Plant-Growth-Promoting Rhizobacteria (PGPR)-Based Biostimulants for Agricultural Production Systems

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The application of biostimulants has been proven to be an advantageous tool and an appropriate form of management towards the effective use of natural resources, food security, and the beneficial effects on plant growth and yield. Plant-growth-promoting rhizobacteria (PGPR) are microbes connected with plant roots that can increase plant growth by different methods such as producing plant hormones and molecules to improve plant growth or providing increased mineral nutrition. They can colonize all ecological niches of roots to all stages of crop development, and they can affect plant growth and development directly by modulating plant hormone levels and enhancing nutrient acquisition such as of potassium, phosphorus, nitrogen, and essential minerals, or indirectly via reducing the inhibitory impacts of different pathogens in the forms of biocontrol parameters. Many plant-associated species such as *Pseudomonas*, *Acinetobacter*, *Streptomyces*, *Serratia*, *Arthrobacter*, and *Rhodococcus* can increase plant growth by improving plant disease resistance, synthesizing growth-stimulating plant hormones, and suppressing pathogenic microorganisms. The application of biostimulants is both an environmentally friendly practice and a promising method that can enhance the sustainability of horticultural and agricultural production systems as well as promote the quantity and quality of foods. They can also reduce the global dependence on hazardous agricultural chemicals.

Keywords: Acinetobacter ; Arthrobacter ; biostimulants ; Enterobacter ; Ochrobactrum ; Pseudomonas ; Streptomyces

1. *Ochrobactrum* spp.

Ochrobactrum spp. belongs to the *Brucellaceae* family and is a class-alpha-proteobacteria [1], commonly identified in the soil within the roots of a plant [2]. *Ochrobactrum* spp., together with the closely related *Brucella*, *Agrobacterium*, and *Rhizobium* genera, belong to the class of *Alphaproteobacteria* [1][2], which are also of interest as plant beneficial bacteria, as some of the strains are able to nodulate roots to fix nitrogen, underlining their close association with the host plants. They can also improve the germination percentage, as well as increase the protease activities, amylase, and relative root elongation, and they can be considered as important in bioremediation as well as an important alternative for plant growth promotion. *Ochrobactrum* is usually found in entomopathogenic nematode symbiotic systems, and it has been reported that the *Ochrobactrum intermedium* strain produces glyco lipopeptide biosurfactant [3]. Ochrosin, which is a multi-functional bio-surfactant produced by *Ochrobactrum* sp. BS-206, shows appropriate anti-adhesive, antimicrobial, antifeedant, and insecticidal activities [4]. *Ochrobactrum* sp. MPV1 is an appropriate candidate for the bioconversion of toxic oxyanions, including tellurite and selenite, to their respective elemental forms, producing intracellular Se and TeNPs possibly accessible in industrial and biomedical applications [5]. *Ochrobactrum anthropi* DE2010 indicated high tolerance and a high removal ability value for Cr(III), as well as being effectual in immobilizing Cr(III) [6]. *Ochrobactrum* JAS2 isolated from paddy rhizosphere soil indicated meaningful advantages of the production of hydrogen cyanide, ammonia, and IAA with significant plant-growth-promoting capabilities [7]. *Ochrobactrum lupini* KUDC1013 consisted of systemic resistance against spots caused by *Xanthomonas axonopodis* pv. *vesicatoria* in pepper, as well as resistance against leaf sport rot caused by *Pectobacterium carotovorum* subsp. *carotovorum* in tobacco [8].

2. *Acinetobacter* spp.

Acinetobacter spp. is a Gram-negative coccobacilli that is aerobic and non-motile, with no glucose-fermentation capability, being found in different environments [9][10][11][12][13]. One of the main reasons for the study of the genus *Acinetobacter* is because of its role in antimicrobial resistance and serious infections [12]. It can fix nitrogen, solubilize minerals, produce siderophores, and even be used as plant epiphytes or endophytes, allowing it to assist hosts in detaching pollutants and tolerating environmental stresses [13]. It is short, plump, and typically 1.0–1.5 μm by 1.5–2.5 μm in size during the rapid phase of its growth [14][15]. Shah et al. [16] observed that zinc sulfide nanoparticles, *Bacillus velezensis*, and *Acinetobacter pittii* have great potential against *Rhizoctonia solani* in tomato to suppress root rot infection and improve yield and growth.

They have also found that this combination can increase tomato plant nutrition such as in terms of potassium, calcium, silicon, and magnesium, as well as improve redox quenching status by increasing the activity of antioxidant defense enzymes [16]. Wang et al. [17] also discovered that *Acinetobacter oleivorans* S4 is important for plant growth and valuable in assisting in phytoremediation. Ke et al. [18] reported that the *Acinetobacter indicus* strain ZJB20129 isolated from an urban sewage treatment plant showed a heterotrophic nitrification-aerobic denitrification ability. *Acinetobacter* sp. TX5 has a valuable ability in terms of nitrite removal with a capability of suppressing N_2O accumulation, and it has been reported that *Acinetobacter* sp. XS21 effectively removes arsenite from soluble-exchangeable fraction [19], with *Acinetobacter calcoaceticus* strains from canola and soybean having been reported to improve plant growth [20]. The improved seedling growth parameters of the treated crop seeds of *Vigna unguiculata*, *Vigna radiata*, *Dolichos lablab*, and *Abelmoschus esculentus* showed the wonderful potential of *Acinetobacter* sp. RSC7 to be used in a bio-fertilizer formulation in a sustainable production system [21]. The strain *Acinetobacter calcoaceticus* DD161 has high inhibitory activity against the *Phytophthora sojae* 01 in soybean [22]. *Acinetobacter* sp. strain Xa6 can be used as a biological control against *Ralstonia solanacearum* as well as increase the final yield of tomato [23]. *Acinetobacter* sp. strain SG-5 is an important candidate as a metal remediation plant, particularly in terms of Cd in edible plant parts and as a plant growth promoter [24].

3. *Arthrobacter* spp.

The genus *Arthrobacter* can effectually utilize inorganic and organic compounds as a metabolism substrate, acting as a tool for bioremediation in agriculture [25][26][27][28]. Certain *Arthrobacter* species, mainly soil-dwelling rhizobacteria, have been considered as plant growth promoters because of their different growth-promoting activities, such as potassium and phosphate solubilization, nitrogen fixation, and indole acetic acid synthesis [29][30]. Zhao et al. [31] reported that *Arthrobacter* sp. ZCY-2 has a circular chromosome and five circular plasmids encoding for the procedure of salt adaptation and pollutant degradation, proving its unique saline tolerance characteristic. Zhao et al. [32] reported that Ap920-WI from *Arthrobacter* sp. H5 has shown high anti-fungal activity and that it inhibited the infestation of *Sclerotinia sclerotiorum* on rape leaves, with it potentially offering a novel solution for controlling plant diseases.

4. *Enterobacter* spp.

The genus *Enterobacter* is a member of the family *Enterobacteriaceae* of the class *Gammaproteobacteria* [33], and the *Enterobacteriaceae* family includes different bacteria such as *Enterobacter* spp., *Klebsiella* spp., and *Escherichia coli* [34][35][36]. Ngigi et al. [37] found that the existence of bacterial strains such as *Enterobacter cloacae* in different sugarcane-cultivated fields can be used to increase the degradation of atrazine in contaminated soil, where atrazine is known to be recalcitrant. *Enterobacter roggenkampii* ED5 has notable application potency in sugarcane production as it can boost plant growth, as well as being able to enhance photosynthetic leaf gas exchange capacity and agronomic trains in sugarcane [38]. Mayak et al. [39] also reported that the plant-growth-promoting bacterium *Enterobacter cloacae* CAL3 has a positive influence on tomato seedlings. Ullah et al. [40] reported that the Zn-solubilizing endophyte *Enterobacter* sp. MN17 with Zn utilization via seed coating can increase the profitability, productivity, bioavailable Zn, and grain quality of *Kabuli* chickpea. Utkhede and Smith [41] also noted that *Enterobacter agglomerans* is appropriate for the control of crown and root rot of apple trees. Zakria et al. [42] also observed the positive effects of *Enterobacter* sp. strain 35-1 and *Enterobacter* sp. SE-5 isolated from sugarcane on both rice (*Oryza sativa*) and wild rice (*Oryza officinalis*). The beneficial impacts of *Enterobacter* species on potassium, nitrogen contents, leaf area, stem girth, and seedling height proved its important role as a bio-inoculant for maize seedling growth and health [43].

5. *Pseudomonas* spp.

One of the most widespread and diverse bacterial groups in the natural environment is *Pseudomonas* [44]; the genus has significant functions in the soil and biosphere [45], belonging to the phylum *Proteobacteria*, including the major abundant quenching Gram-negative bacteria genus, especially in the rhizospheres of all plant samples [46], being considered as versatile biocontrol agents against bacteria and non-bacterial pathogens [47]. The widespread occurrence of *Pseudomonas* shows its adaptability through physiological, molecular, and environmental diversity. Its family consists of general forms like *Xanthomonas*, *Frateuria*, *Zoogloea*, and *Pseudomonas*. Cyclic lipopeptides from *Pseudomonas mediterranea* have 22 amino acids, which can induce plant dell death immunity and confer resistance to bacterial infection in *Nicotiana benthamiana* [48]. Different strains of *Pseudomonas* show numerous ecological qualified characteristics such as antifungal metabolite production, biofilm formation, synergistic attachment with the plant root system, quorum-sensing mediation, chemotactic mediation, uptake, and the catabolism of different plant secretions. *Pseudomonas fluorescens* UM270 has shown a functional role in the promotion of tomato plant growth, especially under salt stress conditions as it resulted in an increase in dry weight, chlorophyll content, and shoot and root length [49]. The application of *Pseudomonas* *plecoglossicida* RGK was found to have a capacity to solubilize potassium, zinc, and phosphate, as well as the potential to produce exopolysaccharide, hydrogen cyanide, ammonia, nitrogen fixation, siderophores, and indole acetic acid in turmeric plant [50]. It has also been found to be suitable to improve the growth metrics of plants, such as rhizome biomass, shoot height, the number of leaves, flavonoids, and phenolic content [51]. *Pseudomonas* sp. EB3 can protect banana plants against fusarium and salinity stress, as well as leading to improved growth under non-stressed conditions [52].

6. *Rhodococcus* spp.

Rhodococcus are well known for their significant capacity to degrade various aromatic chemicals, both short- and long-chain, such as heteroaromatic, halogenated, hydroaromatic, and polycyclic aromatic hydrocarbons [53][54][55][56][57]. The genus *Rhodococcus* consists of Gram-positive, aerobic bacteria, and non-sporulating belongs to the phylum *Actinobacteria* [58], which can tolerate extremely toxic components and unfavorable environments because of their cell wall structure and a large array of enzymes that can degrade and toxify harmful components in hostile habitats [59]. They have shown a wide range of metabolic activities [60], and they have been considered because of their biotechnological, agricultural, and ecological importance [61]. Dhaouadi et al. [62] reported that new plant species have been found to be hosts of the plant pathogenic *Rhodococcus fascians* and other newly found members of the genus *Rhodococcus*, and according to their findings, *Rhodococcus* can be found in pistachio and almond trees and root-stocks. *Rhodococcus fascians* can produce a mixture of cytokinins to modify the hormone landscape of its broad range of plant hosts, inducing developmental changes and tissue deformations. Abraham and Silambarasan [63] also found that *Rhodococcus erythropolis* JAS13 could be applied for the integrated bioremediation of pesticides and it plant-growth-promoting capability in agricultural systems. *Rhodococcus erythropolis* MTC 7905 can alleviate Cr^{6+} and promote the plant growth of pea, especially at a low temperature [55]. *Rhodococcus* sp. Fp2 did not stimulate pea growth in Cd-supplemented soil because it had no 1-aminocyclopropane-1-carboxylate deaminase activity in vitro in the presence of Cd [64]. *Rhodococcus* sp. PBTS1 and PBTS2 were able to produce auxins, cytokinins, and plant-growth-stimulating volatiles with notable influences on plant development [65]. In one experiment, it was reported that plant-growth-promoting characteristics were observed after the isolation of *Rhodococcus qingshengii* RL1 from the surface-sterilized leaves of *Eruca sativa* Mill. [66][67].

7. Serratia

Serratia spp. has various plant growth promotion characteristics, and it stimulates and colonizes the growth of multiple hosts such as non-homologous and homologous forms [68][69][70]. It is a Gram-negative bacterium belonging to *Enterobacteriaceae*, with more than 42 species, and the plant-associated *Serratia* consists of both free-living and endophytic species in the rhizosphere [71]. They can induce root hair development stimulated by their IAA-production and acyl homoserine lactone (AHL) signaling mechanisms [72][73][74]. Lim et al. [75] also found that *Serratia fonticola* DSM 4576^T can confer solubilization of inorganic phosphate, hydrogen cyanide production, indole-3-acetic acid production, siderophore production, and assimilation of ammonia via the glutamate synthase (GS/GOGAR) pathway. *Serratia nematodiphila* RGK has been found to have a high capacity to solubilize zinc, phosphate, and potassium, as well as the potency to produce exopolysaccharide synthesis, hydrogen cyanide, ammonia, nitrogen fixation, and the indole acetic acid of the turmeric rhizome of turmeric (*Curcuma longa*). *Serratia* sp. KUJM3 presents various benefits, such as the metalloid bioremediation, plant growth promotion, and As reduction of cowpea [76]. *Serratia marcescens* can stimulate plant growth and increases resistance against *Nilaparvata lugens* in rice, with colonized plants indicating increased seed germination, shoot and root lengths, and shoot and root fresh weights [77]. *Serratia* sp. 5D and RTL100 can be applied as effectual microbial inoculants, especially in nutrient-deficient soils in rainfed areas, where the cultivation of chickpea is common [78]. Devi et al. [79] also concluded that *Serratia marcescens* AL2-16 can increase the growth of latjeera (*Achyranthes aspera* L.), which is one of the most important medicinal plants of the Amaranthaceae family. *Serratia* sp. CP-13 decreases Cd uptake and concomitant lipid peroxidation in maize cultivars, showing its high potential in terms of plant growth augmentation and Cd remediation plans [80]. *Serratia marcescens* AHPC29 can be considered as a new agent for the management of *Bursaphelenchus xylophilus*, which is a destructive and invasive pathogen in forestry [81], with Obi et al. [82] reporting that *Serratia marcescens* 39-H1 was able to increase the hydrolysis of lignocellulosic biomass, being a plant-growth-promoting organism. Bhatta et al. [83] reported that *Serratia marcescens* DB1 is a plant-growth-promoting rhizobacterium with an innate ability to resist heavy metals such as Cr, Ni, and As, which can stimulate the bioavailability of essential elements for plant uptake and keep the balance of Na^+/K^+ ions in rice shoots. Ting et al.'s [84] pre-inoculation with the endobacterium *Serratia marcescens* strain UPM39B3 led to the production of host defense enzymes, such as polyphenol oxidase, peroxidase, total soluble phenols, and phenylalanine, in banana plantlets. Zhu et al. [85] found that *Serratia* sp. PW7 can be used to colonize wheat for decreasing pyrene contamination [86], and *Serratia plymuthica* BMA1 can be a potential choice to increase the agronomic effectiveness of *Vicia faba* L. plants toward a clean P-nutrition through the formulation of bio-phosphate fertilizers for plant growth promotion [87]. In another experiment, it was reported that *Serratia marcescens* strain B2 suppressed mycelial growth of the rice health blight pathogen *Rhizoctonia solani* AG-1 IA [88]. Restrepo et al. [88] indicated that *Serratia plymuthica* AED38 extracts showed a promising potential as a bioproduct for the control of avocado root rot caused by *Phytophthora cinnamomi*. *Serratia marcescens* are effectual in increasing the growth and growth characteristics such as leaf Cl^{-}, Na^{+} content, and the antioxidant enzyme activities in eggplant under salt stress [89]. Prischmann et al. [90] reported that *Serratia plymuthica* was associated with maize roots and can be considered as a plant-growth-promoting factor through antagonistic action against plant-pathogenic fungi. Youssef et al. [91] also noted that *Serratia proteamaculans* as soil drench effectively increased plant growth and controlled tomato early blight disease. *Serratia marcescens* AS09 was able to reduce disease incidence, promote growth, and increase root length and plant height, and it has shown high potential to be studied as a biocontrol agent against fusarium wilt disease [92].

8. Streptomyces

The major genus of *Actinobacteria* is streptomyces, and various strains of streptomyces can promote biocontrol pests and plant growth, weeds, diseases, and phytopathogenic microorganisms by producing phytohormones such as IAA, enzymes, siderophores, antibiotics, volatile organic compounds, and some other secondary metabolites [93][94][95][96]. *Streptomyces* spp. can also alleviate abiotic stresses, such as drought, salinity, and inorganic and organic contaminants in soil, as well as promoting nutrients bioavailability [97][98]. *Streptomyces* are extensively known for the production of an array of components that can promote plant growth directly by phytohormone production such as of cytokinins, indole acetic acid, and gibberellins; through the increased nutrition acquisition of potassium, phosphorus, nitrogen, and essential minerals; or through the suppression of plant diseases [99]. In fact, species of the genus *Streptomyces* are well known as producers of secondary metabolites such as antifungals, antibiotics, anticancer agents, and virulence parameters [100]. Ngalimat et al. [101] reported that *Streptomyces* spp. showed no phytotoxic impact on rice plants, mitigated the negative effects of bacterial panicle blight, increased rice yield attributes, and elicited defense-related gene transcript levels. Zheng et al. [102] illustrated that *Steptomycetes* sp. strain FJAT-31547, presenting broad-spectrum antibacterial and antifungal activity with high biocontrol effectiveness against tomato *Fusarium* wilt and bacterial wilt, was an important growth-promoting factor, as on the basis of GC-MS, n-hexadecanoic acid was recognized as the main constituent of this strain.

9. Stenotrophomonas

Stenotrophomonas maltophilia linked with plant roots can grow in the availability of different carbon sources such as glucose, chloroform, trichloroethylene, toluene, and benzene, which is also effectual in stimulating plant growth and controlling a wide range of fungal plant pathogens [103]. *Stenotrophomonas maltophilia* is the subclass of γ-β-proteobacteria with a high G + C content, being a Gram-negative bacillus extensively spread in a variety of environmental habitats such as the plant rhizosphere, foods, hospital disinfectant solutions, and soil [104]. It was formerly referred to as *Pseudomonas maltophilia* or *Xanthomonas maltophilia* [105][106]. Its strains can influence and increase plant growth when applied to seedlings, as the strains increase hair development and root growth, and there is always a significant correlation between indole-3-acetic acid and plant growth hormone [107]. *Stenotrophomonas* sp., *Stenotrophomonas chelatiphaga*, *Stenotrophomonas nitritireducens*, and *Stenotrophomonas maltophilia* are among the species that have found to be appropriate in their capability to degrade diverse aromatic components [108]. *Stenotrophomonas maltophilia* is known as the most prevalent organism found in clinical laboratories after *Acinetobacter* spp., *Pseudomonas aeruginosa*, and the *Burkholderia cepacia* complex [109]. Jeong et al. [110] also confirmed that *Stenotrophomonas maltophilia* R13 could be considered as a potential bioinoculant in environments, as well as increasing the nutritional value of feather meal. *Stenotrophomonas* sp. EGS12 has been considered as a wonderful substitute for the bioremediation of repairing a selenium-contaminated environment due to its capability to effectively decrease Se(IV) to form selenium nanospheres [111]. It has been reported that *Stenotrophomonas maltophilia* strain SCS1.1-produces copper nanoparticles, showing its great potency with notable antifungal and antibacterial activity to break down pesticides such as imidacloprid, profenofos, and chlorpyrifos, which are the most well-known organophosphate insecticides against a wide range of pests and insects [112]. *Stenotrophomonas rhizophila* DSM14405^{T} can produce spermidine for both stress protection and growth promotion, and it exerts high Cr(VI) resistance and reductive capability [113]. *Stenotrophomonas maltophilia* strain UN1512 was able to show the causal factor strawberry anthracnose, and its produced volatile compounds can improve tomato seedling growth [114]. Giesler and Yuen [115] reported that *Stenotrophomonas maltophilia* strain C3 prevented the growth of the fungus on leaf blades and decreased the severity of necrosis on seedlings. Li et al. [116] reported that *Stenotrophomonas maltophilia* CGMCC 4254 is an appropriate biocatalyst for the preparation of optically pure L-menthol from diastereomeric mixture. Ercole et al. [117] found that the inoculation of *Stenotrophomonas maltophilia* strains and *Bacillus velezensis* as an important technique to increase salinity tolerance and improve plant growth in maize cultivation.

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