have harmful effects on soil and they can improve, plant growth under stressful conditions (Cardoso et al., 2013; Solanki et al., 2022).

Microbes have emerged as important to enhance strain tolerance and crop productivity (Ali et al., 2014). Microbes are designed with numerous direct and indirect mechanisms that aid plant growth and development in harsh environments. For instance, plant growth-promoting rhi-bacteria (PGPR) produces extracellular proteases, increases osmolyte accumulation and activates Na^+ /H^+ which helps the plants mitigate the adverse impacts of SS (Cao et al., 2016; Jana and Yaish, 2021). PGPR also hydrolyzes the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) by ACC deaminase, reducing stress-induced ethylene production and alleviating the toxic effects of abiotic stress (Mayak et al., 2004; Santana et al., 2022). Therefore, considering the importance of PGPR in reducing the toxic effects of SS in the present review we discussed the different physiological, biochemical, and molecular mechanisms through which PGPR can mitigate salt tolerance in plants. This review also discusses various research gaps that must be fulfilled to ensure better crop production by using PGPR. The present review with provide better insights and potential avenues for future research and it will also provide new suggestions to develop salt-tolerant crops.

Effects and responses of plants to salinity stress

Salt stress suppresses plant growth and reduction in growth rates depends on many things like plant species and stage of plant growth salt concentration (*Table 1*). Plants use stunted growth as a defense mechanism against the toxic effects of SS (Yadav et al., 2019). Salt stress reduces gene expression involved in cell cycle progression, resulting in a reduction in meristem cell numbers and growth inhibition (Yadav et al., 2019). Besides this SS also reduces the root growth which affects the ability of plants to absorb nutrients and water resulting in significant growth losses (Yadav et al., 2019). Photosynthesis is an important process in plants, however, SS impaired photosynthesis by decreasing chlorophyll synthesis (*Figure 1*), altering enzyme activity, damaging photosynthetic apparatus, and reducing the carbon dioxide (CO_2) supply (Denaxa et al., 2022; Al Hinai et al., 2022). Salinity stress reduces chlorophyll synthesis by increasing the degradation and oxidation of chlorophyll owing to increased ROS production (Taïbi et al., 2016). Salinity-induced pseudocyclic electron transport inhibits electron transport and increases ROS production which damages the photosynthetic apparatus and proteins (Zahra et al., 2021). The short-term SS also disrupts the structure of chloroplast due to thylakoid swelling and accumulation of starch (Goussi et al., 2018). The increased absorption of salts under SS also negatively affects plant-water relations. In saline conditions osmotic potentials become more negative which produces an osmotic gradient that removes water from the cell, resulting in a decrease in turgor pressure (Betzen et al., 2019). The salinity-induced reduction in cell turgor pressure reduces the water uptake (0-20%) and transpiration rate (0-30%) (Sheldon et al., 2017).

Salinity also reduces plant growth by decreasing nutrient uptake and acquisition and increasing competition between nutrients and toxic ions (sodium: Na^+ and chloride: Cl^-). Therefore, such interactions lead to a deficiency of calcium (Ca^{2+}), potassium (K^+), and magnesium (Mg^{2+}): (Sultan et al., 2021). Nitrogen is an important nutrient for plants however, in saline soils, the increased accumulation of Cl decreases the N uptake due to Cl^-/NO_3^- antagonism (Munns and Termaat, 1986).

Table 1. *Effect of salinity stress, on growth, physiological, and biochemical processes of different plant species physiological, and biochemical processes of different plant species*

Plant species	Salinity stress	Toxic effects	References
Wheat	200 µM	Salt stress reduced leaf area, photosynthetic pigments, and concentration of GSH, and ASA, and increased NO and H_2O_2 accumulation, GR and APX activities, and lipid peroxidation.	Maslennikova et al. (2023)
Rice	4.09 dS m^{-1}	Soil salinity reduced the photosynthetic rate, SPAD value, grain weight, grain yield, and leaf area.	Hussain et al. (2023)
Malus	0.60%	Salt stress reduced the chlorophyll-a and chlorophyll-b contents and increased MDA, POD, and SOD.	Wang et al. (2022)
Wheat	10 g L^{-1}	Salt stress significantly reduced the germination capacity, induced osmotic stress, reduced seedling vigor, seedling growth, and K accumulation, and increased Na accumulation.	Hmissi et al. (2023)
Canola	100 mM	Soil salinity reduced root and shoot growth, chlorophyll contents, RWC, and increased antioxidant activities and synthesis of proline, and threhalose.	Dawood et al. (2024)
Cotton	1.2%	The fresh weight and root vitality of seeding were significantly decreased under salt stress. However, salt stress increase GR, CAT, POD, and SOD activities and accumulation of MDA.	Dong et al. (2023)
Brassica rapa	150 mM	Salinity stress inhibited the growth, biomass, photosynthetic pigments, soluble sugars, and K^+, Ca^{2+}, and Mg^{2+} accumulation and increased Na accumulation, EL, and MDA production.	Zhang et al. (2023)
Alfalfa	100 mM	Salinity stress reduced aerial weight, and root weight, and increased lipid peroxidation, CAT, and POD activities.	Pacheco-Insausti et al. (2023)
Cotton	150 mM	Saline conditions reduced the seedling growth, biomass, and photosynthetic rate and increased membrane damage and Na accumulation, CAT, POD activities, MDA accumulation, and reduced K accumulation.	Fu et al. (2023)
Eggplant	80 mM	Salinity stresses RWC, chlorophyll, contents, fruit yield, and quality of eggplants and increased Na and Cl accumulation.	Mozafarian et al. (2023)

CAT: catalase, GSH: glutathione, ASA: ascorbic acid, NO: nitric oxide, POD: peroxidase, SOD: superoxide dismutase, RWC: relative water contents

Salinity stress with higher concentration of Cl^- and sulfate (SO_4^{2-}) also reduces phosphorous uptake, because of the media's high ionic strength and the Ca±P minerals' low solubility. Potassium (K) is also a vital nutrient for plants, however, in saline conditions, the competition between Na and K is significantly increased. This competition causes the replacement of K by Na and the reduction in K uptake causes a marked reduction in plant growth and development (Hasana and Miyake, 2017; Betzen et al., 2019; Balasubramaniam et al., 2023).

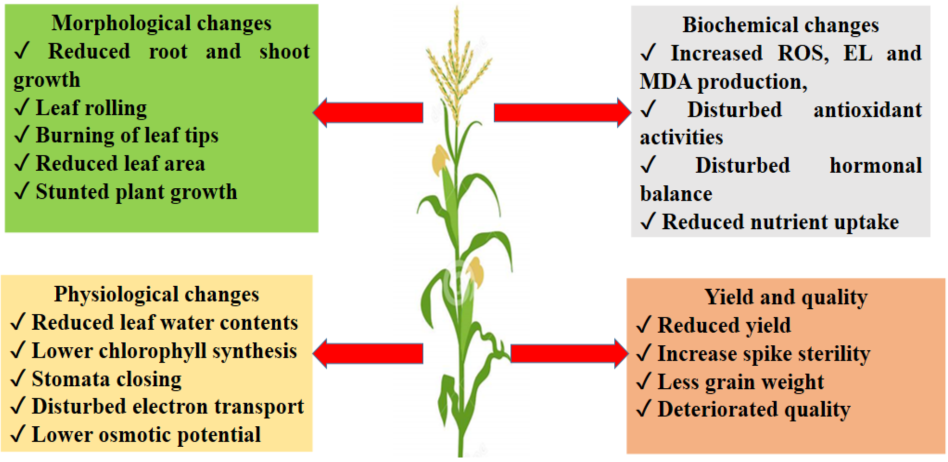

Figure 1. *Effect of salinity stress on growth, morphological, physiological, and biochemical traits of plants*

Besides affecting growth, photosynthesis, and nutrient uptake, SS also harms protein synthesis, cell signaling, and energy metabolism. As a result of the high metabolic expenditure required for plant adaptation, causes a marked reduction in plant growth. The yield reductions and intensity of membrane energy are determined by salinity-induced osmotic stress and salt absorption (Volkmar et al., 1998). The increasing salt concentration under saline soil increases membrane damage by increasing H_2O_2 production and lipid peroxidation (Amombo et al., 2022). This increase in membrane damage leads to the loss of important osmolytes in the form of EL and this aspect is well echoed in many studies (Amombo et al., 2022; Balasubramaniam et al., 2023).

To counter the toxic effects of Ss plants accumulate different osmolytes such as proline, soluble sugars, and GB which help the plants to counter the toxic effects of SS. These soluble solutes serve as an osmoprotectant which maintains osmotic adjustment and detoxifies ROS thus protecting the cellular membranes (Sharma et al., 2019). Glycine-betaine (GB) is an important osmolyte produced by plants in chloroplast and it plays an important role in adjusting the thylakoid membrane therefore, maintaining the plant photosynthetic efficiency (Alasvandyari and Mahdavi, 2018; Zhu et al., 2022). Proline is also an important osmolyte produced by plants in stress conditions and increased proline concentration is considered a hallmark in response to SS (Abdelhamid et al., 2013). Salinity increases the expression of genes (P5CS1, P5CS2, and P5CR) involved in proline bio-synthesis which increases production of proline under saline soils (Nguyen et al., 2013). It is also documented that an exogenous supply of proline reduces the toxic impacts of SS and ensures better growth (Jamil et al., 2018). Soluble sugars also play an important role in salinity tolerance and higher concentrations of soluble sugars protect the soluble enzymes from the toxic effects of SS (Singh et al., 2022). For instance, trehalose (Tre) is an important sugar that enables the plant's reversible capacity of water absorption and it could also protect molecules from osmotic damage (Delorge et al., 2014). Salinity-induced ionic balance negatively affects plants' cellular metabolism, photosynthesis, and root architecture and reduces nutrient uptake.

Salinity stress also increases the accumulation of toxic ions that cause negative impacts on plants. Nonetheless, plants maintain cellular homeostasis to counteract the toxic effects of SS by controlling ionic influx and compartmentalization (Balasubramaniam et al., 2023). Besides this, plants also restrict the Na influence into cells and increase Na exclusion out of cells and maximum Na compartmentalization in vacuole which prevent the toxic effects of salinity (Balasubramaniam et al., 2023). Salinity-induced ROS cause serious damage to plants, though plants have excellent enzymatic and non-enzymatic antioxidant defense systems that help to quench and scavenge ROS (Azeem et al., 2023). SOD is the first defense line against ROS which convert radicals of superoxide radicals into oxygen and hydrogen peroxide (Balasubramaniam et al., 2023). Many authors noted a positive correction between salt tolerance and an increase in antioxidant activities. For instance, the study findings on *A. tricolor* foliage showed that an increase in APX and SOD substantially detoxifies the ROS (Sarker and Oba, 2020; Hussain et al., 2022). MDA production under SS is a sign of membrane damage, however, plants increase antioxidant activities (APX and CAT) which counter ROS and reduce MDA production (Hussain et al., 2022). Another study showed that over-expression of the POD gene (*GsPRX9*) in wild soybeans substantially increases salt tolerance due to increased antioxidant responses (Jin et al., 2019). Anthocyanins are an important group of antioxidants and their accumulation is well-reported in plants in response to SS. The increased synthesis of anthocyanin under salinity stress ensures better plant growth and counter the toxic effects of SS (Van Oosten et al., 2013).

Soil salinity and microbial communities

Salinity stress affects the abundance of the microbes community therefore, it affects their functioning in saline soils. Microbe composition and abundance can differ between saline and normal soils (Chandra et al., 2020) and microbial diversity can also be significantly decreased with increasing salt concentration (Zhang et al., 2019b). The excessive concentration of salts in salt-affected soils also affects the composition of bacteria (Lozupone and Knight, 2007). Different bacteria and archaea also adapt salt in as well as salt mechanisms which neutralize the osmotic stresses and help to withstand the SS (Yang et al., 2016). The composition of the microbial community is also significantly correlated with soil pH and salt concentration (Rath et al., 2019).

The abundance of different taxonomic groups is significantly changed with the increase in salt concentration possibly owing to the sensitivity of taxonomic groups towards stress conditions (Canfora et al., 2014). For instance, maximum *Deltaproteobacteria* abundance was noted in highly saline soils, while maximum abundance of Alpha and Gammaproteobacteria was reported in lower saline soils (Ibekwe et al., 2010). Salinity stress significantly affects the composition of microbial communities as compared to soil pH, temperature, and geographic conditions (Yang et al., 2016).

Plant-microbe interactions

Plants produce various exudates that microbes use as food, and microbes benefit plants by producing various growth and stress-tolerance substances (*Figure 2*). The rhizosphere is rich in microbial diversity and microbes can be found with endo as well as epishere beyond the plant tissues. The microbiota of roots generally moves horizontally, and it comes from a soil environment that contains different microbes like *Acidobacteria*, *Bacteroides*, *Planctomycetes*, *Verrucomicrobiota*, and *Actinobactreia* (Fierer, 2017). Rhizosphere soil contains ten times more microbial communities than bulk soil (Donn et al., 2015). Generally, 1 gram of soil contains >1 million bacterial genomes, and mycorrhizal fungi have been reported to be found in over 200,000 plant species more than 80% are involved in plant growth (Afridi et al., 2022a). The utilization of PGPR proved their ability to increase plant growth and salt tolerance (Ha-Tran et al., 2021). It is documented that PGPR produces ACC deaminase as well as indole-3-acetic acid (IAA), siderophore (Sid), and EPS they also form biofilms and increase N fixation and solubilization of P, thus leading to an increase in plant growth (Bhise et al., 2017).

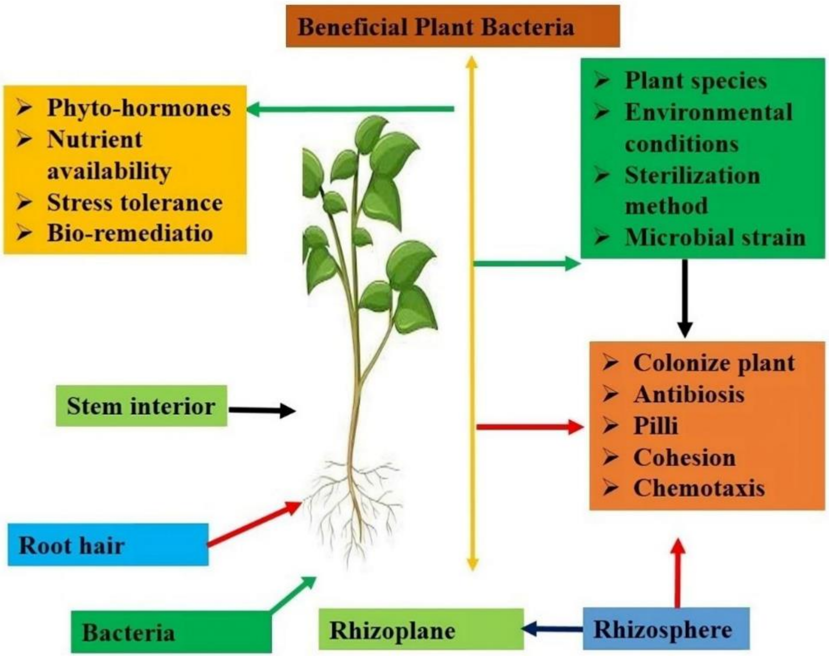

Figure 2. *Interaction of soil microbes with plants and factors affecting the soil microbes*

The phyllosphere is a plant's celestial surface that is nutritionally deficient for the rhizospheric and endospheric microbiota. Plant physiology and microbial composition are also significantly affected by environmental factors. For instance, wind and rain produce temporary changes in the microbiome of the phyllosphere (Lindow, 1996; Bodenhausen et al., 2013). Besides this, plants also harbor diverse microbe communities in different plant organs. For instance, endophytes infiltrate the internal plant tissues leading to the development of endospheric microbiome. AMF and endophytic fungi are considered important endosphere colonizers (Dastogeer et al., 2018; Singh et al., 2020). It is also documented that the population of endophytic has a lower diversity than the microbial community outside the plants (Eid et al., 2019). For instance, some microbes like Pseudomonas can also enter the plant roots which can improve the plant's growth (Mercado-Blanco and Prieto, 2012). Microbes also form intracellular colonization with plants which in turn improve the plant production (Liu et al., 2019).

Endophytes living in the tissues of plants can be isolated after disinfecting the surface of plants (Singh et al., 2020). Plant-friendly bacteria are known as endophytic bacteria and they live within plants and ensure better plant performance under normal and stressful conditions (Lata et al., 2018). For example, *Penicillium* endophytes provide gibberellins to host plants which play an important role in plants under stress conditions (Leitao and Enguita, 2016). Endophytes in the rhizosphere are also known as PGPR, and these bacteria have developed the ability to infiltrate host plants (Santoyo et al., 2021). It is documented that there are more than 300,000 plant species on this planet and they are considered to be hosts of single or multiple entophytes (Ryan et al., 2008). The endophytic bacteria have an appreciable capacity for promoting the host plant growth and they also help to resist the stress conditions confer allelopathic impacts on competing plant species (Cipollini et al., 2012).

Role of PGPR in mitigating salinity effect

The higher concentration of salts induced osmotic, ionic, and oxidative stresses which negatively affect plant growth and development (*Table 2*). The ability of plants to grow without the toxic effects of salinity is referred to as salt tolerance. The use of microbes could be an important way to combat the toxic effects of salinity. PGPB directly and indirectly affects the host plants and subsequently salt tolerance. PGPR has a special mechanism through which they confer salt tolerance in plants. For instance, PGPR produces different hormones such as auxins, cytokinin, and gibberellin and they also produce biofilms and siderophores which help to counter the toxic effects of SS.

Table 2. *The role of different microbial strains in mitigating the salinity stress in various crops*

Plant species	Salinity stress	Microorganism	Mechanisms	References
Cucumber	100 mM NaCl	Acinetobacter baumannii	Improved the growth, and reduced deleterious impacts of salt stress by increasing antioxidant activities	Kartik et al. (2021)
Maize	900 mM NaCl	Bacillus sp. PM31	The plant root and shoot growth, chlorophyll, protein sugars, RWC, and antioxidant capacity significantly increased microbial inoculation.	Ali et al. (2023)
Wheat	EC 13.41 (dS m^{-1})	Bacillus pumilus	Seed inoculation with bacteria improved the root and shoot growth, biomass production, proline, and TSP synthesis, root K and Ca concentration, and activities of POD.	Nawaz et al. (2020)
Wheat	EC 8%	Pseudomonas mendocina	Seed inoculation with bacteria improved the uptake of K, Ca, Mg, and Zn, K/Na ratio, grain weight, and yield.	Ullah et al. (2022)
Wheat	EC 5.14 (dS m^{-1})	Azospirillum lipoferum	The microbial treatment protected the wheat plants against salinity by increasing CAT, POD, SOD activities, and N uptake, and decreasing EL, MDA, and H_2O_2.	Alharbi et al. (2023)
Mung bean	EC 7.81 (dS m^{-1})	Bacillus drentensis	Bacterial inoculation reduced salinity-induced oxidative damages by increasing CAT, POD, and AsA activities, nutrient uptake, and reducing MDA.	Mahmood et al. (2022)
Barley	1000 mM NaCl	Pseudomonas fluorescens	Microbial application improved root and shoot growth, Cl accumulation, germination, and photosynthetic pigments.	Zaib et al., (2023)
Rice	100 mM NaCl	Pseudomonas	Bacterial treatments increased plant height, root length, total dry matter, leaf area, and dry matter accumulation.	Sen and Chandrasekhar (2014)
Pea	EC 8 (dS m^{-1})	Bacillus subtilis	The application of PGPR increased the root and shoot length, pods per plant, pot weight, chlorophyll contents, K uptake, and reduced Na uptake.	Muslim et al. (2023)
Maize	EC 10 (dS m^{-1})	Acinetobacter johnsonii	The bacterial inoculation increased urease, alkaline phosphatase, and dehydrogenase activities, P and N uptake, and CAT, and POD activities reduced MDA production.	Shabaan et al. (2022)

Role of PGPR in improving plant growth under saline conditions

Growth reduction is a common effect of salinity stress, and PGPR improves salinity tolerance via various mechanisms (Bhattacharyya and Jha, 2012). PGPR causes solubilization of nutrients and they increase N fixation, production of hormones, ACC deaminase activity, and siderophores that support plant growth under saline conditions (Mehmood et al., 2021b). For instance, in canola plants, bacteria produced the ACC deaminase which increased salt tolerance by reducing salt-induced ethylene synthesis (Moon and Ali, 2022). Likewise, in groundnut, ACC deaminase produced by bacteria (Pseudomonas fluorescens) enhanced the yield and salt tolerance (Danish et al., 2020). Different authors also found the appreciable potential of Pseudomonas species to counter the toxic effects of salinity. It was found that *P. fluorescens* significantly improved chickpea growth and yield by increasing photosynthetic efficiency and water uptake (Yasin et al., 2018b). Similarly, Upadhyay et al. (2011) also reported the positive impact of *B. subtilis* in increased wheat growth, biomass, yield, and synthesis of proline and soluble sugars (Upadhyay et al., 2011). In another study, Banik et al. (2018) found that excellent antioxidant pigments in *Bacillus* and *Halobacillus* ensured better plant growth (Banik et al., 2018).

Recently, it was reported that *Curtobacterium albidum* improved the growth, chlorophyll concentration, and proline synthesis in rice which protected and stabilized the membranes (Vimal et al., 2019). PGPR not only improves plants' growth but also plays an important role in plants against pathogens. For instance, *Stenotrophomonas maltophilia* can increase the concentration of b-1, 3 glucanases, PAL, PO, and polyphenol oxidase (PPO) against the fungal pathogen (*Fusarium graminearum*) of wheat growing under saline conditions (Singh and Jha, 2017). In another study, it was noted that *Bacillus drentensis* mitigated the adverse impacts of salinity in mungbean by increasing osmolyte synthesis, nutrient uptake, and Na contents (Mahmood et al., 2017). Mungbean plants treated with *Bacillus cereus* increased NPK concentration and proline synthesis which countered the toxic effects of salinity stress (Islam et al., 2016). PGPR also increases the availability of nutrients, soil organic carbon (SOC), and soil enzyme activities which help to counter SS. The current meta-analysis showed that PGPR inoculation increases nutrient acquisition, photosynthetic and counter SS effects, and increases antioxidant activities and osmolyte accumulation (Pan et al., 2019).

PGPR improves nutrient uptake under salinity stress

Salinity stress causes nutritional imbalance in plants which results in a reduction in plant growth. The PGPR linked with the rhizosphere alters the root architecture resulting in improved nutrient and water uptake by the host plant. Further, PGPR also increases the supply of nutrients through N fixation and solubilization of phosphorus which ensures better plant growth (Choudhary et al., 2018). It is documented that P solubilizing microbes produce different kinds of organic acids that reduce the soil pH and this reduction in soil pH enhances phosphate mineral’s solubility (Puente et al., 2004). PGPR also aids legume plants in retaining N and they also help the legumes to fix more nitrogen by improving root nodulation, nitrogenase activity, and leg-hemoglobin content (Abd-Alla et al., 2019).

In salt-affected soils, PGRP also increases the availability of both micro and macro nutrients which maintain the soil fertility and lead to an increase in crop growth (Hafez et al., 2021). The soil bacteria help the host plants to facilitate nutrient uptake and it is well echoed that in saline soils endophytes increase solubilization of Zn, P, K, and fix N and contribute to increasing the plant growth and yield (Santoyo et al., 2016). For instance, Bacillus spp. and *Gracilibacillus* appreciably fix the N and they also produce siderophores and solubilize the phosphate (Mukhtar et al., 2018). Different authors also noted that plants inoculation with bacteria provide better growth and stand establishment in salt-affected soils. For example, Jha et al. (2011) noted that rice seedlings inoculated with *P. pseudoalcaligenes* showed a significant improvement in shoot growth by increasing the synthesis of glycine betaine (Kushwaha et al., 2020). Similarly, *Acinetobacter* sp. ACMS2 and *Bacillus* sp. PVMX4 strains were reported to promote the growth of plants by increasing ACC and IAA production and increasing enzymatic activities (Joe et al., 2016).

PGPR improves phytohormones and osmolyte production to counter salinity stress

PGPR can modulate the production of different hormones like indoleacetic acid (IAA), gibberellic acid (GA), and abscisic acid (ABA) in plants which support root growth and nutrient uptake under SS. Khan et al. (2019) discovered that bacteria (Curtobacterium sp. SAK1) alleviated salinity stress in soybean regulation by regulating IAA, ABA, ACC, and siderophore production. It is well known that ACC deaminase-producing bacteria can convert the plant ethylene precursor ACC to ammonia and -ketobutyrate, lowering ethylene levels under stress conditions. In another study, Ji et al. (2020) noted that *Glutamicibacter* sp. YD01 inoculation regulated ACC concentration, and ethylene production which improved the acquisition of K in rice plants and therefore led to a marked increase in salinity tolerance. Recently, *Kosakonia sacchari* showed appreciable ACC deaminase activity and improved the growth of mungbean plants under saline conditions (Shahid et al., 2021). On the other hand, Kang et al. (2019) discovered that salt-tolerant bacteria (*Leclercia adecarboxylata* MO1) synthesized a significant amount of IAA, sugars, and organic acids, which protected against salinity stress.

The production of ethylene is significantly increased in saline conditions which inhibits root growth (Afridi et al., 2021; Haider et al., 2022). The endophytes with a strong ability to produce ACC deaminase reduce the production of ethylene under saline conditions which reduces the toxic effects of salinity on roots (Del et al., 2020). Many bacterial species secreting IAA have been isolated from the halophyte plants (Navarro-Torre et al., 2017b). Abscisic acid is also an important hormone released by PGPR which improves the salt tolerance in plants (Gerhardt et al., 2017). Microbes also produce different osmolytes in their cytoplasm that maintain cell turgor and improve their survival under SS (Kumar et al., 2020). PGPR promotes osmolyte accretion in the plant cell cytoplasm, which aids in maintaining osmotic balance under SS (Suprasanna et al., 2016). These osmolyte works as molecular chaperones and protect protein integrity, boosting enzyme activities that protect plants against SS (Szabados and Savoure, 2010).

PGPR improves antioxidant activities to counter the toxic effects of salinity

The most common effect of SS is the overproduction of ROS that damages proteins, enzymatic activities, DNA, and membranes (*Figure 3*). However, plants possess an excellent antioxidant defense system to counter ROS and the application of PGRP has been reported to increase antioxidants to induce salt tolerance in plants (Kim et al., 2014; Islam et al., 2016). Rojas-Tapias et al. (2012) found that maize plants treated with PGPR displayed an increase in K^+/Na^+ by increasing K uptake and Na exclusion. Salinity stress increases ROS production (Miller et al., 2010), however, PGPR improves the salinity tolerance either by altering or regulating ROS. For instance, many bacterial species like *Halomonas*, *Kushneria*, and *Micrococcus* have been reported to increase antioxidant activities (CAT, POD, and SOD) which reduces ROS production (Navarro-Torre et al., 2017).

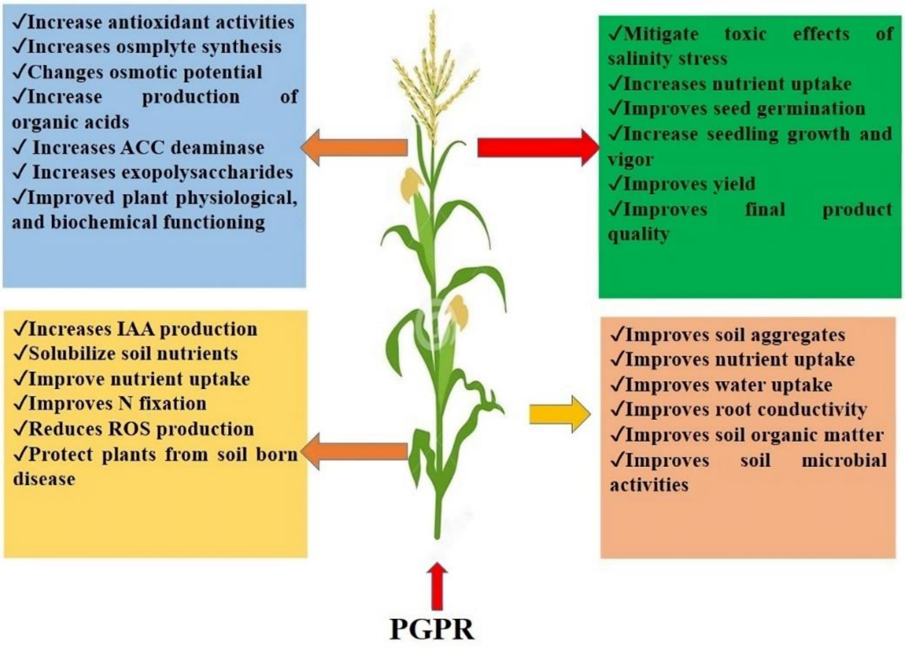

Figure 3. *Role of PGPR in improving plant growth under saline conditions. PGPR improves plant physiological, and biochemical functioning, and soil quality which ensures better plant growth under saline conditions*

Endophytes also activate signaling molecules such as jasmonic acid, salicylic acids, and H_2O_2 which increases salt tolerance by increasing antioxidant activities (Ren and Dai, 2012; Wang et al., 2015). In a study, Redman et al. (2011) found that inoculation with PGRP decreases the production of ROS by increasing antioxidant (CAT, POD, and SOD) activities. In another study, it was found that root colonization by *Piriformospora indica* increases ascorbic acid and antioxidant activities in barley roots. Furthermore, this PGRP improved growth and reduced salinity-induced lipid peroxidation. The potential of *Trichoderma longibrachiatum* was tested in wheat crops under saline conditions and a remarkable increase in APX, CAT, POD, and SOD activities was reported which countered the toxic effects of salinity by ROS scavenging.

PGPR improves gene expression to counter the toxic effects of salinity

PGPR altered the plant's response to salinity by changing the gene expression (*Table 3*). ACC deaminase synthesis, IAA, and other secretions produced by bacteria work as signaling molecules that activate the plant stress responses (Yan et al., 2014). The tomato seedlings treated with *Pseudomonas putida* UW4 showed up-regulation of Toc GTPase genes which increased the synthesis of proteins involved in stress responses

(Yan et al., 2014). In another study, Bharti et al. (2016) found maize plants treated with Kocuriarhizophila Y1 showed an increase in NHX gene expression which lowered the Na ionic strength by removing it from cells and absorbing it on vacuoles and increasing salt tolerance (Bharti et al., 2016). Increased salt tolerance was also observed in maize and *Arabidopsis* plants treated with *Serratia liquefaciens* KM4, *Bacillus amyloliquefaciens* SQR9, and B*urkholderiaphytofirmans* (El-Esawi et al., 2018). It is also reported that Bacillus flexus (KLBMP 4941) increases the activation of GB transporters genes, Na^+/H^+ anti-porters genes, and K^+ transporter genes which can help to counter the toxic effects of SS (Asaf et al., 2018b). Moreover, *Puccinellia tenuiflora* plants inoculated with B. subtilis (GB03) also showed a reduction in Na deposition which was linked with increased expression of PtHKT1 and PtSOS1 (Niu et al., 2016). Moreover, in wheat crops, *DietzianatronolimnaeaSTR1* modulated the signaling of ABA by up-regulating the ABA-responsive genes (TaABARE), and stress-responsive genes (Yao et al., 2010).

Table 3. *The role of bacterial gene expression in improving the salt tolerance in plants*

Plant species	Bacterial species	Genes	Effects	References
Soybean	Pseudomonas simiae	HKT1	The production of organic-induced salt tolerance by up-regulating genes results in less Na accumulation.	Yang et al (2009)
Maize	Bacillus megaterium	ZmPIP	The bacteria gene expression regulated the water potential and improved the transpiration rates and plant performance.	Marulanda et al. (2010)
Maize	Pantoea agglomerans	ZmPIP2-1	The increased gene expression protected the plants from oxidative damage by decreasing NaCl accumulation.	Wang et al. (2017)
Tomato	Pseudomonas putida	Toc GTPase	The increase in gene expression up-regulated the chloroplast apparatus and promoted protein production.	Yan et al. (2014)
Maize	K. rhizophila Y1	ZmGR1	The plant growth and antioxidant defense system was up-regulated which reduced ROS production.	Li et al. (2020)
Pea	Escherichia coli	PsFDH	The gene over-expression increased the chlorophyll contents and salt tolerance.	Joshi et al. (2009)
Tomato	Stenotrophomonas rhizophila IS26	YojM	The increased gene expression improved SOD, CAT, and POD activities to counter the toxic effects of salinity.	Dif et al. (2022)
Sugarcane	Enterobacter roggenkampii E	gpx, osmC	The bacterial genes increased POD and glutathione activities.	Guo et al. (2020)
Wheat	Arthrobacter protophormiae	TaCTR1, TaDRE2	Increased IAA concentration and decreased ABA production which reduced harmful effects of salinity.	Barnawal et al. (2017)

It is also documented that the PGRP causes the activation of ethylene and drought response genes which help mitigate the adverse impacts of SS (Barnawal et al., 2017). The organic acids are considered as a volatile compound and they can reduce Na concentration by down-regulating expression of HKT1 in roots and increasing its expression in shoots. For instance in *Arabidopsis* plants *B. subtilis* increased production of organic acids resulting in improved plant growth under salinity stress (Yang et al., 2009). Moreover, it was also noted maize plants treated with *B. megaterium* showed a significant regulation of zmPIP2-1 gene followed by zmPIP1-1 and zmPIP2-5. Salinity stress also caused an overexpression of zmPIP1-1 and zmPIP1-2 in maize roots which was further increased by B. megaterium which helped the plant roots to uptake more and cope with hazards of SS (Gond et al., 2015).

PGPR produces exopolysaccharide (EPS) from biofilms to counter the toxic effects of salinity

PGPR also makes bio-films under saline conditions, and these bio-films are made of extra-cellular polymers which protect bacterial cells to survive under saline conditions. For instance, *Bacillus pumilus* FAB10 showed an excellent capacity to form a bio-film which improves the wheat growth under saline conditions by increasing antioxidant activities and plant physiological traits (Ansari et al., 2019). Further, inoculation with EPS-producing bacteria also protects the roots of plants from the toxic effects of salinity by providing an exopolysaccharides protective layer (Awad et al., 2012). EPS functional grounds can bind N and inhibit the influx of Na in plant tissues from soil (Amna et al., 2019) which leads to improved plant growth under saline conditions (Kasotia et al., 2016; Amna et al., 2019). EPS-producing bacteria not only improve plant performance but also improve the soil structure of salt-affected soils by increasing soil aggregation. It has been documented EPS producing bacteria showed an increased tolerance to drought and salinity owing to improved soil structure (Qurashi and Sabri, 2012). In saline conditions, EPS increases water availability and acquisition of nutrients which ensures better plant growth (Etesami and Beattie, 2018).

El-Ghany et al. (2020) used EPS-producing bacteria and melatonin (MT) in a field study to test the impacts of fava beans. They found that seed priming with MT and inoculation with EPS-producing bacteria effectively improved the growth, seed yield, water relations, and photosynthetic efficiency in saline conditions. In a pot study, Awad et al. (2012) also noted a significant increase in root and shoot growths and photosynthetic pigments with inoculation with EPS-producing bacteria (*Azotobacter chrococcum*). In another study, it was found that the EPS-producing Pseudomonas PS01 strain increased the expression of stress-responsive genes in *Arabidopsis* (Chu et al., 2019). The recent findings of Shultana et al. (2020) showed that rice plants treated with *Bacillus tequilensis* showed a significant improvement in nutrient uptake, photosynthesis, stomata conductance, and transpiration rates. Moreover, Costa-Gutierrez et al. (2020) also noted a marked increase in growth traits, and biomass production of maize and soybean plants after inoculating with *Pseudomonas putida* KT2440. Recently, Fatima and Arora (2021) also reported that sunflower plants after inoculating with *P. entomophila* showed an increase in NPK and Zn solubilization and improved growth and yield under saline conditions.

Microbial formulations for salt-affected soils

The use of PGPR is considered a friendly and cost-effective way to mitigate the adverse impacts of salinity stress. In recent times different microbial bio-formulations are also being used to mitigate the toxic effects of salinity. Bio-formulations are microbial formulations with suitable carriers that remain stable during manufacturing, as well as storage and transportation. The carrier used in the production of microbial formulations must allow for easy dispersal while also providing a suitable environment for PGPR. If the formulation is used for seed treatment, the carrier must have good adhesive properties to adhere to the seed. A good carrier is also capable of delivering the correct number of cells (Nehra and Choudhary, 2015).

Different microbes showed promising results in improving plant performance under SS. Rhizogold (RG) a multi-strain microbial formulation showed appreciable results for mitigating SS impacts on crops (Shahzad et al., 2017). The use of bio-fertilizers improves plant growth and development, according to the authors. Similarly, different bio-inoculations (BIST, ErMalxami, Subtin, and Fitobisol) also remarkably increased the germination, root and shoot growth, and yield of cotton under saline conditions (Pulatov et al., 2016). Likewise, in another study, Cyanobacterial bio-formulation effectively improved the yield of pearl millet and wheat crops (Nisha et al., 2018). Likewise, Damodaran et al. (2013b) used a bio-formulation containing *B. pumilus*, *B. thermogenesis,* and *T. harzianum* to substantially improve the growth and yield of vegetables, bananas, and gladiolus in saline soils. Moreover, some bio-formulations also showed effective results in improving microbial activities, soil fertility, and productivity (Damodaran et al., 2013a).

Conclusion and future directions

Salinity stress is a serious concern across the globe and it needs dire attention for ensuring crop production on a sustainable basis. The plant-associated microbes can protect against salinity stress by increasing nutrient uptake, osmolyte and hormone synthesis, and antioxidant activities. Besides this microbes also release different extra-cellular compounds and they form different bio-films which can help to counter the toxic effects of salinity. The microbes can also improve the soil properties which can help to counter the toxic effects of salinity. These PGPRs can also survive in salt-affected soils which makes them an effective practice to improve crop production. The microbial use for increasing salt tolerance is well studied, however, still studies are needed to explore the mechanism of release of extra-cellular compounds by PGPR. Field studies are also needed to evaluate the role of different PGPR and microbes-based bio-inoculation in mitigating the adverse impacts of salinity. Besides this more research is required to understand the mechanism of bio-formulations in mitigating toxic effects of salinity, this will provide new insights to design better bio-formulations to remediate salt-affected soils to achieve food security.

The role as well as responses of particular microbial groups toward the salinity are poorly studied, therefore, more extensive studies are needed on this aspect. The use of integrated techniques up to genetic levels on the plants and microbial interaction in saline conditions can help to induce salt tolerance and it will also help to unfold the mechanisms of salinity stress mitigation. Further research is needed on rhizosphere microbes and their secondary metabolites, owing to the fact these metabolites are responsible for microbial interactions with plants. Besides, this use of multi-strain formulation can provide better results to mitigate the adverse impacts of salinity as compared to a single strain. The increased shelf life of PGPR productions, and their non-toxic nature and tolerance to adverse conditions will also help to mitigate adverse impacts of salinity stress. The use of PGPR-based bio-formulation will also protect plants from different pathogens and it will also improve and trigger different biological promotion effects growth. Moreover, field studies are also direly needed to investigate the PGPR inoculation with plants for commercial use of these microbes.

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