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Review

Plant Growth-Promoting Halobacteria and Their Ability to Protect Crops from Abiotic Stress: An Eco-Friendly Alternative for Saline Soils

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Abstract: Arid and semi-arid soils display low productivity due to abiotic stress associated with drought and salinity. Halobacteria can increase the yield of crops grown under these types of stress. These bacteria thrive across a wide salinity range (1–25% NaCl) and also in the absence of NaCl and have direct and indirect mechanisms that promote plant growth. This review summarizes studies conducted over the past five years that have assessed the effect of halobacteria on plants and soil fertility. The criteria used in the selection of halobacteria were also reviewed. Few studies have assessed the impact of halobacteria on soil fertility. The selection of halobacteria has been based on a qualitative criterion considering the morphology of colonies grown in media enriched with salts, mainly Na^+. Not all bacteria growing in salt-enriched media are capable of capturing Na^+ ions. Therefore, a quantitative criterion should be applied for the selection of halobacteria, which could be their ability to capture Na^+ ions in vitro. This, together with the assessment of the effect of halobacteria on soil fertility, may largely contribute to the recovery of saline soils.

Keywords: abiotic stress; drought; plant growth-promoting rhizobacteria; salinity; soil fertility

1. Introduction

Abiotic factors such as salinity, drought, high and low temperatures and heavy metal toxicity reduce crop productivity [1]. Climate change increases the frequency and severity of these abiotic factors. Mainly, high temperatures and low precipitation cause droughts of increasing severity [2]. Recent estimates report that abiotic stress accounts for the loss of 50% of crop production [3]. Etesami & Maheshwari [2] indicated that salinity has led to a 1–2% annual decline in arable land.

Arid and semi-arid zones are the areas most affected by drought and salinity, two types of abiotic stress closely related to each other. Salinization is the increase in the concentration of soluble ions such as Na^+, Ca^{2+}, Mg^{2+} and K^+ as a result of low precipitation and high temperatures. Agricultural activities promote the salinization of soils through irrigation with poor-quality water, inadequate farming systems and excess use of conventional mineral fertilizers and pesticides [4,5], all of which ultimately reduce soil fertility and quality.

Drought influences crop yields as low water availability adversely affects the photosynthetic rate, nutrient uptake and metabolic processes in plants [6]. Facing these issues, several studies have been carried out through different approaches, including the search for new techniques in traditional agriculture, new plant varieties, genetic engineering and the use of biostimulants, with the aim of reducing crop yield losses caused by abiotic factors [1]. Efforts made as part of traditional agriculture and genetic engineering to develop plants resistant to salinity and desiccation are complex because these stressors affect several physiological aspects of the plant and require many years of study [7]. By contrast, biostimulants have shown positive effects on plants to improve tolerance to abiotic stress [8].

The increase in the use of fertilizers and pesticides significantly reduces microbial biodiversity in soil and can cause environmental pollution issues; indeed, the use of some synthetic plant additives is prohibited due to the absorption and accumulation of toxic chemicals in plants, which pose a health risk [9]. One of the approaches to achieve sustainable and environmentally friendly agriculture is the use of inoculants based on beneficial microorganisms, which stimulate the growth of plants or their protection against pathogenic agents and abiotic factors [9].

A widely accepted eco-friendly biological alternative is the use of plant-growth-promoting rhizobacteria (PGPR), such as halobacteria, which have great potential for use in agriculture as they increase crop production and protect plants against different types of abiotic stress [10]. Halobacteria are microorganisms with the ability to grow across a wide salinity range (1–25% NaCl) as well as in the absence of NaCl. The combination of this ability with their capacity to promote plant growth has been used as support to propose the use of halobacteria as a valuable eco-friendly alternative to increase the productivity of salt-stress-sensitive crops and to remediate salinity-impaired soils [11].

In arid regions, microbial metabolic activity is strongly driven by soil water content [12]. This is why PGPR adapted to this type of environment survive long drought periods and exert an improved positive effect on plants when rehydration occurs [5,12]. Halobacteria are microorganisms adapted to the natural salinity of arid regions; for this reason, their application is considered a suitable alternative in this type of environment [13].

This review summarizes some studies conducted over the past five years addressing the effect of halobacteria on the mitigation of salinity and drought stress in different crops, with the consequent promotion of plant growth; these two types of stress were considered for being the abiotic factors with the greatest influence in arid and semi-arid regions. Emphasis is made on those studies that have demonstrated the positive effect of halobacteria on soil fertility properties or that have considered this aspect. Finally, this paper highlights the methodological aspects and approaches that, in our view, may contribute to the potential of halobacteria for use as an eco-friendly strategy to increase crop yield and contribute to soil remediation in saline soils.

2. Halobacteria

During prolonged periods of drought in arid and semi-arid regions, high temperatures and evaporation, as well as high salt content in soil solution, cause physiological stress in microbial communities [14]. Many microorganisms, such as archaeans, bacteria and fungi, have adapted to the different changes in the extreme climatic conditions of these regions.

Saline stress-tolerant bacteria employ a variety of strategies to survive and grow in environments across a wide salinity range. According to their ability to survive in these environments, they are classified as halotolerant or halophilic bacteria. Halotolerant bacteria can survive in media with up to 25% NaCl and media with no NaCl, while halophilic bacteria need salt to grow. The halophilic category includes slightly halophilic bacteria, which show unlimited growth in media within the range of 1–3% NaCl; moderate halophilic bacteria, within a range of 3–15% NaCl; and extreme halophilic bacteria, between 15–25% NaCl [5,15].

Bacterial phyla most commonly found in different saline and xeric soils include Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria and Cyanobacteria. Also present, although less dominant, are Deinococcus and Verrucomicrobiae. Besides, dry soils are also home to some phyla from Archaea, such as Euryachaeota, Crenarchaeota and Thaumarchaeota [16].

Halobacteria comprise various halophilic and halotolerant species; these bacteria have been isolated from saline environments in parts of the world with different degrees of hostility. Roodi et al. [17] isolated species of the genera *Halobacillus*, *Halomonas*, *Thalassobacillus*, *Brevibacterium* and *Bacillus* from the Karak saline mine soil in Pakistan. Several salt lakes of Romania with salinities above 70 g L^{-1} and electrical conductivities up to 168.1 dS m^{-1} hosted bacteria in three phyla: Firmicutes, Proteobacteria and Actinobacteria; within the phylum Firmicutes, the genera *Bacillus*, *Virgibacillus*, *Salinococcus*, *Marinococcus*, *Halobacillus*, *Planococcus*, *Thalassobacillus* and *Salimicrobium* were reported; in the phylum Proteobacteria, *Halomonas* was the most representative genus, with *Vibrio*, *Idiomarina* and *Psychrobacter* also present; in the phylum Actinobacteria, the most representative genus was *Nocardiopsis* [18]. Sharma et al. [19] isolated bacteria of the genera *Bacillus*, *Corynebacterium*, *Acinetobacter*, *Aeromonas* and *Staphylococcus* from soil of the Thar desert in India.

Multiple studies have explored extreme environments to isolate halobacteria; however, these microorganisms are distributed across a broad range of environments, including freshwater, as in the case of *Micrococcus luteos*, *Staphylococcus aureus* and *Staphylococcus lentus*, which have been isolated from the Ezzu river in Nigeria [20].

Several halotolerant bacteria have been isolated from halophyte plants. Thus, these plants may be good sources for the identification of additional halophytic PGPR bacteria, as a potential plant-bacteria relationship has already been established. Halophytes are plants capable of growing in saline environments and can even accumulate Na^+ in plant tissue. The precise hormonal mechanisms by which halophyte plant roots perceive salt stress and translate this perception into adaptive, directional growth toward higher salt concentrations are not well understood [21]. Halotropism is a sodium-specific tropic movement of roots [22]. In halotropism, the gravitropic responses of roots should be inhibited, so this mechanism helps roots modify and fine-tune their movement to optimize growth and survive conditions of high salinity [22].

Mukhtar et al. [23] isolated bacteria of the genera *Bacillus*, *Halobacillus* and *Kocuria* from the rhizosphere of *Salsola stocksii* and *Atriplex amnicola* in Kewra salt mines in Pakistan. Ruppel et al. [24] conducted a review of several halotolerant bacterial genera and species associated with different halophytic plants in coastal and arid hypersaline environments. Szymańska et al. [25] isolated halotolerant endophytic and rhizosphere bacteria of *Aster tripolium*, a halophytic plant that grows in degraded hypersaline soils. Halophytic plants of the genus *Sauceda* also harbor halotolerant bacteria such as *Bacillus subtilis*, *Zhihengliuella halotolerans*, *Erwinia persicina* and some species of the genera *Brachybacterium* and *Brevibacterium* [26].

To survive in environments with high salt concentrations, halobacteria have developed two key strategies: (1) Maintain high intracellular salt concentrations to match the external salt concentration, known as "salt-in" strategy. (2) Maintain low cytoplasmic salt concentrations by compensating osmotic pressure with the accumulation of compatible solutes [27].

The salt-in strategy is commonly used by extreme halophilic archaeans and halophilic anaerobic bacteria of the order Halanaerobiales and involves the active uptake of Na^+ and its accumulation inside the cell [27]. However, other studies have found different levels of in-vitro Na^+ uptake in bacteria of different orders, such as *Vibrio alginolyticus*, *V. metschnikovii*, *Flavimonas oryzihabitans* and *Agrobacterium tumefasciens* [28].

On the other hand, the accumulation of compatible solutes is a common response to salt and drought stress. These compatible solutes can be synthesized de novo within the cell or incorporated from the exogenous medium and stored in large quantities without compromising cell physiology [24]; they increase the fluidity of the cell membrane and stabilize proteins by binding to their surface and preventing stress-related denaturation. The most common compatible solutes in halophilic and halotolerant microorganisms can be classified into (1) amino acids and their derivatives such as glycine betaine, glutamine, glutamate, proline and ectoine and (2) polyols such as sucrose, trehalose, mannosylglycerate and diglycerol phosphate [29].

Salt-in strategies and the accumulation of compatible solutes participate in osmoregulation along with other physiological strategies, including the balance of intracellular Na^+ concentration by pumping ions out of the cell by the electrogenic Na^+/H^+ antiporters and K^+/Na^+ ion transporters that achieves the mass accumulation of K^+ by effectively removing Na^+ [7,27].

Another characteristic of halophilic bacteria is the composition of membrane proteins, which include high levels of acid amino acids such as glutamate and aspartate and low levels of basic amino acids such as lysine and arginine. The negative charge conferred to the membrane by glutamate and aspartate maintains its structure in the presence of salt within the cell and favors water retention for the proper functioning of enzyme activity [24,27].

Many halotolerant bacteria produce exopolysaccharides that form biofilms to improve moisture retention and create a more hydrated microenvironment for the cell; biofilms also act as a barrier and limit the ingress of salts into the cell [11]. Bacterial exopolysaccharides are composed of homo- or heteropolysaccharides formed by glucose, galactose and mannose monomers in combination with neutral sugars (rhamnose and fucose), uronic acids (glucuronic and galacturonic), amino sugars, organic substitutes with ester bonds and pyruvate ketals [30]. The composition of exopolysaccharides varies among species and their production depends on the growth phase, the relative availability of carbon and nitrogen in the environment and environmental conditions [30].

Several genera of rhizosphere bacteria such as *Enterobacter*, *Aeromonas*, *Bacillus*, *Planococcus*, *Halomonas*, *Burkholderia*, *Microbacterium* and *Paenibacillus* produce exopolysaccharides and form biofilms [5]. Almost all species of the genus *Pseudomonas* produce alginate (one of the main exopolysaccharides composed of D-mannuronic and L-glucuronic acids) [31], however, the proportion of the components of alginate changes under stress conditions; for example, *Pseudomonas* spp. GAP-45 changed the composition of the exopolysaccharide produced when subjected to high temperatures, salinity and desiccation [32].

3. Plant Growth-Promoting Halobacteria and Protection against Abiotic Stress

PGPR are bacteria that inhabit the rhizosphere and facilitate plant growth through various direct and indirect mechanisms. Direct mechanisms include biological nitrogen fixation, production of phytohormones, production of the enzyme 1-aminocyclopropane-1-carboxylic acid deaminase (ACC-deaminase) and solubilization of phosphates and K, as well as the production of siderophores that improve Fe uptake. Indirect mechanisms include plant-induced systemic resistance and the production of antimicrobial compounds that inhibit pathogen growth [33,34].

Halobacteria also possess direct and indirect mechanisms capable of promoting plant growth even in highly saline environments [2].

The plant growth-promoting effect of halotolerant and halophilic bacteria has been extensively documented [5,35–37] and occurs through various mechanisms, as follows.

(1) Activating the antioxidant defense machinery of plants by regulating the activity of enzymes such as superoxide dismutase, peroxidase and catalase, which eliminate reactive oxygen species and protect plants from salinity
(2) Improving plant nutrition by fixing atmospheric nitrogen, solubilizing nutrients such as P and K, or by producing siderophores that improve Fe uptake
(3) Increasing selective ion uptake to maintain a high K^+:Na^+ ratio, which can reduce the accumulation of toxic ions such as Na^+ and Cl^-
(4) Reducing the accumulation of Na^+ in the plant by excreting exopolysaccharides that fix this cation in roots and prevent its translocation to leaves and the rest of the plant; the exopolysaccharides produced by halobacteria also improve soil structure by promoting soil aggregation
(5) Generating ACC-deaminase activity to reduce ethylene levels in the plant
(6) Modifying the structure and morphology of roots, thus facilitating the uptake of nutrients and water from soil. Szepesi [21] established that halotropism helps roots navigate and remodel their architecture through cost-effective energy supply to survive high-salinity conditions
(7) Accumulating amino acids such as glutamate and proline, amines such as carnitine, glycine and betaine, and sugars such as sucrose and trehalose to reduce intracellular osmotic stress
(8) Increasing stomatal conductance and photosynthetic activity
(9) Inducing and regulating the expression of stress-response genes in plants

Studies with plant growth-promoting halobacteria have reported increased biometric and physiological parameters, as well as higher yields of many crops of commercial interest, including *Oryza sativa* (rice), *Triticum aestivum* (wheat), *Vigna unguiculata* (L.) (caupi bean), *Medicago sativa* (alfalfa), *Zea mays* (maize), *Cuminum cyminum* (cumin), *Glycine max* L. (soybean), *Solanum lycopersicum* (tomato) and *Beta vulgaris* L. (sugar beet), among others (Table 1). For instance, in wheat (*T. aestivum*)—a crop highly sensitive to salinity—, the inoculation of different halotolerant bacteria improved plant growth and yield under saline stress [38–41]. Peanut plants (*Arachis hypogaea*) inoculated with *Stenotrophomonas maltophilia* BJ01 isolated from saline soil showed improved growth and conservation of photosynthetic pigments and total amino acid content, relative to non-inoculated plants, in the presence of 100 mM NaCl [42]. Under the same salinity concentrations, this same crop showed higher values of germination percentage and parameters such as root length, stem length, number of leaves and shoot biomass, after inoculation of *Bacillus megaterium* (YM13), *Enterobacter* sp. (YM14), *Providencia rettgeri* (TPM23) and *Ensifer adhaeren* (TPMX5), four halotolerant and phosphate-solubilizing bacteria strains [43].

Bacillus pumulus improved tolerance to salinity stress and high boron concentrations in rice, another salt stress-sensitive crop [44]. *Enterobacter* sp. P23, which shows ACC-deaminase activity as the primary plant growth-promotion mechanism and is resistant to salinity, favored the growth of rice seedlings under salt stress [45]; the strain PR14, which shared these same characteristics, showed an increase in the growth of millet seedlings in addition to rice and sorghum under alkaline conditions [46].

Tirry et al. [47] reported that *Pseudomonas putida*, *Alcaligenes* sp., *Klebsiella* sp. and *Pseudomonas cedrine* increased root growth and chlorophyll content in alfalfa plants under salt stress. Inoculated alfalfa plants also showed lower hydrogen peroxide, malondialdehyde and proline contents, which are considered indicators of oxidative damage. Several studies have documented the beneficial effect of plant growth-promoting halobacteria on the oxidative response of the plant [48–52] (Table 1).

Table 1. Effect of plant growth-promoting halobacteria in different crops under salt stress.

Halobacteria	Place of Isolation	Crop Evaluated	Mechanisms That Promote Plant Growth	Effect on the Plant	Ref.
Micrococcus yunnanensis, *Planococcus rifietoensis*, *Variovorax paradoxus*	Halophyte plants from the Gurbanunggut desert, northwest China	*Beta vulgaris* L. (sugar beet)	ACC-deaminase activity, phosphate solubilization and production of siderophores and indole-acetic acid (IAA)	The effect of halobacteria was assessed under five NaCl concentrations (50 mM, 75 mM, 100 mM, 125 mM and 150 mM). Seed germination increased by 37% and 94% under 50 mM and 125 mM NaCl, respectively). The highest increase in growth parameters was observed at 125 mM NaCl (SL = 24%, RL = 13%, SDW = 98%, RDW = 42%)	[53]
Pseudomonas pseudoalcaligenes, *Bacillus subtilis*	Rhizosphere of rice (*Oryza sativa*) and sugarcane (*Saccharum officinarum*) in saline agricultural soils in Pakistan	*Glycine max* L. (soybean)	ACC-deaminase activity, production of siderophores and IAA	Increase in growth parameters: SL = 20%, SFW = 81%, SDW = 48%, RFW = 124%, RDW = 67%, LA = 174%. Increase in relative leaf water content (26%), increase in K^+ level in shoots (61%) and roots (197%), as well as in the levels of antioxidant enzymes in shoots (SOD = 118%, CAT = 20%, APX = 65%, POD = 83%, PAL = 35%, PPO = 50%) and roots (SOD = 12%, CAT = 36%, APX = 87%, POD = 117%, PAL = 18%, PPO = 48%). Leaf proline content increased (118%). Lipid peroxidation decreased in shoots (MDL = 52%) and roots (MDL = 45%)	[51]
B. velenzensis, *B. subtilis* subsp. *spizizenii*	Sfax solar saltern in the central portion of the Eastern Tunisian coast.	*Solanum lycopersicum* var. *Rio Grande* (tomato)	Siderophore production, biofilm formation, exopolysaccharide production, phosphate solubilization and protease and lipase activity	Seed germination improved under salt stress and in the presence of heavy metals (Co, Ni, Cu and Cr) (Vigor index = 166 in inoculated plants, contrasting with 87.33 in non-inoculated plants). 50–90% reduction in the degree of infection caused by the pathogenic fungus *Botrytis cinerea* in fruits	[54]
Halomonas elongata, *Bacillus* sp.	*Salicornia utahensis*, *Salicornia rubra* and *Allenrolfea occidentalis*	*Medicago sativa* (alfalfa)	Biofilm formation and possible sequestration of Na^+ ions during growth	An endophytic interaction with alfalfa roots developed; root length (15.9 cm) and total biomass (386 mg) increased significantly in the inoculated plants (2.6- and 4.5-fold, respectively)	[55]

Table 1. *Cont.*

Halobacteria	Place of Isolation	Crop Evaluated	Mechanisms That Promote Plant Growth	Effect on the Plant	Ref.
Pseudomonas fluorescens, *Enterobacter hormaechei*, *Pseudomonas migulae*	*Setaria italica* L. (moha)	*Setaria italica* L.	ACC-deaminase activity and production of exopolysaccharides	The effect of halobacteria was evaluated under three different levels of hydric stress (drought conditions): −0.3 MPa, −0.49 MPa and −1.03 MPa. Percent germination increased within a range of 13.68–141.82% at all drought levels. Seed dry weight increased by 122%. Exopolysaccharide production facilitated colonization (the CFU ml^{-1} dropped in only 18.93% 30 days after inoculation). Soil moisture increased by 95.27% and the proportion of soil adhered to roots also improved (75.58%)	[56]
Staphylococcus sp.	*Salicornia* sp. (Succulent, halophyte plant)	*Salicornia* sp.	Production of IAA, ACC-deaminase activity and phosphate solubilization	The effect of endophytic and rhizosphere *Staphylococcus* sp. was evaluated at three NaCl concentrations (0 mM, 200 mM, 400 mM and 600 mM). Increases were observed in germination (33.2%), plant weight (71.77% at 0 mM, 88.9% at 200 mM, 72.2% at 400 mM and 85.7% at 600 mM NaCl) and root dry weight (69.7% at 200 mM, 35.6% at 400 mM and 12.7% at 600 mM NaCl). At all concentrations, increases were also recorded in leaf water content (161.1%), K^+ content (22.8% at 200 mM, 21.9% at 400 mM and 86.6% at 600 mM NaCl) and superoxide dismutase activity	[57]
Enterobacter sp.	Rhizosphere of rice (*Oryza sativa*) in fields near the Odisha coast, India	Rice	Phosphate solubilization, production of IAA, siderophores and HCN	Germination percentages (Vigor index = 881.6 versus 57.6 in non-inoculated plants) and morphological parameters of shoots (length = 23.07%, fresh weight = 35.71%, dry weight = 90%) and roots (length = 60%, fresh weight = 40%, dry weight = 50%) increased, as well as the total chlorophyll content (114%). Ethylene concentration decreased (66.6%). The activity of antioxidant enzymes increased (SOD = 40%, CAT = 41.66%, POD = 34.42%, PPO = 50%), as well as sugar (113.5%), protein (50%) and IAA (45.83%) content	[45]

Table 1. *Cont.*

Halobacteria	Place of Isolation	Crop Evaluated	Mechanisms That Promote Plant Growth	Effect on the Plant	Ref.
Klebsiella sp., *Pseudomonas* sp., *Pseudomonas stutzeri*, *Agrobacterium tumefaciens*, *Ochrobactrum anthropi*	Roots of *Arthronemum indicum* in coastal marshes	*Arachis hypogaea* L. (maní)	Nitrogen fixation, IAA production, phosphate solubilization and ACC-deaminase activity	Total nitrogen content in shoots and roots increased significantly (76%) compared to the control. Fewer reactive oxygen species accumulated. Parameters such as shoot (19–31%) and root (45–64%) biomass increased under 4–8% NaCl	[58]
Arthrobacter woluwensis, *Microbacterium oxydans*, *Arthrobacter aurescens*, *Bacillus megaterium*, *Bacillus aryabhattai*	*Artemisia princeps*, *Chenochloa crusgalli*, *Oenothera biennis* growing in sand dunes at Pohang Beach, Korea	*Glycine max* L. (soybean)	Phosphate solubilization and production of IAA, gibberellins and siderophores	Superoxide dismutase (108.95%) and glutathione peroxidase (40.89%) levels increased, K^+ uptake improved (25.56%) and Na^+ concentration decreased (31%). Chlorophyll content (63.24%) and all plant growth parameters (SL = 23.52%, RL = 31.17%, SFW = 106.39%, RFW = 114.94%, SDW = 172.72% and RDW = 118.87%) increased under 200 mM NaCl	[50]
Bacillus cereus, *Serratia marcescens*, *Pseudomonas aeruginosa*	*Triticum aestivum* (wheat)	Wheat	Production of IAA, HCN and siderophores; nitrogen fixation, phosphate solubilization	Under two levels of saline stress (150 mM and 300 mM NaCl), the uptake system of reactive oxygen species was strengthened, especially at 300 mM NaCl (CAT = 77.77%, SOD = 76.25%, POX = 69.23%) and K^+ selectivity increased (19.16% at 300 mM NaCl), restricting Na^+ uptake (Na^+ ion content in leaves = 27.55%)	[52]
Zhihengliuella halotolerans, *Brachybacterium* sp.	*Suaeda* sp. in different areas of Iran	*Suaeda maritima*	Nitrogen fixation	Growth was favored by increasing nutrient uptake through an improved root system, showing higher root and shoot fresh weight (0.0956 g plant^{-1} and 0.2284 g plant^{-1}, respectively). Salinity resistance also increased	[26]
Staphylococcus jettensis, *S. arlettae*, *Bacillus marisflavi*, *Zhihengliuella flava*, *Halomonas nanhaiensis*, *Exiguobacterium mexicanum*	*Suaeda fructicosa* (L.) of north-eastern Pakistan	*Zea mays* L.	Auxin production, ACC-deaminase activity and biofilm formation	Root (98%) and shoot length (59%) significantly increased in the presence of 200 to 400 mM NaCl. Under co-inoculation, plants showed a high accumulation of proline (140%) compared with the non-inoculated plants	[48]

Table 1. *Cont.*

Halobacteria	Place of Isolation	Crop Evaluated	Mechanisms That Promote Plant Growth	Effect on the Plant	Ref.
Pseudomonas putida, *Alcaligenes* sp., *Klebsiella* sp., *Pseudomonas cedrina* subsp. *Fulgida*	Rizosphere of *Medicago sativa* (alfalfa) from southern Morocco	Alfalfa	Phosphate solubilization; nitrogen fixation; cellulase, pectinase and chitinase activity; production of IAA, ammonia and HCN	The dry weight of shoots (69.3%), roots (36.87%) and chlorophyll content (36.69%) increased. The accumulation of hydrogen peroxide (48.13%) in plant tissue and proline content in shoots (68.27%) decreased significantly. Colonization by arbuscular mycorrhizal fungi increased (25.1%) under saline stress. Phosphatase (49.7%) and galactosidase (91.7%) activity increased in the rhizosphere of inoculated plants	[47]
Bacillus subtilis, *Oceanobacillus iheyensis*, *Arthrobacter crystallopoietes*	*Triticum turgidum* subsp. *Durum* cv. *Haurani* in Dead Sea nearby areas	*Triticum turgidum* subsp. *Durum* cv. *Tamaroi* (salt-sensitive) and var. 5004 (salt-resistant)	Nitrogen fixation, ACC-deaminase activity and production of siderophores and IAA	The germination percentage of both plant varieties improved (83.3% in the sensitive variety and 100% in the tolerant variety under 160 mM NaCl); root length (139.12% for the sensitive variety and 59% for the tolerant variety at 160 mM NaCl) increased. The tolerance and survival of salt-sensitive plants improved (var. Tamaroi) under drought stress after 10 days of water withholding	[39]
Bradyrhizobium sp., *Paenibacillus graminis*, *Actinomadura* sp., *Bacillus* sp., *Streptomyces* sp.	Soil with pasture (*Bradyrhizombium* sp.), rhizosphere of Caatinga (*Actinomadura* sp.), maize (*Paenibacillus graminis*), sugar cane (*Bacillus* sp.) and rúcula (*Streptomyces* sp.), Brazil	*Vigna unguiculata* (L.) (cowpea bean)	Nitrogen fixation	The co-inoculation of *Bradyrhizobium* with the other PGPR genera prompted responses to salinity-induced oxidative stress. *Bradyrhizobium* with *Bacillus* sp. showed an increased activity of superoxide dismutase (52%), *Bradyrhizobium* inoculated with *Streptomyces* displayed the highest catalase activity (55%), *Bradyrhizobium* inoculated with *P. graminis* increased phenol peroxidase activity (20%) and *Bradyrhizobium* inoculated with *Bacillus* sp. showed the highest levels of redox glutathione (23.9%) in root nodules	[49]

Table 1. *Cont.*

Halobacteria	Place of Isolation	Crop Evaluated	Mechanisms That Promote Plant Growth	Effect on the Plant	Ref.
Bacillus tequilensis, *Bacillus aryabhattai*	Rice rhizosphere in various saline fields in Malaysia	Rice	IAA production, nitrogen fixation and phosphate and potassium solubilization	Inoculation with halobacteria in three rice varieties (BBRI dhan67, Putra-1 and MR279) was evaluated. Increases were recorded in the photosynthetic rate (56.23% in BRRI dhan67, 69.95% in Putra-1 and 69.04% in MR297), transpiration (92.22% in BRRI dhan67, 89.08% in Putra-1 and 82.87% in MR297) and stomatal conductance (78.94% in BRRI dhan67, 50% in Putra-1 and 47.36% in MR297). Grain yield (in weight; 15.44%, 33.12% and 57.55% in each variety, respectively) also increased, as well as some growth parameters (SL = 14.74%, RL = 19.58%, RDW = 17.64% and RWC = 4.29%). Proline content (22.73%), electrolyte loss (20.08%), malondialdehyde content in shoots (45.13%) and antioxidant enzyme activity decreased significantly (SOD = 56.72% and POD = 39.62%)	[59]
Klebsiella sp.	Wheat rhizosphere	*Avena sativa* (oat)	IAA production and ACC-deaminase activity	Shoot (14.74%) and root (19.58%) length, root dry weight (17.64%) and relative water content (4.29%) increased. Proline content (22.73%), electrolyte loss (20.08%), malondialdehyde content in shoots (45.13%) and antioxidant enzyme activity decreased significantly (SOD = 56.72% and POD = 39.62%)	[60]
Aneurinibacillus aneurinilyticus and *Paenibacillus* sp.	Garlic (*Allium sativum*) rhizosphere	*Phaseolus vulgaris* (French bean)	ACC-deaminase activity, phosphate solubilization, production of IAA, siderophores and ammonium	Ethylene concentration decreased (42%); root (110%) and shoot (60%) length, fresh weight (45% in roots and 255% in shoots), root (220%) and shoot (425%) biomass and total chlorophyll content (57%) increased	[61]
Bacillus pumillus FAB10	Wheat rhizosphere	Wheat	Biofilm formation, ACC-deaminase activity, phosphate solubilization, production of exopolysaccharides and IAA	The effect of halobacteria was evaluated at three NaCl concentrations (75 mM, 125 mM and 250 mM NaCl). Internal CO_2 concentration increased (8.5%, 7.5% and 5.5% for each NaCl concentration, respectively), as well as the transpiration rate (22.7% at 250 mM NaCl). Reduced activity levels of antioxidant enzymes such as catalase (42%, 25% and 22%), superoxide dismutase (10.5%, 10.8% and 12%) and glutathione reductase (50%, 42.9% and 42.9%) with each NaCl concentration were recorded	[62]

Table 1. *Cont.*

Halobacteria	Place of Isolation	Crop Evaluated	Mechanisms That Promote Plant Growth	Effect on the Plant	Ref.
Glutamicybacter halophytcola KLBMP 5180	Rhizosphere of the coastal halophyte *Limonium sinense*	Tomato seeds (Jingpeng No. 1)	Production of siderophores, exopolysaccharides and IAA	Root length and root fresh weight (28.6%) increased; total chlorophyll content in leaves remained unchanged under 200 mM NaCl. Proline content increased in leaves (40.4%) and stems (39.2%) under salt stress and in leaves (110%) and stems (86.7%) of non-stressed plants. The accumulation of antioxidant enzymes (SOD = 7.6% and 9.4% and POD = 35.2% and 160.8% in 0 mM and 200 mM NaCl) and the K^+/Na^+ ratio (102.5% and 170.5% in stems and 10.2% and 33.3% in leafs) increased at 0 mM and 200 mM NaCl, respectively	[63]
Alcaligenes faecalis SBN01 and SBN02	Rhizosphere of native plants (*Sesbania aculeata* and *Atriplex lentiformis*) from the Kewra salt mine in Pakistan	Wheat	Nitrogen fixation, IAA production, phosphate solubilization and catalase and protease activity	Under two levels of salt stress (450 mM and 600 mM NaCl), plant biomass increased (LA = 29.47%, PH = 6.5%, SpL = 11.8%, VT = 90% at 450 mM NaCl and LA = 36.78%, PH = 19.15%, SpL = 21.31%, VT = 114.28% at 600 mM NaCl); accumulation of photosynthetic pigments (Chla = 83.82%, Total Chl = 22.41%, Carotenoid = 39.94% at 600 mM NaCl) and the efficiency of the photosystem II (PI_{ABS} = 63.64% and Fv/Fm = 4% at 450 mM and PI_{ABS} = 45.22% and Fv/Fm = 14% at 600 mM) increased versus non-inoculated plants	[41]

Note: Only the greatest increases in each parameter compared to the non-inoculated control (under stress) are reported. SL = Shoot length, RL = Root length, SDW = Shoot dry weight, RDW = Root dry weight, SFW = Shoot fresh weight, RFW = Root fresh weight, LA = Leaf area, PH = Plant height, RWC = Relative water content, SOD = Superoxide dismutase, POD = Peroxidase, ASC = Ascorbate, APX = Ascorbate peroxidase, CAT = Catalase, GSH = Glutathione, GR = Glutathione reductase, PPO = Polyphenol oxidase, PAL = Phenylalanine ammonia lyase, MDL = Malonaldehyde, SpL = Spike Length, VT = Vegetative tillers, Chl = Chlorophyll, PI_{ABS} = Performance Index, Fv/Fm = Quantum yield.

On the other hand, it has been reported that some bacteria of the genus *Halomonas* that have several plant growth-promoting features such as biological nitrogen fixation, indole-acetic acid production, phosphate solubilization and ACC-deaminase activity are capable of growing under extreme temperatures and low water availability; this suggests that halotolerant bacteria can promote plant growth even under drought conditions [64].

Albdaiwi et al. [39] demonstrated that *Bacillus subtilis*, *Oceanobacillus iheyensis* and *Arthrobacter crystallopoietes* are halotolerant bacteria that improve the germination and survival rate of two lines of *Triticum turgidum* subsp. *durum* under water and saline stress simultaneously.

The accumulation of proline (a compatible solute) in plants is correlated with tolerance to salinity and drought in plants [31], suggesting that plants may share common response mechanisms to these two types of abiotic stress. Many studies show decreased proline accumulation in plants in the presence of halobacteria since plants show no oxidative damage requiring a response when subjected to saline stress (Table 1).

Although studies evaluating the tolerance of halobacteria to various types of abiotic stress simultaneously are scarce, the wide range of mechanisms available to stimulate growth and protect crops from saline stress are very likely to offset the harmful effects of other types of stress, such as water deficit. *Achromobacter piechaudii*, for instance, induces resistance against salinity and drought in tomato and cucumber thanks to ACC-deaminase activity, a very common feature in plant growth-promoting rhizobacteria associated with tolerance to drought and salinity stress in plants by reducing endogenous ethylene levels that increase with stress [30].

Many rhizobacteria that have been tested in drought-stressed crops show ACC-deaminase activity; although this metabolic feature is one of the main factors conferring tolerance to drought and salinity in plants [2,65,66], it has also been found as an important mechanism for the survival of plants under stress from flooding, freezing and heavy metals [2,65].

Heavy metal toxicity has also been considered when evaluating the efficiency of halobacteria in stimulating plant growth and protecting some crops. In fact, Masmoudi et al. [54] reported the efficiency of *Bacillus velenzensis* and *B. subtilis* subsp. *spizizenii* to increase tomato plant growth (*Solanum lycopersicum* var. *Rio grande*) under salt stress in the presence of heavy metals (Co, Ni, Cu and Cr).

Al-Mailem et al. [67] assessed the tolerance to different concentrations of heavy metals (Hg, Cd, Pb, Cu) of halophilic and halotolerant bacteria by adding some biostimulants to boost their resistance in the presence of crude oil. It was found that the addition of proline and Fe_2SO_4 significantly improved the tolerance to heavy metal toxicity of the halobacteria *Archodomonas aquaeolei*, *Marinobacter lacisalsi*, *Halomonas axialensis*, *Kocuria flava*, *Haloferax elongans* and *Halobacterium salinarum* and it increased their bioremediation potential in hydrocarbon-polluted hypersaline areas.

Hassan et al. [68] tested the ability of halo-alkaliphilic species *Sphingobium* sp., *Stenotrophomonas chelatiphaga* and *Rhizobium borbori* to biodegrade tributyltin (TBT)—a compound used as a pesticide in agriculture —, identifying a TBTB-permease gene encoding an ArsB permease responsible for TBT resistance from the gene amplification of *S. chelatiphaga* that showed to be more efficient in transforming tributyltin into di- and monobutyltin.

The ability of halobacteria to tolerate pollution by heavy metals and organic pollutants is a feature of interest in assessing their application for rhizoremediation and recovery of saline soils [69–71].

4. Effect of Halobacteria on Soil Fertility

Most studies on halobacteria have focused on increasing plant growth and crop yield under salinity conditions and, to a lesser extent, under other types of stress such as drought [63] and heavy metal toxicity [54,67,70,72]. Therefore, the impact of halobacteria on soil fertility has not been investigated in depth. Some studies show improved soil structure and fertility after inoculation with halobacteria [11].

Inoculation with this type of microorganisms has been reported to significantly improve the availability of nutrients such as N, P, K and Fe in soil, generally without affecting the structure of the existing microbial community [73]. Some genera such as *Azospirillum*, *Alcaligenes*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Flavobacterium*, *Pseudomonas* and *Rhizobium*, in addition to having shown less negative effects of salinity on different crops, appear to favor organic matter content and the structure and water retention capacity of soil [11].

Mukhtar et al. [23] evaluated the growth of maize plants inoculated with *Bacillus safensis*, *B. pumilus*, *Kucuria rosea*, *Enterobacter aerogenes* and *Aeromonas veronii* under saline stress. These bacteria were isolated from the rhizosphere of halophyte plants and showed the ability to solubilize phosphates. These authors reported that inoculation of these halobacteria, in addition to increasing the growth of maize plants, also increased P availability in soil.

Pankaj et al. [74] determined the efficiency of *Pseudomonas plecoglossicida* (KM233646), *Acinetobacter calcoaceticus* (KM233647), *Bacillus flexus* (KM233648) and *B. safensis* (KM233652) to improve the plant growth and crop yield of *Bacopa monnieri* (L.), a plant that bioaccumulates Na^+ and K^+ in saline soils. The halobacteria-treated soil showed an increase in the activity of dehydrogenase, alkaline phosphatase and acid phosphatase, as well as higher total nitrogen, organic carbon and available P, compared to non-inoculated soil. In contrast, the Na^+/K^+ ratio, electrical conductivity, pH, percentage of exchangeable Na^+ and Na^+ uptake rate decreased in inoculated soils.

Al-Enazy et al. [75] demonstrated that the inoculation of maize plants with *Azotobacter chroocococcum*, *Bacillus megaterium* and *Pseudomonas fluorescens* by adding phosphorus plaster to saline soil in Saudi Arabia significantly reduced electrical conductivity and soil pH after inoculation. Hassan et al. [76] evaluated the effect of the pulverized roots of a halophyte plant containing three halotolerant bacteria (*Bacillus cereus*, *Pseudomonas moraviensis* and *Stenotrophomonas maltophilia*) on wheat growth and soil fertility properties; they found that electrical conductivity and the Na^+ uptake rate decreased significantly, unlike K, P and NO_3^- content, which increased after inoculation.

Anees et al. [77] evaluated the effect of the co-inoculation of halotolerant bacteria (*Pseudomonas* sp., *Thalassobacillus* sp. and *Terribacillus* sp.) and chitinolytic bacteria (*Pseudomonas* spp. Fo1, *Sanguibacter* spp. Ft2, *Bacillus* spp. Ft4 and *Bacillus* spp. Fc3) in spinach (Spinacia oleracea L.) and found that the electrical conductivity of soil decreased from 6.5 to 2 dS m^{-1} and Na^+ content decreased from 22–24 to 9–12 meq L^{-1} after harvest. In addition, the dry weight of roots and shoots increased, while the leaf Na^+:K^+ ratio decreased.

Arora [78] reported a substantial improvement in soil pH (9.42 to 8.91) and a decrease in exchangeable Na^+ content (416 to 238 mg kg^{-1}) after 2 years of continuous inoculation in rice and wheat plants with two commercial bioinoculants made from plant growth-promoting rhizobacteria isolated from halophyte plants. In addition, increases in carbon levels from soil microbial biomass and dehydrogenase activity were observed, compared with soil where bioinoculants were not used.

Based on the above, the inoculation with halobacteria seems to contribute to the recovery of some soil fertility properties, thus achieving a double benefit that implies an increase in plant growth and the restoration of the soil (Figure 1).

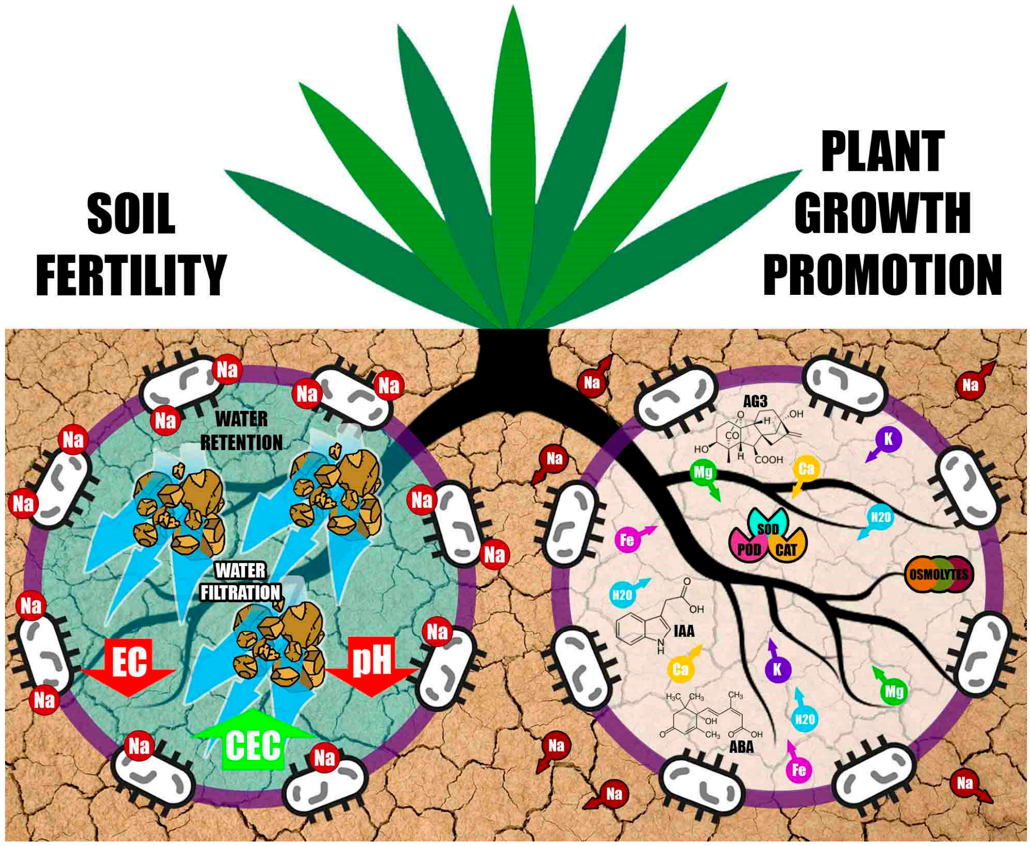

Figure 1. Effect of halotolerant PGPR bacteria on soil and the plant under high salinity. The exopolysaccharide produced by halobacteria plays a key role in Na^+ sequestration and the consequent reduction in soil electrical conductivity (EC). Besides, it favors the formation of aggregates in soil, with macro and micropores that improve water filtration and retention. It also increases cation exchange capacity (CEC), decreases the pH and improves nutrient availability. Altogether, these contribute to increase soil fertility. On the other side, halobacteria solubilize nutrients, release osmolytes, antioxidant enzymes (SOD = Superoxide dismutase, CAT = Catalase, POD = Peroxidase), auxins (IAA = Indol acetic-acid), gibberellins (AG3 = Gibberellic acid), stress signaling and adaptation molecules (ABA = Abscisic acid) that favor plant growth and protection against salinity, and improve water retention and Na^+ extrusion thanks to the exopolysaccharide.

5. Abiotic Characteristics of Arid and Semi-Arid Zones

Arid and semi-arid zones stretch across an estimated area of 66.7 million km^2 of the Earth, and this area is expected to expand as a result of climate change and human activities [16]. Soils in arid and semi-arid zones have a variable depth with textures ranging from sandy to clayey [79]; the existing sparse vegetation resulting from low precipitation accounts for the low organic matter content in soil (1–3%) [80]. These soils are characterized by the accumulation of soluble salts whose distribution, quantity and type depend on the composition of water reaching the soil profile and the fluxes that occur within it.

The most common salts include combinations of Na^+, Ca^{2+}, Mg^{2+} and K^+ with Cl^-, SO_4^{2-} and HCO_3^- [4], although soil salinity is driven primarily by NaCl levels.

Many of these arid regions have geomorphological features characterized by inner basins with no natural outlets, so water evaporation leaves salts in the soil, causing salinization problems if they are not dissolved by rain or redistributed [79].

Soils affected by salinity are classified into three types: saline, sodic and saline-sodic [81]. Saline soils contain enough soluble salts to affect plant growth and are characterized by an electrical conductivity higher than 4 dS m^{-1} and a pH value of less than 8.5. Sodic soils have exchangeable Na^+ levels above 15% and electrical conductivity values below 4 dS m^{-1} since they are not saline and may or may not have an alkaline pH above 8.5. As a result, these soils show structural issues such as dispersion and disaggregation. On the other hand, saline-sodic soils have high levels of soluble salts (predominantly Ca^{2+} chlorides or sulfates and, in smaller amounts, nitrates or borates) and Na^+ ions, with an electrical conductivity greater than 4 dS m^{-1} and not necessarily alkaline [81–83].

Various factors can promote salinization in agricultural soils. In areas with shallow water tables (less than 1.5 m deep), vertical drainage is inadequate and, when groundwater reaches the surface, it recirculates dissolved salts that accumulate on the surface. If the groundwater level is deep but drainage is poor, salts transported by rain, weathering and wind deposits accumulate on the surface; these processes commonly occur in sodic or alkaline soils. On the other hand, if irrigation water is of poor quality, plants are unable to completely absorb the salts dissolved in water and they accumulate in roots; this, together with high evaporation conditions, ultimately leads to increased soil salinity [84].

Soil salinity and drought are considered the main abiotic stressors that severely impair crop growth in arid and semi-arid areas, leading to major negative impacts from the ecological, agronomic and economic perspectives [2]. It is estimated that about 20% of irrigated soils in the world have been affected by salinity; these are classified as arid or desert soils and comprise 25% of the total soils covering the Earth's surface [85]. Drought includes the interaction between water deficit, high temperature and high irradiance. Drought and water deficit are terms used interchangeably in various studies to refer to stress caused by poor water availability and its effect on living organisms.

6. Halobacteria Potential in the Recovery of Saline Soils. A Key Characteristic

The use of halophilic bacteria represents a great potential for the recovery of soils degraded by salinity, drought, or even polluted with heavy metals, due to their tolerance to these stressors; however, the mechanisms through which these bacteria change the original ions that lead to degradation by forming complexes in soil have been little studied [28].

It has been proposed that to capture Na^+ ions from soil, halobacteria should be capable of taking them up to osmotically regulate the intracellular concentration of salt according to the salt concentration in soil—a common strategy in moderate and extreme halophilic microorganisms that strictly require salt for growth [27]. However, it has been reported that other strategies of halobacteria, such as the production of exopolysaccharides, account for the active sequestration of Na^+ ions. This not only reduces Na^+ availability to plants in saline soils but may also contribute to improving soil structure by forming micro- and macroaggregates, with the consequent increase in soil water retention capacity [86]. Mukherjee et al. [86] identified through in-vitro assays that the exopolysaccharide produced by *Halomonas* sp. is directly related to Na^+ sequestration.

The literature review revealed that most studies involving plant growth-promoting halobacteria report the selection of this type of microorganisms considering the morphological characteristics of colonies grown in media supplemented with salt, mainly Na^+, but they did not focus on the ability of halobacteria to sequester Na^+ ions in vitro. Studies addressing the recovery of saline soil fertility have also not evaluated Na^+ uptake in vitro by the inoculated halobacteria, as suggested by Sanchez-Leal & Arguello-Arias [28]. These authors reported that, although all the isolated bacteria initially displayed a halophilic behavior, only *Vibrio alginolyticus* and *V. metschnikovii* were able to capture Na^+ ions in vitro. The above showed that not all bacteria grown in salt-enriched media have the ability to capture Na^+ from the external medium.

We found only two studies that included the quantitative determination of in-vitro Na^+ uptake in the selection of halotolerant bacteria to assess their effect on the growth of rice plants. Shultana et al. [59] reported that *Bacillus tequilensis* and *Bacillus aryabhattai* increased the photosynthetic rate, transpiration rate and stomatal conductance of rice plants, as well as grain yield. Separately, Fatima et al. [87] reported that the inoculation of *Alcaligenes* sp. supplemented with the exopolysaccharide produced by this halobacterium in different concentrations led to a significant increase in the biometric parameters of rice plants compared to the increase observed with the inoculation of the bacterium alone, thus highlighting the importance of the exopolysaccharide during salt stress. However, in both studies, only the results of some crop growth parameters were reported, without an in-depth assessment of the effect of the Na^+ sequestration ability of these halobacteria on soil fertility.

The ability of halotolerant bacteria to actively capture Na^+ from the soil may be critical for reducing the natural salinity of arid and semi-arid soils due to the effect of climatic conditions, as well as of any type of soil affected by salinity.

The use of halotolerant PGPR bacteria in arid and semi-arid regions has been proposed by several authors [2,13,16], as it potentially represents an important option to recover soil fertility in these regions.

The studies mentioned in Section 4 above demonstrated an improvement of soil properties associated with the inoculation of halobacteria; However, other recent studies explored the effect of the combination of halobacteria with organic amendments to recover soil fertility. Arjumend & Turan [88] showed that the inoculation of halotolerant PGPR alone increased the growth and yield of wheat in saline soil in Turkey, noting a decrease in soil parameters such as pH, electrical conductivity and exchangeable Na^+ after harvest. However, the highest values of all parameters were obtained with the combined application of halotolerant bacteria and biochar, a carbon-rich bioproduct, also showing a significant increase in the content of organic matter, total nitrogen and exchangeable cations (Ca^{2+}, Mg^{2+} y K^+) in the soil.

Other approaches for the recovery of soils involving halobacteria are those that use the products of bacterial metabolism, mainly exopolysaccharides and biosurfactants [89], in combination with amendments [90], or with halotolerant microorganisms [87]; these approaches have achieved an improvement in soil fertility coupled with increased crop growth.

Some recent studies are using the potential of halobacteria in various ways, such as the bioremediation of contaminated saline environments with *Pseudomonas aeruginosa* (AHV-KH10) biosurfactants to biodegrade diesel in the Persian Gulf [91]. Other studies have focused on the biological treatment of organic compounds in water with halotolerant bacteria for hydrocarbon removal [92]. Halobacteria are even applied to crops in coastal areas of northeastern United Arab Emirates that are irrigated with seawater [93].

7. Prospects

This review outlines multiple ways through which halobacteria contribute to the development and survival of crops subjected to salinity stress and other abiotic stressors such as water deficit and heavy metal toxicity. Many studies provide knowledge of the effect of halobacteria on crop protection and growth enhancement through different growth promotion mechanisms. However, most studies have focused on crop yield and production. Therefore, further research is needed addressing the effect of plant growth-promoting halobacteria on the physical, chemical and microbiological properties of soil to generate knowledge oriented to the remediation and recovery of the fertility of soils degraded by salinity through the inoculation of this type of microorganisms.

Arid and semi-arid regions are important areas of soils degraded by salinity and drought whose fertility can be recovered through the combined effect of proper management practices and the inoculation of halobacteria. The colonization efficiency of PGPR bacteria is closely related to the effect on the rhizosphere, plant age and genotype, and the intrinsic abilities of the bacterial species. The type of root exudates varies with plant genotype and plant age [94] and determines the composition of the bacterial community associated with the rhizosphere [95]. The intrinsic abilities of the bacterial species refer to the set of features that make it more competitive against other microorganisms to colonize the rhizosphere, including nutrient solubilization, biofilm formation to adhere to roots, production of antimicrobial compounds, motility and chemotaxis and evasion of the plant immune system [96]. For these reasons, ideally, indigenous plant growth-promoting halobacteria should be used in the development of bioinoculants, since they can be easily adapted to local field conditions, as suggested by Kumar et al. [97].

Practices to reduce soil salinity include irrigation with large amounts of water to wash away Na^+ ions; however, these methods may require very expensive drainage systems and are difficult to achieve as irrigation water obtained from adjacent areas is commonly also saline [98]. Practices such as fertilization, the addition of amendments and fertigation are also accepted and recommended, provided the concentration of nutrients added to soil is properly controlled; in combination with drip irrigation, these are suitable alternatives for improving water use efficiency and constantly leaching salt away from the root zone of plants [98]. Another technique is the use of halophyte plants that, due to their ability to hyperaccumulate salts and even heavy metals, are suitable models for the phytoremediation of saline soils [99–102].

The use of plant growth-promoting halobacteria may have pronounced benefits in all aspects mentioned above, since the tolerance to drought conferred by these bacteria on plants can improve water retention and absorption in soil, influencing the efficiency of irrigation water use. Also, the continuous supply of nutrients provided by halobacteria associated with the plant decreases the consumption and amount of fertilizers applied, representing a lower economic expense and a lower precipitation rate of those nutrients not absorbed by the plant that remain in soil, which lead to salinization. Therefore, this type of bacteria can contribute to reducing soil salinity through their plant growth promotion properties and their intrinsic characteristics to reduce soil Na^+ levels.

All these characteristics make halobacteria an eco-friendly alternative for recovering soil fertility in arid regions and other areas facing similar issues from soil deterioration due to abiotic factors or as a consequence of salinization arising from conventional agricultural practices. New bioinoculants may potentially be developed by utilizing diverse halotolerant bacteria and their metabolites for improving the productivity, fertility and quality of saline soils (Figure 2).

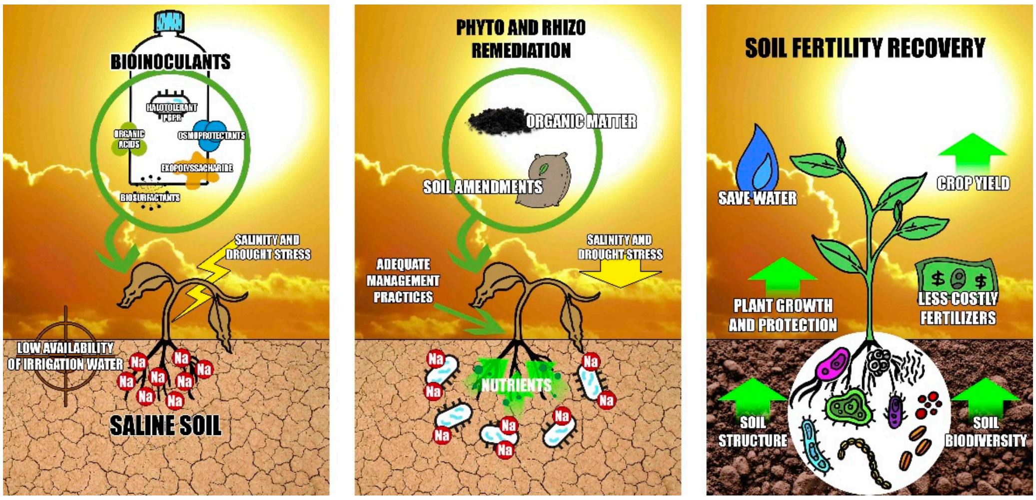

Figure 2. Application of halobacteria and their metabolites to recover soil fertility and increase crop yield in soils degraded by salinity and drought.

Recently, Kumar et al. [97] indicated that it is essential to develop screening protocols for use to evaluate bacteria resistant to different types of abiotic stress, such as salinity, heavy metal toxicity and drought. This will help produce precise data that can be replicated more accurately. In this sense, the literature surveyed reported that halotolerant bacteria have been selected solely considering a qualitative criterion based on the morphological characteristics of the colonies grown in media enriched with salts, mainly Na^+. A stricter quantitative criterion to be applied in the selection of plant growth-promoting halotolerant bacteria may be the assessment of Na^+ uptake in vitro since not all bacteria that grow in salt-enriched media are capable of capturing Na^+ ions [28]. This may add certainty about the efficiency of these microorganisms in the bioremediation of saline and sodic soils.

8. Conclusions

Halobacteria are microorganisms adapted to survive under adverse conditions because they have physiological mechanisms allowing them to tolerate different concentrations of salts in their environment. These microorganisms are distributed across a broad range of environments. The mechanisms for plant growth promotion of this type of bacteria are multiple and include direct and indirect mechanisms through which they have managed to induce an increase in the biometric and physiological parameters of plants, as well as in the yield of multiple crops that are sensitive to salt stress. Most studies related to halobacteria have focused on increasing plant growth and crop yield under saline conditions and, to a lesser extent, under other stressors such as drought and heavy metal toxicity. Therefore, the impact of halobacteria on soil fertility has not been investigated in depth. The inclusion of this latter aspect in studies addressing halobacteria and the selection of halobacteria based on quantitative methods can contribute to a better understanding of the effect of halobacteria on soil properties and the possible recovery of arid and semi-arid soils that are currently degraded by salinity and drought.

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