

Review

Overview of the Role of Rhizobacteria in Plant Salt Stress Tolerance

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Abstract: Salinity is one of the main causes of abiotic stress in plants, resulting in negative effects on crop growth and yield, especially in arid and semi-arid regions. The effects of salinity on plant growth mainly generate osmotic stress, ion toxicity, nutrient deficiency, and oxidative stress. Traditional approaches for the development of salt-tolerant crops are expensive and time-consuming, as well as not always being easy to implement. Thus, the use of plant growth-promoting bacteria (PGPB) has been reported as a sustainable and cost-effective alternative to enhance plant tolerance to salt stress. In this sense, this review aims to understand the mechanisms by which PGPB help plants to alleviate saline stress, including: (i) changes in the plant hormonal balance; (ii) release of extracellular compounds acting as chemical signals for the plant or enhancing soil conditions for plant development; (iii) regulation of the internal ionic content of the plant; or iv) aiding in the synthesis of osmoprotectant compounds (which reduce osmotic stress). The potential provided by PGPB is therefore an invaluable resource for improving plant tolerance to salinity, thereby facilitating an increase in global food production and unravelling prospects for sustainable agricultural productivity.

Keywords: salinity; PGPB; climate change; osmotic stress; ion homeostasis; phytohormones; osmoprotectan; crops



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1. Introduction

At present, there is scientific consensus indicating that the human production model and energetic consumption are involved in climate change [1]. The impact that this global climatic alteration causes is translated into adverse environmental conditions, such as salinity in soils, extreme temperatures, droughts, or floods, which limit the geographical distribution of plant species and crop yields [2,3]. These types of extreme processes mainly affect semi-arid and arid regions, and they have not only environmental impacts but also economic and social repercussions [2,4].

Soil salinity is the result of the accumulation of soluble salts in soils, due to natural (primary salinization) and/or anthropogenic (secondary salinization) processes, and has been defined as an important cause of loss of soil fertility, as well as agricultural productivity and sustainability [5]. A soil is saline when it presents electrical conductivity (EC) of the saturation extract (EC_e) of 4 dS m^{-1} (approximately 40 mM NaCl) or higher at $25 \text{ }^\circ\text{C}$ and has an exchangeable sodium of 15% [6,7]. Although most studies have focused on the effect of NaCl as a cause of saline stress, in some areas of the planet, this stress is due to the presence of Na_2SO_4 [8]. The long-term accumulation of other ions, such as Ca^{2+} , Mg^{2+} , or CO_3^{2-} , has also been shown to have negative effects on plant productivity, when certain thresholds are exceeded [9]. In this sense, it has been estimated that 20% of cultivated lands and 33% of irrigated agricultural lands worldwide are affected by salinity [5–7,10]. According to the Food and Agriculture Organization (FAO) of the United

Nations [11,12], and other scientific literature [2,5,13–16], these percentages represent an approximate area of more than 900 million hectares, of which about 77 million hectares could be human-induced salt-affected soils [13]. Furthermore, the rate of lands degraded by salinity increases annually by 10% due to various factors, such as climate change, poor irrigation practices, and other natural processes [5,7,10].

The impact generated by salinity is predominantly focused in arid and semi-arid regions, where evapotranspiration exceeds precipitation [13,17], although other edaphic, hydrologic, topographic, biological, and anthropogenic factors also interfere in this degradative process [3]. Oceania and Asia are the most-affected continents, as they present 39% and 34% of salt-affected soils globally, respectively; this jointly equates to 374 million hectares [2,11,13]. Considering human-induced salinization, the percentages in Asia are higher than in the other regions (approximately 70%), followed by Africa (20%) and Europe (5%) [13]. This degradation of arable land due to salinity has a negative impact on production and, therefore, on the economy. Taking into account studies carried out in India with different crops (rice, wheat, cotton, or sugar cane), production losses due to salt-affected soils may exceed 30% [18]. Economically, this could represent an annual cost of US\$ 27.3 billion [2,13,18], assuming only losses due to a reduction of crop yield, without counting the additional inputs required to mitigate the impact of saline degradation of soils. However, according to the FAO [12], the annual loss of agricultural productivity has been estimated to be US\$ 31 million, with production losses between 20–40%.

Plants can act through two different strategies to withstand saline stress: On the one hand, through resistance to salinity, consisting of the execution of strategies aimed at reducing the damage caused. On the other hand, through tolerance to salinity, by the reduction of negative fitness impact of damage [19–21]. Crop yield usually decreases when the salt concentration in soils exceeds the salinity threshold (4 dS m^{-1}), although plant species have a huge diversity of tolerance to salt [1]. The effects of salinity on plant growth mainly generate osmotic stress, ion toxicity, nutrient deficiency, and oxidative stress [7]. Firstly, the osmotic phase takes place, due to salt accumulation in the radicular system, thus generating a water deficit in the roots [2,16,22]. This osmotic pressure results in a decrease of the growth rate and stomatal closure, with the aim of reducing the water used by the plant [1,7,16,22]. This is followed by the ion toxicity phase, which is caused by an excess of ions, mainly Na^+ and Cl^- [7,16,23]. When the salt concentration is high, the accumulation of these ions exceeds the rate of exclusion. This results in an aggregation of radicals in vacuoles and cytoplasm (mainly in leaves), which generates structural and functional alterations of the cell [1,2,16]. Furthermore, high salt concentrations can limit macro- (P,N) and micronutrient uptake (e.g., Mg, Fe, Cu, or Zn), by reducing their solubility and competing in uptake with Na^+ and Cl^- [24,25]. In turn, osmotic stress and ion toxicity cause a photosynthetic imbalance, which imposes oxidative stress [1,7,16]. This metabolic alteration increases the formation of Reactive Oxygen Species (ROS), by-products that affect cellular components, such as photosystems, and which are able to induce programmed cell death [1,16,22,26]. Thus, different aspects of plant development, such as germination, vegetative growth, and reproductive development, are disrupted by the actions of all these effects [7].

According to this increasing problem, it is certainly necessary to search for methodologies to provide possible solutions to boost crop yields under salinity. The traditional approach has been based on two main alternatives: appropriate farm management practices and plant breeding [6,7,17]. Although sustainable management of the land can ameliorate the effects of soil salinity, it is limited by hydric resources and their quality, and is often slow and costly [7,17]. The development of salt-tolerant crops by traditional breeding and transgenic approaches is also an expensive and time-consuming alternative, which is not always easy to implement [1,17,23]. Identification of the basic molecular machineries of stress tolerance is a prerequisite for the development of effective varieties, and it is also necessary to increase knowledge in this respect [6,7,18]. In contrast, there are other feasible

and cost-effective strategies, as is the case for the application of beneficial microorganisms that increase salt-tolerance in plants [1,17,23].

In recent years, the application of Plant Growth-Promoting Bacteria (PGPB) has been demonstrated as an effective alternative to enhance plant development and the nutritional content of various crops, even under adverse environmental conditions, such as soil salinity [10,24,27–31]. These soil microorganisms are able to improve crop water relations, alter ion homeostasis, or change phytohormone status through direct and indirect mechanisms that modulate abiotic stress regulation [1,23]. Therefore, the aim of this review is to understand the mechanisms by which PGPB help plants to alleviate saline stress.

2. Physiological Effects of Salinity Stress on Plants

Increased ion concentration in the soil causes salinity. Salt-affected soil includes saline soil, sodic soil, and saline–sodic soil [2]. The common cations associated with salinity are Na^+ , Ca^{2+} , and Mg^{2+} , while the common anions are Cl^- , SO_4^{2-} , and HCO_3^- [22]. Among them, Na^+ and Cl^- ions are considered the most important, owing to their negative effects in plants and soil [1,7,16,22]. The impacts of salinity are complex, ranging from morphological, physiological, and biochemical effects on plants, to erosion and reduced soil productivity [1,7,22]. In this sense, soil salinity affects all aspects of plant growth and development (i.e., germination, vegetative growth, and reproductive development) by imposing damaging effects, involving osmotic imbalance and ionic stress. As a consequence of these primary effects, secondary stresses often occur, such as oxidative damage [1,2,7,16,22].

2.1. Osmotic Stress

Osmotic stress is a type of stress that occurs when there is an imbalance in the water balance of the plant [32]. It is said to be the first phase in the development of salt stress, which starts immediately after the accumulation of salt above a threshold level around the radicular systems, generating a water deficit in the roots [2,16,32]. Osmotic stress affects shoot and reproductive development: the expansion of leaves is reduced, new leaves emerge more slowly, senescence of older leaves occurs, fewer branches or lateral shoots form, and flowering starts earlier [1,2,16]. Radicular system architecture and development is also affected: the elongation of roots is initially diminished, and the formation of lateral roots is repressed [1,16]. Furthermore, alteration of the water balance causes stomatal closure and a reduction in gas exchange. All of the above, together with the feedback inhibition of unused photosynthates (which accumulate in plant meristems and storage organs), results in a decrease in the rate of photosynthesis [1,2,7,16].

2.2. Ionic Stress

According to the literature, ionic stress is defined as the combination of ion accumulation in plant shoots and an inability to tolerate the ions that have accumulated [1,2,16]. The ion toxicity phase is the second stage in the development of salt stress, which appears when the accumulation of these ions exceeds the rate of exclusion. These radicals are transported from the roots to the xylem, through which they move to the leaves, where they accumulate in vacuoles and cytoplasm to toxic levels [1]. Leaves die under these levels of ions and, if the rate of production of new leaves is less than the rate of death, the photosynthetic capacity of the plant is reduced [16]. Moreover, an excess of radical concentration, mainly Na^+ and Cl^- , negatively affects K^+ uptake, due to competition between the two ions to act as substrate in low-affinity potassium uptake systems, as well as other micronutrients [1,7,24,25]. All of this results in structural and functional alterations of the cell: restraint of enzymes involved in photosynthesis and respiration, interference with vesicular trafficking, inhibited cytosolic activities, and/or chloroplast and mitochondrial toxicity [1,7,16].

2.3. Oxidative Stress

Oxidative damage is caused by the production of reactive oxygen species (ROS) in cells, such as singlet oxygen ($^1\text{O}_2$), superoxide (O_2^-), hydrogen peroxide (H_2O_2), or hydroxyl radicals (OH) [1,16,33]. ROS are profoundly reactive with cellular components, and induce programmed cell death. They can cause protein and DNA damage, chlorophyll degradation, and lipid peroxidation, consequently affecting photosynthesis and membrane permeability [1,22,33]. As previously discussed, osmotic and ionic stress cause photosynthetic imbalances and/or stomatal closure, leading to oxidative damage [16,22].

3. Main Mechanisms of Salinity Tolerance/Resistance Induced by PGPB

The physiological effects of salinity cause significant reductions in crop productivity [1,16]; however, the application of PGPB has been shown to improve crop productivity, by reducing the physiological damage caused by high ion concentrations in the soil [1,23]. This effect is due to different mechanisms exhibited by these beneficial bacteria, which act at different levels, regulating the harmful effects of high salt concentrations [1,7,23,34,35].

3.1. Osmotic Balance (Water Homeostasis and Osmolyte Accumulation)

Osmotic stress is the first effect produced by salinity, as previously mentioned. It generates a disruption in the water balance, causing stomatal closure [2,7]. The photosynthesis rate decreases, due to an imbalance in gas exchange and leaf area reduction [1]. Additionally, photosynthate feedback inhibition occurs. The reduction of growth results in an accumulation of carbohydrates in meristems and storage organs, which otherwise would be used in proliferation and the expansion of new tissues [1,23]. Accordingly, plants need to maintain water homeostasis and preserve photosynthetic structures, with the aim to mitigate the impact of salinity. In this sense, the use of PGPB has been demonstrated as an alternative to enhance the osmotic balance, through various mechanisms (see Figure 1, Table 1).

Bacterial extracellular polysaccharides or exopolysaccharides (EPS) are complex hydrated high-molecular weight organic polymers broadly distributed among bacteria [17,36], which have a fundamental roles in the defense of microbiota against stressful environmental conditions (pH or temperature), as well as adhesion to biotic and abiotic surfaces [37]. The composition and amount of ESP depend on the strain and conditions [34]. ESP also have additional functions in plant–microbe interactions. The addition of polysaccharides increases the adherence of soil particles into microaggregates and favors macropore generation, which are beneficial in improving porosity and aeration in soil (Figure 1) [17,23,38,39]. Thus, the effects of the initial osmotic stress are diminished by binding soil particles and improving its structure [7]. It has been shown that co-inoculation of the plant growth-promoting rhizobacteria *Pseudomonas mendocina* and the arbuscular mycorrhizal fungus *Glomus intraradices* onto lettuce resulted in a high percentage of stable aggregates in soil under field conditions, due to the bacterial EPS production [40]. Moreover, according to Qurashi & Sabri [41], the effect of inoculating two bacterial strains, *Halomonas variabilis* HT1 and *Planococcus rifietoensis* RT4, onto *Cicer arietinum* plants subject to soil aggregation under salt stress led to enhancements in chickpea growth and soil structure.

As previously stated, salinity causes growth reduction and feedback inhibition of unused photosynthates. Microorganisms can modulate the source–sink relationships of soluble sugars in plants, favoring osmotic adjustment and avoiding feedback photoinhibition during the salinity osmotic phase (Figure 1) [1,42]. On one hand, plant roots are a strong carbohydrate sink, and their development can be mediated by the hormonal response (IAA) associated with the action of the microbe. On the other hand, the microbes can also consume a considerable part of these photosynthates [23]; for example, the salt resistance of two nodulated *Medicago ciliaris* L. lines was mediated by the maintenance of nodular-symbiotic and source–sink activities [43]. In addition, co-inoculation of *Bradyrhizobium japonicum* 532C, *Rhizobium* sp. SL42, and *Hydrogenophaga* sp. SL48 onto soybean plants under saline conditions improved shoot and root growth, nitrogen assimilation, and

the K^+/Na^+ ratio, which could be a consequence of nodular-symbiotic and source-sink activities [44]. *Capsicum annuum* L. plants co-inoculated with *Azospirillum brasilense* M3 and *Pantoea dispersa* C3 under salinity (40–120 mM NaCl) showed increases in analyzed production parameters, as related to higher stomatal conductance and photosynthesis, without changes in chlorophyll content or photosystem efficiency [45]. In the same way, inoculation with various *Bacillus* strains in strawberry and wheat has increased different leaf physiological parameters, such as photosynthesis or stomatal conductance [46], or productivity and nutritional content [47].

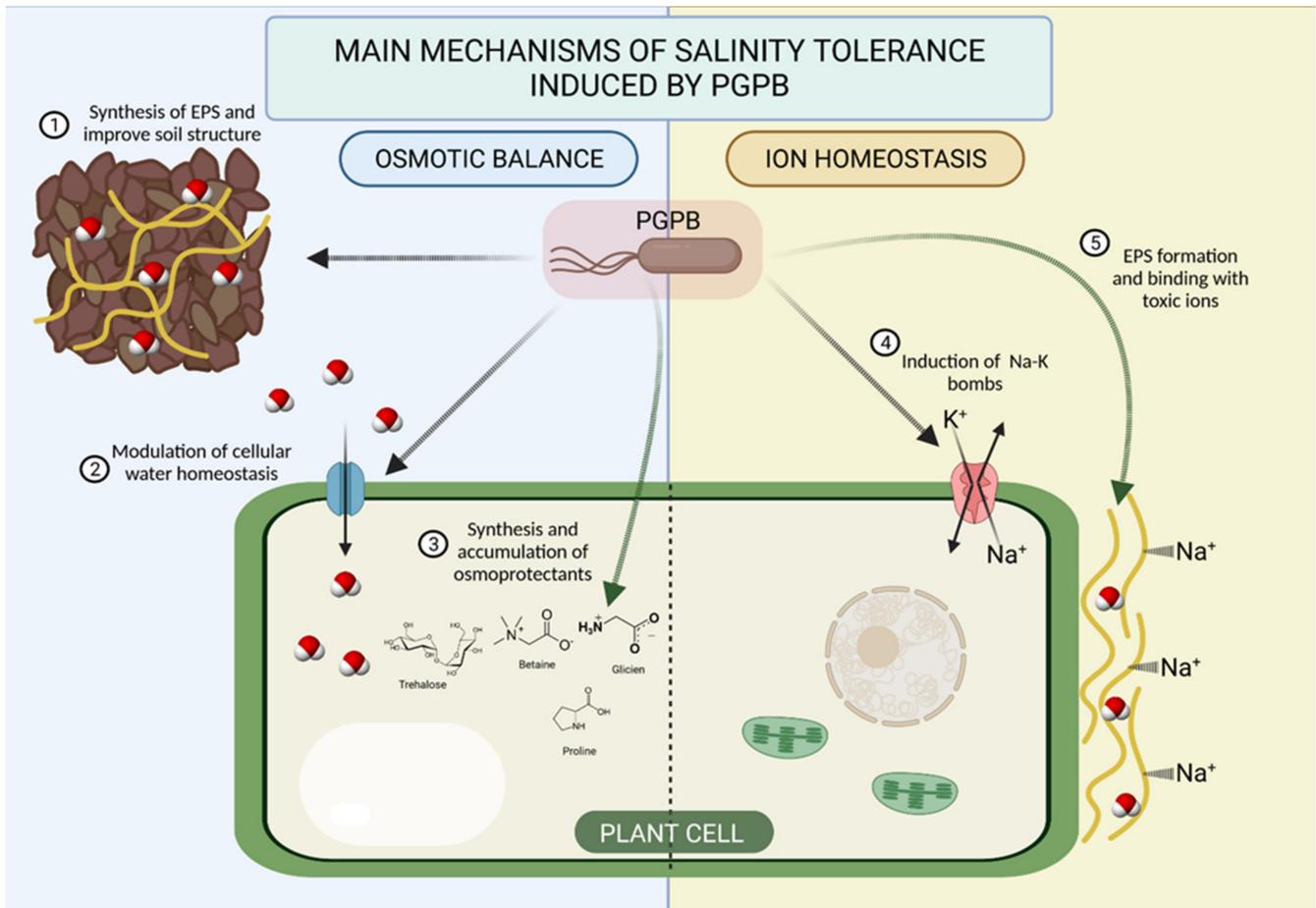


Figure 1. Main mechanisms of salinity stress tolerance induced by Plant Growth Promoting Bacteria.

Saline stress causes a loss of intracellular water in plants [48]. Therefore, vegetal species accumulate organic osmolytes in the cytoplasm, in order to maintain the osmotic cellular state and to improve their response to such stress [34,48]. These compounds include proline, glycine, betaine, or trehalose, among others (Figure 1) [1,23,48]. Salt-tolerant bacteria also employ this mechanism against osmotic fluctuations of the environment [34]. In addition, the biosynthesis of such osmoprotectants is quicker in bacteria than in their associated plants [1]. It has been observed that inoculation with PGPB generated an improvement of osmolytes in plants, which may be due to bacterial solutes being taken up by the roots or de novo synthesis in plants, where the PGPB have been demonstrated to be useful [1,23]. The accumulation of certain osmoprotectants (e.g., proline, betaine) has helped various vegetal species to resist salt-stress conditions in the presence of beneficial bacterial strains, such as *Burkholderia* [49,50], *Arthrobacter* [51], *Azospirillum* [52], *Bacillus* [51,53], *Rhizobium*, and *Pseudomonas* [24]. Similarly, *Oryza sativa* L. inoculated with *Pseudomonas pseudoalcaligenes* YJ1 has shown the accumulation of glycine betaine-like quaternary compounds, while co-inoculation with *P. pseudoalcaligenes* YJ1 and *Bacillus pumilus* YJ2 was also

able to protect the plant from salinity [54]. It has also been shown that the use of three bacterial strains (*B. megaterium* MPP7, *B. tequilensis* MPP8, and *P. putida* MPP18) increased the production of proline and total soluble sugar in salt-stressed wheat plants, which also reduced electrolytic leakage and enhanced enzymatic activity for the scavenging of reactive oxygen species (ROS) [55]. In this sense, pea plant grown under salinity stress and inoculated with various PGPR (*Acinetobacter bereziniae* IG2, *Enterobacter ludwigii* IG10, and *Alcaligenes faecalis* IG27) showed higher proline and total soluble sugar content, as well as a reduction in oxidative damage [56]. Furthermore, the construction of *Pseudomonas* strain mutants for the gene coding trehalose synthase (*treS*) has been carried out, and the function of this bacterial mechanism in the protection of a plant (tomato) against salt stress has been reported [57].

The plant water potential is altered under high salt concentration conditions. PGPB can regulate water homeostasis by improving the hydraulic conductivity (Figure 1) [1,23,58]. Inoculation with *Bacillus megaterium* B26 in maize plants under salinity (2.59 dS m⁻¹) generated an enhancement in the hydraulic conductance, as related to a positive regulation of PIP-type plasma membrane aquaporins [59]. This same effect has also been observed in tropical corn plants exposed to salt stress (200 mM NaCl) and inoculated with *Pantoea agglomerans* SG_JW.01 rhizobacteria [60]. Furthermore, *Azospirillum brasilense* AZ39 inoculation produced improvements in a PIP-type aquaporin transcription for barley plants grown under saline conditions (200 mM NaCl) [61].

Table 1. PGPB-produced mechanisms related to tolerance against salinity stress.

Bacteria	Plant	Mechanism	Effect	Reference
Osmotic balance				
<i>Pseudomonas mendocina</i>	<i>Lactuca sativa</i> L.	EPS production	High percentage of stable soil aggregates	[40]
<i>Halomonas variabilis</i> and <i>Planococcus rifietoensis</i>	<i>Cicer arietinum</i> L.	Biofilm formation and EPS production	Increased plant growth under salinity and soil aggregation	[41]
<i>Sinorhizobium medicae</i>	<i>Medicago ciliaris</i> L.	Nodulation and bacterial source–sink activities	Differential carbohydrate and hormonal changes between source–sink tissues	[43]
<i>Bradyrhizobium japonicum</i> , <i>Rhizobium</i> sp. and <i>Hydrogenophaga</i> sp.	<i>Glycine max</i> L.	Nodulation and bacterial source–sink activities	Improved shoot and root growth, nitrogen assimilation, and K ⁺ /Na ⁺ ratio	[44]
<i>Azospirillum brasilense</i> and <i>Pantoea dispersa</i>	<i>Capsicum annuum</i> L.	Maintaining of higher stomatal conductance	Higher dry weight and K ⁺ /Na ⁺ ratio	[45]
<i>Bacillus licheniformis</i> , <i>Bacillus subtilis</i> , and <i>Bacillus</i> sp.	<i>Fragaria x ananassa</i>	Maintaining of higher stomatal conductance and transpiration rate	Enhanced growth, yield, and fruit quality	[46]
<i>Bacillus aquimaris</i>	<i>Triticum aestivum</i> L.	Accumulation of osmoprotectants (proline and soluble sugars)	Increased biomass, weight, and leaf nutrients	[47]
<i>Burkholderia phytofirmans</i>	<i>Vitis vinifera</i> L.	Bacterial colonization	Higher root growth and plantlet biomass	[50]
<i>Arthrobacter</i> sp. and <i>Bacillus</i> sp.	<i>Capsicum annuum</i> L.	Accumulation of osmoprotectants (proline) and transcriptional changes	Increased fresh biomass	[51]
<i>Azospirillum brasilense</i>	<i>Zea mays</i> L.	Accumulation of osmoprotectants (trehalose)	Increased survival, leaf and root biomass	[52]
<i>Bacillus</i> spp. and <i>Paenibacillus favisporus</i>	<i>Zea mays</i> L.	Accumulation of osmoprotectants (proline and sugars)	Increased plant biomass, water homeostasis, and soil aggregate stability	[53]

Table 1. Cont.

Bacteria	Plant	Mechanism	Effect	Reference
<i>Rhizobium</i> sp. and <i>Pseudomonas</i> sp.	<i>Zea mays</i> L.	Accumulation of osmoprotectants (proline), ion and water homeostasis	Enhanced plant development, biomass, and nutrient uptake	[24]
<i>Pseudomonas pseudoalcaligenes</i> and <i>Bacillus pumilis</i>	<i>Oryza sativa</i> L.	Accumulation of osmoprotectants (glycine betaine-like compounds)	Higher plant weight and height	[54]
<i>Bacillus megaterium</i> , <i>Bacillus tequilensis</i> , and <i>Pseudomonas putida</i>	<i>Triticum aestivum</i> L.	Accumulation of osmoprotectants (proline and soluble sugars) and transcriptional changes in ion transporter genes (SOS-type)	Reduced electrolytic leakage and oxidative damage	[55]
<i>Acinetobacter bereziniae</i> , <i>Enterobacter ludwigii</i> , and <i>Alcaligenes faecalis</i>	<i>Pisum sativum</i> L.	Accumulation of osmoprotectants (proline and soluble sugars)	Reduced oxidative damage	[56]
<i>Pseudomonas</i> sp.	<i>Solanum lycopersicum</i> L.	Accumulation of osmoprotectants (trehalose) and ACC deaminase production	Higher root and shoot length, total dry weight, and chlorophyll content	[57]
<i>Bacillus megaterium</i>	<i>Zea Mays</i> L.	Upregulation of aquaporin genes (PIP-type)	Higher root hydraulic conductance	[59]
<i>Pantoea agglomerans</i>	<i>Dracaena fragrans</i> (L.) KER GAWL.	Upregulation of aquaporin genes (PIP-type)	Increased dry biomass	[60]
<i>Azospirillum brasilense</i>	<i>Hordeum vulgare</i> L.	Upregulation of aquaporin genes (PIP-type)	Increased biomass and height	[61]
Ion homeostasis				
<i>Bacillus subtilis</i>	<i>Puccinellia tenuiflora</i> SCRIBN. & MERR.	Transcriptional changes in ion transporter genes (HKT-type)	Decreased Na ⁺ accumulation and increased shoot and root growth	[62]
<i>Kocuria rhizophila</i>	<i>Zea mays</i> L.	Transcriptional changes in ion transporter genes (HKT and NHX-type) and hormonal changes (IAA and ABA)	Decreased Na ⁺ accumulation and increased productivity parameters	[63]
<i>Pseudomonas simiae</i>	<i>Glycine max</i> L.	Transcriptional changes in phosphatase activity, accumulation of osmoprotectants (proline), and VOCs production	Higher weight, length, and K ⁺ /Na ⁺ ratio	[64]
<i>Pseudomonas mendocina</i>	<i>Lactuca sativa</i> L.	Transcriptional changes in phosphatase activity and accumulation of osmoprotectants (proline)	Increased biomass and water content	[65]
<i>Brachybacterium</i> sp., <i>Brevibacterium</i> sp. and <i>Haererohalobacter</i> sp.	<i>Arachis hypogaea</i> L.	Water homeostasis and IAA plant accumulation	Higher productivity variables and nutrient content	[66]
<i>Pseudomonas putida</i>	<i>Gossypium hirsutum</i> L.	Hormonal changes (IAA and ABA)	Increased germination rate, productivity variables, and nutrient content	[67]
<i>Azotobacter chroococcum</i>	<i>Zea mays</i> L.	Hormonal changes and accumulation of polyphenols	Higher plant length, weight, and ion uptake	[68]
<i>Azospirillum brasilense</i>	<i>Zea mays</i> L.	Transcriptional changes in plant growth genes	Higher K ⁺ /Na ⁺ ratio	[69]

Table 1. Cont.

Bacteria	Plant	Mechanism	Effect	Reference
<i>Rhizobium</i> sp. and <i>Pseudomonas</i> sp.	<i>Zea mays</i> L.	Accumulation of osmoprotectans (proline), ion and water homeostasis	Enhanced plant development, biomass, and nutrient uptake	[24]
<i>Aeromonas</i> sp. and <i>Bacillus</i> spp.	<i>Triticum aestivum</i> L.	EPS production	Increased growth parameters, K ⁺ /Na ⁺ ratio, and soil aggregation an	[70]
<i>Bacillus subtilis</i> and <i>Marinobacter lipolyticus</i>	<i>Triticum aestivum</i> L.	EPS production	Increased growth parameters, K ⁺ /Na ⁺ ratio, and selective nutrient uptake	[71]
<i>Pseudomonas mendocina</i>	<i>Lactuca sativa</i> L.	EPS production, accumulation of osmoprotectans (proline), and raised antioxidant enzyme activities	Higher shoot biomass, water content, and K ⁺ /Na ⁺ ratio	[72]
<i>Pseudomonas</i> sp. and <i>Bacillus</i> sp.	<i>Glycine max</i> L.	ESP, ACC deaminase and IAA production, and accumulation of osmoprotectans (proline)	Enhanced plant biomass, water content, and photosynthesis activity	[73]
<i>Halomonas maura</i> and <i>Ensifer meliloti</i>	<i>Medicago sativa</i> L.	Nodulation and EPS production	Increased plant biomass and leghaemoglobin	[74]
<i>Staphylococcus sciuri</i> , <i>Zobellella denitrificans</i> , and <i>Arthrobacter endophyticus</i>	<i>Pistacia vera</i> L.	EPS production	Increased productivity parameters, and K ⁺ /Na ⁺ ratio	[75]
<i>Bacillus aquimaris</i>	<i>Triticum aestivum</i> L.	Accumulation of osmoprotectans (proline and soluble sugars)	Increased biomass, weight, and leaf nutrients	[47]

3.2. Ion Homeostasis (Regulation of Ion Content)

Salinity causes Na⁺, Cl⁻, Ca²⁺, Mg²⁺, SO₃²⁻, or CO₃²⁻ accumulation, which results in the ion toxicity phase. Ionic stress occurs under prolonged exposure to high salt concentrations, when the influx of these ions overcomes the rate of exclusion [1,16]. Plants initially compartmentalize the excessive salts in vacuoles, avoiding their accumulation in the cytosol and intracellular spaces, which limits photosynthesis and respiration [1]. Elevated Na⁺ concentrations affect K⁺-dependent process, where the replacement of K⁺ by Na⁺ in biochemical reactions results in protein conformation changes and synthesis [7,76]. It has also been observed that there is a dependence between the reduction of productivity and the ionic balance, determined by the K⁺:Na⁺, Mg²⁺:Na⁺, and Ca²⁺:Na⁺ ratios [9]. Soil micro-organisms have been reported to maintain ion homeostasis, which must benefit plant growth and tolerance during salinity [23,77]; however, these studies have focused on NaCl saline stress, but not other ions involved in saline stress.

Maintaining a high K⁺/Na⁺ ratio is one of the ways by which PGPB can regulate toxic ion homeostasis, thus reducing the accumulation of Na⁺ and Cl⁻ in leaves, boosting ion exclusion by the root, or modulating the expression of ion transporters [1,23]. High-affinity K⁺ transporters (HKT) are plasma membrane proteins that mediate Na⁺ transport in plants, preventing the build-up of high concentrations of Na ions in shoots by excluding to the roots (Figure 1) [49,76]. It has been shown that inoculation with rhizobacteria modulates the expression of these types of transporters. The *B. subtilis* GB03 strain conferred salt tolerance *Puccinellia tenuiflora* Scribn. & Merr., by enhancing selective absorption of K⁺ over Na⁺ and (down- and up-)regulating the expression of HKT-family genes in roots and shoots, such as *HKT1* or *HKT2* [62]. Furthermore, the expression of ion affinity transporters (*ZmHKT1*, *ZmNHX1*, *ZMNHX2*, and *ZmNHX3*) has also been up-regulated in *Zea mays* L. after exposure to salt stress and inoculation with *Kocuria rhizophila* Y1, resulting in protection of the plant against salinity [63]. Thus, tissue-specific regulation of HKT-type

genes in plant–microbe interactions is necessary for toxic ion homeostasis in salt-stressed plants [49,62,76]. Moreover, there are other enzymes that act as sodium antiporters, such as Salt Overlay Sensitive (SOS) genes, which can help the plants to cope with salinity stress [55]. In this sense, inoculation with three bacterial strains (*B. megaterium* MPP7, *B. tequilensis* MPP8, and *P. putida* MPP18) on wheat plants grown under saline conditions revealed the higher expression of SOS1 and SOS4 genes, which were associated with a higher relative water content and photosynthetic pigments in wheat seedlings [55].

PGPB can also reduce the accumulation of Na^+ and Cl^- ions, by regulating the exchange of macro- and micro-nutrients [1]. First, microbial activities, such as P_i (inorganic phosphate) solubilization or siderophore production, may make these nutrients more accessible to plants (Figure 1) [23,77]. Second, inoculation with PGPB can induce the up-regulation of proteins related to phosphatase activity (associated with P_i solubilization). As Vaishnav et al. [64] have reported, *Pseudomonas simiae* AU treatment in soybean plants under salt stress increased the expression of VSP (vegetative storage protein) in plants, which had preponderant roles in acid phosphatase activity. In this sense, water-stressed lettuce plants colonised by the *Pseudomonas mendocina* Palleroni strain also increased acid phosphatase activity, among other effects, thus alleviating oxidative stress in plants [65]. Three bacterial strains, belonging to *Brachy bacterium*, *Brevibacterium*, and *Haerero halobacter* genera, improved productivity variables of peanut plants under 100 mM NaCl, as well as K^+/Na^+ ratio and Ca^{2+} , phosphorus, and nitrogen content [66]. Moreover, a *P. putida* strain increased the absorption of Mg^{2+} , K^+ , and Ca^{2+} in cotton plants grown under saline conditions (3.5 g salt/kg soil), and decreased the uptake of Na^+ ; plant growth was also enhanced after its application [67]. According to Rojas-Tapias et al. [62], maize plants grown under saline conditions (2.93 and 5.85 g NaCl/kg soil) and treated with two *Azotobacter chroococcum* strains showed an enhancement in Na^+ exclusion and K^+ uptake, as well as polyphenol and chlorophyll content, with respect to uninoculated controls. Another free-living nitrogen-fixing rhizobacteria also significantly improved the K^+/Na^+ ratio in a salt-sensitive maize cultivar, by restricting Na^+ uptake and selectively increasing K^+ and Ca^{2+} [69]. In addition, NaCl-affected maize (100 mM), co-inoculated with *Rhizobium* and *Pseudomonas*, exhibited some positive adaptative responses to such stress, such as an increase in proline content or the selective absorption of K^+ ions [24].

Exopolysaccharide (EPS) production also provides a way in which microbes can reduce the uptake of toxic ions in plants. These compounds act as a physical barrier around the root system, preventing the effects of the ion toxicity phase [17,35,77]. EPS bind cations, including Na^+ , and thereby decrease the accessibility of toxic ions available for plant uptake, reducing the salinity stress by diminishing its transfer to leaves (Figure 1) [7,17,23,35]. According to Ashraf et al. and Talebi Atouei et al. [70,71], wheat plants affected by salinity and treated with EPS-producing bacteria showed increases in growth parameters and alteration of nutrient uptake, by diminishing Na^+ concentration and boosting the absorption of K^+ and Ca^{2+} . Similarly, a plant growth-promoting rhizobacteria (*P. mendocina*), in combination with an arbuscular mycorrhizal fungus (*G. intraradices*), colonised lettuce plants, which presented higher concentrations of foliar K^+ and lower amounts of Na^+ under saline conditions [72]. The inoculation with other exopolysaccharide-producing rhizobacteria also indicated the important role that they play in alleviating saline stress conditions in different crops, such as soybean, wheat, alfalfa, or pistachio [47,73–75].

4. Molecules Synthesized by Rhizobacteria Involved in Tolerance/Resistance to Osmotic Stress

4.1. Synthesis of Phytohormones

Phytohormones are synthesized by plants in response to salt stress, such as indole-3-acetic acid (IAA), abscisic acid (ABA), or ethylene. These substances alter plant metabolism, morphology, biomass production, and other mechanisms [23,77]. Moreover, soil bacteria may directly alter the plant hormonal balance, by producing exogenous phytohormones. Thus, changes in hormonal signalling arising from plant–microbe interactions are considered as a mechanism for plant soil salinity tolerance (Figure 2) [1,23,77].

In this sense, it has been shown that there is a correlation between bacterial IAA production and plant hormone status modification, which has positive effects on plant growth and development (Figure 2). Thus, both the use of exogenous IAA and inoculation with an IAA-deficient mutant (*A. brasilense* Sp245 indole pyruvate decarboxylase *-ipdC*-mutant, generating only 10% of wild-type auxin production), showed that the growth response of *Phaseolus vulgaris* L. roots is related to a differential response to the bacterially produced auxin, in terms of root dry weight, nodule number, and the number of basal roots formed during germination [83].

4.1.2. Ethylene (ACC-Deaminase)

Ethylene is commonly known as a stress hormone, due to its synthesis in response to abiotic and biotic stress in plants [77]. This organic compound is regarded as an inhibitor of root growth and formation, also negatively influencing plant development as a whole [35,42]. Aminocyclopropane-1-carboxylate (ACC) is the precursor of ethylene biosynthesis, which can be transported specifically to stressed organs, where is converted into ethylene by the ACC oxidase enzyme [42,77]. PGPB influence the ethylene cycle in plants by inhibiting its production, which happens because rhizobacteria can secrete ACC deaminase, an enzyme which converts ACC into ammonia and α -ketobutyrate; possible sources of carbon and nitrogen for bacteria [1,34]. In this context, ACC deaminase-containing PGPB may mitigate stress symptoms and boost plant development, by reducing the levels of this stress hormone and preventing the associated growth inhibition (Figure 2) [34,35,84].

Many studies have shown that ACC deaminase-producing bacteria can diminish the ethylene inhibition due to salinity. Maize inoculated with *Pseudomonas* and *Enterobacter* strains under saline conditions demonstrated that ACC deaminase synthesized by these bacteria led to improvements in plant growth parameters and nutrient absorption, such as higher K^+/Na^+ ratios and NPK uptake [85]. Barnawal et al. [84] have reported a correlation between the protection of *Trigonella* plants against osmotic stress and reduced levels of ACC, due to inoculation with ACC deaminase-containing rhizobacteria (*Bacillus* and *Ensifer*), which also generated improvements in growth and plant-microbe interaction. *Achromobacter piechaudii* inoculation increased the nutrient uptake (P and K), as well as the fresh and dry weights of tomato seedlings grown in the presence of up to 172 mM NaCl salt, and diminished ethylene production [86]. Three ACC deaminase-producing halotolerant bacteria (*Brevibacterium*, *Bacillus*, and *Zhihengliuella*) have been evaluated, in terms of improving red pepper growth under salt stress. Inoculation with these strains reduced ethylene production and enhanced plant development and nutrient acquisition [87]. The correlation between ACC deaminase production and protection against salt stress has been demonstrated in various reports. Thus, the inoculation of groundnut plants with an ACC deaminase-producing *P. fluorescens* strain enhanced their saline resistance and the yield of the plant, as compared with other strains lacking this activity [88]. In this sense, Orozco-Mosqueda et al. [51] and Ali et al. [89] have reported that ACC deaminase-deficient mutants (mutated at *acdS*) inoculated on salt-stressed tomato plants performed worse, in terms of different production parameters, compared to wild-type strains.

Furthermore, there exist microbes which are capable of producing both IAA and ACC deaminase. As previously noted, IAA induces cell division and root growth, and the ACC deaminase produced by these bacteria hydrolyse the excess ACC, as well as promoting plant development [1,35]. Therefore, the combined action of both phytohormones can also help the plant to cope with adverse environmental conditions. For example, IAA- and ACC deaminase-producing *Pantoea dispersa* led to improved production parameters in salt-affected *Cicer arietinum* L. plants (150 mM NaCl). These effects were associated with a higher K^+/Na^+ ratio, chlorophyll content, and relative leaf water content [90].

4.1.3. Abscisic Acid (ABA)

Abscisic acid (ABA) is another phytohormone involved in the plant response to abiotic and biotic stresses, mainly in protection against drought, salt stress, and toxic metals [91].

Under osmotic stress, ABA is produced in roots, and then can be translocated into leaves. It is involved in stomatal closure (reducing transpiration and maintaining water potential), the growth and emergence of roots (enhancing water uptake), and ion homeostasis [77,91]. Many PGPB can alter the ABA status in plants, acting as modulators of plant ABA content and, thus, allowing for the management of salt stress.

Some reports have exhibited that PGPB inoculation prevents ABA accumulation in plants (Figure 2). According to Yao et al. [67], cotton plants inoculated with *P. putida* Rs198 showed biomass enhancements and salt tolerance, induced by higher nutrient uptake and lower ABA production. In this sense, the inoculation of cucumber plants with *Burkholderia*, *Promicromonospora*, and *Acinetobacter* strains under salt and drought stress were revealed to be effective, with consequent increases in biomass, chlorophyll, water, and ion content. These treated plants also presented down-regulation of ABA, compared with uninoculated controls [92]. Additionally, Belimov et al. [93] conducted inoculation trials in tomato plants (using wild-type and negative mutants in ABA), with two ABA metabolizing rhizobacteria, in which it was observed that microbial inoculation decreased ABA concentration in roots and leaves, and altered plant development under saline conditions. Further, *B. aryabhatai* ATL29 and *A. woluwensis* ATL43 strains inoculated on salt-stressed soybean plants caused an enhancement in plant growth productive parameters, as associated with a reduction in ABA endogenous levels and the expression of *GmNARK* genes (related to the induction of ABA production) [94]. Finally, *K. rhizophila* Y1 inoculation protected maize from salt stress by regulating plant hormones: IAA (positively) and ABA (negatively). This study indicated that strain Y1 inoculation reduced ABA content markedly, in comparison with non-inoculated treatments, under salt stress treatment; these results being associated with the down-regulation of *ZmNCED1* (the key gene for ABA synthesis) [63].

On the other hand, other studies have found that PGPB treatments improved ABA content in plants (Figure 2). Thus, Salomon et al. [95] have indicated that *Bacillus* and *Pseudomonas* strains (ABA-producing) act as stress alleviators in *Vitis vinifera* L., by inducing ABA synthesis and, so, reducing water losses. In another report, Cohen et al. [96] proposed that an ABA-producing *Azospirillum lipoferum* strain reversed the negative effects caused by osmotic stress in maize plants, even using ABA synthesis inhibitors. These results were correlated with ABA levels assessed by GC-EIMS. Furthermore, inoculation of maize plants with *B. pumilis* positively modulated the ABA content in leaves, while increases in water content, photosynthetic pigments, and osmotic potential were also recorded. This established the great potential of this bacterium for formulations to alleviate osmotic stress [97]. In this way, the evidence seems to indicate that PGPB are capable of modifying ABA levels, optimizing their function and regulation (which are already complex), while presenting different levels, according to the stage of development of the plant [98,99].

4.2. Other Molecules Synthesized by Rhizobacteria

Certain bacterial mechanisms for modulating salt stress in plants are related to the secretion of extracellular molecules, such as volatile organic compounds or other organic compounds [1,34]. These substances act as inter-organismal signals, which affect plant behaviour by manipulating response pathways and regulatory functions, eliciting positive effects against stress conditions [100,101], and several species are able to produce some which can alleviate osmotic and salinity stress (Table 2).

4.2.1. Volatile Organic Compounds (VOCs)

Volatile Organic Compounds (VOCs) are carbon-containing chemical substances with low molecular masses and boiling points, which can be emitted by rhizobacteria [1,79]. It has been reported that microbial volatiles can induce resistance to diseases and stimulate plant growth [79,102]. Other studies have indicated the effect of these substances in relieving salt stress in plants (Figure 2). The application of a putative *P. simiae* VOCs blend to soybean (under 100 mM NaCl) decreased the Na⁺ concentration in roots, and increased proline and chlorophyll content. Molecular analysis confirmed that this effect

was induced by protein transcription changes [64]. Vaishnav et al. [103] has also found that two VOCs—namely, 4-nitroguaiacol and quinoline—promote soybean seed germination under 100 mM NaCl stress. Accordingly, *Mentha x piperita* L. plants grown under different NaCl levels (0 to 100 mM) were exposed to *B. amyloliquefaciens* GB03 VOCs (acetoin being the main one). This counteracted the negative effects of salinity, also causing a reduction in the endogenous levels of ABA in the plant [104].

4.2.2. Polyamines

Polyamines (PAs) are aliphatic amines with great antioxidant potential, which play an important role in plant development and abiotic stress response, by regulating antioxidant enzymes and genetic activities, as well as ROS homeostasis (Figure 2). Spermidine, spermine, and putrescine are the most significant polyamines [1,101]. It has been shown that exogenous PA application can induce tolerance to salinity, but more exhaustive studies of the effects on plants of the PAs secreted by PGPR are necessary. For example, spermidine secreted by *B. amyloliquefaciens* SQR9 caused a decrease in the effects of oxidative damage, a reduction of Na⁺ toxicity, and an inhibition of ABA accumulation in *Zea mays* L. plants. These resulted in plant salt tolerance enhancement, which was confirmed through the construction of mutants [105,106]. Moreover, tomato plants grown under osmotic stress and inoculated with *B. megaterium* TG1-E1 accumulated a higher level of arginine, a precursor in the synthesis of polyamines (e.g., spermidine, spermine, or putrescine) [107].

4.2.3. Bacteriocins and Lipo-Chito oligosaccharides

Bacteriocins are ribosomally synthesized peptides secreted by bacteria, which are bactericidal and/or bacteriostatic against organisms closely related to the producer, and active at low concentrations [1,108]. These molecules are used as a competitive advantage in the ecological niche. The use of bacteriocins, such as Thuricin, has been focused in the food industry and medicines, but also has agricultural potential [108]. Lipo-chitoooligosaccharides (LCOs) are molecules produced by microbes that trigger their symbiotic interactions with plants [109]. Among them, Nod-factors (NFs) are secreted by rhizobacteria in response to flavonoids in root exudates, which initiate nodule formation [1,110]. For example, LCOs extracted from *B. diazoefficiens* USDA 110 and from *R. tropici* CIAT 889, in conjunction with various rhizobacterial strains (*Bradyrhizobium* and *Azospirillum*), have been shown to enhance grain quality and nodule formation in soybean [111]. Furthermore, NFs can positively affect plant growth, even under abiotic stresses (Figure 2) [110,112,113]. Thuricin 17 (Th17), isolated from *B. thuringiensis* NEB17, has been shown to be a plant growth promoter under saline stress conditions, applied alone or in conjunction with *Bradyrhizobium japonicum* 532C LCOs. *Brassica napus* L. plants treated with Th17 showed a positive response under saline and temperature stress conditions, causing a higher biomass production and root development [113]. In this sense, the application of *B. thuringiensis* NEB17 Th17 and *B. japonicum* 532C LCOs to salt-stressed soybean (100 mM NaCl) altered the plant proteome, by positively regulating proteins involved in photosynthesis, metabolism, and stress-related pathways, such as: PEP carboxylase, rubisco oxygenase large subunit, glutathione-S-transferase (with antioxidant activity), and LEA proteins (involved in cellular dehydration tolerance) [110]. Thus, Th17 and LCO can manipulate the plant proteome profile and improve its physiological tolerance to salinity [110,112].

Table 2. PGPB producing molecules involved in tolerance to salinity stress.

Bacteria	Plant	Mechanism	Effect	Reference
Synthesis of phytohormones				
<i>Pseudomonas putida</i>	<i>Gossypium hirsutum</i> L.	Hormonal changes (IAA and ABA)	Increased germination rate, productivity variables, and nutrient content	[67]
<i>Brachybacterium</i> sp., <i>Brevibacterium</i> sp. and <i>Haererohalobacter</i> sp.	<i>Arachis hypogaea</i> L.	Water homeostasis and IAA plant accumulation	Higher productivity variables and nutrient content	[66]
<i>Azospirillum lipoferum</i>	<i>Triticum aestivum</i> L.	IAA production and N ₂ fixation	Enhanced plant weight and chlorophyll content	[81]
<i>Streptomyces</i> sp.	<i>Triticum aestivum</i> L.	IAA and siderophore production	Increased plant germination rate, length, weight, and nutritional content	[82]
<i>Azospirillum brasilense</i> and <i>Rhizobium etli</i>	<i>Phaseolus vulgaris</i> L.	IAA production	Higher root weight, and number of roots and nodules	[83]
<i>Pseudomonas fluorescens</i> and <i>Enterobacter aerogenes</i>	<i>Zea mays</i> L.	ACC deaminase production	Increased plant height, biomass, K ⁺ /Na ⁺ ratio, and NPK uptake	[85]
<i>Bacillus subtilis</i> and <i>Ensifer meliloti</i>	<i>Trigonella foenum-graecum</i> L.	ACC deaminase production	Improved plant weight with lower ACC concentration	[84]
<i>Achromobacter piechaudii</i>	<i>Solanum lycopersicum</i> L.	ACC deaminase production	Increased fresh and dry weight, and P and K uptake	[86]
<i>Brevibacterium iodinum</i> , <i>Bacillus licheniformis</i> , and <i>Zhiehengluelia alba</i>	<i>Capsicum annuum</i> L.	ACC deaminase production	Higher biomass and nutrient uptake	[87]
<i>Pseudomonas fluorescens</i>	<i>Arachis hypogaea</i> L.	ACC deaminase production	Increased seedling weight, height, and germination	[88]
<i>Pseudomonas</i> sp.	<i>Solanum lycopersicum</i> L.	Accumulation of osmoprotectants (trehalose) and ACC deaminase production	Higher root and shoot length, total dry weight, and chlorophyll content	[57]
<i>Pseudomonas fluorescens</i> and <i>Pseudomonas migulae</i>	<i>Solanum lycopersicum</i> L.	ACC deaminase production	Higher biomass, chlorophyll content, and number of flowers and buds	[89]
<i>Pantoea dispersa</i>	<i>Cicer arietinum</i> L.	IAA and ACC deaminase production	Improved productivity parameters, K ⁺ /Na ⁺ ratio, and water and chlorophyll content	[90]
<i>Burkholderia cepacian</i> , <i>Promicromonospora</i> sp. and <i>Acinetobacter calcoaceticus</i>	<i>Cucumis sativus</i> L.	Downregulation of ABA genes	Increased biomass, and chlorophyll, water, and ion (K and P) content	[92]
<i>Rhodococcus</i> sp. and <i>Novosphingobium</i> sp.	<i>Solanum lycopersicum</i> L.	Metabolizing ABA	Decreased ABA concentration in roots and leaves, and altered plant development	[93]
<i>Bacillus aryabhatai</i> and <i>Arthrobacter woluwensis</i>	<i>Glycine max</i> L.	Reduction in ABA endogenous levels and downregulation of ABA genes	Increased fresh and dry weight, length, and chlorophyll content	[94]
<i>Kocuria rhizophila</i>	<i>Zea mays</i> L.	Transcriptional changes in ion transporter genes (HKT and NHX-type) and hormonal changes (IAA and ABA)	Decreased Na ⁺ accumulation and increased productivity parameters	[63]
<i>Bacillus licheniformis</i> and <i>Pseudomonas fluorescens</i>	<i>Vitis vinifera</i> L.	ABA production and accumulation in plants	Diminished plant water loss rate	[95]

Table 2. Cont.

Bacteria	Plant	Mechanism	Effect	Reference
<i>Azospirillum lipoferum</i>	<i>Zea mays</i> L.	ABA, IAA, and gibberellins production	Reversed negative effects caused by osmotic stress	[96]
<i>Bacillus pumilis</i>	<i>Zea mays</i> L.	ABA production and accumulation in leaves	Increased water content, photosynthetic pigments, and osmotic potential	[97]
Other molecules synthesized by rhizobacteria				
<i>Pseudomonas simiae</i>	<i>Glycine max</i> L.	Transcriptional changes in phosphatase activity, accumulation of osmoprotectants (proline), and VOCs production	Higher weight and length, and K ⁺ /Na ⁺ ratio	[64]
<i>Pseudomonas psimiae</i>	<i>Glycine max</i> L.	VOCs production and transcriptional changes in phosphatase activity	Promoted seed germination	[103]
<i>Bacillus amyloliquefaciens</i>	<i>Mentha × piperita</i> L.	ABA reduction and endogenous levels	Higher total chlorophyll content, and better morphological characteristics	[104]
<i>Bacillus amyloliquefaciens</i>	<i>Zea mays</i> L.	Polyamine production (spermidine)	Decreased oxidative damage and Na ⁺ toxicity, and inhibition of ABA accumulation in plants	[105,106]
<i>Bacillus megaterium</i>	<i>Solanum lycopersicum</i> L.	Production of polyamine precursors	Osmotic stress resistance	[107]
<i>Bradyrhizobium japonicum</i> and <i>Bacillus thuringiensis</i>	<i>Brassica napus</i> L.	Lipo-chitooligosaccharide and bacteriocin production	Affected plant growth, architecture, and biomass	[113]
<i>Bradyrhizobium japonicum</i> and <i>Bacillus thuringiensis</i>	<i>Glycine max</i> L.	Lipo-chitooligosaccharide and bacteriocin production	Changes in the proteome during seed germination	[110]

5. Conclusions

Soil salinity is one of the main causes of abiotic stress in plants, as it generates not only environmental, but also economic and social problems. Crop yields can be reduced by the effects of salinity in plants (e.g., osmotic stress, ion toxicity, nutrient deficiency, and oxidative stress) and soils (loss of structure and fertility). In this sense, the use of plant growth-promoting bacteria (PGPB) has been reported as a sustainable and cost-effective alternative to increase plant tolerance to salt stress. Stress adaptation of plants is induced by the microbiota, through: (i) changes in plant hormonal balance (e.g., IAA and ABA production, or inhibition of ethylene synthesis); (ii) the release of extracellular compounds that act as chemical signals for the plant (e.g., LCOs, PAs, and/or VOCs), or enhancers that improve the soil conditions for plant development (e.g., EPS or Bacteriocins); (iii) regulating the internal ionic content of the plant (e.g., inducing ion transporters or regulating the exchange of macro and micronutrients); and (iv) facilitating the synthesis of osmoprotectant compounds that reduce osmotic stress (e.g., soluble sugars, proline, betaine, or trehalose).

Despite the studies carried out on these mechanisms to date, there exist other beneficial effects of soil microbiota that remain unknown, making it necessary to identify them, in order to optimise the use of PGPB in agronomic systems. Moreover, it is important to bear in mind that the action of these mechanisms is not individual, but that the same microorganism may induce different effects in the plant.

Therefore, the potential that PGPB provide is an incalculable resource favouring the salt tolerance and, thereby, reducing the effects of soil salinity in crops. In this line, many studies have shown that inoculation with halotolerant bacteria can lead to salinity alleviation in plants, but not all of them have investigated the mechanisms underlying these effects. Furthermore, the range of microorganisms capable of growing in saline conditions and promoting plant development is very wide. For all of these reasons, there exists a need

for a deeper understanding and knowledge of plant–microorganism interactions and the PGPB mechanisms which mitigate salt stress in plants.

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