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Review

Sustainable Strategy to Boost Legumes Growth under Salinity and Drought Stress in Semi-Arid and Arid Regions

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Abstract: The escalating risks of drought and salinization due to climate change and anthropogenic activities are a major global concern. Rhizobium–legume (herb or tree) symbiosis is proposed as an ideal solution for improving soil fertility and rehabilitating arid lands, representing a crucial direction for future research. Consequently, several studies have focused on enhancing legume tolerance to drought and salinity stresses using various techniques, including molecular-based approaches. These methods, however, are costly, time-consuming, and cause some environmental issues. The multiplicity of beneficial effects of soil microorganisms, particularly plant growth-promoting bacteria (PGPB) or plant-associated microbiomes, can play a crucial role in enhancing legume performance and productivity under harsh environmental conditions in arid zones. PGPB can act directly or indirectly through advanced mechanisms to increase plant water uptake, reduce ion toxicity, and induce plant resilience to osmotic and oxidative stress. For example, rhizobia in symbiosis with legumes can enhance legume growth not only by fixing nitrogen but also by solubilizing phosphates and producing phytohormones, among other mechanisms. This underscores the need to further strengthen research and its application in modern agriculture. In this review, we provide a comprehensive description of the challenges faced by nitrogen-fixing leguminous plants in arid and semi-arid environments, particularly drought and salinity. We highlight the potential benefits of legume–rhizobium symbiosis combined with other PGPB to establish more sustainable agricultural practices in these regions using legume–rhizobium–PGPB partnerships.

Keywords: sustainability; legumes; arid regions; abiotic stress; root exudates; symbiosis; PGP traits; quorum sensing

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1. Introduction

Arid and semi-arid land areas today occupy nearly 46.2% of the Earth's surface, hosting 3 billion inhabitants [1]. Such extended regions are becoming more widespread because of global warming and are mainly centered in the Middle East, North America, Africa, Oceania, and Asia, where the agricultural system heavily relies on crop production as the primary food resource [2]. However, these areas are subjected to a variety of abiotic constraints, including drought, salt, and extreme temperatures, which significantly impact plant growth, development, and productivity [3]. This stress results from climate change and environmental deterioration caused by human activities [4], affecting crop yields and soil fertility globally.

Drought stress, caused by prolonged precipitation deficits and high temperatures, leads to decreased soil moisture and degradation, affecting plant growth [5]. This results in poorly structured, infertile soil with increased water evaporation and mineral accumulation, especially salt ions [6]. Soil salinization, a major threat to plants and microorganisms, occurs when soil electrical conductivity exceeds 4 dS m^{-1} and NaCl concentration is over 40 mM [7]. This stress can be exacerbated by lack of precipitation, use of chemical fertilizers, irrigation with saline water, and deposition of ocean salt through wind or rain [8]. These stresses degrade soil, reduce agricultural yield, and harm plant growth by causing osmotic and oxidative stress, decreased photosynthesis, and altered soil microbial communities [9,10].

Various approaches have been developed to mitigate drought and salinity impacts on agriculture in arid regions. Rainwater harvesting, micro-irrigation systems, and soil moisture conservation techniques improve water availability [11–13]. Mineral fertilizers and soil amendments enhance soil fertility and crop yields [14]. Despite a few successful attempts, these methods can be costly, time-consuming, and environmentally harmful [15–17]. Similarly, biological techniques, like genetically modified plants, raise concerns about genetic conservation [18]. In addition to plant genomes, the genomes of associated microorganisms serve as a secondary plant genome that can be manipulated to benefit the plant host.

Plants are associated with a diverse community of microorganisms called the “plant microbiota” [19], which includes bacteria, fungi, archaea, and protists [20]. These microorganisms interact with plants in various ways (parasitism, commensalism, or mutualism) and inhabit different plant compartments such as leaves, stems, roots, and the rhizosphere [21,22], significantly influencing plant growth and development [23]. Most plant microbiota originate from the soil [24], with additional sources being air, water, seeds, animals, and insects [25,26]. Microbial communities in the plant microbiome are influenced by soil properties, plant genotype, and environmental stressors like drought and salinity [3,27,28], which significantly impact microbial diversity and function [29–31]. For instance, plant microbiota significantly contributes to plant fitness by enhancing genomic and metabolic capabilities and providing supportive activities, metabolites, and defense mechanisms.

Among these complex microbial communities, plant growth-promoting bacteria (PGPB) stand out due to their ability to improve plant resilience through nitrogen fixation, mineral solubilization, phytohormone secretion, and enhanced stress tolerance [32]. These bacteria are promising candidates for improving plant resilience to abiotic stress in arid and semi-arid regions [19,20]. For instance, nitrogen-fixing symbioses are particularly important in arid regions for several reasons [33]: (i) these symbioses enhance soil fertility by increasing the nitrogen content, which is often limited in arid regions; (ii) nitrogen-fixing bacteria can improve the water-use efficiency of plants, helping them survive and thrive under water-limited conditions; (iii) these symbioses can help plants tolerate environmental stresses common in arid regions, such as high temperatures and salinity, thus increasing resilience and supporting plant survival and productivity; and (iv) nitrogen-fixing symbioses contribute to sustainable agricultural practices by reducing the need for synthetic fertilizers, which is crucial in fragile arid ecosystems where excessive use of chemical inputs can lead to soil degradation. Therefore, the use of efficient rhizobia in legume cultivation has been frequently recommended for areas lacking compatibility or with reduced rhizobia populations [34]. According to Yanni et al. [35], inoculation with native and tolerant rhizobia significantly increased common bean growth, yield, and resilience in saline/drought-stressed fields. Moreover, synergistic interactions between rhizobium and various microorganisms (other PGPB and arbuscular mycorrhizal fungi—AMF) have also been reported as an efficient strategy to promote legume cultivation in dry environments, including alfalfa, faba bean, and cowpea [36–38].

In recent years, special attention has been paid to increasing the cultivation of legumes and legume shrubs, whose persistence and survival depend on symbiotic interactions and PGPB to mitigate the effects of climate change [39,40]. The use of rhizobia and PGPB has been emphasized as a strategy to boost legume tolerance to salinity and drought in the current climate change scenario [34,40–43]. These microbial-based strategies are recognized as green technologies that are cost-effective and can be used as long-term solutions. Additionally, understanding these legume-bacteria interactions in arid and semi-arid regions can aid in the development of synthetic microbial communities to enhance plant resilience and productivity under these specific conditions [44–46]. Therefore, the aim of this review is to provide comprehensive information about the main effects of drought and salinity on nitrogen-fixing leguminous plants and to highlight the green strategies that help legumes cope with such conditions.

2. Legume–Rhizobium Symbiosis: Evolution, Mechanisms and Concerns

Legume–rhizobia symbiosis is vital for global food production and nitrogen cycles. Evolutionary data indicate that this partnership originated from a common ancestor within a single phylogenetic clade [47], approximately 92–110 million years ago [48,49]. This clade includes the four plant orders Fabales, Fagales, Cucurbitales, and Rosales (FaFaCuRo or collectively known as the nitrogen-fixing clade or NFC), of which 10 out of 28 families contain nitrogen-fixing, root nodule-forming species [50]. However, the common ancestor did not form root nodules; the earliest fossil evidence of a potential nodule dates back to 84 million years ago [51]. Recent studies suggest a 30-million-year period between the predisposition of plants to nodulation and the development of the first symbiotic interactions within the NFC [52]. According to the predisposition model, the common ancestor acquired a genetic change that conferred an evolutionary advantage, which persisted until multiple nodule organogenesis evolved [51–53]. During this genetic predisposition phase, the FaFaCuRo clade acquired several evolutionary traits such as the cortical infection threads, a common feature used by all nodulating plant species for bacterial uptake into their root cells [53,54]. In contrast, this symbiosis also comprises a diversity of nodular organ structures, externally actionable developmental programs [55], phylogenetically divergent endosymbiotic bacteria [54,56,57] and a variety of modes of infection [56].

Root nodulation is a symbiotic process wherein a plant host enables rhizobium bacteria to colonize its roots, forming specialized structures known as nodules. Within nodules, rhizobium fixes atmospheric nitrogen, converting it into ammonia, which makes it available to the plant, which, in return, supplies carbon produced through photosynthesis [58]. It is generally accepted that the nodulation process is regulated both spatially and temporally, consisting of four main stages: (1) infection of legume roots by rhizobia; (2) nodule development; (3) nodule function; and (4) nodule senescence [59]. In brief, legume–rhizobia symbiosis initiates with the exudation of flavonoids and isoflavonoids from the plant root. These act as chemo-attractants, drawing motile rhizobial bacteria towards the root hairs [60]. Upon perception of the specific flavonoid signal, rhizobia undergoes the synthesis and secretion of nodulation factors (Nod factors) [61]. These Nod factors act on the root hair epidermis, triggering root hair curling and the formation of an infection thread. The infection thread, a plant-derived structure, extends through the root cortex, ultimately reaching the newly formed nodule primordium [62]. The primordium arises from the division of recently emerged meristematic cells. Following the colonization of the nodule primordium by the rhizobia, these bacteria differentiate into bacteroids, specialized for nitrogen fixation [63]. The subsequent development and metabolic activity within the nodule are primarily under the control of the host plant [64], including the tightly regulated onset and progression of nodule senescence and the programmed breakdown of the symbiotic organ.

Despite the known benefits of this symbiosis, several challenges must be addressed to use rhizobia as commercial inoculants effectively. Firstly, the legume–rhizobia association is highly specific, with each rhizobial strain establishing a symbiosis with only a limited set of host plants and vice versa [65]. This specificity limits the use of highly efficient N_2-fixing rhizobial strains with different legume hosts. The best-known mechanism behind this symbiotic specificity involves the fine-tuned exchange of molecular signals between a host plant and its bacterial symbiont [66]. Aside from the Nod-factor signaling pathway [67], the host control of nodulation specificity remains poorly understood [68]. Secondly, among N_2-fixing rhizobial strains capable of nodulating the same host plant, there is significant variability in the efficiency of fixing atmospheric nitrogen [69,70]. Additionally, rhizobial competitiveness has important practical implications for agriculture. Therefore, elite rhizobial inoculants must be highly effective in providing fixed nitrogen to the plant (N_2-effectiveness) while also being highly competitive in occupying nodules (competitiveness). This is crucial in an environment where native rhizobia may exhibit high competitiveness combined with low N_2-effectiveness [69–71]. Thirdly, whether native to the site or introduced through inoculation, rhizobia must be able to survive in the soil until they infect the roots of a plant. Generally, these microorganisms survive well in soil, but their numbers can be reduced by environmental stresses, such as acidity, drought, high temperatures, or salinity [72]. Therefore, the development of effective strains to develop effective rhizobial inoculants must always take into consideration the importance of stress tolerance [73]. Selecting effective rhizobial strains can be challenging and, at times, quite time-consuming. We anticipate that next-generation agriculture will significantly benefit from the creation of rhizobial bioinoculants derived from elite strains that offer both effectiveness and competitiveness in field conditions, as suggested by [69]. In the long run, these advancements will help address the competition issue by enabling the cost-efficient design and production of site-specific inoculants.

3. The Effect of Drought and Salinity on Legume Growth and Their Symbiotic Interactions

Cultivated legumes, particularly cold-season species (e.g., pea, chickpea, lentil, and faba bean), are a staple of the human diet owing to the beneficial compounds and protein content of their grains [74]. Plants in the Fabaceae family are severely impacted by all types of abiotic stress caused by climate change factors, particularly drought and salinity. This unfavorable influence on the growth and production of these legumes has been widely reported around the world [75,76].

Drought, for example, causes several physiological and metabolic changes in plants [77], with the first developed reaction from a leguminous vegetative system to water scarcity being a reduction in photosynthetic activity, resulting in a decrease in chlorophyll content. In addition, water loss in the guard cells causes stomatal closure, which disrupts the transpiration and gas exchange mechanisms [78]. A study conducted by Mansour et al. [79] on the physiological responses of faba bean genotypes to drought revealed a significant reduction in chlorophyll a and chlorophyll b, as well as transpiration rate, by 21%, 50% and 47%, respectively. Moreover, long-term drought stress causes an overproduction of reactive oxygen species (ROS), creating an imbalance between ROS and their detoxification enzymes. This oxidative stress is responsible for protein denaturation, a decrease in the stability and integrity of the cell membrane and DNA, which can lead to cell death [80]. Moreover, it reduces plant growth by obstructing cell division and elongation, which has a considerable effect on crop maturity [81]. Finally, drought-stressed conditions during the reproductive stage can lower crop pollen fertility, which results in delayed pod formation and a substantial decrease in crop yield and seed quality [82]. Nevertheless, the severity of drought on plant growth parameters remains dependent on several factors, including the plant's vegetative stage, the seasonal period, and the duration of soil water scarcity [83] (Figure 1). Likewise, soil salinization poses a real threat to legume development in drylands [3].

Plants growing under salinity suffer from both osmotic stress and ionic toxicity [4]. Roots are the first organs exposed to high Na^+ and Cl^- ion content, leading to significant physiological alterations in cell function [84]. The accumulation of salts in the rhizosphere creates an osmotic pressure, which affects nutrient uptake and protein transport via root cells to the rest of the plant's organs [85]. In addition, intracellular salt accumulation in plant tissues impairs cell integrity and membrane stability, resulting in cell dehydration, dysfunction, and death [3]. Long-term salt stress causes ion toxicity and metabolic disruption [58] (Figure 1). Plants exposed to salinity, like other types of abiotic stress, are susceptible to oxidative stress, which can potentially alter protein function and nucleic acid integrity [86].

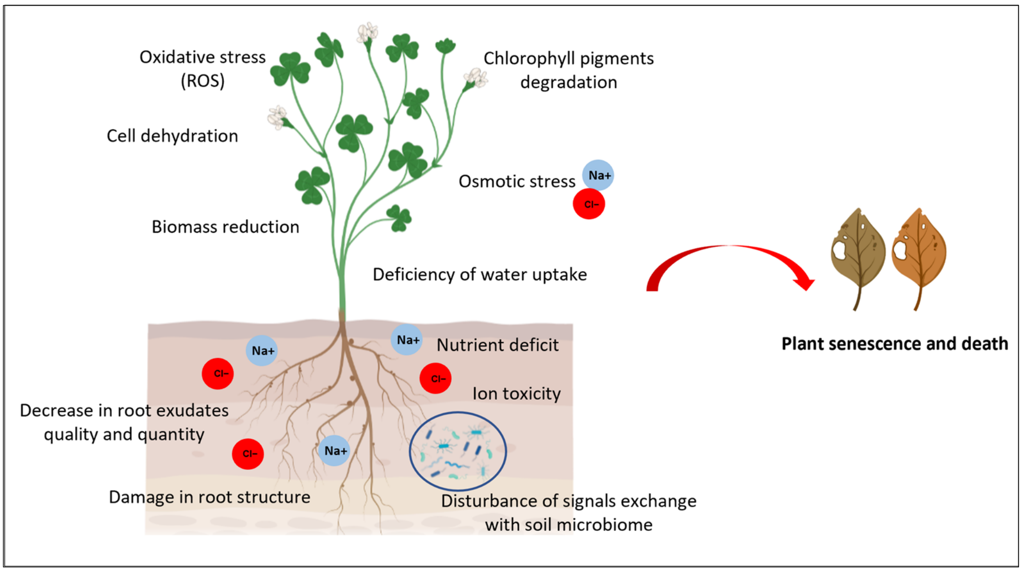

Figure 1. Effects of drought and salinity on legume growth and physiology.

Salinity and drought directly impact soil microbial populations. Water availability in soil is a critical factor influencing bacterial and fungal survival and diversity in arid and semi-arid environments. As a result, a decrease in moisture and water availability in dry soils can cause particle aggregation and the accumulation of insoluble components, such as soil organic carbon (SOC), leading to a decline in microbial abundance [87]. In fact, several studies have reported the influence of drought and salinity stresses on the structure of microbial species present in the rhizosphere soil of legumes. Although the experimental setups in the reviewed studies varied considerably, making direct comparisons challenging, some commonalities can nevertheless be identified. A summary of the most relevant bacterial taxa, associated with different legume species under stress, is presented in Table 1. For instance, analysis of the diversity of bacterial microbes in the rhizocompartment of three desert leguminous plants grown under drought conditions showed similarities at the order level, where different members of the Rhizobiales, Xanthomonadales, Burkholderiales, Sphingomonadales, Solirubrobacterales, and Nitrosomonadales orders have been detected in the rhizosphere soil of all three studied plants but with different relative abundance percentages [88]. These findings suggest that, in arid regions, drought stress exhibits a selective pressure on the structure of soil microbial communities, favoring the emergence of specific bacterial groups that can dominate the rhizosphere of various plant species. In addition, a study examining the influence of drought on peanut (*Arachis hypogaea*) rhizosphere revealed a shift in the abundance of the bacterial community, favoring the dominance of Actinobacteria, Cyanobacteria and Planctomycetes while decreasing the number of Proteobacteria [89]. Similar results have been recently reported by Peng et al. [90], where the application of drought stress on peanut, in mono- or intercropping cultures, altered both the stability and the composition of the rhizosphere microbiome. In another study, the impact of drought on rhizosphere diversity was more pronounced in alfalfa (*Medicago sativa*) than in red clover plants (*Trifolium pratense*), which demonstrated enriched taxa in the rhizosphere, particularly under severe drought treatment (20% field capacity) [91]. This variability in microbial diversity was attributed to the possible differences in the composition of root exudates between the two plant species, resulting in a variety of plant–microbe interactions. Given that water is an ideal transport medium for microbial solutes, a negative water potential can also alter microbial transport pathways and disrupt the hydrological connection between microbial cells and their external environment [92]. Salinization also impacts soil microbial activity through osmotic stress and ion toxicity. In fact, several studies have revealed that salinity induces plant-mediated selection of rhizosphere microbiome, during which plants intend to recruit beneficial bacteria to increase their tolerance to salt stress [93–95]. Among these microbes, members of the phyla Proteobacteria, Actinobacteriota, Chloroflexi, and Planctomycetes were reported as the most abundant taxa in the rhizosphere of legumes exposed to salinity (Table 1). Moreover, increased osmotic potential in the rhizosphere causes cell dehydration and plasmolysis. Additionally, high concentrations of salt ions can strongly inhibit the function of various microbial enzymes such as alkaline phosphatase, β-glucosidase, and urease [96]. In fact, osmotic plasmolysis can cause microbial cells to release intracellular enzymes, which then become susceptible to degradation by soil proteases. In addition, the increase in soil electrical conductivity may alter the ionic conformation of the enzyme's active site, reducing its functionality [97]. Despite the huge impact of abiotic stresses (drought and salinity) on natural ecosystems, only a few research studies have explored their potential effect on the diversity of the rhizosphere microbiome associated with food legumes. However, those inhabiting the rhizosphere soil of wild Fabaceae are currently unexploited, particularly in arid and semi-arid regions.

Table 1. Effect of drought and salinity on the diversity of rhizosphere microbiome in legumes.

Plant Host	Microbial Taxa	Type of Stress	Soil Type	Study
Caragana microphylla *Hedysarum mongolicum* *Hedysarum scoparium*	Rhizobiales, Xanthomonadales, Burkholderiales, Sphingomonadales, Solirubrobacterales, and Nitrosomonadales	Drought (Ningxia Province, northwest China, natural dry area)	Rhizosphere soil	[88]
Arachis hypogaea	Actinobacteriota, Planctomycetes, and Cyanobacteria	45% FC (drought stress) and 85% FC (control)	Rhizosphere soil	[89]
Arachis hypogaea	Actinobacteriota, Proteobacteria, Chloroflexi, Acidobacteriota, and Firmicutes	Short-term drought treatment	Rhizosphere soil	[90]
Medicago sativa *Trifolium pratense*	Actinobacteriota, Proteobacteria, Firmicutes, Acidobacteriota, and Gemmatimonadetes	20% FC (severe drought), 40% FC (moderate drought), and 80% FC (control) for three weeks	Rhizosphere soil	[91]
Glycine max	Acidobacteria, Bacteroidetes, Gemmatimonadetes, and Verrucomicrobia	Drought (plants were watered once per 6–10 days)	Rhizosphere soil	[98]
Albizzia julibrissin	Chloroflexi, Acidobacteria, Gemmatimonadetes, Proteobacteria, and Bacteroidetes	Salinity (natural saline field; salt content 4.1 ± 3.2 g kg^{-1})	Rhizosphere soil	[99]
Glycine max	Actinobacteria, Proteobacteria, Firmicutes, and Gemmatimonadetes	Salinity (natural saline soil)	Rhizosphere soil	[100]

Table 1. *Cont.*

Plant Host	Microbial Taxa	Type of Stress	Soil Type	Study
Glycine soja (Wild soybean) *Sesbania cannabina*	Proteobacteria, Actinobacteriota, Chloroflexi, Acidobacteriota, Firmicutes, Gemmatimonadota and Crenarchaeota (archaea)	Salinity (natural saline soil; EC above 1500 µs cm^{-1})	Rhizosphere soil	[94]
Vigna radiata	Proteobacteria, Planctomycetes, Actinobacteria and Firmicutes	Salinity (150 to 180 mM NaCl)	Rhizosphere soil	[93]
Glycine soja (Wild soybean)	Proteobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Acidobacteriota, Gemmatimonadetes, Planctomycetes, and Firmicutes	Salinity (natural saline soil; EC of 565 ± 33 µS/cm)	Rhizosphere soil	[95]

FC: field capacity; **EC**: electrical conductivity.

To survive under harsh conditions, legumes and their associated microbes have evolved a set of physiological and biochemical interactions primarily controlled by rhizodeposition and highly reliant on the plant's health state [101]. Legumes, for example, recruit a wide range of beneficial microbes, notably rhizobia and arbuscular mycorrhizal fungi (AMF). These microorganisms possess various features that promote plant growth and exhibit strong adaptability to severe environments [102]. Rhizobia improve soil nutrient availability by fixing atmospheric nitrogen in root nodules, while AMF enhances root surface area and development, potentially increasing water absorption in drought-stressed plants [103]. However, maintaining these relationships can be challenging due to the effects of drought and salinity on root structure and exudate profiles [104,105]. Under optimal growth conditions, these exudates contain mainly carbohydrates (e.g., xylose, sucrose and raffinose) [106], amino acids (AAs) (e.g., glycine, arginine, and lysine) [106], and flavonoids (e.g., luteolin, methoxychalcone, apigenin, naringenin, and genistein) [107–109]. However, stress can induce various changes in the composition of root exudates, including the nature of the carbon source and amino acids released into the rhizosphere, altering the signaling exchange between microbial communities and host plants. Some of the compounds secreted by legume plants in response to drought or salinity are mentioned in Table 2. For instance, a study conducted by Canarini et al. [110] showed that, under water deficit, soybean plants did not change their exudation rates, however, the metabolic composition was changed favoring the secretion of the two osmolytes proline and pinitol, which confer an osmoprotection for plant roots. Similarly, Bobille et al. [111] examined the relation between water deficit and the exudation of AAs in pea plants (*Pisum sativum*). Results showed that the quantity of AAs, particularly proline, alanine, glutamate, and homoserine, increased in response to water stress, suggesting that these AAs may represent the key signaling molecules secreted by *P. sativum* under drought stress. Furthermore, the presence of 50 mM NaCl significantly reduced the quality and quantity of isoflavonoids in root exudates of *Glycine max* plants [112]. This alteration was reflected through the absence of daidzein and genistein compared to the control conditions. Moreover, comparative analysis of the phenolic composition of root exudates extracted from two grain legumes—*P. sativum* and *Cicer arietinum*—as previously described by Ben Gaied et al. [34,43], have revealed notable changes in root metabolism of both plant species, following exposure to abiotic stress (salinity and heat stress) (Figure 2). Results showed that the phenolic compounds in root exudates collected under salinity or heat stress were present in significantly lower quantities compared to the control. Nevertheless, the exposure of *P. sativum* to salt stress resulted in the secretion of a new metabolite, acacetin, compared to the control. Similarly, the secretion of quercetin by *C. arietinum* was only observed under heat stress, which demonstrates the specificity of root metabolic responses regarding plant species and the type of stress.

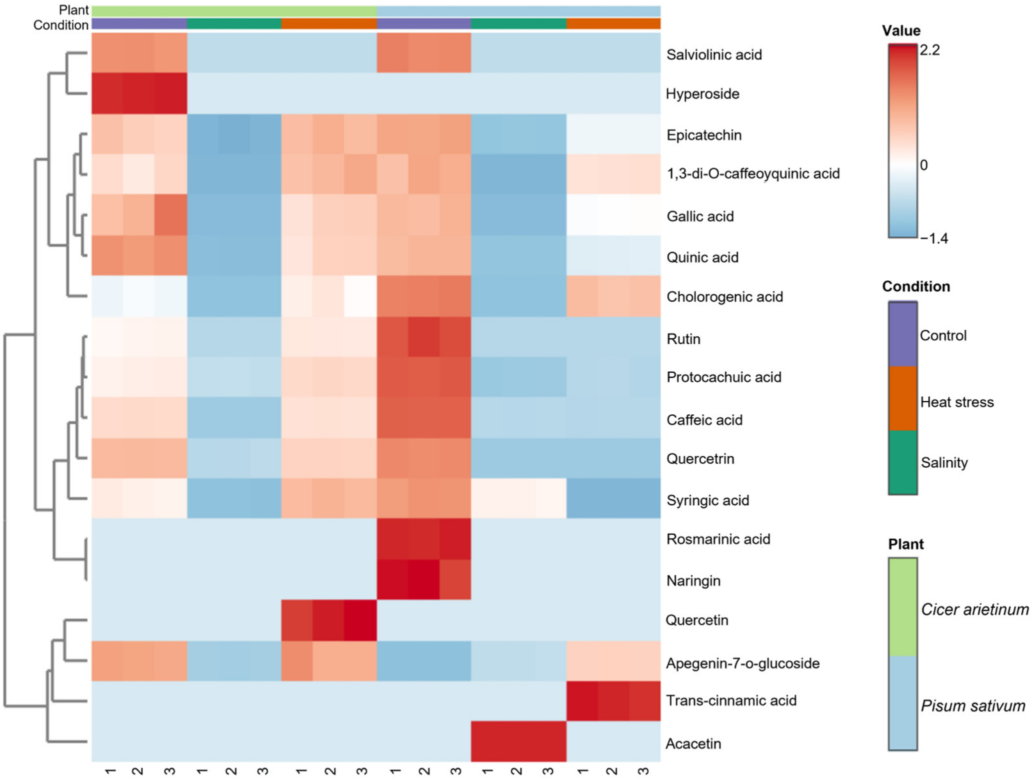

Figure 2. The distribution of phenolic compounds in *Pisum sativum* and *Cicer arietinum* root exudates collected under control, salinity, and heat stress conditions. Data from [34,43]. Numbers 1, 2 and 3 indicate the number of biological replicates under each condition. The color scale ranges from a light blue color, corresponding to the absence or the presence of a very low quantity of the phenolic compound, to a red color, corresponding to a higher quantity of phenolic compound.

Table 2. Type of root exudate compounds released by different legume species under salinity and drought stresses.

Plant Species	Type of Stress	Identified Compound (s)	Reference
Pisum sativum var. Avola	Drought Salinity	Proline	[113]
Glycine max	Drought	Proline and pinitol	[110]
Arachis hypogaea	Drought	Apigenin, Genistein, Luteolin, Naringenin, Naringin, Rutin, IAA, and Tryptophane	[114]
Pisum sativum	Drought	Amino acids (proline, alanine, glutamate, and homoserine)	[111]
Glycine max	Salinity	7,4-Dihydroxyflavone, Apigenin, Quercetin, Naringenin, Isoliquiritigenin (4, 2′, 4′-trihydroxychalcone), and Umbelliferone	[112]

Table 2. *Cont.*

Plant Species	Type of Stress	Identified Compound (s)	Reference
Phaseolus vulgaris	Salinity	7,4-Dihydroxyflavone, Quercetin, Naringenin, Hesperetin, Isoliquiritigenin, Umbelliferone	[115]
Cicer arietinum	Salinity	Quinic acid, Gallic acid, Cafeic acid, Syringic acid, Epicatechin, Quercitrin, and Apegenin-7-o-glucoside	[43]

On the other hand, the alteration in the root exudate profile, under the effect of stress, can impact the specificity and efficacy of plant–microbe interactions, in particular, the early stages of molecular signaling in legume-rhizobium symbiosis and nodule function. In fact, the exposure to salinity reduced the capacity of *G. max* root exudates to induce *nod* gene expression and the formation of Nod factors by the microsymbiont *Sinorhizobium fredii* SMH12 [112]. Similarly, Ben Gaied et al. [43] have reported a significant decrease in the level of expression of *nodD* gene in *Mesorhizobium ciceri* when exposed to root exudates of *C. arietinum* collected under salt stress. Additionally, several studies have demonstrated that when legumes are cultivated under saline conditions, the quantity and weight of root nodules decrease dramatically. L'taief et al. [116] observed a marked decrease of 43% in root biomass and complete prevention of nodule formation in chickpea plants under 25 mM of NaCl. Moreover, the decrease in nodule permeability associated with drought or salt application can lead to the inhibition of nitrogenase activity and nodule respiration. These effects were reported in soybean plants growing in 0.1 M of NaCl, where both nodule respiration and acetylene-reducing activity (ARA) were massively inhibited [117]. Similarly, Babber et al. [118] reported up to 78% decline in ARA in chickpea plants subjected to a mixture of salt ions, along with an acceleration of nodule senescence due to salt proteolysis impact on leghemoglobin molecules. At mild salt concentrations, the leghemoglobin content decreased by 57% after 55 days of sowing and fell to negligible levels by day 85. Additionally, structural degradations of the symbiosome were seen in plants under salinization, mainly marked by a reduction in the size of nodules and a decrease in the meristematic zone [118]. Aside from salt stress, legume–rhizobium symbiosis is highly sensitive to drought stress. After 45 days of growth under water deficit, two leguminous species—*Sesbania aculeata* and *Phaseolus vulgaris*—exhibited a significant decrease in individual fresh and dry nodule weight. Reductions in nodule number, size, and diameter have also been recorded [119]. In conclusion, these findings highlight the need to characterize and select more tolerant microbial candidates capable of surviving under harsh environmental conditions as well as improving plant resilience to drought and salt stress in arid and semi-arid regions.

4. The PGPB: Effective Candidates to Improve the Agricultural System in Drylands

It has been hypothesized that plants growing in harsh environments harbor a naturally adapted microbiome that can provide protection against stressful conditions. Interestingly, several surveys have shown that the soils of extreme ecosystems, typically inhospitable and arid regions that are geographically distant, have identical bacterial communities. High-throughput sequencing analysis revealed that these communities are mostly dominated by Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes, with certain variations in the abundance of each phylum [120,121]. This similarity in the diversity profile between bacterial communities can be attributed to the harsh environmental conditions that are common to all these areas.

Microorganisms from dry soils have developed several mechanisms to tolerate the harsh conditions to which they are subjected. For example, all bacterial isolates from the Thar Desert of Western Rajasthan (India) were found to be able to grow at high temperatures (up to 50 °C), suggesting their ability to tolerate osmotrophic solutes [122]. In a study of bacterial taxonomy associated with the rhizosphere of three halophytes growing in a salt-affected soil in Wujiaqu (China), Gao et al. [123] reported the dominance of halotolerant species along with some beneficial bacterial taxa such as *Halobacillus*, *Rhizobium*, *Klebsiella*, *Actinoplanes* and others. In addition, the phenotypic characterization of bacteria isolated from the native legume *Psoralea corylifolia* L. rhizosphere, growing in a salt-contaminated area of India, showed a high salt-resistance capacity of these isolates [124]. This capacity was attributed to the natural exposure of this bacterial community to high salt concentrations in that semi-arid region.

It is known that the rhizosphere microbiota is dynamic and can adapt to meet plant needs. For instance, the rhizospheric bacterial community associated with *Arabidopsis* changed over time, suggesting that plants can select a subset of microbes for specific functions [28]. Similarly, differences in the bacterial community structures in the rhizosphere of native plants grown in Chilean extreme environments may have resulted from the plants' selection of specific bacterial groups with multiple plant growth-promoting traits (PGP) in order to sustain their growth and tolerance to local conditions [125]. Although these studies support the notion that plant species have a specific effect on the diversity and structure of plant microbiomes, there is still a lack of knowledge regarding the various physiological and metabolic mechanisms adopted by the plants to define their own microbiota, particularly under stress conditions.

Apart from their ability to survive under extreme environmental conditions, arid-soil isolates possess common PGP traits similar to non-arid-soil microbiomes, which directly and/or indirectly improve plant growth (Figure 3). The in vitro screening of rhizobacteria associated with 11 wild plant species from the arid soil in Saudi Arabia revealed different PGP capacities [126]. Of the 66 selected isolates, 92.3% were able to fix nitrogen, among which 60.9% had the ability to produce indole-3-acetic acid (IAA) and solubilize minerals. Along with PGP traits, these isolates exhibited antagonist potential against phytopathogenic fungi, such as *Fusarium oxysporum* and *Sclerotinia sclerotiorum* [126]. In another study, functional characterization of three rhizobacterial isolates from the Cholistan Desert, a hot hyper-arid sandy desert, showed multi-stress tolerance capacities (tolerance to 20% PEG-induced drought and to temperature up to 37 °C). These stress-tolerant bacteria shared various PGP traits such as IAA production, solubilization of different minerals, ACC-deaminase activity, and nitrogen fixation ability [127]. When inoculated into wheat plants, growing under drought, these strains improved plant tolerance to stress and significantly enhanced antioxidant enzyme activity in plant tissues, thus protecting the plant against the damage caused by oxidative stress. Similarly, the phenotypic characterization of rhizobacteria, isolated from degraded soil of the north Shewa Zone in Ethiopia, showed that while all strains were able to grow at high temperatures (45 °C) and pH (pH = 10), only 10 isolates tolerate increased concentrations of PEG (40%) [128]. Inoculated into *Acacia* plants, these strains improved plant biomass significantly. Additionally, bacterial isolates associated with *Prosopis cineraria*, a native species of the saline desert of the United Arab Emirates, showed different PGP capabilities such as phosphate solubilization, nitrogen fixation, and antibacterial activity [129]. However, these conclusions were based on data from high-throughput sequencing using short 16S amplicons (of only 227 nucleotide length), which limits the ability to detect significant fine differences in bacterial species between the studied areas. Additionally, slight differences in sampling depth or geographical coverage can introduce biases on real microbial diversity. Therefore, future studies should address these methodological challenges to better understand the microbial communities of extreme environments.

Considering the PGP potential, different microbial techniques have been developed for the application of native PGPB and non-arid-soil isolates as bioinoculants to successfully improve legume growth and yield in arid and semi-arid regions. Despite the difference in dryland soil quality, native PGP microbial communities remain the most stable and well-adapted microorganisms to extreme abiotic conditions. Therefore, single-inoculated or co-inoculated native PGPB represents an interesting candidate for greenhouse and field trials [130]. Adopting complex adaptation mechanisms, these PGPB can confer plant resistance to drought and salinity stresses.

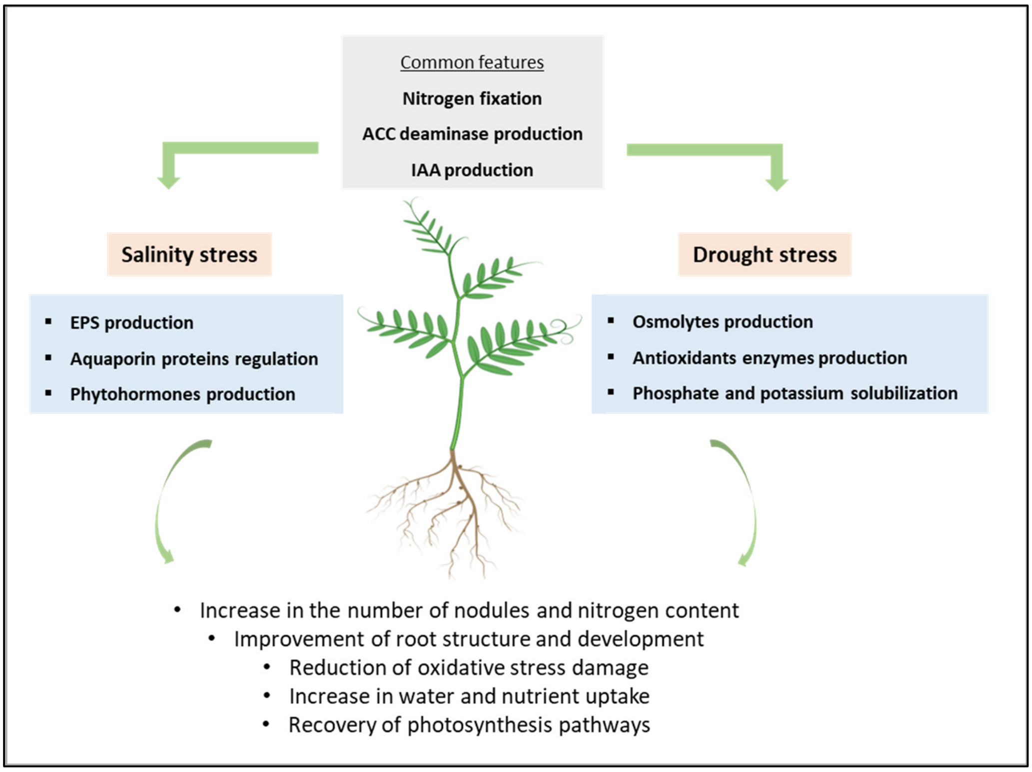

Figure 3. Plant growth-promoting bacterial (PGP) features for salinity and drought stress mitigation.

5. Rhizobia Application in Legume Cultures under Arid Environments

Nitrogen is one of the most essential elements for plant development and production. It is mostly present in a non-assimilable form in the soil, thus highlighting the role of diazotrophic bacteria in fixing the atmospheric nitrogen in the soil later absorbed by plants in ammonia form [131]. Rhizobia, which is Gram-negative soil bacteria able to fix atmospheric nitrogen when associated with leguminous plants, are classified among the best candidates to maintain N supply to compatible leguminous species cultivated in arid regions. Under stress conditions, the ability of rhizobia to survive the detrimental effects of desiccation and osmotic stress allows the establishment of an effective legume–rhizobium symbiosis.

5.1. Drought Stress

Drought stress events have a major impact on soil quality in drylands. Soil becomes poor, infertile, prone to disaggregation, and deficient in major minerals, particularly nitrogen (N), in areas with low water potential. Therefore, biological nitrogen fixation (BNF) remains the most efficient mechanism to increase N input. Plants evolved various interactions with nitrogen-fixing organisms to ensure their survival in arid regions. In this context, much interest has been focused on rhizobium–legume symbiosis as a renewable source of N in arid natural ecosystems [132]. Although drought stress affects bacterial growth and performance, studies have shown that drought-tolerant rhizobia have evolved to survive in low soil moisture environments [133]. These bacterial populations have undergone different genetic and morphologic changes in response to stress. For example, rhizobia isolated from lentil plants and belonging to the *R. leguminosarum* species showed the greatest tolerance to dry conditions with a growth rate of 10^7 cells per g of soil [134]. In a study conducted by Shoushtari and Pepper [135], the desert *Rhizobium* isolate (AZ-M1) exhibited a higher capacity for nodule occupancy compared to a commercial strain. The same Saharan isolate was able to survive in three desert soils for 1 month, while the commercial strain could not persist longer than 14 days. Inoculating legumes with drought-tolerant rhizobia can therefore help alleviate N limitation and enhance crop productivity in arid and semi-arid regions.

In this context, several studies have focused on the isolation, characterization, and application of drought-tolerant rhizobial species in order to increase legume growth and productivity in areas with low water potentials. To increase bean (*Phaseolus vulgaris* L.) and soybean (*Glycine max* L.) yields in south Ethiopia, Aserse et al. [136] studied the capacity of selected drought-tolerant and effective rhizobial strains to stimulate plant growth and increase field yields in low soil fertility during two drought-affected years. A consortium of *Rhizobium* strains (*R. etli* and two strains *R. phaseoli*) was used to inoculate bean plants, whereas soybean was inoculated with a consortium of three Bradyrhizobia (*B. japonicum* and two *B. elkanii* strains). Both consortia showed a high symbiotic efficiency in a greenhouse experiment and field trials by increasing the number of nodules, plant shoot dry weight and N content compared to non-inoculated plants and equaling the effect of N-fertilizer treatment [136]. Similarly, the inoculation of chickpea plants with *Bradyrhizobium japonicum* strains improved both symbiotic N fixation and plant physiological adaptation to drought stress [137]. Additionally, several studies showed a direct interference of biological nitrogen fixation (BNF) in plant photosynthesis. BNF regulates not only the photosynthetic rate but also increases the efficiency of plant transpiration and chlorophyll content in plants under drought [138,139]. For instance, Cerezini et al. [140] reported the capacity of *B. elkanii* strain SEMIA 5019 to stimulate the photosynthetic rates of soybean plants subjected to drought stress. Thus, delaying the degradation of leaf chlorophyll and decreasing the plant senescence rates.

Besides N-fixation, rhizobia have additional PGP traits that might help improve legume growth under drought. Phosphorus (P), the second most limiting element for crop development, is physiologically inaccessible in drylands where soil fertility is frequently reduced due to soil erosion, water scarcity, and high temperatures. To overcome this issue, many studies have focused on identifying rhizobial species with P solubilization capacities and using them as biofertilizers [141]. In this context, a collection of rhizobia was obtained from root nodules of chickpea plants, cultivated across different bioclimatic zones in Tunisia, including semi-arid, arid, and Saharan. Among these isolates, *Mesorhizobium ciceri* (LL10) isolate showed a superior phosphorus solubilization ability and was therefore selected for plant inoculation. A field experiment conducted in a semi-arid region demonstrated that this selected isolate significantly enhanced nodule formation, as well as increased the pod number and shoot dry weight by 400%, 200% and 200%, respectively compared to nitrogen-fertilized seedlings [142].

In addition, certain rhizobia contribute to plant growth by producing osmolyte compounds in response to low water potential. Initially recognized as a defense mechanism employed by plants to regulate the osmotic potential during drought stress [143], recent findings have revealed that soil bacteria utilize a similar pathway. They produce amino acid osmolytes, such as glutamine, taurine, and proline, to reduce their intercellular osmotic potential, thereby preventing cells from oxidative stress-induced damage [144–146]. The accumulation of proline is a consequence of rhizobia's osmo-adaptation, where proline acts as a radical scavenger and antioxidant regulator, as previously demonstrated in other studies [147]. In a recent study by Amine-khodja et al. [148], the capacity of *Rhizobium* within nodules to regulate proline concentrations in the other parts of the plant, such as the leaves and roots, was highlighted as a feature to improve the plant's response to water limitations. In their experiment, the effects of inoculation with *R. leguminosarum* strain OL13, isolated from the nodules of *Lens culinaris* growing in a semi-arid Algerian region, were tested on *Vicia faba* plant drought adaptability. One remarkable finding of this study was the significant increase in proline level in plants inoculated with OL13 strain, with enhancements of 391%, 390% and 630% in leaves, roots, and nodules, respectively. In another study, the inoculation of chickpea plants experiencing a water deficit with the rhizobial strain MC07 led to the accumulation of proline and the increase in both chlorophyll and nitrogen contents, thus improving plant tolerance to drought [149]. These findings highlighted the ability of rhizobium within nodules to regulate the levels of osmolytes, particularly proline, in different plant organs. However, the mechanisms and metabolic pathways by which rhizobia can regulate the internal osmolarity of plant cells remain unknown.

In addition to osmotic stress, drought-stressed legumes produce a high concentration of ethylene (a phytohormone endogenously produced by plants and responsible for different physiological processes), which causes abscission, accelerates plant aging and inhibits root elongation and nodule formation [150]. Bacteria that produce ACC (1-aminocyclopropane-1-carboxylate) deaminase can regulate ethylene levels in plant tissues by converting ethylene precursor ACC into ammonia or α-ketobutyrate [151]. This reduces the detrimental effects of ethylene on plant growth under stress [152]. Belimov et al. [153] conducted an experiment using ACC deaminase-producing strain *R. leguminosarum* bv. *viciae* 1066S and its Δ*acdS* mutant derivative to demonstrate the strain's capacity to enhance pea plant tolerance to drought and combined drought-cadmium stress. The results showed that ACC deaminase activity had a favorable influence on different plant growth parameters, including increased shoot biomass, nitrogen fixation levels and water use efficiency, suggesting improved root and nodule development under water-limited conditions in the presence of the wild-type strain. Additionally, recent studies have aimed to enhance the functionality of the ACC deaminase enzyme through genetic engineering approaches to establish more effective symbiotic interaction under stress. For instance, the inoculation of Mung bean plants (*Vigna radiata* L.) with a genetically modified *Bradyrhizobium* sp. SUTN9-2 strain under water deficit conditions resulted in an approximately 8-fold increase in ACC deaminase activity compared to the wild-type strain. This modified strain promoted nitrogen fixation, increased plant biomass, and enhanced resistance to drought stress [154]. Despite the large number of studies demonstrating the importance of ACC deaminase-producing rhizobia in promoting legume tolerance to abiotic stress, these findings have not fully elucidated the metabolic pathways involving this enzyme.

5.2. Salinity

The increase in soil salinization in arid and semi-arid regions represents a significant challenge for legume-cultivation [155], particularly due to its impact on soil microbial diversity and function [145]. Nevertheless, several halo-tolerant rhizobia have been shown to grow at NaCl concentrations ranging from 170 mM to 1.7 M. For instance, the growth response of *Bradyrhizobium* strains, obtained from root nodules of a forage legume *Stylosanthes* spp., to salt stress demonstrated the emergence of a salt-tolerant isolate RJS9-2, which was able to grow in 0.3 M of NaCl [156]. Osmotolerant rhizobia develop specific metabolic processes to counteract the negative effects of salt. To maintain an osmotic balance between the cytoplasm and the surrounding medium, these cells produce a variety of compatible osmolytes, including sugars, amino-acids, and proline. This production leads to endosmosis of water, which increases turgor pressure and preserves membrane integrity [157]. For instance, studies on the intrinsic salt tolerance of *Astragalus cicer* microsymbionts under high salinity showed their capacity to use glycine betaine as an osmoprotectant to sustain their cell growth [158]. Additionally, the synthesis of high molecular weight compounds, known as exopolysaccharides (EPS), has been identified as another salt resistance mechanism in rhizobia. Under unfavorable conditions, bacteria secrete EPS to cover cell walls, thus ensuring cell resistance against desiccation by absorbing large amounts of water, which create a hydrating environment outside the cells [159]. In addition, EPS are a crucial component of the biofilm matrix. Biofilm formation enhances microbial adhesion to root surfaces, helps maintain bacterial biomass, and facilitates signal exchange with host plants [160]. Multiple studies have highlighted the importance of EPS production for bacterial cells by generating different mutant derivates from different rhizobial species. Consequently, the loss of EPS function in these mutants resulted in impaired biofilm formation and in increased cell sensitivity to desiccation and osmotic stress [161,162]. Considering the different strategies adopted by rhizobia to tolerate salt stress, the application of halo-tolerant isolates in agriculture can successfully enhance a legume's tolerance to salt stress in comparison with conventional agricultural practices.

Earlier studies have reported the adverse impacts of salt accumulation on the photosynthesis process and plant metabolism, resulting in the degradation of chlorophyll content and a decrease in mineral uptake. Mushtaq et al. [163] conducted a study to investigate the role of *Rhizobium* inoculation in regulating plant physiology under salinity stress. Chickpea plants (*Cicer arietinum*, var. Pusa-BG5023) were inoculated with a *Rhizobium* species and subjected to two different doses of salt (50 and 150 mM NaCl). As expected, *Rhizobium* inoculation had a positive effect on plant photosynthesis, resulting in an increase of 13.52% in total chlorophyll content compared to uninoculated seedlings, which suffered a significant reduction in shoot and root biomass (48.68% and 45.93%, respectively). Additionally, the results demonstrated the positive influence of *Rhizobium* on other physiological traits such as proline content, antioxidant enzymes, and nutrient absorption. The enhancement of these different parameters boosted the plant's defense system against salinization and helped to maintain a balanced water status.

Salt stress alters water availability by reducing root capacity for water absorption. Under high osmotic potential, the decrease in leaf transpiration and stomatal width generates a dangerous dehydration of the plant's aerial part [164]. Studies on root hydraulic conductivity reported the presence of key proteins responsible for water homeostasis. These proteins are identified as the aquaporins proteins (including PIPs family) localized in different plant compartments [165]. PIPs or the plasma membrane-intrinsic proteins represent the largest subfamily of plant aquaporins, responsible for the regulation of water permeability in organs with large fluxes of water, such as roots and leaves [166]. Interestingly, previous reports identified the presence of several aquaporins proteins on the peribacteroid membrane of the root nodule in some legume species, such as *Glycine max* and *Pisum sativum* [167,168], suggesting an impressive relation between rhizobia symbiosis and PIPs gene expression and regulation in legumes [169]. To investigate the relationship between symbiosis and aquaporin protein abundance under salinity stress, *Phaseolus vulgaris* plants were inoculated with *R. leguminosarum* strain CIAT 899. Twenty days post-inoculation, different physiological changes were reported. The number of nodules in salt-treated inoculated plants increased by 134% compared to the control group. This improvement in symbiotic performance reflects the increase in osmotic water flow (Jv) and more essentially the accumulation of PIP proteins upon *Rhizobium* inoculation, which helped elevate the water status in bean plants. Moreover, a decline in sodium (Na^+) accumulation in the roots of inoculated plants has been observed. According to the authors, the lower levels of Na^+ concentration could explain the higher leaf relative water content (RWC) under saline conditions [170].

Under salinization, EPS help to alleviate the negative effect of ion toxicity on plant growth through binding cations, which decreases the abundance and availability of Na^+ for plant uptake. A recent study by Chakraborty et al. [171] highlighted the link between EPS production and plant response to salt stress. In this study, the model plant *Medicago truncatula* was inoculated with the halo-tolerant strain *Sinorhizobium meliloti* (Rm1021). Interestingly, the absence of succinoglycan (EPSI) molecules, a specific EPS produced by *S. meliloti*, blocked the nodulation process under salt stress. Conversely, a transcriptomic analysis of the plant response to salinization showed a significant increase in plant defenses in the presence of EPS, underscoring the importance of EPS in maintaining legume-rhizobium symbiosis under high salt concentrations.

All in all, these findings highlight the importance of drought-tolerant and halo-tolerant rhizobial strains in improving legume growth under arid environments. However, not all compatible microsymbionts possess PGP traits and/or adaptation mechanisms to stress conditions, which can interfere with the establishment of an efficient symbiosis under hostile environments. Consequently, multiple studies have focused on the isolation and characterization of non-rhizobial bacterial endophytes associated with the rhizosphere or root nodules of legume plants to test their ability to ameliorate legume growth and symbiotic interaction under different types of stress [23,172].

6. Non-Rhizobial Endophytes: Plant Biofertilizers in Arid and Semi-Arid Regions

6.1. Application under Drought Stress

Thanks to the vast diversity of plant-associated microorganisms, other potential PGPB candidates (non-rhizobia) have been identified and categorized as promising biofertilizers owing to their tolerance to various abiotic stresses and their ability to establish beneficial interactions with legumes [172]. For instance, a combined inoculum of phosphate-solubilizing bacteria (*Pseudomonas putida* and *Panteoa agglomerans*) and potassium solubilizing bacteria (*Bacillus circulans* and *Bacillus megatherium*) was used by Chavoshi et al. [173] to inoculate red beans (*Phaseolus vulgaris* cv. Goli) subjected to water stress at different vegetative stages. The results demonstrated a significant increase in the biomass of inoculated plants and a recovery of their physiological functions compared to the control. Additionally, analyses of chlorophyll and seed protein content revealed the positive impact of the bioinoculant, with an increase of 21.73% in protein content, which corresponds to the average protein content obtained from fully irrigated plants. Moreover, a variety of other mechanisms employed by non-rhizobial strains to alleviate plant stress have been well studied. Isolates from genera such as *Azotobacter*, *Azosprillum*, *Bacillus* and *Pseudomonas*, for example, are currently among the most studied due to their ability to produce high quantities of phytohormones and growth regulators, such as gibberellins and cytokinins [174]. Auxin, a phytohormone widely synthesized by PGPB, directly or indirectly influences plant development at different stages [175]. In fact, the presence of indole-3-acetic acid (IAA) in plant stems stimulates cell division and increases bud formation. Moreover, it improves root structure and proliferation by increasing the number of tips and root hairs, thereby increasing water availability for the plant and facilitating nutrient uptake under water-limited conditions [176]. Recognized as plant growth promoters, five strains of *Pseudomonas aeruginosa* were selected to explore their ability to enhance the growth of two varieties of mung bean (*Vigna radiana*) under drought stress. Functional screening of the tested strains revealed a high capacity for IAA production (around 116 μg/mL), along with other PGP traits such as phosphate solubilization and siderophores production. Under field conditions, the positive interaction between *P. aeruginosa* strains and *Vigna radiata* plants had significantly improved the growth parameters, with a maximum increase of 125% in shoot length, 139% in root length, 293% in total yield, 68% in water content and a 19%increase in antioxidant activity. These findings underscore the importance of IAA-producing bacteria and their role in mitigating the effect of drought stress by increasing root elongation, thus assisting the plant in coping with water limitations [177]. However, it is well established that elevated levels of bacterial IAA can inhibit plant growth, particularly root development. Therefore, it is interesting to explore the underlying mechanisms and potential signaling molecules used by the plant and/or its associated bacteria to regulate the levels of phytohormones produced by the bacterial cells to meet the host's needs.

A recent study conducted by Brunetti et al. [178] highlighted the significance of PGPB inoculation practices in improving soil quality and boosting plant defense mechanisms against abiotic stress. Two previously characterized strains *Enterobacter* HS9 and *Bacillus* G9 [179], known for their dual ability to produce both ACC deaminase and IAA, were selected to inoculate *Mucuna pruriens* L. (also called velvet bean), an endemic Indian plant species, under drought stress. Results showed that co-inoculated plants maintained the same biomass production under both moderate (50%) and severe (10%) water stress. Moreover, the co-inoculation with these two strains leads to a more effective regulation of ethylene levels, thus reducing ACC content in both leaves and root tissues [179].

6.2. Application in Saline Soils

Advanced microbiological analysis of soil microorganism population and dynamics led to the identification of a wide range of halo-tolerant isolates from many genera such as *Pseudomonas*, *Azospirillum*, *Bacillus*, *Enterobacter*, etc. [180]. The application of these salt-tolerant microbes in saline-soil-based agriculture showed remarkable success in the amelioration of crop growth and yield [41]. Hmaeid et al. [181] conducted a study on the native rhizosphere of the wild legume *Sulla carnosa* (*Hedysarum carnosum* Desf.), growing in northeast Tunisia, resulting in the characterization of salt-tolerant isolates exhibiting many PGP features. In order to increase the salt tolerance of *S. carnosa*, three halo-tolerant isolates (up to 10% NaCl) identified as *Pseudomonas putida*, *Acinetobacter* sp. and *Curtobacterium* sp. were used for inoculation trial under 200 mM of salt. Results showed a positive impact of endophytic inoculation on the quality of soil by decreasing the level of electrical conductivity (EC), which reflects the reduction in NaCl ionic toxicity in the rhizosphere. According to the authors, the reduction in soil EC is mainly due to soil acidification by the inoculated strain caused by the secretion of organic acids. Hence, inoculated plants showed an apical improvement in their biomass, along with the accumulation of photosynthetic pigments and antioxidant enzymes, which reflects the increase in plant adaptation to salt damage [181].

Similar to some wild legumes, food legumes such as chickpea, faba bean and pea are sensitive to salinity stress. Their productivity is reduced under high salt levels, as well as their metabolic activities. A disturbance in osmotic potential and ionic balance negatively affects their growth parameters and leads to cellular damage. In this context, the strain *Kocuria rhizophila*, a halo-tolerant and ACC deaminase-producing endophyte previously isolated and characterized by Mufti et al. [182], was able to improve salt tolerance in two varieties of pea plants. As expected, inoculation with *K. rhizophila* had a direct effect on water uptake, resulting in a significant increase in leaf relative water content (RWC) by 70–73% compared to the control. This increase can be attributed to the reduction in Na^+ levels in the plants (a decrease of 17–22% in both varieties), which indicates an enhancement of the plant's capacity to overcome osmotic stress and ion toxicity upon inoculation [183].

Azospirillum sp., one of the most utilized PGPBs globally, exhibits a wide range of PGP activities, including nitrogen fixation, IAA, and ACC-deaminase production. Previous reports showed the capacity of some *Azospirillum* species to alleviate the inhibitory effects of abiotic stress in different plant species [184,185]. To evaluate the ability of these endophytes to attenuate the adverse impacts of salt stress on crop growth, El-Esawi et al. [186] conducted a plant trial to improve chickpea plant response to salinization using *A. lipoferum* FK1, which can grow under 250 mM NaCl. The results aligned with previous studies [187], showing significant adaptation of *Cicer arietinum* to salinization following inoculation. The presence of *A. lipoferum* endophyte stimulated the production of photosynthetic pigments and the accumulation of osmolytes such as gibberellin and proline in plant tissues, thereby alleviating the damage caused by oxidative stress [186].

7. PGPB Consortia for Alleviating Drought and Salinity Stresses in Legumes

The use of *Rhizobium* inoculum or other non-rhizobial strains individually has shown great promise in establishing a sustainable agricultural system. These PGPB serve as biofertilizers, reducing the reliance on chemical fertilizers and enhancing plant defense mechanisms against both abiotic and biotic stress. However, recent findings suggest that the co-inoculation of *Rhizobium* together with other non-rhizobia provides even more favorable results, as the interaction between *Rhizobium* and other endophytic bacteria not only enhances plant growth parameters but also boosts the efficiency of rhizobia's symbiosis with their hosts. This symbiotic efficiency is crucial, as it is highly affected by adverse environmental conditions such as drought and salinity [172]. In this context, a study conducted by Abd El-Ghany and Attia [188] showed the positive effects of the co-inoculation with a mixture of *R. leguminosarum* and EPS-producing bacteria *Azotobacter chroococcum* on the growth of faba bean plants, growing in a salt-affected site. Inoculation significantly increased plant yield, relative water content (RWC), photosynthesis pigments and proline content at high salt stress (100 mM NaCl). Moreover, biochemical analysis revealed an improvement in nutrient uptake (N, P and K) against the reduction in toxic concentrations of ions (Na^+, Cl^-). These findings are consistent with those presented by Abdiev et al. [189] who showed the beneficial effects of dual-inoculation of *Rhizobium* and *Azotobacter* on plant growth and productivity of two chickpea varieties cultivated in saline arid soil with an electrical conductivity of 5.8 dS m^{-1}. The results revealed that co-inoculation promoted several physiological and biochemical plant parameters compared to single inoculation. Similarly, the co-inoculation of chickpea plants with the *M. ciceri* strain and a consortium of non-rhizobial endophytes (*Phyllobacterium* and *Xanthomonas*), isolated from legumes native to arid regions, resulted in the enhancement of plant growth and *Mesorhizobium* symbiotic performance under salinity [43]. Additionally, a recent study conducted by Gritli et al. [190] has demonstrated the positive outcomes of the co-inoculation of *Lathyrus cicera* (red pea) with *R. laguerreae* and three endophytic strains belonging to the *Bacillus* genus under salt stress. Interestingly, this study not only reported a significant improvement in plant growth and biochemical parameters post-inoculation but also noted a remarkable increase in the expression of salt tolerance markers, specifically the HKT1 and NHX7 genes. These genes act as transporters and exchangers of sodium ions within plant tissues. Similarly, scientists' attention has been drawn to the evaluation of the impact of co-inoculation on mitigating the detrimental effects of drought, a main environmental problem, especially in drylands. In one instance, chickpea plants co-inoculated with *M. ciceri* and *P. fluorescens* under 40% of field water capacity showed a synergetic performance of both strains, enhancing chickpea tolerance to water deficit. An analysis demonstrated that consortium inoculation led to improved chickpea resilience to water scarcity [191]. In addition, another study highlighted the use of the *Pseudomonas* species, notably *Pseudomonas putida*, to enhance *R. leguminosarum* symbiotic interaction with its host plant (*Vicia faba* L.) in a low-fertility soil under water stress. Co-inoculated plants exhibited alleviated drought stress, with relative water content (RWC) and plant biomass, particularly root length, increasing by 10.4% and 32.4%, respectively, compared to those under well-watered conditions [139]. Lastly, a recent study analyzed the combined effects of inoculation with the native endosymbiont *R. laguerreae* and its two associated endophytic strains *Bacillus* sp. and *Enterobacter aerogenes* on *Lens culinaris* (lentil) growth when exposed to water limitation. This study showed promising results for plant tolerance to drought stress after co-inoculation, revealing the efficacy of consortium containing multiple strains, and suggests its future selection as an eco-friendly strategy to enhance lentil resistance to osmotic stress [192]. Overall, these findings underscore the efficacy of co-inoculation with consortia combining both rhizobial and non-rhizobial endophytes in enhancing legume growth and symbiosis under drought and salinity stress. However, many of these promising results may not translate effectively to field conditions due to the limited ability of certain inoculants to compete and establish themselves within the complex indigenous soil biome. Therefore, future studies must delve deeper into defining the physiological and functional core required for rhizosphere competitiveness and colonization. Moreover, there is a pressing need to unravel the complex rhizobium-endophyte interactions and the mutual mechanisms by which they influence both plant and nodule development under extreme environments.

8. PGPB Interactions in the Rhizosphere: Cell-to-Cell Communication

The rhizosphere is a dynamic and complex environment in which plant roots interact with a large community of microorganisms, including bacteria. Within this ecosystem, bacterial cell-to-cell communication is crucial for controlling population dynamics and coordinating physiological responses to various environmental stimuli [193]. Root exudates present the first metabolic compound affecting the communication between bacteria and plants. Studies have demonstrated that the composition of carbon sources and other exudate compounds released by plants can dictate whether there's cooperation or competition between members of the rhizobacterial community [194]. In addition, taxonomic correlation within bacterial networks has revealed the presence of diverse signaling pathways used by bacteria to regulate specific behaviors and control population density, especially under stress conditions. Bacteria have the potential to produce a large panel of secondary metabolites used for cell–cell signaling within the same specie or inter-species, referred to as a quorum sensing mechanism [195].

Quorum sensing (QS) is one of the most studied and well-described mechanisms for bacterial cell communication. It involves the production of a variety of signaling molecules, autoinducers (AI), that are synthesized within the cells and transported to the intercellular space. Recently, three classes of AI molecules have been identified A-1, A-2, and A-3, with different functions and chemical structures [196]. The first group of AI (AI-1) is represented by the N-acyl-l-homoserine lactones (AHLs) and is responsible for interspecies communication. Natural AHLs are mainly synthesized by the *ain* and *lux* systems [197]. The *lux* system is activated through the synthesis of N-3-oxo-hexanoyl homoserine lactone (3-oxo-C6-HSL) by the LuxI enzyme. This 3-oxo-C6-HSL will bind to the transcriptional factor LuxR and form together a complex that can induce the transcription of luxICDABEG operon. The *ain* system, however, is based on the AHL synthase activity of the AinS protein, which is responsible for the synthesis of N-octanoyl-homoserine lactone (C8-HSL) [196]. This molecule has two main effects: a direct activation of the LuxR and the inactivation of LuxO, a gene responsible for QS repression at low cell densities. The second class of AI is mediated through the synthesis of furanosyl borate diester by a LuxS enzyme [197]. This group of AI is also responsible for interspecies communication. On the other hand, bacterial interactions with higher organisms require the biosynthesis of the autoinducer AI-3 a pyrazinone derivative, whose synthesis involves the dual action of the threonine dehydrogenase and tRNA synthetases [198]. Diffused into the rhizosphere, these signaling molecules can induce bacterial assemblies (Biofilm), plant growth and improve plant resistance to phytopathogens [196].

Biofilm formation serves as the best example of bacteria–bacteria cooperation. This special structure represents one of the different strategies used by bacterial endophytes for plant surface colonization and for adaptation under drought and salinity stresses. Recent studies suggested that this cooperation occurs via genetic material transfer between the biofilm members and under the regulation of QS systems, particularly AHLs molecules [199]. Moreover, recent research has identified other types of cell-to-cell communication systems in the rhizosphere, including diffusible signal factor (DSF)-mediated signaling and extracellular vesicle (EV)-based communication. DSF-QS involves the secretion and detection of fatty acids such as cis-2-unsaturates fatty acids. These autoinducers were first identified in the phytopathogen *Xanthomonas campestris* as regulators of virulence expression [200]. More recently, DFS-mediated signaling has been identified in the biocontrol agent *Stenotrophomonas maltophilia* as a stimulus of several genes related to plant colonization, plant growth promotion and stress protection [201].

Despite the huge number of studies on plant microbiome evolution and interactions, there remains a significant challenge in cultivating all bacterial species in association with plant systems. This is due to the difficulty in recreating the complex natural habitat of plants under laboratory conditions. Consequently, there is still a lack of full understanding of the exact composition of the phytomicrobiome and its impact on plant development. Therefore, advanced experiments are needed to elucidate the connections between all members of the phytomicrobiome. These findings will be crucial in developing effective synthetic microbial communities (SynCom's) that can enhance plant health and productivity under rapidly changing climatic conditions.

9. Concluding Remarks

Over recent decades, it has become clear that traditional agricultural practices cannot keep up with the growing demands of the world population. This issue is especially pressing in arid and semi-arid countries, where drought and salt stress significantly hinder agricultural productivity. The rhizobium–legume symbiosis, involving either herbs or trees, is suggested as an optimal solution to enhance soil fertility and restore arid lands, marking an essential focus for future research. The use of adapted and improved legume genotypes (either by plant breeding or genetic modification) shows promise for increased cultivation under such conditions, but their survival, growth, and persistence also depend on their associated microorganisms. Inoculation with PGPB has emerged as a potential strategy for enhancing legume yield and sustainability in these areas. By improving soil fertility, water use efficiency, and stress resistance, PGPB offer an eco-friendly and compatible solution to help farmers in arid and semi-arid regions overcome the detrimental impacts of drought and salinity stress, achieving higher yields with fewer inputs. Inoculation of legumes with bacterial consortia resistant to salinity or able to survive under drought conditions has proved to be a promising and cost-effective technology for salt- and drought-stressed areas, allowing the re-vegetation of affected lands. Despite the promising results of PGPB-based approaches, there is still a lack of knowledge regarding the complex interactions between PGPB and their hosts. Therefore, developing advanced genetic and molecular technologies is fundamental for identifying new effective PGPB candidates, including rhizobia, and characterizing the core genes responsible for their unique adaptability to various stressors. Once identified, this genetic material can be exploited to enhance the normal functioning of stress-sensitive bacterial cells, particularly rhizobia, through genetic engineering or genetic editing approaches. The application of such genetically modified and/or stress-tolerant microorganisms will guarantee stress mitigation in a wide range of legume host plants and help maintain the specificity of symbiotic interactions in hostile environments. Ultimately, the successful integration of PGPB-based agriculture in arid and semi-arid regions will be determined by several socio-economic factors, as well as farmers' willingness to embrace innovation and adopt new agricultural practices.

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