

Review

Plant-Growth-Promoting Bacteria Mitigating Soil Salinity Stress in Plants

Stefan Shilev 

Department of Microbiology and Environmental Biotechnologies, Agricultural University—Plovdiv,
12 Mendeleev Str., 4000 Plovdiv, Bulgaria; stefan.shilev@au-plovdiv.bg

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Abstract: Soil deterioration has led to problems with the nutrition of the world's population. As one of the most serious stressors, soil salinization has a negative effect on the quantity and quality of agricultural production, drawing attention to the need for environmentally friendly technologies to overcome the adverse effects. The use of plant-growth-promoting bacteria (PGPB) can be a key factor in reducing salinity stress in plants as they are already introduced in practice. Plants having halotolerant PGPB in their root surroundings improve in diverse morphological, physiological, and biochemical aspects due to their multiple plant-growth-promoting traits. These beneficial effects are related to the excretion of bacterial phytohormones and modulation of their expression, improvement of the availability of soil nutrients, and the release of organic compounds that modify plant rhizosphere and function as signaling molecules, thus contributing to the plant's salinity tolerance. This review aims to elucidate mechanisms by which PGPB are able to increase plant tolerance under soil salinity.

Keywords: plant-growth-promoting bacteria; salinity; halotolerant; phytohormones; nutrients; sustainable agriculture

1. Introduction

Global food needs are growing significantly, in line with population growth, raising a number of nutrition issues as well as the need for new approaches and actions. Climate change raises a number of questions for the coming decades and furthers uncertainty on how to deal with these questions and how to provide food. Rising temperatures, declining freshwater supplies, and the increasing frequency of extreme events such as floods, fires, and drought, require an integrated approach, joint action, and indepth research to overcome and adapt. As one of the most important factors, soil salinity occurs all over the world, causing diverse effects on soil biota and soil properties. Salinity is a major problem in agriculture, reaching about 20% of cultivated lands and more than 30% of the irrigated ones [1]. Crops have a very diverse response to soil salinity, which is basically related to their ability to survive and to produce a satisfactory amount of yield while growing in salinity conditions. Soluble salts aggravate soil fertility, causing diverse negative effects on plant health [2]. Soil electrical conductivity (EC) concentrations of up to 0.7 dS.m^{-1} do not lead to damage in crop plants, but when it is more than $2.5\text{--}3 \text{ dS.m}^{-1}$, the yield decreases dramatically [3].

Soil microbes possess the ability to modify the rhizosphere and thus can ameliorate its deleterious effects on plant growth and development under stressful conditions. The field method is the most acceptable method to justify the ability of a population or consortium to improve plant development in real conditions. Nowadays, the introduction of selected microbes in soil and, especially, in soil rhizosphere is often found as an approach for field application [4,5]. It is clear that rhizosphere bacteria interact with the plant roots, exchanging different molecules. Plant roots excrete exudates and signal molecules until 40% of their carbon is fixed photosynthetically; thus, plants select or modify the microbial consortium in the rhizosphere. Exudates are very diverse, and their type depends on the

specific plant species and ecosystem, stage of development, or soil biota. [6]. Previous studies have demonstrated that PGPB alleviated the negative effects of salinity on the growth of tomato, pepper, canola, sunflower, and cotton [4,7,8].

Problems related to the cultivation of agricultural crops, expressed as stressors, have led to a number of scientific developments. Publications related to this area in one of the major abstract and citation databases worldwide, such as Scopus, have shown increasing research work done during the last few years. Those devoted to general stress have reached more than 3000 documents in the last decade, and publications specifically targeting salinity and the use of PGP microorganisms are also growing, albeit at a slower pace, reaching about 32% of the total (Figure 1a). At the same time, the distribution of the type of documents shows an increase in reviews, books, and book chapters dealing with soil salinity and the use of PGP microorganisms (Figure 1b).

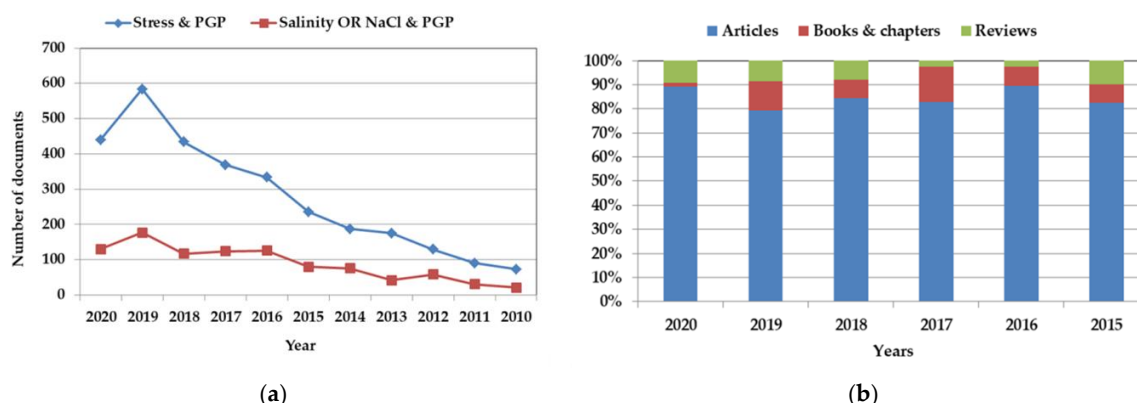


Figure 1. Publications featuring the use of plant-growth-promoting (PGP) microorganisms: (a) in stressful conditions and, particularly, salinity for the last 10 years; (b) distribution of publications by type of document, including, in particular, salinity. Source: Scopus; search parameters: “stress” AND “plant growth-promoting”; “salinity” OR “NaCl” AND “plant growth-promoting”. The search was performed in August 2020.

Despite the gradually increasing number of review papers dealing with the role of PGPB in the attenuation of salinity stress to plants [5,9–17], the need for these kinds of documents has increased due to the rapid development of knowledge in the field. Most of the papers discuss the damage produced by salinity to plants and the general mechanisms that describe the bacteria as plant-growth promoters. There are not many documents summarizing the exact mechanisms by which PGPB alleviate salinity stress.

This review focuses on the recent scientific findings on the role of PGPB in alleviating plant growth and development under soil salinity.

2. Soil Salinity-Induced Harmful Effects on Plants

Fertile agricultural soil is able to offer the plant all the necessary environmental and nutritional conditions for its growth and successful development, having, as a result, sustained and consistent yield of high quality. In contrast, in saline soils, the concentration of soluble salts increases to certain levels that deteriorate plant growth through diverse adverse effects. The definition was given in the middle of the 20th century by Richards [18], and it says that the saline soils are those that have an electrical conductivity higher than 4 dS.m^{-1} at 25°C . The presence of different kinds of soluble salt ions in the soils (anions: chlorides, sulfates, nitrates; cations: sodium, potassium, magnesium, calcium) is called salinization [19]. The salinization occurs in two ways: *naturally* or *primary*, when the soils are supplied by salts as an innate characteristic, including salt lakes or scalds formation, seawater influence, and the release of soluble salts of rocks and minerals, and *artificially* or *secondary*, by anthropogenic activities such as chemical contamination, inappropriate crop rotations, excessive irrigation, flooding, and inadequate

drainage [20]. Soil salt concentration also depends on the soil type: there is low accumulation capacity in sandy soils and high affinity in clay loamy soil because sodium ions bind to negatively charged clay particles. Generally, saline stress is considered one of the most severe stresses affecting living and nonliving environments, aggravated by climate change as salinity and water are very closely linked. It can be exacerbated as a consequence of drought, especially in arid and semiarid areas, representing a quite important and widespread problem [9,21].

The effect of soil salinity depends on plant sensitivity, salt kind and concentration, agronomic practices, and the existence of additional stressors. Crops such as the horticultural (tomatoes, potatoes, lettuce, spinach) and cereals (rice, maize, wheat, legumes) are known to be sensitive to salinity [22–24]. They suffer from soil salinity stress, resulting in the reduction of yield of up to 50–70% in rice (*Oryza sativa* L.), chickpea (*Cicer arietinum* L.), barley (*Hordeum vulgare* L.), maize (*Zea mays* L.), soybean (*Glycine max* L.), and wheat (*Triticum aestivum* L.), although deleterious effects are recorded even at the beginning of seed germination [25–28]. Plants exposed to elevated salt concentrations are shorter, with smaller leaves and pale color. The response of plants to salinity is a reduction in growth and yield as a consequence of osmotic adjustment and salt-specific response. The first is related to the reduction in the ability of the plant to absorb water, while the second is connected to changes in enzyme activity and metabolism, in general, and hormonal imbalance, including membrane transport of nutrients and water [29,30]. Salinity stress to plants is associated with water shortage and related to a decrease in photosynthesis, oxidative and osmotic stresses, ion toxicity, and nutrient balance; thus, the concentration of some ions increase and they became harmful [31]. The K^+/Na^+ ratio is very important for plants, and salt stress causes disturbances in the balance between these ions, reducing this proportion and decreasing nutrient availability [4,10]. In addition to the above effects, the stress can lead to the generation of reactive oxidative species (ROS), leading to DNA damage and protein metabolism [32].

3. Plant Response to Salinity Stress

Many plants are susceptible to soil salinization, the result of which their turgor, quality, and quantity of harvest decreases and the rate of growth and development slows down. Some of them, however, tolerate certain concentrations of soluble salts in the soil solution throughout their life cycle, which is the tolerance of plants to salinization. It depends on many factors, but the main one is the biology of the specific plant species and variety. There is a huge diversity in salinity tolerance among species. Some of the species are glycophytes and are sensitive to salinity, while others are halophytes and “need” salt [33]. In this sense, they have both built different strategies to exist in such an environment. The first type of plant tries to exclude the salt from their root cells in order to survive and ameliorate the stress effect, while the second accumulate the salt in their tissues, mainly in the leaves via xylem flux. While sensitive plant species do not have many mechanisms of their own to adapt to this abiotic stress, some halophytes tolerate up to 1 M of NaCl in the soil due to genes that are activated in response to salinity [34], which lead to the formation of specific proteins [11].

Halophytes use different mechanisms to adapt to salty environments [5,11,33,35–37]. The basic mechanisms include sophisticated changes at physiological, molecular, and biochemical levels: (i) modulation of hormone levels together with associate enzymes [11,38]; (ii) production of solutes and osmoprotectants [11,37,39]; (iii) modulating the K^+/Na^+ relationship at high values, as potassium is vital for stomata and enzyme functioning, regulating toxic ion accumulation and nutrient status [5,37,40]; (iv) selective intake or extrusion of ions [41]; (v) synthesizing polyamides that take part in ROS modulation [11,42]; (vi) antioxidant compound production [11,43]; (vii) regulation of salt overly sensitive (SOS) genes as a response to salinity-produced stress [37,44]; (viii) nitric oxide generation, which activates diverse gene expression and antioxidant enzymes [11,45]; (ix) changing photosynthetic activity [12,34,46]; (x) regulation of salinity tolerance gene expression [13]. The halophytes can be classified into three major groups: obligate, facultative, and habitat-indifferent. The *obligate halophytes* (*Chenopodiaceae*) require salt to live and complete their biological cycle, and some

of them are assigned as extremophiles [11], whereas the *facultative halophytes* tolerate certain salt concentrations and can grow in salty soils, achieving maximum yield and growth in salt-free soils. Some authors have established another called *habitat-indifferent halophytes* that are not affected by the salinity in their own habitats [5,33,35].

4. Bacteria and Salinity Stress

Microorganisms, as well as plants, have developed diverse mechanisms to adapt to salinity stress. They can be characterized as halotolerant and halophilic depending on the attitude towards salinity. The first can grow in the case of high concentrations of NaCl in the medium or without it; thus, they do not “need” salt, they just tolerate it. In contrast, halophiles are widely spread around the world in salt-rich ecosystems and habitats, representing natural communities. They require Na^+ for their metabolisms and development, so they need it to live [47]. In that sense, the halophiles can be divided into three categories according to their optimal NaCl concentration in the medium: slight halophiles, 1–3% of sodium chloride; moderate halophiles, 3–15% of sodium chloride; extreme halophiles, who love to grow at 15% to 30% of NaCl. Physical or chemical properties are involved in the bacterial perception and tolerance to the abovementioned concentrations, such as temperature, pH value, and nutrients [48]. In the present study, it can be summarized that the most common bacteria that tolerate elevated concentrations of NaCl (1–15%) are *Ochrobactrum intermedium*, *Bacillus subtilis*, *Pseudomonas fluorescence*, *Kocuria rhizophila*, consortium, *Bacillus amyloliquefaciens*, *Bacillus firmus*, *Azotobacter chroococcum*, *Ps. stutzeri*, *Az. brasiliense*, *Az. lipoferum*, *Pseudomonas putida*, *Curtobacterium flaccumfaciens*, *Arthrobacter* sp., and *B. safensis* (Table 1). These strains were found to improve plant growth and enhance the tolerance to sodium chloride in maize, wheat, barley, rice, soybean, sunflower, and tomato.

Soil salinity affects the structure, activities, and biodiversity of rhizosphere bacterial communities [49], which is not a well-explored area. Wang and collaborators found that the EC of soils was the most influential driving force of bacterial community composition (20.83%), while the second most important factor was sodium content (14.17%), suggesting a clear separation of bacterial communities in accordance with the EC. The dominant bacterial groups were *Planctomycetes*, *Proteobacteria*, and *Bacteroidetes* among different salty soils. As the salt concentration increased, the indicators changed from *Planctomycetes* and *Bacteroidetes* to *Proteobacteria* and *Firmicutes* [49]. One factor that indirectly affects the structure of bacterial communities in the rhizosphere is the quality and quantity of root exudates being influenced by the salinity [50]. In addition, halotolerant bacteria have built mechanisms to survive in salinity-rich environments. The main mechanisms are related to cell-wall construction and the capacity to pump ions out of the cell, as follows: (i) generation of extracellular polymeric substances (EPSs) that support biofilm formation, limiting the salt import into the cell [14,37,51]; (ii) soluble salt production through protein and enzyme adaptation [5]; (iii) optimizing the intracellular concentration of Na^+ ions using the Na^+/H^+ antiporter of the cell membrane [51–53]—the vital function of this “pump” is to maintain the elevated values of the K^+/Na^+ ratio in the cytosol compared to the low value in the surrounded habitat; (iv) avoiding the entry of high salt concentrations through the cell membrane because of the specific structure of the cell wall (structural and integral proteins, lipid composition, polysaccharides, between others) [15,52,53]; (v) endogenous synthesis of amino acids and solutes [37,51,54].

5. Role of PGPB in Alleviating Salinity Stress to Plants

Some PGPB are able to alleviate the negative effects on plants caused by salinity [4,11,27,36,38,54–56]. There is evidence of the application of these mechanisms to promote growth and enhance the salinity tolerance of plants (Table 1), and, in most cases, more than one mechanism is involved.

5.1. Phytohormone Signals

Phytohormones are very important for plants as they use them to regulate their own processes [57,58]. They are involved in plant interactions with their environment. The synthesis of phytohormones is precisely regulated by the plant, but bacteria are also able to produce phytohormones and to release them out of the cell, either in the rhizosphere (rhizobacteria) or in plant tissues (endophytes). The excretion of these molecules by bacteria affects plant behavior under salinity stress, as, in some situations, plants do not generate sufficient quantities for optimal development [59,60].

5.1.1. Auxins

The auxin is a phytohormone that affects several plant processes, including root hair and stem cell formation and elongation, and has a momentous function on plant growth under salinity stress [59,61]. One of the most common and studied auxins is indole-3-acetic acid (IAA), also produced by PGPB, functioning as a signaling molecule. The level of endogenous IAA in roots can be defined as optimal or suboptimal, so PGPB excreting that phytohormone could change the level and, thus, promote or suppress plant growth [62,63]. IAA is synthesized by different pathways that use tryptophan released from root exudates as a precursor. Most of the PGPB synthesize that phytohormone through the indole-3-pyruvate pathway, while the biosynthesis in plants is inducible [55,64]. Thus, the ability to generate IAA seems to be a common trait for halotolerant PGPB [59].

In a study, the halotolerant strain *Kocuria rhizophila* Y1, isolated from maize rhizosphere and tolerating up to 10% NaCl, presented two growth-promoting traits: phosphate solubilization and IAA production [65]. The inoculation of the strain showed it could protect maize from salt stress by regulating plant hormone (IAA and ABA) levels and improving nutrient acquisition. This resulted in significantly improved growth, photosynthetic capacity, biomass production, antioxidant levels, relative water content, seed germination rate, and chlorophyll accumulation in maize under saline conditions compared to the noninoculated plants. The inoculated maize also showed higher transcript levels of genes encoding antioxidants (ZmGR1 and ZmAPX1) and genes involved in salt tolerance (ZmNHX1, ZmNHX2, ZmNHX3, ZmWRKY58, and ZmDREB2A) than in noninoculated plants.

In the present review, most of the authors reported IAA production by the beneficial bacteria, tolerant to salt (Table 1). This ability is expressed even in salinity stress conditions, which is a beneficial effect and a valuable result of the environmental adaptation [4,16,17,66,67].

In an investigation, *Sulla carnosia*, an important legume for animal feed grown in salt-affected areas, was positively influenced by PGPR *Bacillus subtilis*, with or without coinoculation of the actinomycorrhizal fungus *Rhizophagus intraradices* [16]. The authors suggested that the efficiency of *B. subtilis* was due to the high IAA production by this strain under salinity stress. An isolate, identified as rhizobacteria *Arachis hypogaea*, was able to stimulate the growth of peanuts by producing IAA and siderophores and reducing the nitrate to nitrite. The authors stated that the strain was also able to adapt to the tested saline environment through phospholipid and fatty acid (to the degree of unsaturation) modifications; that is, the most important mechanism for maintaining the physical properties of the plasma membrane [68].

Inoculation of a *Bacillus firmus* SW5 population that exhibited the production of IAA and siderophores, and phosphate mobilization increased the growth and biomass yield of salinity-stressed soybean plants, expressed as chlorophyll content, nutrient uptake, osmolytes levels, total phenolic and flavonoid contents, and antioxidant enzyme activities [69]. The antioxidant enzyme-encoding genes and stress-related genes exhibited the highest expression levels in soybean plants inoculated with *B. firmus* SW5 and treated with 80 mM NaCl. Generally, the authors suggested that *B. firmus* SW5 bacteria play an important role in the amelioration of adverse effects of salinity on soybean, improving root system architecture, stimulating the antioxidant systems, and expressing stress-responsive genes.

5.1.2. Cytokinins, Gibberellic Acid, and Absciscic Acid

Both cytokinins and gibberellic acid play important roles in plant physiological processes in the regulation of protein synthesis, seed germination and cell division and elongation, and chlorophyll accumulation, among others [11,60,70]. They are generated by PGPB but have not been studied in depth under salinity stress [58]. *Bacillus*, *Pseudomonas*, *Rhizobium*, *Azotobacter*, and *Azospirillum* are reported to synthesize cytokinins and gibberellic acid and to promote plant growth [58,71]. There is evidence that cytokinin levels generated by PGPB are lower than those from phytopathogens; thus, the effect on plants is inhibitory in the case of the pathogens, while it is stimulatory in the case of PGPR [72]. Egamberdieva (2009) reported wheat growth stimulation of about 50% under salinity stress conditions when *Pseudomonas* strains, producing cytokinins, were presented in the rhizosphere [27]. The role of gibberellins under salt stress is also associated with the mitigation of the harmful effects of salt shock by increasing water availability to plants [5,73].

Globally, wheat is one of the most important crops, and a lot of studies are directed to the use of PGPB to increase the yield of wheat and alleviate the environmental stresses to it [17,74–77]. In one of them, four rhizobacteria that produced different phytohormones, such as IAA, gibberellic acid, cytokinins, and abscisic acid, were isolated in in-vitro experiments under salt stress. *Bacillus* sp., *Azospirillum brasilense*, *Azospirillum lipoferum*, and *Pseudomonas stutzeri*, applied together as a consortium, improved plant biomass and relative water content significantly. At the same time, wheat plants exposed to salinity stress of 150 mM NaCl showed tolerance-reducing electrolyte leakage and increasing production of chlorophyll *a*, *b*, and total chlorophyll, and osmolytes such as soluble sugar, proline, amino acids, and antioxidant enzymes (superoxide dismutase, catalase, peroxidase) [74].

A confirmation of the promotion effect that PGPB hormones render to plants is the application of *P. putida* H-2-3 in soybean rhizosphere [78]. The strain ameliorated the stress effects, enhancing shoot length, fresh weight, and chlorophyll content of the plants. Plants under salinity stress shown a higher level of superoxide dismutase and total polyphenol, but, at the same time, the radicals' formation was decreased. Finally, *P. putida* H-2-3 was able to induce tolerance to abiotic stress by a reduction of Na⁺ in plants [78].

5.1.3. Modulation of Plant Ethylene Levels

The ethylene is generated endogenously by the plant for the regulation of plant growth (roots, stems, leaves, flowers). It is associated with environmental stress, so when the plant is stressed, it synthesizes ethylene, thus increasing the endogenous concentration of that phytohormone [79]. This response to an environmental stress, including salinity, drought, and toxic elements, decreases the plant's own root elongation, alters the root structure, decreases biomass, and reduces whole plant development [80]. This is done by the activation of plants' precursor of ethylene, called S-adenosyl methionine, which is further converted to 1-amino-cyclopropane-1-carboxylic acid (ACC) by the ACC-synthase pathway, followed by conversion to ethylene by the enzyme ACC-oxidase [81]. In addition, PGPB are able to use the ACC, thus preventing the ethylene synthase. Some PGPB may produce the enzyme ACC-deaminase that splits the ACC molecule into α -ketobutirate and NH₄⁺, which is the most widely found mechanism among PGPB. Thus, the concentration of endogenous plant ethylene decreases, affecting the expression of the genes encoding the enzymes ACC-synthase and ACC-oxidase [82].

This trait of PGPB is well known under different stressful conditions, such as heavy metals, drought, and salinity. The expression of ACC-deaminase under salinity results in the induction of plant growth, alleviating the adverse effects of ethylene by the modulation of ACC accumulation and ACC-oxidase and ACC-synthase activities [83]. The *Bacillus* sp. consortium, presenting halotolerant species and applied in maize rhizosphere, also induced a plant response for protection enzymes, proline, chlorophyll, and soluble sugars, in a salt stress environment (100 mM NaCl).

Rice is a very important crop all over the world, especially in Asia. In a salinity stress study, *Bacillus amyloliquefaciens* NBRISN13 confers salt tolerance in rice by modulating the response of

transcription in a set of 14 genes [84]. The study was conducted in hydroponic and soil conditions, expressed in the inoculation of a bacterial population in such a salty environment, thus increasing plant growth and tolerance. The authors suggested that this is a stimulation of osmoprotectants, utilizing microbial populations as a mechanism of inducing salt tolerance in rice, and it is possibly due to increased root colonization, ACC-deaminase activity of *B. amyloliquefaciens*, maintained chlorophyll content, and enhanced proline accumulation [85].

In another project, the effect of PGPB *P. fluorescens* biotype A, containing ACC-deaminase maize under salt stress, showed more than a 3-fold increase in root length at the EC of 9 dS.m⁻¹, and an increase in plant height of 2.3-fold after the inoculation of a *P. putida* biotype A population at the EC of 12 dS.m⁻¹ [86]. In addition, *P. fluorescens* and *Enterobacter* spp. expressing ACC-deaminase increased maize yield under salinity, but also improved NPK nutrition and the K⁺/Na⁺ ratio [87]. In a recent study, several *Bacillus* isolates showed high ACC-deaminase activity, siderophore production, and phosphate solubilization, besides extracellular enzymes such as lipase, amylase, and cellulose, among others [88]. The isolates were able to promote the growth of pepper seedlings, alleviating the harmful effects of salinity and inducing the plants to accumulate proline. Some of the strains also induced plant antioxidant enzymes.

5.2. PGPB Support Nutrient Acquisition in Plants

Plant nutrition is one of the most serious issues that excite researchers, agronomists, nutritionists, technologists, and plant protection specialists. It is related in the first place to the quantity of the crop yield, but also to its quality, especially under environmental stress. Salinity stress is one of the most damaging stresses in terms of quality and quantity of production because it affects the transport of nutrients and water to the roots. Low levels of some important elements, such as nitrogen, phosphorus, and potassium, are some of the main reasons for reduced growth and crop quality. Soil salinity causes a reduction of essential nutrient uptake because of ion toxicity and osmotic pressure. There are micronutrients that are essential for the plants, although they are needed in small quantities [37,54,89]. These microelements, such as copper, zinc, iron, magnesium, sulfur, and molybdenum, are very important as they participate in the composition of various proteins, DNA, enzymes (nitrate reductase, catalases, hydrogenases), amino acids (methionine, tryptophan, threonine), and photosynthetic processes [89]. At the same time, soil bacteria can improve plant nutrient status under salinity stress through different ways using the proper traits that define them as plant-growth promoters [42,54,90].

5.2.1. Nitrogen Fixation

Nitrogen is one of the most important elements for life on Earth, and it is an integral part of proteins, nucleic acids, and chlorophyll. It is a limiting factor in terms of production from agricultural plants. Although 78% of the Earth's atmosphere is nitrogen, it cannot be used by organisms other than microorganisms that bind and molecules that convert it to organic and mineral forms. In salinity-rich environments, access to N is restricted by its availability, but the same process of nitrogen fixation is negatively affected through low access to soil ammonium salts, nitrates, and sulfates. [42,91]. As N availability is an important obstacle for yield production in salinity, lots of farmers excessively use agrochemicals in their agricultural practices, thus resulting in increased contamination (eutrophication and acidification) and financial costs [92]. The excellent ability of N-fixing bacteria to convert atmospheric nitrogen into easily accessible mineral compounds is a substantial help in the growth of plants and their nutrition under salinity stress.

The ability to fix soil nitrogen is a vital characteristic of two kinds of microorganisms, symbiotic and free-living, which contribute to the global nitrogen load of about 180×10^6 t.y⁻¹, divided into 80%/20% [93]. Organic inputs in the rhizosphere from the roots modify microbial diversity, resulting in an enormous number of free-living N-fixing bacteria (diazotrophs) that colonize plant roots of nonleguminous plants. They are mainly from genera *Azotobacter*, *Azospirillum*, *Pseudomonas*,

Agrobacterium, *Erwinia*, *Bacillus*, *Serratia*, *Klebsiella*, and *Burkholderia*, among others [94,95]. Because of elevated energy requirements and low metabolic activity, the intensity of N-fixation in diazotrophs is limited, and their contribution to the nitrogen nutrition of plants can reach 20 kg.ha⁻¹.y⁻¹ [96]. Undoubtedly, salinity affects the activity of N₂-fixing bacteria as some of them are sensitive, but others are tolerant to salt. PGP diazotrophs may ameliorate the osmotic-stress-producing osmolites that permit plants to maintain their metabolisms at acceptable levels [37]. Authors have suggested that halotolerant PGP diazotrophs can be found and easily isolated from the rhizosphere of halophytes [97]; thus they can be useful as biofertilizers in salinity-inhibited crops [54].

Investigators have reported that salinity inhibits nodule formation in mutualistic legume–rhizobia relationships [98]; thus, the nitrogen nutrition of legumes is negatively affected. Inoculation of PGPB, together with *Rhizobium*, helps in the increase in nodule numbers under salinity in various cases [99–102]. In addition, the plant secretes flavonoids from the root that provoke the *Rhizobium* bacteria to secrete a Nod-factor, initiating nodule formation [103]. These Nod-factors may also act as stress-response signals of salinity stress in legumes, especially when they are generated by PGPB. In that sense, *Bradyrhizobium japonicum* significantly improved nodule formation and the biomass of soybean (more than 20%) under salinity stress, and such positive effects become more evident with time [104].

5.2.2. Phosphate Solubilization

Phosphorus (P) is an essential plant nutrient that limits plant growth and, in many agricultural lands, is of low bioavailability. This nutrient is required for diverse metabolic processes such as respiration, biosynthesis, photosynthesis, energy transfer, and signal transduction, so plants need it in proper amounts. There are two forms of P compounds: organic and inorganic phosphates. Soil bacteria are capable of converting insoluble forms into bioavailable forms; thus, plant growth and development is promoted [105,106]. Generally, the concentration of soluble P in soil is quite low, usually at levels of 0.001% or less. Plants can take up diverse forms of P, but of the greatest importance is absorption in the forms of HPO₄⁻² or H₂PO₄⁻¹, while the state of the compounds in the soil depends on pH and soil type [107]. Apatite is a common mineral form of P that is characterized by low solubility [108], while the most common organic forms are phytate and phosphomono(di-, tri-)esterase, being mostly bioavailable to plants [5,109].

Phosphate-solubilizing PGPB involve the genus *Arthrobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Erwinia*, *Mesorhizobium*, *Flavobacterium*, *Rhodococcus*, and *Klebsiella*, among others [9,37,54,59,110]. Some of them may fix soluble P in their cells or convert P from organic to inorganic forms using different phosphatases [91,111]. In saline soils, the bioavailability of nutrient elements is low because the salt modifies the balance of ions. However, halotolerant PGPB are able to mitigate, on a certain level, some of the deleterious effects of salinity, improving plant growth, biomass accumulation, and yield [2,111]. *Achromobacter piechaudii* ARV8 had a quite positive influence on the growth of tomato plants under salinity, improving P uptake and water balance [112].

It is clear that halotolerant PGPB improve plant nutrient status, but the effect in most of the studies cannot be attributed to only one trait, e.g., P-mobilization or production of IAA and siderophores, or ACC-deaminase activity. The application of beneficial bacterial populations results in multiple positive results on the whole plant. Salt-tolerant bacterial strains expressing PGP abilities were found to produce EPS, auxin, and proline, reducing sugars and total soluble sugars, and to solubilize phosphate [17]. These abilities of the native isolate of the wheat rhizosphere are associated with plant growth and biomass enhancement in saline soil. Plant-growth-promoting strains support the restriction of Na⁺ uptake by the roots caused by a decreased quantity of the apoplasmic flow of sodium ions. The authors also informed us that the use of a consortium of four strains, two *Bacillus* sp. increasing EPS production and two *Enterobacter* sp., was the most efficient way to reduce cation uptake by plants in soil salinity environments. Populations of two isolates determined as *Azotobacter chroococcum* alleviated the saline stress in maize through the integration of several mechanisms that improve plant growth and mineral

nutrition. These mechanisms included Na^+ exclusion and K^+ uptake in maize, thereby increasing their K^+/Na^+ ratio, enhancing polyphenol and chlorophyll content, and decreasing the proline concentration, increased by the salinity, in leaves. At the same time, both *Az. chroococcum* isolates possessed several PGP traits such as nitrogen fixation, phosphate solubilization, and auxin synthesis [113].

5.2.3. Iron Mobilization

Iron is an essential micronutrient for all living cells, in particular plant cells, because it is involved in plenty of processes, proteins, and enzymes and is a cofactor in photosynthesis, N_2 -fixation, and respiration, including the reparation processes of RNA and DNA. It is one of the most common elements on Earth (second or fourth, according to different sources) [5,114–116]. Despite the above, iron is not widely accessible in soils forming complexes of hydroxides and oxyhydroxides; thus, its bioavailability decreases below 10% in loamy soils [117]. In soil matrix, iron exists in two convertible states as Fe^{2+} and Fe^{3+} , depending on pH, oxygen, and organic matter content. There are reports that soil salinity is an additional negative factor for plant iron nutrition [5,118]; thus, growth, development, and yield suffer. Plants respond to such limitations through excreting organic molecules by the root, acidifying the rhizosphere and resulting in a certain increase of iron availability. An additional toll is the synthesis of some compounds that bind Fe^{3+} by the plants to make it more accessible to the roots [119], but even that is not sufficient to satisfy the plants' need for iron [38].

Different PGPB, such as *Pseudomonas*, *Bacillus*, and *Serratia*, possess the ability to synthesize low molecular weight (<1000 Da) compounds named siderophores, having a high affinity to Fe^{3+} and forming complexes with them. They act as solubilizing agents for many more ions (with less affinity) from minerals or organic compounds such as Al, Cd, Pb, Cu, and Zn. Although the siderophores are very diverse, the iron-chelating group of the siderophores includes three types: hydroxycarboxylic acid, catechol, or hydroxamic acid [120]. These complexes are taken up by the same PGPB, but in the rhizosphere, the bacterial population is numerous due to the specific conditions created by the root secretions, so the concentration of siderophores becomes significant. This leads to the mobilization of available iron, which is largely absorbed by the plant roots. [121]. Table 1 presents the different studies on how PGPB-producing siderophores mitigate some of the salinity stress effects. In one study with sunflower plants and maize, improvement in growth was reported [122]. A similar investigation was made using wheat plants and PGPR populations isolated from halophytes, presenting multiple PGP traits, including siderophores. That investigation confirmed the utility of PGPR in saline soils as the plants had enhanced salinity tolerance, increased growth and K^+/Na^+ ratio, and reduced endogenous ethylene production. Moreover, diverse genes were reported to be upregulated in the roots of salt-stressed plants [77]. In other studies on iron-deficient soil, the growth of *Arabidopsis thaliana* was induced by the inoculation of siderophores producing a *Pseudomonas fluorescens* strain [123]. Researchers suggested that siderophore production could even be preventive in response to environmental stress; thus, *Azospirillum brasiliense* produced siderophores in the iron-rich rhizosphere of cucumber [124].

Table 1. Studies showing the application of plant-growth-promoting bacteria (PGPB) to alleviate plant growth and salinity tolerance.

Plant	Beneficial Effect(s)	Halotolerant PGPR	PGP-Traits	Conditions	Source
<i>Phaseolus vulgaris</i>	enhanced growth, yield, and biochemical activity	<i>Bacillus subtilis</i> MTCC 441 and <i>Pseudomonas fluorescence</i> MTCC 103 ^T	-	greenhouse, pots, soil, and vermicompost, 150 mM NaCl	[125]
<i>Arachis hypogaea</i>	shoot and root growth promotion	<i>Ochrobactrum intermedium</i>	IAA, siderophores	growth chamber, pots, sterilized nitrogen-free vermiculite	[68]
<i>Zea mays</i>	increase of growth, seed germination rate, photosynthetic capacity, antioxidant levels, relative water content, chlorophyll	<i>Kocuria rhizophila</i> Y1 (10% NaCl)	P solubilization, IAA	greenhouse, pots, soil:vermiculite:perlite (2:2:1), 100 and 200 mM NaCl	[66]
<i>Sulla carnosa</i>	improved growth, nutrition, and salt tolerance	<i>Bacillus subtilis</i>	IAA, urease, alkaline phosphatase, β -glucosidase and dehydrogenase	greenhouse, pots, soil/sand mixture, 200 mM NaCl	[16]
<i>Hordeum vulgare</i>	improved growth	<i>Curtobacterium flaccumfaciens</i> E108	IAA, phosphate mobilization	greenhouse, tonsubstrat ED 73 substrate, 4.4% or 4.8% NaCl	[66]
<i>Triticum aestivum</i>	increased biomass	11 isolates, 8% NaCl	EPS and auxin production, phosphate solubilization	growth chamber, pots, soil, 1% NaCl	[17]
<i>Oryza sativa</i>	increased growth and tolerance to salt	<i>Bacillus amyloliquefaciens</i> NBRISN13, 50–2500 mM NaCl	ACC deaminase, root colonization	hydroponics and soil, 100–300 mM NaCl	[84]
<i>Glycine max</i>	plant growth and performance	<i>Bacillus firmus</i> SW5, 500 mM NaCl	IAA, siderophores, phosphate mobilization	hydroponics, 80 mM NaCl	[69]
<i>Zea mays</i>	improved plant growth and mineral nutrition	<i>Azotobacter chroococcum</i> C5 & C9, 5.8% NaCl	N fixation, phosphate solubilization, auxin	greenhouse, pots, soil, 0.58% NaCl	[112]
<i>Helianthus annuus</i>	plant biomass, improved K ⁺ /Na ⁺ ratio	<i>P. fluorescens</i> biotype F, <i>P. fluorescens</i> CECT 378 T, 50 mM NaCl	IAA, siderophores	growth chamber, pots, soil:peat (1:1), 100 mM NaCl	[4]
<i>Lycopersicum esculentum</i>	increased salt tolerance in tomato, enhanced plant biomass, shoot and root length,	<i>Sphingobacterium</i> sp. BHU-AV3, 0.85 M NaCl	IAA, siderophores, phosphate solubilization	growth chamber, pots, soil, 200 mM NaCl	[126]

Table 1. Cont.

Plant	Beneficial Effect(s)	Halotolerant PGPR	PGP-Traits	Conditions	Source
<i>Triticum aestivum</i>	induced salinity tolerance, increased plant biomass and relative water content	<i>Bacillus</i> sp., <i>Ps. stutzeri</i> , <i>Az.brasiliense</i> , <i>Az.lipoferum</i> , 2–15% NaCl	IAA, gibberellic acid, cytokinin, abscisic acid	greenhouse, pots, soil, 150 mM NaCl	[74]
<i>Glycine max</i> , <i>Zea mays</i>	improved seed germination, root and stem length	<i>Pseudomonas putida</i> KT2440, 0.5 M NaCl	phosphate solubilization, indoles and siderophores	growth chamber, pots, soil, sand, 80 and 100 mM NaCl	[127]
<i>Zea mays</i>	improved growth, induced plant response for defense enzymes, chlorophyll, proline, soluble sugars	<i>B. subtilis</i> , <i>B. subtilis</i> , <i>B. safensis</i> , 1 M NaCl	ACC-deaminase, IAA, P-solubilization, EPS	greenhouse, pots, soil, 100 mM NaCl	[83]
<i>Lycopersicum esculentum</i>	improved fresh and dry biomass, chlorophyll contents, and a greater number of flowers and buds	<i>P. fluorescens</i> YsS6 and <i>P. migulae</i> 8R6	IAA, siderophores, phosphate solubilization, ACC-deaminase	greenhouse, soil, pots, 165 and 185 mM NaCl	[62]
<i>Glycine max</i>	length, shoot biomass, chlorophyll content	<i>Pseudomonas putida</i> H-2-3	gibberellins, abscisic and salicylic acids	greenhouse, pots, peat mixture, 120 mM NaCl	[78]
<i>Oryza sativa</i>	dry matter, chlorophyll content, K^+/Na^+ ratio,	<i>B. tequilensis</i> , <i>B. aryabhattai</i> , <i>Providencia stuartii</i>		glasshouse, pots, soil, 4 g.L ⁻¹ NaCl (EC = 8 dS.m ⁻¹)	[128]
<i>Zea mays</i>	increase K^+/Na^+ ratio, plant growth	<i>Arthrobacter</i> sp., <i>Bacillus</i> sp.	auxin, abscisic acid, cytokinins, gibberellins	greenhouse, pots, sand:vermiculite, NaCl (EC = 12 dS.m ⁻¹)	[129]
<i>Triticum durum</i>	Growth promotion, chlorophyll content, K^+/Na^+ ratio	<i>Pantoea agglomerans</i> , 1 M NaCl	auxin, ACC-deaminase, phosphate solubilization	growth chamber, pot, soil, 100 and 200 mM NaCl	[75]
<i>Zea mays</i>	improving growth and salt stress tolerance, regulating ion homeostasis, redox potential, leaf gas exchange, stress-related genes expression	<i>Serratia liquefaciens</i> KM4, 450 mM NaCl	IAA, siderophores, phosphate solubilization	growth chamber, pots, soil, 160 mM NaCl	[76]
<i>Lolium perenne</i>	enhanced growth and salt tolerance and K^+/Na^+ ratio, chlorophyll, root volume and activity, leaf catalase activity, soluble sugar and proline	<i>Pseudomonas</i> sp. M30-35,	phosphorus solubilization, auxin	greenhouse, pots, soil, 300 mM NaCl	[130]
<i>Triticum durum</i>	increasing light absorbed by PSII antenna, PQ ratio and total quenching of chlorophyll fluorescence, increased yield of grains	consortium (<i>A. pittii</i> , <i>A. oleivorans</i> , <i>A. calcoaceticus</i> , <i>Comamonas testosteroni</i>)	Phosphate, K, and Zn solubilization, N ₂ fixation	greenhouse, pots, soil, 150 mM NaCl	[131]

5.3. Contribution to Osmolyte Accumulation in Plants

Plants accumulate osmolytes to maintain osmotic balance in the cells. The most widely used osmolytes by the plants are oligo- and disaccharides, alcohols, proline, and glycine [132]. In addition, some of these compounds are used by the PGP endophytes [133]. Some sugar alcohols are, in fact, signaling molecules, or they participate in osmoregulation under salinity stress. Beneficial bacteria can regulate water potential and stomatal opening in plants by the accumulation of diverse organic compounds, such as sugars, amino acids, alcohols, and glycerol, via hydraulic conductivity [14,134]. There is evidence that betaine and proline, such as mannitol and sorbitol, function as osmoregulators of plants in such deleterious environments [132]. In maize rhizosphere, *B. megaterium*, a capsule-forming microbe, support plants by improving root hydraulic conductivity under salinity [135]. Similarly, the *B. amyloliquefaciens* strain, in the presence of 200 mM of NaCl, stimulated salt tolerance in rice plants by the upregulation of expression of some genes in the soil environment, while in hydroponics, other genes were downregulated [84].

5.4. Plant Ion Homeostasis

The excess of Na^+ results in an imbalance of nutrients due to the elevated uptake of this element, so the K^+/Na^+ ratio decreases, which reduces plant growth in this circumstance. Some plants have mechanisms to compensate for this imbalance by controlling the Na^+ influx through the roots and the xylem flux back [136]. Halotolerant PGPB increase K^+ uptake by upregulating one K^+ transporter and decreasing the accumulation of Na^+ in leaves; thus, the K^+/Na^+ ratio increases. *Azotobacter* populations were able to decrease Na^+ uptake and to stimulate the K^+ influx, which resulted in increased chlorophyll content and plant stress response mechanisms [113]. Other studies have reported that the inoculation of PGPB (*P. fluorescens* biotype F, *P. fluorescens* CECT 378T, *B. tequilensis*, *B. aryabhatai*, *Providencia stuartii*, *Pantoea agglomerans*, or *Arthrobacter* sp.) in plant rhizosphere under salinity stress resulted in an increased K^+/Na^+ ratio [4,76,128,129]. All PGPB presented various PGP traits, the combined action of which leads to the amelioration of salinity stress to plants.

5.5. Extracellular Polymeric Substances (EPSs)

Different biopolymers are secreted by the microbial cell (polysaccharides, polyesters, polyamides) into its surroundings. The biopolymers play an irreplaceable role in plant–microorganisms relationships, especially in the alleviation of plant salinity stress [17,36,55,137], as they are excreted out of the cells and bind cations like Na^+ in decreasing bioavailable concentration, but also serve as signal molecules for the defense response to infections. These EPSs help PGPB to survive in saline environments; thus, most of the halotolerant bacteria possess the ability to extrude this kind of compound [5]. Moreover, they are an instrument that permits microorganisms and plant roots to communicate, establishing a number of interactions. In that sense, EPSs are very useful to microorganisms in order to survive in root surroundings and benefit from the exudates. Of course, the composition of the EPSs excreted by the PGPB cells differs among genera and species and change with time, environmental conditions, and circumstances. There are data that EPSs improve nutrient uptake and water potential in the rhizosphere [138,139]. PGPB gently adhere to plant roots, secreting EPSs and forming biofilms against desiccation [137].

Particularly, exopolysaccharide-producing *Enterobacter* sp. and *Bacillus* sp. have been found to improve water balance in roots of quinoa under the saline stress of 400 mM NaCl [140]. Many of the EPS-producing PGPB play a vital role in soil fertility and agricultural sustainability, such as *Azotobacter vinelandii*, *Rhizobium* sp., *Enterobacter* sp., *Agrobacterium* sp., *Xanthomonas* sp., and *Bacillus* sp.; thus, they indirectly improve soil structure and aggregation in the rhizosphere [55,138].

6. Conclusions

Plants respond to salinity stress in different ways, but most of them are susceptible to increased salt concentrations and suffer from reduced growth and development. Soil microbiome and especially halotolerant PGPB possess plenty of mechanisms by which to promote plant access to nutrients or improve their growth. These tools are diverse, including phytohormone generation, the dissolution of phosphate compounds, and the production of siderophores, among others. Special attention should be paid to the modulation of plant ethylene levels by utilizing the ACC as the sole carbon source of nitrogen, due to its overall impact on plant growth and development. Regulation in plant phytohormone signaling by PGPB is a promising way to boost the yield. In addition, the combined possession of different traits has the most noticeable positive effect on plants when subjected to the stress of salinization.

The studies over the past few years have demonstrated the ability of some halotolerant PGPB to improve plant existence under salinity and also in nonstressful conditions. Most of the trials were conducted in controlled conditions or even in vitro, while when they were applied in the field, the promoting effect dramatically decreased. The main reason is that PGPB come from different environments than the one in which they are inoculated. Nevertheless, a consortium of PGPB presents multiple traits and may have more success in real conditions as different mechanisms can be applied. Moreover, fundamental studies of the interactions between different populations and different communities and plants need to be deepened by moving more and more to studies at the molecular level. Further studies should be directed to reveal all intimate mechanisms of plant-growth promotion under salinity stress and adjust the PGP biotechnology to be applied in real field conditions, as the most important goal of this area of science is related to agricultural production.

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