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Review

Current Advances in Plant Growth Promoting Bacteria Alleviating Salt Stress for Sustainable Agriculture

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Abstract: Humanity in the modern world is confronted with diverse problems at several levels. The environmental concern is probably the most important as it threatens different ecosystems, food, and farming as well as humans, animals, and plants. More specifically, salinization of agricultural soils is a global concern because of on one side, the permanent increase of the areas affected, and on the other side, the disastrous damage caused to various plants affecting hugely crop productivity and yields. Currently, great attention is directed towards the use of Plant Growth Promoting Bacteria (PGPB). This alternative method, which is healthy, safe, and ecological, seems to be very promising in terms of simultaneous salinity alleviation and improving crop productivity. This review attempts to deal with different aspects of the current advances concerning the use of PGPBs for saline stress alleviation. The objective is to explain, discuss, and present the current progress in this area of research. We firstly discuss the implication of PGPB on soil desalinization. We present the impacts of salinity on crops. We look for the different salinity origin and its impacts on plants. We discuss the impacts of salinity on soil. Then, we review various recent progress of hemophilic PGPB for sustainable agriculture. We categorize the mechanisms of PGPB toward salinity tolerance. We discuss the use of PGPB inoculants under salinity that can reduce chemical fertilization. Finally, we present some possible directions for future investigation. It seems that PGPBs use for saline stress alleviation gain more importance, investigations, and applications. Regarding the complexity of the mechanisms implicated in this domain, various aspects remain to be elucidated.

Keywords: alleviation; mechanisms; PGPB; plant; salinity stress; soil

1. Introduction

The worldwide enhancement of both human population and the associated environmental deterioration has the unfortunate influence that global food manufacture might soon become unsatisfactory to nourish all of the world's people. It is therefore crucial to increase farming productivity within the next few decades [1]. On the other hand, in the natural environment, plants are constantly exposed to various abiotic and biotic factors, which may affect their increase and yield [2]. Stress is described as any external abiotic (salinity, water, heat) or biotic (herbivore) constraint that restricts the level of photosynthesis and decreases a plant's capacity to transform energy to biomass [3]. Especially, abiotic factors are main constraints for global food security, food quality, and crop productivity [4].

Salinity is recognized to affect almost one fourth of world cultivable land, a main cause of desertification [5]. It is responsible for the degradation of 10 million ha of world farming per year [6], influencing about 1 million ha in the European Union, mainly in the Mediterranean countries. Various salt ions in the soil, that are dissoluble in water like chloride (Cl^-), sodium (Na^+), magnesium (Mg^{2+}), potassium (K^+), bicarbonate (HCO_3^-), sulfate (SO_4^{2-}), carbonate (CO_3^{2-}), and calcium (Ca^{2+}) may cause salinization [7]. Salinization is a natural process in semiarid and arid zones and may additionally be stimulated by anthropogenic practices. It significantly influences land fertility [8], and therefore comprises a huge effect on food security and economy at local, regional, and global levels [7]. Although plant tolerance to salinity varies with species and even varieties as well as with biotic and abiotic factors, the growth of most of the plant cultures is negatively influenced by salinity [9,10]. Excess accumulation of salts in the root zone often deteriorates the soil properties, viz. physical, chemical, and biological to such an extent that crop production is adversely affected [11]. In addition, excessive salinity in soil suppresses growth, decreases species diversity, and alters the community composition of plants; however, the effect of salinity on soil microbial communities is poorly understood [12].

Some of the microorganisms that live in close combination with the plant roots ensure a significant function in improving plant growth [13], and/or in stress mitigation of crops cultivated under salinity conditions [14]. Plant growth-promoting bacteria (PGPB) may be active through a diversity of processes [15] including the regulation of the transcription of various genes and cellular communication through quorum sensing [16], and mainly by production of various secondary metabolites [17]. For instance, through the production of exopolysaccharides (EPS), indole acetic acid (IAA), nitrogen fixation, and P-solubilization [18]. PGPB may form symbiotic relations with plants and improve their performance in the face of salinity stress [19,20]. Moreover, PGPB are an environmentally sustainable tool to mitigate the impacts of salinity on crop yields [2].

2. Implication of PGPB on Soil Desalinization

Soil hosts an enormous number of bacteria (often between 10^8 and 10^9 cells per gram of soil) but only about 1% of those bacteria are culturable [21]. Soil microorganisms belong to various groups of fungi, archaea, bacteria, and protozoa. Some of these microorganisms are recognized for their capacity to tolerate and improve plant salinity tolerance [22]. To date, several bacterial genera, like *Streptomyces*, *Azospirillum*, *Clostridium*, *Alcaligenes*, *Bacillus*, *Rhizobium*, *Pseudomonas*, *Thiobacillus*, *Serratia*, and *Klebsiella* are recognized as PGPB working under saline conditions [23]. They are being tested under field trials applied as a one species inoculant or as part of microbial consortia with very encouraging results [24].

They may alleviate salinity stress by resynchronization stress-stimulated physiological modifications in plants through different mechanisms [25,26]. Additionally, PGPB promoting impact during stress conditions has also been proposed to be advantageous for crop effectiveness, dry weight of root and shoot and root length, and the plant height [27]. The various ways in which microbes stimulate plant growth and alleviate stress responses include efficient nutrient mobilization in the soil, protection from phytopathogens, and improvement of soil structure and quality by sequestration of toxic heavy metals. Microbes can also aid degradation of various xenobiotic compounds [28]. The primary action of PGPM (plant growth promoting microorganisms) is investigated as their role in maintaining osmotic balance, ion homeostasis, and turgor pressure to combat the toxicity of salinity in plants [19]. The salinity-resistant microbial community improves the health of salinity-impacted soil, maintains ecological functions, and sustains and promotes the growth of plants [29]. Hence, the application of beneficial stress-tolerant microbes not only helps in improving the microbial community structure but also in enhancing plant and soil health under salinity. Further research will be required to reveal the hidden mechanisms of stress-tolerant microbial diversity [30]. Moreover, various researchers have demonstrated that the associations between rhizospheric microbes and stressed plants help the plants to adapt to their microenvironment [11].

3. Impacts of Salinity on Crops

All crops may be killed by salt solutions if the amount is excessive. The salinity of a field is such that individuals of a specific crop die, although most farming interests (and most research) are focused on the impacts of sublethal salinities. A wide spectrum of physiological and biochemical alterations of plants are induced by salinity, which causes lowered water potential in the soil solution, ionic disequilibrium, specific ion effects, and a higher accumulation of reactive oxygen species (ROS) [31]. Generally, the consequence of salinity was initially involved with NaCl, as these ions are the most frequent reason for salinity in plants that have been established not in requirements of survival, nevertheless, in its impact on plant increase [32]. Notably, salinity may reduce crop productivity [32]. Biomass yield is adversely associated and rapidly reactive to osmotic stress whereas the potency of the subsequent membrane injury is determined by the level of salt fixation and the capacity to compartmentalize the salts in diverse tissues [33]. In addition, salt influences density and germination of plant cultures, and also crop development, decreasing yield, and, in the particularly difficult cases, causing widespread plant death, decreasing the attribute of the usable water and restricting absorption of nutrients [34]. It decreases grain productivity and seed set by affecting pollination. Seed germination in glycophytes is severely inhibited under salinity due to both osmotic stress and ionic toxicity stress [35]. In addition, in [36], several crops such as barley, cotton, bean, rice, and wheat reduce their productivity considerably during saline stress. Similarly, earlier investigation, in [37], mentioned a significant impact of salinity rates, varieties, and the correlations among yield and yield constituents in rapeseed. For instance, in [38], in tomato the exhibition of salinity stress results in Na⁺ aggregation in style, ovaries, and anther intermediate layers that generated an improved survival of the plant, level of flower abortion, and diminution of pollen number. In addition, several main field crops like rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), sorghum (*Sorghum bicolor* L. Moench), maize (*Zea mays* L.), sugarcane (*Saccharum officinarum*), and cotton (*Gossypium hirsutum*) show adverse reaction against salinity [39].

4. Salinity Origin and Its Impacts on Plants

Salinity is a cumulative process over time and may have a natural origin (Figure 1) or may be due to anthropogenic practices [39,40]. Different types of mineral salts (Na⁺, K⁺, Cl⁻, Mg, Ca, etc.) at the origin of salinity in the soil and can prevent impacts from several sources such as climatic factors (erosion and evaporation), and manufacturing. Hemophilic PGP (Plant growth promoting) bacteria present in soil can alleviate salt stress, stimulate vegetal nutrition and growth through enhancement of various vital plant mechanisms.

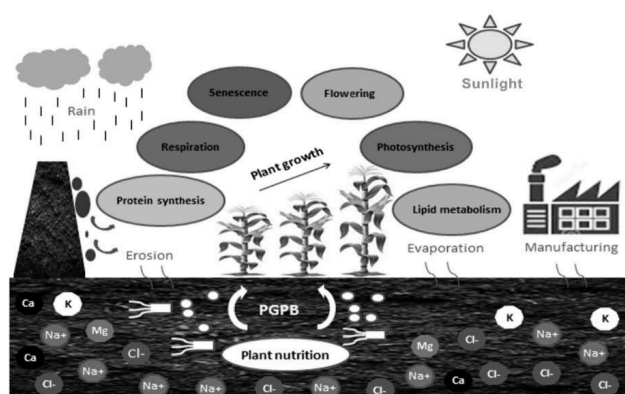


Figure 1. Origin of salinity in the soil and the main impacts of salicylic acid produced by PGPB (plant growth promoting bacteria) on plant primary metabolism.

Salinity is a consequence of inorganic salt solubilization, dust deposition, unbalance between precipitation and evapotranspiration rates, or an increased capillary infiltration of saline underground

water [41]. Salinization affects plant development when salt concentrations build up in the root zone [40]. To maintain productivity under saline conditions, crops need higher water and fertilizer inputs, which probably enhances soil salinity in the end [5], extending the zone affected by secondary salinization [42].

Salinity is a two-phase stress to plants comprising a rapid osmotic phase followed by a slower one related with ion accumulation [43]. During the first phase, salinity elicits disorder of water and ionic homeostasis increasing the energetic costs of cellular metabolism [44,45] affecting, among others, nutrient uptake [46,47], photosynthesis and respiration [48], lipid metabolism and protein synthesis [49,50], phytohormone production, oxidative stress, gene expression, and long distance transport [51], which affects plant seed germination and seedling survival, as well as plant phenotype. The plant osmotic response of salinity stimulates physiological modifications in the plant that are similar to those generated by water stress [52]. Apart from its influence in plant biomass accumulation, salinity may interfere in the process of biomass partitioning between shoots and roots [44].

Plant resistance or tolerance to salinity involves the root capacity to restrain Cl^- and Na^+ uptake or to induce their efflux, while maintaining the adequate uptake rates of essential ions such NO_3 and K^+ [51], which may be associated with the accumulation of compatible solutes such as proline and soluble sugar able to participate in the osmotic balance [45–53]. With varying salt concentrations, transcription of genes responsible for osmoprotectant synthesis may express differentially in some HT-PGPR (Halo-tolerant plant growth promoting rhizobacteria). For example, in *Bacillus. amyloliquefaciens* FZB42 trehalose and proline synthesis were found to be differentially expressed at 0 and 100 mM NaCl concentrations facilitating stress adaptation in *A. thaliana* [54].

4.1. Seed Germination

Plants exhibit great variability toward salinity resistance [55,56]. Many seeds, including those of *L. cossonianum*, present their highest germination rate in distilled water and are extremely sensitive to salinity [57,58]. Salinity delays the germination process in a process that is dependent on abiotic and biotic factors such as light, temperature [59,60], and plant microbiome [61]. Overall, salt stress adversely influenced seed germination; both osmotically via decreased water absorption or ionically via the accumulation of Cl^- and Na^+ causing toxicity impact and an imbalance in nutrient uptake [61]. It affects the sowing increase of plants by less or slow mobilization of preserve foods, suspending the division of cells, injuring and enlarging hypocotyls [62]. For instance, germination percentage in Lettuce (*Lactuca sativa*) showed substantial reduction with cumulative salinity up to 14.1 dS m^{-1} NaCl. The essential time for germination likewise increased with increasing salinity levels. The seedling growth was meaningfully repressed [63]. Furthermore, the study conducted by Bagwasi et al. [64], showed that salinity influenced seed germination of different wheat and barley cultivars. Although, all cultivars showed a reduction in total germination percentage, with increasing salinity levels from EC 0 to EC 20 dS m^{-1} . Wheat cultivars outperformed barley cultivars at EC levels 0, 4, 8, 12, and 16 dS m^{-1} .

4.2. Primary Metabolism

While a plant endures abiotic stress, a variety of genes are switched on or off, leading to changes in many metabolites and proteins, responsible for triggering salinity stress defense [65].

4.2.1. Photosynthesis

Photosynthesis is a major essential physiological process and is potentially influenced by salinity at all stages [66,67]. However, disentangling the cause–effect nexus between photosynthesis inhibition and decline in sink demand due to salinity is controversial. Many roads lead to photosynthesis inhibition by salinity including increased oxidative stress-related impacts [68], changes in chlorophyll concentration [69,70], and osmotic stress. The water deficit associated with salinity induces a reduction in leaf cells turgor and the concomitant stomata closure, decreasing stomatal

conductivity (gs) and the intrinsic CO₂ concentration, which leads to reduced carboxylation rates by RuBisCo (ribulose-1,5-bisphosphate carboxylase) [69]. Moreover, the response of the sesame (*Sesamum indicum* L.) plants to salinity stress was analyzed by estimating the levels of photosynthetic enzymes activity. Photosynthetic rate, activities of RuBisCo, and sucrose phosphate synthase (SPS) decreased with increasing salinity. In addition, the activities of Dichlorophenol Indophenol (DCPIP) reduction were decreased [71].

4.2.2. Respiration

Respiration and mitochondrial metabolism ensure a central function in establishing plant salinity resistance like ion removal, osmotic resistance, and ROS (reactive oxygen species) responses [72]. Salinity has been shown to contribute to increased respiration levels in a large variety of plant species [73,74]. In some cases, the increase in the respiration rate is related with changes in the plasmalemma composition and permeability, higher protein turnover [75], and higher energetic costs associated with ion homeostasis. Nevertheless, respiration itself can be inhibited by salinity through distinct sensitivity of the enzymes involved in the respiration pathway towards salinity [76,77]. For example, salt treated wheat leaves exhibit higher respiration rate and extensive metabolite changes. The activity of the tricarboxylic acid (TCA) cycle enzymes pyruvate dehydrogenase complex and the 2-oxoglutarate dehydrogenase complex were shown to be directly salt sensitive. Multiple lines of evidence showed that the γ -aminobutyric acid (GABA) shunt was activated under salt treatment [78].

4.2.3. Senescence

Under long-period exposition to salinity, plants undergo ionic stress, which may contribute to premature senescence of mature foliage and hence a decrease of the required photosynthetic zone to maintain biomass accumulation and growth [79,80]. Salt-stimulated senescence is claimed to be due to ionic pressure of high Na⁺ quantities and nutritional deficiencies like a decreased cytoplasmic K⁺: Na⁺ proportion [81,82] causing chlorosis and necrosis in mature leaves by destruction of protein production and disruption of enzyme function [83]. In rice leaves, salinity affects several senescence-related variables including membrane permeability, fluorescence of chlorophyll a, and leaf concentration of chlorophyll and protein. The anticipation of increased activity of senescence characteristic enzymes such as isocitrate lyase (ICL) can be observed under saline conditions [84,85]. The involvement of ICL, a central enzyme of the glyoxylate cycle [86], in the crossroads between salinity and senescence was demonstrated in an experiment showing that the AtICL knockout tomato (Aticl mutant without ICL activity) was much less tolerant to salinity than the isogenic wild type [85].

4.2.4. Flowering

Flowers produced higher P and Zn comparably to the control crops, while the targeted vegetation was exposed to either salinity levels. Salinity reduced the composition of Mg in flowers at 100 mM NaCl concentration. Interestingly, 50 mM NaCl salinity generated Ca in flowers approximately three times relative to the control of crops not treated with salt [87]. In addition, phenological findings of bud flowering and forming were found in plants handled with high amounts of NaCl occurred in contrast to control plants [88]. For instance, in [89], with rising salinity rates, days to flowering were expanded, however, in rapeseed rice varieties days to maturation were reduced. Additionally, early flowering in plants species decreased dry matter, enhanced root, shoot ratio as a response to salinity stress [90]. On the other side, plant tolerance to salinity stress requires biochemical modifications in the metabolism of nitrogen and carbon including improvements in proline and polyamines [91]. Production of polyamines in bacteria and plants starts with the production of putrescine, diamine, from decarboxylase ornithine (ODC) or arginine decarboxylase (ADC). During vegetative growth ADC activation was correlated with smaller internodes, necrotizing and (in one line) rapid flowering [92]. Additionally, differences in flavonoid, polyphenol, and pro-anthocyanidin compositions have been

observed in *C. tinctorius* flowers during salt stress at two improvement phases including full and post flowers formation [93].

4.2.5. Protein Synthesis

Many plants respond to salinity through modifications in their protein status. Salinity may interfere with the regulation of protein activity, protein synthesis, and even with the availability of the substrates needed for protein synthesis (namely N). Cellular suspensions of *Nicotiana tabacum* and *Citrus* sp. plants sensitive to salinity have distinct proteomic profiles under saline and non-saline conditions [94]. The disturbance of protein synthesis tends to be a major cause of Na^+ damage [82]. Similarly, high Na^+ concentration or $\text{Na}^+:\text{K}^+$ ratio may disturb several enzymatic mechanisms. K^+ stimulates and/or regulates the activity of more than 50 enzymes and is a critical component of the protein synthesis as it attaches tRNA to ribosomes [95].

Salinity inhibits root nitrate uptake [96] and thus the availability of N needed for protein synthesis [97,98], as it was evidenced by the decrease of free amino acid concentration in *Glycine max* roots under salinity [99]. However when grown under saline conditions tolerant plants may increase the concentration and/or the activity of key proteins that contribute to salt resistance reactions, such as heat shock proteins (HSPs), ribulose-1,5-bisphosphate carboxylase (RuBisCo), antioxidative enzymes, late embryogenesis abundant (LEA) proteins, glycerate dehydrogenase, glucose-6-phosphate 1-dehydrogenase, glutamate synthase, NADPH-producing dehydrogenase, and glutamine synthetase [100].

4.2.6. Lipid Metabolism

The fine tuning of plant lipid profile is a key tool in crop adaption to environmental changes, but the process by which lipid contouring modulates a respond to salt stress is not clear [101,102]. Salinity causes structural changes in the lipid composition of the plasma membrane, like increasing the degree of free fatty acid saturation and enhancing concentration of free sterols, leading to a reduction in cellular membrane fluidity [103]. For example, the lipid composition of the root plasma membrane of *Phaseolus vulgaris* grown under salinity differed in phospholipid groups, saturated and unsaturated fatty acids, and sterol groups from that of plants grown under non-saline conditions [104]. Furthermore, the intensity of salinity induced a considerable decrease in overall lipids derived from the black cumin seed [105].

Salinity induced oxidative stress in *C. roseus* cells, as seen by the rise in lipid peroxidation, increased lipoxygenase (LOX) function, following antioxidant enzyme activation [104]. Plant response to salinity may decrease the concentration of sterol ester, oleic acid, and free fatty acids, and reduces that of linoleic acid ($\text{C}_{18}\text{H}_{32}\text{O}_2$) and triacylglycerol [106]. Under salinity, the expression of the genes involved in the lipid metabolism may suffer changes [107]. Novel discoveries have greatly expanded the importance of autophagy during lipid metabolism. An emerging model suggests that autophagy can operate in various aspects of lipid and membrane recycling. Current evidence also highlights the complexity of this system, given that autophagy is required for energy-producing organelle maintenance under stress conditions. This is of paramount importance because the removal of damaged and potentially ROS over producing energy organelles can circumvent cell death and promote lipid catabolism [108].

5. Impacts of Salinity on Soil

The remediation of salt-affected soils is difficult and costly [109], if not impossible. Globally, salinity has a negative effect on crucial soil mechanisms like respiration, degradation of residues, denitrification, nitrification, root function, and soil biodiversity [110], by affecting crucial soil enzyme activities during stress that were implicated in soil degradability, nutrients cycling, organic matter composition, and intercellular metabolic responses of living organisms [34]. The activity of soil enzymes tends to decrease with salinity, despite the rate of inhibition being variable according to the enzyme and the salinity level [111]. Salinity and, in particular, sodium contributes to soil degradation, particularly of clay agglomerates,

which generally leads to structure loss, reduced hydraulic conductiveness, disrupted air and water flow, erosion, and run off [112].

Salinity may lead to higher soil moisture content; however, it significantly decreases the osmotic potential of the soil solution, resulting in lower water absorption by the plants and other living organisms [113]. A soil may be identified as salt-impacted when white salt-crusts and/or salt-spots are present on/in the bare soil; there is persistent or sustained waterlogging following rainfall; crumbling and road erosion are visible; surface water is unpalatable to animals and humans; and the appearance of salt crystals under extremely saline lands [114].

Salinity affects the distinct functional characteristics (biological, chemical, and physical) making soil recovery very difficult. In contrast with other current alternatives, organic fertilization seems to be extremely efficient as a mitigation solution to the problems outlined above [115]. For instance, saline-sodic soil has many negative characteristics including high values of electrical conductivity (EC), sodium adsorption ratio (SAR), and exchangeable sodium percentage (ESP) [116]. Additionally, high levels of soil salinity and sodicity can limit the activities of enzymes and microbes [117].

5.1. Soil Biological Activity

Salts are an important component of soil, and certain salts (e.g., nitrates, sulfates, phosphates) are critical for soil fertility [118]. Salt-impacted soils contain high concentrations of soluble salts in both the micro and macro-pores [119]. Therefore, soil salinity inhibits soil respiration and C mineralization, as demonstrated by lower the CO₂-C evolution rates of saline soils in comparison to non-saline soils [120]. Similarly, the osmotic potential of the soil solution increases and thus minimizes the potential plant and microbial water availability [121]. Saline soils have higher permeability to soluble salts and lower potential assimilation rates of nutrients like N [122]. Additionally, the absorption of nutrients is inhibited by ion competitiveness and higher pH, whereas the weak soil structure generated by high sodium levels adversely affects soil water quality and plant growth [123].

5.2. Soil Microbial Function and Diversity

In good conditions, 1 g of soil may incorporate 600 million bacteria appertaining to 15,000 or 20,000 distinct species. These amounts reduce to 1 million bacteria in desert soils comprising between 5000 and 8000 species [124]. This soil microbiota plays a vital role in preserving and/or improving the consistency of the soil by controlling the degradation of organic matter and the supply of nutrients, facilitating the production of macro-aggregates [125]. However, soil microbiota responsible for the formation and maintenance of soil aggregates are vulnerable to environmental changes because of their wide area to volume ratio, highly permeable cell membrane, and high turnover rates resulting in a quick reaction to nutritional supply variations [126].

It is evident that salinity decreases microbial activity, microbial modifications, biomass, and the structure of the microbial community [127,128]. Furthermore, knowing the microbial group structure and its role in saline soil is a key ecological goal, as it will help to explain the biological regulatory processes for the nutritional cycles in saline soil [129]. Many other studies concentrate on the examination of the effects of salinity on microbial communities [130,131]. Salinity has an adverse effect on quantity, distribution, structure, and functionalities of the microbiota [132]. Additionally, salinity was observed to lower soil microorganism's biomass and microbial growth rate [133,134]. The disruption of the symbiotic relationship between plant and microorganisms is another damaging consequence of salinity. For instance, disruption in plant interaction with bacteria is induced by deterioration in proteins implicated in the anchoring and adsorption phases of the symbiotic interactions between bacteria and plant roots [135]. Salinity often has an adverse impact on biotransformation of the biogeochemical cycles like mineralization of N and C [129]. Microbes are engaged in nitrification, oxidation, ammonization, nutrient absorption, and other processes that contribute to soil organic matter nutrient cycling and degradation [136].

Fungi are usually considered to be less salinity tolerant than prokaryotes. However, this claim is only because only prokaryotes are tolerant to extreme levels of salinity [137]. However, in fact, the total number of soil fungi is significantly reduced with increased levels of salinity. The total number of Actinobacteria and bacteria also decreases under salinity, but only at salinity levels above 5% [138]. The low osmotic potential characteristic of soil salinity declines hyphae production and spore germination, and induces modifications in the mycelium morphology [139]. Archaea is one of the microbial groups reported to increase its relative abundance in extremely saline ecosystems. However, the functional relevance of the association between plants and archaea is still unknown, since only a few reports of the association between archaea and plants (rice, maize cress, *Abutilon*, *Suaeda nudiflora*, and *Sporobolus*) have been established [140,141].

6. Halophile PGPB for Sustainable Agriculture

In the rhizosphere, plant–microorganism relationships are indicators of plant health, production, and soil fertility. Particularly, plant growth-promoting bacteria (PGPB) are microorganisms that could also promote plant increase and prevent plants from infection and abiotic factors via a wide range of processes. Those PGPBs that develop more intimate interactions with plants, like the endophytes, may be more effective in plant growth improvement [16]. Usage of PGPB as an important part of farming activity is an innovation whose time has arrived [1]. More particularly, some halophilic bacteria were proved able to alleviate plant salt stress, improving the development and productivity of crop production under salinity [142].

PGPB represent a possible solution to mitigate salinity-induced plant stress [143]. The impact of five plant growth stimulating halotolerant bacteria on wheat growth [142] revealed that bio-formulation of these halotolerant bacterial strains can improve salinity stress (80, 160, and 320 mM) in wheat seedlings, resulting in a 70% improvement of root length comparatively to negative controls. In addition, variations in the bacterial community formulation with the soil salinity were observed, and attention is growing in experiments regarding functional interactions between plants and microbes that lead to salt stress tolerance [25]. The use of microorganisms for saline soil restoration may be an environmentally sustainable, safer, and more efficient method, as the halophilic microorganisms have the potential to eliminate salt from saline soils [144]. Such microbes also provide exceptional prototypes for studying the stress resistance, adaptation, and response processes which might consequently be integrated into agricultural crops to cope with the pressures caused by climate modification [145].

6.1. Biofertilization

PGPB can successfully be manipulated in the agro-farming system as alternative strategies to control most of the stated abiotic stresses faced by crops and to increase their yields and would lead to the minimal use of synthetic fertilizers [146]. Arbuscular mycorrhizae fungi and plant growth promoting bacteria are beneficial microbes in the soil which provide assistance to plants in many ways. Directly they are concerned with hormones and organic compounds synthesis while indirectly they reduce salinity stress. They can be employed in agriculture as biofertilizers [147]. Improved plant growth under saline soils has been attained with the use of PGPB [148]. Significant increase in growth attributes of rice plants with *Bacillus amyloliquefaciens* as compared to non-inoculated control plants under salinity stress [149]. *Bacillus licheniformis* SA03 inoculated with *Chrysanthemum* plants grown under saline-alkaline conditions significantly decreased saline-alkaline stress in plants along with augmented biomass and survival rates via mediating cellular ABA (abscisic acid) levels [150].

6.2. Biopesticides

Many strains of PGPB have been found to be positively linked with suppressing diverse plant pathogens (both in the rhizosphere and above ground) by producing antagonistic metabolites and enhancing the immunity potential of crops to pathogenic stress [151]. Moreover, Nadeem et al. [152] have comprehensively provided evidence about the growth promotion and biocontrol potentials of

AMF and PGPR in agriculture. Egamberdieva et al. [153] found that *Pseudomonas chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 reduced the *Fusarium* infection by 23% and 14% under non-saline conditions and by 42% and 25% under saline conditions, respectively. Tewari and Arora [154] reported EPS (exopolysaccharides) and salicylic acid producing *P. aeruginosa* PF23EPS+ showed biocontrol against *M. phaseolina* up to 500 mM NaCl.

6.3. Bioremediation

The concept of using PGPB to facilitate bioremediation of contaminated soil has only recently emerged. For example, Pacwa-Płociniczak et al. [155] proposed that two petroleum hydrocarbon-degrading *Rhodococcus* spp., with plant growth promoting traits, are likely to be good candidates for the phytoremediation of petroleum hydrocarbon contaminated sites. In recent years, the ecological functions of halophyte symbiotic microorganisms, including the growth promotion of host and crops, enhanced salt tolerance, and joint phytoremediation of contaminated soil, have been clarified by increasing studies [156,157]. As bioremediation agents, *Streptomyces* (in particular halophiles), participate in alleviating the toxic effect of xenobiotics on plants, using the strategies previously mentioned. *Streptomyces* are widely used in the remediation of soils contaminated with different pollutants. Moreover, they are studied as PGP in salt-affected soils, where they provide plants with salt resistance to face this major problem for agriculture [158,159].

Table 1 illustrates various roles of PGPB in enhancing yield and growth of different plants/crops under salt stress.

Table 1. Various roles of PGPB (Plant growth promoting bacteria) in enhancing yield and growth of different plants/crops under salt stress.

Crops	PGPB	NaCl (mM)	Beneficial Effects	Reference
Lettuce	<i>Azotobacter chroococcum</i>	50 and 100	Enhanced the radicle lengths and plumule of germinated seeds	[160]
Sunflowers	<i>Pseudomonas fluorescens</i> <i>CECT 378T</i>	100	Fresh weight significantly improved by more than 10%; K ⁺ /Na ⁺ proportion	[161]
Strawberry	<i>Bacillus</i> sp.	35	Ameliorated fruit productivity, leaf water amount, ionic constitution, and membrane permeability	[162]
Wheat	<i>Serratia</i> sp. <i>SL-12</i>	150–200	Improvement in plant increase, as determined by factors like root/shoot length, dry/fresh weight, and augmentation of photosynthetic pigment	[163]
Maize	<i>Trichoderma harzianum</i> <i>Th-6</i>	50–150	Improves water composition and stomatal conductance, elevated pigment amounts, and increases photosynthetic performance	[164]
Barley	<i>Azospirillum brasilense</i> <i>NO40</i>	250 and 350	Mitigate photosynthetic pigments in the roots and shoots, photosynthetic effectiveness, transpiration level, stomatal conductance, agglomeration of Mg, P, K, Fe, and Ca	[165]

7. Mechanisms of PGPB (Plant Growth Promoting Bacteria) towards Salinity Tolerance

The key mechanisms involved in PGPR (plant growth promotion rhizobacteria) salinity tolerance include specific membrane or cell wall structures, draining ions out of the cell through salt efflux, or modification of their intracellular environment through accumulation of nontoxic organic osmolytes, and adapting enzymes and proteins to function under high solute ion concentrations [25]. The ability of PGPB to improve crop yields during salt stress includes many direct and indirect pathways such as ferrous iron minerals and inorganic phosphate solubilization, exopolysaccharides and biofilms synthesis [166], production of phytohormones [167], increased ACC (1-aminocyclopropane-1-carboxylate) deaminase activity [168], and nitrogen fixation [169]. The Figure 2 shows PGPB (Plant growth promoting bacteria) salinity resistance strategies and mechanisms of plant growth improvement under salt stress. PGP bacteria may survive high salinity via three main mechanisms (pumping out the cell, intracellular adaptation processes, and cell wall construction). These bacteria stimulate plant growth during salt stress by means of several mechanisms including

phytohormones production, amelioration of nutrients uptake, ACC deaminase, P solubilization, EPS synthesis, biofilms formation, and N₂ fixation.

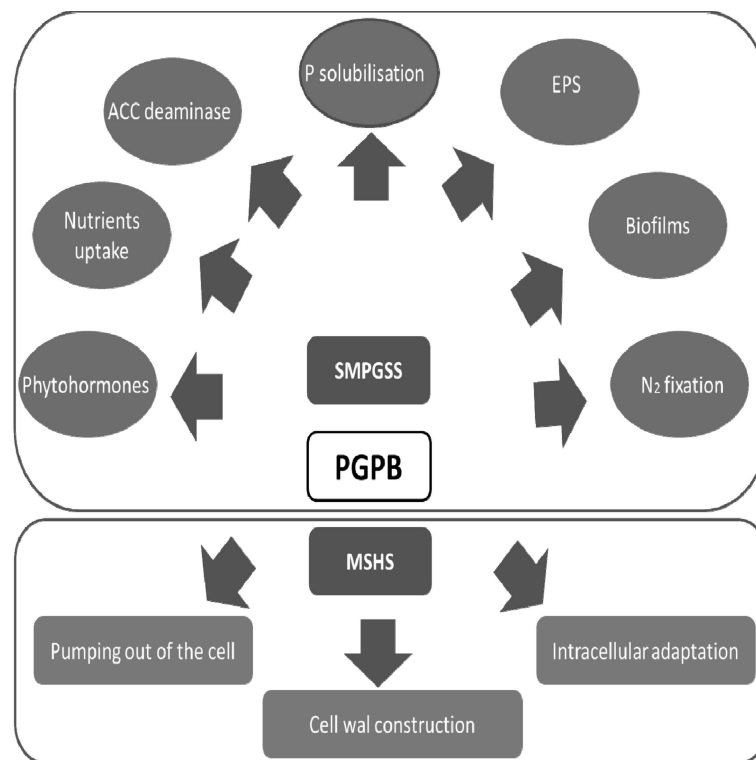


Figure 2. PGPB (Plant growth promoting bacteria) salinity resistance strategies and mechanisms of plant growth improvement under salt stress (SMPGSS: stimulation mechanisms of plant growth under salt stress; MSHS: mechanisms surviving high salinity, PGPB: plant growth-promoting bacteria, EPS: exopolysaccharides).

7.1. Direct Mechanisms

7.1.1. Nitrogen Fixation

Nitrogen is an essential plant nutrient [170]. In particular, legumes are influenced by salt stress frequently related to a lower growth of the host plant, weak symbiotic formation of root-nodule microorganisms [171] with a decrease of the nitrogen-fixing capacity [172]. Symbiotic associations of plants with soil microbes such as nitrogen-fixing bacteria (*Frankia* and *Rhizobia*) and mycorrhizal fungi may have a positive impact on plant salt stress tolerance [173]. Additionally, stress-tolerant rhizobial strains may help legume plants to preserve the level of N fixation and plant productivity [174]. Salinity tolerant *Rhizobium* bacteria are more efficient in promoting plant growth under saline conditions [175]. Consequently, it is advisable to select indigenous rhizobial strains that are efficient even under salinity [176]. For example, *A. nilotica* inoculated with a salinity resistant *Rhizobia* strain was capable of maintaining an N-fixing rate of almost 70% at 12 dS/m compared to its highest fixing rate (2 dS/m) [177]. The simultaneous treatment of cowpea seedlings with arbuscular mycorrhizal fungi (AMF) and N-fixing bacteria like *Azospirillum brasilense* enhanced plant N concentration by 230% in comparison to 151% and 94% in seedlings treated individually with N-fixing strains or AMF at 7.2 dS/m salinity [178]. It has been shown that the association of stress-tolerant varieties and stress-tolerant rhizobia can lead to synergistic benefits in legume plant development under saline conditions [179].

7.1.2. Phosphate Solubilization

Phosphorus (P) is another essential nutrient needed by living organisms for transduction, biosynthesis of macromolecules, energy transfer, respiration, and photosynthesis [180]. Most of the soil phosphorus is found in the form of insoluble phosphates and phytate, which cannot be used by plants [181]. Environmental factors are likely to affect the organization and efficiency of phosphate-solubilizing microorganisms, particularly under conditions [182], namely the efficiency of soil bio weathering of phosphates [183]. Recently it was highlighted that many microorganisms (*Pseudomonas*, *Erwinia*, *Achromobacter*, *Enterobacter*, *Flavobacterium*, *Serratia*, *Mycobacterium*, *Bacillus*, *Escherichia*, and *Agrobacterium*) improve their inorganic phosphate solubilization rates when NaCl is present in moderate concentrations [184]. However, this beneficial effect of moderate saline conditions is counterbalanced by the fact that salinity diminished the phosphorus adsorbed to soil particles and inhibits phosphate absorption by plant roots [185].

Some PGPB are able to solubilize phosphate salts at high salinity levels (10% NaCl) [186]. It is possible that this efficiency of PGPB under high salinity is related to the fact that the production of organic acids responsible for phosphate solubilization (2-ketogluconic, gluconic, oxalic, acetic, citric, succinic, and malic acids), are also responsible for a local decrease of the alkaline pH usually associated with saline soils [187,188]. For instance, the isolate *Pseudomonas stutzeri* SGM-1 could grow at increasing salt concentrations up to 12% w/v NaCl with wide temperature and pH ranges. *Pseudomonas stutzeri* SGM-1 exhibited diazotrophy by growing on nitrogen free media along with expression of other PGP traits such as phosphate solubilization. The amelioration of the salt stress to the *Cicer arietinum* plant by isolate's bio-fertigation was observed up to 300 mM of NaCl [189]. A novel halo-tolerant strain *Kocuria rhizophila* Y1 was isolated from maize rhizosphere soil. This strain tolerated up to 10% NaCl and showed growth promoting traits like phosphate solubilization [190].

7.1.3. Production of Phytohormones

Phytohormones play a crucial role in plant development and responsiveness to stress [191]. External phytohormones may help to improve crop productivity by improving biotic and abiotic stress tolerance [192]. Phytohormones like salicylic (SA), abscisic acid (ABA), and jasmonic acids (JA) also play key functions in plant response to salinity [193,194]. Particular enzymes that facilitate seed germination and plant development are also responsible for enhancing the concentration of certain phytohormones such as gibberellins (GAs) and indole-3-acetic acid (IAA) [195]. IAA is the major natural auxin with a well-documented capacity to control certain aspects of plant performance [196].

IAA is involved in cell division and extension; and root initiation. The regulation of these processes by IAA is negatively affected by saline conditions. Declining concentrations of IAA in the seedling roots of constrained plants result in reduced and slower germination rates [197]. Additionally, IAA can promote plant defense, for instances application of exogenous IAA decreased tomato infection by *Fusarium oxysporum* f. sp. *radicis-lycopersici* [198]. For example, the IAA producing ability under salt stress was assessed was observed to be 250 ± 0.1 , 220 ± 0.1 , and 200 ± 0.1 $\mu\text{g/mL}$ for *Rheinheimera* sp., *Rhizobium* sp., and *Bacillus subtilis*, respectively [199].

Phytohormones, e.g., Gas and IAA, are considered as growth hormones, which enhance the number of root tips, as well as root and shoot length resulting in improved nutrient absorption and thus improved plant health during stress and non-stress conditions [200]. It is recognized that phytohormones synthesized by bacteria may contribute to determining plant phenotype [201]. In addition, PGPB modulates ABA biosynthesis and ABA regulated signaling pathways, which can lead to increased salt-stressed crop production. Halotolerant *Dietzia natronolimnaea* STR1 stimulated salinity (150 mM NaCl) tolerance in rice seedlings through regulation of the ABA signaling cascade [24]. *Novosphingobium* sp. and *Pseudomonas putida* are reported to decrease salinity stress in citrus seedlings by enhancing leaf IAA concentration and decreasing accumulation of root chloride under salt stress [202]. Phytohormone signaling cascades influence osmotic equilibrium and other processes of salt resistance and control adaptation of plants to salinity [197,203,204]. Auxin-producing root-colonizing bacteria

can provide additional auxin to the rhizosphere, and can help root development during stress, while maintaining leaf growth [205].

7.1.4. Exopolysaccharides and Biofilm Formation

In many salt tolerant bacteria, the formation of exopolysaccharides (EPSs) is a strategy for growth, adherence to solid areas, and survival of adverse conditions. In particular, the synthesis of exopolysaccharides by these bacteria can also lead to stress reduction, in addition to improving their salinity-condition survival and competence [206]. Certainly, they have a defensive character: EPSs, which generate a layer around a cell, provide powerful defense towards elevated salinity [207]. EPSs are the most crucial component of extracellular matrix, representing 40–95% of bacterial weight [208]. They are located on microbial cellular surfaces where the cells are preserved by stabilizing membrane organization toward unfavorable environmental stresses. They are mainly formed by large organic macromolecules; polysaccharides, along with smaller uronic acid and protein percentages [209]. Microorganisms to protect themselves against ionic toxicity and desiccation form polysaccharides, most of them are in the ionic form contributing to chelate and sodium ions. This decreases the toxicity and concentration of such ions in the rhizosphere, rendering the soil ideal for root proliferation [54–210].

Increased exopolysaccharides generation in response to salt stress favors biofilm formation [211,212], contributing towards plant adaptation to salinity [213]. In addition, biofilms are formed on specific surfaces, such as roots and soil particles, contributing to reinforce soil structure and physicochemical characteristics [214,215]. The fact that *Pseudomonas anguilliseptica* SAW 24 exhibited the maximum PGPB effectiveness at its maximum biofilm formation capacity confirms the relation between biofilm formation and PGPB effectiveness under saline and non-saline conditions [215]. Halophilic microorganisms can form biofilm and accumulate EPS at increasing salt stress. EPSs promote bacterial colonization of plant roots and soil particles, and they can eventually be added to soil to improve its structure and, consequently, to improve plant growth. In a long-term vision, alleviation of derelict soil, improved crop yield, and restoration of mangrove diversity are possible by mechanistic use of EPS-producing halotolerant microorganisms [216]. For instance, Fathalla [216] showed that biofilm formation and EPS-production by *Az. chroococcum* significantly contribute to soil fertility and improve plant growth.

7.1.5. Enhancement of Plant Nutrient Uptake

The excessive uptake and respective accumulation of ions may result in toxicity. Salinity is particularly associated with high Na^+ , Cl^- concentrations, the persistence of excessive concentrations of these ions in the soil may disturb ion balance in soil solution, and uptake by the plant roots [217]. High sodium and chloride concentrations in the soil can create Na/K and Na/ Ca_2 unbalances in crop plants responsible for increased susceptible to osmotic stress and lower yields [218]. Especially, high concentrations of Na^+ in the soil solution inhibit K^+ , N, and Ca^{2+} uptake [219]. Plant growth-promoting bacteria also release/increase the availability of mineral elements like Cu, Fe, Mn, Zn, etc., to plants by chelation and acidification of soil [220]. For example, potassium has a significant role in the growth and development of the plant. To achieve maximum yield, K is needed in adequate quantities ($50\text{--}300\text{ kg ha}^{-1}$) by all crops. However, most of the K of soil is not directly available for plant uptake. Moreover, K availability to plants decreases due to salinity stress. In this situation, K-solubilizing bacteria (KSB) are an effective tool to fulfill the K requirement of crops [221].

PGPB enhance crop development and thereby increase the availability of mineral nutrients to plant roots [222]. For example, PGPBs from *Rhizobium* and *Serratia* genus were shown to be able to increase the nutrient absorption of lettuce growing under different soil salt concentrations [222,223], and several isolates of *Azospirillum* sp. and *Pseudomonas* sp. were shown to improve the development and biomass of canola plants by ameliorating essential nutrients uptake under saline conditions. There is now increasing recognition that the use of PGPB could enhance plant resistance to adverse nutrient deficiency [224]. Although, PGPB functions in nutrient availability and stress mitigation are

emerging areas of farming that are not yet well established; it is accepted that they are a potential tool to improve productivity and sustainability in many areas of the world [225].

7.1.6. Osmolytes Accumulation

Under salinity, a higher fraction of the cellular energy deviated towards the synthesis of osmolytes is able to defend the cells from osmotic fluctuations [226]. In response to osmotic stress induced by high concentrations of NaCl, bacteria may reprogram their gene expression and synthesize specific stress proteins [227]. In some halophilic bacteria, the internal amount of organic osmolytes can reach 1 M under salt stress and has a significant function in lowering the T_m (Temperature of Melting) of DNA and stabilizing the double helix [228]. Consequently, bacterial cells accumulate compatible solutes, like amino acids, sugars, and quaternary amines, which prevent degenerative processes and improve cell growth under harmful osmotic conditions [229]. They host various groups of compounds comprising soluble sugars like trehalose, sucrose [230], celllobiose, maltose, turanose, palatinose, and gentiobiose [231]. In addition, sucrose, glycine, betaine, and proline are among the osmolytes greatest investigated and that are accumulated during salt stress in a number of plant species regrouping halophytes [232]. Notably, compatible solutes exert their influence by modifying the solvent structure and/or slight modifications in the dynamic characteristics of the protein, rather than by altering the protein structure itself [233]. Such osmolyte accumulations preserve turgor pressure and balance the different macromolecular structures towards the physiological drought stress caused by salinity [234]. These organic solutes can be generated in the cytoplasm where they help to maintain turgor and preserve enzymes and cell organelles from deterioration or dehydration [235].

7.2. Indirect Mechanisms

7.2.1. ACC Deaminase

Some microorganisms possess the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase that transforms 1-aminocyclopropane-1-carboxylic acid (the immediate precursor to ethylene biosynthesis in higher plants) into ammonia and α -ethylene chetobutyrate instead of ethylene [236]. Additionally, as the enzyme ACC deaminase breaks the ethylene substrate ACC, which is transformed into alpha-ketobutyrate and ammonium, it supplies the microorganisms with N [237]. PGPB such as *Rhodococcus*, *Variovorax*, *Alcaligenes*, *Bacillus*, and *Ochrobactrum* have been identified to synthesize ACC deaminase [238], and have been shown to improve plant nodulation under salinity [239]. Recent findings on the synergetic functioning of ACC deaminase and other bacterial mechanisms of salt stress tolerance, such as trehalose accumulation, are also established [240].

ACC deaminase based PGPB can also reduce the harmful impacts of environmental stress and enhance crop resistance through multiple processes including improvement of mineral solubilization, phytohormone synthesis, leaf area raising, nutrient absorption, enhanced antioxidant enzyme activity, and soluble protein and chlorophyll concentration [241]. Direct demonstration for such processes derives from the observation that *Pseudomonas* sp. *acdS* mutants UW4 (ACC deaminase minus) lost the capacity to stimulate canola root extension during gnotobiotic growth [242], and that canola plants inoculated with the mutant are not able to develop under salinity [243].

Salt tolerant PGPBs producing ACC deaminase have impacts on many biochemical characteristics of plant cells, including production of biocompatible solutes, membrane stability, and the synthesis of photosynthetic pigments during salinity stress [244]. For instance, Jaemsaeng et al. [159] demonstrated that the strain *Streptomyces* sp. GMKU 336 developing ACC deaminase might improve rice development and salt tolerance by reducing ethylene concentration, scavenging ROS, and preserving ion homeostasis. Biomass and root length of maize plants grown under saline conditions increase in plants inoculated with *P. fluorescens* possessing ACC deaminase [242]. During abiotic stress, rhizobacteria endowed with ACC deaminase activity may ameliorate plant development by controlling ethylene production [245]. Enhanced ethylene synthesis due to exogenous use of 1-aminocyclopropane-1-carboxylic acid (ACC)

or salinity may reduce the root development [246], and subsequently increase plant performance. Similarly, supplementation of legume crops with ACC deaminase-synthesizing rhizobia isolated from saline soils boosted nodule construction [247]. The halophilic bacteria *Microbacterium* sp., isolated from rhizosphere of rice, is another strain that revealed ACC deaminase function [248].

7.2.2. Induced Systemic Resistance

Induced systemic resistance (ISR) is the increased protective ability produced by a plant towards a large range of plant pathogens following root microbial colonization [249,250]. Besides jasmonate and ethylene, other microbial substances like O-antigenic side chain of the microbial outer membrane protein lipopolysaccharide, pyoverdine, flagellar proteins, β -glucans, chitin, salicylic acid, and cyclic lipopeptide surfactants have all been identified to operate as signals for the stimulation of systemic tolerance [1]. On the other hand, plants establish tolerance in reaction to pathogen invasion, insect attack, colonization by microorganisms or after processes, but this mediated condition is reflected by the activation of “dormant” immune responses reflected in reaction to external interactions of insects, pathogens, and other invaders [251]. For example, bacteria belonging to taxa such as *Bacillus* and *Pseudomonas* sp. have been recognized to stimulate tolerance to pathogenic fungi and bacteria [252]. Plant inoculation with *Serratia marcescens* strain CDP-13 diminished the intensity of the infection caused *Fusarium monaliformiae* and *Fusarium graminearum*, which demonstrated its potential to generate induced systemic resistance in target plants of wheat (*Triticum aestivum* L.) during salt stress (150–200 mM) [233].

7.2.3. Ethylene

Plants, against various stress factors [253], produce ethylene. Ethylene ensures a fundamental function in plant development in a plethora of ways. Ethylene is associated with seed germination, root development (beginning and extension repression), leaf abscission, inactivation of mycorrhiza and plant relationship, and fruit ripening [254]. Ethylene additionally serves as a signal transducer for the detection of salt stress [255]. Accumulation of ethylene in reaction to abiotic stress prevents root development and, eventually, plant growth [256]. Salinity-induced ethylene accumulation caused by high production of 1-aminocyclopropane-1-carboxylic acid (ACC) hinders rice plant growth and development. Nevertheless, ACC deaminase may alleviate salt stress and high ethylene production in rice cultivars under salinity stress [257]. Another crucial enzyme in ethylene biosynthesis is ACC-oxidase (ACO). Maize plants under salt stress have demonstrated enhanced ACO activity as compared to plants under normal condition. Application of PGPR resulted in a significant reduction in ACO activity; *Bacillus safensis* NBRI 12 M-treated maize plants have exhibited maximum reduction which is consistent with the low ethylene production under salt stress [258].

8. PGPB Inoculants under Salinity Can Reduce Chemical Fertilization

While the production of genetically engineered and salt-tolerant varieties, resource management methods, synthetic fertilizers, etc., are cost-intensive and have damaging consequences on humans and the environment, the use of PGPB seems to be a viable option [158–259]. Recently, the use of advantageous halophilic microbes has generated interest in sustainable and environmentally friendly farming [14], with the consequent increase in the exploitation and utilization of microbial fertilizers worldwide [260]. In particular, these microorganisms have multiple characteristics of plant development and these effective and potential microorganisms can be used as biofertilizers to improve soil health and crop productivity for sustainable farming [260]. It is estimated that the market share of biofertilizers will achieve USD 1.66 billion by 2022 and will rise to a CAGR (compound annual growth rate) of 13.2% in 2015–2022 [261].

Several methods have been used to mitigate the impact of soil salinity on crops: the application of plant growth regulators, the selection of salt resistant cultivars, and the treatment of seeds with halophilic rhizobacteria [262]. The use of biofertilizers can also minimize the impact of salinity on crops. A biofertilizer may be characterized as a formulated commodity incorporating one or more microbes

that improve plant nutrient capacity (and increase and productivity) both by replacement soil nutrients, rendering plant nutrients most available, and/or enhancing plant nutrient accessibility [5]. Many other innovations have been involved in increasing salt resistance in plant cultures, along with PGPB to alleviation of salinity stress. Such chemicals' use could be decreased/substituted by P-solubilizing, nitrogen-fixing, and K-solubilizing/mobilizing microorganisms (NPK) as biofertilizer environmentally friendly advancements [8]. The use of microbes in wheat and maize may minimize salt stress effects by about 50% [263]. The most effective solution to improve productivity and yield in salinity-impacted regions is predominantly the use of PGPB as inoculums in cultivation to mitigate salt stress. The great opportunity for investigations concerning crop salinity resistance is actually their capacity to be associated with PGPR [264].

9. Conclusions

Salinity is a great threat for agriculture by affecting soil, microorganisms, and plants throughout their development cycle, from germination to maturation. Moreover, salinity may influence different vital processes in plant such as photosynthesis, respiration, senescence, and flowering. Particularly, PGPBs show a great capacity for saline stress alleviation mainly because of their resistance, adaptability, and a huge variability of the mechanisms involved in this process. Several investigations and experiments have demonstrated that the PGPB is a potential alternative to chemical fertilizers, biopesticides, and bioremediators under salt stress. Additionally, the most important PGPBs progress to date was the elucidation of various molecular mechanisms involved in plant microorganism interactions, in different plants and their utilization efficiently as bioinoculants in soil salinity mitigation. Recently, a genotypic approach was adopted through the characterization of different salinity tolerance implicated genes.

In the future, we recommend using soil autochthonous microorganisms that were mentioned in a number of investigations to be more efficient in soil salinity bioremediation. That may remediate the problem of survival and durability of PGPB in soil. Additionally, synergetic effects through the combination of hemophilic plants (phytoremediation) to PGPB seem to be very promising in soil salinity mitigation. The challenge of host specificity can be determined by adopting a multidisciplinary approach like proteomic, meta-transcriptomic, meta-genomic, etc. For reducing commercial formulation cost, traditional fermentation techniques can be used in small farming systems. Low price fermentation substrates like compost may be developed.

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