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Review

Tailoring Next Generation Plant Growth Promoting Microorganisms as Versatile Tools beyond Soil Desalinization: A Road Map towards Field Application

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Abstract: Plant growth promoting bacteria (PGPB) have been the target of intensive research studies toward their efficient use in the field as biofertilizers, biocontrol, and bioremediation agents among numerous other applications. Recent trends in the field of PGPB research led to the development of versatile multifaceted PGPB that can be used in different field conditions such as biocontrol of plant pathogens in metal contaminated soils. Unfortunately, all these research efforts lead to the development of PGPB that failed to perform in salty environments. Therefore, it is urgently needed to address this drawback of these PGPB toward their efficient performance in salinity context. In this paper we provide a review of state-of-the-art research in the field of PGPB and propose a road map for the development of next generation versatile and multifaceted PGPB that can perform in salinity. Beyond soil desalinization, our study paves the way towards the development of PGPB able to provide services in diverse salty environments such as heavy metal contaminated, or pathogen threatened. Smart development of salinity adapted next generation biofertilizers will inevitably allow for mitigation and alleviation of biotic and abiotic threats to plant productivity in salty environments.

Keywords: salt stress; next generation PGPB; soil desalinization; bioformulation; endophytes; rhizospheric microorganisms

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1. Introduction

Plant growth is strongly influenced by many biotic and abiotic factors [1,2]. Salinity is one of the major factors, limiting the productivity of plants and therefore agricultural production. Globally, 380 million ha of agricultural land are affected by salinity [3]. This salinization is especially encountered in arid and semi-arid areas. It leads to the depletion of organic matter in soils and the accumulation of toxic ions [4]. As a result, productive agricultural land has deteriorated. On the other hand, the increase in population has increased the demand for agricultural products. This not only threatened the sufficiency

of available food resources, but also necessitated the exploitation of marginal cultivated land [5].

If crops on soils moderately affected by salinity could be improved, the productivities of these lands would be multiplied. In this case, there is an urgent need to develop appropriate techniques for better crop production capacity in inefficiently cultivated or non-cultivated places. Various research aimed at developing technological approaches, consisting of modifying salty soil through reclamation measures or adopting biotic approaches through the use of salt-tolerant vegetable crops, is not an easy and economical step for sustainable agriculture [5,6].

The use of microbial technologies in agriculture is spreading very quickly by the identification of new bacterial strains effective in improving plant growth (PGPR, Plant Growth Promoting Rhizobacteria). Rhizospheric microorganisms, in general, exert various effects on plants, influencing their development [7–11]. They can also improve their competitiveness and their responses to external stressors. Thus, inoculation of stressed plants with PGPR strains attenuates salt stress [3]. As a result, the growth of halotolerant microorganisms associated with plant roots can lead to better fertility of saline soils [12]. Microorganisms present in the saline zone or in the rhizosphere of halophytic plants can be a valuable resource for improving the tolerance of crops to salinity [13]. PGPRs are a promising alternative to chemical fertilizers and pesticides. However, the ability of these bacteria to colonize the roots and survive in the soil is often limited. The selection and use of PGPRs should take into account the adaptation of the inoculant to a particular plant and ecosystem [14]. Developing effective measures for microbial inoculants remains a major scientific challenge. The application of the formulation for the development of new types of fertilizers is considered as one of the promising solutions to significantly boost global agricultural production in order to meet the growing food needs of the population. Encapsulation technology can be used as a versatile tool to protect these biofertilizers from desiccation, improving their shelf life and dispersal in fertilizer formulation and enabling the controlled release of microorganisms [15].

Moreover, the selection of an efficient PGPR strain is linked to the characterization of its properties promoting plant growth, which are most often the fixation of nitrogen, the production of phytohormones; the solubilization of minerals and the production of siderophores, enzymes, and organic acids. Their biocontrol activities are attributed to the production of antibiotics, iron chelation, cyanide production, induced resistance, synthesis of extracellular enzymes, and intra-rhizosphere competition [16].

These particular biofertilizers are used not only to replace chemical fertilizers but, in addition, to overcome any limits associated with the contamination of the environment by toxic compounds generated by anthropogenic and industrial activities that have caused considerable damage to aquatic and terrestrial ecosystems. In addition to salinity, pollution has led to a significant loss of agricultural land [17]. Therefore, it is very important to develop a reliable, simple, and practical strategy for the screening of effective inoculants, and having broad-spectrum resistance against several environmental constraints. Stacking multiple desirable traits in a single inoculant could, therefore, be used successfully in future studies to mitigate the effects of various biotic and abiotic stresses on plant growth and productivity [18]. It is expected that this strategy will provide a new generation of PGPRs targeting highly stress resistant plants that thrive in harsh environments and will restore degraded lands. This review is a synthesis of the beneficial effect of rhizobacteria improving plant growth and the important role of halotolerant PGPRs in the desalination of degraded soils, in improving plant productivity in extreme environments, and in the induction of their resistance in the fight against various other stresses (salinity, aridity, temperature, and pH extremes, pollutants, heavy metals, phytopathogens, etc.). The potential future uses of these multitask PGPRs as an environmentally sustainable agricultural input and the strategy for the isolation and selection of these bacteria in vitro have been screened.

2. Plant Growth Promoting Microorganisms

The plant microbiome and knowledge about the dynamics and evolution of microbial communities associated with plants are currently a growing field. Studies on the composition and diversity of the microbiota of several plants of economic interest have shown that the association of bacteria with roots has important influences on plant health, productivity, and soil quality [19]. Colonization of the roots by bacteria has long been known, but now its importance for the growth and development of plants has become more attractive [20]. The bacteria associated with the roots of plants are then defined as rhizobacteria. In this zone, plants and microorganisms interact, where chemical communications and the exchange of compounds and nutrients occur [19]. In general, highly competitive and promoter bacteria are those that manage to survive and successfully colonize nutrient-rich roots. Rhizobacteria are typical heterotrophs, so they require organic compounds as a source of energy. Their needs are fully met within the rhizosphere itself. The abundance of bacteria in the soil is explained by their rapid multiplication and their ability to use a wide variety of substrates as sources of energy and nutrients [16]. These bacteria which, when applied to seeds, plant surfaces or soil, colonize the rhizosphere or the interior of plants and promote their growth. These PGPRs play a special role in increasing nutrient uptake, improving root and shoot formation, improving seed germination, and disease prevention and resistance of plants [20]. PGPRs can promote plant growth through various mechanisms (Table S1).

2.1. Bioavailability of Nutrients

PGPRs use different mechanisms to make certain nutrients available to plants. Nitrogen-fixing bacteria generally classified as symbiotic bacteria of legumes (e.g., *Rhizobium*) and non-legumes (e.g., *Frankia*), and non-symbiotic bacteria (free life, associative, and endophytes) convert atmospheric N_2 into assimilable ammonia by plants using a complex enzyme system known as nitrogenase [21]. PGPRs also use mechanisms to solubilize phosphate (P) complexes [22]. The main mechanism used by bacteria for the solubilization of inorganic P is the production of mineral compounds such as hydroxyl ions, protons, carbon dioxide (CO_2) and organic acids (including gluconic acid, acid α-ketobutyric acid, and 2-ketogluconic acid), which reduce the pH of the soil to release P. To mineralize organic P, PGPRs producing phosphatases (e.g., phytase, phosphonoacetate hydrolase, D-α-glycerophosphatase and C-P lyase) which stimulate the hydrolysis of phosphoric esters and convert organic P into the form available to plants [23]. Among PGPRs, *Pseudomonas*, *Rhizobium*, *Enterobacter*, *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, and *Pantoea* are the most potent solubilizers [24]. PGPRs are also able to solubilize insoluble potassium sources through the production and secretion of organic acids (oxalate, succinate, and citrate) in the rhizosphere. Therefore, these bacteria improve soil fertility and the bioavailability of potassium to plants [25]. Potassium solubilizing PGPRs such as *Acidothiobacillus ferrooxidans*, *B. edaphicus*, *B. mucilaginosus*, *Burkholderia*, *Paenibacillus* sp., and *Pseudomonas* have been reported [26].

Another important component, catalyzing many metabolic reactions in plants and necessary for production of phytohormones is zinc (Zn). Therefore, Zn deficiency severely affects various life processes in plants [23]. PGPRs solubilize Zn by producing different organic acids such as 2-ketogluconic acid and 5-ketogluconic acid for the mobilization of Zn. Other mechanisms possibly involved in the solubilization of zinc include the production of siderophores and protons [27].

PGPRs can secrete low molecular weight metal chelating compounds with high affinity called siderophore. The siderophore chelates iron and other metals from mineral phases through the formation of soluble siderophore–metal complex, which then binds to specific receptors on the bacterial cell surface for uptake an energy-dependent membrane transport mechanism, and to make it available to plants [16] (Figure 1).

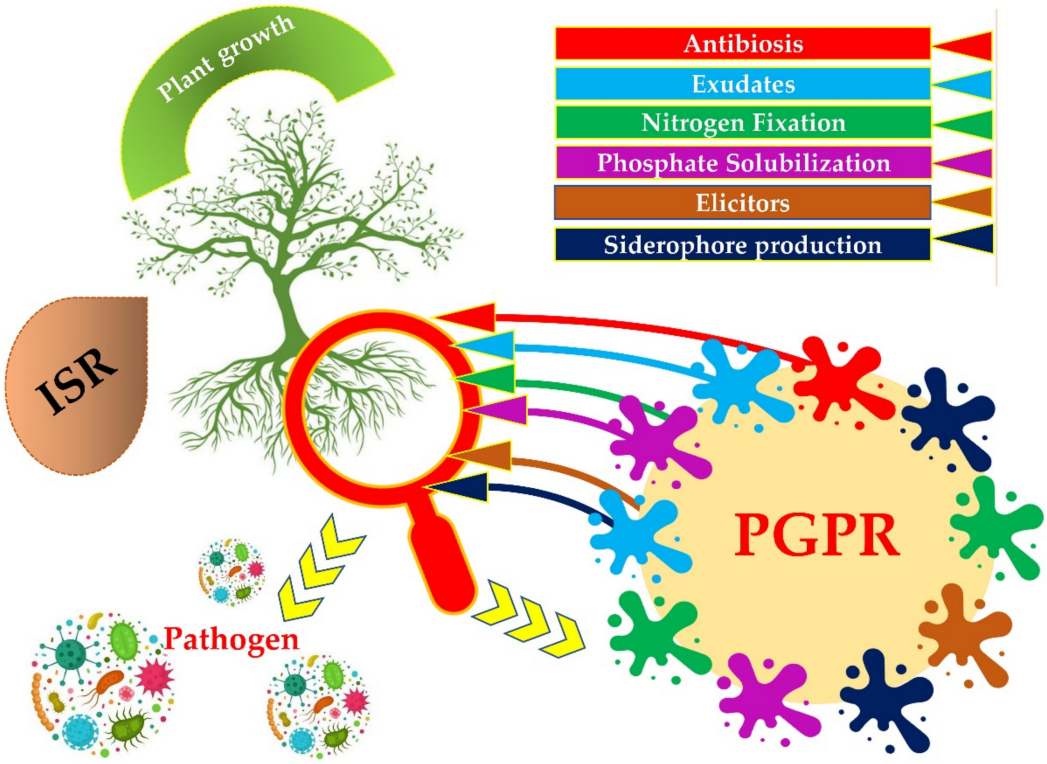

Figure 1. Different strategies of Plant Growth Promoting Rhizobacteria (PGPRs) to enhance plant growth.

2.2. Modulation of Phytohormone Levels

Phytohormones and plant growth regulators such as gibberellins, cytokinins, and auxins are organic substances, which, at low concentrations, promote plant growth and development [28]. The production of these phytohormones can be induced by certain PGPRs. Auxin is a phytohormone that directly or indirectly regulates most plant processes. It triggers a number of cellular functions ranging from vascular tissue differentiation, lateral root initiation, stimulation of cell division, stem and root elongation, and direction of stem growth in response to light [28,29]. Indole-3-acetic acid (IAA) is a common phytohormone belonging to the class of auxins and quantitatively the most produced by PGPRs. It plays an important role in the growth and development of plants because it induces the elongation and division of cells [30]. Cytokinin is a hormone derived from adenine involved in the regulation of various plant development processes such as plant cell division, disruption of dormant bud quiescence, activation of seed germination, growth roots, leaf expansion and retardation of senescence of many PGPRs including *Azotobacter*, *Azospirillum*, *Rhizobium*, *Bacillus*, and *Pseudomonas* spp. are producers of this hormone [31]. Gibberellins are a group of hormones that perform various functions in the plant organism. Gibberellins are the main regulators of the formation of reproductive organs and the ripening of viable fruits and seeds. They are synthesized by rhizospheric bacteria, including the genera *Azospirillum*, *Bacillus*, *Pseudomonas*, *Rhizobium*, *Azotobacter*, *Arthrobacter*, *Agrobacterium*, *Clostridium*, *Flavobacterium*, and *Xanthomonas* [32].

2.3. Biocontrol Activities

The use of specific microbial antagonists further stimulates plant growth in degraded ecosystems. PGPRs used as biological control agents against phytopathogens, synthesize a variety of antibiotic and antifungal compounds including lytic enzymes, siderophores, and hydrogen cyanide (HCN) [33].

The production of one or more antibiotics is the most important mechanism of PGPRs, which facilitates antagonism against many phytopathogens There are several classes of antibiotics produced by PGPRs and related to the control of root diseases: 2,4 Di-

acetyl phloroglucinol, phenazine-1-carboxyclic acid, phenazine-1-carboxamide, pyoluteorin, pyrrolnitrin, etc.). Bacilli are among the most predominant microorganisms in soil and produce a significant number of different types of antibiotics [34–36]. PGPRs also produce metabolites contributing to antibiosis and to the control of phytopathogenic agents, used as defense systems involving the production of hydrolytic enzymes such as chitinases, glucanases, proteases, lipases, and cellulases. These enzymes digest or deform the fungal cell wall components of plant pathogens. In addition to enzymes, the siderophores produced by PGPRs are considered to be biological control agents since they prevent certain phytopathogens from acquiring a sufficient quantity of iron, thus limiting their ability to proliferate. Although, plant pathogenic fungi also synthesize siderophores, these generally have a lower affinity for iron compared to those produced by PGPRs. This feature is beneficial in the process of colonization and competition for the substrate in the rhizosphere [7,37]. HCN is a volatile antimicrobial compound produced by numerous species of rhizobacteria involved in broad-spectrum biological control of root diseases since they prevent the proliferation and development of pathogenic microorganisms [38]. Many bacterial genera such as *Rhizobium*, *Pseudomonas*, *Alcaligenes*, *Bacillus*, and *Aeromonas* have been shown to be producers of HCN. Volatile organic compounds (VOCs) are low molecular weight gaseous metabolic compounds. They play a useful role in the control of plant pathogens by inducing systemic resistance and stimulating plant growth [39]. Particular bacterial species of various genera, *Pseudomonas*, *Arthrobacter*, *Stenotrophomonas*, *Serratia*, and *Bacillus* species produce VOCs. PGPRs provide an alternative strategy to protect plants against disease via induced systemic resistance (ISR) [22]. This strategy is generally defined as the activation of latent defense mechanisms in plants prior to a pathogen attack. It is not specific against a particular pathogen, but it helps the plant to control many diseases [40]. This "immunity" is initiated as a result of the plant's perception of so-called "elicitor" molecules produced by PGPRs. Thus, the transmission of the signal emitted following the perception of the infectious agent relies on different pathways in which salicylic acid, jasmonic acid, and ethylene play a crucial role [41]. However, these pathways interpenetrate and act with other mechanisms to form a modular regulatory network allowing the plant to initiate a specific defensive response depending on the nature of the pathogen, be it virus, bacteria, fungus, insect or nematode [38].

These beneficial effects of PGPRs are conditioned by their capacity for colonization and survival, which appear to be well established under normal conditions, but what about the application of these PGPRs under extreme conditions. The selection of PGPRs having the capacity for tolerance, growth promotion and protection of plants requires another selection strategy. In this case, the performance of these bacteria will be defined first in relation to their ability to adapt to especially saline stresses. Therefore, the new generation of PGPR should be sought in the rhizosphere of plants adapted to extreme saline and arid conditions. The exploitation of the microbiota of saline and arid soils will allow desalination and increase in cultivation on marginal surfaces thus meeting an ultimate objective.

3. Plant Growth Promoting Microorganisms for Use in Soil Desalinization

Saline soils currently cover a large area of the earth. Salinization is a process of increasing the total concentration of dissolved salts (sodium, potassium, magnesium, calcium, chloride, sulfate, and carbonate) in water and soil. Soil is saline when it contains an excess of soluble salts and when the electrical conductivity of the saturated soil extract exceeds 4 dS/m. In addition, the soil has a pH of 8.5 or less and its salinity is greater than 0.2% [14].

Two types of salinization are known. Primary salinization occurs naturally in both arid and temperate, maritime or continental climates induced by environmental factors, salts are released following an alteration of certain sedimentary, volcanic and hydrothermal rocks [7]. They can also be released from old salt accumulations [42]. The released salts are transported by groundwater, which accumulates on the surface of low-lying areas where

the rate of evapotranspiration is high and exceeds rainfall precipitation. [17]. Secondary salinization caused by human interventions is the result of the accumulation of salts from additional water induced by human activities. The worldwide development of irrigated crops leads to a secondary extension of salty lands. Irrigation of cropland leads to the salinization of many soils, especially those in arid and semi-arid regions [42]. The amounts of water added over time cause an accumulated deposition of salt in the topsoil as the water evaporates [14].

In desert or sub-desert countries, the chotts are salty lands or sometimes pastures which surround a closed depression or ephemeral lake (Sebkha). The Sebkhas, are a flat-bottomed depression, generally liable to flooding, where salty soils limit vegetation. The water comes from runoff, but also from groundwater. All desert regions have Sebkhas. In the far Sahara, groundwater is also very salty with more than 4 to 5 g/L of dry residue and often much more. They cannot be used for irrigation. The evaporation of hydromorphic soils causes a salinity, which only increases causing desertification by salt, due not to lack of water but to its excess. The final stage of the process is a Sebkha whose sediments are completely sterile, drowned by a few tens of centimeters of water in winter and covered in summer with a white layer of crystallized salts. During the dry season, these areas are subjected to wind erosion, which accentuates the basin topography [43]. In Algeria, as elsewhere in the world, salty soils occupy large areas (3.2 million hectares of the total area). Almost 10–15% of irrigated land is affected by these problems. The salinized lands will be difficult to recover. Most of these soils is located in arid and semi-arid regions [44]. The salty soils of Algeria are characterized, in general, by an electrical conductivity greater than 7 dS/m and a percentage of exchangeable sodium, which varies from 5 to 60% of the CEC. The salinity is observed in the plains and valleys, around the Chotts and Sebkhas and in the far South (Figure 2).

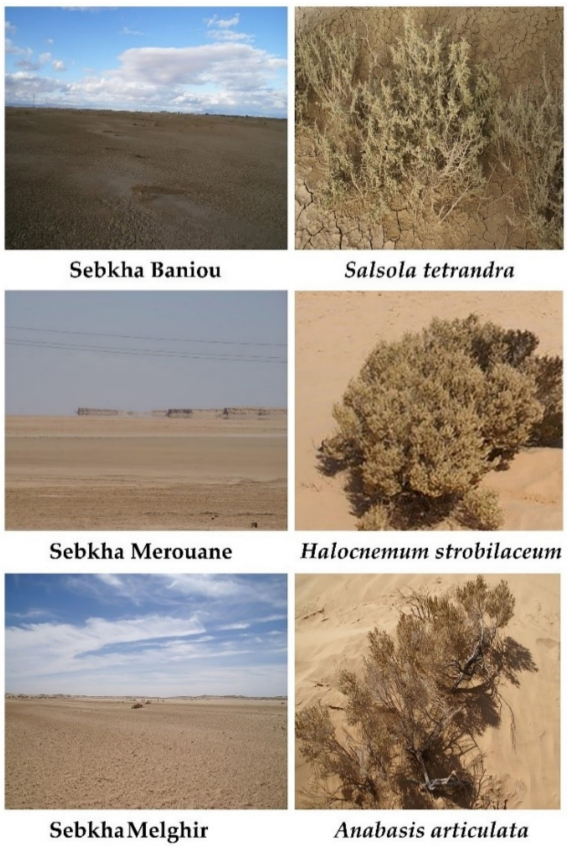

Figure 2. Different plains and valleys with their related plants.

3.1. Effects of Salinity on Plants

Salinity affects the growth and yield of plants. Crops are sensitive to high concentrations of salts dissolved in irrigation water or present in the soil. Osmotic stress induces a decrease in cell growth, a reduction in leaf area and chlorophyll content with an acceleration of senescence [3]. The photosynthetic capacity of the plant, being the main cause of plant productivity, is greatly reduced under salt stress. The reduction in photosynthesis is linked to the decrease in leaf water potential, which causes stomata to close, leading to a reduction in stomatal conductance [3]. Salinity also disturbs the gas exchange parameters. The diffusion of CO_2 inside the stomata then becomes limited and its fixation in the chloroplasts decreases. Closure of stomata in response to salinity stress usually occurs due to decreased leaf turgor and atmospheric vapor pressure, as well as chemical signals generated by the roots. Plants synthesize a stress hormone, abscisic acid (ABA), transported to the aerial parts where it triggers the closure of the stomata [3,45], the ABA acts as the stress signal, from the root to the leaf. The increased concentration of ABA in the xylem correlates with reduced leaf conductance and general inhibition of leaf growth. The production of ABA and the dehydration of membranes increase the resistance of the mesophyll to CO_2 diffusion. A nutritional deficiency therefore accompanies the water deficit [45].

Plants subjected to salt stress showed a decrease in biometric parameters such as fresh shoot weight, plant height, and number of leaves. When the concentration of salts in the soil makes water unavailable, plants develop changes in root morphology to cope with it. The root architecture is strongly affected, with a consequent reduction in the size of the secondary roots [46]. Plants can also suffer from membrane destabilization and nutritional imbalance, in response to increased absorption of Na^+ ions or decreased absorption of Ca^{2+} and K^+ ions [47]. An excess of Na^+ and especially Cl^- can affect plant enzymes and lead to reduced energy production. In the event of excessive concentrations of Na^+ and Cl^- in the rhizosphere, competitive interactions with other nutrient ions (K^+, NO_3^- and $H_2PO_4^-$) are established with transport proteins at the root level [48]. The effects of salinity give rise to many other effects such as oxidative stress, which is characterized by the accumulation of reactive oxygen species (ROS), potentially dangerous for the membrane, proteins, enzymes, and nucleic acids. Once the capacity of cells is depleted, salts accumulate in the intercellular space leading to dehydration and cell death [7].

Faced with this danger, certain plants, called glycophytes, are not able to withstand the presence of salt and are apparently devoid of the genetic basis for salt tolerance, they include the majority of vegetable crops. When exposed to saline conditions, these plants undergo nutritional disorders [49]. This sensitivity is due to their inability to effectively remove Na^+ ions from the cytoplasm [50]. Halophytes, on the contrary, are natural plants in salty environments, they survive in the presence of high concentrations of electrolytes in their environments [17] (Figure 2). Halophytes develop physiological responses to ensure their water supply while preserving their metabolism. Different categories of halophytes exist [49].

3.2. Strategies for Adapting Plants to Salinity

Plants respond to salt stress with numerous changes, revealing the multifactorial nature of the mechanisms of tolerance and adaptation to abiotic stresses. Under stressful conditions, plants can react by setting up physiological and biochemical mechanisms. Thus, the synthesis of organic compounds, which act as osmoprotectors or osmotic regulators, accumulate in the cytoplasm and replace water in chemical reactions. These compatible solutes mainly include proline, glycine betaine, sugars and polyols [51]. Certain species, both halophytes and glycophytes, use the mechanism of excluding excess salts [52] which consists of excluding sodium from the cytoplasm outside the cell by limiting the entry of saline elements and reject them in the apoplasmic compartment [42,53]. Vacuolar compartmentalization is another mechanism that involves the removal of excess Na^+ ions from the cytoplasm into the vacuole in order to avoid their toxic and inhibitory effect against enzymatic processes. Plants also defend themselves by inducing the activities of

certain antioxidant enzymes such as catalase (CAT), glutathione S-transferase (GST), and superoxide dismutase (SOD) which eliminate ROS. Plants have other adaptive mechanisms to reduce oxidative damage resulting from salt stress. In response to this stress, the biosynthetic pathway of phenylpropanoids is stimulated and results in the production of various phenolic compounds which have strong antioxidant potential. In this case, polyphenolic compounds such as phenolic acids, flavonoids, proanthocyanidins, and anthocyanins play an important role in the fight against free radicals. The antioxidant activity is mainly due to their redox properties, which allow them to act as reducing agents, hydrogen donors and oxygen scavengers [54,55]. In addition, abiotic stress imposes a series of adaptive changes on the plant cell to maintain growth, including upregulation or downregulation of various genes. Under these conditions, regulatory proteins such as C_2H_2 zinc finger proteins directly target downstream stress-related genes to activate or inhibit their expression [46]. These proteins directly target antioxidant genes associated with scavenging reactive oxygen species (ROS) and may confer stress tolerance by increasing the content of abscisic acid (ABA), proline, soluble sugars, or chlorophyll, and reducing the rate of water loss [56].

In halophytes, the endodermis and exodermis form a tight hydrophobic barrier that regulates and maintains the flow of solutes in the cytoplasm through the plasma membrane. In addition, they have a thickened primary root which acts as a sink for the sequestration of Na^+ ions in order to prevent the accumulation of Na^+ in the lateral roots and young leaves, thus protecting the plants from salt stress [46]. However, it is quite complex to describe a universal scenario of root responses to an external stimulus, as it varies from species to species as well as between different stages of root development. In conclusion, the pronounced ability of roots to adapt to various external stress conditions is a result of their significant root plasticity [57,58] (Figure 3).

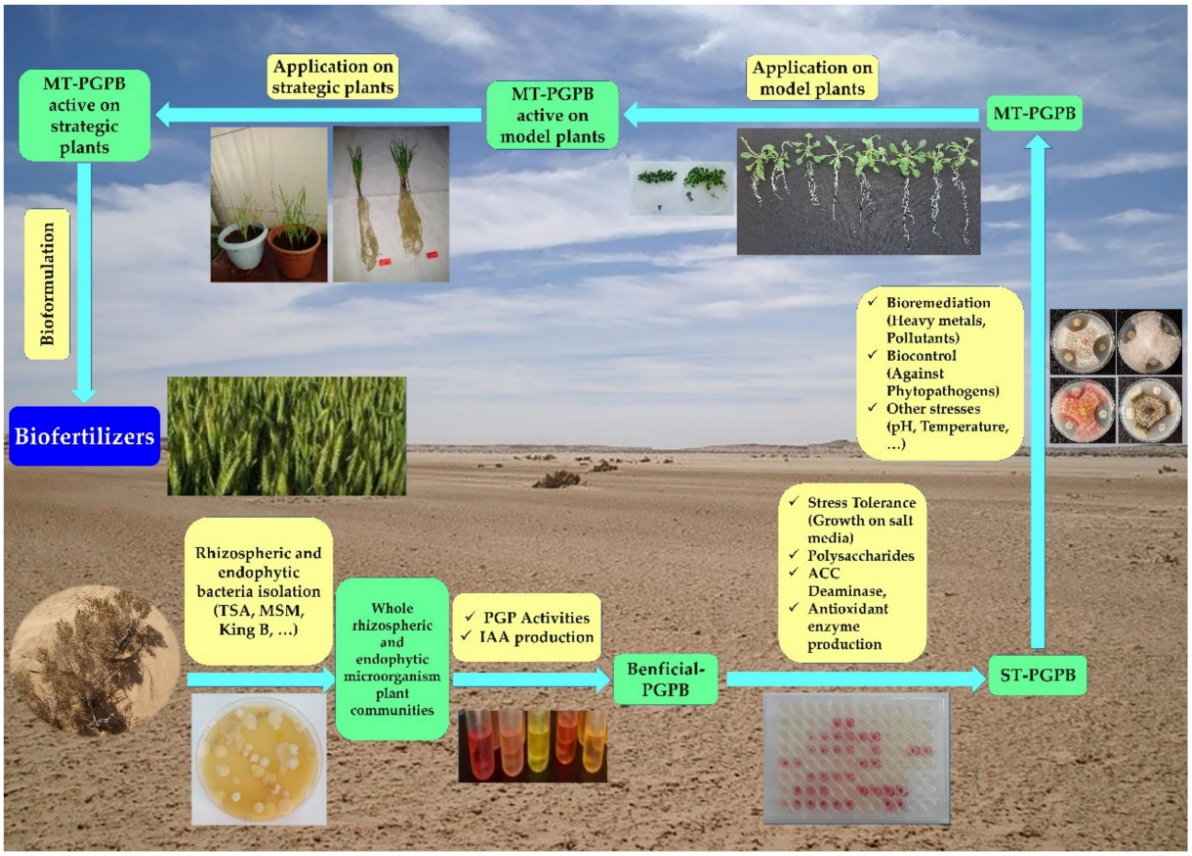

Figure 3. Strategies of plant growth promoting (PGP) bacteria for adapting plants to salinity.

3.3. Microbiota Tolerance Strategies Associated with Halophytes

Microorganisms are said to be halotolerant when they able to grow without salts, while tolerating varying concentrations of salts. On the contrary, they are halophilic when they can only develop in the presence of salts. A basic property of halophiles is that the cytoplasm of these microorganisms is iso-osmotic with the surrounding environment. To maintain continual turgor, cells must maintain their intracellular osmotic pressure higher than that of their environment. An organism's ability to adapt to changes in external osmotic pressure (osmoadaptation) and the development of mechanisms to achieve this goal (osmoregulation) are essential to its survival [59]. Halophilic bacteria have adapted during evolution (phenotypic and genotypic adaptation) to develop optimally in hypersaline environments. To survive and multiply these bacteria adopt certain strategies. Recognition of the osmotic imbalance by an osmosensor, which can be macromolecules undergoing conformational transitions in response to changing extracellular activities of water or resulting from changes in cell structure. This regulatory mechanism is made up of two systems. It is a protein sensor, which detects the signal and a regulatory protein that binds to deoxynucleic acid (DNA) and controls gene expression. The regulatory system of components that respond to osmotic changes is the EnvZ/OmpR found in Eubacteria. EnvZ is a transmembrane histidine kinase that monitors changes in osmolarity on both sides of the cytoplasmic membrane via OmpR [60]. The accumulation of osmolytes or compatible solutes in response to the pressure difference imposed, is carried out to achieve an osmotic balance. Solutes can be accumulated at high concentrations, either by de novo synthesis or by absorption from the medium without interfering with vital cellular processes. These osmotically active molecules retain the positive turgor pressure necessary for cell division. However, when the turgor becomes too high, the microorganisms must excrete these solutes from their cytoplasm. Compatible solutes can be inorganic ions (intracellular concentrations of inorganic cations: potassium K^+, magnesium Mg^{2+}, and sodium Na^+) and organic solutes (betaines, ectoines, and glycine). Thus, bacteria using the organic solute strategy can tolerate fluctuations in ambient salinity much better than bacteria using the salt strategy in the cytoplasm. However, the disadvantage of the synthesis of organic solutes consumes more energy than the accumulation of K^+ [61].

Changes in water activity can also have a profound effect on the stabilization of macromolecules. Cells respond to changes in osmotic pressure with mechanisms designed to promote the correct folding of proteins. Moderate halophilic bacteria increase the number of negative charges on an increased salt concentration in their growth medium. Halophilic bacteria have intracellular proteins with a higher proportion of acidic amino acids, and a lower proportion of non-polar residues than usual proteins. On the contrary, for halotolerant bacteria organic solutes act as osmoprotectants, these accumulated solutes can have different effects on proteins, their structures and their activities. It is not necessary to modify a large group of proteins when the salt concentration of the environment changes. Therefore, halotolerant bacteria can tolerate fluctuations in ambient salinity much better than halophilic bacteria.

In addition, all halophilic microorganisms contain powerful transport mechanisms, usually based on Na^+/H^+ antiports, to expel sodium ions from inside the cell [62]. Majority of functions responsible for the survival of halophilic and halotolerant bacteria in their environment are encoded by megaplasmids [63].

3.4. Potential of HALOTOLERANT PGPRs in Desalinization

The potential to use salt tolerant species associated with halophytes would improve agricultural production in arid and semi-arid regions of the world. The microflora associated with plants (phyllosphere, rhizosphere, and endophyte) is recognized for improving the capacity of plants to resist environmental stresses [64,65]. Recently, numerous studies have documented that the tolerance of plants to stress is attributed partially or totally to their associated microbiota [64]. Due to their active role in regulating a wide variety of plant physiological responses, bacteria associated with host plants from extreme environ-

ments appear to be the most promising biological alternatives in the development and improvement of plant production. [66,67]. This could be the consequence of the natural adaptability of these bacteria in extreme environments, and also the selection pressure of these types of ecosystems imposes specific biological responses during the interaction plants–microorganisms [68]. Halophytes are a reservoir for isolating halotolerant PGPRs [46].

Several studies exploring the diversity of salt tolerant bacteria found that most isolates could tolerate a concentration of 1–15% NaCl [69]. The microbial composition in the rhizosphere, due to the various plant–microorganism interactions, often differs considerably from one plant species to another. Phylogenetic analysis of the salt tolerant strains showed that they belong to the orders Bacillales, Actinomycetales, Rhizobiales, and Oceanospirillales. Several bacterial genera, such as *Streptomyces*, *Azospirillum*, *Alcaligenes*, *Bacillus*, *Rhizobium*, *Pseudomonas*, *Serratia*, and *Klebsiella* are recognized as PGPBs working under saline conditions [70]. The genus *Bacillus* is widely distributed in different natural habitats [65], suggesting a remarkable capacity for physiological and genetic adaptability of this genus in nature. Salt-tolerant PGPR *Bacillus licheniformis* strain SA03 isolated in saline–alkaline soil conferred increased salt tolerance [71]. Moreover, a study carried out on halotolerant bacteria, *Hallobacillus* sp. and *Bacillus halodenitrificans* showed a significant increase in root elongation and dry weight of wheat compared to the uninoculated control in saline soil [72]. Various species as, *Bacillus*, *Acinetobacter*, *Microbacterium*, and *Arthrobacter*, have also been isolated from saline soils and are currently used in highly saline and degraded soils to support plant growth and development [73]. Salt tolerant *Rhizobium* species have also been isolated from saline soils. These salt-resistant isolates by intracellular accumulation of compatible solutes have shown their potential to improve salt tolerance, growth and yield of plants under salt stress conditions. Other PGPRs, including, *Acetobacter* and *Flavobacterium* and many strains of *Azospirillum* can maintain their PGP capacity even under high salt conditions. The saline tolerant strain *Azospirillum* increased shoot dry weight, grain yield and nitrogen concentration of wheat grown in saline soil [74].

These PGPBs originating from bacterial communities of the rhizosphere, the phyllosphere, or endophytes of plants are defined as those capable of colonizing the tissues of a wide variety of plant species. These bacteria, despite their ability to promote the growth of host plants through their beneficial mechanisms, cope with stress by adopting other means of responding to osmotic stress.

3.4.1. ACC (1-Aminocyclopropane-1-Carboxylate) Deaminase

In response to the constraints of salinity, PGPRs producing ACC deaminase stimulate plant growth by regulating the massive production of ethylene. The bacteria reduce ethylene production in plants after exposure to increasing concentrations of salt. However, the sodium content of the plant did not decrease while the absorption of phosphorus and potassium was slightly increased, which partly contributed to the activation of the processes involved in reducing the harmful salt effect. The bacteria also increased the efficiency of water use in saline conditions and reduced the suppression of photosynthesis. Recently, several studies have reported that *P. fluorescens* containing ACC deaminase improves the resistance of plants to saline solutions and provides an increased yield compared to those inoculated with strains of Pseudomonas lacking ACC deaminase [75]. The decrease in high ethylene content can be achieved by degradation of its direct precursor, 1-Aminocyclopropane-1-carboxylic acid (ACC), using ACC-deaminase. This enzyme can relieve stress caused by several stresses. This enzyme is expressed in several rhizobacteria (ex: *Alcaligenes* spp., *Bacillus pumilus*, *Burkholderia cepacia*, *Enterobacter cloacae*, *Methylobacterium fujisawaense*, *Ralstonia solanacearum*, *Pseudomonas* spp., and *Variovorax paradoxus*). These can degrade ACC in α-ketobutyrate and in ammonium. Other strains, such as *R. leguminosarum* bv. viciae, *R. hedysari*, *R. japonicum*, *R. gallicum*, *B. japonicum*, *B. elkani*, *M. loti*, and *S. meliloti* may also produce ACC deaminase. Inoculation of *Rhizobium* producing

ACC deaminase reduces the level of ethylene in the soil. Inoculation with these bacteria promotes root elongation, nodulation and mineral absorption [16,76].

3.4.2. Exopolysaccharides

Bacteria that produce exopolysaccharides (EPS) play a crucial role in plant growth and agricultural production by maintaining water potential, aggregating soil particles, ensuring contact between plant roots and rhizobacteria and protecting the host under stressful conditions. EPS are a complex of high molecular weight polymers (MW $\geq$ 10,000) secreted by bacteria in response to environmental stresses [77]. EPS-producing PGPRs can improve soil structure by increasing the volume of rhizospheric soil macropores resulting in high water retention and availability of nutrients to plants. EPS can also retain Na^+ ions by reducing its content absorbed by plants, and therefore attenuate the effect of salt stress. The ability of EPS to bind cations is associated, mainly, with hydroxyl, sulfhydryl, carboxyl and phosphoryl groups [70,77]. Bacterial EPS plays an important role in soil aggregation and adhesion. PGPR EPS-producing strains induce tolerance to soil salinity, promote plant growth and limit Na^+ uptake by the roots [70]. Bacterial EPS would protect bacteria from desiccation by modifying their microenvironment. Inoculation not only reduces the concentration of Na^+ and Cl^- in the plant, but also induces a marked and gradual increase in the concentration of N, P, and K under the stress of salinity. The concentrations of N, P, and K in lettuce inoculated with *Bacillus* sp. under stressful conditions increase by about 5, 70, and 50%, respectively [78]. Certain rhizobacteria including *Aeromonas hydrophila*, *Bacillus* sp., *Planococcus rifietoensis*, *Halomonas variabilis*, *Burkholderia*, *Enterobacter*, *Microbacterium*, and *Paenibacillus* produce EPS and facilitate biofilm formation [79]. The EPS produced by *Pseudomonas putida* GAP-P45 play a positive role in the regulation of water content and the diffusion of the carbon source to plants in particular under fluctuating conditions of stress [80].

3.4.3. Antioxidant Activity

Under saline conditions, ROS causes oxidative damage to biomolecules such as lipids and proteins and ultimately leads to plant death [81]. Attenuation of oxidative degradation by antioxidant enzymes mediated by ROS scavenging is an important mechanism in plants for increasing tolerance to salinity stress. Bacteria moderate the redox state of salt-affected plants by increasing antioxidants and polyamines, resulting in enhanced photosynthetic efficiency [82]. PGPRs produce antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT), and non-enzymatic antioxidants such as ascorbate, glutathione, and α-tocopherol [83].

Studies of the transcriptome profiles of tissues of Arabidopsis shoots affected by salinity have shown, after inoculation with *Bacillus amyloliquefaciens* FZB42, a stimulation of the upregulation of genes associated with photosynthesis, trapping of ROS, osmoprotectors such as trehalose and proline, the translocation of Na^+ as well as the signaling of jasmonic acid, auxin and ethylene under conditions of salt stress [84]. The expression of the variance of the antioxidant genes may possibly be involved in the regulation of the level of ROS in plants inoculated with PGPR under salinity stress. This corresponds to previous studies where PGPR treatment stimulated antioxidant defense mechanism, thus resulting in a decrease in the concentration of ROS in plants exposed to salt stress.

4. Next Generation Plant Growth Promoting Microorganisms

Climate change and anthropogenic activities have created more stressful conditions limiting crop production around the world [85]. Huge crop losses are likely to be over the years. It has been estimated that around 30% of global agricultural production is lost due to abiotic stresses [22], including drought, salinity, desertification, pollution, and erosion [86]. Among the abiotic stresses, salinity is a major stress affecting agricultural land. In addition, and beyond the salinity, other stresses are not tolerable by plants. It is obvious that drought, desertification, and extreme temperatures are phenomena associated with arid and saline

regions. In addition, soils can be polluted by effluents from mining, tannery, textiles, and petrochemical sectors. These effluents are rich in salts as well as in heavy metal ions. To overcome all these constraints and restore environmental stability, great attention is being paid to sustainable agriculture by inoculating the soil with beneficial bacteria [87]. There is evidence that plant growth promoting bacteria (PGPB) can improve crop production under stressful conditions [88,89]. Therefore, the current trend would be the choice and selection of new PGPBs having the capacity to solve several problems at the same time. This new generation of so-called multitask PGPBs (MT-PGPB) would be selected from halotolerant bacteria. These bacteria are the best options for the bioremediation of degraded soils due to their tolerance and ability to thrive under extreme conditions and their high sequestration capacity. Inoculation with these MT-PGPBs improves the physico-chemical and biological properties of the soil [90].

Salt-Tolerant-PGPB (ST-PGPB) Converted to MT-PGPB Mitigate More Stress

Numerous studies have revealed that the use of PGPBs possessing pollutant detoxification characteristics, combined with beneficial properties for plants, is a promising, cost-effective, and ecological method [91]. Bacterial bioremediation makes it possible to reduce/eliminate organic and metallic contaminants by several biotechnological processes [92]. Many bacteria are capable of reducing heavy metals and potentially degrading pesticides and hydrocarbons, using these pollutants as the sole source of carbon and energy.

Numerous studies have reported that PGPBs are potential agents tolerating heavy metal stress [93]. These bacteria are exploited to improve plant growth as well as for the bioremediation of contaminated sites by adopting various strategies [94].

Bacterial bio-sorption is a process primarily used for the removal of non-biodegradable pollutants, such as heavy metals. It is an accumulation independent of metabolism, by living or inactive biomass [95]. This process involves the sequestration of metals in different cellular compartments. The cell wall of bacteria comes into contact with metal ions and is responsible for the bio-sorption of metals by their chemical functional groups which have an affinity for heavy metals [96]. In addition, the exopolysaccharides produced by bacteria have a strong capacity for binding to heavy metals. They are able to absorb heavy metals, due to their particular structure, their physicochemical properties and their chemical stability, due to the presence of functional groups (hydroxyl, carboxyl, amino, and phosphate groups) [97]. These groups react with oppositely charged metal ions to form metal-EPS complexes [98].

Bioaccumulation is a complex process that involves the uptake of metals into bacterial cells where the metal is sequestered. This requires active transport of metal ions to reduce the availability of heavy metals [49]. Exposure of bacteria to toxic concentrations of heavy metals induces the expression of peptides rich in cysteine (metallothioneins, glutathione, or phytochelatin) [99] which have a high affinity for metals [95]. The metallothionein of *Synechococcus* PCC7942, sequesters and detoxifies Cd^{2+}. Through a phenomenon of bioassimilation, PGPBs are able to produce siderophores which chelate iron as well as other heavy metals (cadmium, lead, nickel, arsenic, and cobalt, etc.) [100]. Many bacteria synthesize these substances to capture metal ions. Bioprecipitation is the most common method for removing dissolved pollutants [101]. Bacteria produce and/or excrete substances which react chemically with metallic species and produce insoluble metallic compounds; insoluble hydroxides, carbonates, phosphates, and sulfides [102]. PGPBs also produce low molecular weight organic acids (e.g., gluconic, oxalic and citric acids, etc.), which play an important role in the detoxification of polluted sites by the complexation of heavy metals and by increasing their mobility and their absorption [49]. Biotransformation can alter the chemical form of heavy metals by methylation/reduction, dealkylation/oxidation, altering their mobility, toxicity, and bioavailability [91]. PGPBs have the potential to minimize the deleterious effects of heavy metals through methylation [103]. The strain *Bacillus* sp. CX-1 isolated from manure compost has a high capacity to methylate Arsenic (As). This biological transformation is catalyzed by the enzymes As (III) S-adenosylmethionine methyl-

transferase [104]. According to Pires et al. [105], *Bacillus*, *Pseudomonas*, and *Arthrobacter* are considered to be the predominant genera of the bacterial population in sites contaminated by metals.

Pesticide toxicity or contamination can be reduced by the natural detoxifying ability of PGPBs. Pesticides can be completely mineralized in water and carbon dioxide. Among the various microbial communities, PGPRs such as the genera *Alcaligenes*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhodococcus*, *Serratia*, *Sphingomonas*, *Stenotrophomonas*, and *Streptomyces*, have potential applications in the bioremediation of pesticides by different mechanisms [106]. Hydrolytic enzymes are most often used for reducing the toxicity of pesticides as they disrupt major chemical bonds of toxic organic compounds such as esters, peptide bonds, carbon-halide bonds, etc. Among these enzymes, the dehalogenase DhaA from *Pseudomonas pavonaceae* 170 and LinB from *Sphingomonas paucimobilis* UT26 which are the most studied haloalkane dehalogenases used for the degradation of pesticides [79]. The purified carbaryl hydrolase from Arthrobacter sp. hydrolyzes three insecticides N-methylcarbamate: carbaryl, xylylcarb, and metolcarb [107].

Remediation of environments contaminated by hydrocarbons remains difficult due to their low solubility, lack of polarity, and hydrophobic nature. The strategy of bacteria in the degradation of hydrocarbons is generally based on the use of enzymes and biosurfactants [108]. Enzymes play a major role in the biodegradation of hydrocarbons because they convert them into harmless compounds (carbon dioxide and water). Oxygenases are the main enzymes in the aerobic degradation of aromatic hydrocarbons [86]. P450 monooxygenase isolated from *Bacillus megaterium* BM3 has the ability to degrade a variety of substrates such as fatty acids and aromatic compounds, naphthalene dioxygenase isolated from *Pseudomonas putida* involved in the degradation of naphthalene, toluene dioxygenase produced by *Pseudomonas putida* F1 catalyzes the degradation of toluene [86]. In addition, bacteria can come into contact with hydrocarbons by the production of biosurfactants allowing them to form micelles which accumulate at the interphase between liquids of different polarities such as water and oil, thus reducing surface tension and facilitating the absorption and emulsification of hydrocarbons [109]. Khan et al. [110] report the potential of four bacterial strains *Pseudomonas poae* BA1, *Acinetobacter bouvetii* BP18, *Bacillus thuringiensis* BG3, and *Stenotrophomonas rhizophila* BG32 for the degradation of hydrocarbons by biosurfactants. Biosurfactants have been widely studied in the bioremediation of pollutants [111]. They are amphiphilic molecules containing polar (hydrophilic groups) and nonpolar (hydrophobic groups) groups and have surface or interface related properties [111]. They have several advantages: biodegradability, low toxicity, high surface activity, and high yield even under extreme environmental conditions [112]. They have been classified according to their chemical composition and their microbial origin, into four groups: Glycolipids (rhamnolipids produced by *Pseudomonas aeruginosa* and *Pantoea* sp.), Lipopolysaccharides (emulsan produced by *Acinetobacter*), lipopeptides (surfactin produced by *Bacillus subtilis*), and phospholipids (fatty acids, neutral lipids of *Corynebacterium*) [113].

Drought is also a stress that limits plant growth and soil fertility resulting in major loss of productivity across the world. Drought disrupts the water potential of plants, by lowering the water content and nutrients in the soils [114]. Microbial inoculants facilitate the amelioration of drought stress through the production of cytokinin, antioxidants, ACC deaminase, EPS, and other metabolites associated with growth. Cytokinins increase the abscisic acid (ABA) content of plants, which further closes the stomata to reduce leaf water loss [115].

The increase in temperature and decrease in precipitation, gave rise to the problem of heat stress. Under these conditions, soils lose their water due to excessive evaporation and are subject to erosion by wind and water. Plants under this stress show a reduced growth due to decreased water and nutrient uptake, impaired photosynthesis, and increased leaf senescence [114]. To promote plant growth and revive soil fertility, PGPBs have been a sustainable solution configuring the mechanism of tolerance. They induce the production of osmoregulators for osmotic balance preventing plasmolysis and increased synthesis of

heat shock proteins (HSPs) which tolerate heat stress and regulate biological enzymatic mechanisms. Both HSPs and chaperones instruct the correct folding of proteins ensuring proper enzymatic functioning even under high temperature stress [116] another strategy for protection from heat stress damage consists of an accumulation of trehalose which inhibits protein denaturation and supports aggregation by maintaining the normal conformation of proteins under stress conditions. Unlike heat stress, cold stress is also a climatic limit that impairs plant growth. At low temperatures, the cellular metabolism of plants is disturbed. Inoculation with cold tolerant bacteria stabilizes membrane fluidity and ensures proper functioning of enzymatic processes. The tolerance mechanisms adopted by these cold tolerant bacteria include an increased concentration of unsaturated fatty acids in the cell membrane to improve fluidity [117], cold shock proteins (CSP) such as chaperones ensuring correct protein folding, and accumulation of trehalose [118].

Another challenge that limits the productivity of agriculture is pH stress. Deviations in pH lead to decreased plant growth due to loss of beneficial plant–microorganism interactions, reduced chelation of nutrients, and loss of essential anions. The offset from normal pH shows substantial changes in gene expression and cellular metabolism. Beneficial bacteria initiate adaptive responses to support growth and maintain osmotic balance and cellular vitality [119]. Under this type of stress, PGPBs produce enzymes that adapt to pH changes to control their metabolic activities. Biofilm (composed of EPS) is also a mechanism by which microorganisms form a local environment protecting against extreme external pH.

Plants under stressful conditions become more vulnerable to diseases caused by phytopathogens. The use of specific microbial antagonists further stimulates plant growth in degraded ecosystems [120]. PGPRs used as biological control agents against phytopathogens are beneficial, naturally occurring microorganisms which are environmentally friendly and non-toxic compared to conventional chemical control compounds. They possess a diverse range of modes of action, including antibiosis, siderophore production, cell wall degrading enzymes, bio-surfactants and volatiles, and also the induction of systemic resistance to plants [7].

PGPBs beneficial for improving agricultural production under conditions of environmental stress adopt various strategies to counter the limitations of abiotic and biotic stresses; although, these bacteria respond to each stress differently by adopting a specific mechanism. However, some degree of overlap is observed in the responses of these PGPBs to several stresses. PGPBs can cause "induced systemic tolerance" (IST), involving various physiological and biochemical changes in plants that confer tolerance to biotic and abiotic stresses [121]. The mechanisms include the production of VOCs which are low molecular weight gaseous metabolic compounds that control phytopathogens and induce systemic resistance [39] to various abiotic stressors such as than salinity, drought, high and low temperatures, and heavy metals [122]. Antioxidants work by reducing the damaging effects of ROS, thereby securing the cell, membranes, and biomolecules [123]. SPEs produced by bacteria help maintain the hydrological balance of the soil through the aggregation of soil particles trapping water molecules, thereby increasing nutrient uptake and sequestering heavy metals [124]. PGPBs with ACC deaminase activity reduce the level of stress-induced ethylene in host plants and stimulate plant growth. The effectiveness of this enzyme has been reported to alleviate various environmental stressors such as salinity, flooding, heat, drought, metal contamination, organic pollutants, injury, pathogens, and infections by insects [125]. Finally, in the event of stress, the cells also call on compatible organic solutes of low molecular weight. The accumulation of these solutes, within intrinsic limits, is a very widespread response of bacteria and plants in response to these stresses [98]. In addition, some PGPBs can also play a protective role against biotic stresses by triggering reactions following the emission of signals or the production of pathogenesis-related proteins (PR) which propagate systemically in the plant. In sum, the molecular mechanism behind tolerance includes the upregulation of stress response marker genes [126].

5. A Road Map for Tailoring Plant Growth Promoting Microorganisms as Versatile Tools beyond Soil Desalinization

The microbiomes of plants native to extreme environments can be rich sources of stress-relieving microorganisms. The phytomicrobiome plays an essential role in the survival of the holobiont, especially for plants growing in extreme environments. In recent years, much interest has been focused on the strategy of inoculating soil with beneficial microorganisms known to promote plant growth under various stresses [87]. The use of PGPBs as inoculants has been a technique known for a long time; the use of these inoculants on legumes and cereals has existed since antiquity [127]. The development of new inocula is based on laboratory screening tests. The selection of effective PGPB strains is linked to the characterization of properties promoting plant growth. Therefore, this part aims at the prospect of selecting the isolates with the highest PGP potential and their identification by molecular approach.

For the development of a new inoculum, we target the rhizo-microbiome of halophytic plants because in this area there is the greatest microbial diversity. The halotolerant bacteria associated with the roots of the halophytes taken from various Sebkhas are isolated on culture media. In order to increase diversity and recover a large number of cultivable bacteria, the isolation of rhizospheric and root endophytic bacteria is carried out on different media. Generally, a rich medium trypticase soy agar (TSA) and a minimum medium allowing the growth of bacteria that are not very demanding for the total flora is recommended. For the search for specific flora, other media can be used such as ISP2 medium to isolate Actinobacteria, King B medium for *Pseudomonas* or Yeast Extract Mannitol Agar (YMA) allowing the growth of Rhizobia. Once the isolated strains are cultivated and purified, they are screened for their ability to improve plant growth by analyzing direct PGP activities (nitrogen fixation, phosphate solubilization, hormone production including IAA, production of siderophores) and indirect (production of NH_3 from HCN, antagonism towards phytopathogens and production of lytic enzymes). The biosynthetic capacity of auxin can be used as a tool for screening for effective PGPB strains [121]. Particularly, IAA production appears to be a most prevalent plant growth promoting property among PGPBs.

However, given the large number of strains to be assessed at this stage, we must accept this risk and consider reviewing the situation once the initial screening is complete. These strains are then screened for their ability to tolerate stress. The easiest stress to apply evenly is salt stress. Responses to salt stress are generally representative of expected responses to other stresses. A first selection is made according to the best PGP activities and the ability to tolerate salt stress. These bacteria are checked for their PGP potential in a saline medium and then tested for their ability to induce stress tolerance by the production of ACC deaminase, production of polysaccharides or the measurement of antioxidant enzymes. Promising isolates can then be tested for their ability to tolerate other stresses. Water stress is tested in vitro by measuring growth on culture medium deficient in available water (e.g., added with polyethylene glycol). Growth is also measured at pH and temperature extremes to assess the ability to tolerate these stresses. In order to achieve the ultimate goal for the selection of MT-PGPBs, more stressful and complex conditions are applied. To do this, the strains are appreciated for their ability to metabolize pollutants (hydrocarbons, insecticides, etc.) and to sequester heavy metals by checking their growth on culture media supplemented with these compounds used as the sole carbon sources. In addition, the screening of strains performing in the protection against phytopathogenic diseases is also carried out on a Petri plate of potato dextrose agar (PDA) by testing the activity of the strains in the biological fight against pathogens. This activity results in the determination of a zone of inhibition between the bacteria and the fungal strain [12]. Germination of Arabidopsis or cultivated plants allows these promising bacteria to accelerate the emergence and early growth of plants, under controlled environmental conditions. Experimentation with germination and early growth of plants should be carried out under optimal and stressful conditions. The results can be validated in planta, under controlled conditions and possibly under field conditions. It is clear that some

strains will be overlooked with this approach. In addition, there might be strains that do not show promising results in the early stages (e.g., do not affect germination) but that would improve subsequent growth [128,129]. At this stage, the strains are identified by a molecular approach and their metabolites are characterized and identified.

The combination of bioremediation and the promotion of plant growth would be a beneficial approach to solve this global agricultural problem. The most promising and demanding PGPB in the field, will be the most efficient for commercialization after bioformulation. In the case of consortia, the strains must be managed so that they are in constant proportions in the final product. Combining strains around or at the end of their growth cycles can give the most reliable results. However, consortia, due to interactions between strains, may very well offer advantages over single-strain inoculum.

Stacking of several desirable traits in a single agent could, therefore, be generalized for the selection of putative candidates and the application of these selected agents in plant experiments. This pyramid strategy could be used successfully in future studies to mitigate the effects of various biotic and abiotic stresses on plant growth and productivity. It is anticipated that this strategy will provide a new generation of PGPBs targeting highly resistant to biotic and abiotic stress plants that thrive in hostile environments.

Bacteria with multiple benefits can be beneficial in commercial agriculture and are relevant to the bioeconomy. Many economically important plants require amendments for optimal growth and yield as well as protection against pathogenic organisms [130]. Bioformulations of these PGPBs for promoting plant growth, soil fertility and suppressing plant pathogens offer green alternatives to conventional agrochemicals [131] and can be extremely effective in alleviating the effects of abiotic stress on a wide variety of crop plants [124]. Assessment of possible combinations of strains and/or signals, product delivery formulation, registration, and regulatory approval will lead to product availability on the market.

6. Conclusions and Perspectives

The problems of desertification, the degradation of agricultural areas, and the loss of soil fertility are an obstacle that affects most Mediterranean countries. The development of suitable bio-fertilizers, based on bacterial strains isolated from the most arid areas and resistant crops, could therefore have the potential to increase crop yields and resistance to various stresses. They will have a positive influence on crop productivity and the sustainability of agriculture. Their successful implementation in the agricultural system has become a necessity. The research and development of effective PGPRs will become a reality in their use and a fundamental process leading towards an ideal agricultural system that maintains, and improves human health, benefits the environment, and produces sufficient food for the growing world population.

However, despite extensive research already carried out in this area, there is a lack of knowledge on some important aspects. Interactions between plants and microorganisms are still limited. In addition, the mechanisms for promoting growth in the presence of PGPBs under salinity stress should be described in more detail down to the gene level. The development of efficient inocula with a high colonization rate in the rhizosphere is a major challenge. The adaptation of the bacteria selected according to the type of soil in the application area is also to be considered. PGPBs must be present on the roots in sufficient numbers to have a beneficial effect and be able to compete for nutrients in the rhizosphere. In addition to the intrinsic growth rate, the other properties enhancing the colonizing potential of a strain are of prime importance (mobility, chemotaxis, and the usability of compounds excreted by the roots as sources of carbon and nitrogen). To make this approach practical, it is necessary to select or develop strains that can be applied in low numbers but multiply rapidly following their release into the environment. In addition, efficient colonization requires the development of inocula containing microbes with long survival under field conditions, due to competition with resident soil micro- and macro-fauna. The formulation of biofertilizers and the application in the field will verify

the reliability of the proposed protocol, its proper functioning and the monitoring of its stability. The viability and shelf life of the bacteria will be assessed after bioencapsulation, as well as the survival rate is checked after inoculation. Future research should focus on the evaluation and valuation of PGP bacteria in the field. The passage to the stage on the ground requires the participation and the assistance of agronomic institutes which guarantee the diffusion and the distribution of the products. There is a need to sensitize farmers on the potential benefits that could be obtained by using these PGPBs and on these cost-effective approaches based on the use of biofertilizers versus the use of chemical fertilizers. On the other hand, although a number of rhizobacteria capable of tolerating extreme climates have been identified, their potential synergistic effects on plants or their antagonistic effects on pests and soil diseases should be considered. The combined use of PGPBs from the rhizosphere and endophytic microbiomes can have a synergistic effect to alleviate stress and to sustainably improve agricultural productivity in dry, saline, or polluted environments for an extended period of time and under real natural conditions. PGPBs have also been proven to be excellent model systems in the field of biotechnology that can provide new genetic constituents and bioactive chemicals with various uses in agriculture and environmental sustainability.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/su13084422/s1, Table S1. Bacterial species with different strategies to overcome on stresses.

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