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Review Article

Unravelling the Roles of Plant Growth Promoting Rhizobacteria (PGPR) in Growth Promotion, Phytoremediation and as Biocontrol Agents to Suppress Plant Diseases

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Abstract

Agriculture in the twenty-first century has several issues, including soil fertility, climate changes, environmental degradation, urbanisation & rising food consumption to feed the world's growing population. Meanwhile, scientists are grappling with major obstacles in expanding food yield from the present land base. Traditional farming has seen increased per-acre crop yields due to the haphazard and injudicious use of agrochemicals, such as pesticides and synthetic fertilisers, but at a significant environmental cost. Crop pests developing pesticide resistance is another big worry in modern agriculture. Therefore, alternative ecologically friendly crop yield-increasing techniques are necessary for the future of sustainable crop production. Scientists are very interested in utility of rhizobacteria, particularly PGPR, as an alternative to pesticides. These rhizobacteria employ a range of tactics to encourage plant growth, thwart plant pests, and foster resilience to abiotic stresses. The mechanisms of rhizobacteria involved in soil bioremediation, pest biocontrol, and plant growth promotion are reviewed in this article. It also looks at how PGPR vaccination affects plant growth and survival in challenging conditions. An in-depth examination is also given of the benefits and drawbacks of rhizobacterial application as well as potential solutions for rhizobacteria's long-term use in agriculture.

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Introduction

The persistent use of chemical fertilisers to boost fertility and feed the world's rising population growth has led to a slew of environmental hazards. To feed the world's rising population, the total fertiliser nutrient demand (N, P, and K) is expected getting there 200 million tonnes by 2020 (www.fao.org). Traditional nutrient management, on the other hand, depends on exogenous chemical input, which results in lower nutrient utilisation efficiency and increased environmental risks. There is a push to develop an alternative to make better use of land, use less fertiliser, maintain soil health, and maintain ecological balance (Hasler et al., 2017). The goal is to maximise the capacity of soil and plant systems for biological activity to achieve the vision of a healthy environment. The decreased carbon components that makeup soil are a source of a variety of microbial communities in general (Backer et al., 2018). Plants with root-knot nematodes show symptoms above and below ground. The aboveground indicators are needful development and smaller, pale green leaves that fade in hot weather. (Elnahal et al., 2022). A sophisticated and organised microbial community is associated with a plant growing in the soil. However, due to its numerous beneficial benefits, Agriculture benefits more from the microbiota linked to roots. The close relationship between plant roots and bacteria has a wide range of effects, including improved plant physiology, signal exchange, resistance, and so on. PGPR are an essential tool for protecting the plant's health through a variety of mechanisms. They consume the root's nutrient-rich exudates and repay the

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favour with biofertilizers and biocontrolling. In order to shift to environmentally friendly agriculture, a complete understanding of these interactions is crucial for improving soil fertility as well as plant health.

Roles of PGPR in various aspects

According to Bhattacharyya et al. (2012), PGPR was first utilised in order to boost yields and protect plants from environmental challenges including floods, droughts, high salt, phytopathogens and other environmental variables. PGPR will be enjoyed by heavy metal lovers. High levels of heavy metal content in the soil must be tolerated by phytoextraction. To develop this tolerance, mechanisms that reduce metal ion toxicity must be put in place. The transformation of metal ions into less harmful forms or their encapsulation in extracellular or intracellular polymers are examples of these processes (Rajkumar et al., 2013). Metal-resistant Increased plant tolerance to high levels of heavy metals in soil is the main result of PGPR, which controls ethylene concentrations by producing ACC deaminase (Hrynkiewicz et al., 2011). Gibberellins, cytokinins, and auxins, as well as siderophores that change nutrient and metal bioavailability, are produced by plants as a result of PGPR. Plant growth-promoting endophytes (PGPE) are microbes that inhabit plants and provide the nutrients they need to develop and survive (Lodewyckx et al. 2002). Most of the time, PGPR employed in phytoextraction investigations is isolated from rhizosphere of plants growing in contaminated soils (Mendoza-Hernández et al., 2019, Jinal et al,. 2019)andis therefore adapted to high metal concentrations, while PGPE utilised to improve phytoextraction is often isolated from hyperaccumulator plants or other polluted soil-growing plants (Tang et al. 2020). Examples of recent PGPR/PGPE utilisation in phytoremediation employing Brassica species are shown in Table 1.

Mechanisms exhibited by PGPR

PGPR can boost various ways, either directly or indirectly, to evolution of plants (Figure 1 & Figure 2) (Ahmed et al., 2017). Vitamins, phytohormones, HCN, ammonia, siderophore synthesis, phosphorus solubilization and nitrogen-fixing (such as auxin, cytokinin, and gibberellins) are examples of direct mechanisms, whereas indirect mechanisms are those that are not directly involved in growth promotion but play a role in the synthesis path. ACC deaminase activity, antibiotic synthesis, hydrolytic enzymes, and phytopathogen ISR are examples of indirect processes (Aloo et al. 2019).

Direct Mechanisms of action

Biological Nitrogen Fixation

The growth of plants depends on the presence of nitrogen. Among other things, it can be found in proteins, enzymes, and nucleic acids. Unfortunately, plants and animals cannot access nitrogen, a gas that predominates in the atmosphere. The conversion of atmospheric nitrogen to ammonia is required for plant nitrogen absorption. Nitrogen-fixing bacteria that include an enzyme complex termed nitrogenise facilitate the process, which is known as biological nitrogen fixation (Smith et al., 2013). A symbiotic relationship is a mutualistic relationship in which both microbes and plants benefit (Ahemad et al., 2012). *Rhizobium* and *Mesorhizobium* create symbiotic relationships with *leguminous* plants, but *Frankia* forms symbiotic relationships with non-leguminous trees & shrubs (Zahran et al., 2001). *Cyanobacteria* (*Nostoc*, *Anabaena*), *Azotobacter*, *Gluconacetobacter* & *Pseudomonas* form a non-symbiotic relationship that can be both free-living and endophytic (Meena et al., 2021). Thus, inoculating seeds, seedlings, or soil with nitrogen-fixing microorganisms stimulates plant growth, improves soil quality, and maintains nitrogen levels in the soil (Damam et al. 2016). Encouragement of plant growth is done by PGPR in a number of direct and indirect methods. The most advantageous growth strategy for PGPR is biological nitrogen fixation, and molecular analysis of isolates of PGPR that fix nitrogen has revealed the presence of several *nif* genes, which encode the nitrogenase enzyme. A membrane complex that aided in electron transfer to the nitrogenase enzyme was made by the fixABCX gene, which was discovered in nitrogen-fixing Rhizobium species & other diazotrophs, in addition to *nif* genes (Mahmud et al., 2020).

Solubilisation of phosphate

A crucial component for the growth and development of plants is phosphorus. It participates in almost all of a plant's metabolic activities, including photosynthesis; respiration, signal transduction and energy transfer (Ahmed et al., 2017). The majority of phosphorus is contained in the soil as insoluble organic and inorganic phosphate. Phosphate solubilizing bacteria (PSB) is significant in this area since they can release phosphates from organic molecules and solubilize insoluble inorganic phosphate. Plants can only absorb monobasic and dibasic phosphate ions (HPO4−and H2PO42−, respectively) (Gouda et al., 2018). Phosphorus is extracted from organic molecules using several methods. Phosphatases break down phospho-ester linkages; phytases liberate phytic acid; phosphonatases employ magnesium (II) as a cofactor to catalysethe hydrolysis of phos-phonoacetaldehyde to produce acetaldehyde and phosphate and C-P lyases catalyse the C-P cleavage of phosphonates. (Morais et al., 2000).

Table 1. Represents the uses of PGPR in phytoremediation with *Brassica* species

Host	Bacteria	PGPR Effect	Reference
Brassica juncea	*Bacillus* sp. PZ-1	Increased biomass (up to 35%) Pb absorption by roots (28.3-83.6%) and shoots (52-106%) increased. A higher TFroot-shoot (12–55%)	Yu et al. (2017)
Brassica juncea	*Bacillus toyonensis* (MG430287) *Rhodococcus hoagii* (MG432495) *Lysinibacillus mangiferihumi* (MG432492) *Lysinibacillus fusiformis* (MG430290)	Increased rot length (47–106%) lengthened shoots (by 49–71%) Enhanced absorption of Fe (57.91-128%) production of antioxidant compounds has increased.	Jinal et al. (2019)
Brassica napus	*Bacteroidetes bacterium, Pseudomonas fluorescens Variovorax* sp.	Biomass has not increased. Increased roots and shoots Cd uptake (up to 12% and 10%, respectively) greater uptake of Zn (18% in shoots and 8% in roots)	Tang et al. (2020)
Brassica juncea	Isolates SMV242, SMV244, SMV248, SMV250, and Actinobacteria, Proteobacteria, and Firmicutes are the three phyla that SMV251 belongs to.	Biomass has not increased. As uptake increased only in roots (55%) Only when the mobilising chemical K2HPO4 (150%) is present do shoots exhibit increased As absorption.	Franchi et al. (2018)
Brassica juncea	*Burkholderiaphytofirmans*PsJNT	No increase in biomass Increased shoot uptake of Cd (22%) and Zn (38%)	Konkolewska et al. (2020)
Brassica juncea	*Rhizobium leguminosarumbv. I strain RCAM1066, Variovorax. paradoxus strain 5C-2, and Glomus sp. strain 1Fo of the AMF are three examples.*	Biomass has not increased. Uptake of Cd increases (by up to 10%)	Belimov et al. (2020)

Production of siderophores

Surface iron in aerobic conditions is converted into an insoluble form like oxyhydroxide, which leads to the production of ferric oxide, microbes have trouble getting enough iron to maintain their growth in the rhizosphere. Iron is needed for enzyme cofactors, oxygen metabolism, electron transport, DNA and RNA synthesis, as well as biofilm formation (Patel et al., 2018). PGPR-produced siderophores help plants get the iron they need by making it soluble and chelating it from accessible complex organic and inorganic iron (Singh et al. 2017). Some microbes create a siderophore that chelates available iron and competes with phytopathogens for iron feeding (Shaikh et al., 2016). *Alcaligenes*, *Pseudomonas*, *Bacillus* and *Rhizobium* all produce siderophore (Shaikh et al., 2015). The ability to colonise roots and exclude other bacteria due to siderophore synthesis gives PGPR a competitive advantage. The ability to obtain iron via siderophores may decide the outcome of competition for diverse carbon sources accessible as a result of root exudation andrhizodeposition under highly competitive situations (Tsegaye et al., 2017).

Production of IAA

80 % of PGPR produces IAA, an auxin that is physiologically active and encourages several growths including cell division, elongation, and differentiation (Ahmed et al. 2017). The most prevalent genera of bacteria involved in the production of IAA rhizosphere of different crops are *Acinetobacter*, *Rhizobium*, *Bacillus* and *Klebsiella* (Choudhary et al. 2018). *Pseudomonas spp.* is the most powerful producer of IAA among these bacterial genera, with *Pseudomonas putida*

producing more IAA than *Pseudomonas fluorescens* (Singh et al., 2019).

Indirect Mechanisms of Action

Production of hydrogen cyanide

HCN synthesis is required for strains that encourage plant growth to function. Due to its great toxicity against plant diseases, ability to chelate metal ions, and indirect ability to increase the availability of phosphate, In the agricultural production system, hydrogen cyanide is commonly used as a biocontrol agent (Rijavec et al., 2016). HCN-producing PGPR and their usage as a biofertilizer for promoting growth, increasing yields, and preventing disease have been described by a number of studies (Ahmed et al., 2017). Numerous bacterial taxa, such as *Aeromonas*, *Pseudomonas*, *Bacillus*, and *Enterobacter*, have been found to emit HCN in the rhizosphere (Vaikuntapu et al,.2014).

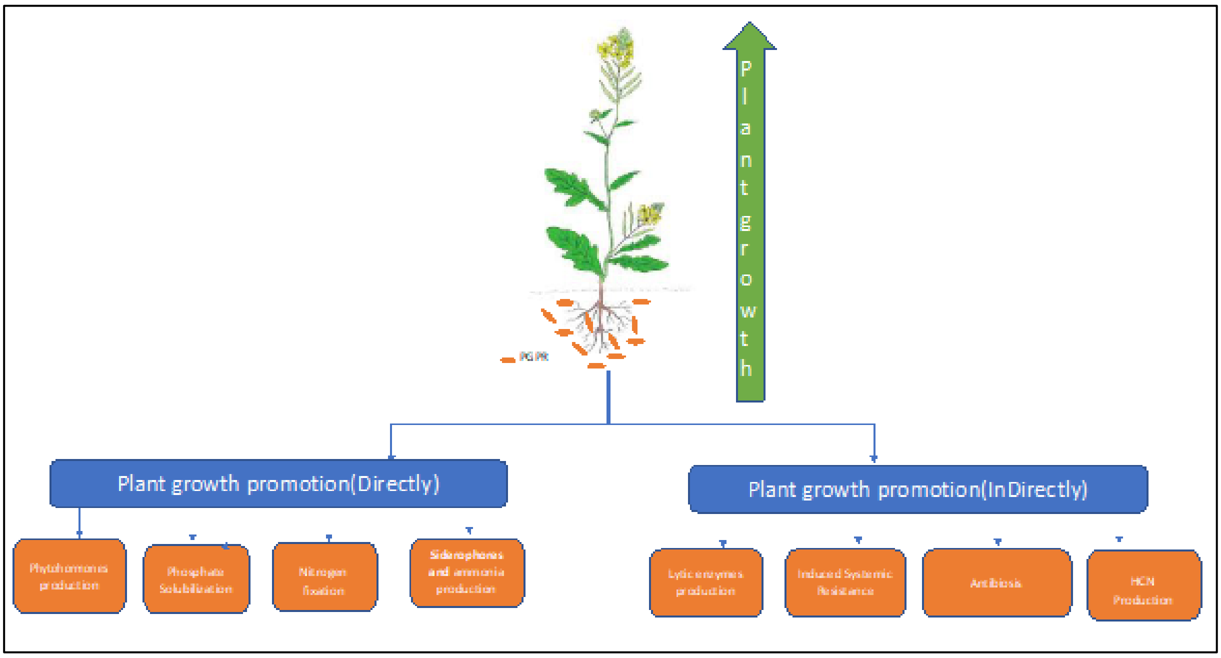

Figure 1. Direct and indirect plant growth promotion in a diagram (Mhatre *et al.* 2019)

Induced systemic resistance (ISR) and antibiotic production

PGPR strains produce antibiotics like phenazines, pyrrole-type compounds, butyrolactones, 2,4-diacetyl phloroglucinol, pyrrolnitrin, polyketides, and peptides that strengthen plant defence systems against infections (Govind et al., 2015). Numerous plant diseases have been discovered to be suppressed by PGPR strains that produce antibiotics, including *P. fluorescens* MKB 100, B. subtilis BMB 26, and *P. fluorescens* BL915 (Khan et al., 2005). Induced systemic resistance, also known as rhizobacterial strains, has been proven to give plants protection against pathogenic fungus, bacteria, viruses, nematodes, and pests (ISR) (Lugtenberg and Kamilova, 2009). The host plant's defence response is triggered when it is subjected to a high level of pathogenic infections by the PGPR increasing jasmonate/ethylene reliant on ISR-specific signals, which either induces specific jasmonic acid sensitive genes or upregulates ISR-associated genes (Glick, 2012).

PGPR is employed as a biocontrol agent

Several PGPR strains are utilised to manage a wide range of plant diseases by secreting a number of chemicals, including phenazine, DAPG, viscosinamide and tensin, which are frequently found to be disease suppressors. *Pseudomonas*, *Azotobacter*, *Bacillus* and *Streptomyces* are among the bacteria (Bharti et al., 2016). *Rhizobacteria* can inhibit the growth of several phytopathogens by competing for nutrients and space, creating lytic enzymes, bacteriocins, antibiotics, and siderophores, among other things (Tariq et al., 2017).

Biofertilizers

The words "biofertilizer" and "bioinoculant" have been derived in a variety of ways as a result of the remarkable advancements made in the study of the interaction between microorganisms and plants during the past 20 years. According to Vessey et al. (2003), "a material containing living microorganisms that, when applied to seed, plant surfaces, or soil, colonises the rhizosphere or the inside of the plant and encourages growth."A revised definition of biofertilizers was later proposed by Dineshkumar et al. (2018) as "products (carrier or liquid based) containing living or dormant microbes (bacteria, actinomycetes, fungi, algae) only or in combination, which helps in fixing

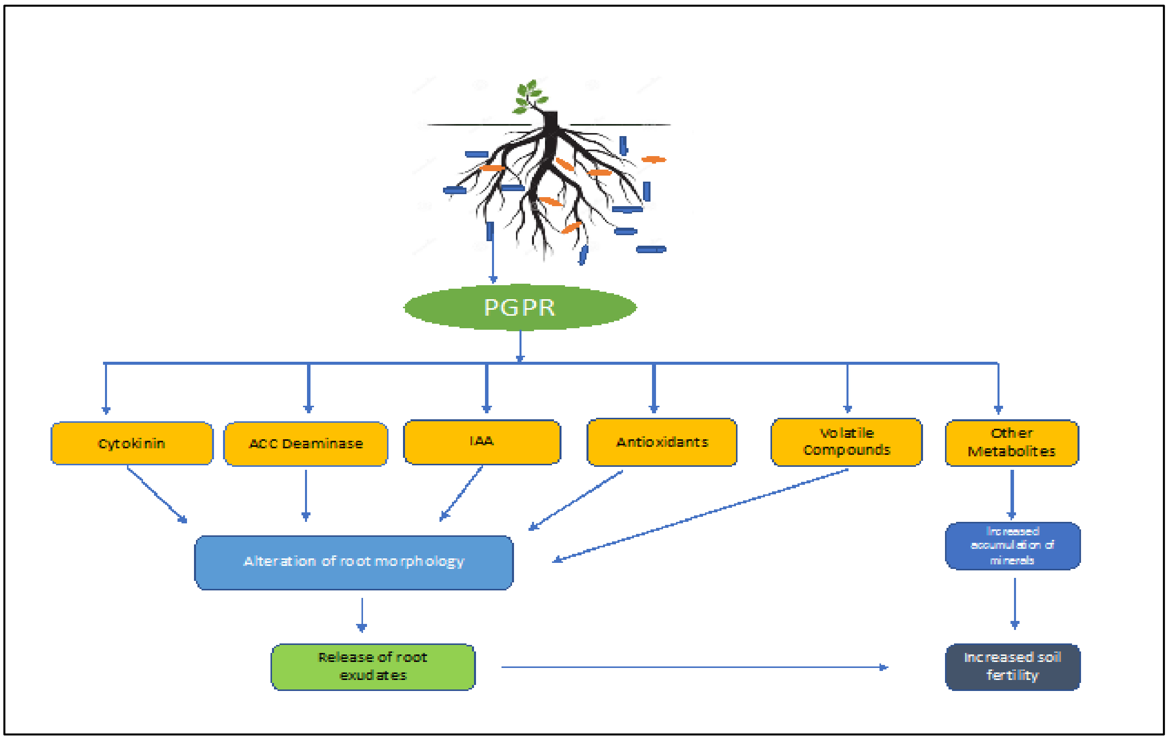

Figure 2. PGPR plays in creating sustainable crop production systems (Sharma et al. 2017)

atmospheric nitrogen or solubilizing soil nutrients further to secreting growth promoting substances for improving crop growth and yield." The microorganisms in biofertilizers use a number of techniques to assist agricultural plants. They may be adept in promoting plant growth, phosphate solubilization, and nitrogen fixation, or they may combine these abilities. (Mahanty et al., 2017). Compared to chemical inoculants, microbial inoculants provide a variety of benefits. (Meena et al., 2020). They are trustworthy sources of renewable nutrients needed for soil biology and wellness that are also environmentally benign (Sun et al., 2020). Additionally, they defend against different crop diseases and combat abiotic stresses (Ilangumaran et al., 2017). A number of microbial taxa have been employed commercially as efficient biofertilizers because of their ability to draw nutrients from the soil, fix atmospheric N2, enhance nutrient solubilization, and act as biocontrol agents (Schütz et al., 2018).

Ideal PGPR Characteristics

(1) It ought to be rhizosphere-capable and environmentally friendly.
(2) After inoculation, it should colonise the plant roots in substantial quantities.
(3) It should be capable of encouraging plant development.
(4) It should have a wide range of actions.
(5) The bacteria in the rhizosphere must get along with one another.
(6) Physical and chemical factors including heat, humidity, radiation, and oxidants must not harm it.
(7) It should outperform existing rhizobacterial communities in terms of competitive abilities.

PGPR's Mechanisms

Being the dominant microbial population in the rhizosphere, PGPR either actively or passively contributes to the support of plant growth. By enhancing biotic and abiotic stress tolerance and supplying nutrients to host plants, they can act as biofertilizers, boosting plant growth and development (Sagar et al. 2020, Mahdi et al. 2020). These helpful bacteria defend plants and aid in their growth through a number of processes, including root colonisation, favourable effects on plant physiology and growth, biofertilization, inducing systemic resistance, and biocontrol of phytopathogens, among others. The precise mechanisms of PGPR action and their distinctive role in promoting plant growth have been widely investigated (Swarnalakshmi et al. 2020). According to general definitions, the direct and indirect ways that PGPR promotes plant growth take place inside and outside of the plant, respectively (Goswami et al. 2016).

Commercialization of PGPR

In addition to promoting plant development, improving soil fertility, and controlling phytopathogens, PGPR is used as a nematode biocontrol agent and as an ecologically friendly substitute for synthetic agrochemicals like chemical fertilisers and pesticides promoting sustainable agriculture. PGPR-based biocontrol agent development and commercialization guidelines. Although different strains of PGPR are already offered as biological nematicides on the market, a straightforward query (i.e., repeatability) needs to be resolved before PGPR may be commercialised. However, more research on these products' efficacy is required. To be profitable, PGPR products need to have a variety of uses, a long shelf life, safety during use, a viable market, accessibility, consistency in terms of efficacy, and a cheap investment cost.

Plant Gene Expression and the PGPR

In addition to nitrogen fixation, phosphate solubilization is a well-known property of PGPR isolates. The six core genes of the PQQ operon, which codes for the membrane-bound enzyme glucose dehydrogenase and its enzymatic cofactor pyrroloquinoline quinine (PQQ), namely *pqqA*, *paqB*, *pqqC*, *pqqD*, *pqqE*, and *pqqF*, solubilize mineral phosphates (Matsushita et al., 1982). Another key aspect of PGPR is the creation of a siderophore, which aids plant growth by solubilizing and transferring iron through the generation of soluble Fe^{3+}.The up-regulation of the sid gene by PGPR is said to be responsible for siderophores synthesis (Ovaa et al., 1995). Plant gene expression is altered by PGPR, which controls genes involved in metabolism, stress response, defence, and phytohormones. Plant exudates operate as signalling chemicals, influencing microbiont gene expression (Sharma et al., 2019), ISR and hormonal homeostasis were associated with the majority of differentially regulated activated genes. The gene expression of the nitrate and ammonium absorption genes in Arabidopsis thaliana was altered by PGPR, as demonstrated by Calvo et al. (2019). Reduced expression of the cell wall and root defence mechanism genes was observed after B. subtilis colonisation of A. thaliana plants (Blake et al., 2021). During the colonisation of rice plantlets' roots, B. subtilis RR4 has been shown to repress several defense-related genes in order to enhance plant immunity (Rekha et al., 2018). The molecular processes by which PGPR isolates stimulate plant growth are still being researched, and further research is needed to confirm how PGPR regulate phytobeneficial features during plant colonisation, there is gene regulation between bacteria and plants.

Conclusions and Implications for the Future

Among the several sectors of the economy in a nation, the agriculture sector not only ensures its citizens' subsistence moreover helps the nation satisfy its export and population growth demands. Following the Green Revolution, the agroindustry has experienced a number of technological advances that have enhanced agricultural productivity but come with negative environmental effects. While biofertilizers are natural products with no environmental danger, chemical fertilisers are bad for the health of the soil and the environment. Therefore, in terms of maintaining long-term soil fertility and crop yield, fertilisers made from natural products demonstrate that they are a crucial and integrated part of sustainable agriculture. A revolution has unavoidably occurred in the preceding ten years due to the growing usage of biological inoculants in place of agrochemicals for sustainable agriculture. In addition to being essential for overall crop plant development and production. Our planet's health and appropriate biogeochemical cycling depend on the interactions between the bioinoculant microorganism(s), local soil microbiota, and host plant(s).

Farmers' emphasis is predicted to shift toward organic farming and adoption of sustainable agricultural practises as concerns about food safety and the need to control food production quality to meet shifting customer demand develop. As a result, when looking for environmentally acceptable alternatives to harmful chemicals, it's important to keep the three "Ps" in mind: people, prosperity, and the environment. Biofertilizers should be promoted by governments and federal agencies as environmentally acceptable crop development choices. Entrepreneurs ought to invest more in the biofertilizer sector and support startups financially. To secure a greener future, it is additionally necessary to raise general public awareness in order to inform farmers and consumers about the advantages of using microbe-based biofertilizers.

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