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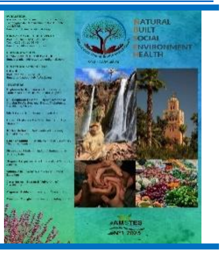


Functional dynamics of Plant Growth-Promoting Bacteria (PGPB) in Adaptation to Abiotic Stress and Enhancement of Crop Productivity

Karima Jmaili[1a], Bouchaib Bahlaouan[2b], Alla Silkina[3c], Mohamed Lahrairi[1d]
& Nadia Boutaleb[1e]*

[1] *Hassan II University of Casablanca (https://ror.org/001q4kn48), Laboratory of Biotechnology, Agri-Food, Materials and Environment, Team: Biotechnologies, Resource Valorisation, Quality, Health and Ecotoxicology, Faculty of Science and Technology Mohammedia, BP 146, Mohammedia 20650, Morocco*

[2] *Higher Institutes of Nursing and Health Technical Professions (ISPITS) (https://ror.org/007h8y788), Laboratory of Care, Health and Sustainable Development 2S2D, Higher Institutes of the Nursing Professions and Techniques of Health ISPITS Casablanca 22500, Morocco*

[3] *Swansea University (https://ror.org/053fq8t95), Algal Research Group, Department of Biosciences, College of Science, Singleton Park, Swansea SA2 8PP, United Kingdom*

[a] ***ORCID**: 0009-0009-3153-0825; **Email:** karima.jmaili@etu.fstm.ac.ma*

[b] ***ORCID**: 0000-0002-0976-1274; **Email**: b.bahlaouan@ispitscasa.ac.ma*

[c] ***ORCID**: 0000-0002-1804-8083; **Email**: a.silkina@swansea.ac.uk*

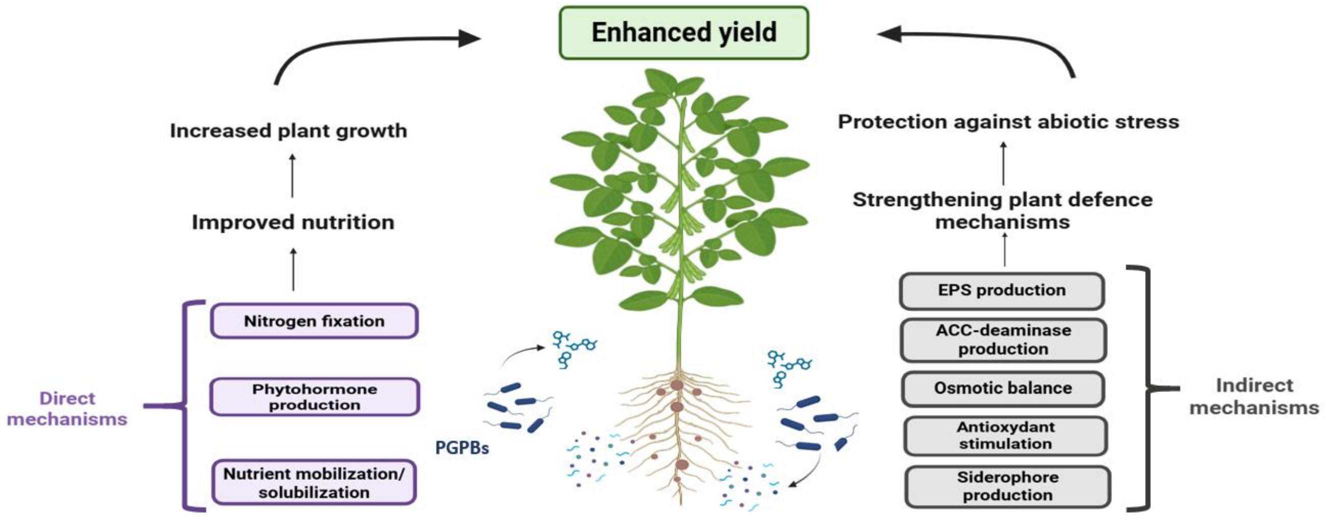
[d] ***ORCID**: 0009-0006-9408-9190; **Email**: mohamed.lahrairi-etu@etu.univh2c.ma*

[e] ***ORCID**: 0000-0003-1628-4311; **Email**: nadia.boutaleb@fstm.ac.ma*

Corresponding author:** Nadia Boutaleb; ***Email: nadia.boutaleb@fstm.ac.ma ; **Telephone:** +212 661485088

Graphical abstract

This study explores the functional mechanisms by which Plant Growth-Promoting Bacteria (PGPB) enhance crop productivity and strengthen resilience to abiotic stress. Both through direct actions—such as nitrogen fixation, phytohormone production, and nutrient solubilization—and indirect strategies—including antioxidant activity, regulation of osmotic balance, and the production of ACC-deaminase, siderophores, and exopolysaccharides—PGPB contribute to improved plant growth and defence. By reinforcing nutrition and triggering protective mechanisms, these beneficial microbes are central to sustainable agriculture. They are an alternative to chemical inputs, particularly under conditions characterized by environmental stress.



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Abstract: In the context of sustainable agriculture, plant growth-promoting bacteria (PGPB) are key microbial biostimulants. These beneficial microorganisms enhance nutrient uptake, strengthen plant defence mechanisms, and improve tolerance to abiotic stresses, contributing to reduced reliance on chemical inputs. Bacterial genera such as *Azospirillum*, *Rhizobium*, *Bacillus*, and *Pseudomonas* have demonstrated positive effects on crop yield and quality, even under challenging conditions including salinity, drought, and heavy metal contamination. Their beneficial actions include several mechanisms, such as phytohormone production, nutrient solubilization, nitrogen fixation, and modulation of gene expression linked to plant defence and metabolism. The efficacy of these bacteria varies according to microbial strain, plant species, and environmental context. This review shows the agronomic value of PGPB and emphasizes the importance of continued research into their functional interactions in resilient and environment-friendly farming systems.

Keywords: *Microbial biostimulant, PGPB, Abiotic stress.*

Introduction

Urbanization, climate change, and unfavourable local conditions are reducing the amount of arable land available for agriculture worldwide. This has serious consequences for crop productivity and quality, threatening global food security [1]. Abiotic stresses such as drought, excessive rainfall, extreme cold or heat, soil salinity, and nutrient imbalance account for approximately 50 to 70% of yield losses. These stresses impair plant growth, development, productivity, and crop quality. In some regions, they have led to the extinction of local species [2].

Abiotic stress disrupts key physiological and biological functions. These include membrane dysfunction, reduced photosynthesis and protein synthesis, and hormonal imbalance. Under saline conditions, salt enters the transpiration stream and damages leaf tissue. Sodium chloride also reduces water uptake and introduces toxicity. This limits plant growth and reduces shoot length, leaf area, and leaf number [3]. Roots are especially vulnerable. Direct contact with salt impairs cell division at the root tips and reduces root length. The most harmful effect of salinity is the ionic imbalance and hyperosmotic stress it creates. These are driven by excess reactive oxygen species (ROS) and disrupted antioxidant defences. High ROS levels cause oxidative damage, leading to cell death in crops [4].

Drought stress lowers water potential because of increased solute concentration. This results in loss of turgor, leaf wilting, desiccation, and, in severe cases, plant death. Water quality is critical. Contaminated water used in fruit and vegetable production can contain heavy metals, pathogens, urban waste, or salts. All of these reduce crop health [3]. Water scarcity may increase soil mineral toxicity and make plants more vulnerable to heat and solar radiation. High temperatures disrupt metabolism and respiration. This slows plant development and, in extreme cases, causes plant death. Cold stress limits crop cultivation. It causes chlorophyll loss, plasmolysis, and reduced photosynthetic activity. Waterlogging, caused by heavy rainfall, is another threat. It saturates the soil, forcing air out of the pores. This creates oxygen shortages and carbon dioxide buildup, which impair root and shoot growth. Taken together, these environmental stresses pose a serious and growing threat to global food production [4].

Furthermore, the excessive use of chemical inputs causes long-term harm because of their persistence and slow breakdown. These substances affect the environment, soil, plants, and living organisms [5]. Once they enter the food chain, they accumulate and cause carcinogenic, mutagenic, and toxic effects at higher trophic levels. They also alter the physicochemical structure of soils and disrupt microbial activity and diversity, leading to ecotoxicological damage [6]. In plants, xenobiotics interfere with growth and germination. They disturb both morphology and physiology and may alter gene regulation and expression. Some also block signalling by interfering with receptors. Pesticides, fertilizers, and herbicides are the main xenobiotic pollutants in agriculture. They bind to free metal ions in the soil and form complexes that reduce the bioavailability of essential nutrients [7].

Remedial action is needed to prevent land degradation. About 98% of the world’s food is produced on land. Soil and water degradation caused by human activity reduces fertility, biodiversity, and the environmental functions that support food production and resilient livelihoods. There is an urgent need for an ecological, efficient, and productive system that improves agronomic performance [5]. Biostimulants have become one of the most promising tools for supporting crop growth and productivity through natural means. They also help reduce the harmful effects linked to synthetic fertilizers.

Biostimulants are alternatives to chemical inputs. Their bioactivity, low toxicity, limited persistence in the environment, and ability to support plant performance under suboptimal conditions make them highly valuable [3]. They reduce the need for fertilizers, which is crucial in organic farming where synthetic inputs are not permitted. Microbial biostimulants form a distinct subgroup within the wider category of plant biostimulants. These products are easy to apply under field conditions and produce measurable effects [4].

They stimulate physiological and biochemical functions that improve nutrient absorption, nutrient use efficiency, stress tolerance, crop quality, and yield; thus, they help to counter the negative effects of intensive farming. The global biostimulant market is growing at an average rate of 10.2% per year. About 25% of commercially available biostimulants are microbial in origin. These microbes help to restructure the biological activity of the soil and encourage the growth of other beneficial organisms. This improves soil fertility and increases crop yield while restoring the native microflora.

Microbial biostimulants act on different levels. At the shoot level, they affect stomatal function and xylem water transport. In the root zone, they improve water availability and modulate hormones such as ethylene and auxin. At the whole-plant scale, they support ROS detoxification, osmotic regulation, and membrane protection [1]. According to EU Regulation 2019/1009, microbial biostimulants are classified under CMC 7. This category includes arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) from the genera *Azotobacter*, *Azospirillum*, and *Rhizobium* [8].

These microbes release various exudates into the rhizosphere; including organic and inorganic substances such as hormones, organic acids, amino acids, exopolysaccharides, siderophores, hydrogen cyanide (HCN), and volatile organic compounds (VOCs). Some of these compounds can be extracted and applied directly to crops in acellular formulations. In this way, microbial products enhance plant performance without the use of living cells.

The use of beneficial microbes represents a credible alternative to agrochemicals. Microbial biostimulants may be applied as single-strain formulations or as microbial consortia. Application methods include seed coating, foliar spraying, and rhizosphere inoculation. One of the most promising approaches is bio-priming, when seeds or seedlings are inoculated with beneficial microbes to support early growth and activate systemic resistance to stress [4]. These microorganisms and their exudates are essential for regenerative and organic farming. They offer bioprotective, bioremediating, and biostimulant effects that contribute to a more sustainable food system [9].

Soil contains a vast diversity of living organisms, including fungi, algae, and protozoa. About 95% of these microorganisms are bacteria. The rhizosphere provides nutrients and ecological niches that support microbial development. Plants release a large share of their photosynthetically fixed carbon into the soil through root exudates. This carbon stimulates microbial metabolism. As a result, bacterial populations near the roots are 10 to 1,000 times greater than those in bulk soil. The highest concentrations are found in the rhizosphere, closest to the root surface [10].

Plant growth-promoting bacteria (PGPB) support multiple processes. These include soil structure improvement, organic matter breakdown, nutrient recycling, mineral solubilization, and the synthesis of growth regulators. They enhance plant biomass, root and shoot length, seed germination, photosynthesis, and the production of secondary metabolites. They also thrive under stressful environmental conditions and help plants absorb nutrients and cope with biotic and abiotic stress by influencing stress-response mechanisms [11,12].

This review aims to present a clear explanation of how microbial biostimulants, particularly those based on PGPB, support plant growth under both optimal and suboptimal conditions. The authors describe the mechanisms through which these microbes mitigate abiotic stress and improve plant performance. Recent findings and case studies on the application of microbial biostimulants to horticultural crops are summarized. The review examines how PGPB influence morpho-anatomical, biochemical, physiological, and functional traits. There is a detailed analysis of the biochemical and molecular mechanisms activated by PGPB. This knowledge will help guide the design of new bioformulations for sustainable agriculture. The review also includes a section on challenges and future priorities for integrating PGPB-based biostimulants into horticultural systems.

The information is based on articles published between 2018 and 2025 in peer-reviewed journals. Sources include Google Scholar, Scopus, ScienceDirect, PubMed, MDPI, and other academic platforms. The literature search used the following terms: plant biostimulants, plant growth-promoting microbial biostimulants, microbial biostimulant, PGPB, PGPR, Azospirillum, Azotobacter, horticultural crops, sustainability, bioactive compounds, and microbial exudates. These terms were refined through exploratory searches to improve relevance. The review aims to consolidate current knowledge, assess both the benefits and limits of PGPB, and support the development of sustainable and productive agricultural systems.

Definition and Mechanisms of Action

Plant growth-promoting bacteria (PGPB) are beneficial microbes that either live freely in the soil or interact directly with plants. These include rhizospheric bacteria that adhere to root surfaces and are classified as PGPR; endophytes that colonize internal plant tissues without causing harm; and phyllospheric bacteria found on leaves and stems. Each group contributes to plant growth through different biological mechanisms [1,10]. PGPB form a highly diverse group that includes genera such as *Bacillus*, *Arthrobacter*, *Pseudomonas*, *Rhodococcus*, *Enterobacter*, *Ochrobactrum*, *Acinetobacter*, *Azospirillum*, *Rhizobium*, and *Streptomyces*. These microbes are now recognized as cost-effective agroecological tools for improving crop productivity [1]. They support plant development and reinforce resistance to abiotic stress factors [13]. PGPB can be applied to seeds or introduced directly into the soil, often in a carrier such as peat, manure, compost, sawdust, or vermiculite [14].

Their beneficial effects depend on several key functions. These include the solubilization of minerals such as zinc (Zn), phosphorus (P), and potassium (K); nitrogen (N) fixation; the production of iron (Fe)-chelating compounds; and the synthesis of phytohormones such as indole-3-acetic acid (IAA), abscisic acid (ABA), ethylene (ET), cytokinin (CK), and jasmonic acid (JA). PGPB also produce secondary metabolites, enzymes that break down organic matter, and volatile organic compounds (VOCs), including fatty acids and their derivatives, hydrocarbons, carbohydrates, and lipopolysaccharides [7]. These substances influence root morphology, including root biomass, surface area, and lateral root development. They also enhance shoot growth, leaf expansion, soil structure, water retention, porosity, and nutrient availability. PGPB improve the uptake of essential minerals (N, P, Fe, Zn), increase photosynthetic activity, and help plants tolerate abiotic stress. They achieve this by activating genes in antioxidant defence, and by promoting the synthesis of phenolics, osmolytes, enzymes, amino acids, organic acids, exopolysaccharides (EPS), and 1-aminocyclopropane-1-carboxylate (ACC) deaminase [1]. The detailed cellular and biomolecular processes remain under investigation. To understand these mechanisms better, researchers are now using molecular biology tools, proteomics, transcriptomics, and metabolomics [5].

Table 1. Key functional mechanisms of PGPB in plant growth promotion

Mechanism of Action	Primary Function	Examples of Bacterial Genera	Impact on Plants
Biological Nitrogen Fixation (BNF)	Converts atmospheric N_2 into plant-available ammonia via nitrogenase enzyme	*Rhizobium*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Beijerinckia*	Enhances nitrogen supply, promotes growth, reduces need for chemical N fertilizers
Phosphate Solubilization	Converts insoluble phosphorus into available forms ($H_2PO_4^-$, HPO_4^{2-}) through organic acids and enzymes	*Bacillus*, *Pseudomonas*, *Burkholderia*, *Rhizobium*, *Enterobacter*	Improves phosphorus nutrition and root development
Siderophore Production	Chelates insoluble Fe^{3+} and increases iron availability for plant uptake	*Pseudomonas*, *Bacillus*, *Azospirillum*, *Arthrobacter*, *Sphingomonas*	Alleviates iron deficiency, enhances chlorophyll synthesis, suppresses pathogens
Phytohormone Synthesis	Produces auxins (IAA), gibberellins (GA), cytokinins (CK) and reduces ethylene via ACC deaminase	*Bacillus*, *Pseudomonas*, *Rhizobium*, *Azospirillum*, *Methylobacterium*	Promotes root elongation, delays senescence, increases stress tolerance
Antioxidant System Activation	Boosts activity of antioxidant enzymes (SOD, CAT, APX, etc.) and induces osmolyte accumulation	*Bacillus*, *Rhizobium*, *Pseudomonas*	Protects against oxidative damage from abiotic stresses
Exopolysaccharide (EPS) Production	Stabilizes soil, enhances water retention, and mitigates salt stress	*Bacillus subtilis*, *Pseudomonas chlororaphis*, *Lactobacillus plantarum*	Improves soil structure, water availability, and salt stress resilience

Effect of PGPBs on Plant Growth

PGPB-based biostimulants are increasingly used as part of agroecological strategies to support plant growth and improve nutrient use efficiency in crops. These microbial products help plants cope with abiotic stress by activating defence responses from the moment of stress perception through to cellular and molecular regulation [15]. Their use in agriculture has been widely documented in scientific research and agronomic manuals (Table 2). Many studies show the symbiotic relationship between rhizobacteria and leguminous plants. In these systems, the bacteria fix atmospheric nitrogen (N_2) and provide the plant with organic nitrogen in the form of amides or with mineral nitrogen as ammonia.

Rhizobacteria also form associations with non-leguminous plants. Through chemotaxis, they are guided by compounds exuded from roots and migrate towards them. This targeted movement leads to the formation of beneficial interactions that support plant health and nutrition [13]

Table 2. The effects of Plant Growth-Promoting Bacteria (PGPBs) on various plant species.

Bacteria	Plants	Effects	References
PGPB	*Brassica rapa* L.	● Enhancement of plant growth, biomass, yield parameters, and seed fatty acid content ● Increase in plant biomass, leaf number, root length, and total IAA, phosphorus, and nitrogen contents	[16]
	Coriandrum sativum	● Increase in relative water content (RWC), photosynthetic activity, and pigment concentration ● Improvement in plant growth	[17]
	Sorghum bicolor	● Enhancement of plant growth and chlorophyll pigment levels ● Positive regulation of genes active in iron uptake and transport (IRT1, IRT2, YS1, and YS2)	[16]
A. lipoferum, *A. brasilense*, *A. irakense* and *Azospirillum* strain 21	*Foeniculum vulgare*	● Increase in seed weight uniformity and essential oil yield, particularly in α-pinene and limonene	[13]
Azospirillum brasilense Cd (DSM-1843)	*Ocimum basilicum* L.	● Enhancement of fresh biomass ● Increase in root growth, unsaturated fatty acids, flavonoids, alkaloids and several terpene derivatives	[18]
Azospirillum brasilense	*Triticum aestivum*	● Release of auxins by *Azospirillum brasilense* and activation of auxin signaling pathways involved in wheat root morphogenesis	[14]
Azospirillum sp. and *Azotobacter* sp.	*Capsicum annuum* L.	● Improvement of vitamin C, carotenoids, total soluble solids concentration ● Enhancement of N and P uptake under reduced N rate	[13]
Azospirillum brasilense and *Azotobacter chroococcum*	*Ocimum basilicum* L.	● Increase of fresh and dry yield independent of the cropping system. ● Increase of essential oil content (methyl chavicol)	[19]
Azotobacter chroococcum and *Azotobacter vinelandii*	*Zea mays*	● Increase in shoot and root length, number of leaves and roots, and chlorophyll content	[20]

Rhizobium laguerreae strain HUTR05	*Lactuca sativa* L. var. romaine	● Increase of N and P content, phenolic acids (dicaffeoylquinic and cichoric acids) and quercetin 3-O-glucoside flavonoid	[21]
Rhizobium legiminosarum strain TPV08 and *Rhizobium* sp. strain PETP01	*Solanum lycopersicum* L. *and* *Capsicum annuum* L.	● Promotion of growth of both tomato and pepper, especially in pepper fresh weight and tomato nutrient quality (higher N, P, K or Mg)	[13]
Rhizobium laguerreae strain PEPV40 and *Bacillus halotolerans* SCCPVE07	*Cichorium endivia* L.	● Promotion of overall plant development ● Increase of concentration of K, Fe, Mg, N, phenolic acids (cichoric acid and caffeoyl-tartaric acid) and flavonoids (kaempferol 3-O-glucuronide).	[22]
Bacillus licheniformis NJ04 and *Bacillus velezensis* 83	*Solanum lycopersicum* L.	● Increase of root and shoot length of treated plants and improvement of length and lateral root	[1]
Bacillus subtilis QST 713	*Zinnia violacea* *and* *Petunia ×atkinsiana*	● Production of abscisic acid and other growth regulators promoting stomatal closure and reducing water loss ● Synthesis of osmolytes such as proline, which stabilize proteins and cell membranes ● Production of antioxidant enzymes reducing oxidative damage under stress	[23]
Bacillus subtilis and *Bacillus licheniformis*	*Cucumis sativus*	● Increase in fresh weight, chlorophyll content, and improved cell division ● Increase in cytokinin content in roots and shoots	[14]
Bacillus amyloliquefaciens	*Glycine max* L.	● Improvement in plant growth, biomass, yield parameters, and seed fatty acid content ● Enhancement, under saline stress, of biomass, gibberellin and abscisic acid levels, and plant development	[24]
Bacillus megaterium	*Triticum estivum* L.	● Improvement in the uptake of low-mobility nutrients like calcium and zinc ● Improvement in plant growth ● Enhancement of total microbial biomass ● Improvement in gluten quality	[25]
Bacillus halotolerans and *Pseudomonas frederiksbergensis*	*Triticum estivum* L. and *Glycine max* L.	● Improvement in germination, growth, and yield ● Improvement in nitrogen, potassium, and zinc uptake	[26]
Bacillus sp. and	*Solanum lycopersicum* L.	● Increase in plant biomass, RWC, healthy fruit yield, and micronutrient content	[24]

Pseudomonas putida			
P. fluorescens (C7R12) and *P. putida*	*Pisum sativum*	● Enhancement of root and shoot ratio by promoting plant iron nutrition	[7]
Pseudomonas fluorescens	*Brassica napus* L.	● Increase in plant height, biomass, and grain yield	[14]
Burkholderia sp. Strain N3	*Solanum lycopersicum* L.	● Improvement of tomato seedling height, dry weight, and nutrient uptake ● Facilitation of gene expression and alleviation of Cd toxicity in tomato plants	[1]

Studies on chickpea inoculated with *Rhizobium* sp. have reported significant improvements in biomass and yield. Higher chlorophyll levels and increased NPK content were also observed. The nutritional quality of the seeds improved as well [21]. Other findings confirm the benefits of *Rhizobacteria* spp. in non-leguminous plants. For example, *Rhizobium jaguaris* CCGE525 enhanced growth in *Arabidopsis thaliana*, increasing both biomass and chlorophyll concentration under normal conditions [16].

Inoculation of cherry tomato and sweet pepper plants with *Rhizobium leguminosarum* strains TPV08 and PETP01 also improved growth. In peppers, the main effect was on fruit production, with a marked increase in fresh weight. In tomatoes, improvements were more related to fruit quality, especially increased levels of nitrogen, phosphorus, potassium, and magnesium [13].

Romaine lettuce seedlings treated with *Rhizobium laguerreae* strain HUTR05 showed higher nitrogen and phosphorus content, as well as elevated levels of phenolic acids, such as dicaffeoylquinic and cichoric acids, and flavonoids including quercetin 3-O-glucoside [21]. *Rhizobium meliloti* improved growth and nitrogen use efficiency in peanuts, and enhanced pod quality [27]. Many of these strains produce phytohormones, including gibberellic acid (GA) and **indole-3-acetic acid (IAA).**

Among PGPB, *Azospirillum* is one of the most studied genera. Many strains are approved for use in wheat and maize [20]. In fennel (*cv.* Isfahan), seed treatment with *Azospirillum* increased seed weight and the yield of essential oils, particularly α-pinene and limonene. β-pinene increased only when plants were treated with strain 21 [13].

Kolega *et al.* [18] inoculated two cultivars of basil with *Azospirillum brasilense* Cd (DSM-1843). They noted enhanced root growth and elevated levels of unsaturated fatty acids, flavonoids, alkaloids, and terpenes, especially in the Red Rubin cultivar. Strains Sp7b and Sp245b of *A. brasilense* also promoted IAA synthesis and improved germination, root length and weight, and seedling vigour in cucumber, tomato, and lettuce [1].

Azospirillum lipoferum DO12, applied to the rhizosphere of tomato (*cv.* Menhir F1), improved fruit quality. Lycopene, vitamin C, and total polyphenol content increased, suggesting improved shelf life [19]. Research on *Arthrobacter agilis* UMCV2 applied to *Sorghum bicolor* has shown improved plant growth and higher chlorophyll levels. These effects were likely linked to enhanced iron uptake [16]. Genes active in iron absorption and transport, including *IRT1*, *IRT2*, *YS1*, and *YS2*, were upregulated, indicating that this strain influences gene expression.

Azotobacter chroococcum strain CL13 increased leaf number, stem height, fresh biomass, and curcumin content in *Curcuma longa* L., a crop valued for its pharmaceutical properties [1]. Native rhizospheric bacteria isolated from *Solanum lycopersicum* L., including strains similar to *Ochrobactrum anthropi*, promoted tomato growth even under reduced fertiliser input [28]. The radiobacterium *Rhizobium* InaCCB835 enhanced biomass, leaf number, and root length in *Brassica rapa* L. It also increased total levels of IAA, phosphorus, and nitrogen in the plant [25].

Bacillus spp. function both as biofungicides and biostimulants. They produce beneficial metabolites and solubilize nutrients into forms more accessible to plant roots. Although nitrogen scarcity in soil can restrict growth, certain *Bacillus* strains convert atmospheric nitrogen into plant-available forms, supporting growth and yield. These microbes also produce compounds such as cytokinins, spermidines, gibberellins (GA), and IAA [16]. *Bacillus pumilus* has been shown to increase nutrient content and fruit yield in tomato (*Solanum lycopersicum* L.) [29]. *Bacillus licheniformis* improved fresh weight, cell division, and chlorophyll content in cucumber [27]. Three strains of *Bacillus velezensis* applied to wheat (*Triticum aestivum* L.) enhanced early plant development and raised macro- and micronutrient levels under greenhouse conditions. Inoculation with *B. velezensis* FZB24 also led to higher grain yields under low-nitrogen conditions [30].

These findings highlight the dual function of *Bacillus* spp. as both growth promoters and nutrient mobilisers. Their flexibility in different nitrogen environments makes them valuable tools for improving crop performance across a wide range of agricultural systems.

Pseudomonas spp. are among the most important plant-associated bacteria. Many strains show biostimulant activity by improving nutrient uptake, releasing vitamins, and synthesizing ACC deaminase [16]. *Pseudomonas fluorescens* LBUM677 has been shown to increase seed weight, seed number, and oil content in *Brassica napus*, *Buglossoides arvensis*, and *Glycine max*. These benefits are linked to its production of ACC deaminase, IAA, and its capacity to solubilize micronutrients. Other studies have reported that *P. fluorescens* enhances grain yield, plant height, and biomass in rice, sweet potato, and rapeseed [31].

In hybrid amaranth (*Amaranthus hybridus* L.), *P. fluorescens* increased the leaf content of calcium, magnesium, potassium, phosphorus, and zinc, with a modest reduction in total plant growth. *Pseudomonas pseudoalcaligenes* and *P. putida* also improved water content and pigment concentration, leading to better plant development [17]. In *Trifolium repens* (white clover), *P. putida* enhanced both shoot and root biomass, as well as water content [27].

Biostimulant formulations that combine several bacterial strains also offer promising results. Co-inoculation with *Pseudomonas* BA-8 and *Bacillus* OSU-142 significantly improved growth, yield, and nutritional quality in sweet cherry (*Prunus avium* L.). The combined treatment increased zinc and iron concentrations in leaves by up to 50.5% and 35.5%, respectively, compared to untreated controls [32].

Strains of *Bacillus pumilus*, *B. amyloliquefaciens*, *B. mojavensis*, and *Pseudomonas putida* supported IAA production, nitrogen fixation, and phosphorus solubilization. These actions improved tomato growth and nutrient uptake [29]. A mix of *Bacillus halotolerans*, *Pseudomonas frederiksbergensis* RG2, and *Enterobacter hormaechei* enhanced germination, yield, and the uptake of phosphorus, nitrogen, and zinc [27].

Other PGPR strains such as *P. fluorescens*, *Bacillus subtilis*, *Sinorhizobium meliloti*, and *Bradyrhizobium* sp. promoted increases in shoot length, shoot biomass, leaf number, node count, and root dry weight in sweet marjoram (*Origanum majorana* L.) [1].

In basil, inoculation with a commercial mix of *Azospirillum brasilense* and *Azotobacter chroococcum* raised both fresh and dry yield, regardless of whether the plants were intercropped with maize. Full nitrogen fertilization and partial nitrogen supply combined with inoculation increased methyl chavicol content, a major component of basil essential oil with nutraceutical value [19].

In lettuce (*cv.* Santoro and Quintus), inoculation with a bacterial mix of *Azospirillum* and *Azotobacter* raised fresh yield. Carotenoid content and antioxidant activity improved only in *cv.* Quintus (romaine type) [13]. The application of *Azospirillum brasilense*, *Gluconacetobacter diazotrophicus*, *Burkholderia ambifaria*, and *Herbaspirillum seropedicae* induced hormone production in onion. These hormones support nutrient solubilization and uptake [1].`

Effect of PGPBs on Stress Tolerance

Abiotic stress leads to physiological, biochemical, and molecular disruptions in plants. Bacteria with biostimulant potential have been isolated from ecosystems with saline, alkaline, and arid soils. These microbes are highly adapted to such harsh environments [1]. PGPB can improve plant tolerance to drought and salinity through multiple mechanisms [27]:

1. Production of phytohormones, including abscisic acid (ABA), gibberellic acid (GA), indole-3-acetic acid (IAA), and cytokinins (CKs);

2. Synthesis of ACC deaminase, which reduces plant ethylene levels by breaking down its precursor (ACC), promoting growth;
3. Secretion of extracellular polysaccharides (EPS);
4. Modulation of genes active in cell wall architecture, synthesis of choline and glycine betaine, and stomatal regulation;
5. Mitigation of oxidative stress by scavenging reactive oxygen species (ROS), through enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), and through antioxidant metabolites like ascorbate and phenolic compounds;
6. Accumulation of osmolytes, including soluble sugars, proline, and glycine betaine;
7. Maintenance of ion homeostasis by increasing potassium levels and preserving the K^+/Na^+ balance;
8. Enhancement of nutrient availability, including nitrogen, phosphorus, potassium, iron, zinc, manganese, copper, and boron, via solubilization, mineralization, nitrogen fixation, and siderophore production.

Common plant adaptations include changes in cell wall structure and increased synthesis of soluble solutes. These responses improve water retention and boost tolerance to osmotic and ionic stress. The cell wall is enriched with EPS, lipopolysaccharides, and polysaccharide–protein complexes. Together, these elements form a protective biofilm around roots. EPS are sugar-based molecules secreted by microbes, including PGPB. They help retain water around roots and support the recovery of water potential gradients during drought. EPS production is particularly beneficial under salt stress, extreme temperatures, water scarcity, and pH changes [24]. EPS may also bind free sodium ions in the soil, reducing their availability to plants. The protective role of PGPB against abiotic stress has been documented in many crops, including tomato, lettuce, pepper, potato, soybean, cabbage, broccoli, maize, wheat, pea, faba bean, chickpea, sorghum, and rice. These treatments consistently lead to improved growth and yield (Table 3) [15].

Table 3. The effects of Plant Growth-Promoting Bacteria (PGPB) on plant growth and stress tolerance under various abiotic stress;

Stress	Bacteria	Plants	Effects	References
Heat stress	*Bacillus cereus* SA1	*Helianthus annuus* L.	● Improvement of tomato biomass and chlorophyll content ● Increase in SA and ABA, different antioxidant (APX, SOD, LPO and GSH) and ion uptake (Fe, P and K) ● Upregulation of heat stress transcription factor *SiHsfA1a*, along with *SlHKT1*, *SlATG5*, and *SlWRKY33b* genes in SA1 treated plants	[15]
		Glycine max	● Increase in IAA, GA, and organic acids content, along with improved growth and chlorophyll accumulation in soybean plants due to reduced ABA levels ● Enhancement of antioxidant activities (POD, SOD, CAT) and increased amino acid concentrations ● Upregulation of heat shock proteins (*GmHSP*) and stress-responsive genes *GmLAX3* and *GmAKT2*	
	Bacillus tequilensis SSB07	*Glycine max*	● Improvement in growth, gibberellins levels, indole-3-acetic acid and abscisic acid concentration ● Increase in shoot length and biomass, leaf development, and photosynthetic pigment ● Increase in the endogenous jasmonic acid and salicylic acid contents along with down-regulation of ABA level	[33]
Drought stress	*Bacillus subtilis* A31	*Solanum tuberosum*	● Maintenance of enhanced growth and favourable physicochemical traits in plants treated with *Bacillus subtilis* HAS31 under drought conditions; inoculated plants showed higher relative growth rate, dry matter, leaf area, tuber number, tuber weight, and yield ● Improvement in growth attributes along with tuber weight and yield ● Maintenance of higher soluble sugar levels and enzymatic activities such as CAT, POD, and SOD	[34]
	Bacillus sp.	*Megathyrsus maximus* and *Lolium spp.*	● Increase in proline, antioxidant enzymes (CATandPOD) ● Reduction in MDA, relative membrane permeability and H_2O_2 accumulation ● Reduce in proline accumulation, in GR activity and increase in APX levels.	[5]

	Bacillus cereus	*Solanum lycopersicum* L.	● Improvement of plant growth and development, accompanied by the expression of genes such as *SlHKT1*, *SlATG5*, *SlWRKY33b*, endogenous phytohormones (ABA, SA), antioxidants (APX, GSH, LPO, SOD), and essential amino acids	[27]
	Bacillus megaterium and *Bacillus licheniformis*	*Triticum estivum* L.	● Increase in proline and antioxidant enzymes (SOD, CAT, APX, POD, GR)	[35]
	Bacillus butanolivorans	*Capsicum annuum*	● Upregulation of proline biosynthesis genes (*P5CS*, *P5CR*), drought-responsive genes (*Cadhn*, *sHSP*), ABA-related (*bZIP1*), JA-related (*LOX*, *COI1*), and oxidative stress-related (*POX*, glutathione), along with reduction in CAT and SOD activity	[36]
	Enterobacter ludwigii AFFR02 and *Bacillus megaterium* Mj1212	*Medicago sativa* L.	● Recovery of the growth attributes (shoot/root length, fresh/dry weight, shoot diameter and chlorophyll content) in post-drought stressed alfalfa plants ● Decrease in electrolyte leakage and ABA content while increase in RWC were observed. ● Increase of different antioxidant, in phenolic content, DPPH scavenging activities and total flavonoid content in bacterial inoculated alfalfa plants. Increase in K, P, Ca and Mg content in post-drought stressed	[15]
	Azotobacter chroococcum, and *Azospirillum brasilense*	*Mentha spicata* L.	● Elevation of ABA, SOD, proteins, soluble sugars, phenolic, flavonoid and oxygenated monoterpenes ● Decrease in antioxidant enzymes GPX and CAT activity	[5]
Salinity stress	PGPB	*Zea mays*	● Improvement in root growth ● Increase in chlorophyll and soluble sugar contents ● Reduction in lipid peroxidation ● Enhancement of POD and CAT enzymatic activity ● Positive regulation of *RuBisCO*, *NHX1*, *NHX7*, *H^+-PPase*, and *HKT1* genes	[16]
	Bacillus sonorensis, *Bacillus cereus*, *Bacillus subtilis*, *Bacillus safensis*, *Bacillus paramycoides*, *Bacillus*	*Gossypium* spp.	● Increase in K^+ uptake, and reduction in Na^+ uptake ● Maintenance of proline content, Chlorophyll Content Index (CCI), Relative Water Content (RWC), and Relative Electrolyte Leakage (EL) ● Modulation of ascorbate, aldarate, glyoxylate, dicarboxylate metabolism and pentose and glucuronate interconversions pathway	[37]

	pumilus and *Bacillus tequilensis*			
	Bacillus thuringiensis PM25	*Zea mays*	● Increase in antioxidants (APX, POD, SOD, AsA), total soluble sugars, proteins, flavonoids, osmolytes (free amino acids, glycine betaine and proline)	[38]
	Bacillus amyloliquefaciens	*Zea Mays*	● Improvement of root growth under saline stress ● Increase in chlorophyll and soluble sugar content ● Reduction in lipid peroxidation ● Stimulation of POD and CAT enzymatic activity ● Positive regulation of *RuBisCO*, *NHX1*, *NHX7*, H^{+}-*PPase*, and *HKT1* genes	[24]
	Bacillus cereus and *Pseudomonas aeruginosa*	*Triticum estivum* L.	● Decrease in antioxidant enzymes (SOD,CATandPOX), non-enzymatic antioxidants (GSH,AsA,anda-TOC)	[5]
	Bacillus subtilis and *Pseudomonas* sp.	*Solanum melongena* L.	● Increase in free polyamines (spermine, spermidine, putrescine) ● Positive expression of *psbD*, *GR*, *GST*, and *Protease I/II* genes, along with decreased lipase levels	[39]
	Pseudomonas citronellolis strain (SLP6)	*Helianthus annuus*	● Significant enhancement of chlorophyll content, antioxidant enzyme production, and plant growth under salinity stress	[7]
	Pseudomonas oryzihabitans AXSa06	*Solanum lycopersicum*	● Enhancement of plant growth and photosynthetic characteristics ● Activation of antioxidant metabolism and priming of *AXSa06*-inoculated plants, supported by lipid peroxidation, ascorbate levels, amino acids (serine, threonine, glutamate), and genes active in ethylene or abscisic acid signaling	[40]
	Azospirillum brasilense Sp245	*Lactuca sativa* L.	● Enhancement of fresh and dry leaf weight, leaf area, chlorophyll and ascorbic acid content ● Increase of product quality and improvement of storage life	[1]
	Enterobacter ludwigii IG10 and *Alcaligenes faecalis* IG27	*Pisum sativum*	● Decrease in levels of electrolyte leakage and H_2O_2 contents ● Improvement of chlorophyll and proline content, and total soluble sugar	[41]

	Stenotrophomonas maltophilia BJ01	*Arachis hypogaea*	● Support of peanut plant growth and development ● Reduction of electrolyte leakage, lipid peroxidation, proline, and H_2O_2 contents ● Enhancement of auxin and total amino acid synthesis	[15]
	Kocuria rhizophila	*Zea mays*	● Increase in antioxidant enzyme (APX, GPX and GR), proline and expression of *ZmGR1*, *ZmAPX* (antioxidants-related genes), *ZmNHX1*, *ZmNHX2*, *ZmNHX3*, *ZmWRKY58* and *ZmDREB2A* (salt tolerance genes), with a decrease in MDA	[5]
Heavy metal stress	*Bacillus gibsonii* and *B.xiamenensis*	*Sesbania sesban* L.	● Production of ACC deaminase, IAA and EPS ● Significant increase in growth parameters including height of plant, fresh dry biomass and chlorophyll content ● Regulation of physiochemical traits and increase in proline, SOD and POD content	[34]
	Bacillus cereus ALT1	*Glycine max*	● Secretion of IAA and production of different organic acid ● Enhancement of fresh/dry biomass, root/shoot length ● Increase in Chlorophyll content ● Decrease in endogenous ABA and different antioxidants such as GSH, LPO, POD and SOA and increase in SA content along with total protein and SOD content ● Reduction in Cd uptake and enhancement of K uptake	[6]
	Bacillus atrophaeus	*Chenopodium quinoa*	● Improvement of the germination rate, and seedling biomass and growth vigour index	[42]
	Bacillus megaterium	*Celosia argentea*	● Increase in shoot biomass, shoot Cd accumulation ● Enhancement of phytoextraction ● Increase in soil enzyme activities in contaminated soil	[43]
	Bacillus spp.	*Lolium perenne* L.	● Increase in biomass yield, phytoextraction efficiency, and Cu extraction efficiency and increase in soil Cu bioavailability by secreting siderophores and organic acid	[12]

	Paenibacillus mucilaginosus, Curesistant rhizobia and *Sinorhizobium meliloti*	*Medicago sativa* L.	● Increase in Cu phytostabilization and prevention of toxic metals entering the food chain ● Increase in shoot and root biomass ● Increase in total nitrogen, available potassium, soil organic matter content, microbial community structure, and soil enzymatic activity	[6]
	Enterobacter ludwigii GAK2	*Oryza sativa*	● Increase in fresh/ dry weight, root shoot length and chlorophyll content ● Reduction in endogenous JA and down-regulation of JA related gene (*OsJAZ1*) and cadmium transporter gene (*OsHMA2*)	[15]
	Sphingomonas sp. PbM2. *Providencia* sp. and *Serratia* sp.	*Zea mays*	● Enhancement of plant growth, pigments, protein, phenolics and relative water content ● Improvement of remediation performance of contaminated soil	[11]
	Rhodococcus erythropolis Rhizobium sp.	*Lolium perenne* L.	● Increase in photodegradation efficiency through enzyme secretion	[12]
	Streptomyces pactum	*Triticum estivum* L.	● Increase in wheat growth, reduction in soil pH, enhancement of metal chelation and production of IAA and siderophores ● Decrease in antioxidant activity and lipid peroxidation	[15]

Salinity Stress

More than 6% of global land is affected by soil salinization. This leads to a reduction in agricultural productivity on approximately of all cultivated and irrigated soil. Projections suggest that by 2050, salt-affected soils could threaten nearly half of the world's arable land [34].

High salt concentrations create osmotic stress that disrupts plant physiology. Photosynthesis, stomatal conductance, enzyme activity, and the uptake of water and nutrients are all impaired. These effects limit plant growth and reduce crop yields [5]. Saline soils also cause ionic imbalance and hyperosmotic stress, which trigger oxidative responses. In addition, salt stress raises ethylene levels, a typical plant reaction under adverse conditions [12]. Microbial inoculation offers multiple pathways for alleviating salinity stress. PGPB reduce the effects of salt on crops through a range of coordinated actions. One key mechanism is the production of ACC deaminase, which lowers ethylene precursors and moderates stress signalling. PGPB also form biofilms on root surfaces. These structures act as barriers, limiting direct contact between roots and toxic soil particles.

Many strains synthesize phytohormones such as auxins, cytokinins, and salicylic acid. They promote the production of antioxidant enzymes and VOCs. PGPB also enhance the synthesis of osmoprotective molecules, including proline, trehalose, alanine, glycine, glutamic acid, serine, threonine, aspartate, choline, betaine, and several organic acids.

These bacteria help regulate ion transporter activity, supporting ionic, osmotic, and water balance. They also improve water use efficiency by modulating transpiration and stomatal conductance. Inoculated plants typically show reduced levels of reactive oxygen species (ROS), contributing to stress mitigation and improved resilience under saline conditions [41].

Several recent studies have reported the use of *Azospirillum* and *Azotobacter* to improve yield and quality in vegetable crops under saline conditions. *Azospirillum lipoferum* strain FK1 reduced the harmful effects of salt stress in chickpea and improved plant performance. This strain also enhanced the biosynthesis of osmolytes, boosted antioxidant activity, and upregulated stress-responsive genes under saline conditions. Wheat inoculated with *A. lipoferum* and irrigated with 80 mM NaCl showed significantly greater leaf and root dry weight than uninoculated controls [24].

Lettuce plants treated with *Azospirillum* produced higher-quality heads at harvest, with elevated chlorophyll content and longer shelf life under salt stress [1]. Treatments using *Azospirillum brasilense* have shown similar results in crops such as lettuce (*Lactuca sativa* L.), pepper (*Capsicum annuum* L.), chickpea (*Cicer arietinum* L.), and faba bean (*Vicia faba* L.) grown in salt-affected environments [44]. In lettuce (*cv.* Mantecosa), inoculation with *A. brasilense* Sp245 improved survival under 40 mM NaCl. Treated plants had higher fresh and dry leaf weights, greater leaf area, increased chlorophyll content, and more ascorbic acid than controls [13]. Further trials confirmed higher biomass, antioxidant levels, and post-harvest quality in inoculated plants exposed to salinity.

In pepper, plants inoculated with *A. brasilense* and *Pantoea dispersa* tolerated salinity levels up to 80 mM NaCl. By contrast, uninoculated plants showed reduced dry weight at only 40 mM NaCl. Inoculated pepper plants accumulated more biomass and maintained higher stomatal conductance and photosynthetic rates. Chlorophyll levels and photosystem II efficiency remained stable despite salt exposure [9].

In wheat (*Triticum aestivum*), inoculation with *A. brasilense* improved growth under severe salt stress (320 mM NaCl) and osmotic stress induced by polyethylene glycol (20–30% PEG 6000). Treated plants showed higher fresh and dry weights and better relative water content (RWC). Lipid analysis revealed altered phospholipid profiles in inoculated roots, suggesting a role in membrane stability and improved stress tolerance [27].

Azotobacter chroococcum, a free-living nitrogen-fixing species, has demonstrated salt tolerance. Inoculation with this species has improved yields in pea, potato, rice, wheat, and cotton under saline and arid conditions. Treated plants also showed greater root length and shoot growth [45]. In maize, *Azotobacter* species promoted potassium uptake and sodium exclusion, and improved the availability of phosphorus and nitrogen under salt stress [9].

A commercial mix of *Azospirillum* and *Azotobacter* applied 15 days after transplanting enhanced growth and yield in cherry tomato. Treated fruits had higher dry matter, greater acidity, and more soluble solids, even in saline conditions [13].

Inoculation with specific *Bacillus* strains improved plant responses to salt. *Bacillus aryabhattai* H19-1 and *B. mesonae* H20-5 increased antioxidant enzyme activity, stimulated abscisic acid (ABA) metabolism, and promoted proline accumulation [12]. In rice, *B. aryabhattai* MS3, which produces siderophores, increased yield by 60% under normal conditions and by 43% under 200 mM NaCl [7].

In soybean, *B. amyloliquefaciens* raised endogenous gibberellin (GA) and ABA levels under salinity. The strain SQR9 synthesised IAA and GA, enhanced maize root growth, and influenced the expression of *RubisCO* genes, which code for key photosynthetic enzymes [24]. This strain also upregulated *NHX1* and *HKT1*, genes active in sodium transport and sequestration. Metabolites from the culture supernatant of salt-tolerant *B. amyloliquefaciens* improved germination and radicle length in maize and soybean grown under saline conditions [46].

In *Arabidopsis thaliana*, inoculation with *Pseudomonas koreensis* Ps 9–14 reduced the negative effects of salt stress. This was attributed to enhanced antioxidant enzyme activity, including ascorbate peroxidase (APX), catalase (CAT), and peroxidase (POD) [16]. The endophytic strain *Pseudomonas* OFT5, which produces ACC deaminase, reduced ethylene levels and improved salt tolerance in tomato [5]. *Pseudomonas* PS01 improved salt tolerance in *Arabidopsis* by modulating stress-related gene expression. This included upregulation of *LOX2* (linked to jasmonic acid biosynthesis) and downregulation of *APX2* and *GLY17* (active in ROS detoxification) [47].

Pseudomonas citronellolis SLP6H improved chlorophyll content, antioxidant enzyme activity, and growth in *Helianthus annuus* under salinity. Its action was partly linked to hydroxamate-type siderophore production [7]. Cucumber treated with *Rhodopseudomonas palustris* G5 showed higher expression of *SOD*, *POD*, polyphenol oxidase (PPO), and soluble sugars compared to untreated plants under salt stress [38]. In soybean, the endophyte *Curtobacterium* SAK1 lowered ABA, JA, ROS, PPO, and POD levels, while increasing glutathione content, an essential antioxidant [33].

In rice, the halotolerant strain *Curtobacterium albidum* SRV4 enhanced the expression of *SOD*, *CAT*, and *APX*, and helped maintain Na^+/K^+ homeostasis. This strain also produced EPS, which limited sodium ion availability to roots and reduced salt toxicity [41]. *Planococcus* sp. MSSA-10 regulated antioxidant activity, phenolic compound levels, and nutrient mobilization in pea. Inoculated plants showed increased uptake of phenolics, POD, CAT, and nutrients (N, P, K), which improved growth under salinity [5]. In barley, *Hartmannibacter diazotrophicus* E19(T) colonized roots and enhanced both shoot and root biomass in saline soil. Treated plants exhibited relative water content (RWC) more than three times higher than controls [24].

In tomato, *Leclercia adecarboxylata* MO1 improved growth under salt stress. This effect was associated with higher levels of sugars (sucrose, glucose, fructose), organic acids (citric and malic acid), and amino acids (serine, glycine, methionine, proline), along with lower endogenous ABA [33]. In rice, *Glutamibacter* sp. YD01 upregulated antioxidant genes (*OsPOX1*, *OsFeSOD*, *OsGR2*) and abiotic stress-related genes (*OsWRKY1*, *OsDREB2*, *OsHKT1*), while suppressing *OsERF1* (linked to ethylene synthesis), thereby improving salt tolerance [40]. In soybean, five halotolerant strains—*Arthrobacter woluwensis* AK1, *Microbacterium oxydans* AK2, *Arthrobacter aurescens* AK3, *Bacillus megaterium* AK4, and *Bacillus aryabhattai* AK5—enhanced SOD and glutathione activity, increased K^+ uptake, and reduced Na^+ and ABA levels. These strains also upregulated *GmLAX3* (auxin-related) and *GmST1* (salt tolerance) genes [33].

Pseudomonas putida KT2440 and *Novosphingobium* sp. HR1a improved the growth of *Citrus macrophylla* under salt stress. HR1a increased IAA levels in leaves, and KT2440 reduced chloride and proline accumulation in roots [12]. In soybean grown hydroponically, *Pseudomonas pseudoalcaligenes* SR16 and *Bacillus subtilis* SR3 improved salt tolerance. SR16 raised protein levels, proline content, and the activity of antioxidant enzymes including SOD, CAT, PX, POD, and PPO [5].

Rhizobacterial inoculation also enhanced the activity of soil enzymes such as dehydrogenase, alkaline phosphatase, acid phosphatase, and urease. These enzymatic responses helped maintain soil nutrient balance and supported plant growth under salinity stress [48].

Hydric and Heat Stress

About 60% of global land lies in arid and semi-arid zones. These regions depend heavily on irrigation for agriculture. Climate change is expected to reduce rainfall, raise temperatures, increase atmospheric CO_2, and intensify weather variability. This will result in more frequent droughts and floods. In the coming years, agriculture will face growing water shortages. Crops will be exposed to both drought and heat stress, limiting productivity.

Drought stress occurs when soil moisture and humidity are low, and temperatures are high. Heat stress refers to temperatures exceeding the physiological limits of plant growth [5]. Drought triggers cellular signals that increase reactive oxygen species (ROS). Without adequate detoxification, ROS damage membranes, proteins, and DNA [12]. Water movement from the xylem to growing cells is reduced. This suppresses cell elongation and slows development. Leaf area and plant height also decline, as mitosis and cell expansion are inhibited.

Osmotic adjustment allows plants to cope with drought by actively accumulating solutes in the cytoplasm. This helps maintain water balance in cells [49]. Beneficial bacteria can enhance water use efficiency and improve tolerance to drought and heat. These microbes release various compounds, including phytohormones, organic acids, sugars, trehalose, choline, proline, glycine betaine, amino acids, polyamines, EPS, and ACC deaminase. They also promote the synthesis of heat shock proteins (HSPs), dehydrins, and volatile organic compounds (VOCs). Together, these metabolites help plants survive and recover from both drought and heat stress [34].

Several studies have shown that PGPR used as biostimulants improve plant responses to drought and heat stress [35]. Under water deficit, *Bacillus amyloliquefaciens* FZB42 produced extracellular polysaccharides (EPS) that enhanced biofilm stability in *Arabidopsis thaliana* [7]. In soybean exposed to heat stress, *Bacillus tequilensis* SSB07 raised levels of jasmonic acid (JA) and salicylic acid (SA), and reduced ABA content. Treated plants showed increased biomass and photosynthetic pigments compared to controls [33]. Under drought, a strain of *Bacillus subtilis* increased cytokinin content by 30% in *Platycladus orientalis*, improving foliage health [10].

In *Arabidopsis*, *B. subtilis* GOT9 induced the expression of drought-related genes such as *RD29B*, *RD20*, *RAB18*, and *NCED3*. In *Brassica*, it also upregulated *BrDREB1D*, *BrWRKY7*, and *BraCSD3*. These responses were linked to ABA accumulation and better stress tolerance [50]. In wheat, *Bacillus safensis* modulated heat shock protein (HSP) expression. Plants withstood heat stress at 40°C without excess ROS production [15]. *Streptomyces* strains reduced drought stress in tomato and activated transcription factors *ERF1* and *WRKY70* [5]. In *Brassica*, inoculation with *Bacillus* sp. stimulated *DREB2* and *DREB1-2*, which are independent of ABA signalling [35].

Pseudomonas sp. AKMP6 and *P. putida* AKMP7 protected plants from heat stress by reducing ROS levels and increasing sugars, proteins, starch, proline, chlorophyll, and amino acids [1]. In tomato, *P. fluorescens* increased cytokinin levels and improved drought tolerance [10]. In wheat, inoculation with thermotolerant *P. putida* AKMP7 increased shoot and root biomass, seed size, and heat tolerance. ROS levels were reduced, along with the expression of *SOD*, *APX*, and *CAT* [24]. In pepper, *Pseudomonas aeruginosa* and *Bacillus licheniformis* activated stress-related genes such as *ERD15*, *HSP*, *CaPR-10*, *VA*, and *Cadhn*, conferring drought resistance [24].

In maize grown under Mediterranean conditions, *Azotobacter chroococcum* increased photosynthesis, chlorophyll content, and transpiration. Root treatments with *Bacillus megaterium* and a 1:1 mix of *A. chroococcum* and *B. subtilis* gave the highest yields [15].

In wheat, antioxidant enzymes such as *SOD*, *CAT*, and *POX* increased after inoculation with *Bacillus* spp., *Azospirillum lipoferum*, and *A. brasilense* under drought conditions with 40% field capacity [51].

The overexpression of *TaFER-5* in wheat increased tolerance to multiple stresses, including heat, when seedlings were exposed to temperatures below 40°C. This response was linked to ROS detoxification [5]. In *Phaseolus vulgaris*, *Rhizobium tropici* and *Paenibacillus polymyxa* induced the expression of the *trehalose-6-phosphate synthase (TPS)* gene, which contributes to drought resistance. *Bacillus* strains also regulated *P5CS*, a gene involved in proline biosynthesis, enhancing osmotic tolerance in maize and cucumber seedlings [24].

Wheat seedlings inoculated with *Bacillus amyloliquefaciens* and *Azospirillum brasilense* showed improved heat tolerance during early growth [4].

Under osmotic stress, *Acinetobacter calcoaceticus* AC06 and *Bacillus amyloliquefaciens* BA01 produced high levels of osmolytes. These included proline (2.21 and 1.75 µg ml^{-1}), salicylic acid (18.59 and 14.21 µg ml^{-1}), trehalose (28.35 and 22.74 µg mg^{-1} FW), and glycine betaine (11.35 and 7.74 mg g^{-1}), respectively. These strains were tested in *Arachis hypogaea* L. (peanut) under two drought regimes: 60% and 40% field capacity. Inoculated plants showed better osmotic adjustment. This was reflected in improved biomass, pigment content, relative water content (RWC), proline levels, and soluble sugar concentration. Stress indicators such as electrolyte leakage and malondialdehyde (MDA) content were reduced. Enzyme activity of CAT, APX, and SOD also increased, supporting drought tolerance through antioxidant defence [50].

In *Mentha pulegium* L. (pennyroyal mint), co-inoculation with *Azotobacter chroococcum* and *Azospirillum brasilense* improved physiological and phytochemical traits. Treated plants under severe water stress accumulated more ABA, proteins, sugars, phenolic monoterpenes, flavonoids, oxygenated compounds, and showed stronger DPPH radical-scavenging activity [1]. In *Triticum aestivum*, *Azospirillum lipoferum* increased proline content in seedlings. This enhanced water retention and drought tolerance during a 10-day pre-irrigation period [5].

Cold Stress

Low temperatures restrict crop productivity in temperate regions. In these areas, cold stress contributes to annual yield losses ranging from 51% to 82%. Cold exposure disrupts physiological functions including ROS regulation, energy metabolism, photosynthesis, root hydraulics, and biomolecule stability. Membrane structure, protein function, and nucleic acid integrity are all affected. Plants respond by altering gene expression and triggering the production of compatible solutes, enzymes, phytohormones, and antioxidants [5].

Psychrotolerant and psychrophilic bacteria offer mechanisms to improve cold tolerance in crops [49]. In tomato, inoculation with *Pseudomonas vancouverensis* OB155 and *P. frederiksbergensis* OS261 raised proline and antioxidant enzyme levels (SOD, APX, and GSH), reducing damage from cold stress [45]. In beans, *P. fragi*, *P. chlororaphis*, and *P. fluorescens* improved cold tolerance by increasing the activity of SOD, CAT, POX, APX, and glutathione reductase (GR). These enzymes reduced ROS levels and lipid peroxidation [1].

In wheat, treatment with *Bacillus* spp. reduced ABA, ethylene (ET), and MDA content under cold stress. Expression of *P5CS*, *expA1*, *CKX2*, and *ARF* genes increased. These changes improved osmotic balance, leaf expansion, cytokinin metabolism, and auxin signalling [5].

In *Medicago truncatula*, *Rhizobium* inoculation raised the levels of SOD, CAT, APX, ascorbate, glutathione, proline, sugars, and glycine betaine. It also reduced nitro-oxidative stress and improved nitrogen uptake by increasing nitrate reductase activity [52]. In tomato, *Streptomyces* sp. 506 (TOR3209) activated ABA-related genes through the HY5 transcription factor. Expression of *ZEP1*, *NCED1*, beta-carotene hydroxylase, and *TASI4* increased. TOR3209 also improved photosynthesis by regulating RUBISCO and NAD/NADP-malate dehydrogenases (MDH), confirming an ABA-mediated response [24]. In rice, strains of *Pseudomonas*, *Enterobacter*, and *Stenotrophomonas* enhanced cold tolerance. Treated plants showed higher levels of proline, sugars, proteins, and nutrients (N, P, K), along with greater antioxidant activity (SOD, POD, CAT) [53]. In wheat, *Pantoea dispersa* improved growth and nutrient uptake under cold stress. This response was attributed to phosphorus solubilization and the production of IAA and ACC deaminase [1]. In grapevine (*Vitis* *vinifera*), the psychrotolerant bacterium *Burkholderia phytofirmans* enhanced cold tolerance by increasing the expression of ROS-scavenging genes and the accumulation of stress metabolites. Inoculated plants recovered faster and returned to normal metabolism more quickly than controls. *B. phytofirmans* also modulated carbohydrate metabolism and protected photosynthetic function during cold exposure [7].

Heavy Metals Stress

Soil contamination by heavy metals is a growing environmental problem. Industrial effluents released into water bodies contribute directly to the accumulation of toxic elements in agricultural soils. This contamination affects food safety and crop productivity [54]. The use of nitrogen, phosphorus, and potassium fertilizers, along with herbicides, insecticides, and fungicides, compounds the problem.

Heavy metals alter soil pH and texture. They also interfere with biological processes that are essential for plant growth. These include enzyme activity, antioxidant responses, and cell integrity. Metal stress reduces photosynthesis, disrupts nutrient uptake, and damages plant tissues. Several microbial biostimulants reduce the effects of heavy metal stress. They act through biosorption, chelation, and precipitation, limiting the absorption and translocation of metals in plant tissues [34]. Microbial siderophores, which bind iron, can also immobilize toxic metals such as Cr^{3+}, Al^{3+}, Cu^{2+}, U^{3+}, and Pb^{2+}.

Siderophores from *Azotobacter chroococcum* improve tolerance to metal stress in maize. *Agrobacterium radiobacter* has been shown to remove up to 54% of arsenic from contaminated soils through siderophore activity [49]. Extracellular polysaccharides (EPS) produced by bacteria can reduce hexavalent chromium (Cr^{6+}) to trivalent chromium (Cr^{3+}). This form is less toxic, less soluble, and more stable in soils [6]. EPS-based reduction of Cr^{6+} offers a promising strategy for improving the quality of groundwater in polluted environments. In rice, co-inoculation with *Pseudomonas stutzeri* and *Cupriavidus taiwanensis* reduced arsenic toxicity by converting arsenic into a stable arsenic sulphide form [10]. These strains also produced ACC deaminase, synthesised IAA, solubilized phosphate, and fixed nitrogen.

Functional metagenomic studies identified genes encoding phosphodiesterase enzymes in *Koribacter*, *Acidomicrobium*, *Bradyrhizobium*, and *Burkholderia*, suggesting the potential for degradation of organophosphorus pesticides in contaminated soils [7]. Three copper-resistant strains—*Burkholderia cepacia* J62, *Pseudomonas thivervalensis* Y1-3-9, and *Microbacterium oxydans* JYC17—improved biomass in *Brassica napus* L. and increased copper accumulation in shoots by 63.4%, 55.3%, and 63.4%, respectively, compared to untreated plants [12].

Pseudomonas and *Bacillus* strains also promoted the hyperaccumulation of zinc and cadmium in *Helianthus annuus* L., increasing shoot concentrations by 1.7–2.5 times. Metal uptake and transport were linked to transporter families such as YSL (Yellow Stripe-Like), COPT (Copper Transporter), P1B-type HMAs, CE (Cation Efflux), ZIP (Zinc and Iron-Regulated Transporters), and ZIF1 (Zinc-Induced Facilitator 1). ZNTs, part of the ZIP family, are essential for micronutrient transport and metal tolerance. These transporters may be manipulated to improve plant resistance to metal stress.

In spinach, three highly metal-tolerant isolates—*Bacillus subtilis* subsp. *spizizenii* DSM, *Paenibacillus jamilae*, and *Pseudomonas aeruginosa*—enhanced tolerance under cadmium and lead stress. Treated plants showed improved fresh and dry weight, chlorophyll content, transpiration rate, net photosynthesis, stomatal conductance, RWC, and membrane stability index. Metal stress alone reduced these physiological attributes and suppressed antioxidant activity [15]. *Pseudomonas fluorescens* Sasm05, a cadmium-resistant endophyte, increased Cd accumulation in *Sedum alfredii* by enhancing IAA production and upregulating genes involved in cadmium transport and uptake [12].

Bacillus altitudinis KP14, a Pb-tolerant strain, improved biomass in *Miscanthus* × *giganteus* by 77%. This was linked to its ability to solubilize phosphate, produce IAA, ACC deaminase, ammonia, siderophores, and hydrogen cyanide, and to exert antifungal activity [34].

Several scientific studies confirm that the application of PGPRs enhances plant resilience against rapid weather changes, rising temperatures, salinity, drought, disease, and insect attack. The interaction between plants and rhizospheric microbes is dynamic and responsive. Environmental changes are detected early, triggering stress-related responses that support plant adaptation. Although transgenic crops offer certain advantages, their acceptability for human consumption remains debated. In contrast, PGPRs provide a scientifically grounded, sustainable, and environmentally friendly approach to developing stress-resilient crops.

Conclusion, Challenges and Future Prospects

The use of PGPBs in sustainable agriculture offers a promising strategy. These bacteria can improve crop productivity, modulate physiological responses, and enhance stress tolerance, while reducing reliance on chemical inputs. PGPBs also contribute to soil health and nutrient availability, addressing major challenges linked to climate change and global food security [10].

But, several limitations remain. The effectiveness of PGPBs varies depending on soil type, climate, and microbial interactions. Introducing non-native strains may disrupt indigenous microbial communities and reduce soil biodiversity. Modified strains may persist or spread in unintended ways, posing ecological risks. Their use may also affect nutrient cycling, with cascading impacts on ecosystem functions. Horizontal gene transfer between PGPBs and native microbes raises additional concerns.

To mitigate these risks, thorough research, risk assessments, and good application practices are essential. Regulatory barriers and the lack of standardized protocols hinder large-scale use. High production costs may limit access for smallholder farmers. Scalability, approval processes, and deeper insight into plant–microbe interactions are needed to ensure successful integration into farming systems. There is a need for continued research, technological innovation, and a comprehensive understanding of the interactions between PGPBs, plants, and the environment.

For the scientific community and commercial organizations considering the use of PGPBs, the first step is a soil analysis to determine composition and nutrient levels. This is followed by the selection of PGPB strains that match specific crops and local conditions. Customized microbial consortia, biotechnological applications, and continual research advances can further optimize PGPB effectiveness for targeted crops and environments. Current studies are exploring molecular and physiological stimulation processes, as well as the intricate interactions between PGPBs and plants at the molecular level, with the aim of unlocking their full potential, expanding their applicability, and ensuring consistent outcomes in sustainable agriculture [11].

Omics technologies—including transcriptomics, proteomics, metabolomics, and metagenomics—alongside advanced molecular biology tools, are used to identify biochemical targets, elucidate regulatory roles within cellular pathways, and characterize and optimize PGPB strains for specific crops and environments [34]. High-throughput phenotyping at multiple scales is regarded as the most effective method for identifying new biostimulants, given the complexity of matrices containing diverse groups of bioactive molecules. Multi-trait screening enables discovery of promising biostimulants and clarification of their modes of action under both optimal and challenging conditions.

An integrated strategy combining omics technologies with high-throughput phenotyping offers a robust scientific basis for understanding biostimulant traits and activities [2]. The main actors in the biostimulant industry—including researchers, companies, policymakers, and stakeholders—are now focused on developing second-generation products (*biostimulant 2.0*) featuring synergistic action from microbial and non-microbial components, to enhance sustainability and resilience in agriculture.

Microorganisms produce diverse bioactive compounds that allow them to establish complex associations with plants. Each plant species—and subspecies—releases specific small molecules that attract beneficial microbes and deter potential pathogens [10]. Optimizing culture conditions, biochemical characterisation, comprehensive investigation of mechanisms of action, and precise determination of dosage and formulation are essential steps for scaling up microbial exudates commercially.

Accurate qualitative and quantitative profiling of microbial secretions, combined with transcriptomic, metabolomic, and proteomic studies, is critical to elucidate biosynthetic pathways and to make full use of microbial exudates as biostimulants. Research and development can integrate microbial exudates into environmentally responsible and sustainable farming systems. Continued research and application of PGPB-based approaches, tailored to specific crops and agroecosystems, remain essential to maximize their contribution to crop productivity and agricultural sustainability.

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