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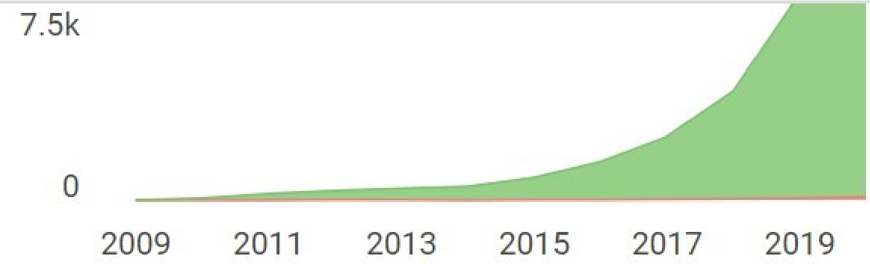

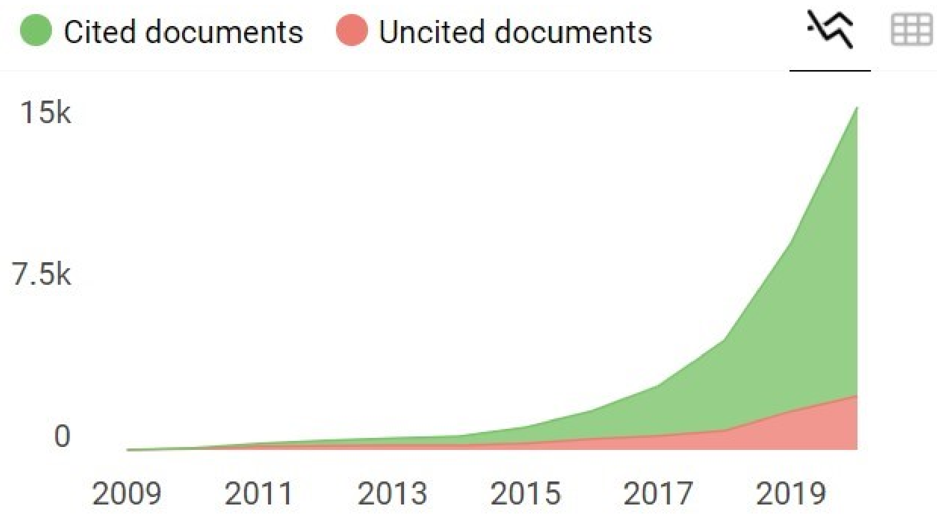

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Review

Bacterial Plant Biostimulants: A Sustainable Way towards Improving Growth, Productivity, and Health of Crops

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Abstract: This review presents a comprehensive and systematic study of the field of bacterial plant biostimulants and considers the fundamental and innovative principles underlying this technology. Plant biostimulants are an important tool for modern agriculture as part of an integrated crop management (ICM) system, helping make agriculture more sustainable and resilient. Plant biostimulants contain substance(s) and/or microorganisms whose function when applied to plants or the rhizosphere is to stimulate natural processes to enhance plant nutrient uptake, nutrient use efficiency, tolerance to abiotic stress, biocontrol, and crop quality. The use of plant biostimulants has gained substantial and significant heed worldwide as an environmentally friendly alternative to sustainable agricultural production. At present, there is an increasing curiosity in industry and researchers about microbial biostimulants, especially bacterial plant biostimulants (BPBs), to improve crop growth and productivity. The BPBs that are based on PGPR (plant growth-promoting rhizobacteria) play plausible roles to promote/stimulate crop plant growth through several mechanisms that include (i) nutrient acquisition by nitrogen (N_2) fixation and solubilization of insoluble minerals (P, K, Zn), organic acids and siderophores; (ii) antimicrobial metabolites and various lytic enzymes; (iii) the action of growth regulators and stress-responsive/induced phytohormones; (iv) ameliorating abiotic stress such as drought, high soil salinity, extreme temperatures, oxidative stress, and heavy metals by using different modes of action; and (v) plant defense induction modes. Presented here is a brief review emphasizing the applicability of BPBs as an innovative exertion to fulfill the current food crisis.

Keywords: abiotic stress; ethylene; jasomic acid; mineral solubilization; phytostimulants

1. Introduction

The global environment is changing continuously and the incidence of global warming caused by extreme climatic events is also on the rise, consequently disturbing the world ecosystems, including agro-ecosystems [1]. Such extreme changes in climate can affect the quality and quantity of crops severely by inducing various environmental stresses to crops, threatening food security worldwide [2]. An increase in global temperature, atmospheric CO_2 level, tropospheric O_3, and acid rains can cause multifarious chronic stresses to plants, reducing their capability to respond in case of pathogen attacks [3]. Among these stresses, drought, water scarcity, and soil salinization are the most problematic and complicated factors of agricultural losses resulting from human-induced climate changes [4]. Fluctuations in temperature and rainfall variations are key indicators of environmental stresses [5]. Elevated temperatures lead to an amplification of the rates of respiration and evapotranspiration in crops, a higher infestation of pests, shifts in weed flora patterns, and reduction in crop duration [6]. Water scarcity is also considered one of the prime global issues that have direct effects on agricultural systems and according to climate projections, its severity will increase in the future [7]. Water scarcity piercingly influences a crop's gaseous exchange capacity, causing the closure of stomata [8]. This leads to the impairment of the evapotranspiration and photosynthetic activities of plants, affecting overall biomass production [9]. Impaired evapotranspiration reductions also affect the nutrient uptake ability of plants [8]. In semi-arid and arid climatic zones where rainfalls are already less intense and sporadic, the damages caused by drought stress can be exacerbated due to excessive accumulation of salts in soil [10].

Furthermore, the liberal use of inorganic fertilizers and pesticides to increase crop productivity and meet the food requirement of the ever-growing human population, which is projected to reach 9.7 billion by 2050, has severely affected the health of agro-ecosystems and human beings. Confrontational challenges of improving agriculture production with limited arable land rely on sustainable technologies. Several technical advances have been suggested in the past three decades to increase the productivity of agricultural production processes by reducing toxic agrochemical substances such as pesticides and fertilizers. An emerging technology tackling these critical problems includes the creation of novel plant biostimulants and successful methods for their application [11–15]. Plant biostimulants differ from other agricultural inputs such as fertilizers and plant protection products because they utilize different mechanisms and work regardless of the presence of nutrients in the products. They also do not take any direct action against pests or diseases and therefore complement the use of fertilizers and plant protection products. According to the latest European Regulation (EU 2019/1009), a biostimulant is an EU fertilizer that seeks to promote processes for plant feeding, regardless of the product's nutrient quality, solely to boost the following plant or plant rhizosphere characteristics: (i) increased nutrient utilization efficiency, (ii) abiotic stress alleviation/tolerance, (iii) quality traits, and (iv) soil or rhizosphere supply of stored nutrients [16,17]. Over the past decade, microbiome research has changed our understanding of the complexity and composition of microbial communities. The intense interest of industry and academics in biostimulants based on live microbes has increased due to the reason that the growth and development of a plant can be improved under field conditions more effortlessly than other biostimulants [18,19]. Biostimulants are not nutrients, but encourage the utilization of nutrients or help foster plant growth or plants' resistance/tolerance to various types of stresses [9,20]. Beneficial plant fungi and bacteria can be considered the most promising microbial biostimulants [21]. The recent trend has underscored the fact that plants are not autonomous agents in their environments but are associated with bacterial and fungal microorganisms, and that many external and internal microbial interactions respond to biotic and abiotic stresses [22,23]. Therefore, biostimulants are gradually being incorporated into production systems to alter physiological processes in plants to maximize productivity [24].

Bacterial plant biostimulants (BPBs) comprise a major category of plant biostimulants. Plant growth-promoting rhizobacteria (PGPR) that colonize the plant rhizosphere are the most prominent group in this category [24]. These PGPR improve plant growth, control plant pathogens, improve nutrient and mineral uptake in plants, and increase plants' resistance to various types of biotic stresses and tolerance towards abiotic stresses (Figure 1). The representative beneficial groups of PGPR-based BPBs include nitrogen-fixing *Rhizobium*, *Azotobacter* spp., *Azospirillum* spp., *Pseudomonas* spp., and *Bacillus* spp. [25,26]. The present review describes the recent knowledge concerning beneficial BPBs and their role in improving crop health through various mechanisms. The article concludes by highlighting the main findings of an in-depth analysis of research articles published between 2015 and 2020, sorted using different databases such as Google Scholar, Science direct, Pub Med, Web of Science, etc.

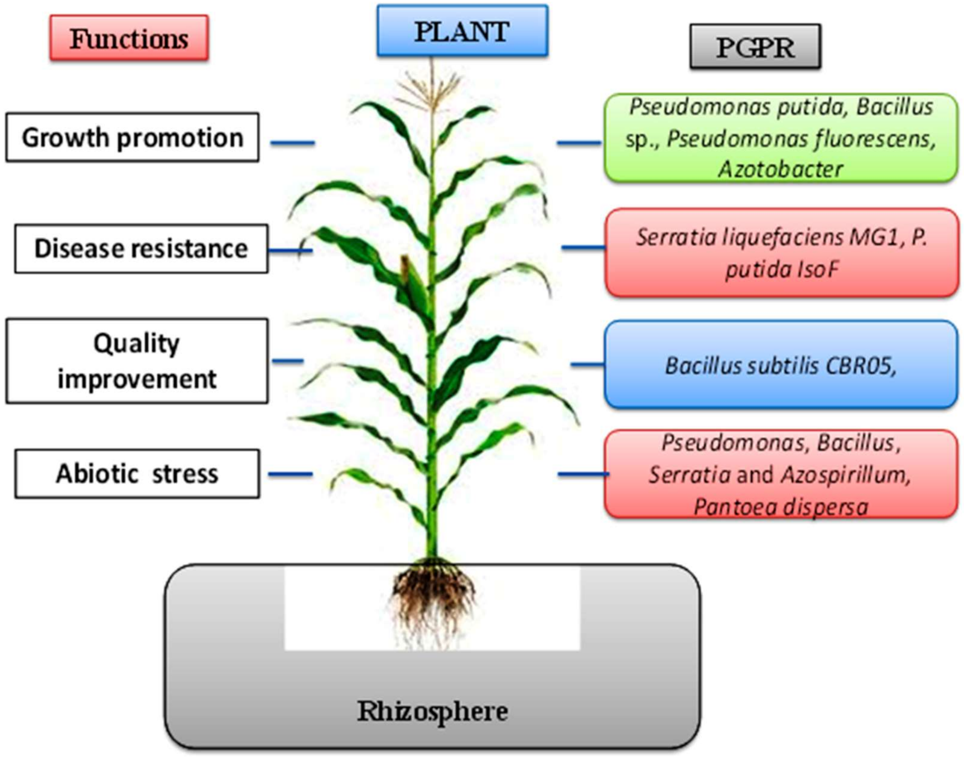

Figure 1. The beneficial influence of PGPR on crop plants.

2. Global Market for PGPR-Based Biostimulants

Biostimulants are emerging as an essential component in sustainable agricultural practices. Instances of environmental hazards and soil contamination from injudicious and excessive application of chemical-based products on crops have been a key issue for the industry in recent times. The global biostimulants market size was estimated at USD 1.74 billion in 2016, and projected to expand at a Compound Annual Growth Rate (CAGR) of 10.2% from 2017 to 2025. A rising focus on enhanced productivity, coupled with rapid soil degradation, is likely to drive the market over the forecast period. The global biostimulants market size was estimated at USD 2.30 billion in 2019 and is expected to reach USD 2.53 billion in 2020. The global biostimulants market is expected to grow at a compound annual growth rate of 10.2% from 2017 to 2025 to reach USD 4.14 billion by 2025 [27]. Although not all biostimulants are biological in nature [28], the bacteria are ancestral companions of a plant in all conditions. Moreover, according to the currently available literature, less than 25% of the commercial products of biostimulants are microbial based [9]. Table 1 provides a list of some popular PGPR-based commercial biostimulants [29–31]. Although some formulations contain fungal associations, the preparations are mainly based on PGPR.

Table 1. Examples of commercial PGPR-based plant biostimulants [29–31].

Commercial Products (Manufacturer)	PGPR Strains	Target Crops for Use	Target of Function
FZB24®fl Rhizovital 42® (ABiTEP GmbH, Germany)	*Bacillus amyloliquefaciens* and *B. amyloliquefaciens* sp. *plantarum*	Ornamentals, vegetable field crops	Phosphate availability and protection against pathogens

Inomix® Biostimulant, Inomix® phosphore, and Inomix® Biofertilisant (IAB (Iabiotec), Spain)	*B. subtilis* (IAB/BS/F1) and *B. polymyxa* (IAB/BP/01); *Saccharomyces cerevisiae; B. megaterium* and *P. fluorescens*; and *Rhizobium leguminosarum*, *Azotobacter vinelandii*, *B. megaterium*, and *Saccharomyces cerevisiae*	Cereals	Plant growth promotion increases root and shoot weight, strong root system
BactoFil B10® (AGRO.bio Hungary Kft., Hungary)	*Azotobacter vinelandii, Azospirillum lipoferum*, *P. fluorescens*, *B. circulans*, *B. megaterium*, and *B. subtilis*	Dicotyledons (potato, sunflower, rapeseed)	Soil amelioration; produce plant growth-promoting hormones auxin, gibberellins, and kinetin; N_2 fixation; a biocontrol agent
Bio-Gold (BioPower, Sri Lanka)	*Pseudomonas fluorescens* and *Azotobacter chroococcum*	All agricultural and horticultural crops	Growth promotion via nitrogen fixation, drought tolerance, control of root rot and wilt diseases, phosphorus solubilization
Cedomon® (Lantmannen BioAgri AB, Sweden)	*P. chlororaphis*	Barley and oats	Highly effective against various types of seed-borne diseases
Rhizosum N Liquid PSA (Mapleton Agri Biotec Pty Limited, Australia)	*Azotoformans* (N_2-fixing bacteria) and *Pseudomonas sp*	Wheat	Phosphate availability, N_2 fixation, plant growth promotion
BactoFil A10® (AGRO.bio Hungary Kft., Hungary)	*Azotobacter vinelandii*, *Azospirillum brasilense*, *P. fluorescens*, *B. polymyxa*, and *B. megaterium*	Monocotyledons (cereals)	Increased soil nutrient content that results in plant growth promotion

Micosat F® Uno;
Micosat F® Cereali
(CCS Aosta Srl, Italy)
Agrobacterium radiobacter AR 39,

subtilis BA 41
and flowers
Increased nutrient and water absorption, increases stress tolerance and enhances ISR
Paenibacillus durus PD 76, *B. subtilis*
Cereals, soybeans,
F
ruits,
vegetable
s,
Streptom
yces sp.
SB 14,
and *B.*

beet, tomatoes,
BR 62, and *Streptomyces* spp.
ST 60

Table 1. *Cont.*

Commercial Products (Manufacturer)	PGPR Strains	Target Crops for Use	Target of Function
		and sunflowers	
Bioscrop BT16 (Motivos Campestres, Portugal)	*Bacillus thuringiensis* var. kurstaki	Deciduous fruit trees, horticultural brassicas, cotton, citrus, cauliflower, olives, pepper, banana, and tomato	Protection against pests (beetles)
Amase® (Lantmannen Bioagri, Sweden)	*Rhizobium*, *Azotobacter*, *Pseudomonas*, *Bacillus*, and *Chaetomium*	Cucumber, lettuce, tomato, pepper, eggplant, cabbage, and broccoli	Growth promotion, quick production of the large and strong root system, and increases stress tolerance
PGA® (Organica technologies, USA)	*Bacillus* sp.	Fruits and vegetables	Improved biomass accumulation, stress tolerance
Nitroguard®	*Azorhizobium caulinodens* NAB38, *Azospirillum brasilense* NAB317, *Azoarcus indigens* NAB04, and *Bacillus* sp.	Cereals, rapeseed, and sugar	Growth promotion via nitrogen fixation
TwinN® (Mapleton Agri Biotec Pty Ltd. Australia)	*Azospirillum brasilense* NAB317, *Azoarcus indigens* NAB04, and *A. caulinodens* NAB38	Beet, sugarcane, and vegetables	Helps with nitrogen fixation and phosphorus solubilization and produces growth-promoting hormones
Symbion®-N, Symbion®-P, and Symbion®-K (T. Stanes & Company Ltd., India)	*Rhizobium*, *Azotobacter*, *Azospirillum*, *Acetobacter*; *B. megaterium* var. *phosphaticum*; and *Frateuria aurantia*		Promotion of plant growth, improved root and shoot weight, and a stronger root system
Ceres® (Biovitis, France)	*Pseudomonas fluorescens*	Field and horticultural crops	Biocontrol agent against pathogens
Gmax® PGPR (Greenmax AgroTech, India)	*P. fluorescens*, *Azotobacter*, and *phosphobacteria*	Field crops	Nitrogen and phosphatic nutrition, disease prevention and helps in plant growth promotion.

3. Bacterial Plant Biostimulants, Beneficial Effects, and Mode of Action

Bacteria are known to interact with plants in all possible ways [32], including (i) continuum of symbiosis; (ii) bacteria niches extending from the substrate to the interior of cells, which are called intermediate locations for rhizosphere and rhizoplane; (iii) associations that are transient or lifelong; and (iv) functions that affect lots, including engagement in biogeochemical cycles, the supply of nutrients, increased nutrient consumer efficiency, induction of resistance, increased stress tolerance, plant growth regulators, and morphogenesis control. In this regard, a large amount of work presented in recent literature has a sharp emphasis on potential applications of the bacterial association of plants largely as agents for promoting plant growth and maintaining soil and crop health [33–36]. Plant growth-promoting bacteria are generally associated with numerous (if not all) crop plant species and are habitually present in varied environments. The most extensively investigated category of PGPB is the plant growth-promoting rhizobacteria (PGPR) primarily colonizing the surfaces of roots and closely adhering to the soil interface, namely, the rhizosphere. As overviewed by recent reviews [37–39], several PGPR can enter the root interior, thereby establishing endophytic associations. Some of them can even surpass the endodermis barrier, transcending from root cortex to vascular system, and afterward thrive as endophytes (inside stem, tubers, leaves, and other organs). The extent of the endophytic associations of host plant tissues (and/or organs) reflects the capability of these bacteria to selectively acclimatize to various specific ecological niches [40,41]. As a result, such intimate bacterial associations with host plants are formed with no damage to the plant [42,43]. In regard to taxonomic, functional, and ecological diversity in developing agriculture biostimulants, PGPR seize the most prominent place.

Although numerous soil bacteria were documented to help plant growth promotion and production, the mode(s) of action by which the bacteria exhibit beneficial activities are hardly understood. The molecular basis for association processes between bacteria and crop plants that induce/stimulate physiological modifications is starting to be understood, primarily because of the emerging approaches to "omics." A varied number of pathways have been employed to aid the acquisition of plant nutrients, including improved plant root surface, phosphorus solubilization, nitrogen fixation, production of HCN, and development of siderophores, which are further discussed under subsections [44]. PGPR differ and have consequences for all facets of the plant life cycle: promoting growth and nutraceutical values of plants, morphological and physiological development, stress responses (biotic and abiotic), interactions of agro-ecosystems with other species forms, and enhanced production. Numerous direct and indirect mechanisms are involved in the development of these responses that are shown in Figure 2.

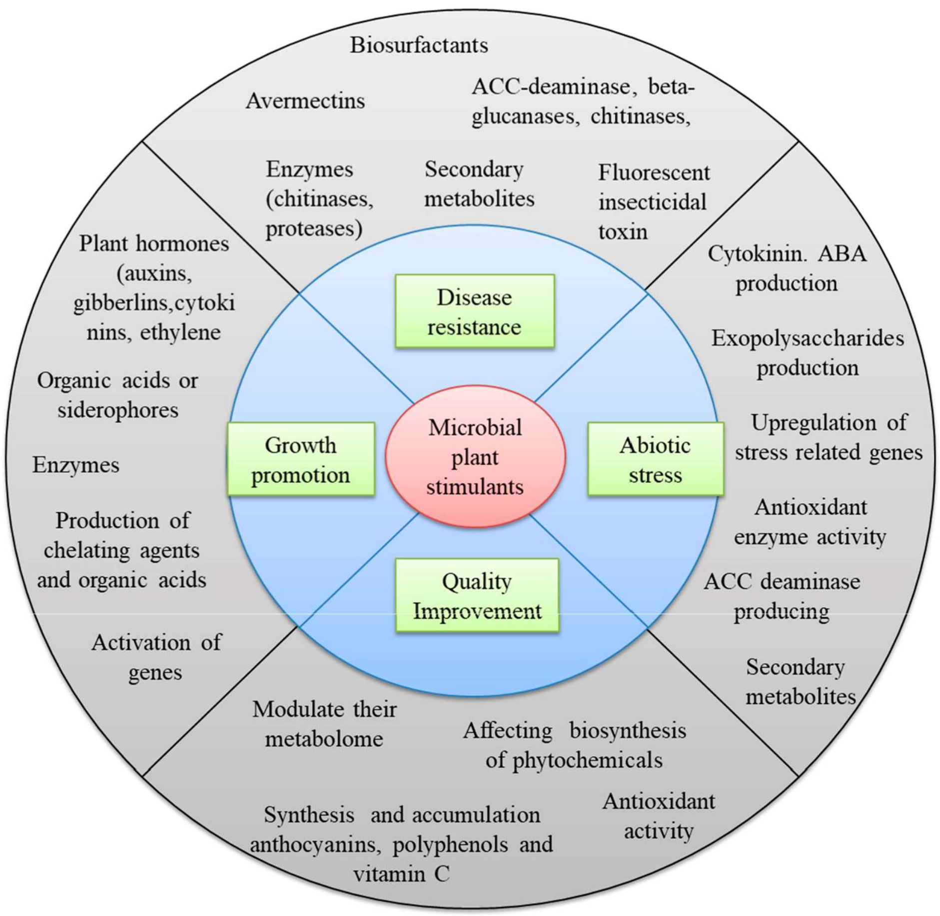

Figure 2. Mode of action of PGPR on the growth of crop plants.

3.1. Plant Growth Promotion and Nutrient Acquisition

The modulation of bacterial behavior has tremendous potential for the procurement of nutrition for plants. PGPR formulations are a significant biostimulant class, as they allow root growth, mineral availability, and efficiencies in the utilization of nutrients in the crop rhizosphere to increase crop growth [45]. Many PGPR are known to stimulate phytohormone production through a combination of various mechanisms [46–53] represented in Table 2.

Table 2. Beneficial effects of reported PGPR biostimulants on different crops and their modes of action.

PGPR Biostimulant	Crop	Beneficial Effects	Mode of Action	References
Bacillus sp.	Lettuce	Growth, biomass, and yield of plants	Increased production of phytohormones and availability of nutrients	[46]
Azospirillum brasilense, *Gluconacetobacter diazotrophicus*, *Herbaspirillum seropedicae*, and *Burkholderia ambifaria*	Onion	Plant growth, crop yield, and increased number of bulbs	Production of plant hormones and solubilization of nutrients that cause uptake of nutrients	[47]
Bacillus pumilus, *B. mojavensis*, *B. Amyloliquefaciens*, and *P. putida.*	Tomato	Growth and production and nutrient uptake	Synthesis of indole-3-acetic acid N_2-fixation and P solubilization	[48]
PGPR *(Bacillus subtilis)*	Tomato	Improved fruit quality	Enhanced production of phenols, flavonoids, carotenoids, and antioxidants	[49]
Pseudomonas aeruginosa	Wheat	Nutrient uptake	N_2 fixation involving many reactions and synthesis of organic acids	[50]
Azospirillum brasilense (Sp7b and Sp245b)	Cucumber, lettuce, and tomato	Enhanced germination, root length, and weight; vigor index of germinating seeds	Production of a substantial amount of phytohormones such as IAA	[51]
Bacillus pumilus and *Pseudomonas pseudoalcaligenes*	Rice	Stimulated growth and production	Phosphate solubilization and production of IAA, gibberellins, siderophores, and ACC utilization	[52]
Azospirillum brasilense	Maize, sorghum, wheat, barley, and legumes	Biostimulated growth and production	Synthesis of indoleacetic acid (IAA), nitric oxide, carotenoids, and numerous cell surface components	[53]

3.1.1. Phytohormone Stimulation

Auxins such as 3-Indole Acetic Acid (IAA) are involved in processes such as the germination of seeds, control processes for vegetative increase, and the establishment of lateral or adventurous roots, and can mediate light and heavy reactions, photosynthesis biosynthesis of metabolites, and stress tolerance [54]. It has been observed that PGPR produces hormones that provide protection and wall-related transcription changes [55], induce long roots, increase the biomass of roots, and reduce the density and dimensions of stomata [56], in addition to activating auxin reaction genes that enhance plant development [21]. As IAA producers, separate PGPR genera have been recognized, such as *Rhizobium* [57], *Aeromonas* and *Azotobacter* [32], *Bacillus* [21], and *Pseudomonas* [58]. A great number of PGPR produce cytokinins and gibberellins [59], although the roles of bacteria in the regulation of plant hormones and the bacterial mechanism involved in their synthesis are largely not understood yet. Some strains of PGPR can support relatively large quantities of gibberellins, which contribute to increased growth in plants [60]. PGPR also regulate the proper amounts of ethylene to maintain plant growth, as confirmed by previous studies [61].

3.1.2. Nitrogen

Nitrogen (N) is a very essential macronutrient needed for plant growth and development, but it is not available to most plants due to its inertness. Atmospheric nitrogen (N_2) is converted into ammonia by PGPR by nitrogen fixation and this source of nitrogen (ammonia) can be utilized by crop plants for productivity purposes [62]. The application of N_2-fixing bacteria as growth enhancers has become known as one of the most effective and environmentally feasible methods and concurrently replaces the use of inorganic nitrogen fertilizers [63]. Biological nitrogen fixation (BNF) is accomplished by free-living microorganisms such as *Azotobacter, Azospirillum, Bacillus, Enterobacter, Pseudomonas, Burkholderia*, and *Serratia,* etc., and symbiotic or associated microorganisms such as *Rhizobium, Bradyrhizobium,* and certain species of *Azospirillum* sp., which contribute fixed nitrogen to the associated crop plants [64,65]. Moreover, a small group of woody non-legumes, known as actinorheic plants, can also be colonized by diazotrophs belonging to the *Frankia* sp., which can induce the development of nitrogen-fixing root nodules. Leguminous inoculants are the first example of industrial bacterial products in agriculture and are now the most commonly used inoculants in agriculture [66]. Beginning in the early 21st century, interest began rising around the mass production of commercial inoculants from wild, live N-fixing bacteria, including *Azoarcus* sp., *Burkholderia* sp., *Gluconacetobacter* sp., and *Diazotrophicus* sp. These free-living diazotrophs are more efficient in providing N to a wider variety of crops than rhizobia. *Azospirillum* sp.-based commercial inoculants from small and mediumsized businesses worldwide have improved the production yields of different cereal crops effectively [67]. Other bacteria that do not primarily fix N_2 have also shown increased N in many plants possibly due to root growth enhancement, allowing plants to gain more soil [68] and thus, increase the efficiency of nitrogen usage.

3.1.3. Phosphorus

Phosphorus is another essential macronutrient in metabolic and physiological processes in plants such as photosynthesis, biological oxidation, and cell division [69], and is also an important nutrient for crop growth and productivity. Chemical phosphorus fertilizers are subjected to chemical fixation (in soil) with some other metal cations and are lost by leaching, and their unavailability to plants limits their ability to perform these crucial functions [70]. The application of stimulants that contain PGPR that are capable of solubilizing insoluble phosphate by discharging organic acids increases the accessibility of this element to crop plants, thereby improving soil fertility and productivity [71,72]. Numerous strains among bacterial genera including *Pseudomonas, Rhizobium, Bacillus,* and *Enterobacter* are the most potent P-solubilizers. Phosphorus solubilizing bacteria (PSB) may facilitate plants' access to the non-labile phosphorus reserve by liberation of its recalcitrant form and making it more accessible to crops by secreting organic acids and/or hydrochloric ions. Likewise, PSB-manufactured phytase can release reactive phosphates from organic compounds [73].

3.1.4. Potassium

Potassium is another fundamentally important macronutrient required for crop growth and improvement owing to the rhizospheric deficiency of crops and consequently has always been a major constraint in crop production [74,75]. The shortage of the solubilized form of rhizospheric potassium is also because it tends to form insoluble complexes when applied as an inorganic fertilizer. However, PGPR can solubilize insoluble potassium through secretions of inorganic acids and by making it available to crop plants, thus improving the agricultural productivity and health of crops [76,77]. Hence, they offer an attractive option as biostimulators in place of conventional fertilizers. PGPR such as *Bacillus edaphicus, Acidothiobacillus* sp., *Ferrooxidans* sp., *Pseudomonas* sp., *Bacillus mucilaginosus, Burkholderia* sp., and *Paenibacillus* sp. have been known to release potassium in its available form from potassium-bearing minerals in soils [78].

3.1.5. Micronutrients

Many strains of bacteria improve Fe (iron) availability by generating siderophores or organic acids. The commercial preparation of the genus *Acidithiobacillus ferrooxidans* developed and produced by AgriLife (India) [79] solubilizes Fe through the release of organic acids [80]. Zinc is another crucial micronutrient that is needed in smaller quantities for the healthy growth and improved production of crops. About 96–99% of the zinc applied to crop plants is converted into an insoluble form that depends on soil type and other physiological reactions [81]. Several bacteria strains increase Zn mobilization, thereby increasing Zn uptake by plants and boosting the yield in many crops [82]. Although the mechanisms involving Zn mobilizers still remain uncertain, they are more likely similar to PSBs and Fe mobilizers and involve mainly the production of organic acids and chelating agents.

3.2. Quality Improvement of Crop and Yield by Bacterial Plant Biostimulants

Plant biostimulants, which increase plant evolution, flowering, fruit forming, and crop production, can provide a desirable and environmentally friendly agricultural modernization [83]. A variety of living and non-living bacterial isolates such as *Bacillus licheniformis, Bacillus megaterium, Bacillus pumilus, Bacillus safensis, Microbacterium* sp., *Nocardia globerula, Pseudomonas fluorescens, Pseudomonas fulva, Pseudoxanthomonas dajeonensis, Rhodococcus coprophilus, Lactobacillus plantarum, Sphingopyxis macrogoltabida, Streptomyces* sp., *Bifidobacterium bifidus, Lactobacillus acidophilus, Lactobacillus* sp., *Lactobacillus buchneri, Lactobacillus paraplantarum, Lactobacillus delbrueckii,* and *Lactobacillus pentosus* have been reported to increase concentrations of total carbohydrates, nutrients (magnesium, nitrogen, and phosphorus, etc.), pigments (such as chlorophyll, carotenoids), and antioxidant substances and therefore improve plant quality, productivity, and yield [21,83,84]. As an example, the impact on common bean plants cultivated under water stress shows substantial enhancement in the phenolic contents of the inoculated plants of four biostimulant products with *Bacillus subtilis* in their formulations [84]. In addition, by inoculation of the *Bacillus subtilis* CBR05 PGPR strain, the quality of tomatoes is known to improve for the carotenoid profile (carotene and lycopene) [49]. The influence of the biopreparation containing some bacterial species such as *Streptomyces* sp., *Bacillus subtilis,* and *Pseudomonas fluorescens* on the growth enhancement of fruits through organic farming was reported as improving the growth of sour cherry and apple trees [85]. The regulation of horticultural primary and secondary metabolisms in microbial biostimulants culminates in the synthesis and build-up of lipophilic as well as hydrophilic antioxidant molecules, also referred to as phytochemicals [86,87]. Microbial biostimulant applications containing beneficial bacterial cultures often improve fruit quality by suppressing diseases that may cause economic loss [88].

3.3. Abiotic Stress Tolerance Induced by Bacterial Plant Biostimulants

Global climate change dictates that abiotic stresses, particularly nutrient deficiency, salinity, drought, hypoxia, and heat stress, are responsible for 60–70% of yield deficit [14]. Under these situations, plant biostimulant application is suggested as an effective agronomic method to improve tolerance to adverse soil and harsh environmental conditions and to address the adverse effects of the suboptimal conditions on agricultural and horticulture crops [9]. Plant growth rhizobacteria (PGPR) can enhance plant reactions to abiotic pressures (Figure 3), and promote physical, chemical, and biological activities [89] through various mechanisms [90–100], as presented in Table 3. Much work has been done on bacterial isolates that can be employed to promote the mitigation of abiotic stress in various crops.

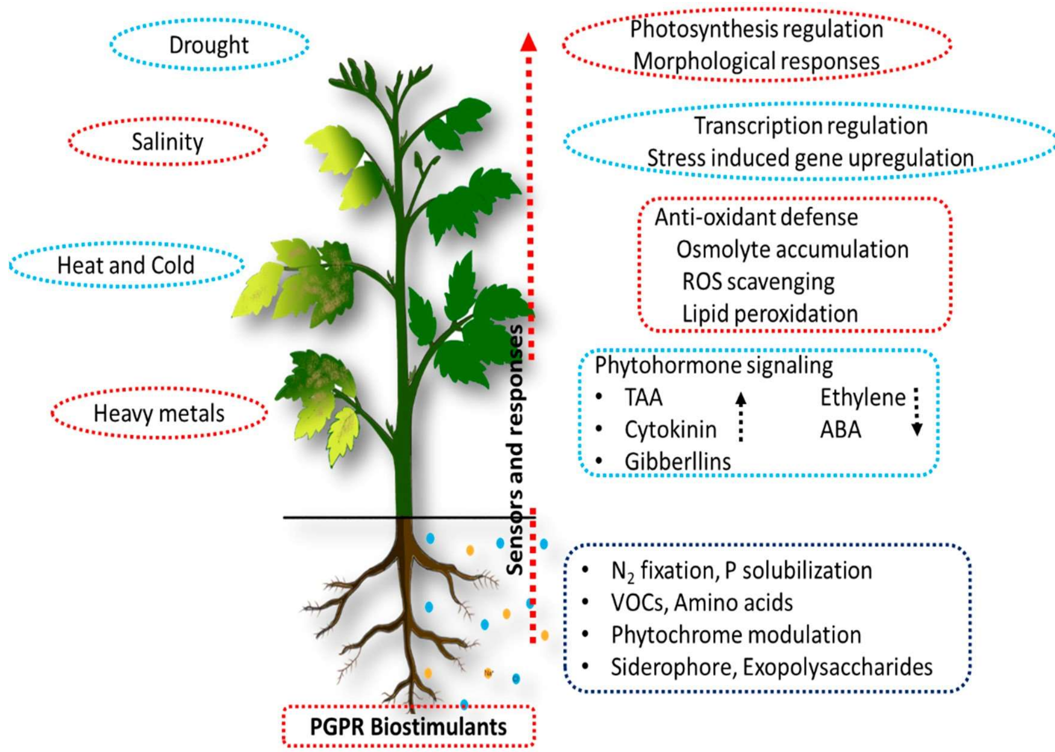

Figure 3. Illustration of abiotic stress tolerance induced by bacterial plant biostimulants.

Table 3. Influence of PGPR biostimulants on abiotic stress tolerance in various crop plants.

PGPR Biostimulants	Crop Plants	Type of Abiotic Stress	Mode of Action	References
Glutamicibacter sp. YD01	Rice	Salt tolerance	Ethylene mediation, reacive oxygen species (ROS) accumulation, maintaining photosynthetic efficiency and ion homeostasis, increasing expression of stress-related genes, the activity of ACC oxidase, and acquisition of K^+	[90]
Bacillus sp., *Azospirillum lipoferum*, *Azospirillum brasilense*, and *Pseudomonas stutzeri*	Wheat	Salt stress	Production of phytohormones and osmoregulators, and enzyme (ROS scavenging) activation	[91]
Gluconacetobacter diazotrophicus Pal5	Red rice	Drought stress alleviation	Increased production of Abscisic acid (ABA), osmoprotectants (proline and glycine betaine) and e AT-hook motif nuclear-localized (AHLs)	[92]
Gluconacetobacter diazotrophicus Pal5	Red rice	Water stress alleviation	Increased ABA production, enhanced chlorophyll synthesis, and increased trehalose and α-tocopherol content in roots.	[93]
Azospirillum spp. (Az19)	Maize	Water/drought stress alleviation	Increased production of proline, trehalose (glutamate) and glycine-betaine	[94]

Table 3. *Cont.*

PGPR Biostimulants	Crop Plants	Type of Abiotic Stress	Mode of Action	References
Bacillus spp XT13, XT38, and XT110	Maize	Drought stress	Increased proline content accompanied by reduced Ascorbate Peroxidae (APX) and glutathione reductase (GR) activities, increased nutrient uptake	[95]
Pseudomonas entomophila (PE3)	Sunflower	Salinity stress alleviation	Exopolysaccharides, IAA, gibberellic acid, and siderophores	[96]
P. fragi, *P. proteolytica*, *P. fluorescens*, *P. chloropaphis*, and *Brevibacterium frigoritolerans*	Bean	Cold stress	Reduced chill injury, lipid peroxidation, and ice-nucleating activity corresponding to ROS level, and stimulation of apoplastic antioxidant enzyme activities	[97]
Pseudochrobactrum kiredjianiae	Wheat	Cold stress	Growth promotion and biocontrol	[98]
Pseudomonasfluorescens	Maize	Heavy metal stress	Production of IAA	[99]
Azotobacter chroococcum	Maize	Heavy metal stress	Production of siderophores, ammonia, and 1-aminocyclopropane-1-carboxylate deaminase (ACCD)	[100]

3.3.1. Drought Stress

Recent attention has turned to the application of beneficial microorganisms that mediate drought tolerance and improve plant water-use efficiency. These efforts have been augmented due to technological advances in next-generation sequencing and microbiomics [101,102]. The application of plant growth-promoting rhizobacteria (PGPR) is considered a sustainable synergistic biological approach to cope with water deficiency in crop production [103]. PGPR can impart tolerance to drought stress by releasing phytohormones, volatile compounds, ACCD, exopolysaccharides, and antioxidants by regulating osmolytes and stress-responsive genes and aggravating modifications in the roots [102–104].

3.3.2. Salinity Stress

Soil salinization accounts for more than 6% of global land, rendering 22% and 33% of total cultivated and irrigated agrarian land, respectively, under stress that adversely affects crop productivity [105]. By the year 2050, approximately 50% of arable area will be under threat due to soil salinity, as it increases rapidly at the rate of 10% annually due to numerous reasons including implausible irrigation practices, irrational fertilization, poor drainage, and climate change [106,107].

PGPR can alleviate salinity stress in plants through many synergistic mechanisms including osmotic regulation by prompting accumulation of osmolytes and signaling of phytohormones, increasing nutrient uptake and attaining homeostasis of ions, and reducing oxidative stress through enhanced antioxidant activity, volatile organic compounds (VOCs), and photosynthesis amelioration [108,109].

3.3.3. Heat Stress

The prime alarming effect of climate change is the rise in global temperature and is directly linked to crop productivity. High temperatures increase respiration and transpiration rates, alter the allocation of photosynthates, and affect photosynthesis (particularly C_3 plants), thereby influencing plant physiology [110]. Intense heat can cause plant cell protein denaturation or affect cell wall and membrane permeability [111]. PGPR help mitigate the heat stress in plants through properties such as the production of osmolytes and the reduction of carbon flux [112]. They can secrete several polysaccharides involved in biofilm formation, covering root nodules that enhance the water retaining capability of plant roots. PGPR, especially the heat-tolerant/evolved strains, possess the ability to enhance the production of lipopolysaccharides (LPS) and exopolysaccharides (EPS) and specific proteins known as heat shock proteins (HSPs) [113]. The application of ethylene reducing bacteria, especially with ACC deaminase activity, can avoid the detrimental effects of heat stress in plants [3].

3.3.4. Cold Stress

Cold stress is detrimental to plants, as it directly affects the rate of nutrient and water uptake, which may lead to cell starvation, desiccation, and consequent death. Reduced metabolism, which occurs in cold tension, results in photo inhibition, inhibition of the activity of photosystem II, and destabilization of the phosphorus lipid bilayers, thereby affecting the normal architecture of cell membranes [44,114]. In harsh environments, psychrophilic (cold-adapted) microorganisms can thrive and have possible resistance enhancement pathways that benefit plants [115]. Cold-adapted PGPR belong to various genera, including *Pseudomonas*, *Bacillus*, *Arthrobacter*, *Exiguobacterium*, *Paenibacillus*, *Providencia*, and *Serratia*. There are several attributes of psychrotolerant PGPR that make their application as biostimulants beneficial in alleviating cold stress. These attributes include solubilization of nutrients, Fe-chelating compounds, ACC deaminase production, IAA, and bioactive compounds. In plants, cold tolerance can be imparted by PGPR through the enhanced accumulation of carbohydrates, the regulation of stress-responsive genes for modulation of osmolytes, and increasing specific proteins, including cold shock proteins (CSPs) [113]. In addition, the application of such biostimulants with the ability to outcompete the icenucleating activity of microorganisms is becoming an effective method to overcome the losses caused by cold/frost damage [3].

3.3.5. Heavy Metal Stress

Heavy metal stress due to hyperaccumulation of toxic metals, including Hg, As, Cd, Pb, and Al, greatly decreases crop productivity. Their accumulation in the soil directly affects its texture and pH, which consequently reduces crop growth by exerting negative effects on several biological processes [116]. In plants, heavy metal stress shows both direct effects, including cytoplasmic enzyme inhibitions and cell structure damage as well as indirect consequences, including oxidative stress through several indirect mechanisms (e.g., glutathione depletion or binding to proteins—sulf-hydryl (SH) groups) or inhibiting anti-oxidative enzymes, inducing ROS-producing enzymes (e.g., Nicotinamide Adenine Dinucleotide Phosphate Hydrogen (NADPH) oxidases) [117]. Heavy metal-tolerant PGPR such as *Pseudomonas*, *Bacillus*, *Methylobacterium*, and *Streptomyces* can reduce the deleterious effects of heavy metals and improve the growth and yield of crops. PGPR biostimulants are very effective in alleviating the toxicity of heavy metals in plants. They reduce the translocation of heavy metals to different parts of the plant by altering their mobilization through chelation, precipitation, complexation, redox reactions, and adsorption [118,119]. Rhizospheric bacteria also release extracellular polymeric substances (EPS) [93] such as polysaccharides, glycoprotein, lipopolysaccharide, and soluble peptide, which possess a substantial quantity of anion binding sites to help in the removal or recovery of heavy metals from the rhizosphere via biosorption. However, in highly contaminated sites, the mobilization and consequent bioavailability of heavy metals in excess by siderophores, organic acids, or through bioleaching remains debatable.

3.4. Disease Suppression/Defense against Plant Pathogens through Antagonism

Nowadays, the biological control of pathogens is managed by the activities of several microbiomes. Additionally, PGPR are known to develop resistance to various diseases through various direct or indirect mechanisms [120–128], shown in Table 4. The application of bacterial biostimulants encourages the healthy growth of crops through the suppression of different plant pathogens and pests. The PGPR inhibition of microbial/pathogen growth occurs synergistically through several chief mechanisms, including antibiosis, volatile organic compound (VOC) production, extracellular enzymatic lysis, bacteriocin, and siderophore-mediated inhibition [129].

Table 4. Influence of PGPR biostimulants on biotic stress resistance in different crop plants.

PGPR Biostimulants	Crop	Biotic Stress	Mode of Action	References
Bacillus cereus (PX35), *Serratia sp.* XY21, and *Bacillus subtilis* SM21	Tomato	Root-knot nematodes	Synergistic biocontrol	[120]
Pseudomonas aeruginosa LV	Tomato	Bacterial stem rot	Extracellular-bioactive compounds (phytoalexins, flavonoids, defensins, proteins, and phenolics)	[121]
B. subtilis 26DCryChS	Potato	Late blight agent and damaged by Colorado potato beetle larvae	Production of Cry1Ia δ-endotoxin, stimulating transcription of jasmonate reliant genes promoting transcription of salicylate reliant gene (PR1)	[122]
Lactobacillus plantarum PM411 and *Lactobacillus plantarum* TC92	Strawberry	Disease prevention in strawberry and kiwi fruit	Antimicrobial metabolites (lactic acid) production that disrupts pathogen's cell membranes	[123]
B. subtilis BS2	Tomato	Tomato wilt	Production of defense enzymes such as peroxidase, polyphenol oxidase, chitinase, and phenylalanine	[124]
Bacillus safensis and *Bacillus altitudinis*	Cabbage	Black rot	IAA production	[125]
B. velezensis, *B. mojavensis*, and *B. safensis*	Soybean	Phytophthora root rot	IAA production	[126]
Bacillus cereu, *B. subtilis BSV*, and *B. subtilis BSP*	Ginger	Blister blight	1-aminocyclopropane,1, carboxylic acid production	[127]
B. cepacia GRB35	Ginger	Soft rot in ginger	Fungicide production	[128]

3.4.1. Antibiosis

PGPR produce antibiotics that are the most significant antagonistic agents effective against phytopathogens. Antibiotics produced by PGPR are known to have antimicrobial, antiviral, cytotoxic, insecticidal, antihelminthic, and phytotoxic (against weeds) effects [130,131]. Antibiotic production usually allows better competition between microbes and thus enhances the efficiency of beneficial PGPR associations [132]. Numerous species of *Pseudomonas* produce a broad range of antifungal antibiotics, including butyrolactones, cepaciamide A, ecomycins, 2,4-diacetylphloroglucinol (2,4-DAPG), phenazines, pyrrolnitrin, pyocyanin, pyoluteorin, oomycin A, rhamnolipids, N-butylbenzene sulfonamide, and viscosinamide [133]. *Bacillus* species also secrete a large variety of antibiotics, including bacilysin, bacillaene, difficidin, mycobacillin, rhizocticins, sublancin, subtilintas A, subtilosin A, etc. They also produce numerous lipopeptide biosurfactants, such as bacillomycin, iturins, surfactin, etc. with antibiotic activity [134].

3.4.2. VOC Antagonism

In plants, VOCs help in the biocontrol of bacteria and fungi nematodes and also act as elicitors of the induced systemic resistance against phytopathogens [135]. Several VOC metabolites with antagonistic activities are secreted by PGPR. These include benzene, cyclohexane, 2-(benzyloxy)-1-ethanamine, methyl, dodecane, decane, 1-(*N*-phenyl carbamyl)-2morpholinocyclohexene, benzene (1-methylnonadecyl), dotriacontane, 1-chlorooctadecane, tetradecane, and 11-decyldocosane, although their type and quantities released vary among different species [136]. Among VOCs, HCN produced by rhizospheric bacteria is known to play an important function in the biocontrol of phytopathogens and pests [137]. *Pseudomonas* sp. synthesizing HCN can inhibit some pathogenic fungi [138]. HCN released by *P. chlororaphis* O6 is known to show nematicidal activity [139]. In addition, VOCs (acetoin and 2,3-Butanediol) secreted by *Bacillus* spp. are very effective fungal inhibitors [140]. In addition to biological control, VOCs are associated with beneficial tradeoffs in attracting pollinators via the mediation of communication signals [141].

3.4.3. Lysis by Extracellular Enzymes

Lytic enzymes produced by PGPR provide another effective mechanism for combating pathogen attacks. Rhizobacteria release extracellular enzymes such as chitinase and β-1,3glucanase, which are involved in cell wall lysis, killing pathogens [142]. Since the fungal cell wall is mainly composed of chitin and β-1,4-*N*-acetyl-glucosamine, rhizobacteria secreting chitinase and β-1,3-glucanase are potent antifungals. For example, *P. fluorescens* LPK2 and *S. fredii* KCC5 release β-glucanases and chitinases and suppress wilts caused by *Fusarium udum* and *F.oxysporum* [133]. Bacteria with protease, lipase, and chitinolytic activities have been reported to show insecticidal activity [143]. PGPR with ACC deaminase activity also play a very important role in all types of stresses, including biocontrol.

3.4.4. Bacteriocins

Bacteriocins or bacterial toxins are narrow-spectrum antimicrobial peptides produced by bacteria, including PGPR. Their production is another mechanism for eliminating competitor strains that are narrow-spectrum, proteinaceous antibiotics that target and kill related bacterial species [144]. Bacteriocins are produced by both Gram -negative (colicins, S-piocins, microcins, etc.) as well as Gram -positive (nisin, helvecin, mersadicin, etc.) bacteria [145]. The direct application of bacteriocins has shown promising results under laboratory conditions against bacterial spot disease in tomato [146]. Typically, bacteriocins are highly selective of their targets without affecting off-targets and provide a safer substitute to field applications of chemicals [147].

3.4.5. Siderophores

Siderophores are the largest class of known compounds that can bind and transport, or shuttle, iron (Fe). These low-molecular-weight coordination molecules are excreted by a wide variety of fungi and bacteria to aid Fe assimilation [148]. Siderophore production by PGPR is an indirect mechanism involving the reduction or prevention of destructive effects caused by phytopathogens [149]. Siderophores possess an antagonistic effect and prevent the escalation of other pathogenic bacteria and fungi in the plant's rhizosphere [150]. Their low molecular weight and ability to sequester Fe^{3+} ions in the rhizospheric zone makes iron inaccessible to the plant pathogens, thus preventing their growth.

3.5. Induction of Systemic Resistance (ISR)

The first line of the defense system of plants is comprised of a precise surveillance system that, by perceiving several elicitors, allows them to switch on plant defense mode and reject potentially dangerous pathogens or microbes. The elicitors are small structures referred to as pathogen/microbe-associated molecular patterns (PAMPs or MAMPs), which are recognized by the pattern recognition receptors (PRRs) of the plant's innate immune system [151]. Similar to this innate mechanism, PGPR are also capable of stimulating the defense system of their associated plants against pathogen attack through the induction of systemic resistance (ISR) by SAR (system acquired resistance) and ISR (induced systemic resistance) pathways [152]. Furthermore, PGPR can be exploited for the stimulation of induced systemic tolerance (IST) against various abiotic stresses, including water scarcity, drought, salinity, osmolyte stress, temperature extremes, heavy-metal stress, and mechanical injuries [153] (Figure 4). Therefore, the application of multi-stress-resistant PGPR biostimulants has become important for enhancing agricultural production, resolving global climate change concerns and low annual crop yields, and combatting increasing food demands [13].

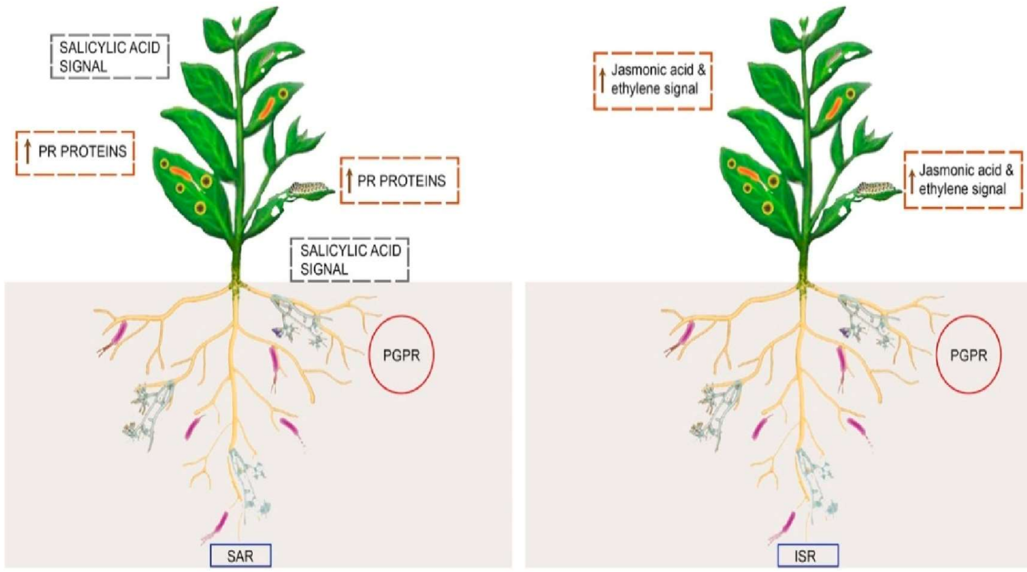

Figure 4. Types of induced resistance in plants by bacterial biostimulants.

3.5.1. Systemic Acquired Resistance (SAR)

Systemic acquired resistance (SAR) is a mechanism of induced defense that confers long-lasting protection against a broad spectrum of microorganisms. It is an induced immune mechanism found in plants with a broad spectrum that is not specific to the initial infection [154] and can be systematically expressed in all organs [155]. SAR requires the salicylic acid (SA) signaling that accumulates within the infected plant tissues after pathogen attack, which stimulates immune responses such as pathogenesis-related (PR) gene expression and antimicrobial substance encoding [156]. The SA signal transduction requires activation of PR (pathogenesis-related) genes, of which the NPR1 regulatory (activator) protein is an essential gene that operates within the terminal of the SAR signal pathway [157].

SAR is generally activated by pathogens or chemical stimuli; however, some PGPR are also known to trigger the SA (salicylic acid)-dependent pathway through the production of SA at the root surface [158]. Treatment of tomato plants with *Bacillus amyloliquefaciens* (strain MBI600), which is an active component of the fungicide Serifel®, was shown to produce antiviral action against Potato virus Y (PVY) and tomato spotted wilt virus (TSWS) in tomato plants through the SA-dependent signaling pathway [159]. In another example, leaf infiltration with *Bacillus cereus* (AR156), a PGPR was reported to enhance disease resistance against *Pst* (*P. syringae* pv. tomato) in *Arabidopsis* through the activation of a SAR pathway [160]. However, the salicylic acid released by rhizobacteria does not necessarily need to mediate the SAR mechanism, as SA produced by rhizobacteria may require siderophores for its assimilation [161].

3.5.2. Induced Systemic Resistance (ISR)

Induced systemic resistance (ISR) emerged as an important mechanism by which selected plant growth-promoting bacteria and fungi in the rhizosphere enhanced defense against a broad range of pathogens and insect herbivores [162]. ISR induction requires components of the jasmonic acid (JA) signaling pathway followed by the ethylene signaling pathway [163]. For many biological control agents, ISR has been recognized as the mechanism that at least partly explains disease suppression. It is of significant importance from an agronomic perspective for its effectiveness against a wide range of microbial pathogens, nematodes, and insects that damage crops [164,165]. It was reported that the PGPR *Bacillus amyloliquefaciens* induces systemic resistance in bean plants against aphids through the production of higher contents of jasmonic acid [166]. The attack of insect herbivores on plant roots and leaves imposes different selection pressures on plants, which in turn produces contrasting responses in terms of gene expression and the production of secondary metabolites and wound hormones [167]. PGPR-triggered ISR does not involve severe defense-related gene changes and assists the plant in the induction of resistance against various pathogens by the production of several extracellular metabolites that act as elicitors [153]. Several PGPR metabolites include N-Acyl homoserine lactones [168], siderophores [169], VOCs [170], rhamnolipids [171], and cyclic lipopeptides [172]. However, most of these elicitors have been identified from strains of *Bacillus* and *Pseudomonas* sp. and elicitors from many other species remain mostly undiscovered.

These elicitors require higher µM concentrations to activate the immune responses compared to MAMPs, indicating that they may not be sensed through high-affinity receptors [173]. Quorum-sensing molecules such as acyl homoserine lactones produced by PGPR represent novel elicitors of biotic stress resistance in plants. In a recent study, a halotolerant plant growth-promoting bacterium, *Staphylococcus equorum* EN21, triggered ISR against *Pseudomonas syringae* (pv. Tomato) through quorum quenching of acyl homoserine in *Arabidopsis* and tomato plants [174]. ISR activity of the elicitor oxo-C14-HSL was observed in tomato and wheat against *Phytophthora infestans* and Puccinia graminis f., respectively [175]. In monocots (such as rice) cyclic lipopeptides released by *Pseudomonas* are crucial in eliciting the ISR. For example, cyclic lipopeptides such as lokisin, endolysin, and white line inducing principle (WLIP) were described recently as successfully inducing resistance against *Magnaporthe oryzae* [176] whereas orfamide (at 25 µM concentration) is known as an elicitor of ISR against *Cochliobolus miyabeanus* [177]. Accumulation of ROS following the inoculation of bacteria *Gluconacetobacter diazotrophicus* has also been observed at the early stages of rice root colonization. This study indicates that bacterial ROS-scavenging enzymes, glutathione reductase, and superoxide dismutase help trigger a typical ISR plant defense response against pathogens [178].

3.5.3. Induced Systemic Tolerance (IST)

Similar to ISR against biotic stresses, the defense responses induced by different PGPR to withstand abiotic stresses generally involve highly regulated mechanisms, including the regulation of phytohormones, ROS accumulation, EPS (exopolysaccharide) production, ACC-deaminase activity, the secretion of secondary metabolites, VOCs, antioxidant machinery, and the activation of defense-related genes that lead to induced systemic tolerance (IST) and has been well documented by [153]. Such responses also involve a web of highly coordinated plant hormones such as abscisic acid (ABA), gibberellins (GA), ethylene (ET), auxins (indole acetic acid, IAA), cytokinins (CK), jasmonic acid (JA), salicylic acid (SA), and brassinosteroids (BRs). These plant hormones habitually act as the key signaling molecules triggering intricate signaling cascades that subsequently lead to the stimulation of physiological and morphological changes, eventually leading to tolerance or resistance of abiotic stresses [179]. Several molecular studies have described that PGPR induce stress tolerance (biotic as well abiotic) through crosstalk between various phytohormones and the proper signaling network [180].

Different mechanisms of IST by several elicitors stimulated by inoculation of PGPR have been also demonstrated for the mitigation of abiotic stresses [92,93]. Under the conditions of salt stress, the inoculation of tomato by PGPR *Sphingobacterium* BHU-AV3 showing whole plant protection through IST was due to reduced ROS levels, increased antioxidant enzyme activities, and the multiple-isoform expression of superoxide dismutase (SOD), polyphenol oxidase (PPO), and peroxidase (POD) in the plant roots [181]. In wheat, IST was elicited by a halotolerant *Aeromonas* sp. (strains SAL17 and SAL21) via the production of many acyl homoserine lactones (AHLs) to mitigate salt stress [182]. During heavy metal stress, *Pseudomonas* SFP1, which is a metal-tolerant species, produces IAA [183]. It also secretes many enzymes for degradation of the cell wall that include chitinases, cellulose, protease, glucanase, lipopolypeptides, and HCN, which provide inhibition to plant pathogenic fungi, bacteria, and viruses, and also restrain nematodes [184]. Different PGPR treatments known to induce systemic tolerance in wheat against abiotic stresses including salinity, drought, heat, and cold have been well studied.

4. Conclusions

Feeding the world's rising population is one of the biggest challenges, especially when the agriculture system is facing a multitude of complex problems arising from changing environments due to global climate change. This global phenomenon triggers and worsens already existing abiotic stresses due to the shifting of normal climatic patterns such as water budgets, resulting in frequent droughts, floods, salinization, and temperature extremes. These problems become factors for shifting patterns of weeds and phytopathogens and reduce the beneficial microbial population associated with plants that affect plant health while leaving plants susceptible to biotic stress. Furthermore, to guarantee and ensure a sufficient yield and the biocontrol of pests, agriculture is increasingly relying on chemical fertilizers and pesticides, which unfortunately have a very negative environmental effect. Therefore, in recent years, to establish environmentally sustainable alternatives to such agrochemicals, the use of PGPR plant biostimulants (PBs) has attracted worldwide interest. The PB market is rising rapidly, with an expected exponential growth rate in the near future. PGPR-based BPBs have shown effectiveness in nutrition use, mitigation of abiotic/biotic stress, and/or crop quality characteristics when applied to agricultural and horticultural crop plants (fruits, vegetables, ornamental plants, and medicinal plants). PGPR make soil elements such as iron, phosphorus, potassium, and zinc more available to plants through the phytohormone regulation, production, and release of siderophores, organic acids, and enzymes.

Furthermore, PGPR fight various abiotic and biotic stresses through a multitude of mechanisms or a combination of an array of mechanisms such as phytohormone regulation, signaling pathways, gene regulation and expression, secondary metabolites, VOCs, bioactive compound enhancement, ROS enzyme activities, etc. However, detailed work also needs to be carried out for an additional explanation of mechanisms related to plant– microbe interactions, their bilateral "molecular dialogue," and the "omics" approaches, particularly under the synergistic pressures of abiotic and biotic stress under field conditions. Such cognizance will expound on the development of new biostimulant formulations and their implementation as an innovative solution to the current food crisis.

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