

## Sustainable agriculture through rhizosphere bacteria for plant growth promotion, nutrient acquisition, and stress alleviation

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### Abstract

Rhizosphere bacteria are attracting a lot of interest in sustainable agriculture because of their capacity to stimulate plant growth, improve nutrient uptake, and reduce stress in plants. A review of recent discoveries in the field of using rhizosphere bacteria for these advantageous agricultural techniques is given in this article. Rhizosphere bacteria facilitate plant growth by solubilizing inaccessible elements like phosphorus, potassium, zinc, and manganese by producing a variety of enzymes and organic acids. Furthermore, these bacteria support plant nutrition by fixing atmospheric nitrogen, a necessary component for plant growth and development. Moreover, some rhizosphere bacterial strains can inhibit plant diseases, which lessen the need for artificial chemical pesticides. Rhizosphere bacteria have improved plant stress tolerance by producing stress-related substances, including phytohormones and osmoprotectants. These bacteria also give rise to systemic resistance in plants, successfully allowing them to survive various biotic and abiotic challenges. Concerning climate change and environmental variations, this rhizosphere bacteria-mediated stress reduction component holds a tremendous potential for sustainable agriculture. But for rhizosphere bacteria-based agricultural techniques to be successfully utilized, a thorough grasp of their variety, ecological relationships, and mode of action are necessary. Optimizing application techniques, formulating bioinoculants, and considering environmental aspects are crucial for consistent and dependable outcomes through rhizosphere bacteria.

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## Introduction

Microbial abundance in the soil causes biochemical transformations of nutrients in the presence of

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minerals, air, water, and organic matter (Paul, 2016). Many microorganisms, including bacteria, fungi, protozoa, algae, and actinomycetes, are present in the soil; however, bacteria most commonly influence nutrient transformation and plant growth. Bacteria colonizing in the rhizosphere enhance nutrient availability and soil fertility (De Zelicourt et al., 2013; Zhao et al., 2016). The bacterial assortment is affected by the soil conditions, including the presence of plants in the soil, organic carbon, temperature, moisture, electrical conductivity, and other chemical parameters (Glick, 2012). Many plant species require bacterial association for better growth (Ma et al., 2016). Plants choose the microflora of their own choice and have specific microbes. A balanced assortment of plants and bacterial responses is necessary to maintain mutually beneficial link between plants and soil microorganisms (De et al., 2013). The slow release of chemicals and signals gives plants a better chance to communicate with rhizosphere microflora. By releasing host functional signals, they make an associative symbiosis with plants (Chaparro et al., 2013; Ma et al., 2016). Endophytic bacteria colonize the internal tissues of the plants without degrading the host. Among them, *Rhizobium* spp. is symbiotically associated with the legume and is involved in the fixation of atmospheric nitrogen (Afzal et al., 2019; Lindström and Mousavi, 2020). Free-living bacteria form non-symbiotic associations by colonizing the rhizosphere and root surface.

The bacteria-plant-soil interaction is a complex and dynamic relationship in shaping soil health, plant growth, and ecosystem functioning. Soil is a home to various microorganisms, including bacteria, fungi, archaea, and viruses. There are several billion bacterial cells in a single gram of soil, which are abundant in nature (Ortiz et al., 2021). Organic matter content, moisture temperature, and pH are the soil factors that enhance bacterial abundance and diversity in the rhizosphere (Liu et al., 2020). Several mechanisms are adopted by the plants to interact with the microbes present in the soil (Jayaraman et al., 2021). Some nitrogen-fixing or mineral-solubilizing bacteria are produced by producing several organic acids produced by plants (Fasusi et al., 2021). These bacteria provide essential nutrients to plants, such as nitrogen, phosphorus, potassium, and other micronutrients (Pronk et al., 2022).

The soil nutrient cycle is significantly linked to soil microorganisms, including bacteria, as they convert fixed forms of organic or inorganic minerals into readily available nutrients for plant uptake (Basu et al., 2021). Various rhizobacteria solubilize insoluble minerals, including phosphorus, potassium, zinc, calcium, magnesium, and manganese (Thomas and Singh, 2019). Not all bacteria have symbiotic relations with plants, and some can also harm the growth and production of plants. Soil rotation and cover crops are unique treatments that can improve the proliferation of beneficial microbial communities in soil (Ghani et al., 2022). Thus, in the current review, we discuss how the bacterial-plant-soil interaction is a complex and dynamic process and how does it play a vital role in soil health, plant growth, and ecosystem functioning. It also describes the interactions that are essential for developing sustainable agricultural practices that promote plant growth and soil health while minimizing negative environmental impacts.

## Plant growth-promoting bacteria

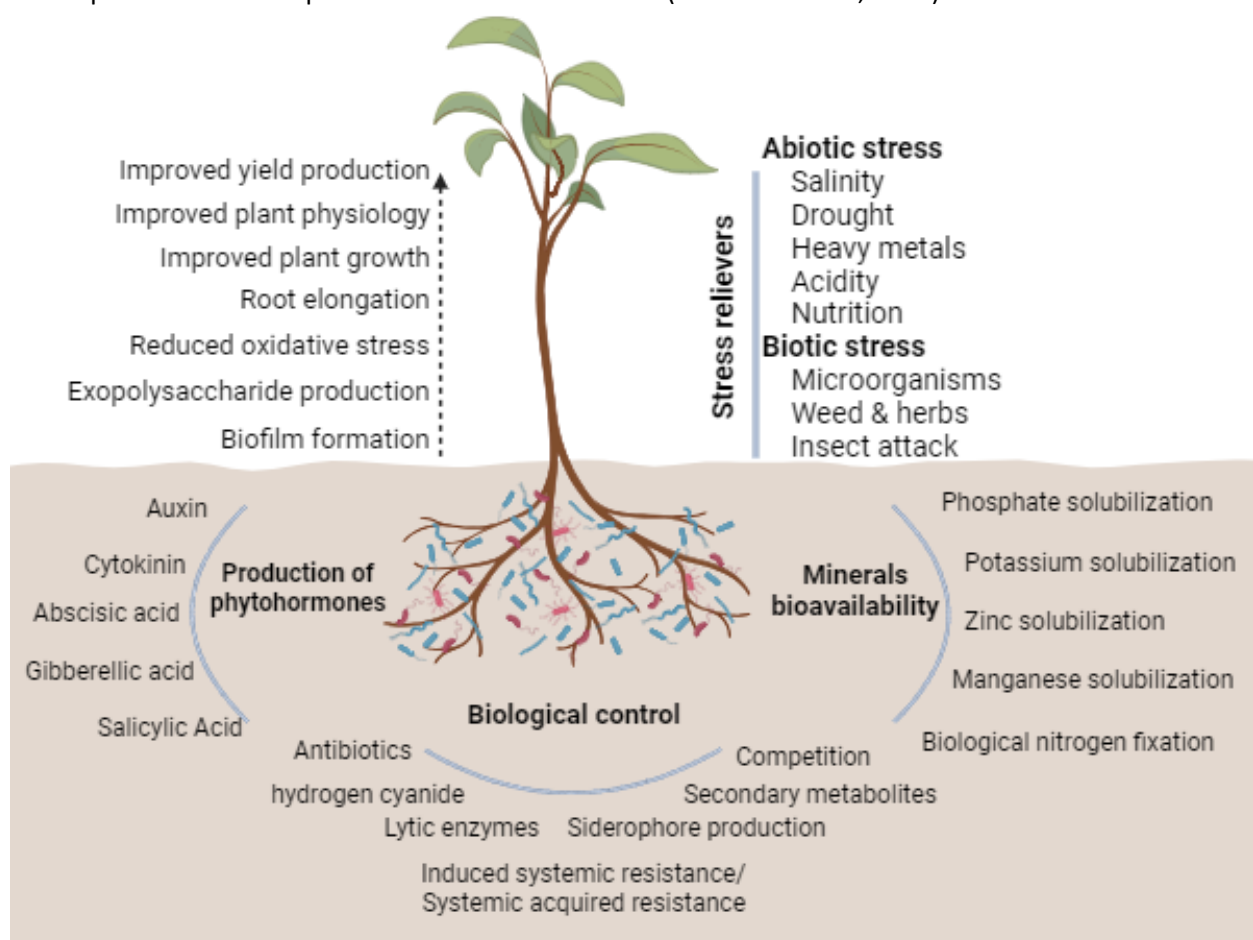
Some rhizosphere microorganisms may support their host's plant growth, yield, and defense against phytopathogens and abiotic stress tolerance, known as plant growth-promoting bacteria (PGPB). Extracellular plant growth-promoting bacteria located in the rhizosphere and rhizoplane, and intracellular plant growth-promoting bacteria present in the unique structure of root cell nodules are beneficial for the biostimulation of plant growth (Martínez-Viveros et al., 2010). Rhizosphere bacteria are prevalent in soils and help increase nutrient availability, reduce soil-borne diseases, and improve water infiltration into the soil (Abdelaziz et al., 2023). They form a symbiotic relationship with many legumes and other plants, increasing root growth and improving crop yield. Rhizobacteria can also fix atmospheric nitrogen, increasing plant nutrient availability (Sedri, 2022).

Rhizosphere bacteria have been used as a natural fertilizer for years and can be applied to crops directly or incorporated into soils to improve soil health. Rhizosphere bacterial-mediated plant growth promotion is crucial in sustainable agriculture and can increase crop yields and reduce fertilizer input (Sedri et al., 2022). These bacteria can also help restore degraded soils and provide long-term plant benefits. They are eco-friendly substitutes for traditional fertilizers and can sustainably improve crop production (Gupta et al., 2015). Rhizobacteria can colonize the root surface or inside the plant's root and promote plant health through various mechanisms. Rhizobacteria can activate the plant's innate defense mechanisms by inducing systemic resistance. This involves triggering a cascade of signaling pathways within the plant that help it resist diseases and pests (Ding et al., 2022). Rhizobacteria can enhance plant nutrient uptake by solubilizing insoluble nutrients such as phosphorus, iron, and potassium, making them available for plant uptake. They are involved in biological N-fixation and promote N availability for plant growth (Sheoran et al., 2021). Some rhizobacteria take part in the production of phytohormones such as auxins, cytokinins, and gibberellins, which can stimulate plant growth by promoting cell division,

elongation, and differentiation (Mekonnen and Kibret, 2021). Rhizobacteria can form biofilms on the root surface, a protective barrier against phytopathogens and abiotic stresses, and they also can compete with pathogenic microorganisms for resources such as nutrients and space, and exclude them from colonizing the root system (Herms et al., 2022). Overall, the mechanistic approach used by rhizospheric bacteria has been summarized in **Figure 1** and discussed in the sections below.

## Indole acetic acid-producing bacteria

Phytohormones are essential for controlling several physiological processes in plants. Plants primarily produce phytohormones, although some bacteria have also been found to produce these hormones (Egamberdieva et al., 2017). By producing phytohormones, these bacteria penetrate the rhizosphere and plants' roots and facilitate plant growth (Souza et al., 2015). They generate auxins, cytokinins, gibberellins, and abscisic acid. Indole-3-acetic acid (IAA), an auxin produced by PGPB bacteria, helps to promote root development, lateral root formation, cell elongation, and nutrient absorption (Shah et al., 2022). Bacteria produce zeatin (cytokinins) to encourage bud formation, lateral shoot development, and cell division (Kurepin et al., 2014). Gibberellins produced by bacteria affect flowering, seed germination, and stem length, and endorse plant growth (Olanrewaju et al., 2017). Some bacteria can produce the abscisic acid hormone, which helps plants adapt to abiotic stresses and increase water stress tolerance. Ethylene is involved in aging, leaf abscission, and fruit ripening. It controls growth and development and is also produced in reaction to stress (Chandra-kuntal, 2022).



**Figure 1. Representation of rhizosphere bacteria-mediated plant growth promotion and alleviation of abiotic and biotic stresses. The model shows promoted plant growth through phytohormone production, mineral solubilization, exopolysaccharides, biofilm production, and induced phytopathogen biocontrol**

Auxins are involved in the promotion of plants' growth and development (Gupta et al., 2023). These bacteria interact with the plant in the rhizosphere and promote its growth. These bacteria produce IAA, improving stress tolerance, boosting nutrient absorption, encouraging root development, and protecting plants from infections (Chieb and Gachomo, 2023). IAA-producing bacteria have the potential to enhance crop productivity and general health, which makes them advantageous for agriculture. It leads to sustainable farming techniques by lowering the requirement for chemical fertilizers and synthetic auxins.

Researchers and farmers are investigating the potential of IAA-producing bacteria in agricultural systems to boost yields and plant growth (Prasad, 2023). Several taxonomic groups, including genera like *Bacillus*, *Pseudomonas*, *Rhizobium*, *Azospirillum*, and *Enterobacter*, are inhabited by IAA-producing bacteria (War et al., 2023). Numerous environments, including soil, the rhizosphere, and plant tissues, are host to these bacteria.

Bacteria use tryptophan-dependent and tryptophan-independent mechanisms to produce IAA (Naureen et al., 2022). Tryptophan is converted to IAA by bacteria in the tryptophan-dependent pathway (Jahn et al., 2021). Tryptophan decarboxylase catalyzes the decarboxylation of tryptophan, creating tryptamine (Bajguz and Piotrowska, 2023). Tryptamine 2-monooxygenase is often referred to as indole-3-acetamide hydrolase, which converts tryptamine into indole-3-acetamide. Indole-3-acetamide hydrolase hydrolyzes indole-3-acetamide to produce IAA. Tryptophan is a prerequisite for IAA synthesis in this route, and its presence is required (Huang, 2023). Certain bacteria can produce IAA even in the lack of tryptophan. This pathway is called tryptophan-independent pathway. IAA is produced by converting alternate precursors in the tryptophan-independent route (Ortiz-García et al., 2023). Indole-3-pyruvic acid, a frequent precursor in this pathway, is generated by a series of enzymatic processes beginning with intermediates in the shikimate pathway. The indole-3-pyruvate decarboxylase (IPDC) catalyzes the decarboxylation step to generate IAA and then converts indole-3-pyruvic acid into IAA (Xiao et al., 2023). It is pertinent to remember that not all bacteria have both routes, and different bacterial strains may or may not be able to make IAA. Bacteria can create mutualistic interactions with plants and influence numerous physiological processes by generating IAA, which is advantageous to both the bacteria and the host plants (Mazoyon et al., 2023).

Certain bacteria can produce IAA and interact with plants to benefit them in several ways (Tang et al., 2023). They encourage the development of lateral roots, which aid in a plant's ability to search a broader soil region for nutrients and water. IAA production produces more robust and healthier root systems (Das et al., 2022). These bacteria can improve plant nitrogen uptake efficiency. They generate IAA, which helps the root to absorb vital minerals, including potassium, phosphate, and nitrogen. These bacteria lessen the detrimental impacts of environmental conditions on plants, such as desiccation, or high temperatures (Kaushal and Wani, 2016). IAA strengthens plant resilience, enabling them to endure and bounce back from challenging circumstances. Bacterial IAA may also support plant defense mechanisms against diseases (Meena et al., 2020). It increases plant defense against harmful microbes by triggering the plant's immune system. In many plant species, IAA encourages fruit development and flowering. Bacteria can affect these processes by generating IAA, which increases the number of flowers and the yield of high-quality fruits (Duca et al., 2014). Various studies conducted by researchers that elaborate the importance of IAA produced by bacterial species have been summarized in [Table 1](#).

## Nitrogen-fixing bacteria

Nitrogen (N) is the basis of all life on earth and is necessary for synthesizing nucleic acids, proteins, and enzymes (Raza et al., 2020). A considerable increase in atmospheric N<sub>2</sub> due to the synthesis of chemical fertilizers has caused a shift in emphasis towards biological nitrogen fixation (BNF) by legumes (Soumare et al., 2020). Nitrogen fixation is a crucial mechanism for determining the primary crop yield. The BNF has been widely used as a substitute for chemical N-fertilizers for legume production. The *Rhizobium*-legume association in the BNF process is considered an immensely effective process that can meet the N needs of the host plants (Kebede, 2021). The symbiotic relationship between rhizobia and the legume for biological nitrogen fixation is preferred since it is secure and safe for the environment. For example, like several other legumes, *Sesbania* spp. could employ biologically fixed nitrogen to solve soil problems owing to salt stress and waterlogging (Singh et al., 2021). Low nitrogen fixation and declining soil productivity are usually linked to low productivity of legumes (Slattery et al., 2001).

The inoculation of effective rhizobia can improve the yield production in legumes. Since this approach is mainly limited to leguminous plants in agricultural settings, researchers are very interested in discovering whether comparable symbiosis might also arise in non-legumes to produce the highest possible food yield for humans (Mus et al., 2016). An ancient practice known as "green manuring" with legumes provides physiologically altered N<sub>2</sub> to subsequent crops grown alternately. Legumes' rotation promotes N availability for succeeding cereals (Saadani et al., 2019). *Sesbania* can exchange nitrogen through its aerial parts, including stems, branches, and roots in the soil. Rao and Gill (1993) reported a high nutrient intake in shoots and an increase in nodulation and biomass production in their extensive studies on *Sesbania* species in alkaline stress. In contrast, the Na concentration was low, indicating the plant's value as a source of integrated biofertilizer (Ravshanov et al., 2023). Various roles of nitrogen-fixing rhizosphere and endophytic bacterial strains have been summarized in [Table 2](#).

**Table 1. The role of indole acetic acid-producing bacteria in plant growth promotion**

Bacterial species	Enzymatic mechanisms	Function in plants	References
<i>Burkholderia phytofirmans</i>	ACC-deaminase, aminocyclopropane-1-carboxylate oxidase (ACO)	1- Regulates ethylene level and takes part in the formation of lateral roots	Kaur et al., 2023
<i>Pseudomonas fluorescens</i>	Chitinase, protease, cellulase, lipase and phytase	Breakdown of chitin, amino acids, carbohydrates, fatty acids, and phytic acid	Kaur and Pandove, 2023
<i>Bacillus amyloliquefaciens</i>	Amylase, cellulase, protease, chitinase, lipase and phytase	Hydrolyze starch into glucose and maltose; breakdown of cellulose, proteins, lipids, and chitin	Liu and Kokare, 2023
<i>Azospirillum irakense</i>	Nitrogenase enzymes	Biological nitrogen fixation	Nair, 2023
<i>Burkholderia</i> spp.	1-aminocyclopropane-1-carboxylate (ACC) deaminase	Cell elongation and root development	Orozco-Mosqueda et al., 2023
<i>Azospirillum picis</i>	Nitrogenase enzymes	Biological nitrogen fixation	Rabara et al., 2023
<i>Azospirillum melinis</i>	Nitrogenase enzymes	Protein synthesis, chlorophyll production, and biological nitrogen fixation	Rana et al., 2023
<i>Pseudomonas putida</i>	Oxidase, chitinase, cellulase, protease and lipase	Root initiation and elongation, breakdown of chitin, cellulose protein, and lipids.	Rani et al., 2023
<i>Pseudomonas aeruginosa</i>	ACC deaminase	Promotes plant growth under stressful conditions	Ratnaningsih et al., 2023
<i>Bacillus</i> spp.	Indole-3-acetate hydrolase, indole-3-acetyl-amide hydrolase, isopentenyl transferase, and cytokinin oxidase	Stress tolerance	Roy et al., 2023a
<i>Burkholderia gladioli</i>	Oxidase and chitinase	Cell elongation, root initiation, flowering, protection of plants from fungal pathogens, and biological nitrogen fixation	Shahid et al., 2023
<i>Azospirillum oryzae</i>	Nitrogenase enzymes, reductases, and hydrogenases	Biological nitrogen fixation	Tokas et al., 2023
<i>Pseudomonas</i> spp.	Indole acetyltransferase, gibberellin oxidase, and jasmonate carboxyl methyltransferase	Defense response against pathogens	Vanková et al., 2023
<i>Rhizobium</i> spp., <i>Bradyrhizobium</i> spp.	Oxidase, and isopentenyl transferase	Root development and nodulation, and cytokinin production	Wang et al., 2023
<i>Bacillus pumilus</i>	Cellulase acetyl esterase	Cellulose degradation	Yang et al., 2023
<i>Azospirillum brasilense</i>	ACC deaminase, nitrogenase, and phosphate solubilizing enzymes	N <sub>2</sub> fixation, phosphate solubilization and lowering of the ethylene level	Zamanzadeh-Nasrabadi et al., 2023
<i>Bacillus subtilis</i>	Amylase, protease, cellulase, chitinase, and lipase	Hydrolysis of starch into simple sugars, and breakdown of proteins, cellulose, chitin & lipids	Zhou et al., 2023
<i>Azospirillum lipoferum</i>	Nitrogenase enzyme	Biological nitrogen fixation	Lee et al., 2021
<i>Streptomyces</i> spp.	Indole-3-acetate hydrolase, isopentenyl transferase and gibberellin 3-oxidase	Resistance against diseases	Vurukonda et al., 2018
<i>Azospirillum</i> spp.	Oxidase, indole-3-acetamide (IAM) hydrolase	Promotion of root growth and nutrient absorption	Duca et al., 2014

To increase soil biodiversity conservation, it is therefore preferable to apply native rhizobial strains as biofertilizers (De Mandal and Bhatt, 2020). The detrimental properties of chemical fertilizers on biodiversity are minimized by biofertilization. Rhizobia are not highly mobile in soil; hence, the point at which they are introduced into the soil determines the nodulation pattern (Otaiku et al., 2022). Farmers can use rhizobial inoculation to maximize grain legume yields with suitable and appropriate rhizobia where a low population of local rhizobial strains predominates. Debela et al. (2021) reported increased plant growth and nodulation efficiency by 80-90% through inoculation with abiotic stress-tolerant cluster

**Table 2. An overview of nitrogen-fixing bacteria and their role in plant growth promotion**

Microorganisms	Interaction	Findings	References
<i>Bradyrhizobium</i> sp.	Symbiotic	Enhanced guar growth attributes and seed yield	El-Sawah et al. (2021)
<i>Bacillus xiamenesis</i> PM14	Non-symbiotic	Strain PM14 promoted plant growth and metal accumulation in <i>Sesbania sesban</i>	Din et al., 2020
<i>Pasteuria penetrans</i>	Non-symbiotic	Increased marketable yield of sweet potato	Subedi et al., 2020
<i>Azorhizobium caulinodans</i> ORS571	Symbiotic	Strain ORS571 showed its ability for atmospheric nitrogen fixation in free-living and symbiotic association	Liu et al., 2019
<i>Rhizobium</i> sp. (strain NEPMR1, NETBR1)	Symbiotic	Promoted tolerance against salt and temperature stress	Nohwar et al., 2019
<i>Lactobacillus plantarum</i> PM411	Non-symbiotic	Increased survival on plant surfaces and overexpression of stress-related genes	Daranas et al., 2018
<i>Sinorhizobium saheli</i> , <i>Ensifer</i> sp. AC01b	Symbiotic	Bioremediated the glyphosate toxicity	Chauhan et al., 2017
<i>Agrobacterium salinitolerance</i>	Symbiotic	Improved salt stress tolerance in host plant	Yan et al., 2017
<i>Pseudomonas fluorescens</i> DACG3, <i>Burkholderia</i> sp. DACG1	Non-symbiotic	Promoted biomass and root and shoot growth of chickpea	Dasgupta et al., 2015
<i>Bacillus amyloliquefaciens</i> BZ6-1	Non-symbiotic	Production of antimicrobial compounds	Wang and Liang, 2014
<i>Burkholderia</i> spp. KJ006	Symbiotic	KJ006 was involved in <i>Nif</i> gene cluster and antifungal activity	Kwak et al., 2012
<i>Enterobacter cloacae</i> ENHKU01	Non-symbiotic	This strain promoted plant growth	Liu et al., 2012
<i>Pseudomonas fluorescens</i> EB69	Non-symbiotic	Produced siderophores and inhibitory compounds	Ramesh and Phadke, 2012
<i>Burkholderia phytofirmans</i> PsJN	Symbiotic	IAA synthesis, ACC deaminase activation	Weilharter et al., 2011
<i>Azospirillum lipoferum</i> 4B	Symbiotic	Strain 4B was involved in nitrogen fixation and production of phytohormones	Wisniewski-Dye et al., 2011
<i>Azospirillum</i> sp. B510	Symbiotic	Strain B510 produced IAA and was involved in BNF	Kaneko et al., 2010
<i>Bacillus amyloliquefaciens</i> Bg-C31	Non-symbiotic	Production of anti-microbial proteins	Hu et al., 2010
<i>Rhizobium</i> strain IRBG74	Symbiotic	This strain facilitated nodulation and biomass production	Cummings et al., 2009
<i>Serratia plymuthica</i> HRO-C48	Non-symbiotic	Quorum sensing, and growth promotion	Müller et al., 2009
<i>Enterobacter</i> sp. 638	Non-symbiotic	Produces siderophores, IAA, 2,3-butanediol, and acetoin	Taghavi et al., 2009
<i>Methylobacterium</i> sp. Strain NPFM-SB3	Symbiotic	This strain produced IAA, cytokinins, and promoted lateral roots in rice seedlings	Senthilkumar et al., 2009
<i>Azorhizobium doebereinae</i> , <i>Rhizobium etli</i>	Symbiotic	Increased dry matter production	Blanco et al., 2008
<i>Klebsiella pneumoniae</i> 342	Symbiotic	Nitrogen fixation	Fouts et al., 2008
<i>Serratia marcescens</i> UPM39B3	Non-symbiotic	Growth promotion	Ting et al., 2008
<i>Pseudomonas stutzeri</i> A1501	Symbiotic	N <sub>2</sub> -fixation	Yan et al., 2008
<i>Rhizobium</i> sp.	Symbiotic	Synthesis of IAA	Sridevi and Mallaiyah, 2007
<i>Rhizobium</i> sp. U9709-SC	Symbiotic	Solubilization of insoluble phosphate	Daimon et al., 2006
<i>Pantoea agglomerans</i> EPS125	Non-symbiotic	Accumulation of trehalose & glycinebetaine for desiccation tolerance	Bonattera et al., 2005
<i>Paenibacillus</i> sp. K165	Non-symbiotic	Induced systematic resistance	Tjamos et al., 2005

bean rhizobial isolates. However, there are two most popular methods for utilizing BNF: the first is improved crop, soil, and water management to maximize BNF potential; the second is *Rhizobium* inoculation or host genotype selection to ensure increased nitrogen fixation in the plant (Pankievicz et al., 2019). The rhizobia-legume symbiosis accounts for a significant amount of the nitrogen available to the leguminous crops. Among these, the most sustainable agricultural technique is the use of efficient rhizobial strains as biofertilizers to increase the output of legumes (Saharan and Nehra, 2011). It becomes necessary to improve rhizobia to increase their symbiotic efficiency and a wide range of host options (Gopalakrishnan et al., 2015). Recent developments in high-throughput next-generation technology make it possible to investigate the depth of biological nitrogen fixation. For improving nitrogen fixation in legumes, omics-based approaches are very effective and instructive (Qi et al., 2023).

## Mineral solubilizing bacteria

Microorganisms that can increase the solubility and bioavailability of various minerals in their natural surroundings are called mineral-solubilizing microorganisms. Mineral-solubilizing bacteria play a critical role in biogeochemical cycles by releasing vital nutrients from minerals and making them available for plant uptake and other biological activities (Etesami and Adl, 2020). Mineral-solubilizing bacteria use a variety of techniques to make minerals accessible. Producing organic acids like gluconic acid, oxalic acid, and citric acid is one of the main strategies bacteria use to solubilize insoluble minerals (Bhadrecha et al., 2023). The bacterial strains produce these organic acids, which have chelating properties. They bond to metal ions in minerals to promote their breakdown. Bacteria also produce siderophores and various enzymes participating in mineral solubilization (Walpola et al., 2022). Phosphate-containing minerals are hydrolyzed with enzymes like phosphatases, which release soluble phosphate ions. Bacterial siderophores attach to ferric ions and help in their breakdown to be readily available for plant uptake (Cui et al., 2023). Mineral solubilization by these bacteria has significant consequences for both farming and the restoration of the environment. In nutrient-deficient soils, mineral-solubilizing bacteria increase plant growth and production by increasing the availability of vital minerals. Furthermore, their capacity to extract heavy metals from minerals and detoxify them, can support bioremediation processes, which clean up contaminated areas to lower contamination levels (Timofeeva et al., 2022). Mineral solubilizing bacteria can promote the release and breakdown of vital nutrients from minerals via various processes, such as the synthesis of organic acids, the secretion of enzymes, and siderophore-mediated solubilization.

**Table 3. Mechanisms of mineral solubilizing bacteria through enzymolysis and production of organic acids**

Mineral solubilization	Bacteria	Enzyme produced	Organic acid produced	References
Phosphate solubilization	<i>Pseudomonas fluorescens</i>	Gluconate dehydrogenase	Gluconic acid	Cheng et al., 2023
	<i>Bacillus subtilis</i>	Phosphatase	Citric acid	Cheng et al., 2023
	<i>Burkholderia cepacia</i>	Malate dehydrogenase	Malic acid	Espinosa-Hernández et al., 2023
	<i>Pantoea agglomerans</i>	Citrate synthase	Citric acid	Maldani et al., 2023
	<i>Rhizobium leguminosarum</i>	Nitrogenase	Citric acid and Malic acid	Rabani et al., 2023
	<i>Enterobacter cloacae</i>	Pyruvate carboxylase, Phosphatase	Citric acid	Wang et al., 2023
	<i>Klebsiella pneumoniae</i>	Phosphatases and Proteases	Acetic acid, Lactic acid	Gupta et al., 2021
	<i>Serratia marcescens</i>	Phosphatases and Proteases	Gluconic acid	Mulani et al., 2021
	<i>Pseudomonas fluorescens</i>	Phosphatases and Proteases	Gluconic acid and Oxalic acid	Rawat et al., 2021
	<i>Microbacterium arborescens</i>	Proteases	Citric acid and Malic acid	Bhagat et al., 2021
	<i>Burkholderia cepacia</i>	Phosphatases and Proteases	Gluconic acid and Oxalic acid	Chawngthu et al., 2020
	<i>Enterobacter</i> spp.	Phosphatases and Proteases	Gluconic acid	Kour et al., 2020
	<i>Azospirillum lipoferum</i>	Phosphatases and Nitrogenase	Gluconic acid and Malic acid	Ayyaz et al., 2016

*Table 3 continues on next page*

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Potassium solubilization	<i>Azotobacter chroococcum</i>	Nitrogenase		Gluconic acid and Keto-gluconic acid	Kumar et al., 2016
	<i>Pseudomonas putida</i>	Oxalate decarboxylase		Oxalate	Shahid et al., 2023
	<i>Burkholderia gladioli</i>	Succinate dehydrogenase		Succinic acid	Silva et al., 2023
	<i>Enterobacter asburiae</i>	Citrate synthase		Citric acid	Jini et al., 2023
	<i>Pantoea dispersa</i>	Malate dehydrogenase		Malic acid	Singh et al., 2023
	<i>Rhizobium leguminosarum</i>	Nitrogenase		Citric acid and Malic acid	Ghorai and Ghosh, 2022
	<i>Klebsiella pneumoniae</i>	Phosphatases and Proteases		Acetic acid and Lactic acid	Gupta et al., 2021
	<i>Bacillus megaterium</i>	Gluconic dehydrogenase, Phosphatases and Proteases	and	Gluconic acid, Citric acid and Lactic acid	Mei et al., 2021
	<i>Serratia marcescens</i>	Phosphatases and Proteases	and	Gluconic acid	Mulani et al., 2021
	<i>Pseudomonas fluorescens</i>	Phosphatases and Proteases	and	Gluconic acid and Oxalic acid	Rawat et al., 2021
	<i>Burkholderia cepacia</i>	Phosphatases and Proteases	and	Gluconic acid and Oxalic acid	Chawngthu et al., 2020
	<i>Azotobacter chroococcum</i>	Nitrogenase		Gluconic acid and Keto-gluconic acid	Jin et al., 2020
	<i>Enterobacter</i> spp.	Phosphatases and Proteases	and	Gluconic acid	Kour et al., 2020
	<i>Bacillus subtilis</i>	Phosphatases		Citric acid and Malic acid	Behera et al., 2017
	<i>Azospirillum lipoferum</i>	Phosphatases and Nitrogenase	and	Malic acid and Succinic acid	Ayyaz et al., 2016
	Zinc solubilization	<i>Pseudomonas putida</i>	Glucose dehydrogenase		Gluconic acid
<i>Pantoea dispersa</i>		Lactate dehydrogenase		Lactic acid	Ma et al., 2023
<i>Pantoea dispersa</i>		Proteases and Phosphatases	and	Citric acid and Gluconic acid	Mondal et al., 2023
<i>Acinetobacter</i> sp.		Malate dehydrogenase		Malic acid	Singh et al., 2023
<i>Bacillus megaterium</i>		ACC deaminase		Gluconic acid	Wang et al., 2023
<i>Burkholderia vietnamiensis</i>		Citrate synthase		Citric acid	Ghorai and Ghosh, 2022
<i>Enterobacter cloacae</i> , <i>Bacillus aryabhatai</i>		Proteases and Phosphatases	and	Citric acid and Oxalic acid	Hakim et al., 2021
<i>Burkholderia cepacia</i>		Proteases and Phosphatases	and	Gluconic acid and Itaconic acid	Seenivasagan and Babalola, 2021
<i>Rhizobium leguminosarum</i>		Proteases and Phosphatases	and	Citric acid and Malic acid	Kour et al., 2020
<i>Bacillus subtilis</i>		Proteases and Phosphatases	and	Citric acid and Malic acid	Dash and Dangar, 2019
<i>Pseudomonas fluorescens</i>		Proteases and Phosphatases	and	Gluconic acid and Succinic acid	Kumawat et al., 2019
<i>Bacillus licheniformis</i>	Proteases and Phosphatases	and	Citric acid and Malic acid	Kumar et al., 2014	
Manganese solubilization	<i>Burkholderia cepacia</i>	Manganese oxidase and Laccase		Gluconic acid and Itaconic acid	Dudhagara et al., 2023
	<i>Rhizobium leguminosarum</i>	Manganese oxidase and Laccase		Gluconic acid and Oxalic acid	Devi et al., 2022
	<i>Enterobacter cloacae</i>	Manganese oxidase and Laccase		Citric acid and Oxalic acid	Athukorala, 2021
	<i>Bacillus subtilis</i>	Manganese oxidase and Laccase		Gluconic acid and Malic acid	Athukorala, 2021

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<i>Agrobacterium tumefaciens</i>	Manganese oxidase and Laccase	Gluconic acid and Succinic acid	and	Devi et al., 2020
<i>Pseudomonas aeruginosa</i>	Manganese oxidase and Laccase	Gluconic acid and Oxalic acid		Kumar and Chandra, 2020
<i>Azotobacter chroococcum</i>	Manganese oxidase and Laccase	Gluconic acid and Itaconic acid	and	Mahala et al., 2020
<i>Pseudomonas putida</i>	Manganese oxidase and Laccase	Citric acid and Malic acid		Wan et al., 2020
<i>Bacillus cereus</i>	Manganese oxidase and Laccase	Gluconic acid and Itaconic acid	and	Javaid et al., 2019
<i>Arthrobacter globiformis</i>	Manganese oxidase and Laccase	Citric acid and Malic acid		Rahi and Soni, 2007

Microorganisms involved in solubilizing insoluble phosphate are termed phosphate solubilizing bacteria (PSB) and are significantly present in many habitats. The primary function of these bacteria is to solubilize insoluble forms of phosphorus and ensure its availability to plants and microbes (Kafle et al., 2019). The PSB perform various actions and mechanisms to solubilize insoluble minerals, including organic acids. These organic acids produced by bacteria in phosphate solubilization are citric acid, gluconic acid, oxalic acid, and malic acid, which can act as chelating agents. These organic acids help break down mineral phosphate by adhering to the metal ions of those minerals (Chai et al., 2023).

Along with organic acids, enzymes also facilitate phosphate solubilization. Phosphatases are one of the significant enzymes that take part in this process. PSB produce alkaline and acidic phosphatases, which ensure the availability of soluble phosphate by reacting with phosphate-containing minerals and esters (Peng et al., 2023). Microorganisms, including *Bacillus megaterium*, *Pseudomonas fluorescens*, *Burkholderia* spp., *Enterobacter* spp., and *Azotobacterium chlorococcum*, are involved in phosphate solubilization (Sharma et al., 2023). PSB are an essential research subject due to their phosphorus restriction capacity and helping in improving and developing several agricultural and environmental scenarios (Ramirez-Gil et al., 2023).

The rhizobacteria involved in solubilizing insoluble potassium and ensuring potassium availability in the rhizosphere are termed potassium solubilizing bacteria (KSB) (Etesami and Adl, 2020). To solubilize the insoluble form of potassium, these bacteria use several techniques; one is the production of organic acids that can act as chelating agents. By forming complexes with potassium ions, organic acids production by KSB, including citric acid, malic acid, oxalic acid, and gluconic acid, assist in solubilizing insoluble potassium compounds (Sindhu et al., 2022). In addition, KSB-produced enzymes are essential for the solubilization of potassium. Potassium is released from organic materials and minerals via phosphatases, specifically acid phosphatases and alkaline phosphatases (Kumar et al., 2022). These enzymes catalyze the release of soluble potassium ions by hydrolyzing phosphorus molecules. Among the bacteria recognized for their capacity to solubilize potassium are *Bacillus subtilis*, *Burkholderia cepacia*, *Pseudomonas* spp., *Azospirillum* spp., and *Enterobacter* spp. (Devi et al., 2022). Several studies focus on the capacity of these bacteria, among others, to solubilize potassium and encourage plant development. The ability of KSB to enhance plant uptake of potassium renders them advantageous in the context of sustainable agriculture and nutrient management approaches (Sarkar et al., 2021).

A category of microorganisms known as zinc solubilizing bacteria (ZSB) assists in releasing zinc from the soil, so plants can absorb it more easily. These bacteria increase zinc availability in the rhizosphere by solubilizing zinc from insoluble sources in multiple processes (Khoshru et al., 2020). One method that ZSB use for zinc solubilization is the synthesis of organic acids. Organic acids secreted by ZSB, including acetic, citric, gluconic, and oxalic acids, function as chelators by forming compounds with zinc ions and promoting their solubility (Khoshru et al., 2023). Enzymes also play a crucial role in zinc solubilization by ZSB. Acid phosphatases and alkaline phosphatases release zinc from organic matter and minerals. These enzymes release soluble zinc ions by catalyzing the hydrolysis of substances containing phosphorus (Chen and Arai, 2023). The few examples of bacteria well-known for their capacity to solubilize zinc are *Bacillus cereus*, *Pseudomonas fluorescens*, *Agrobacterium* spp., *Enterobacter* spp., and *Gluconacetobacter diazotrophicus* (Mehmood et al., 2023). Various microbes have also been examined for their ability to solubilize zinc and encourage plant development. By absorbing zinc, these bacteria have become significant in sustainable agriculture and nutrient management (Gaubal et al., 2023).

A group of bacteria that takes part in solubilizing the insoluble form of manganese is called manganese solubilizing bacteria (MSB). They also ensure the Mn absorption in plants (Khoshru et al., 2023). Manganese solubilizing bacteria perform organic acids and enzyme production processes. Organic acids, including citric acid, oxalic acid, malic acid, and gluconic acid, convert insoluble manganese into soluble nutrients; they act as chelating agents by forming mineral complexes (Ijaz et al., 2021). The

production of enzymes by MSB also helps in manganese solubilization. For example, acid phosphatases release manganese, and phytases remove organic matter (Lall and Dumas, 2022). When these phosphate-containing molecules break down, a soluble form of manganese is released. *Bacillus subtilis*, *Pseudomonas putida*, *Arthrobacter* spp., *Cellvibrio* spp., and *Streptomyces* spp. are some of the main bacteria species that are known for their manganese solubilizing potential (Shinde et al., 2022). These microbes ensure the availability of manganese to plants. With the help of MSB, manganese uptake in plants is increased, which is vital for plant growth and nutrient uptake.

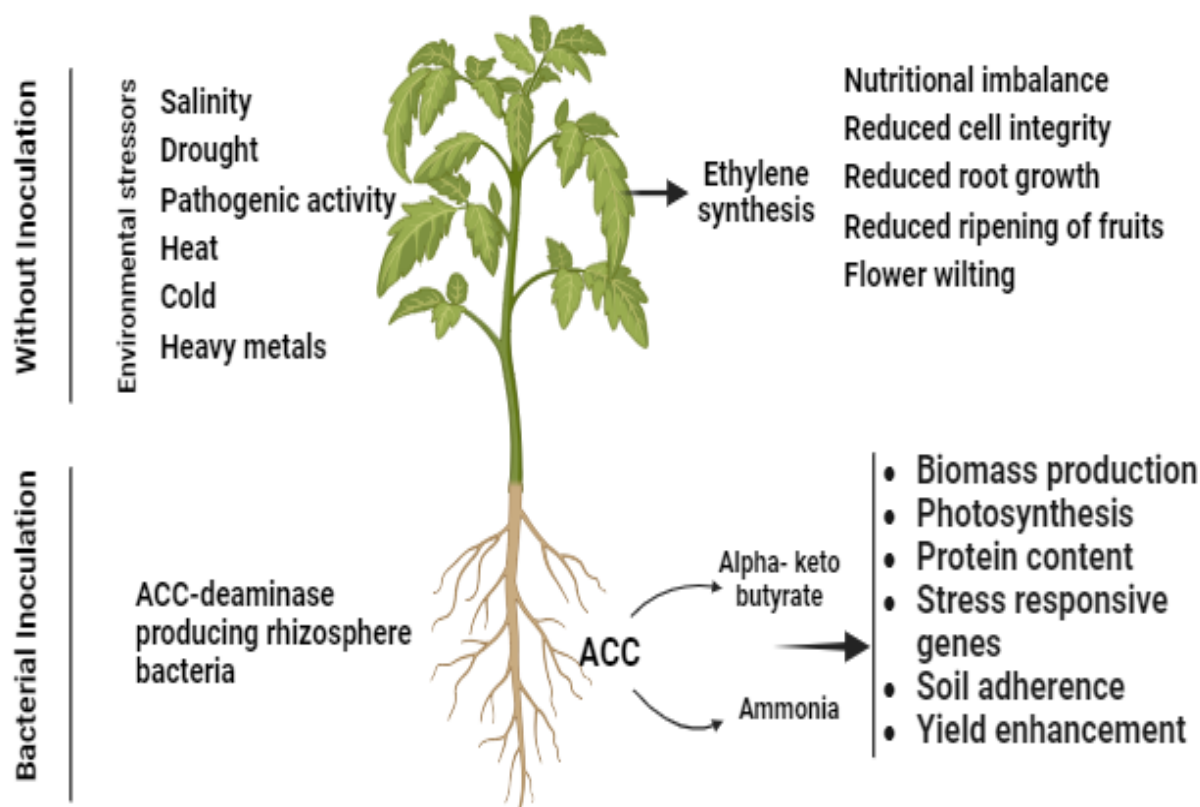
The breakdown of complex organic compounds with phosphate-solubilizing bacteria releases soluble orthophosphate ions by producing citric acid and gluconic acid. They also secrete phosphatases (Cheng et al., 2023). By proton extrusion, they also decrease pH and increase phosphate solubility. Potassium solubilization occurs when bacteria create organic acids, such as acetic and oxalic acids, which chelate potassium ions and make them more soluble (Setiawati et al., 2022). They might also produce siderophores, iron-chelating substances that indirectly increase potassium availability by relocating potassium ions from clay minerals (Potysz and Bartz, 2023). Zinc solubilizing bacteria use the secretion of organic acids (such as malic and citric acids) to chelate zinc ions and help release them from insoluble forms. They produce enzymes that degrade organic materials and release bound zinc, including proteases and organic acid decarboxylases (Singh et al., 2023). By separating manganese from mineral complexes, bacteria solubilize it by using organic acids as chelating agents. Manganese ions are released during the breakdown of organic matter by enzymes produced by bacteria, such as phytase and acid phosphatase (Mondal et al., 2023). Microorganisms use a variety of approaches to solubilize minerals, including phosphate, potassium, zinc, and manganese, including the secretion of organic acids, the synthesis of enzymes, and pH regulation (Khoshru et al., 2023) are summarized in **Table 3**. Ultimately, these processes improve the accessibility and uptake of these vital nutrients, which is advantageous for plant development and the environment's nutrient cycle.

### ACC deaminase-producing bacteria

Certain bacteria produce the ACC (1-aminocyclopropane-1-carboxylate) deaminase enzyme, especially under stress conditions. ACC deaminase-producing bacteria favor plant development and growth (Singh et al., 2022). Under stressful environmental conditions such as salinity, drought, temperature, and heavy metal toxicity, ACC deaminase production by bacteria can mitigate these stresses, and is pivotal for plant-microbe interaction (Chandwani and Amaresan, 2022).

Ethylene is involved in various physiological processes because it is a naturally occurring plant hormone. In ethylene biosynthesis, ACC is a critical precursor. Plants produce a surplus of ethylene under stressful environmental conditions, inhibiting growth, reducing cell integrity, and lowering yield (Khan et al., 2017). To alleviate the effect of these stresses, ACC deaminase catalyzes the conversion of ACC into  $\alpha$ -ketobutyrate and ammonia thereby lowering down ethylene production in plants (Jha et al., 2021). Several investigations have shown that ACC deaminase-producing bacteria have enhanced plant ability to tolerate various abiotic stresses, such as salinity, heavy metals, drought, and high temperature, that improve plant growth and development by increasing protein content, seed germination, root elongation, and biomass production in the plant (Gowtham et al., 2020; Han et al., 2021; Naing et al., 2021).

ACC deaminase-producing bacteria colonize plant roots and form a symbiotic association with the host plant (Roy et al., 2023b). These bacteria predominantly interact with the plant and initiate a series of beneficial effects. In return, plants provide the bacteria nutrients and a protected niche to grow and survive. ACC deaminase-producing bacteria help plants to overcome stress by decreasing ethylene levels, as summarized in **Figure 2** (Bittencourt et al., 2023). Metabolizing ACC lowers ethylene production and mitigates the adverse effects of stress-induced ethylene accumulation (Etesami et al., 2020). ACC deaminase-producing bacteria exhibit another attractive characteristic, i.e, the ability to modulate plant stress-responsive genes directly. By eliciting changes in gene expression, these bacteria help plants to activate stress-responsive pathways, reinforce their defense mechanisms, and adapt to adverse environmental conditions (Ali et al., 2022; Naing et al., 2021). The bacterial ACC deaminase activity could be due to the *acdS* gene broadly distributed in most soil microorganisms (Gupta et al., 2021). For example, Nascimento et al. (2014) reported the presence of this gene in a diverse group of bacteria, including Actinobacteria, Deinococcus,  $\alpha$ -Proteobacteria,  $\beta$ -Proteobacteria,  $\gamma$ -Proteobacteria, and Firmicutes. The Lrp-like regulatory proteins, such as AcdR, regulate the expression of *acdS* genes in proteobacteria (Ekimova et al., 2022). This gene is also found in the fungus *Trichoderma asperellum*, which showed plant growth promotion characteristics and biocontrol of phytopathogenic microorganisms (Rauf et al., 2021).



**Figure 2. A schematic representation of ACC deaminase-producing bacteria involved in stress alleviation through reducing alleviated ethylene level**

The range of stress conditions that ACC deaminase-producing bacteria address is nothing short of remarkable. These bacteria alleviate water stress in drought-stricken environments by maintaining root growth and inhibiting ethylene-triggered growth (Yavuz et al., 2023). Salinity stress is a challenge that disrupts nutrient uptake and cellular processes, which can be managed through the exact ethylene-regulating mechanism. ACC deaminase-producing bacteria help plants to adapt to saline conditions without compromising growth (Misra and Chauhan, 2020). The role of these bacteria in combatting pathogen attacks is equally significant. When plants encounter pathogens, ethylene production surges as part of the defense response (Tyśkiewicz et al., 2022). However, excessive ethylene can lead to tissue damage and inhibit growth. ACC deaminase-producing bacteria fine-tune this ethylene response, enabling a balanced defense reaction without causing harm to the plant (Katiyar et al., 2021). Temperature extremes, heavy metal exposure, nutrient deficiencies, and even the transplant shock experienced during replanting, are all challenges that these bacteria assist plants in surmounting. By reducing ethylene accumulation, these microorganisms facilitate stress tolerance across a spectrum of adverse conditions (Chandwani and Amaresan, 2022). This adaptability highlights the versatility of ACC deaminase-producing bacteria and their potential to reshape our environmental sustainability and ecosystem restoration strategies.

**Table 4. Role of ACC deaminase-producing rhizosphere bacteria in alleviating stress in host plants**

Stress	Organism	Host plant	Findings	References
Salt stress	<i>Pantoea agglomerans</i> R1, <i>Pseudomonas fragi</i> R4	French bean ( <i>Phaseolus vulgaris</i> )	These strains improved root architecture, plant growth, and micronutrient uptake under salt-stressed conditions	Gupta et al., 2023
	<i>Aneurinibacillus aneurinilyticus</i> AIOA1, <i>Paenibacillus</i> sp. SG_AIOA2	Common bean ( <i>Phaseolus vulgaris</i> )	These strains mitigated the negative impact of salt stress on plants	Gupta et al., 2021
	<i>Bacillus marisflavi</i> (CHR 203), <i>Bacillus cereus</i> (BST YS1_42)	Pea ( <i>Pisum sativum</i> )	These strains possessing PGP traits promoted plant growth under saline stress	Gupta et al., 2021

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	<i>Bacillus subtilis</i> (NBRI 28B, NBRI 33 N), <i>B. safensis</i> (NBRI 12 M)	Maize ( <i>Zea mays</i> )	These strains exhibiting multiple PGP attributes alleviated salt stress by reducing ethylene levels in the host plant	Misra and Chauhan, 2020
	<i>Methylobacterium oryzae</i> CBMB20	Rice ( <i>Oryza sativa</i> )	Strain CBMB20 promoted cell viability of roots by regulating the ethylene emission pathway under salt stress	Choudhury et al., 2020
	<i>Bacillus siamensis</i> (PM13), <i>Bacillus</i> sp. (PM15), <i>Bacillus methylotrophicus</i> (PM19)	Wheat ( <i>Triticum aestivum</i> )	These bacterial strains efficiently reduced the impact of salinity on wheat growth	Din et al., 2019
	<i>Aneurinibacillus aneurinilyticus</i> ACC02, <i>Paenibacillus</i> sp. ACC06	French bean ( <i>Phaseolus vulgaris</i> )	Bacterial consortia alleviated the negative effects of salinity stress and promoted plant growth	Gupta and Pandey, 2019
Drought stress	<i>Pseudomonas</i> sp. MRBP4, <i>Pseudomonas</i> sp. MRBP13, <i>Bacillus</i> sp. MRBP10	Maize ( <i>Zea mays</i> )	The synergistic effect of the bacterial strains was observed in maize in terms of biochemical and physiological attributes under drought stress in arid regions	Ojuederie and Babalola, 2023
	<i>Pseudomonas stutzeri</i> AK17, <i>Paenibacillus polymyxa</i> KM6	Cluster bean ( <i>Cyamopsis tetragonoloba</i> )	These bacteria improved drought tolerance in cluster bean seedlings	Jain and Saraf, 2023
	<i>Serratia marcescens</i> RRN II 2, <i>Pseudomonas</i> sp. RRC I 5	Wheat ( <i>Triticum aestivum</i> )	These bacteria improved the physiological traits, productivity, and nutrient status in wheat during drought stress	Khan and Singh, 2021
	<i>Variovorax paradoxus</i> RAA3, <i>Pseudomonas</i> sp. DPC12, <i>Achromobacter</i> spp. PSA7, <i>Ochrobactrum anthropi</i> DPC9	Wheat ( <i>Triticum aestivum</i> )	These bacteria were effective inoculants to improve the growth of wheat plants in water-stressed rain-fed environments	Chandra et al., 2019
	<i>Bacillus subtilis</i> Rhizo SF 48	Tomato ( <i>Solanum lycopersicum</i> )	Rhizo SF 48 served as a useful bioinoculant for sustainable tomato production in arid and semi-arid regions with water deficit	Gowtham et al., 2019
	<i>Pseudomonas fluorescens</i> DPB15, <i>P. palleroniana</i> strain DPB16	Wheat ( <i>Triticum aestivum</i> )	Bacterial inoculation enhanced the growth of wheat in terms of root and shoot biomass, height, and foliar nutrient content	Chandra et al., 2018
	<i>Pseudomonas</i> sp. RJ15, <i>Bacillus subtilis</i> RJ46	<i>Vigna mungo</i> , <i>Pisum sativum</i>	Bacterial application improved crop health in drought-affected acidic agricultural fields	Saikia et al., 2018
	Heavy metal stress	<i>Burkholderia pyrrocinia</i> LWK2	Katsura tree ( <i>Cercidiphyllum japonicum</i> )	LWK2 was resistant to Cu, Zn, Cd, and Co, with maximum tolerance to 4 mM, 10 mM, 3 mM, and 1 mM, respectively.
<i>Sphingomonas</i> sp. PbM2		Maize ( <i>Zea mays</i> )	PbM2 remediated the contaminated soil,	Lee et al., 2023
<i>Enterobacter cloacae</i> (ZNP-4)		Wheat ( <i>Triticum aestivum</i> )	ZNP-4 alleviated the heavy metal stress and improved wheat production	Singh et al., 2022
<i>Pseudomonas</i> sp. TR15a, <i>Bacillus aerophilus</i> TR15c		Sunflower ( <i>Helianthus annuus</i> )	Bacterial strains enhanced Cu uptake and improved biomass production, and decontaminated Cu-contaminated natural ecosystems	Kumar et al., 2021

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<i>Achromobacter</i> sp. A1	Maize ( <i>Zea mays</i> )	A1 had a great potential to immobilize Cd and reduce its uptake in maize in Cd-contaminated environments	Sun et al., 2022
<i>Bacillus gibsonii</i> (PM11), <i>Bacillus xiamenensis</i> (PM14)	Flax plant ( <i>Linum usitatissimum</i> )	These bacterial strains elevated phytoextraction of multi-metals from industrially contaminated soils	Zainab et al., 2020
<i>Agrobacterium fabrum</i> , <i>Leclercia adecarboxylata</i>	Maize ( <i>Zea mays</i> )	Inoculation of these bacterial strains alleviated chromium toxicity and promoted plant growth in maize	Danish et al., 2019

The mechanisms by which ACC deaminase-producing bacteria positively affect plants are not fully understood. However, the bacteria are believed to decrease ethylene levels, stimulate plant growth-promoting hormones, enhance nutrient availability, and induce systemic resistance against pathogens (Han et al., 2021; Baslam et al., 2023). These multifaceted interactions demonstrate the complex nature of the plant-microbe relationship and highlight the potential of ACC deaminase-producing bacteria as biofertilizers and biocontrol agents in agriculture (Baslam, 2023). The crop inoculation with ACC deaminase-producing bacteria leads to enhanced root elongation, improved nutrient uptake, and plant growth promotion. Moreover, these bacteria enhance plant resilience by producing PGP substances, such as IAA, gibberellins, and cytokinins. They can modulate the levels of these phytohormones, which play critical roles in plant development and stress tolerance (Kaur and Karnwal, 2023). Chandra et al. (2019) reported that ACC deaminase-producing *Variovorax paradoxus* RAA3, *Pseudomonas* spp. DPC12, *Achromobacter* spp. PSA7 and *Ochrobactrum anthropi* DPC9 promoted wheat growth under water-stressed rain-fed environments. Similarly, Gupta and Pandey (2019) reported the alleviation of the negative effects of drought and salt stress in *Phaseolus vulgaris* by inoculating with ACC deaminase-producing bacteria. The findings of other researchers in salinity, heavy metals, and drought stress alleviation through ACC deaminase-producing bacteria are summarized in [Table 4](#).

## Biological control of phytopathogens

The significance of developing ecologically acceptable alternatives to the heavy use of chemical pesticides for managing crop diseases has spurred interest in the biological control of plant pathogens during the past ten years (Heydari and Pessarakli, 2010). One of the most promising approaches to safer and more sensible crop management is the employment of helpful microorganisms (biopesticides) (Dlamini et al., 2022). In the past ten years, interest in the biological management of plant pathogens has increased due to the importance of environment-friendly alternatives to the extensive use of chemical pesticides for managing crop diseases (Ab Rahman et al., 2018).

Biocontrol of plant diseases may be able to deal with conditions that are wholly or partially resistant to current control approaches in addition to acting as a replacement for chemical pesticides (Bardin et al., 2015). Using beneficial microorganisms (biopesticides) is one of the most promising strategies for safer and more reasonable crop management. The suppression of plant pathogen populations by living organisms is known as the biological control of plant diseases (Heimpel and Mills, 2017). It is possible to choose isolates of helpful microorganisms that are very powerful against infections and can grow on artificial media. Augmentative biological control applies carefully selected and mass-produced antagonists once or multiple times throughout a growing season (Eilenberg et al., 2001; Van Lenteren et al., 2018).

Growers employ microbial biological control agents (MBCAs), living microorganisms that are commercially augmentative for the biological control of diseases (Sabbahi et al., 2022). Other products contain antimicrobial metabolites produced by specific microbial species, and other items even contain only antimicrobial metabolites without living organisms. These substances are regarded as chemical actives legally (Kohl et al., 2019). Additionally, bacteriophages and mycoviruses have the potential to operate as MBCAs against plant diseases (Van Lenteren et al., 2018). These MBCAs use various modes of action to shield crops from disease damage. Without direct antagonistic contact with the pathogen, they may produce resistance against infections by a pathogen in plant tissues (Pieterse et al., 2014; Conrath et al., 2015). Competition for nutrients and available space is another indirect interaction with pathogens (Spadaro and Droby, 2016). MBCAs can interact with the pathogen directly through antibiosis or hyperparasitism. Ghorbanpour et al. (2018) reported that hyperparasites infect host cells and bacterial pathogens' mycelium, spores, and resting structures. Another direct route of action is the generation of antimicrobial secondary metabolites that have inhibitory effects against infections (Raaijmakers and Mazzola, 2012).

Bacteria and plants coexist closely within agricultural environments. Bacteria may create symbiotic associations with plants by adhering to the root surface or phyllosphere or surviving in soils as free-living organisms (Ayangbenro and Babalola, 2021). Secondary metabolites secreted *in situ* in small amounts increase antagonists' competitive advantage (Grandlic et al., 2009). For the control of nematodes, bacteria species from the genera *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Clostridium*, *Desulfovibrio*, *Serratia*, *Burkholderia*, *Azospirillum*, *Bacillus*, *Chromobacterium*, and *Corynebacterium* have been reported for their biocontrol role (Tapia-Vázquez et al., 2022). The ability of microorganisms to efficiently compete for ecological niches, colonize plant surfaces, and create nematicidal and antimicrobial chemicals (antibiotics, toxins, siderophores, hydrolytic enzymes, etc.) allows bacteria to suppress plant-parasitic nematodes in various ways (Lahlali et al., 2022). Competition for resources or infection sites, parasitism, antibiosis, or other mechanisms can all produce a direct antagonistic effect. Bacteria may indirectly strengthen the host's defenses, leading to induced systemic resistance (ISR) (Prajapati et al., 2020). The *Bacillaceae* and *Pseudomonadaceae* members are given special consideration, emphasizing how they can control the nematode of the *Meloidogyne* genus (Berlanga et al., 2020). Bacterial endophytes are advantageous as possible biocontrol agents against wilt diseases because they can occupy an ecological niche comparable to that of vascular wilt pathogens (Kavino and Manoranjitham, 2018). Beneficial bacteria have been linked to many potential disease-suppressing processes, including the induction of systemic resistance, growth promotion, and competition (Kolytaité et al., 2022; Fadji and Babalola, 2020).

## Conclusion

Rhizosphere bacteria have enormous potential for sustainable agriculture by encouraging plant growth, improving nutrient uptake, and reducing plant stress. The information in this review shows how important rhizosphere bacteria are beneficial to agricultural sustainability and provide encouraging solutions to current and upcoming problems. Rhizosphere bacteria significantly improve plant nutrition by solubilizing essential minerals, fixing nitrogen, and suppressing plant diseases. This biological intervention minimizes environmental pollution and ecosystem damage and increases crop production while reducing reliance on chemical pesticides and synthetic fertilizers. Furthermore, in considering climate change and uncertain climatic conditions, the capacity of rhizosphere bacteria to minimize plant stress and confer resistance to biotic and abiotic stresses is crucial. The utilization of rhizosphere bacteria presents a viable approach to sustainable agriculture. By acknowledging and investigating the capabilities of these advantageous microbes, we can create a more resilient and eco-friendly agricultural system that guarantees nutrition, preserves natural resources, and lessens the effects of climate change.

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Conceptualization and designing the study: MQH, SF, AN, SH, MWA, SUD, TAC, SAB, MAS, MZM. Review of initial draft: MQH, SF, TAC, SAB, MAS, MZM. Revisions and corrections: MQH, SF, AN, SH, MWA, MZM.

### Ethical approval

This study does not involve human/animal subjects, and thus no ethical approval is needed.

### Handling of bio-hazardous materials

Since this a review article, so it does not involve any experimentation or use of any types of materials or chemicals

### Availability of primary data and materials

As per editorial policy, experimental materials, primary data, or software codes are not submitted to the publisher. These are available with the corresponding author and/or with other author(s) as declared by the corresponding author of this manuscript.

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All authors contributed in designing and writing the entire review article. All contributors have critically read this manuscript and agreed for publishing in IJAaEB.

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### Declaration of Generative AI and AI-assisted technologies in the writing process

It is declared that we the authors did not use any AI tools or AI-assisted services in the preparation, analysis, or creation of this review article submitted for publication in the International Journal of Applied and Experimental Biology (IJAaEB).

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