





Review

Halotolerant Rhizobacteria for Salinity-Stress Mitigation: Diversity, Mechanisms and Molecular Approaches

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Abstract: Agriculture is the best foundation for human livelihoods, and, in this respect, crop production has been forced to adopt sustainable farming practices. However, soil salinity severely affects crop growth, the degradation of soil quality, and fertility in many countries of the world. This results in the loss of profitability, the growth of agricultural yields, and the step-by-step decline of the soil nutrient content. Thus, researchers have focused on searching for halotolerant and plant growth-promoting bacteria (PGPB) to increase soil fertility and productivity. The beneficial bacteria are frequently connected with the plant rhizosphere and can alleviate plant growth under salinity stress through direct or indirect mechanisms. In this context, PGPB have attained a unique position. The responses include an increased rate of photosynthesis, high production of antioxidants, osmolyte accumulation, decreased Na⁺ ions, maintenance of the water balance, a high germination rate, and well-developed root and shoot elongation under salt-stress conditions. Therefore, the use of PGPB as bioformulations under salinity stress has been an emerging research avenue for the last few years, and applications of biopesticides and biofertilizers are being considered as alternative tools for sustainable agriculture, as they are ecofriendly and minimize all kinds of stresses. Halotolerant PGPB possess greater potential for use in salinity-affected soil as sustainable bioinoculants and for the bioremediation of salt-affected soil.

Keywords: antioxidants; bioformulation; direct or indirect mechanisms; plant growth-promoting bacteria (PGPB); salinity stress; sustainable agriculture

1. Introduction

The growing population and the food demand are challenging for any country's government, resulting in pressure shifts towards agricultural practices and crop productivity enhancement. Enhanced crop productivity is quite complicated in different agro-ecosystems, and is mainly affected by climatic conditions, edaphic factors, farming practices, and management techniques [1]. A series of abiotic factors comprising temperature, drought, soil pH, salinity, heavy metal, and the application of pesticides and chemical fertilizer hamper crop productivity [2]. Among all of these, salinity stress is recognized as a real threat to agricultural production [3]. In the past few years, soil salinity

and continuously changing climatic conditions have created food insecurity in several countries and have affected arid and semiarid areas of the world, at the rate of 1–2% every year [4,5]. According to some reports, more than a third of irrigated land may become barren because of the accelerated rate of salinization [6]. According to the data released by using the latest version of the FAO main report [7], soil salinity has been identified as an emerging threat to sustainable agriculture. Several recent kinds of research have estimated that around 1,128 million ha are globally aggrieved by high salinity, including 20% of the total cultivated land, and 33% of irrigated agricultural land [8]. In India, approximately 5% of the net cultivated area is salinity-affected, and that covers the Indo-Gangetic plains-lined states [9].

Zorb et al. [10] list the factors that directly influence salinity: low precipitation, higher rates of evapotranspiration, the leaching of minerals from the plant rhizosphere, anthropogenic activity, farming practices, and the formation of water-stressed conditions in plants. These factors lead to soil salinization that seriously affects the biodiversity of flora and fauna, the water quality, the water supply critical for human needs, industry, agricultural productivity, and quality, and cause a reduction in the cultivable area as well as in crops [11]. A high salt concentration contrarily strikes the physiological and biological soil processes of plants, such as the decomposition of residue, respiration, denitrification, nitrification, microbial activity, soil biodiversity, and the plant–microbe interaction [12]. The excessive application of agrochemicals and chemical fertilizers enhances the salinity input in soil and reduces crop productivity [13]. In this sequence, some agricultural practices, such as down plowing and tilling, more profoundly increase the evaporation rate of water from the soil and the deposition of salts that affect crop production. In addition, the salinity of the soil can also increase because of the salts present in the irrigation water, which reduce productivity [14]. Soil is defined as saline when its electrical conductivity (EC) exceeds 4 dSm⁻¹ (approximately 40 mM Na⁺Cl⁻). Salinity levels are essential for reducing the yields of many crop plants [15]. Different types of salts, e.g., sodium chloride (Na⁺Cl⁻), sodium sulphate (Na₂SO₄), sodium nitrate (NaNO₃), magnesium sulphate [MgSO₄], magnesium chloride (MgCl₂), potassium sulphate (K₂SO₄), calcium carbonate (CaCO₃), etc., are present in saline soil, in which Na⁺Cl⁻ causes severe problems for higher plants [16]. The mitigation of the saline effect from the soil is an exhaustive method and involves considerable time and money. However, for a long time, saline soils have been improved mainly by physical and chemical processes. Removing soluble salts from the root zone is considered in the physical process, including scraping, flushing, and leaching methods [17]. Although chemical approaches use gypsum and lime as counteracting agents, when the salt concentration is too high, these methods are not supportable and are inefficient at mitigating the salinity effects [15].

Therefore, achieving manageable crop yields is the need of the hour in saline lands, and sustainable methods should also be employed, in addition to using salinity-tolerant crops or improvement approaches, including chemical neutralizers. In the last few decades, the search for salt-tolerant plant growth-promoting bacteria [PGPB] has been accelerated in order to improve the soil fertility and the nutrient acquisition in saline soil, and to enhance the productivity of crops [18]. Their inherent reaction toward salt stress is associated with their capability to produce compatible solutes, osmoprotectants, and specific transporter channels. Salt-tolerant PGPB are now a thirst of researchers and are also being used as bioinoculants to increase crop yields, improve soil health, and protect from phytopathogens. The current review targets diversity, salt-tolerant PGPB-mediated mechanisms, and the up-regulation of the regarding genes that are transferred through various methods, for example, *Agrobacterium*-mediated gene transfer having an evolutionary impact on their respective hosts (plants). Their application as bioinoculants to increase crop yields has also been targeted. In addition, approaches to salt-tolerant PGPB-mediated crop improvements, new understandings, and the productivity improvement of crops facing salinity pressure are similar discourses for future concern [19,20].

2. Impact of Salinity on Plant Growth and Development

Several researchers have documented the effects of soil salinity on plant enlargement and development [germination, and vegetative and reproductive enlargement], biomass production, and the grain yields of several crops [21]. High salinity has significantly reduced the leaf relative water content, the uptake of nutrients, the pigment content, the gaseous exchange attributes of the leaf, the total flavonoid, the phenolic contents, the plant growth, and the biomass production [22]. The plant organs show significant differences at the anatomical, morphological, and physiological levels, adversely affected by salinity stress. The plant usually shows dynamic enlargement, physiology, metabolic pathways, and gene expression in response to salt stress. The salinity mitigation approaches include proline accumulation within cells [23], the modulation of hormones, and the gathering of metabolic products, such as glycine betaine and polyols. These also include nitric oxide (NO), and compounds to combat the formation of reactive oxygen species (ROS). NO directly or indirectly triggers the expression of several redox-regulated genes. NO also reacts with lipid radicals, and thus inhibits lipid oxidation, exerting a protective effect by scavenging superoxide radicals and forming peroxynitrite, which other cellular processes can neutralize. NO also helps activate several antioxidant enzymes, including catalase (CAT), ascorbate or thiol-dependent peroxidase (APX), glutathione reductase [GR], and superoxide dismutase (SOD).

The plant's growth in salinity conditions is revealed at two stages: the osmotic stage (early response), and the ionic stage (late response). High salinity has harmful effects on most essential plant processes, such as disrupting photosynthesis, protein synthesis, lipid metabolism, osmotic and ionic equilibrium, and energy (Figure 1).

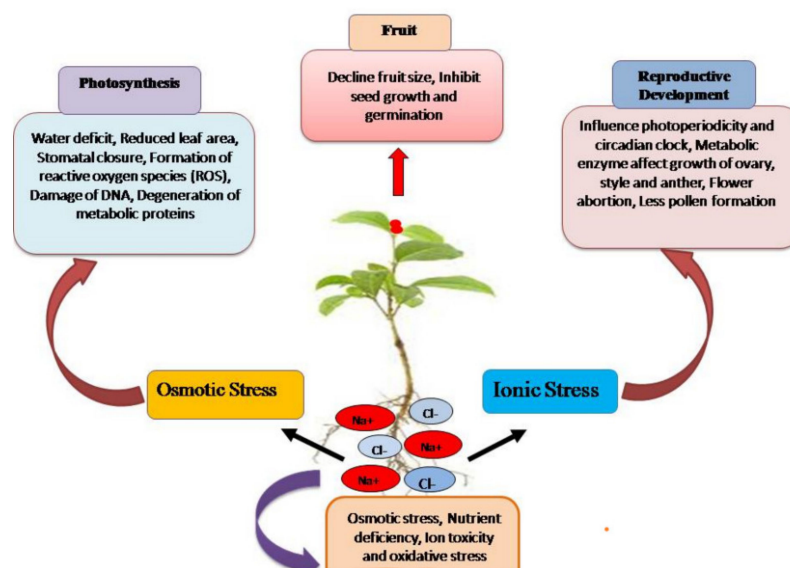


Figure 1. Transduction of salinity stress (osmotic and ionic stress) in plants.

The initial stage of salt stress is caused by salt present outside of the rhizospheric compartment, while the later-stage salinity stress is a consequence of the toxic effects of the salt within the plant [24]. Osmotic stress can be improved through ABA-dependent and ABA-independent pathways, whereas ionic stress is alleviated through ion homeostasis, the salt hypersensitive [SOS] pathway, and the involvement of ion transporters. Osmotic imbalance leads to water loss, reduced leaf area expansion, and stomata closure, ultimately impairing growth and the photosynthetic rate [25]. The shoot and reproductive development are affected by osmotic stress, which manifests in smaller leaves and slower emergence, and the lateral buds endure the quiescent phase and earlier flowering. The growth-modulating mechanisms use hormones and their precursors for stimulating long-distance signals from

the roots to the shoots. Phytohormone signaling triggers cell growth, the division rate, and differentiation, thus regulating the developmental morphogenesis of the plant [26].

Salinity stress in plants is a cumulative effect of osmotic and ionic stress that adversely affects plant growth and productivity. Osmotic adjustment, ion homeostasis, and detoxification are involved in the salt-stress response of plants [27]. Ionic stress develops when plants increase the Na^+ accumulation in their leaves above the threshold levels, leading to chlorosis and decreased photosynthesis, and other metabolic activities. Ionic stress leads to the excessive accretion of Na^+ in older leaves, leading to the premature aging of salt stored in grown-up leaves [28].

Various salt ions, such as bicarbonate (HCO_3^-), sodium (Na^+), potassium (K^+), carbonate (CO_3^{2-}), calcium (Ca^{+2}), sulfate (SO_4^{2-}), chloride (Cl^-), and magnesium (Mg^{+2}) cause salinization. In most salts, sodium chloride is the chief component, and its chloride ions are known to be toxic to plants and to inhibit plant growth at high levels [29]. Higher concentrations of Na^+ and Cl^- ions in the soil affect other essential elements and reduce the plant's access needed to absorb essential nutrients and minerals [30]. Fertilizers with high-salt indexes have an osmotic effect, making it challenging to extract the water needed for plant growth. Multiple genes have been found to be associated with the salt-tolerance mechanism. A plethora of stress-related genes conferring salt-stress tolerance in plants has been reported to be involved in metabolic pathways, transcription regulation, signal transduction, and ion transporters [31].

3. Halotolerant/Salinity-Tolerant PGPB

Studies on halotolerant PGPB occurrence, the plant–microbe interaction, and signaling in the agricultural crop microbiome, or influence on the crop production, rank second for their copiousness, proposing in what manner the salinity is affected globally (Figure 2). The resistant breeding method is the third most relevant Halotolerant PGPB concerning the research topic, which includes developing and evaluating the mutant, screening for resistance, conventional breeding, and transgenic crops, which reduce salinity issues.

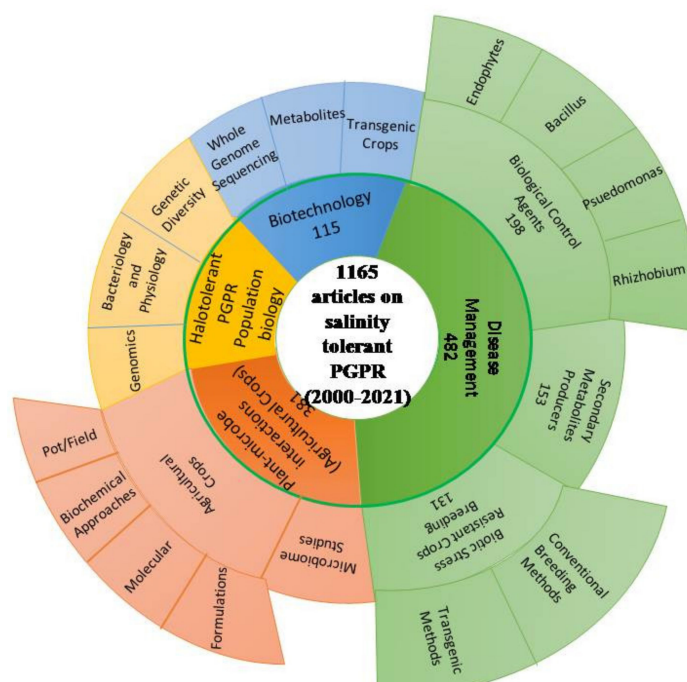


Figure 2. Main topics of scientific articles related to PGPB. Articles were retrieved from the PubMed database and the Google Scholar search engine (2000–2021).

Consequently, biological monitoring and the host's genetic resistance have been deliberated as the most imperative strategies for salinity-tolerant crops and disease man-

agement. In 153 papers, the naturally produced secondary metabolites of Halotolerant PGPB were studied with regard to their production, their application, and their effect on phytopathogens. The interaction of the Halotolerant PGPB with other microbes, and its population studies, have been worked on using “omics” approaches. However, most articles discuss biocontrol agents (BCAs) that comprise endophytic microbes and strains of *Bacillus* spp., *Pseudomonas* spp., and *Rhizobium* spp. In the current research, the trials shown under pot, field, and in vitro conditions are also mentioned in Figure 2.

Biodiversity of Salt-Tolerant Plant Growth-Promoting Bacteria [PGPB]

Soil and plant microbiomes possess a diversity of microbes belonging to diverse bacteria, archaea, and fungi [32]. Similarly, salinity-prevalent soil and crops facilitate halotolerant microbes. Among microbes, halotolerant plant growth-promoting bacteria demonstrate their inherent metabolic capability to tolerate salinity stress and promote plant growth through different mechanisms. Several researchers have reported on the diversity, tolerance mechanisms, and plant growth-promoting-predominant halotolerant bacterial genera, such as *Agrobacterium*, *Arhrobacter*, *Ochromobacter*, *Azospirillum*, *Alcaligenes*, *Bacillus*, *Enterobacter*, *Burkholderia*, *Microbacterium*, *Klebsiella*, *Streptomyces*, *Pseudomonas*, *Rhizobium*, and *Pantoea*, which have been reported to alleviate salt stress in crops [33–35]. In a study by Phour et al. [36], the inoculation of halotolerant *Pseudomonas argentinensis* HMM57 and *Pseudomonas azotoformans* JMM15 in *Brassica juncea* resulted in a significant increase in the shoot, root, and plant dry weights [36].

Zhang et al. [37] explored the genetic diversity of salt-tolerant PGPB (150 g/L Na⁺Cl⁻) isolated from a paddy rhizosphere in Taoyuan and China. The phylogenetic analysis showed 74 salt-tolerating isolates belonging to the orders, *Rhizobiales* (1%), *Oceanospirillales* (4%), *Actinomycetales* (22%), and *Bacillales* (72%) that further effectively enhanced the growth and productivity of rice under salinity stress. Aslam et al. [38] revealed that a halotolerant *Staphylococcus jettensis* F-11 significantly increased [threefold] the plant biomass (*Zea mays*), in dry weight, under 200-mM salinity stress. A current study demonstrates that the occurrence of salinity-tolerant *Pseudomonas putida* and *Novosphingobium* sp. reduce the negative effects of salt stress in citrus plants by lowering the levels of salicylic acid (SA) and abscisic acid (ABA). IAA's growing stock in the leaf inhibits photosystem II's processing (Fv/Fm) and prevents root congregation proline and chloride during salt stress [39]. Several researchers have documented the diversity, salt tolerance, and plant growth-promoting activity of coastal-soil-isolated PGPB, and their application as inoculates in pot and field experiments [40]. Amaresan et al. [41] deciphered the diversity of 121 bacterial strains isolated from Tsunami-affected regions in the Andaman and Nicobar Islands of India. The selected 23 isolates displayed salinity tolerance (10% Na⁺Cl⁻), with PGP characteristics, and belonged to the genera, *Lysinibacillus* spp., *Bacillus* spp., *Microbacterium* spp., *Alcaligenes faecalis*, and *Enterobacter* spp., and they are applied as bioinoculants for salinity-mitigation approaches in different crops. Several examples of halotolerant plant-beneficial microbes, their diversity, tolerance mechanisms, and plant growth-promoting responses are documented in Table 1. The role of salt-tolerant PGPB in the mitigation of salinity stress and the enhancement of crop productivity is well-studied. However, the interactions, colonization, and mechanisms between these microbes and plants, and the up-regulation of genes during salinity stress, need to be explored.

Table 1. PGPB with their salt tolerance values.

Crop	Strain	Na ⁺ Cl ⁻ Tolerance(mM)	Condition	Effect	Country	Reference
Wheat (<i>Triticumaestivum</i>)	<i>Azotobacter chroococcum</i> AZ6	200	Pot	Proline and amino acid	Algérie	[42]
	<i>Bacillus Subtilis</i>	200	Field	Improvement in plant growth	Russia	[43]
	<i>Enterobacter cloacae</i> ZNP-3	150–200	Pot	Enlargement of agronomic traits and chlorophyll content	India	[44]
	<i>Enterobacter cloacae</i> SBP-8	200	Pot	Antioxidant activity	India	[45]
	<i>P. fluorescens</i>	18–36	Invitro	Enhancement of agronomic traits	Iran	[46]
	<i>Pseudomonas</i> sp. and <i>Bacillus</i> sp.	Soil salinity	Pot	Plant growth promotion	India	[47]
Rice (<i>Oryza sativa</i>)	<i>Bacillus</i> and <i>Pseudomonas</i> spp.	Saline soil	Field	Phytostimulation	India	[48]
	<i>Bacillus amyloliquefaciens</i> RWL-1	120	Pot	Increase in essential amino acids	Korea	[49]
	<i>Pseudomonas aeruginosa</i> [PRR1 and PHL3] and <i>Lysinibacillus</i> sp. [BPC2]	100 mM	Pot	Germination percentage and root length	India	[50]
	<i>Curtobacterium albidum</i> SRV4	100–300	Pot	Improve photosynthetisis, osmolytes, and antioxidative enzymes	India	[51]
	<i>Enterobactersp.</i> P23	0 to 200	Invitro	Promote rice-seedling growth	India	[52]
	<i>Enterobactersp.</i> PR14	150–900	Invitro	Growth promotion	India	[53]
Maize (<i>Zea mays</i>)	<i>Pseudomonas</i>	150	Pot	Improve POD activity, proline, and soil moisture	Pakistan	[54]
	<i>Enterobactercloacae</i> [KP226569]	100–200	In vitro	Increased growth parameters	India	[55]
	<i>Azotobacternigricans</i> [KP966496]	100–200	In vitro	Enlargement, growth parameters, and germination	India	[56]
	<i>Bacillus subtilis</i>	0–200	Plastic pots	Increased the relative water content in leaves	Brazil	[57]
	<i>Rhizobium tropici</i> and <i>Azospirillum brasilense</i>	170	Leonard jars	Antioxidant enzymes	Brazil	[58]
	<i>Azospirillum lipoferum</i> and <i>Azotobacter chroococcum</i>	100	Pot	Significantly enhanced growth parameters and pigments	S.Arabia	[59]
Millets	<i>E. cloacae</i> [KP226575]	100–200	Greenhouse	Increase in seed germination andenhanced root and shoot elongation	India	[60]

Table 1. Cont.

Crop	Strain	Na ⁺ Cl ⁻ Tolerance(mM)	Condition	Effect	Country	Reference
Sorghum (<i>Sorghum bicolor</i>)	<i>Azotobacter salinestris</i> NBRC 102,611	50	Pot	Improved plant growth, carbohydrate, proline, and macroelements	Egypt	[61]
Mung bean (<i>Vigna radiata</i>)	<i>Enterobacter cloacae</i> strain KBPD	80	Pot	Increase growth parameters, fresh and dry weights	India	[62]
Tomato (<i>Solanumly copersicum</i>)	<i>Azotobacter chroococcum</i>	100	Jar	Employed as bioeffectors	China	[63]
	<i>Azotobacter chroococcum</i> 76A	100	Pot	Promoted plant growth	Italy	[64]
	<i>Pseudomonas</i> spp. OFT2 and OFT5	75	pot	Promoted shoot uptake of other macronutrients and micronutrients	Japan	[65]
Pea (<i>Pisum sativum</i>)	<i>Bacillus subtilis</i> RhStr_71, <i>Bacillus safensis</i> RhStr_223, and <i>Bacillus cereus</i> RhStr_JH5	10	Pot	Enhanced the antioxidant enzymes	India	[66]
	<i>Enterobacter ludwigii</i> <i>Acinetobacter bereziniae</i> , and <i>Alcaligenes faecalis</i>	150	Field trials	Seedling enlargement and yield	India	[67]
Chickpea (<i>Cicerarietinum</i>)	<i>Bacillus subtilis</i> [BERA 71]	200	Plastic pots	Increased the synthesis of photosynthetic pigments and plant biomass	Saudi Arabia	[68]
	<i>Rhizobium</i> sp.	150	Pot	Influenced photosynthesis and improved yield attributes	India	[69]
Capsicum (<i>Capsicum annum</i> L.)	<i>Bacillus</i> WU-9, WU-5, and WU-13	60	Pot	Growth parameters and freshand dry weights	china	[70]
Red Pepper (<i>Capsicum annum</i>)	<i>Pseudomonas frederiksbergensis</i> OB139 and <i>vancouverensis</i> OB155	150	Plastic pots	Increased content of photosynthetic pigments	Republic of Korea	[71]
Okra (<i>Abelmoschuse sculentus</i>)	<i>Enterobacter</i> sp. UPMR18	75	Plastic pots	Increased antioxidant enzyme activities	Malaysia	[72]
Shalgam (<i>Brassica rapa</i>)	<i>Pseudomonas stutzeri</i> ISE12	200	Pot	Antioxidant defense system	Poland	[73]
Soybean (<i>Glycine max</i>)	<i>Bacillus subtilis</i> and <i>P.pseudoalcaligenes</i>	100	Hydroponics	Enhancement of growth parameters	India	[74]
Soybean	ALT29 and ALT43	80–2400	Pot	Improvement in agronomic parameters, fresh and chlorophyll content	Korea	[75]

Table 1. Cont.

Crop	Strain	Na ⁺ Cl ⁻ Tolerance(mM)	Condition	Effect	Country	Reference
Canola (<i>Brassica napus</i>)	<i>Enterobacter cloacae</i> [HSNJ4]	50–100	Pot	Enhancement of IAA and ethylene content	China	[76]
Canola (<i>Brassica napus</i>)	<i>Rhizobium</i> sp.	90	GH	The increased dry weight of the root	Iran	[77]
Faba bean (<i>Vicia faba</i>)	<i>Rhizobium leguminosarum</i>	0–120	Marrakech-Haouz region	Increased plant biomass, nodule number, and nitrogen content	Morocco	[78]
Snap Bean (<i>Phaseolus vulgaris</i>)	<i>Rhizobium</i> –arbuscularmycorrhizal fungi [AMF]	6–200	Organic garden-shade house	Increased yield	Florida	[79]
Pegion Pea (<i>Cajanus cajan</i>)	<i>Funneliformis mosseae</i> and <i>Rhizophagus irregularis</i>	0–100	Pot	Symbiosis	India	[80]
Hopbush Shrub (<i>Dodonaea viscosa</i> L.)	<i>Azospirillum lipoferum</i> and <i>Azotobacter chroococcum</i>	150–200	Pot	Improved seedling growth parameters	Iran	[81]
<i>Artemisia annua</i> L.	<i>Piriformospora indica</i> [Pi] and <i>Azotobacter chroococcum</i> [Az]	200	Pot	Enhanced activities of antioxidant enzymes	India	[82]
Sunflower (<i>Helianthus</i>)	<i>Pseudomonas citronellolis</i> SLP6	80	pot	Increase in antioxidant enzymes and chlorophyll content	India	[83]
<i>Arabidopsis thaliana</i>	<i>Pseudomonas putida</i>	200	Pot	Auxin Activity RAR shows tryptophan trust for growth	India	[84]
Alfalfa (<i>Medicago sativa</i> L.)	<i>S. meliloti</i> ARh29, <i>K. cowanii</i> A37, <i>Klebsiella</i> sp. A36, and rhizobial strain	1200	Greenhouse and invitro	Plant growth	Iran	[85]
Alfalfa (<i>Medicago sativa</i> L.)	<i>B. subtilis</i> NRCB002, NRCB002, NRCB003 [NRCB003]	130	Greenhouse	Significantly increased dry weight	China	[86]
<i>Medicago sativa</i>	<i>Klebsiella</i> sp., <i>Alcaligenes</i> sp., <i>Pseudomonas cedrina</i> , and <i>Pseudomonas putida</i>	20–60	Pot	Plant development, chlorophyll content, and root AM colonization	Morocco	[87]
	<i>Pseudomonas aeruginosa</i>	170	Field experiments	Significant increase in shoot length	Pakistan	[88]
Talh Tree <i>Acacia gerrardii</i> Benth.	AMF and <i>B. subtilis</i>	250	Pot	Increase in phenols, fiber content, and total lipids	Riyadh, KSA	[89]

4. Mechanisms of Halotolerant PGPB-Mediated Salinity-Stress Tolerance

Numerous systems have been accounted for by Halotolerant PGPB for the exercises of salinity amelioration [18]. The halotolerant PGPB exploits numerous systems (Figure 3) that indirectly or directly participate in the amendment of salinity [90]. Halotolerant PGPB produces numerous plant growth regulators, such as cytokinins, auxins [IAA], gibberellins. PGPB produce ACC deaminase [90], exopolysaccharides [91], and siderophores [92–94]. They also mobilize nutrients, such as phosphorous solubilization [95], nitrogen-fixing [96,97], and osmolytes (trehalose, proline, and glycine betaines), activate the antioxidative enzymes of plants, and regulate plant defense systems under salt stress [98] (Figure 3).

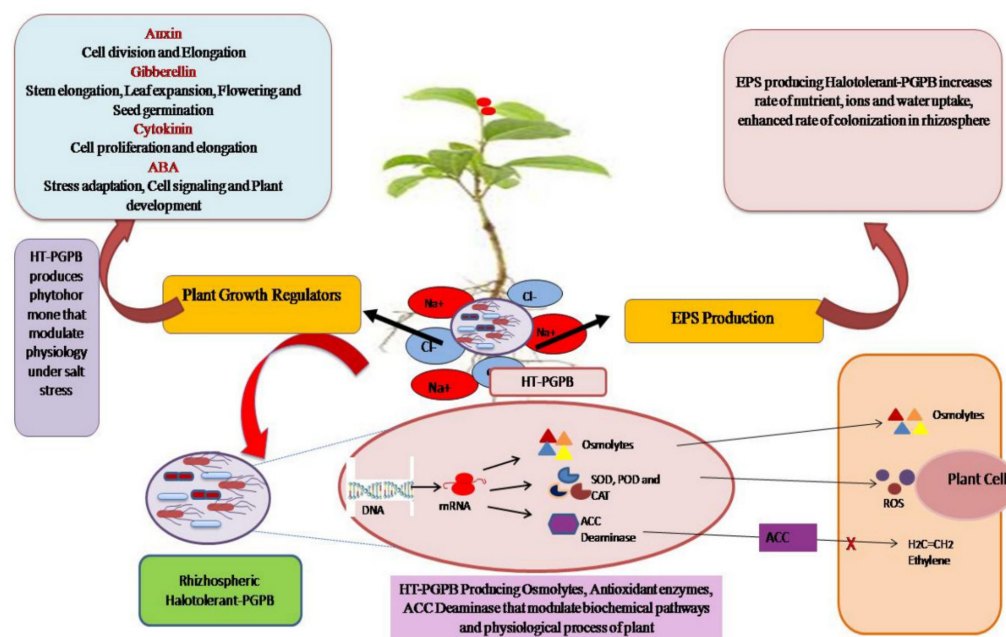


Figure 3. The alleviation of salt stress in plants mediated by halotolerant PGPB.

4.1. Phytohormone Production

Phytohormones secreted by halotolerant PGPB play a vital role in regulating plant metabolic pathways and physiological processes under salinity conditions. There are reports where halotolerant PGPB is known to produce more than one type of phytohormone. Gibberellin-positive bacterial strains, such as *Bacillus. licheniformis*, *Azospirillum spp.*, and *B. pumilus* have also been identified by recent studies [99,100]. Patel and Saraf [101] report that bacterial strains of *Stenotropho monasmaltophilia*, *P. stutzeri*, and *P. putida*, isolated from the *Coleus* rhizosphere, produced gibberellic activity, IAA, and CK in salt environments. In recent times, Tewari et al. [102] documented the involvement of SA in improving salt stress and promoting the enlargement of sunflower in alkaline soils.

4.1.1. Auxin [Indole Acetic Acid, IAA]

The biosynthesis of IAA occurs via multiple pathways in halotolerant PGPB that convert precursor tryptophan into IAA, which is used by the plant and which stimulates cell growth and proliferation under salinity conditions [103]. IAA produced by halotolerant PGPB is the most ordinary and broadly studied. Phytohormones inside salt stress mitigate plant–microbe interactions [18]. There are several well-known IAA-producing halotolerant PGPB under salt stress: *Stenotrophomonas spp.*, *Pseudomonas spp.*, *Rahnella spp.*, and *Bacillus spp.* [104,105]. Inoculation of the halotolerant PGPB has also been shown to protect plants from ion toxicity, improve mineral absorption, and increase growth parameters in saline environments [106]. Several recent studies have established that PGPB produces both ACC deaminase and IAA under salt stress to successfully protect plant growth from salinity

stress. The accumulation of IAA in plant tissues stimulates transcriptional factors related to ACC synthase genes, which enhances the concentration of ACC, and, in response, the production of ethylene increases [107]. *Pantoea dispersa* PSB3 is an indigenous bacterium in chickpea (*Cicer arietinum*) and produces ACC deaminase and IAA. It significantly increases the seed number, the plant biomass, the seed weight, and the salt in the pods of affected plants [108]. *Bacillus tequilensis* UPMRB9 was the best IAA producer for enhancing the root surface and for modifying the root morphology to obtain more nutrients and water from the soil [109]. In addition to EPS production, this breed's exceptional IAA production is vigorous for adventitious roots and lateral root growth, resulting in increased nutrient availability and water absorption. Banerjee et al. [110] conclude that the inoculation of the IAA-producing isolates of rice plants results in significant root- and seedling-length enlargements. Recently, Kang et al. [107] demonstrated that the IAA-producing halotolerant PGPB, *Leclercia adecarboxylata*, has been characterized for sugar activity and chlorophyll fluorescence development in tomato.

4.1.2. Cytokinin

Apart from IAA, cytokinins are compulsory phytohormones for the cell-cycle succession and for mitigating the influences of salinity stress in plants [99]. The cytokinins are involved in various physiological functions of plants, such as cellular proliferation and differentiation, chlorophyll biosynthesis, and chloroplast biogenesis [111]. Inoculating cytokinin-producing bacteria enhances the shoot and fruit formation, as well as the plant resistance to abiotic stress. Several researchers have reported salt-tolerant PGPB that mitigate salinity through cytokinins, including *Halomonas*, *Arthrobacter*, *Pseudomonas* sp., *Bacillus* sp., and *Azospirillum* species [112–114]. Furthermore, our findings were strengthened by the results that show that increased resistance to the abiotic stresses of *Platyclusus orientalis* occur with the cytokinin-producing *Bacillus subtilis*. [115]. ABA is produced by numerous strains of ST-PGPR, comprising *Pseudomonas fluorescens*, *Bacillus licheniformis*, *B. megaterium*, *Proteus mirabilis*, and *Achromobacter xylosoxidans*, which disrupts the activity of cytokinin in root-to-shoot signaling [116]. The up-regulation of cytokinin synthesis genes promoted an increased production of cytokinins in tomato plants, reflecting the organic volatiles excreted by the PGPB *Bacillus subtilis*, SYST2, under salinity-stress conditions [113].

4.1.3. Antioxidant Activity

Several researchers report that halotolerant PGPB-inoculated plants combat the deleterious impacts of oxidative stress by producing antioxidative enzymes [25,117,118]. Several antioxidant mechanisms demonstrated by the halotolerant PGPB-involved enzymes, such as glutathione reductase, peroxidases nitrate, superoxide dismutase, and catalase, as well as secretory molecules, protect tissues from oxidative damage by suppressing and detoxifying ROS [66,119–131]. There are many PGPB strains, such as *Rhizobium* sp., *Azotobacter* sp., *Pseudomonas* sp., and *Serratia* sp., which can be used as inoculants for improving plant growth under salinity stress [75,122,132]. The upregulation of the antioxidant gene responses, in terms of antioxidant production and metabolite synthesis, are measured as the sensitive physiological markers of salt stresses [123,124]. El-Esawi et al. [125] demonstrate that *Azospirillum lipoferum* FK1-inoculated plants exhibited the advanced expression of antioxidant genes and, therefore, improvements in the nutrient uptake, phenol, flavonoid content, antioxidant enzymes, and non-enzymatic metabolize, enlargement, and the rising of chickpeas. In addition, an antioxidant enzyme involved in ROS scavenging activities and ascorbate peroxidase showed enhanced tolerance in tomato plants inoculated with halotolerant PGPB under salt stress [117]. Habib et al. [72] report the enhanced salt tolerance of okra (*Abelmoschus esculentus*) plants when inoculated with *Enterobacter* sp. UPMR18 increased antioxidant enzyme activity, and the ROS cascade gene expression was shown when inoculated with 75 mM of Na⁺Cl⁻. Several documented ST-PGPR, including *Pseudomonas pseudoalcaligenes* and *Enterobacter cloacae*, improved the levels of CAT and APX in *Jatropha* leaves in response to salinity stress and also increased

the biomass, encouraged the development of the root, potassium [K], and phosphorus, the uptake of nutrients, and the chlorophyll content in different tissues of the plant [15].

Polyamines [PAs] are another abundant antioxidant with low molecular weight aliphatic amines, ubiquitously present in plants/microbes, which regulate ROS homeostasis by scavenging free radicals by triggering antioxidant enzymes. The researchers report different polyamines, such as spermidine, putrescine, and spermine, associated with numerous developmental processes and stress responses in plants [126]. The antioxidant system also comprises non-enzymatic systems, such as salicylic acid and carotenoid production [127]. Similarly, Cappellari et al. [128] observed a decreased level of malondialdehyde (MDA, an indicator of lipid peroxidation and membrane damage) in peppermint seedlings under saline conditions when treated with microbial volatile organic compounds (mVOC) and reduced oxidative damage through an increased production of the antioxidant molecule, [DPPH-2,2-diphenyl-1-picrylhydrazyl]. Side by side, the findings observed by recent research suggest the significance of Halotolerant PGPR in plant stress tolerance through the modulation of biochemical processes and plant physiology, for example, osmolytes, stress-related genes, and enzymatic and non-enzymatic antioxidants. Abdelaal et al. [129] describe that salt stress adversely affected the relative water content, the chlorophyll content, and the fruit yields, whereas proline-concentration-electrolyte leakage, malondialdehyde [MDA], reactive oxygen species [ROS], and the activities of antioxidant enzymes increased in salt-stressed plants. Several studies have recognized the capability of microbes to moderate the effects of oxidative reuptake by increasing the osmolyte content and the activity of antioxidant enzymes [117,123,124,127,130–140].

4.1.4. Osmoprotectants

Osmoprotectants (compatible solutes with neutral charges) are low-molecular-weight compounds that help plants or microorganisms survive in adverse saline conditions. Usually, plants gather organic-natured compound osmolytes, including quaternary ammonium compounds, polyamines, glycine, betaine, proline, and other amino acids, in response to salinity stress [131]. Halotolerant PGPR employ a similar mechanism counter to osmotic stress, the collective phenomenon of alkaline soils [132]. Although subjected to salt stress, halotolerant bacteria may upsurge their K^+ ions, the accretion of osmolytes, and their cytoplasmic content to help the persistent stress response and to avoid water loss [133]. Recently, Kushwaha et al. [134] revealed the role of osmoprotectants in (SBS 10) *Halomonas* sp. and showed that low Na^+Cl^- concentrations accelerate the betaine level that overturns the de novo production of ectoine; however, at high Na^+Cl^- concentrations, the ectoine concentration increases brusquely as compared to the betaine.

Furthermore, they determined that the accumulation of ectoine is regulated by transcription elements and that it enhances the expression of transcription factors during salinity stress. In other studies, it was perceived that *Azospirillum* spp. produce proline, betaine, glycine, trehalose, and support plants in order to endure osmotic tension. A halotolerant PGPR strain of *Bacillus* sp. was documented to produce proline and soluble sugars, and significantly enhanced the growth of maize under salinity and drought conditions [18]. Several researchers report the significance of the trehalose as an osmoprotectant and of producing halotolerant PGPR that comprises the genes for trehalose biosynthetic pathways under salt stress [135–137].

4.1.5. Exopolysaccharide (EPS) Production

Some rhizosphere bacteria produce exopolysaccharides (EPSs) or surface polysaccharides, which is a common feature. However, the composition and quantity of EPS might differ in diverse halotolerant PGPR cultures; ample EPS is secreted in hostile conditions, which work as a physical obstruction near the root and protect plant growth in high-saline conditions [16]. Singh and Jha [44] report the enhanced uptake of ions in plants under saline conditions when inoculated with EPS-producing halotolerant PGPR. The ACC-deaminase and EPS-producing halotolerant PGPR, *Mesorhizobium ciceris*, enhanced chickpea growth,

stabilized the soil texture, and enhanced colonization under salinity. In the context of yield improvement, the role of EPS-producing halotolerant PGPB is significant as they are being used as the priming agents of seeds and to help enhance germination [98]. Atouei et al. [138] found that the inoculation of wheat with EPS-producing and salt-tolerating *Marinobacter lipolyticus* SM19 and *B. subtilis* decreases the adverse effects of abiotic stresses. In recent times, Chu et al. [139] observe that the EPS-producing ST-PGPR, *Pseudomonas* PS01, improved *Arabidopsis thaliana* growth and the regulation of genes under salinity stress. They found that a LOX2 gene was up-regulated and that it participated in the jasmonic acid [JA] pathway and enhanced the accumulation of JA plants under abiotic stress, whereas bacterial EPS provides complimentary profit for tolerance below salt stress.

4.1.6. 1-Aminocyclopropane-1-Carboxylic Deaminase [ACCD]

Halotolerant plant growth-promoting bacteria secrete enzymes to reduce salinity stress, including reducing ethylene levels via hydrolyzing 1-aminocyclopropane-1-carboxylic acid [ACC] by the enzyme, ACC deaminase. ACC is the immediate precursor of the hormone ethylene in plants. It is widely reported that PGPB possesses ACC deaminase enzymes that can degrade ACC to ammonia and α -ketobutyrate, thus reducing the levels of ethylene inside the plants [37,100,140–142]. Bacterial ACCD activity, or the induced systemic resistance in plants are both factors that would have led to reduced ethylene biosynthesis [142]. The increased SOD activity of wheat tissues [both root and seedling] in plants planted with ACC-producing rhizobacteria suggests better antioxidant performances, stimulated by ACC-producing rhizobacteria, thereby reducing the harmful effects caused by ROS. Several studies have shown that bacterial consortium inoculation with high ACCD activity and auxin production can modify and improve the antioxidant system in wheat seedlings. ACCD-producing bacteria are classified as halotolerant, with the ability to grow in the range of 2–11% Na^+Cl^- [44,63]. Wheat seedlings planted with two selected ACCD-producing *Klebsiella* sp., 8LJA and 27IJA, significantly ($P \leq 0.05$) enhanced the biomass (45–62%) content and the SOD activity in roots (18–35%), under normal as well as under salt conditions [143]. The seed bacterization by ACC02 and ACC06 reveals that the treatment of plants with bacterial consortia significantly declined the salinity stress through ACC deaminase activity (approximately 60%) and stimulated the ethylene levels [144]. Several reports have recommended that the function of ACC deaminase producers manifest salt stress in plants by reducing ethylene emissions and by providing plant growth promotion and stress tolerance in stressed plants [46,145].

5. Role of Halotolerant PGPB in the Enhancement of Crop Production under Salinity

It is now widely accepted that halotolerant PGPB has the inherent potential to cope with high-saline conditions and to facilitate plant growth through different direct/indirect beneficial mechanisms [50]. Halotolerant PGPB have been reported as bioinoculants/bioformulations, biostimulants, and biofertilizers that enhance the crop yields and facilitate the survival of plants, even under high-temperature concentrations of salt [146,147] (Table 2).

They are present in the soil and directly promote the plant growth of many types of cereals and other important crops [29,32,147]. It has been realized that significant crops, for example, cereal crops (maize, barley, oats, sorghum, rice, wheat, and millet), legumes, vegetables, and oil-yielding crops, are affected by salinity, but that the inoculation with the halotolerant PGPB not only helped in maintaining the crops, but also increased the yields [44]. The role of Halotolerant PGPB in increasing the productivity of several crops is discussed in this section.

Table 2. Role of Halotolerant PGPB in the enhancement of crop production.

Crop	Halotolerant PGPB	Tolerance Mechanism	Reference
		Cereals	
	<i>Thalassobacillus denorans</i> and <i>Oceanobacillus kapialis</i>	Increase in germination %	[148]
	strains S6 and S7	Yield increased	[149]
	<i>Enterobacterudwigii</i> [AF134] and <i>P. Putida</i> [AF137]	Increased root and shoot biomass	[150]
Rice	<i>Enterobacter cloacae</i> [KP226569]	Increase in germination percentage, root, and shoot	[151]
	<i>Azotobacter</i> sp. [KH-2]	Enlargement of plant height, yield, and biomass	[152]
	<i>Alcaligenes</i> sp. [AF7]	Increasingly support the vegetative growth parameters of crop	[153]
	<i>Exiguobacterium</i> sp., <i>Stenotrophomonas</i> sp., <i>Enterobacter</i> sp., <i>Microbacterium</i> sp., and <i>Achromobacter</i> sp.	Significantly improve proline, total chlorophyll, and total phenol	[154]
	<i>Glutamicibacter</i> sp. [YD01]	Enhanced stress-responsive gene expression and photosynthetic	[155]
	<i>Bacillus tequilensis</i> [UPMRB9], <i>Providencia stuartii</i> [UPMRG1], and <i>B. aryabhatai</i> [UPMRE6]	Improved chlorophyll content and reduced electrolyte leakage	[156]
	<i>P. fluorescens</i> , <i>B. pumilus</i> , <i>Exiguobacterium aurantiacum</i>	Enhancement of agronomic traits	[157]
	<i>Klebsiella</i> sp.	Increase in total protein content and proline	[158]
Wheat	<i>Azospirillum brasilense</i> 65B [Abr65B]	Enhanced enlargement and nutrient access	[159]
	<i>Erwinia</i> sp.	Enhanced growth and yield parameters	[160]
	<i>Bacillus megaterium</i> , <i>P. fluorescens</i> and <i>B. subtilis</i>	Increased grain yield	[161]
	<i>Azospirillum</i> sp., <i>Azoarcus</i> sp., and <i>Azorhizobium</i> sp.	Increase in biomass and the activity of enzymes	[162]
	<i>Azotobacter</i> sp. [Az1-Az6]	Improved agronomic characteristics	[163]
	<i>Staphylococcus sciuri</i>	Significantly increased growth parameters and biochemical characteristics	[164]
	<i>Pseudomonas</i> sp. P8, <i>Peribacillus</i> sp. P10, <i>Streptomyces</i> sp. X52	promoted the growth	[165]
Maize	<i>Bacillus aquimaris</i> DY-3	Increased chlorophyll content antioxidant enzymes and osmotic regulation	[166]
	<i>Bacillus</i> sp. SR-2-1/1	increased contents of chlorophyll, total phenolics and proline	[167]
	<i>Serratialiquefaciens</i> [KM4]	Antioxidant enzymes, decrease in ABA biosynthesis, and nutrient uptake	[168]
	<i>Bacillus</i> sp. [HL3RS14]	Increased dry weights of roots and shoots	[169]
	<i>B.safensis</i> [NBRI 12 M]	Increased amounts of chlorophyll, proline, and soluble sugar	[170]
	<i>Bacillus</i> sp. [NBRI YN4.4]	Improved biochemical traits and soil enzymes	[171]
Oat	<i>Klebsiella</i> sp. [IG 3]	Enhanced plant growth	[172]

Table 2. Cont.

Crop	Halotolerant PGPB	Tolerance Mechanism	Reference
Oil-yielding grains			
Soybean	<i>Bradyrhizobium</i> sp.	Increased grain yield	[173]
	<i>P. fluorescens</i> [LBUM677]	Improved plant biomass, lipid composition, and oil content	[174]
	<i>Bradyrhizobium</i> sp and <i>L. adecarcoxylata</i>	Enhanced plant growth and productivity	[175]
	<i>B. velezensis</i> [S141], and <i>B. diazoefficiens</i> [USDA110]	Improved nodulation and N ₂ -fixing efficiency	[176,177]
Sunflower	<i>Bradyrhizobium</i> sp.	nodY/K and nifH gene expression for salinity tolerance	[178]
Groundnut	<i>Klebsiella</i> , <i>Pseudomonas</i> , <i>Agrobacterium</i> , and <i>Ochrobactrum</i>	Enhanced PGP traits	[179]
Cotton seed	<i>B. amyloliquefaciens</i> , <i>Curtobacterium oceanosedimentum</i> , and <i>Pseudomonas oryzihabitans</i>	Seed germination	[180]
Legumes			
Chickpea	<i>Bradyrhizobium</i> and <i>Actinomadura</i> , <i>Paenibacillusgraminis</i>	Induced increased antioxidant enzymes, and	[181]
Peanut (<i>Arachis ypogaea</i> L.)	<i>Serratia</i> sp. S119; <i>Acinetobacter</i> sp. L176;	Increased growth parameters and P content	[182]
	<i>Planomicrobium</i> sp. MSSA-10	Increased growth	[183]
Black gram	<i>P. fluorescens</i>	Improved photosynthetic content	[184]
Faba bean	<i>Pseudomonas anguilliseptica</i> [SAW 24]	EPS production and biofilm production	[185]
Vegetables			
Tomato	<i>Bacillus pumilus</i>	Significantly improved the fresh shoot weight and dry weight	[186]
	<i>B. thuringiensis</i>	Seed germination and shoot elongation	[187]
	<i>Pseudomonas jessenii</i> and <i>Pseudomonas synxantha</i>	Significantly enhanced plant growth	[188]
	<i>Pseudomonas</i> sp. KP966497 [PR21]	Seed germination and shoot elongation	[189]
	<i>Pseudomonas</i> sp. UW4	Enhanced plant growth	[190]
Chinese cabbage, Lettuce, Radish	<i>Lactobacillus</i> sp. and <i>P. putida</i> , <i>A. chroococcum</i>	Increased the plumule and radicle lengths of germinated seeds	[191]
Capsicum	<i>B. fortis</i> strain [SSB21]	Reduced phytohormones	[184]
Potato (<i>Solanum-tuberosum</i> L.)	<i>Bacillus</i> strains	Enhancement of plant growth	[192]

6. Molecular Understanding of Halotolerant PGPB-Mediated Salt Tolerance in Plants

Different genes are affected by PGPB to confer salt tolerance in plants. The efficient colonization of *Enterobacter* sp. EJ01 in tomato and *Arabidopsis* plants alleviate salt stress by stimulating the expression of responsive genes, including the RD29A, DREB2b, and RAB18 genes related to the ABA-dependent pathways. There is scientific evidence that Halotolerant *Pantoeaag glomerans* defend tropical corn plants from salt stress by up-regulating the expression of aquaporin genes (*zmPIP2-1*, *zmPIP1-1*, and *zmPIP2-5*). Similarly, the induction of salt tolerance and the stimulation of a set of genes accountable for salinity tolerance in wheat by the halotolerant *Dietziana tronolimnaea* STR1 strain have been reported by Bharti et al. [25]. The halotolerant PGPB-inoculated plants always have higher SOS gene expression under salt conditions than uninoculated salt-stressed plants, proposing their involvement in salt tolerance mechanisms. *SOS4* gene expression is associated with the auxin and ethylene mechanisms, as well as root hair development in *Arabidopsis*. The improved *SOS4* gene up-regulation in PGPR-inoculated wheat roots can thus be correlated with prolific growth in the root length and the overall plant growth in salt-stressed plants [25]. The dominant pathways, such as ion transporters, ABA-signaling, osmoprotectants, the SOS pathway, and antioxidant machinery usually protect the plant from oxidative damage caused by high salt concentrations. These are accessed by the up-regulation of salt-tolerant genes, such as transcriptional factors (TaABARE, TaWRKY, and TaOPR1), ion transporters (TaHKT1, TaNHX1, and TaHAK), and SOS-pathway-related genes (*SOS1* and *SOS4*) [24]. The activation of the WRKY gene has been reported in response to salinity stress in soybean [193], and *Arabidopsis* [194]. Wheat plants inoculated with the PGPR strains, *B. subtilis* and *Arthrobacter protiformia*, under salinity-stress conditions produced IAA content and there was an observed upregulation of the TACTR1 and TADRE2 genes to reduce salinity stress [195]. The inoculation of the halotolerant PGPB strain, IG3, in oat under salinity conditions increased the auxin concentration in plants under the same condition. It was noted that an increase in the concentration of auxin in tomato plants helped to improve the osmotic stress generated by salinity [196]. de la Torre-González et al. [196] decoded the expression of the cytokinin synthesis gene, *SICKX1*, and promoted high cytokinin production when tomato plants were exposed to the halotolerant PGPB *Bacillus subtilis* SYST2 strain exuding organic volatiles. The knockdown of cytokinin oxidase, *OsCKX2*, in rice, using the RNAi-based approach, resulted in a significant increase in cytokinins under salt-stress conditions. Cytokinin oxidase, *OsCKX2*, knockdown plants displayed enhanced vegetative growth, photosynthetic efficiency, and relative water content compared to wild types under salinity stress [197]. Asaf et al. [198] decoded the whole genome sequence of the salt-tolerant endophytic *Sphingomonas* sp., LK11, containing many genes encoding glycine betaine from choline by encoding the betTcholine transporter, the betacholine dehydrogenase, and the betaine aldehyde dehydrogenase, and further validating the genetic role of the LK11 gene in resisting salinity stress and promoting plant growth. Similarly, Chen et al. [199] report the expression of an upregulated Na^+/H^+ antiporter, [NHX], and H^+ -PPase genes under saline conditions in *Bacillus amyloliquefaciens* SQR9-inoculated maize, and enabled Na^+ confiscation into the vacuoles of maize shoots. The recirculating of Na^+ from shoot to root via an elevated expression of the high-affinity K^+ transporter 1 [HKT1] gene was observed in the treated maize plants. Forni et al. [136] demonstrated the potential role of the salt-tolerant strain, PS01 *Pseudomonas*, causing EPS in regulating genes connected to stress tolerance in *Arabidopsis thaliana* [194]. Upregulated genes related to transcription factor [WRKY] modulate osmotic balance, scavenge ROS, and reduce salinity and drought stress by triggering stress-related genes. The study also proved that the inoculation of wheat with *A. nitroguajacolicus* had a higher WRKY28 gene expression and showed significant crop growth under salinity stress. Similarly, Kazerooni et al. [200] reveal that halotolerant PGPR-inoculated pepper plants showed the upregulated gene expression of *XTH* (Xyloglucan Endotrans glucosylase/Hydrolase) and the decreased expression of *BI-1*, *PTI1*, and *WRKY2*, and the binding immunoglobulin protein (BiP) genes (*CaBiP1*, *CaBiP2*, and *CaBiP3*), under salinity and

drought conditions and enhanced plant growth. In contrast, PGPR-uninoculated pepper seedlings showed decreased cell-wall extensibility and retardation in plant growth. In another study, halotolerant PGPR-treated stressed plants displayed higher XTH (XTH1 and XTH3) gene expression to tolerate salt and drought stress in tobacco and pepper plants and revealed plant heights and leaf lengths/widths. In this order, Liu et al. [201] demonstrate the expression of salinity-induced genes related to the Aux, CK, and GA signaling pathways, as well as the WRKY and MYB transcription factors (TFs) in *Paenibacillus polymyxa* YC0136-inoculated tobacco plants (*Nicotiana tabacum* L.) and promote plant tolerance in stress conditions. Akram et al. [202] demonstrate the multiple mechanisms in the *Bacillus megaterium* strain, A12, for the amelioration of salinity stress in tomato plants. In this order, several genes of halotolerant PGPB, their gene products, tolerance mechanisms, and related crops are documented in Table 3.

Table 3. Genes for salt-stress tolerance in different PGPB.

Halotolerant PGPB	Crops	Gene	Gene Product/Protein/ Enzyme	Significance	Reference
<i>Bacillus megaterium</i>	Tomato	Expression of MT2 and GR1	Metallothionein Glutathione reductase enzyme synthesis	Antioxidant enzyme production, tolerance to salinity	[203]
<i>Bacillus megaterium</i> strain A12 [BMA12]	Tomato	<i>PsbA</i> and <i>PBGD</i>		Increased biosynthesis of chlorophyll	[203]
<i>Pseudomonas putida</i> PS01	<i>A. thaliana</i>	Upregulation of <i>LOX2</i>	Jasmonic acid synthesis pathway, SOS pathway, abscisic acid [ABA] production	ROS activity, abscisic acid	[139]
<i>Arthrobacter nitroguajacolicus</i>	Wheat	Upregulation of AA0618700, AA0359620, APX, and GPX Expression of AA0410390, AA1982260, AA0412840, and AA1872340	SOS pathway and antioxidant enzyme	Plant-cell-wall biosynthesis, ROS activity osmotic balance	[117]
ALT29 and ALT43	Soybean	[GmFLD19 and GmNARK]	Antioxidants [GSH, LPO, TPP, PPO, and POD], ion uptake [Na and K]	Significantly increased growth parameters and biochemical traits	[75]
<i>Bacillus amyloliquefaciens</i>	Pepper	Upregulation of <i>XTH</i> [Xyloglucan Endotrans glucosylase/Hydrolase]	High biochemical traits and antioxidant activities	Enhanced plant growth and tolerance for salinity and drought conditions	[201]

7. Conclusions and Future Prospects

Salinity stress causes high costs in agriculture production, and its destructive effects limit plant growth and reproduction, resulting in reduced food production. Plants have the inherent ability to respond to specific types of stress, but the application of PGPB to stimulate crop growth, through direct and indirect mechanisms, under salt-induced stress conditions, is an emerging strategy for enhancing global food production. Inoculated plants with PGPR make the plant more resistant to salinity, and PGPB strains boost the growth parameters and enhance plant productivity under salinity stress. PGPB play a vital role in enhancing plant enlargement and crop productivity, maintaining balanced nutrient cycling, controlling pesticide pollution, and producing secondary metabolize. The recent thirst of researchers is to develop a combination of formulations that will help stress tolerance and promote plant growth for sustainable agriculture. The use of advanced molecular techniques to search for halotolerant PGPB, to mediate the conservation of salt-affected soil, and for the exploration of biochemical mechanisms, genes, and signaling to neutralize salinity stress in crops can play a revolutionary role in applying halotolerant PGPR for growing crops under salinity stress.

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References

- Shah, F.; Wu, W. Soil and Crop Management Strategies to Ensure Higher Crop Productivity within Sustainable Environments. *Sustainability* **2019**, *11*, 1485. [[CrossRef](#)]
- Wei, B.; Yu, J.; Cao, Z.; Meng, M.; Yang, L.; Chen, Q. The Availability and Accumulation of Heavy Metals in Greenhouse Soils Associated with Intensive Fertilizer Application. *Int. J. Environ. Res. Public Health* **2020**, *17*, 5359. [[CrossRef](#)] [[PubMed](#)]
- Isayenkov, S.V.; Maathuis, F.J.M. Plant Salinity Stress: Many Unanswered Questions Remain. *Front. Plant Sci.* **2019**, *10*, 80. [[CrossRef](#)] [[PubMed](#)]
- Shahid, S.A.; Zaman, M.; Heng, L. Soil Salinity: Historical Perspectives and a World Overview of the Problem. In *Guideline for Salinity Assessment, Mitigation and Adaptation Using Nuclear and Related Techniques*; Springer: Cham, Switzerland, 2018; pp. 43–53.
- Kumar, P.; Sharma, P.K. Soil Salinity and Food Security in India. *Front. Sustain. Food Syst.* **2020**, *4*, 174. [[CrossRef](#)]
- Sunita, K.; Mishra, I.; Mishra, J.; Prakash, J.; Arora, N.K. Secondary Metabolites From Halotolerant Plant Growth Promoting Rhizobacteria for Ameliorating Salinity Stress in Plants. *Front. Microbiol.* **2020**, *11*, 567768. [[CrossRef](#)]
- Panagos, P.; Borrelli, P.; Robinson, D. FAO calls for actions to reduce global soil erosion. *Mitig. Adapt. Strat. Glob. Chang.* **2019**, *25*, 789–790. [[CrossRef](#)]
- Mandal, S.; Raju, R.; Kumar, A.; Kumar, P.; Sharma, P.C. Current status of research, technology response and policy needs of salt-affected soils in India—A review. *Ind. Soc. Coast. Agric. Res.* **2018**, *36*, 40–53.
- Szabo, S.; Hossain, M.S.; Adger, W.N.; Matthews, Z.; Ahmed, S.; Lázár, A.N.; Ahmad, S. Soil salinity, household wealth and food insecurity in tropical deltas: Evidence from south-west coast of Bangladesh. *Sustain. Sci.* **2016**, *11*, 411–421. [[CrossRef](#)]
- Zörb, C.; Geilfus, C.-M.; Dietz, K.-J. Salinity and crop yield. *Plant Biol.* **2019**, *21*, 31–38. [[CrossRef](#)]
- Arora, S.; Sharma, V. Reclamation and management of salt-affected soils for safeguarding agricultural productivity. *J. Safe Agric.* **2017**, *1*, 1–10.
- Schirawski, J.; Perlin, M.H. Plant–Microbe Interaction 2017—The Good, the Bad and the Diverse. *Int. J. Mol. Sci.* **2018**, *19*, 1374. [[CrossRef](#)]
- Rütting, T.; Aronsson, H.; Delin, S. Efficient use of nitrogen in agriculture. *Nutr. Cycl. Agroecosyst.* **2018**, *110*, 1–5. [[CrossRef](#)]

14. Arora, N.K.; Fatima, T.; Mishra, I.; Verma, M.; Mishra, J.; Mishra, V. Environmental sustainability: Challenges and viable solutions. *Environ. Sustain.* **2018**, *1*, 309–340. [[CrossRef](#)]
15. Egamberdieva, D.; Wirth, S.J.; Bellingrath-Kimura, D.S.D.; Mishra, J.; Arora, N.K. Salt-Tolerant Plant Growth Promoting Rhizobacteria for Enhancing Crop Productivity of Saline Soils. *Front. Microbiol.* **2019**, *18*, 2791. [[CrossRef](#)]
16. Vaishnav, A.; Kumari, S.; Jain, S.; Varma, A.; Tuteja, N.; Choudhary, D.K. PGPR-mediated expression of salt tolerance gene in soy-bean through volatiles under sodium nitroprusside. *J. Basic Microbiol.* **2016**, *56*, 1274–1288. [[CrossRef](#)]
17. Ayyam, V.; Palanivel, S.; Chandrakasan, S. Approaches in land degradation management for productivity enhancement. In *Coastal Ecosystems of the Tropics—Adaptive Management*; Ayyam, V., Palanivel, S., Chandrakasan, S., Eds.; Springer: Singapore, 2019.
18. Shilev, S. Plant-Growth-Promoting Bacteria Mitigating Soil Salinity Stress in Plants. *Appl. Sci.* **2020**, *10*, 7326. [[CrossRef](#)]
19. Wang, C.; Wang, H.; Li, Y.; Li, Q.; Yan, W.; Zhang, Y.; Wu, Z.; Zhou, Q. Plant growth-promoting rhizobacteria isolation from rhizosphere of submerged macrophytes and their growth-promoting effect on *Vallisneria natans* under high sediment organic matter load. *Microb. Biotechnol.* **2021**, *14*, 726–736. [[CrossRef](#)]
20. Ha-Tran, D.M.; Nguyen, T.T.M.; Hung, S.-H.; Huang, E.; Huang, C.-C. Roles of Plant Growth-Promoting Rhizobacteria (PGPR) in Stimulating Salinity Stress Defense in Plants: A Review. *Int. J. Mol. Sci.* **2021**, *22*, 3154. [[CrossRef](#)]
21. Machado, R.; Serralheiro, R. Soil Salinity: Effect on Vegetable Crop Growth. Management Practices to Prevent and Mitigate Soil Salinization. *Horticulturae* **2017**, *3*, 30. [[CrossRef](#)]
22. El-Esawi, M.A.; Alaraidh, I.A.; Alsahli, A.A.; Alamri, S.A.; Ali, H.M.; Alayafi, A.A. *Bacillus firmus* (SW5) augments salt tolerance in soybean (*Glycine max* L.) by modulating root system architecture, antioxidant defense systems and stress-responsive genes expression. *Plant Physiol. Biochem.* **2018**, *132*, 375–384. [[CrossRef](#)]
23. Mokrani, S.; Nabti, E.; Cruz, C. Current Advances in Plant Growth Promoting Bacteria Alleviating Salt Stress for Sustainable Agriculture. *Appl. Sci.* **2020**, *10*, 7025. [[CrossRef](#)]
24. Muchate, N.S.; Nikalje, G.C.; Rajurkar, N.S.; Suprasanna, P.; Nikam, T.D. Plant Salt Stress: Adaptive Responses, Tolerance Mechanism and Bioengineering for Salt Tolerance. *Bot. Rev.* **2016**, *82*, 371–406. [[CrossRef](#)]
25. Bharti, N.; Pandey, S.S.; Barnawal, D.; Patel, V.K.; Kalra, A. Plant growth promoting rhizobacteria *Dietzia natronolimnaea* modulates the expression of stress responsive genes providing protection of wheat from salinity stress. *Sci. Rep.* **2016**, *6*, 34768. [[CrossRef](#)]
26. Ilangumaran, G.; Smith, D.L. Plant Growth Promoting Rhizobacteria in Amelioration of Salinity Stress: A Systems Biology Perspective. *Front. Plant Sci.* **2017**, *8*, 1768. [[CrossRef](#)]
27. Vaishnav, A.; Varma, A.; Tuteja, N.; Choudhary, D.K. PGPR-Mediated Amelioration of Crops under Salt Stress. In *Plant-Microbe Interaction: An Approach to Sustainable Agriculture*; Springer: Singapore, 2016; Volume 10, pp. 205–226. [[CrossRef](#)]
28. Almeida, D.M.; Oliveira, M.M.; Saibo, N.J.M. Regulation of Na⁺ and K⁺ homeostasis in plants: Towards improved salt stress tolerance in crop plants. *Genet. Mol. Biol.* **2017**, *40*, 326–345. [[CrossRef](#)]
29. Numan, M.; Bashir, S.; Khan, Y.; Mumtaz, R.; Shinwari, Z.K.; Khan, A.L.; Khan, A.; Al-Harrasi, A. Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: A review. *Microbiol. Res.* **2018**, *209*, 21–32. [[CrossRef](#)]
30. Kamran, M.; Parveen, A.; Ahmar, S.; Malik, Z.; Hussain, S.; Chattha, M.S.; Saleem, M.H.; Adil, M.; Heidari, P.; Chen, J.-T. An Overview of Hazardous Impacts of Soil Salinity in Crops, Tolerance Mechanisms, and Amelioration through Selenium Supplementation. *Int. J. Mol. Sci.* **2019**, *21*, 148. [[CrossRef](#)]
31. Mirdar Mansuri, R.; Shobbar, Z.-S.; Babaieian Jelodar, N.; Ghaffari, M.; Mohammadi, S.M.; Daryani, P. Salt tolerance involved candidate genes in rice: An integrative meta-analysis approach. *BMC Plant Biol.* **2020**, *20*, 452. [[CrossRef](#)]
32. Rai, S.; Solanki, A.K.; Anal, A.K.D. Modern biotechnological tools: An opportunity to discover complex phytobiomes of horticulture crops. In *Microbiomes and Plant Health: Panoply and Their Applications*; Solanki, M.K., Kashyap, P.L., Ansari, R.A., Kumari, B., Eds.; Elsevier: Berkeley, CA, USA, 2020; pp. 85–124.
33. Saxena, A.K.; Kumar, M.; Chakdar, H.; Anuroopa, N.; Bagyaraj, D.J. *Bacillus* species in soil as a natural resource for plant health and nutrition. *J. Appl. Microbiol.* **2020**, *128*, 1583–1594. [[CrossRef](#)]
34. Arora, N.K.; Fatima, T.; Mishra, J.; Mishra, I.; Verma, S.; Verma, R.; Verma, M.; Bhattacharya, A.; Verma, P.; Mishra, P.; et al. Halo-tolerant plant growth promoting rhizobacteria for improving productivity and remediation of saline soils. *J. Adv. Res.* **2020**, *26*, 69–82. [[CrossRef](#)]
35. Albdaawi, R.N.; Khyami-Horani, H.; Ayad, J.Y. Plant Growth-Promoting Rhizobacteria: An Emerging Method for the Enhancement of Wheat Tolerance against Salinity Stress-(Review). *Jordan J. Biol. Sci.* **2019**, *12*, 525–534.
36. Phour, M.; Sindhu, S.S. Amelioration of salinity stress and growth stimulation of mustard (*Brassica juncea* L.) by salt-tolerant *Pseudomonas* species. *Appl. Soil Ecol.* **2020**, *149*, 103518. [[CrossRef](#)]
37. Zhang, S.; Fan, C.; Wang, Y.; Xia, Y.; Xiao, W.; Cui, X. Salt-tolerant and plant-growth-promoting bacteria isolated from high-yield paddy soil. *Can. J. Microbiol.* **2018**, *64*, 968–978. [[CrossRef](#)] [[PubMed](#)]
38. Aslam, F.; Ali, B. Halotolerant Bacterial Diversity Associated with *Suaeda fruticosa* (L.) Forssk. Improved Growth of Maize under Salinity Stress. *Agronomy* **2018**, *8*, 131. [[CrossRef](#)]
39. Vives-Peris, V.; Gomez-Cadenas, A.; Perez-Clemente, R.M. Salt stress alleviation in citrus plants by plant growth-promoting *Pseudomonas putida* and *Novosphingobium* sp. *Plant Cell Rep.* **2018**, *37*, 1557–1569. [[CrossRef](#)]

40. Palacio-Rodríguez, R.; Coria-Arellano, J.L.; López-Bucio, J.; Sánchez-Salas, J.; Muro-Pérez, G.; Castañeda-Gaytán, G.; Sáenz-Mata, J. Halophilic rhizobacteria from *Distichlis spicata* promote growth and improve salt tolerance in heterologous plant hosts. *Symbiosis* **2017**, *73*, 179–189. [[CrossRef](#)]
41. Amaresan, N.; Kumar, K.; Madhuri, K.; Usharani, G.K. Isolation and Characterization of Salt Tolerant Plant Growth Promoting Rhizobacteria from Plants Grown in Tsunami Affected Regions of Andaman and Nicobar Islands. *Geomicrobiol. J.* **2016**, *33*, 942–947. [[CrossRef](#)]
42. Allaoua, S.; Hafsa, C.S.; Bilal, Y. Growing varieties durum wheat (*Triticum durum*) in response to the effect of osmolytes and inoculation by *Azotobacter chroococcum* under salt stress. *Afr. J. Microbiol. Res.* **2016**, *10*, 387–399. [[CrossRef](#)]
43. Lastochkina, O.; Pusenkova, L.; Yuldashev, R.; Babaev, M.; Garipova, S.; Blagova, D.; Khairullin, R.; Aliniaiefard, S. Effects of *Bacillus subtilis* on some physiological and biochemical parameters of *Triticum aestivum* L. (wheat) under salinity. *Plant Physiol. Biochem.* **2017**, *121*, 80–88. [[CrossRef](#)]
44. Singh, R.P.; Jha, P.N. A Halotolerant Bacterium *Bacillus licheniformis* HSW-16 Augments Induced Systemic Tolerance to Salt Stress in Wheat Plant (*Triticum aestivum*). *Front. Plant Sci.* **2016**, *7*, 1890. [[CrossRef](#)]
45. Singh, R.P.; Runthala, A.; Khan, S.; Jha, P.N. Quantitative proteomics analysis reveals the tolerance of wheat to salt stress in response to *Enterobacter cloacae* SBP-8. *PLoS ONE* **2017**, *12*, e0183513. [[CrossRef](#)]
46. Safari, D.; Jamali, F.; Nooryazdan, H.; Bayat, F. Evaluation of ACC deaminase producing *Pseudomonas fluorescens* strains for their effects on seed germination and early growth of wheat under salt stress. *Aust. J. Crop Sci.* **2018**, *12*, 413–421. [[CrossRef](#)]
47. Vimal, S.R.; Gupta, J.; Singh, J.S. Effect of salt tolerant *Bacillus* sp. and *Pseudomonas* sp. on wheat (*Triticum aestivum* L.) growth under soil salinity: A comparative study. *Microbiol. Res.* **2018**, *9*, 26–32. [[CrossRef](#)]
48. Jha, Y.; Subramanian, R.B. Regulation of Plant Physiology and Antioxidant Enzymes for Alleviating Salinity Stress by Potassium-Mobilizing Bacteria. In *Potassium Solubilizing Microorganisms for Sustainable Agriculture*; Springer: New Delhi, India, 2016; pp. 149–162. [[CrossRef](#)]
49. Shahzad, R.; Khan, A.L.; Bilal, S.; Waqas, M.; Kang, S.-M.; Lee, I.-J. Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa*. *Environ. Exp. Bot.* **2017**, *136*, 68–77. [[CrossRef](#)]
50. Kumar, K.; Amaresan, N.; Madhuri, K. Alleviation of the adverse effect of salinity stress by inoculation of plant growth promoting rhizobacteria isolated from hot humid tropical climate. *Ecol. Eng.* **2017**, *102*, 361–366. [[CrossRef](#)]
51. Vimal, S.R.; Patel, V.K.; Singh, J.S. Plant growth promoting *Curtobacterium albidum* strain SRV4: An agriculturally important microbe to alleviate salinity stress in paddy plants. *Ecol. Indic.* **2019**, *105*, 553–562. [[CrossRef](#)]
52. Sarkar, A.; Ghosh, P.K.; Pramanik, K.; Mitra, S.; Soren, T.; Pandey, S.; Maiti, T.K. A halotolerant *Enterobacter* sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. *Res. Microbiol.* **2018**, *169*, 20–32. [[CrossRef](#)]
53. Sagar, A.; Sayyed, R.Z.; Ramteke, P.W.; Sharma, S.; Marraiki, N.; Elgorban, A.M.; Syed, A. ACC deaminase and antioxidant enzymes producing halophilic *Enterobacter* sp. PR14 promotes the growth of rice and millets under salinity stress. *Physiol. Mol. Biol. Plants* **2020**, *26*, 1847–1854. [[CrossRef](#)]
54. Fazal, A.; Bano, A. Role of Plant Growth-Promoting Rhizobacteria (PGPR), Biochar, and Chemical Fertilizer under Salinity Stress. *Commun. Soil Sci. Plant Anal.* **2016**, *47*, 1985–1993. [[CrossRef](#)]
55. Sagar, A.; Dhusiya, K.; Shukla, P.K.; Ramteke, P.W. Salt tolerance plant Growth promoting bacterium *Enterobacter cloacae* (KP226569) in sustainable maize production under salt stress. In Proceedings of the International Conference on Advancing Frontiers in Biotechnology for Sustainable Agriculture and Health (AFBSAH-2016), Allahabad, India, 25–26 February 2016.
56. Sagar, A.; Shukla, P.K.; Ramteke, P.W. Salt tolerance plant growth promoting bacterium *Azotobacter nigricans* (KP966496) in sustainable maize Production under salt stress. In Proceedings of the XXV Italo–Latin American Congress of Ethnomedicine—SILAE, Modena, Italy, 11–15 September 2016.
57. Ferreira, N.C.; Mazzuchelli, R.D.C.L.; Pacheco, A.C.; De Araujo, F.F.; Antunes, J.E.L.; de Araujo, A.S.F. *Bacillus subtilis* improves maize tolerance to salinity. *Ciência Rural* **2018**, *48*. [[CrossRef](#)]
58. Fukami, J.; De La Osa, C.; Ollero, F.J.; Megías, M.; Hungria, M. Co-inoculation of maize with *Azospirillum brasilense* and *Rhizobium tropici* as a strategy to mitigate salinity stress. *Funct. Plant Biol.* **2018**, *45*, 328–339. [[CrossRef](#)]
59. Latef, A.; Abu, A.A.H.; Alhmad, M.F.; Kordrostami, M.; Abo-Baker, A.-B.A.-E.; Zakir, A. Inoculation with *Azospirillum lipoferum* or *Azotobacter chroococcum* Reinforces Maize Growth by Improving Physiological Activities Under Saline Conditions. *J. Plant Growth Regul.* **2020**, *39*, 1293–1306. [[CrossRef](#)]
60. Sagar, A.; Kuddus, M.; Singh, B.P.; Labhane, N.M.; Srivastava, S.P.W. Plant Growth Promotion of millets under Abiotic stress using *Enterobacter cloacae* PR10 (KP226575b). *J. Indian Bot. Soc.* **2020**, *100*, 30–41. [[CrossRef](#)]
61. Omer, A.M.; Emara, H.M.; Zaghloul, R.A.; Abdel-Monem, M.O.; Dawwam, G.E. Potential of *Azotobacter Salinestrus* as Plant Growth Promoting Rhizobacteria under Saline Stress Conditions. *RJPBCS Res. J. Pharm. Biol. Chem. Sci.* **2016**, *7*, 2572–2583.
62. Bhise, K.K.; Bhagwat, P.K.; Dandge, P.B. Plant Growth-Promoting Characteristics of Salt Tolerant *Enterobacter cloacae* Strain KBPD and Its Efficacy in Amelioration of Salt Stress in *Vigna radiata* L. *J. Plant Growth Regul.* **2016**, *36*, 215–226. [[CrossRef](#)]
63. Viscardi, S.; Ventorino, V.; Duran, P.; Maggio, A.; De Pascale, S.; Mora, M.; Pepe, O. Assessment of plant growth promoting activities and abiotic stress tolerance of *Azotobacter chroococcum* strains for a potential use in sustainable agriculture. *J. Soil Sci. Plant Nutr.* **2016**, *16*, 848–863. [[CrossRef](#)]

64. Van Oosten, M.J.; Di Stasio, E.; Cirillo, V.; Silletti, S.; Ventorino, V.; Pepe, O.; Maggio, A. Root inoculation with *Azotobacter chroococcum* 76A enhances tomato plants adaptation to salt stress under low N conditions. *BMC Plant Biol.* **2018**, *18*, 205. [[CrossRef](#)] [[PubMed](#)]
65. Win, K.T.; Tanaka, F.; Okazaki, K.; Ohwaki, Y. The ACC deaminase expressing endophyte *Pseudomonas* spp. Enhances NaCl stress tolerance by reducing stress-related ethylene production, resulting in improved growth, photosynthetic performance, and ionic balance in tomato plants. *Plant Physiol. Biochem.* **2018**, *127*, 599–607. [[CrossRef](#)]
66. Gupta, A.; Rai, S.; Bano, A.; Khanam, A.; Sharma, S.; Pathak, N. Comparative Evaluation of Different Salt-Tolerant Plant Growth-Promoting Bacterial Isolates in Mitigating the Induced Adverse Effect of Salinity in *Pisum sativum*. *Biointerface Res. Appl. Chem.* **2021**, *11*, 13141–13154.
67. Sapre, S.; Gontia-Mishra, I.; Tiwari, S. Plant Growth-Promoting Rhizobacteria Ameliorates Salinity Stress in Pea (*Pisum sativum*). *J. Plant Growth Regul.* **2021**, *189*, 1–10. [[CrossRef](#)]
68. Abd_Allah, E.F.; Alqarawi, A.A.; Hashem, A.; Radhakrishnan, R.; Al-Huqail, A.A.; Al-Otibi, F.O.N.; Malik, J.A.; Alharbi, R.I.; Egamberdieva, D. Endophytic bacterium *Bacillus subtilis* (BERA 71) improves salt tolerance in chickpea plants by regulating the plant defense mechanisms. *J. Plant Interact.* **2018**, *13*, 37–44. [[CrossRef](#)]
69. Mushtaq, Z.; Faizan, S.; Gulzar, B.; Hakeem, K.R. Inoculation of Rhizobium Alleviates Salinity Stress Through Modulation of Growth Characteristics, Physiological and Biochemical Attributes, Stomatal Activities and Antioxidant Defence in *Cicer arietinum* L. *J. Plant Growth Regul.* **2021**, *40*, 2148–2163. [[CrossRef](#)]
70. Wang, W.; Wu, Z.; He, Y.; Huang, Y.; Li, X.; Ye, B.-C. Plant growth promotion and alleviation of salinity stress in Capsicum annuum L. by Bacillus isolated from saline soil in Xinjiang. *Ecotoxicol. Environ. Saf.* **2018**, *164*, 520–529. [[CrossRef](#)] [[PubMed](#)]
71. Samaddar, S.; Chatterjee, P.; Choudhury, A.R.; Ahmed, S.; Sa, T. Interactions between *Pseudomonas* spp. and their role in improving the red pepper plant growth under salinity stress. *Microbiol. Res.* **2018**, *219*, 66–73. [[CrossRef](#)]
72. Habib, S.H.; Kausar, H.; Saud, H.M. Plant Growth-Promoting Rhizobacteria Enhance Salinity Stress Tolerance in Okra through ROS-Scavenging Enzymes. *BioMed Res. Int.* **2016**, *2016*, 6284547. [[CrossRef](#)]
73. Szymańska, S.; Dąbrowska Grażyna, B.; Jarosław, T.; Katarzyna, N.; Agnieszka, P.; Katarzyna, H. Boosting the Brassica napus L. tolerance to salinity by the halotolerant strain *Pseudomonas stutzeri* ISE12. *Environ. Exp. Bot.* **2019**, *163*, 55–68. [[CrossRef](#)]
74. Yasmin, H.; Naeem, S.; Bakhtawar, M.; Jabeen, Z.; Nosheen, A.; Naz, R.; Keyani, R.; Mumtaz, S.; Hassan, M.N. Halotolerant rhizobacteria *Pseudomonas pseudoalcaligenes* and *Bacillus subtilis* mediate systemic tolerance in hydroponically grown soybean (*Glycine max* L.) against salinity stress. *PLoS ONE* **2020**, *15*, e0231348. [[CrossRef](#)]
75. Khan, M.A.; Sahile, A.A.; Jan, R.; Asaf, S.; Hamayun, M.; Imran, M.; Adhikari, A.; Kang, S.; Kim, K.M.; Lee, I. Halo-tolerant bacteria mitigate the effects of salinity stress on soybean growth by regulating secondary metabolites and molecular responses. *BMC Plant Biol.* **2021**, *21*, 176. [[CrossRef](#)]
76. Li, H.; Lei, P.; Pang, X.; Li, S.; Xu, H.; Xu, Z.; Feng, X. Enhanced tolerance to salt stress in canola (*Brassica napus* L.) seedlings inoculated with the halotolerant *Enterobacter cloacae* HSNJ4. *Appl. Soil Ecol.* **2017**, *119*, 26–34. [[CrossRef](#)]
77. Saghafi, D.; Ghorbanpour, M.; Lajayer, B.A. Efficiency of Rhizobium strains as plant growth promoting rhizobacteria on morpho-physiological properties of *Brassica napus* L. under salinity stress. *J. Soil Sci. Plant Nutr.* **2018**, *18*, 253–268. [[CrossRef](#)]
78. Benidire, L.; Lahrouni, M.; Khalloufi, F.; Gottfert, M.; Oufdou, K. Effects of *Rhizobium leguminosarum* inoculation on growth, nitrogen uptake and mineral assimilation in vicia faba plants under salinity stress. *J. Agric. Sci. Technol. (JAST)* **2017**, *19*, 889–901.
79. Garcia, L.; Dattamudi, S.; Chanda, S.; Jayachandran, K. Effect of Salinity Stress and Microbial Inoculations on Glomalin Production and Plant Growth Parameters of Snap Bean (*Phaseolus vulgaris*). *Agronomy* **2019**, *9*, 545. [[CrossRef](#)]
80. Garg, N.; Pandey, R. High effectiveness of exotic arbuscular mycorrhizal fungi is reflected in improved rhizobial symbiosis and trehalose turnover in Cajanus cajan genotypes grown under salinity stress. *Fungal Ecol.* **2016**, *21*, 57–67. [[CrossRef](#)]
81. Yousefi, S.; Kartoolinejad, D.; Bahmani, M.; Naghdi, R. Effect of *Azospirillum lipoferum* and *Azotobacter chroococcum* germination and early growth of hopbush shrub (*Dodonaea viscosa* L.) under salinity stress. *J. Sustain. For.* **2016**, *36*, 107–120. [[CrossRef](#)]
82. Arora, M.; Saxena, P.; Abdin, M.Z.; Varma, A. Interaction between *Piriformospora indica* and *Azotobacter chroococcum* diminish the effect of salt stress in *Artemisia annua* L. by enhancing enzymatic and non-enzymatic antioxidants. *Symbiosis* **2019**, *80*, 61–73. [[CrossRef](#)]
83. Silambarasan, S.; Logeswari, P.; Valentine, A.; Cornejo, P.; Kannan, V.R. *Pseudomonas citronellolis* strain SLP6 enhances the phytoremediation efficiency of *Helianthus annuus* in copper contaminated soils under salinity stress. *Plant Soil* **2020**, *457*, 241–253. [[CrossRef](#)]
84. Srivastava, S.; Srivastava, S. Prescience of endogenous regulation in *Arabidopsis thaliana* by *Pseudomonas putida* MTCC 5279 under phosphate starved salinity stress condition. *Sci. Rep.* **2020**, *10*, 5855. [[CrossRef](#)]
85. Noori, F.; Etesami, H.; Najafi Zarini, H.; Khoshkholgh-Sima, N.A.; Hosseini Salekdeh, G.; Alishahi, F. Mining alfalfa (*Medicago sativa* L.) nodules for salinity tolerant non-rhizobial bacteria to improve growth of alfalfa under salinity stress. *Ecotoxicol. Environ. Saf.* **2018**, *162*, 129–138. [[CrossRef](#)]
86. Zhu, Z.; Zhang, H.; Leng, J.; Niu, H.; Chen, X.; Liu, D.; Chen, Y.; Gao, N.; Ying, H. Isolation and characterization of plant growth-promoting rhizobacteria and their effects on the growth of *Medicago sativa* L. under salinity conditions. *Antonie Leeuwenhoek* **2020**, *113*, 1263–1278. [[CrossRef](#)]

87. Tirry, N.; Laghmari, A.K.G.; Lemjereb, M.; Hnadi, H.; Amrani, K.; Bahafid, W.; Ghachtouli, N.E. Improved salinity tolerance of *Medicago sativa* and soil enzyme activities by PGPR. *Biocatal. Agric. Biotechnol.* **2021**, *31*, 101914. [\[CrossRef\]](#)
88. Rahman, A.; Sultana, V.; Ara, J.; Ehteshamul-Haque, S. Induction of Systemic Resistance in Cotton by the Neem Cake and *Pseudomonas aeruginosa* under Salinity Stress and *Macrophomina phaseolina* Infection. *Pak. J. Bot.* **2016**, *48*, 1681–1689.
89. Hashem, A.; Abd-Allah, E.F.; Alqarawi, A.; Al-Huqail, A.A.; Shah, M.A. Induction of Osmoregulation and Modulation of Salt Stress in *Acacia gerrardii* Benth by Arbuscular Mycorrhizal Fungi and *Bacillus subtilis* (BERA 71). *BioMed Res. Int.* **2016**, *2016*, 6294098. [\[CrossRef\]](#) [\[PubMed\]](#)
90. Egamberdieva, D.; Jabborova, D.; Berg, G. Synergistic interactions between *Bradyrhizobium japonicum* and the endophyte *Stenotrophomonas rhizophila* and their effects on growth, and nodulation of soybean under salt stress. *Plant Soil* **2015**, *405*, 35–45. [\[CrossRef\]](#)
91. Raghuwanshi, R.; Prasad, J.K. Perspectives of Rhizobacteria with ACC Deaminase Activity in Plant Growth under Abiotic Stress. In *Root Biology; Soil Biology*; Giri, B., Prasad, R., Varma, A., Eds.; Springer International Publishing: Cham, Switzerland, 2018; Volume 52, pp. 303–321. [\[CrossRef\]](#)
92. Khan, N.; Bano, A. Exopolysaccharide producing rhizobacteria and their impact on growth and drought tolerance of wheat grown under rainfed conditions. *PLoS ONE* **2019**, *14*, e0222302. [\[CrossRef\]](#)
93. Shameer, S.; Prasad, T. Plant growth promoting rhizobacteria for sustainable agricultural practices with special reference to biotic and abiotic stresses. *Plant Growth Regul.* **2018**, *84*, 603–615. [\[CrossRef\]](#)
94. Sayyed, R.Z.; Seifi, S.; Patel, P.R.; Shaikh, S.S.; Jadhav, H.P.; El Enshasy, H. Siderophore production in groundnut rhizosphere isolate, *Achromobacter* sp. RZS2 influenced by physicochemical factors and metal ions. *Environ. Sustain.* **2019**, *2*, 117–124. [\[CrossRef\]](#)
95. Etesami, H.; Emami, S.; Alikhani, H.A. Potassium solubilizing bacteria (KSB): Mechanisms, promotion of plant growth, and future prospects—A review. *J. Soil Sci. Plant Nutr.* **2017**, *17*, 897–911. [\[CrossRef\]](#)
96. Zaidi, A.; Khan, M.S.; Saif, S.; Rizvi, A.; Ahmed, B.; Shahid, M. Role of Nitrogen-Fixing Plant Growth-Promoting Rhizobacteria in Sustainable Production of Vegetables: Current Perspective. In *Microbial Strategies for Vegetable Production*; Springer: Berlin/Heidelberg, Germany, 2017; pp. 49–79.
97. Tang, A.; Haruna, A.O.; Majid, N.M.A.; Jalloh, M.B. Potential PGPR Properties of Cellulolytic, Nitrogen-Fixing, Phosphate-Solubilizing Bacteria in Rehabilitated Tropical Forest Soil. *Microorganisms* **2020**, *8*, 442. [\[CrossRef\]](#)
98. Abbas, R.; Rasul, S.; Aslam, K.; Baber, M.; Shahid, M.; Mubeen, F.; Naqqash, T. Halotolerant PGPR: A hope for cultivation of saline soils. *J. King Saud Univ.-Sci.* **2019**, *31*, 1195–1201. [\[CrossRef\]](#)
99. Tsukanova, K.A.; Chebotar, V.K.; Meyer, J.J.M.; Bibikova, T.N. Effect of plant growth-promoting Rhizobacteria on plant hormone homeostasis. *S. Afr. J. Bot.* **2017**, *113*, 91–102. [\[CrossRef\]](#)
100. Grover, M.; Bodhankar, S.; Sharma, A.; Sharma, P.; Singh, J.; Nain, L. PGPR Mediated Alterations in Root Traits: Way toward Sustainable Crop Production. *Front. Sustain. Food Syst.* **2021**, *4*, 287. [\[CrossRef\]](#)
101. Patel, T.; Saraf, M. Biosynthesis of phytohormones from novel rhizobacterial isolates and their in vitro plant growth-promoting efficacy. *J. Plant Interact.* **2017**, *12*, 480–487. [\[CrossRef\]](#)
102. Tewari, S.; Arora, N.K. Fluorescent *Pseudomonas* sp. PF17 as an efficient plant growth regulator and biocontrol agent for sunflower crop under saline conditions. *Symbiosis* **2016**, *68*, 99–108. [\[CrossRef\]](#)
103. Li, M.; Guo, R.; Yu, F.; Chen, X.; Zhao, H.; Li, H.; Wu, J. Indole-3-Acetic Acid Biosynthesis Pathways in the Plant-Beneficial Bacterium *Arthrobacter pascens* ZZ21. *Int. J. Mol. Sci.* **2018**, *19*, 443. [\[CrossRef\]](#)
104. Joshi, G.; Kumar, V.; Brahmachari, S.K. Screening and identification of novel halotolerant bacterial strains and assessment for insoluble phosphate solubilization and IAA production. *Bull. Natl. Res. Cent.* **2021**, *45*, 83. [\[CrossRef\]](#)
105. Egamberdieva, D.; Jabborova, D.; Wirth, S.; Alam, P.; Alyemeni, M.N.; Ahmad, P. Interactive Effects of Nutrients and *Bradyrhizobium japonicum* on the Growth and Root Architecture of Soybean (*Glycine max* L.). *Front. Microbiol.* **2018**, *9*, 1000. [\[CrossRef\]](#)
106. Egamberdieva, D.; Wirth, S.; Jabborova, D.; Räsänen, L.A.; Liao, H. Coordination between *Bradyrhizobium* and *Pseudomonas alleviates* salt stress in soybean through altering root system architecture. *J. Plant Interact.* **2017**, *12*, 100–107. [\[CrossRef\]](#)
107. Kang, S.-M.; Shahzad, R.; Bilal, S.; Khan, A.L.; Park, Y.-G.; Lee, K.-E.; Asaf, S.; Khan, M.A.; Lee, I.-J. Indole-3-acetic-acid and ACC deaminase producing *Leclercia adecarboxylata* MO1 improves *Solanum lycopersicum* L. growth and salinity stress tolerance by endogenous secondary metabolites regulation. *BMC Microbiol.* **2019**, *19*, 80. [\[CrossRef\]](#)
108. Panwar, M.; Tewari, R.; Gulati, A.; Nayyar, H. Indigenous salt-tolerant rhizobacterium *Pantoea dispersa* (PSB3) reduces sodium uptake and mitigates the effects of salt stress on growth and yield of chickpea. *Acta Physiol. Plant.* **2016**, *38*, 278. [\[CrossRef\]](#)
109. Shultana, R.; Tan Kee Zuan, A.; Yusop, M.R.; Mohd Saud, H.; Ayanda, A.F. Effect of Salt-Tolerant Bacterial Inoculations on Rice Seedlings Differing in Salt-Tolerance under Saline Soil Conditions. *Agronomy* **2020**, *10*, 1030. [\[CrossRef\]](#)
110. Banerjee, A.; Bareth, D.A.; Joshi, S.R. Native microorganisms as potent bio inoculants for plant growth promotion in shifting agriculture (Jhum) systems. *J. Soil Sci. Plant Nutr.* **2017**, *17*, 127–140.
111. Cortleven, A.; Schmölling, T. Regulation of chloroplast development and function by cytokinin. *J. Exp. Bot.* **2015**, *66*, 4999–5013. [\[CrossRef\]](#)
112. TrParray, A.P.; Jan, S.; Kamili, A.N.; Qadri, R.A.; Egamberdieva, D.; Ahmad, P. Current perspectives on plant growth promoting rhizobacteria. *Plant Growth Regul.* **2016**, *35*, 877–902.

113. Tahir, H.A.S.; Gu, Q.; Wu, H.; Raza, W.; Hanif, A.; Wu, L.; Colman, M.V.; Gao, X. Plant growth promotion by volatile organic compounds produced by *Bacillus subtilis* SYST2. *Front. Microbiol.* **2017**, *8*, 171. [[CrossRef](#)]
114. Ijaz, M.; Tahir, M.; Shahid, M.; Ul-Allah, S.; Sattar, A.; Sher, A.; Mahmood, K.; Hussain, M. Combined application of biochar and PGPR consortia for sustainable production of wheat under semiarid conditions with a reduced dose of synthetic fertilizer. *Braz. J. Microbiol. Publ. Braz. Soc. Microbiol.* **2019**, *50*, 449–458. [[CrossRef](#)]
115. Mukhtar, T.; Rehman, S.U.; Smith, D.; Sultan, T.; Seleiman, M.F.; Alsadon, A.A.; Amna; Ali, S.; Chaudhary, H.J.; Solieman, T.H.I.; et al. Mitigation of Heat Stress in *Solanum lycopersicum* L. by ACC-deaminase and Exopolysaccharide Producing *Bacillus cereus*: Effects on Biochemical Profiling. *Sustainability* **2020**, *12*, 2159. [[CrossRef](#)]
116. Akhtar, S.S.; Mekureyaw, M.F.; Pandey, C.; Roitsch, T. Role of Cytokinins for Interactions of Plants with Microbial Pathogens and Pest Insects. *Front. Plant Sci.* **2020**, *10*, 1777. [[CrossRef](#)]
117. Vaishnav, A.; Singh, J.; Singh, P.; Rajput, R.S.; Singh, H.B.; Sarma, B.K. Sphingo bacterium sp. BHU-AV3 Induces Salt Tolerance in Tomato by Enhancing Antioxidant Activities and Energy Metabolism. *Front. Microbiol.* **2020**, *11*, 443. [[CrossRef](#)]
118. Supriya, P.; Kusale, S.; Attar, Y.; Sayyed, R.; Malek, R.; Ilyas, N.; Suriani, N.; Khan, N.; El Enshasy, H. Production of Plant Beneficial and Antioxidants Metabolites by *Klebsiellavariicola* under Salinity Stress. *Molecules* **2021**, *26*, 1894. [[CrossRef](#)]
119. Arora, D.; Bhatla, S.C. Melatonin and nitric oxide regulate sunflower seedling growth under salt stress accompanying differential expression of Cu/Zn SOD and Mn SOD. *Free Radic. Biol. Med.* **2017**, *106*, 315–328. [[CrossRef](#)]
120. Sukweenadhi, J.; Balusamy, S.R.; Kim, Y.J.; Lee, C.H.; Kim, Y.J.; Koh, S.C.; Yang, D.C. A growth-promoting bacteria, *Paenibacillus yonginensis* DCY84T enhanced salt stress tolerance by activating defense-related systems in *Panax ginseng*. *Front. Plant Sci.* **2018**, *9*, 813. [[CrossRef](#)] [[PubMed](#)]
121. Ansari, F.A.; Ahmad, I.; Pichtel, J. Growth stimulation and alleviation of salinity stress to wheat by the biofilm forming *Bacillus pumilus* strain FAB10. *Appl. Soil Ecol.* **2019**, *143*, 45–54. [[CrossRef](#)]
122. Khan, M.A.; Asaf, S.; Khan, A.L.; Adhikari, A.; Jan, R.; Ali, S.; Imran, M.; Kim, K.-M.; Lee, I.-J. Halotolerant Rhizobacterial Strains Mitigate the Adverse Effects of NaCl Stress in Soybean Seedlings. *BioMed Res. Int.* **2019**, *2019*, 9530963. [[CrossRef](#)] [[PubMed](#)]
123. Khanna, K.; Jamwal, V.L.; Kohli, S.K.; Gandhi, S.G.; Ohri, P.; Bhardwaj, R.; Abd-Allah, E.; Hashem, A.; Ahmad, P. Plant growth promoting rhizobacteria induced Cd tolerance in *Lycopersicon esculentum* through altered antioxidative defense expression. *Chemosphere* **2018**, *217*, 463–474. [[CrossRef](#)]
124. Rajput, R.S.; Ram, R.M.; Vaishnav, A.; Singh, H.B. Microbe-based novel biostimulants for sustainable crop production. In *Microbial Diversity in Ecosystem Sustainability and Biotechnological Applications*; Satynarayan, T., Ed.; Springer: Singapore, 2019; pp. 109–144. [[CrossRef](#)]
125. El-Esawi, M.A.; Al-Ghamdi, A.A.; Ali, H.M.; Alayafi, A.A. *Azospirillum lipoferum* FK1 confers improved salt tolerance in chickpea (*Cicer arietinum* L.) by modulating osmolytes, antioxidant machinery and stress-related genes expression. *Environ. Exp. Bot.* **2018**, *159*, 55–65. [[CrossRef](#)]
126. Chen, D.; Shao, Q.; Yin, L.; Younis, A.; Zheng, B. Polyamine Function in Plants: Metabolism, Regulation on Development, and Roles in Abiotic Stress Responses. *Front. Plant Sci.* **2019**, *9*, 1945. [[CrossRef](#)]
127. Ma, Y.; Dias, M.C.; Freitas, H. Drought and Salinity Stress Responses and Microbe-Induced Tolerance in Plants. *Front. Plant Sci.* **2020**, *11*, 1750. [[CrossRef](#)]
128. Cappellari, L.; Banchio, E. Microbial Volatile Organic Compounds Produced by *Bacillus amyloliquefaciens* GB Ameliorate the Effects of Salt Stress in *Mentha piperita* Principally Through Acetoin Emission. *J. Plant Growth Regul.* **2019**, *39*, 764–775. [[CrossRef](#)]
129. Abdelaal, K.A.; El-Maghraby, L.M.; Elansary, H.; Hafez, Y.M.; Ibrahim, E.; El-Banna, M.; Elkesh, A. Treatment of Sweet Pepper with Stress Tolerance-Inducing Compounds Alleviates Salinity Stress Oxidative Damage by Mediating the Physio-Biochemical Activities and Antioxidant Systems. *Agronomy* **2019**, *10*, 26. [[CrossRef](#)]
130. Zahir, Z.A.; Nadeem, S.M.; Khan, M.Y.; Binyamin, R.; Waqas, M.R. Role of Halotolerant Microbes in Plant Growth Promotion Under Salt Stress Conditions. In *Saline Soil-Based Agriculture by Halotolerant Microorganisms*; Kumar, M., Ed.; Springer: Singapore, 2019; pp. 209–253. [[CrossRef](#)]
131. Sharma, A.; Shahzad, B.; Kumar, V.; Kohli, S.K.; Sidhu, G.P.S.; Bali, A.S.; Zheng, B. Phytohormones Regulate Accumulation of Osmolytes under Abiotic Stress. *Biomolecules* **2019**, *9*, 285. [[CrossRef](#)]
132. Mishra, J.; Fatima, T.; Arora, N.K. Role of Secondary Metabolites from Plant Growth-Promoting Rhizobacteria in Combating Salinity Stress. In *Plant Microbiome: Stress Response*; Ahmad, P., Egamberdieva, D., Eds.; Springer: Singapore, 2018; pp. 127–163.
133. Bremer, E.; Krämer, R. Responses of Microorganisms to Osmotic Stress. *Annu. Rev. Microbiol.* **2019**, *73*, 313–334. [[CrossRef](#)]
134. Kushwaha, B.; Jadhav, I.; Verma, H.N.; Geethadevi, A.; Parashar, D.; Jadhav, K. Betaine accumulation suppresses the de-novo synthesis of ectoine at a low osmotic concentration in *Halomonas* sp SBS 10, a bacterium with broad salinity tolerance. *Mol. Biol. Rep.* **2019**, *46*, 4779–4786. [[CrossRef](#)]
135. Qin, S.; Feng, W.-W.; Zhang, Y.-J.; Wang, T.-T.; Xiong, Y.-W.; Xing, K. Diversity of Bacterial Microbiota of Coastal Halophyte *Limonium sinense* and Amelioration of Salinity Stress Damage by Symbiotic Plant Growth-Promoting *Actinobacterium Glutamicibacter halophytocola* KLBMP 5180. *Appl. Environ. Microbiol.* **2018**, *84*, e01533-18. [[CrossRef](#)]
136. Forni, C.; Duca, D.; Glick, B.R. Mechanisms of plant response to salt and drought stress and their alteration by rhizobacteria. *Plant Soil* **2017**, *410*, 335–356. [[CrossRef](#)]

137. Shim, J.S.; Seo, J.-S.; Seo, J.S.; Kim, Y.; Koo, Y.; Choi, Y.D.; Jung, C. Heterologous expression of bacterial trehalose biosynthetic genes enhances trehalose accumulation in potato plants without adverse growth effects. *Plant Biotechnol. Rep.* **2019**, *13*, 409–418. [[CrossRef](#)]
138. Atouei, M.T.; Pourbabaee, A.A.; Shorafa, M. Alleviation of Salinity Stress on Some Growth Parameters of Wheat by Exopolysaccharide-Producing Bacteria. *Iran. J. Sci. Technol. Trans. A Sci.* **2019**, *43*, 2725–2733. [[CrossRef](#)]
139. Chu, T.N.; Tran, B.T.H.; Van Bui, L.; Hoang, M.T.T. Plant growth-promoting rhizobacterium *Pseudomonas* PS01 induces salt tolerance in *Arabidopsis thaliana*. *BMC Res. Notes* **2019**, *12*, 11. [[CrossRef](#)]
140. Ali, S.; Kim, W.-C. Plant Growth Promotion under Water: Decrease of Waterlogging-Induced ACC and Ethylene Levels by ACC Deaminase-Producing Bacteria. *Front. Microbiol.* **2018**, *9*, 1096. [[CrossRef](#)]
141. Saleem, A.R.; Brunetti, C.; Khalid, A.; Della Rocca, G.; Raio, A.; Emiliani, G.; DE Carlo, A.; Mahmood, T.; Centritto, M. Drought response of *Mucuna pruriens* (L.) DC. inoculated with ACC deaminase and IAA producing rhizobacteria. *PLoS ONE* **2018**, *13*, e0191218. [[CrossRef](#)]
142. Del Carmen Orozco-Mosqueda, M.; Glick, B.R.; Santoyo, G. ACC deaminase in plant growth-promoting bacteria (PGPB): An efficient mechanism to counter salt stress in crops. *Microbiol. Res.* **2020**, *235*, 126439. [[CrossRef](#)]
143. Acuña, J.J.; Camposa, M.; Morab, M.D.L.; Jaisic, D.P.; Jorquera, M.A. ACCD-producing rhizobacteria from an Andean Altiplano native plant (*Parastrephia quadrangularis*) to alleviate salt stress in wheat seedlings. *Appl. Soil Ecol.* **2019**, *36*, 184–190. [[CrossRef](#)]
144. Gupta, S.; Pandey, S. ACC Deaminase Producing Bacteria with Multifarious Plant Growth Promoting Traits Alleviates Salinity Stress in French Bean (*Phaseolus vulgaris*) Plants. *Front. Microbiol.* **2019**, *10*, 1506. [[CrossRef](#)]
145. Maxton, A.; Singh, P.; Masih, S.A. ACC deaminase-producing bacteria mediated drought and salt tolerance in *Capsicum annuum*. *J. Plant Nutr.* **2017**, *41*, 574–583. [[CrossRef](#)]
146. Yoo, S.; Weon, H.Y.; Song, J.; Sang, M.K. Induced Tolerance to Salinity Stress by Halotolerant Bacteria *Bacillus ary-abhattai* H19-1 and *B. mesonae* H20-5 in Tomato Plants. *J. Microbiol. Biotechnol.* **2019**, *29*, 1124–1136. [[CrossRef](#)]
147. Santoyo, G.; Moreno-Hagelsieb, G.; del Carmen Orozco-Mosqueda, M.; Glick, B.R. Plant growth-promoting bacterial endophytes. *Microbiol. Res.* **2016**, *183*, 92–99. [[CrossRef](#)]
148. Shah, G.; Jan, M.; Afreen, M.; Anees, M.; Rehman, S.; Daud, M.; Malook, I.; Jamil, M. Halophilic bacteria mediated phytoremediation of salt-affected soils cultivated with rice. *J. Geochem. Explor.* **2017**, *174*, 59–65. [[CrossRef](#)]
149. Aw, X.; Li, Z.; Wc, L.; Zh, Y. The effect of plant growth-promoting rhizobacteria (PGPR) on arsenic accumulation and the growth of rice plants (*Oryza sativa* L.). *Chemosphere* **2019**, *242*, 125136. [[CrossRef](#)]
150. Habibi, S.; Djedidi, S.; Ohkama-Ohtsu, N.; Sarhadi, W.A.; Kojima, K.; Rallos, R.V.; Ramirez, M.D.A.; Yamaya, H.; Sekimoto, H.; Yokoyama, T. Isolation and Screening of Indigenous Plant Growth-promoting Rhizobacteria from Different Rice Cultivars in Afghanistan Soils. *Microbes Environ.* **2019**, *34*, 347–355. [[CrossRef](#)]
151. Sagar, A.; Shukla, P.K.; Ramteke, P.W. Stimulation of Seed Germination and Growth Parameters of Rice var. Sahbhagi by *Enterobacter cloacae* (KP226569) in Presence of Ammonia Sulphate as Substitute of 1-Aminocyclopropane-1-Carboxylate. In *Plant Growth Promoting Rhizobacteria (PGPR): Prospects in Sustainable Agriculture*; Springer-Nature: Singapore, 2019; pp. 117–124.
152. Javed, H.; Riaz, A.; Qureshi, A.; Javed, K.; Mujeeb, F.; Ijaz, F.; Akhtar, M.S.; Ali, M.A.; Gul, R.; Aftab, M. Isolation, characterization and screening of PGPR capable of providing relief in salinity stress. *Eurasian J. Soil Sci.* **2020**, *9*, 85–91. [[CrossRef](#)]
153. Fatima, T.; Mishra, I.; Verma, R.; Arora, N.K. Mechanisms of halotolerant plant growth promoting *Alcaligenes* sp. involved in salt tolerance and enhancement of the growth of rice under salinity stress. *3 Biotech* **2020**, *10*, 361. [[CrossRef](#)]
154. Prittesh, P.; Avnika, P.; Kinjal, P.; Jinal, H.N.; Sakthivel, K.; Amaesan, N. Amelioration effect of salt-tolerant plant growth-promoting bacteria on growth and physiological properties of rice (*Oryza sativa*) under salt-stressed conditions. *Arch. Microbiol.* **2020**, *202*, 2419–2428. [[CrossRef](#)] [[PubMed](#)]
155. Ji, J.; Yuan, D.; Jin, C.; Wang, G.; Li, X.; Guan, C. Enhancement of growth and salt tolerance of rice seedlings (*Oryza sativa* L.) by regulating ethylene production with a novel halotolerant PGPR strain *Glutamicibacter* sp. YD01 containing ACC deaminase activity. *Acta Physiol. Plant.* **2020**, *42*, 42. [[CrossRef](#)]
156. Sultana, S.; Paul, S.C.; Parveen, S.; Alam, S.; Rahman, S.; Bushra Jannat, B.; Hoque, S.; Rahman, M.T.; Karim, M.M. Iso-lation and identification of salt-tolerant plant-growth-promoting rhizobacteria and their application for rice cultivation. *Can. J. Microbiol.* **2020**, *66*, 144–160.
157. Nawaz, A.; Shahbaz, M.; Imran, A.; Marghoob, M.U.; Imtiaz, M.; Mubeen, F. Potential of salt tolerant PGPR in growth and yield augmentation of wheat (*Triticum aestivum* L.) under saline conditions. *Front. Microbiol.* **2020**, *11*, 2019. [[CrossRef](#)]
158. Singh, R.P.; Jha, P.N. Analysis of fatty acid composition of PGPR *Klebsiella* sp. SBP-8 and its role in ameliorating salt stress in wheat. *Symbiosis* **2017**, *73*, 213–222. [[CrossRef](#)]
159. Nguyen, M.L.; Spaepen, S.; Du Jardin, P.; Delaplace, P. Biostimulant effects of rhizobacteria on wheat growth and nutrient uptake depend on nitrogen application and plant development. *Arch. Agron. Soil Sci.* **2018**, *65*, 58–73. [[CrossRef](#)]
160. Sagar, A.; Thomas, G.; Rai, S.; Mishra, R.K.; Ramteke, P.W. Enhancement of Growth and Yield parameters of Wheat variety AAI-W6 by an organic farm isolate of plant growth promoting *Erwinia* species KP226572. *Int. J. Agric. Environ. Biotechnol.* **2018**, *11*, 159–171.
161. Akbar, M.; Aslam, N.; Khalil, T.; Akhtar, S.; Siddiqi, E.H.; Iqbal, M.S. Effects of seed priming with plant growth-promoting rhizobacteria on wheat yield and soil properties under contrasting soils. *J. Plant Nutr.* **2019**, *42*, 2080–2091. [[CrossRef](#)]

162. Cortivo, C.D.; Ferrari, M.; Visioli, G.; Lauro, M.; Fornasier, F.; Barion, G.; Panozzo, A.; Vamerali, T. Effects of Seed-Applied Biofertilizers on Rhizosphere Biodiversity and Growth of Common Wheat (*Triticum aestivum* L.) in the Field. *Front. Plant Sci.* **2020**, *11*, 72. [CrossRef]
163. El-Nahrawy, S.; Yassin, M. Response of Different Cultivars of Wheat Plants (*Triticum aestivum* L.) to Inoculation by *Azotobacter* sp. under Salinity Stress Conditions. *J. Adv. Microbiol.* **2020**, *20*, 59–79. [CrossRef]
164. Akram, M.S.; Shahid, M.; Tariq, M.; Azeem, M.; Javed, M.T.; Saleem, S.; Riaz, S. Deciphering *Staphylococcus sciuri* SAT-17 Mediated Anti-oxidative Defense Mechanisms and Growth Modulations in Salt Stressed Maize (*Zea mays* L.). *Front. Microbiol.* **2016**, *7*, 867. [CrossRef]
165. Peng, J.; Ma, J.; Wei, X.; Zhang, C.; Jia, N.; Wang, X.; Wang, E.T.; Hu, D.; Wang, Z. Accumulation of beneficial bacteria in the rhizosphere of maize (*Zea mays* L.) grown in a saline soil in responding to a consortium of plant growth promoting rhizobacteria. *Ann. Microbiol.* **2021**, *71*, 40. [CrossRef]
166. Li, H.; Jiang, X. Inoculation with plant growth-promoting bacteria (PGPB) improves salt tolerance of maize seedling. *Russ. J. Plant Physiol.* **2017**, *64*, 235–241. [CrossRef]
167. Rafiq, K.; Akram, M.S.; Shahid, M.; Qaisar, U.; Rashid, N. Enhancement of salt tolerance in maize (*Zea mays* L.) using locally isolated *Bacillus* sp. SR-2-1/1. *Biologia* **2020**, *75*, 1425–1436. [CrossRef]
168. El-Esawi, M.A.; Alaraidh, I.A.; Alsahli, A.A.; Alzahrani, S.A.; Ali, H.M.; Alayafi, A.A.; Ahmad, M. *Serratia liquefaciens* KM4 improves salt stress tolerance in maize by regulating redox potential, ion homeostasis, leaf gas exchange and stress-related gene expression. *Int. J. Mol. Sci.* **2018**, *19*, 3310. [CrossRef]
169. Mukhtar, S.; Zareen, M.; Khaliq, Z.; Mehnaz, S.; Malik, K.A. Phylogenetic analysis of halophyte-associated rhizobacteria and effect of halotolerant and halophilic phosphate-solubilizing biofertilizers on maize growth under salinity stress conditions. *J. Appl. Microbiol.* **2019**, *128*, 556–573. [CrossRef]
170. Misra, S.; Chauhan, P.S. ACC deaminase-producing rhizosphere competent *Bacillus* spp. mitigate salt stress and promote *Zea mays* growth by modulating ethylene metabolism. *3 Biotech* **2020**, *10*, 119. [CrossRef]
171. Dixit, V.K.; Misra, S.; Mishra, S.K.; Tewari, S.K.; Joshi, N.; Chauhan, P.S. Characterization of plant growth-promoting alkalotolerant *Alcaligenes* and *Bacillus* strains for mitigating the alkaline stress in *Zea mays*. *Antonie Leeuwenhoek* **2020**, *113*, 889–905. [CrossRef]
172. Sapre, S.; Gontia-Mishra, I.; Tiwari, S. *Klebsiella* sp. confers enhanced tolerance to salinity and plant growth promotion in oat seedlings (*Avena sativa*). *Microbiol. Res.* **2018**, *206*, 25–32. [CrossRef]
173. Chibeba, A.M.; Kyei-Boahen, S.; Guimarães, M.D.F.; Nogueira, M.A.; Hungria, M. Feasibility of transference of inoculation-related technologies: A case study of evaluation of soybean rhizobial strains under the agro-climatic conditions of Brazil and Mozambique. *Agric. Ecosyst. Environ.* **2017**, *261*, 230–240. [CrossRef]
174. Jiménez, J.A.; Novinscak, A.; Fillion, M. *Pseudomonas fluorescens* LBUM677 differentially increases plant biomass, total oil content and lipid composition in three oilseed crops. *J. Appl. Microbiol.* **2020**, *128*, 1119–1127. [CrossRef]
175. Kumawat, K.C.; Sharma, P.; Singh, I.; Sirari, A.; Gill, B.S. Co-existence of *Leclercia adecarboxylata* (LSE-1) and *Bradyrhizobium* sp. (LSBR-3) in nodule niche for multifaceted effects and profitability in soybean production. *World J. Microbiol. Biotechnol.* **2019**, *35*, 172. [CrossRef]
176. Sibponkrung, S.; Kondo, T.; Tanaka, K.; Tittabutr, P.; Boonkerd, N.; Yoshida, K.-I.; Teaumroong, N. Co-Inoculation of *Bacillus velezensis* Strain S141 and *Bradyrhizobium* Strains Promotes Nodule Growth and Nitrogen Fixation. *Microorganisms* **2020**, *8*, 678. [CrossRef]
177. Zeffa, D.M.; Fantin, L.H.; Koltun, A.; De Oliveira, A.L.; Nunes, M.P.; Canteri, M.G.; Gonçalves, L.S. Effects of plant growth-promoting rhizobacteria on co-inoculation with *Bradyrhizobium* in soybean crop: A meta-analysis of studies from 1987 to 2018. *PeerJ* **2020**, *8*, e7905. [CrossRef]
178. Delamuta, J.R.M.; Menna, P.; Ribeiro, R.A.; Hungria, M. Phylogenies of symbiotic genes of *Bradyrhizobium* symbionts of legumes of economic and environmental importance in Brazil support the definition of the new symbiovars pachyrhizi and sojae. *Syst. Appl. Microbiol.* **2017**, *40*, 254–265. [CrossRef]
179. Sharma, S.; Kulkarni, J.; Jha, B. Halotolerant Rhizobacteria Promote Growth and Enhance Salinity Tolerance in Peanut. *Front. Microbiol.* **2016**, *7*, 1600. [CrossRef]
180. Irizarry, I.; White, J.F. Application of bacteria from non-cultivated plants to promote growth, alter root architecture and alleviate salt stress of cotton. *J. Appl. Microbiol.* **2017**, *122*, 1110–1120. [CrossRef]
181. Santos, A.A.; Da Silveira, J.A.G.; Bonifacio, A.; Rodrigues, A.C.; Figueiredo, M.D.V.B. Antioxidant response of cowpea co-inoculated with plant growth-promoting bacteria under salt stress. *Braz. J. Microbiol.* **2018**, *49*, 513–521. [CrossRef]
182. Anzuay, M.S.; Ciancio, M.G.R.; Ludueña, L.M.; Angelini, J.G.; Barros, G.; Pastor, N.; Taurian, T. Growth promotion of peanut (*Arachis hypogaea* L.) and maize (*Zea mays* L.) plants by single and mixed cultures of efficient phosphate solubilizing bacteria that are tolerant to abiotic stress and pesticides. *Microbiol. Res.* **2017**, *199*, 98–109. [CrossRef]
183. Shahid, M.; Akram, M.S.; Khan, M.A.; Zubair, M.; Shah, S.M.; Ismail, M.; Shabir, G.; Basheer, S.; Aslam, K.; Tariq, M. A phyto-beneficial strain *Planomicrobium* sp. MSSA-10 triggered oxidative stress responsive mechanisms and regulated the growth of pea plants under induced saline environment. *J. Appl. Microbiol.* **2018**, *124*, 1566–1579. [CrossRef]
184. Yasin, N.A.; Akram, W.; Khan, W.U.; Ahmad, S.R.; Ahmad, A.; Ali, A. Halotolerant plant-growth promoting rhizobacteria modulate gene expression and osmolyte production to improve salinity tolerance and growth in *Capsicum annum* L. *Environ. Sci. Pollut. Res.* **2018**, *25*, 23236–23250. [CrossRef] [PubMed]

185. Mohammed, A.F. Effectiveness of exopolysaccharides and biofilm forming plant growth promoting rhizobacteria on salinity tolerance of faba bean (*Vicia faba* L.). *Afr. J. Microbiol. Res.* **2018**, *12*, 399–404. [[CrossRef](#)]
186. Khan, A.; Ali, L.; Chaudhary, H.J.; Hussain Munis, M.F.; Bano, A.; Masood, S. *Bacillus pumilus* alleviates boron toxicity in tomato (*Lycopersicon esculentum* L.) due to enhanced antioxidant enzymatic activity. *Sci. Hortic.* **2016**, *200*, 178–185.
187. Qi, J.; Aiuchi, D.; Tani, M.; Asano, S.I.; Koike, M. Potential of Entomopathogenic *Bacillus thuringiensis* as Plant Growth Promoting Rhizobacteria and Biological Control Agents for Tomato Fusarium Wilt. *Int. J. Environ. Agric. Res.* **2016**, *2*, 55–63.
188. Sharma, I.P.; Sharma, A.K. Physiological and biochemical changes in tomato cultivar PT-3 with dual inoculation of my-corrhiza and PGPR against root-knot nematode. *Symbiosis* **2017**, *71*, 175–183. [[CrossRef](#)]
189. Sagar, A.; Ramteke, P.W. Isolation, characterization and evaluation of Multi traits *Pseudomonas* sp. KP966497 (PR21) for their growth promoting effect on Tomato (*Lycopersicon esculentum* Mill.). In Proceedings of the International Conference Climate Change, Biodiversity and Sustainable Agriculture (ICCBSA-2018), Jorhat, India, 13–16 December 2018.
190. Orozco-Mosqueda, M.D.C.; Duan, J.; Dibernardo, M.; Zetter, E.; Campos-García, J.; Glick, B.R.; Santoyo, G. The Production of ACC Deaminase and Trehalose by the Plant Growth Promoting Bacterium *Pseudomonas* sp. UW4 Synergistically Protect Tomato Plants Against Salt Stress. *Front. Microbiol.* **2019**, *10*, 1392. [[CrossRef](#)]
191. Hussein, K.A.; Joo, J.H. Plant Growth-Promoting Rhizobacteria Improved Salinity Tolerance of *Lactuca sativa* and *Raphanus sativus*. *J. Microbiol. Biotechnol.* **2018**, *28*, 938–945. [[CrossRef](#)]
192. Tahir, M.; Ahmad, I.; Shahid, M.; Shah, G.M.; Farooq, A.B.U.; Akram, M.; Tabassum, S.A.; Naeem, M.A.; Khalid, U.; Ahmad, S.; et al. Regulation of antioxidant production, ion uptake and productivity in potato (*Solanum tuberosum* L.) plant inoculated with growth promoting salt tolerant *Bacillus* strains. *Ecotoxicol. Environ. Saf.* **2019**, *178*, 33–42. [[CrossRef](#)]
193. Yu, Y.; Wang, N.; Hu, R.; Xiang, F. Genome-wide identification of soybean WRKY transcription factors in response to salt stress. *Springerplus* **2016**, *5*, 920. [[CrossRef](#)]
194. Wu, M.; Liu, H.; Han, G.; Cai, R.; Pan, F.; Xiang, Y. A moso bamboo WRKY gene PeWRKY83 confers salinity tolerance in transgenic Arabidopsis plants. *Sci. Rep.* **2017**, *7*, 11721. [[CrossRef](#)]
195. Barnawal, D.; Bharti, N.; Pandey, S.S.; Pandey, A.; Chanotiya, C.S.; Kalra, A. Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and TaCTR1 /TaDREB2 expression. *Physiol. Plant.* **2017**, *161*, 502–514. [[CrossRef](#)]
196. De la Torre-González, A.; Navarro-León, E.; Albacete, A.; Blasco, B.; Ruiz, J.M. Study of phytohormone profile and oxidative metabolism as key process to identification of salinity response in tomato commercial genotypes. *J. Plant Physiol.* **2017**, *216*, 164–173. [[CrossRef](#)]
197. Joshi, R.; Sahoo, K.K.; Tripathi, A.K.; Kumar, R.; Gupta, B.K.; Pareek, A.; Singla Pareek, S.L. Knockdown of an inflo-rescence meristem-specific cytokinin oxidase—OsCKX2 in rice reduces yield penalty under salinity stress condition. *Plant Cell Environ.* **2018**, *41*, 936–946. [[CrossRef](#)]
198. Asaf, S.; Khan, A.L.; Khan, M.A.; Al-Harrasi, A.; Lee, I.-J. Complete genome sequencing and analysis of endophytic *Sphingomonas* sp. LK11 and its potential in plant growth. *3 Biotech* **2018**, *8*, 389. [[CrossRef](#)]
199. Chen, L.; Liu, Y.; Wu, G.; Njeri, K.V.; Shen, Q.; Zhang, N.; Zhang, R. Induced maize salt tolerance by rhizosphere inoculation of *Bacillus amyloliquefaciens* SQR9. *Physiol. Plant.* **2016**, *158*, 34–44. [[CrossRef](#)]
200. Safdarian, M.; Askari, H.; Shariati, V.S.; Nematzadeh, G. Transcriptional responses of wheat roots inoculated with *Arthrobacter nitroguajacolicus* to salt stress. *Sci. Rep.* **2019**, *9*, 1792. [[CrossRef](#)]
201. Kazerooni, E.A.; Maharachchikumbura, S.S.N.; Adhikari, A.; Al-Sadi, A.M.; Kang, S.-M.; Kim, L.-R.; Lee, I.-J. Rhizospheric *Bacillus amyloliquefaciens* Protects *Capsicum annuum* cv. Geumsu gangsan From Multiple Abiotic Stresses via Multifarious Plant Growth-Promoting Attributes. *Front. Plant Sci.* **2021**, *12*, 669693. [[CrossRef](#)]
202. Liu, H.; Wang, J.; Sun, H.; Han, X.; Peng, Y.; Liu, J.; Liu, K.; Ding, Y.; Wang, C.; Du, B. Transcriptome Profiles Reveal the Growth-Promoting Mechanisms of *Paenibacillus polymyxa* YC0136 on Tobacco (*Nicotiana tabacum* L.). *Front. Microbiol.* **2020**, *11*, 2384. [[CrossRef](#)]
203. Akram, W.; Aslam, H.; Ahmad, S.R.; Anjum, T.; Yasin, N.A.; Khan, W.U.; Ahmad, A.; Guo, J.; Wu, T.; Luo, W.; et al. *Bacillus megaterium* strain A12 ameliorates salinity stress in tomato plants through multiple mechanisms. *J. Plant Interact.* **2019**, *14*, 506–518. [[CrossRef](#)]