



Review

Exopolysaccharides Synthesized by Rhizospheric Bacteria: A Review Focused on Their Roles in Protecting Plants against Stress

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Abstract: Plants are constantly exposed to a wide range of environmental factors that cause different kinds of stress, such as drought, salinity, heat, frost, and low nutrient availability. There are also biotic sources of stress, which include pathogens (bacteria, viruses, pests), herbivores, and plant competitors. These various types of stress affect normal plant physiology and development, and may lead to significantly lower yields. However, certain microorganisms (MOs), known as plant growth-promoting rhizobacteria (PGPR), can interact with and benefit plants in stressful environments. They do so through a series of mechanisms which contribute to minimizing the negative effects of plants' responses to stress. This review summarizes current knowledge about those mechanisms, with a focus on the production of exopolysaccharides (EPSs). These compounds can act as osmoprotectants, promote the production of phytohormones, prevent the entry of pathogens through roots, bioremediate metals, and improve soil structure and permeability, among many other beneficial effects. This makes them suitable alternatives to guarantee food security while reducing the excessive use of chemical agricultural inputs and their harmful consequences for the environment.

Keywords: exopolysaccharides; PGPR; stress



Citation: Carezzano, M.E.; Alvarez Strazzi, F.B.; Pérez, V.; Bogino, P.; Giordano, W. Exopolysaccharides Synthesized by Rhizospheric Bacteria: A Review Focused on Their Roles in Protecting Plants against Stress. *Appl. Microbiol.* **2023**, *3*, 1249–1261.

<https://doi.org/10.3390/applmicrobiol3040086>

Academic Editor: Ian Connerton

Received: 29 October 2023

Revised: 14 November 2023

Accepted: 14 November 2023

Published: 16 November 2023



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1. Introduction

Many pathogenic and nonpathogenic bacteria have the ability to synthesize polysaccharides, a kind of carbohydrate, after the exponential growth phase. These compounds may be located within the cytosol or the cell membrane, or be secreted into the extracellular environment in the form of capsules (which surround the cell) or biofilm. In the last case, they are known as exopolysaccharides or EPSs [1].

Xiao et al. (2020) [2] classify EPSs into two groups depending on their distribution in the microbial medium. There are those that are dissolved and thus separated from the bacterial cell, and those that are bound to the cell. According to the model proposed by these authors, the EPSs in the second group are arranged on two layers: the innermost layer, which is tightly bound, denser, and contains a higher concentration of the compounds, and the outer layer, which is loosely bound and, as a consequence, more likely to disperse.

In terms of structure, some EPSs are linear or branched homopolymers, i.e., all their building blocks or repeating sugar units (monomers) belong to a single type. Most of them, however, are heteropolymers made up of monomers of different natures. There are low- and high-molecular-weight forms depending on their degree of polymerization, which is of crucial importance for certain physiological processes [3].

EPS synthesis broadly comprises three steps: the assimilation of a carbon source, the intracellular production of polysaccharides, and their final excretion [1]. The considerable expenditure of energy demanded by this process is practically compensated for by the advantages that EPSs can offer. These molecules intervene in multiple events of biological importance, such as protection against environmental stress, attachment to surfaces, nutrient absorption, nitrogen-fixing symbiosis with plants, and even the pathogenesis of many diseases [4,5]. This review focuses on the EPSs synthesized by rhizospheric bacteria, which live in close contact with plant roots, and on the roles they may play in mitigating the different types of stress to which plants are exposed.

2. EPSs in Bacterial Biofilms

Microorganisms (MOs) were traditionally studied as free-living or planktonic cells [6]. The focus has gradually shifted to the study of sessile communities, since planktonic growth appears to be rare in nature [7]. In other words, characterizing an MO in isolation does not contribute to our understanding of its real behavior in nature, where it shares an ecological niche with diverse microbial populations.

Bacteria of the same or different species are known to associate into biofilms, which are well-structured, multicellular communities embedded in a self-produced matrix attached to a living or inert surface [8,9]. This extracellular matrix is mostly composed of water, but also contains proteins (including enzymes), DNA, RNA, and EPSs [10]. The latter are particularly important because they stabilize the 3D structure of the biofilm [11], and they can represent between 40 and 95% of the biofilm biomass [12].

The life cycle of a biofilm begins when it attaches to a compatible surface. Planktonic cells make use of their motility mechanisms (pili, flagella, proteins, EPSs) to gather on such a surface and establish reversible connections with other cells [10]. After these initial interactions, the cells adhere irreversibly to the substrate and start reproducing into microcolonies, thanks to the exchange of molecular signals. During this time, they secrete the components of the extracellular matrix, which becomes crisscrossed with water-filled channels that transport nutrients and eliminate waste [13]. Eventually, planktonic cells may become detached from the biofilm for different reasons, e.g., because they have been newly formed [14], and go on to create new colonies elsewhere. This last stage in a biofilm's life is known as dispersion.

An important phenomenon for the formation and continued existence of a biofilm is "quorum sensing" (QS). This is a collective communication system that relies on the production and reception of small signal molecules by individual bacterial cells. The denser a bacterial population, the higher the concentration of these molecules. QS-related genes are activated only above a certain signal concentration (i.e., when a certain quorum has been reached), which means the process entails a positive feedback loop: when bacteria sense the molecules building up, they synthesize more of them; the more molecules are released, the higher the likelihood that the expression of QS genes will be induced. For this reason, QS molecules are referred to as "autoinducers" [15].

Three types of autoinducers have been extensively studied in bacteria: N-acyl homoserine lactones (AHLs), autoinducer peptides (AIPs), and AI-2. Different ones are specific to different bacterial groups. In general, QS genes are regulated by AHLs in Gram-negative bacteria, and by AIPs in Gram-positive bacteria [15].

A typical AHL-based system works as follows. A QS gene is activated which encodes LuxI synthase. This enzyme synthesizes an N-3-oxohexanoyl-homoserine lactone (3-oxo-C6) that is passively diffused out of the cell and then binds to a LuxR receptor inside another cell, which is encoded by another, separately regulated gene. The AHL-receptor complex binds to a consensus DNA sequence and triggers the expression of luciferase. Many systems of this kind have been described in Gram-negative bacteria, including more than 70 species of Proteobacteria [15].

The cooperative behavior enabled by QS enhances access to nutrients, defensive responses against competitors, and survival under adverse environmental conditions.

3. EPSs Synthesized by Plant Growth-Promoting Rhizobacteria

The rhizosphere (from the Greek “rhiza”: root) is a microbe-inhabited microzone located at the soil–plant root interface. Three subzones have been described within it, based on their proximity to the roots: the endorhizosphere, which includes parts of the root cortex and endodermis; the rhizoplane, made up of the root epidermis and mucilage; and the ectorhizosphere, which consists of the soil that closely adheres to the root [16]. The size and structure of the rhizosphere vary according to the complexity and diversity of the root systems developed by different plant species, as well as to the microbial populations that live within it [17].

Between 15 and 40% of the total rhizospheric surface is occupied by microcolonies or biofilms. Root exudates act as chemoattractants that draw MOs to the rhizosphere [16] and provide them with nutrients (e.g., sugars and amino acids) [18]. In turn, these MOs exert positive effects on the plant in the context of symbiotic or nonsymbiotic relationships. For instance, they can promote plant growth, improve the health of the soil by regulating its pH, increase the plant’s tolerance to biotic and abiotic stress, offer protection against pathogens, and enhance the plant’s uptake of nutrients [19,20].

The development of rhizospheric communities is influenced not only by the availability of nutrients produced by the plant, but also by the properties of the soil, especially temperature, pH, aeration, and physicochemical composition [21]. These communities include fungi, protozoa, algae, and plant growth-promoting rhizobacteria or PGPR [21]. The latter were initially identified in nodular formations in desert plants. The EPSs they produced were found to provide long-term protection against desiccation. Since then, many other PGPR have been described, and they are now categorized into two major classes depending on their interaction with the host plant. The first comprises endophytes, i.e., bacteria that colonize the inside of root tissues. The second includes rhizospheric bacteria that colonize the root surface, where they often form nodules [22,23].

PGPR belong to many different genera, such as *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Enterobacter*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, *Serratia*, and *Frankia* [22,23]. All of them synthesize EPSs which, as described in 1.2., allow them to become attached to the root surface in the form of biofilms. These biofilms protect bacteria against adverse conditions (salinity, extreme temperatures, biotic stress, drought). EPSs themselves are produced in response to stressful stimuli [21]. In addition to conforming to the biofilm structure, these sugar macromolecules can benefit the plant [24], both through direct action and indirectly, by improving soil properties. They can form aggregates that make the soil more stable, fertile, and porous, and improve its enzymatic activity. This means there is a larger availability of nutrients and water to fuel plant growth. In addition, some polysaccharides can retain as much as seven times their mass in water, which further contributes to water availability for the roots [25,26]. EPSs have also been linked with longer roots and seedlings, a higher chlorophyll content, and an altogether larger plant biomass [27,28].

In short, plant–rhizobacteria interactions (in which EPSs play major roles) can make plants better able to cope with stress, improve the soil, and promote plant growth directly and indirectly. In turn, this may pave the way for agricultural schemes that are both economically viable and sustainable [27].

4. PGPR Activity and the Role of EPSs during Abiotic Stress

Any external factor that hinders correct growth and development is considered stressful [29]. Abiotic or environmental stress does not only affect plant metabolism and physiology; it also alters these aspects in MOs and has an impact on the soil.

Furthermore, the effects of abiotic stress vary depending on the moment it occurs, its degree of aggressiveness, the particular characteristics of the plant and microbial species exposed to it, and other factors. On account of this, plant–MO interactions are highly dynamic and complex. A comprehensive understanding of how abiotic stress modifies plants,

MOs, and plant–plant and plant–MO relationships is crucial to harness the agricultural potential of the plant-associated microbiota [30].

4.1. Salt Stress

A high concentration of sodium (Na^+) in the soil alters its physical and chemical structure, in a way that reduces its aggregation stability [31], permeability, and hydraulic conductivity [32]. Saline soils are darker (due to organic matter disaggregating), more alkaline, and in general less capable of sustaining plant growth [33].

In plants, the effects of salt stress can be divided into two phases. Osmotic stress occurs when a high concentration of salt in the root area inhibits water absorption. This is followed by ionic toxicity: when the concentration of Na^+ rises in the leaves, other ions cannot be absorbed and different metabolic pathways are affected, including that for photosynthesis. These processes are accompanied by secondary reactions like the activation of Ca^{2+} signaling; the accumulation of mineral ions, metabolites, and abscisic acid (ABA); and the production of reactive oxygen species (ROS) [34,35]. In turn, these changes may diminish water and nutrient availability; disturb enzymatic activity, protein metabolism, and hormone regulation; and damage the membrane and its cell constituents. Other aspects that are harmed include root architecture, the composition of plant exudates, the structure of the soil, and the plant-associated microbial community (in terms of biomass, enzymatic activity, soil respiration, and the mineralization of carbon and nitrogen) [36]. As a result, plant growth is stunted and yields are lower.

PGPR conserve their growth-promoting abilities in the face of salt stress. Some of the best-known halotolerant genera are *Halomonas*, *Bacillus*, *Streptomyces*, *Oceanobacillus*, and *Pseudomonas* [35]. There are several things these bacteria can do to counteract the effects of salinity. They can induce systemic tolerance (IST) in the host plant; solubilize phosphates; produce siderophores, ammonia, indole-3-acetic acid (IAA), and 1-aminocyclopropane-1-carboxylate deaminase (ACC); and accumulate osmolytes to maintain the balance between the intracellular and the osmotic pressure. Stress may also be relieved through the secretion of biopolymers, e.g., EPSs, polyesters, and polyamides [37,38]. These biopolymers constitute a physical barrier that absorbs excess Na^+ and reduces its concentrations in the rhizosphere [39,40]. EPSs are able to do this thanks to their anionic nature, which allows them to capture free Na^+ ions. This not only helps plants but also offsets some of the negative consequences of salt stress on the soil. Improved growth in wheat after inoculation with salinity-tolerant PGPR, such as *Bacillus amyloliquefaciens*, *Bacillus insolitus*, *Microbacterium* spp., and *Pseudomonas syringae*, was attributed to the formation of a protective EPS sheath around the roots [24,37,41]. Similarly, another study ascribed increased sunflower growth post-inoculation with halotolerant *Pseudomonas aeruginosa* to the EPSs produced by the bacterium [37,41]. Still, the specific roles played by EPSs in the plant–MO interactions during salt stress need to be researched further [30].

4.2. Drought Stress

Low water availability in the environment causes an imbalance between transpiration and water absorption in plants, and is thus another source of abiotic stress. Drought inflicts mechanical damage on plant cells by decreasing their turgor and volume and increasing their content of solutes. In plants subjected to this kind of stress, the development of leaves and of the apical and lateral meristems is inhibited, and the end result is a reduction in growth [42].

Some of the mechanisms deployed by PGPR to benefit plants during drought are very similar to those that take place during salt stress. For instance, these bacteria may mediate regulations in plant hormones, lead to modifications in root morphology, enhance ACC activity, help the plant accumulate antioxidants and osmolytes, and produce organic volatile compounds, IAA, gibberellins, cytokinins, and EPSs [43,44]. In fact, water scarcity has been observed to induce the expression of genes involved in EPS synthesis in bacteria such as *Azospirillum brasilense* Sp7 and *P. aeruginosa* [37].

EPSs benefit plants exposed to drought through several mechanisms. They induce the production of ABA, which leads to partial stomatal closure and reduces water evaporation through transpiration, a key factor to enhance plant drought resistance [41]. They promote the accumulation of osmolytes, which can increase osmotic pressure in plant cells and, therefore, their capacity to expand. As a result, these cells are better at uptaking and/or conserving water. For example, two osmolytes (proline and soluble sugar) increased significantly in the leaves of rice seedlings treated with bacterial EPSs [41]. These osmolytes also help eliminate free radicals, which tend to build up during drought stress and damage the cell membrane. Furthermore, much as it occurs during salt stress, the EPSs in bacterial biofilms formed around plant roots can be physically protective in the case of drought, since they are hydrophilic and function as water reservoirs (see Section 3) [45]. The ability of EPSs to retain water and trigger plant antioxidant mechanisms (such as the production of ABA) varies depending on their specific composition [37]. Finally, EPSs can improve soil structure and water-retention capacity. When released into the soil by PGPR, they are absorbed onto clay particle surfaces and enhance soil stability through cation bridges, hydrogen bonding, Van der Waals forces, and anion adsorption [37]. This has obvious effects on plant growth, since a stable soil that is better able to retain water is crucial for normal plant development.

The exogenous application of EPS-producing PGPR on plants during times of drought and high salinity, therefore, may be a promising strategy to improve yields in a sustainable manner [1,12]. Many examples in the literature point in this direction. An increase in maize yields was linked to inoculation with *P. aeruginosa* and, in particular, to the effects of the EPSs produced by this bacterium [46]. Wheat plants exposed to drought and inoculated with *Bacillus thuringiensis* AZP2 were 63% more efficient in their use of water than uninoculated specimens, likely thanks to bacterial biofilms formed on their root hairs [47]. The adverse effects of both salt and drought were diminished in wheat after inoculation with *Bacillus subtilis* subsp. *inaquosorum* and *Marinobacter lipolyticus* SM19 [48]. *Sinorhizobium meliloti* and its EPS production aided the survival of alfalfa plants under water deficiency stress and salt stress [49].

4.3. Temperature Stress

Environmental temperature influences several aspects of the soil, e.g., its temperature, humidity, aggregation stability, pH, and nutrient diffusion [50–52]. Naturally, changes in any of these factors will disturb the MOs living in the soil and plant growth. Besides affecting plants through its effects on the soil, temperature has a direct impact on plants, too [53].

Generally speaking, temperature stress can be responsible for low germination, respiration, and photosynthesis, as well as for the inactivation of proteins and detoxification pathways; the accumulation of ROS; alterations in the synthesis of phytohormones; and changes in the lipid composition of the membrane, which render it less fluid and permeable. All of this stunts plant growth and in some cases may even lead to death [30,54,55]. As with other kinds of stress, however, the specific effects of extreme temperatures depend on their intensity and duration, as well as on the resilience of the plants and MOs themselves, and other concomitant environmental factors [53].

Stress caused by very low or freezing temperatures has serious consequences for plant germination, growth, and reproduction [55]. It creates irreversible lesions, cell dehydration, and dysfunctions in the membrane. Inoculated PGPR can mitigate this by fostering plant defenses through a series of strategies, which include the upregulation of ABA; lipid peroxidation; proline accumulation; and an increase in chlorophyll, anthocyanins, starch, and/or iron. As for EPSs, certain plant-associated bacteria have actually been found to produce more of them under low temperatures (0–15 °C). Psychrotolerant *Pseudomonas* from the northwestern Himalayas, for example, synthesize more EPSs when exposed to the cold than at ambient temperatures. As explained earlier, a higher number of EPSs improves water availability, alleviates membrane lesions, and betters the Na⁺/K⁺ balance. The ability

of EPSs to chelate sodium ions limits their uptake by roots, thereby protecting plants from cold-induced dehydration [21]. The thin biofilm formed by inoculated *Bacillus* spp. CJCL2 and RJGP41 was reported to alleviate cold stress in wheat seedlings, since it appears to have allowed the bacterial cells within it to survive and secrete specific metabolites to protect themselves and the host plant from the cold, as well as to promote root colonization under these conditions [21].

Stress created by very high temperatures may similarly decrease germination or even prevent it from happening altogether: it reduces cell size and metabolism, damages plumules and radicles, and produces pollen infertility. It may also generate serious damage during the stage of vegetative growth [56]. Once again, PGPR are able to counteract this through many mechanisms. They can promote nutrient absorption and N₂ fixation; produce siderophores; reduce ROS; increase the content of proteins, chlorophyll, and ABA (which leads to stomatal closure), and stimulate the synthesis of phenolic compounds and secondary metabolites involved in the plant's defense system. Moreover, just as cold stress enhances EPS production in some plant-associated bacteria, the heat can have a similar effect on other species and subsequently foster the synthesis of new proteins (such as heat shock proteins) and increased cell viability and resistance [30,57]. Tomato growth was conserved under very high temperatures (42 °C) after inoculation with *Bacillus cereus*, a bacterium in which EPS synthesis and 1-aminocyclopropane-1-carboxylate (ACC) cleavage were observed to increase upon exposure to heat stress [58]. The inactivation of phaR, a transcription factor controlling poly-3-hydroxybutyrate synthesis, increased EPS production and improved heat stress tolerance in *Bradyrhizobium diazozoum*. These results suggest that EPSs may directly alleviate heat stress in PGPR. This effect may then extend to the biofilm matrix surrounding plant roots, which may act as a heat-resistant agent that improves water retention and reduces the impact of high temperatures on the plant itself [21].

4.4. Stress by Metal(loid)s

In the last few decades, there has been a worldwide increase in metal toxicity in the soil. This is due to a variety of natural phenomena, as well as rapid industrialization and other anthropogenic activities that involve the massive release of different kinds of waste and chemicals into the environment, such as pesticides and fertilizers. Metals, e.g., cadmium (Cd), mercury (Hg), lead (Pb), copper (Cu), chromium (Cr), and nickel (Ni), and metalloids, e.g., arsenic (As), have high molecular density and can be toxic even at low concentrations. When they accumulate in soil that is destined for agricultural activities, they quickly enter the food chain and also accumulate in living organisms. This is known as bioaccumulation, and has direct and indirect effects on human, animal, and plant health. Besides being ingested in food, metal(loid)s can be inhaled or consumed in water, given that they are able to percolate into different water sources [21,59].

In plants in particular, stress caused by rising levels of metal(loid)s in the soil can modify physiological and biochemical processes, and thus affect normal growth and yield. The most considerable damage is usually registered in roots, because they are the initial area of contact with these compounds. However, toxicity does not remain localized: it goes on to have an impact on other tissues and organs, like the stem and the leaves [60]. Harmful effects include decreased nutrient absorption and translocation, the generation of ROS, the inhibition of antioxidant enzymes, damage to the cells (including nucleic acids), the oxidation of proteins, reduced carbon dioxide fixation and photosynthesis, alterations in chloroplasts, etc. [60].

As is the case with other adverse environmental factors, exposure to contaminants such as metal(loid)s exerts selective pressure on populations and favors those individuals capable of prospering under such conditions. Plants are remarkable examples of adaptation and survival in this context [61], since they have evolved many mechanisms to respond to stress caused by those metals. These include the sequestration and/or accumulation of

these compounds in vacuoles and apoplasts (which restricts their absorption), and their conversion into nontoxic forms through detoxification pathways.

Beyond plants' own evolutionary responses to this kind of stress, a human-made solution consists of remediating or decontaminating soils through physical, chemical, and biological strategies. Unfortunately, the first two are often costly in terms of materials and labor, and can produce secondary contaminants. Biological remediation, on the other hand, is much more ecofriendly and economically viable, given that it involves harnessing the detoxifying abilities of living microorganisms, such as PGPR [59].

Several mechanisms help PGPR survive in the presence of metal(loid)s, and may in turn benefit plants by protecting them from elevated exposure to these elements. Metal(loid)s may undergo biosorption onto the bacterial biomass through interactions between functional groups on the cell surface and metal cations. Here is where EPSs play a role once again, since positively charged metal ions can interact with negatively charged functional groups in EPSs (carboxyl, hydroxyl, and noncarbohydrate substituents like acetamide, amine, sulfhydryl, etc.) A study by Nocelli et al. (2016) [62] highlighted the importance of EPSs synthesized by inoculated *S. meliloti* in the improvement of alfalfa growth in soils contaminated with metal(loid)s. ACC deaminase, which contributes to the regulation of ethylene synthesis, also increases metal(loid) adsorption. Moreover, PGPR can bioaccumulate heavy metals, i.e., retain them inside the cell by chelation. Alternately, metals may be transported from the inside to the outside of the bacterial cell through efflux systems. In general, these processes involve biotransformations which reduce the toxicity of the original molecules [30].

5. PGPR Activity and the Role of EPSs during Biotic Stress

Biotic stress is caused by viruses, fungi, bacteria, and pests, among others. Like its abiotic counterpart, it provokes metabolic changes in plants, and reduces their ability to uptake nutrients, their vigor, and their germination power. In severe cases, it can lead to plant death. Plant diseases brought about by pathogens, both pre- and postharvest, are a leading cause of yield and economic losses worldwide [63].

Research has shown that plants engage in several strategies to deter pathogenic MOs. The first line of defense is passive and physical. Trichomes, waxes, and cuticles are components of the epidermis that make it difficult for pathogens to establish themselves on the plant surface. Another barrier is made up of secondary metabolites and antimicrobial compounds that the plant secretes in response to pathogenic invasion. At this level, there are two possible immune responses triggered by the plant's molecular signaling system. One of them is systemic acquired resistance (SAR), which relies on the production of salicylic acid (SA). It acts against biotrophic and hemibiotrophic pathogens, and once deployed, offers long-term protection for future infections by the same kinds of MOs. The other response is induced systemic resistance (ISR), which occurs thanks to the production of jasmonic acid (JA) and can be used against necrotrophic pathogens [14].

Besides inducing plant resistance, many rhizosphere MOs are efficient biocontrol agents in their own right, since they inhibit plant pathogens that indirectly interfere with beneficial microbial consortia [64]. They may do this by outcompeting them, or by synthesizing substances with antibiotic, antifungal, and bactericidal properties; biosurfactants; hydrogen cyanide (HCN); and volatile organic compounds (VOCs) [29,65]. A great number of these compounds are produced by members of the genera *Pseudomonas* and *Bacillus* [66].

In spite of the abundant literature describing the relationship between PGPR and plant tolerance to biotic stress, very little is known about the specific part played by bacterial EPSs in this context. Since ISR is triggered through interactions with rhizobacteria, EPSs may act as signaling molecules in the process [67]. Moreover, biofilms may constitute a physical barrier to the entry of pathogens through the roots, just as they prevent the entry of excess sodium ions.

More generally, researchers believe that all the effects attributed to EPSs regarding the mitigation of abiotic stress (osmoprotection, higher nutrient uptake, higher tolerance

to extreme temperatures, etc.) have an indirect but evident impact on a plant's ability to resist disease. In other words, EPSs contribute to preserving plant health in the face of adverse abiotic factors, and this makes the plant more capable of withstanding pathogenic attack [12,68]. This is particularly important considering that biotic and abiotic stress can occur simultaneously. A study by Tewari et al. (2014) [69], for example, suggested that the EPSs produced by *P. aeruginosa* PF23 acted both as osmoprotectants and biocontrol agents in sunflower. Inoculated plants were not only more tolerant of high salinity, but also more successful at fighting infection by the phytopathogen *Macrophomina phaseolina*, and there was in fact a noticeable reduction in disease incidence.

6. Beneficial Rhizobacteria and Sustainable Agriculture

A remarkable improvement in agricultural productivity occurred from the late 1960s onwards, when fertilizers and pesticides started to be massively used, heavy rural machinery and advanced irrigation systems became widespread, and agricultural practices were generally intensified. This set of processes was dubbed the Green Revolution, and its negative consequences, such as pollution and biodiversity loss, soon became evident [70–72].

Modern agriculture still consists of manipulating the environmental structure of large areas. Natural biodiversity is replaced with a small number of plants (sometimes just one, in the case of monocropping) and farm animals, which are constantly exposed to exogenously applied chemicals (pesticides and fertilizers). These alterations in natural ecosystems affect native MOs, predators, and pollinizers, for which habitat specificity is reduced, but tend to favor pests through selection pressure. This means that pests are now more difficult to control, and that in an effort to do so, even higher doses of chemicals are applied [73,74]. Moreover, due to an increased use of water to grow plants, the uppermost layers of the soil are no longer as fertile as they used to be. In short, the higher yields which are the result of the Green Revolution have been achieved at a high environmental cost [75–78].

Pesticides can contaminate water bodies, phreatic zones, the air, the soil, and the plants themselves, and thus pose risks to food safety [79]. Since plants cannot absorb more than 30–40% of the nutrients they have at their disposal, fertilizers may equally end up in different environmental matrices where they endanger human, animal, and environmental health [80,81]. This has led many countries, especially developed ones, to seek sustainable alternatives for agriculture, i.e., farming practices that ensure productivity while minimizing the harm done to the environment. Some of these alternatives include rotating crops, planting legumes as cover crops, and the use of bioinputs [82,83].

Bioinputs are natural products that can improve crop yield and quality when applied on plants, without having a large impact on the environment [84,85]. They may be classified according to their origin (plant, animal, microbial) or according to their effects on plants, in which case they may be biopesticides or biofertilizers.

Biopesticides eliminate/repel pests and pathogens, or induce the plant's natural defenses against these threats (as when rhizosphere MOs induce SR). Biofertilizers (MO-based inoculants and biological stabilizers, humus, guano, manure, etc.) enrich the soil and/or stimulate plant growth through different active principles (mineral salts, free amino acids, organic chelates, lignosulfonates, humic and fulvic acids, hormones, etc.), whose positive effects on plant physiology and productivity have been widely documented [86]. Some bioinputs work as both biofertilizers and biopesticides, i.e., they may favor plant growth and also induce innate plant immunity against biotic stress factors [87,88].

In the last decades, a large amount of evidence has accumulated on the favorable effects of microbial consortia on plants: improved growth and resistance to stress and disease, as well as better soil quality, all of which lead to higher yields. For this reason, they can be ecofriendly and cost-effective farming tools to satisfy the nutritional demands of a growing global population in the short and long term [81,83].

Many microbial consortia used in agriculture include PGPR (see Figure 1) such as *Pseudomonas*, which solubilize less mobile nutrients in the soil so that they may be available

for the plant (phosphorus, iron, zinc), or *Rhizobium* and *Bradyrhizobium* spp., which improve the fixation of N_2 [23]. Seeing that the bacterial EPSs produced by many PGPR can help reduce the negative impact of stress on plants, contribute to soil quality, and promote phytohormone production, their application on crops may go a long way towards reducing the use of chemical pesticides and fertilizers which are used for the same purposes.

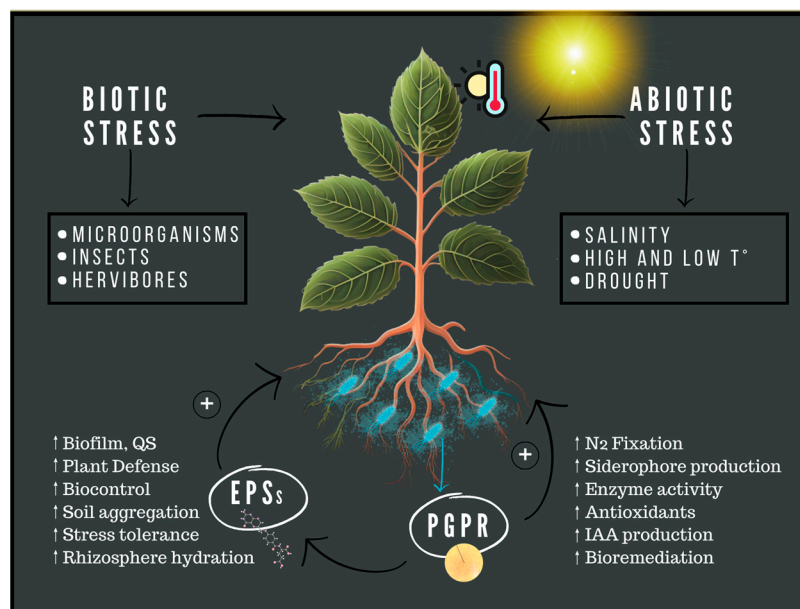


Figure 1. Diagram that summarizes the mechanisms of action of PGPR on plant growth, and the role of their EPSs in counteracting the effects of biotic and abiotic stress. The blue arrow indicates the presence of PGPR bacteria in the rhizosphere. The black arrows indicate, on the right side, the positive effects produced by PGPR bacteria and, on the left side, the beneficial actions produced by the synthesis of EPSs by PGPR bacteria.

7. Conclusions

Stress affects different aspects of plants and of plant-associated microbial communities in the soil, such as photosynthesis, respiration, and ion and nutrient absorption. This review summarized relevant findings on how the EPSs produced by beneficial bacteria (PGPR) can mitigate the damage caused by biotic stress (pathogenic attacks) and abiotic stress (adverse environmental factors including salinity, drought, and extreme temperatures). Bacterial EPSs are important constituents of bacterial biofilms on roots, as they can create a physical barrier that prevents the entry of pathogens and excess Na^+ in cases of salinity. They are capable of storing water and thereby improving its availability for the plant, with their synthesis being necessary for the production of proteins that can offset the effects of heat. The aggregates they form in the soil increase its permeability and stability, which benefits the plant by facilitating nutrient uptake and enabling recalcitrant and toxic compounds such as metal(loid)s to be degraded. Moreover, by promoting the accumulation of osmolytes they protect against desiccation and may act as signaling molecules that intervene by triggering the plant's innate immune response against pathogenic invasion. Although their specific mechanisms of action still need to be fully elucidated, EPSs produced by PGPR can be safe, ecofriendly, and cost-effective biotechnological tools for sustainable agriculture as they can protect plants from stress and stimulate their growth, thus ensuring adequate yields (i.e., food security) in a way that minimizes the impact of agriculture on the environment.

Author Contributions: Conceptualization, M.E.C., P.B. and W.G.; resources, M.E.C. and P.B.; investigation, M.E.C., F.B.A.S. and V.P.; writing—original draft preparation, M.E.C., F.B.A.S., V.P., P.B. and W.G.; writing, reviewing, and editing, M.E.C., P.B. and W.G.; supervision, P.B. and W.G.; funding acquisition, P.B. and W.G. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), grant number PIP 11220200100867CO. M.E.C., F.B.A.S., and V.P. have a fellowship from CONICET. P.B. and W.G. are career members of CONICET.

Data Availability Statement: All of the data are included in the manuscript.

Acknowledgments: The authors would like to thank Candela Winter for his expert help with the design of the illustration; Florencia Sgarlatta for proofreading the English of the manuscript; and Paul Hobson, a native English speaker, for editorial assistance.

Conflicts of Interest: The authors declare no conflict of interest.

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