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REVIEW ARTICLE

Bacterial biostimulants for climate smart agriculture practices: Mode of action, effect on plant growth and roadmap for commercial products

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Abstract

Amidst the global food shortage and the global climate change challenge, there is an urgent need to double food production by 2050. However, the modern crop production methods, including the use of fertilizers and pesticides, have adverse environmental consequences, exacerbating the climate crisis. To address this challenge, a transition to sustainable agriculture is imperative that can harmonize the issue. Biostimulants offer an eco-friendly solution, especially bacterial biostimulants centred on plant growth-promoting rhizobacteria (PGPRs). These biostimulants hold the promise of offering environmentally sustainable solutions to enhance crop productivity. The adoption of PGPR-based biostimulants in agriculture has gained significant momentum in agricultural research. PGPRs enhance plant growth through multifaceted mechanisms. This review delves into the various modes of action employed by PGPRs to improve plant growth, including their impact on nutrient availability (such as nitrogen fixation and mineral solubilization) and stress mitigation. In addition, the practical implication of PGPR strains in field research has been discussed extensively. Besides, the review outlines the roadmap for commercializing PGPR-based biostimulants and discusses the associated challenges and limitations. A balanced perspective on the practical implementation of PGPRs in modern agriculture is presented. Exploration of future strategies and directions rounds out the review, emphasizing the necessity of a comprehensive approach to address research gaps and unlock the full potential of PGPR-based biostimulants for sustainable agriculture. In conclusion, this review underscores the applicability of PGPR-based biostimulants as an innovative solution to address the current food crisis in the context of climate change.

KEYWORDS

biofertilizer, biostimulant products, nutrient availability, plant growth-promoting rhizobacteria, sustainable agriculture

1 | INTRODUCTION

The projected global population of 9 billion by 2050 has created a pressing need for sustainable agricultural technologies that can effectively address the increasing demand for food while mitigating climate-related challenges (Smith and Gregory, 2013). The remarkable success of the 20th century's green revolution, facilitated by scientific advancements, led to a significant increase in global food production (Pingali, 2012). Developing improved crop plants through conventional breeding and advanced genetic manipulation has undoubtedly brought about significant advancements in agriculture (Qaim, 2020). However, it is important to acknowledge that the cultivation of genetically enhanced crops often relies heavily on applying chemical inputs such as inorganic fertilizers, herbicides and pesticides. In fact, these inputs continuously play a crucial role in maximizing crop yields and managing pests and weeds under suboptimum or optimum conditions. However, their excessive usage threatens the environment (Aktar et al., 2009; Davidson et al., 2012; Rani et al., 2021).

Nitrogen (N) fertilizer use in the United States witnessed a significant increase, rising nearly fourfold from 2.9 to 11.8 Tg N per year between 1961 and 2021 (FAOSTAT, 2023). The United States accounts for ~13% of global inorganic-N fertilizer usage of 86 Tg N annually, with a per-unit-area rate 2.2 times higher than the global average (Howarth et al., 2002; Lal, 2021). However, the mismanagement of N fertilizer has led to nitrate leaching, creating eutrophication in natural water bodies, and emission of nitrous oxide (N_2O), a potent greenhouse gas (Sharma & Bali, 2017). The recognition of risks associated with human health and environmental integrity due to nitrate leaching necessitates a focused effort to alleviate the pollution of water bodies stemming from nitrates originating from agricultural sources (Bibi et al., 2016). In addition to leachate losses, N is also lost in gaseous form. Agriculture is a major contributor, accounting for about 30% of global anthropogenic emissions (Lal, 2021). Phosphorus (P) is the second most limiting nutrient for plant growth and is vital for processes such as photosynthesis and cell division (Singh, 2022). Although abundant in soils, its availability to plants is often restricted due to fixation by elements like aluminium (Al), iron (Fe) and calcium (Ca) in acidic and alkaline soils (Hemwall, 1957). As a precaution, growers try to compensate for the fixed P, resulting in environmental issues, including runoff-induced eutrophication in water bodies. Agricultural chemicals also contribute to water contamination and pose a grave danger to the quality of surface and groundwater (Zhang et al., 2018).

Balancing the need for high agricultural productivity with the imperative to address these challenges requires exploring and adopting sustainable farming practices. These practices should minimize the negative impacts on climate, ecosystems and water resources, while ensuring long-term soil fertility. A new bio-based revolution in agriculture is required to address the challenges of feeding a growing global population and mitigating the impact of climate change (Backer et al., 2018). Climate change necessitates a paradigm shift in agricultural practices. In this context, plant biostimulants have emerged as a promising eco-friendly solution to enhance plant growth and productivity (Basu et al., 2021). The definition of biostimulant varies among different regulatory agencies and researchers. According to the 2018 US Farm Bill, biostimulants are described as 'a substance or microorganism that, when applied to seeds, plants, or the rhizosphere, stimulates natural processes to enhance or benefit nutrient uptake, nutrient efficiency, tolerance to abiotic stress, or crop quality and yield' (Congress, 2018). The European Commission defines biostimulants as products that stimulate plant growth and improve at least one plant function, such as nutrient-use efficiency, yield, quality, disease resistance, nutrient availability in soil and plant performance (EU, 2019). Biostimulants are also defined as materials that promote plant growth when applied in low quantities, distinct from fertilizers (Kauffman et al., 2007).

In the absence of a globally accepted legal or regulatory definition for plant biostimulants, the classification of biostimulant products varies across jurisdictions. In the European Commission's classification, biostimulants are divided into two primary classes: microbial and nonmicrobial biostimulants. Within the realm of biostimulants, there has been a notable surge of interest from industry and academia in microbial plant biostimulants based on live microbes. The appeal stems from their ability to enhance plant growth and development under field conditions more effectively than other types of biostimulants (Wozniak et al., 2020).

It is critical to recognize that plants growing in the field do not exist autonomously but instead interact with complex microbial communities. This dynamic microbiome relationship significantly influences numerous aspects, such as nutrient acquisition, pathogen tolerance and responses to abiotic stresses (Lebeis, 2014). Among various microbes, certain beneficial bacteria play a pivotal role in enhancing plant growth through both direct and indirect mechanisms, making them promising candidates as bacterial biostimulants. Among these bacteria, plant growth-promoting rhizobacteria (PGPR) that colonize the rhizosphere stands out as the most prominent group (Prasad et al., 2019). Extensive research has focused on genera such as *Bacillus* (Hashem et al., 2019), *Pseudomonas* (Oteino et al., 2015), *Azotobacter* (Gurikar et al., 2016) and *Azospirillum* (Okon et al., 2015) within the PGPR category. These PGPR strains have consistently demonstrated their remarkable ability to promote plant growth and confer resistance against both biotic and abiotic stressors (Figure 1).

The advancement of research in the field of phytomicrobiome has significantly contributed to our improved understanding of beneficial bacterial species that can be cultured and subsequently reintroduced into the soil through commercial products to enhance their population and diversity. The past few years have witnessed a remarkable expansion in the availability and utilization of these products by growers. In 2022, the global biostimulant market was valued at USD 3.5 billion, reflecting its significant market presence. Projections indicate that by 2027, the market value is poised to exceed USD 6.2 billion (Markets & Markets, 2023).

This comprehensive review will examine the significant role of PGPR, elucidating their mechanisms in enhancing plant growth. This manuscript also delves into some recent studies that used

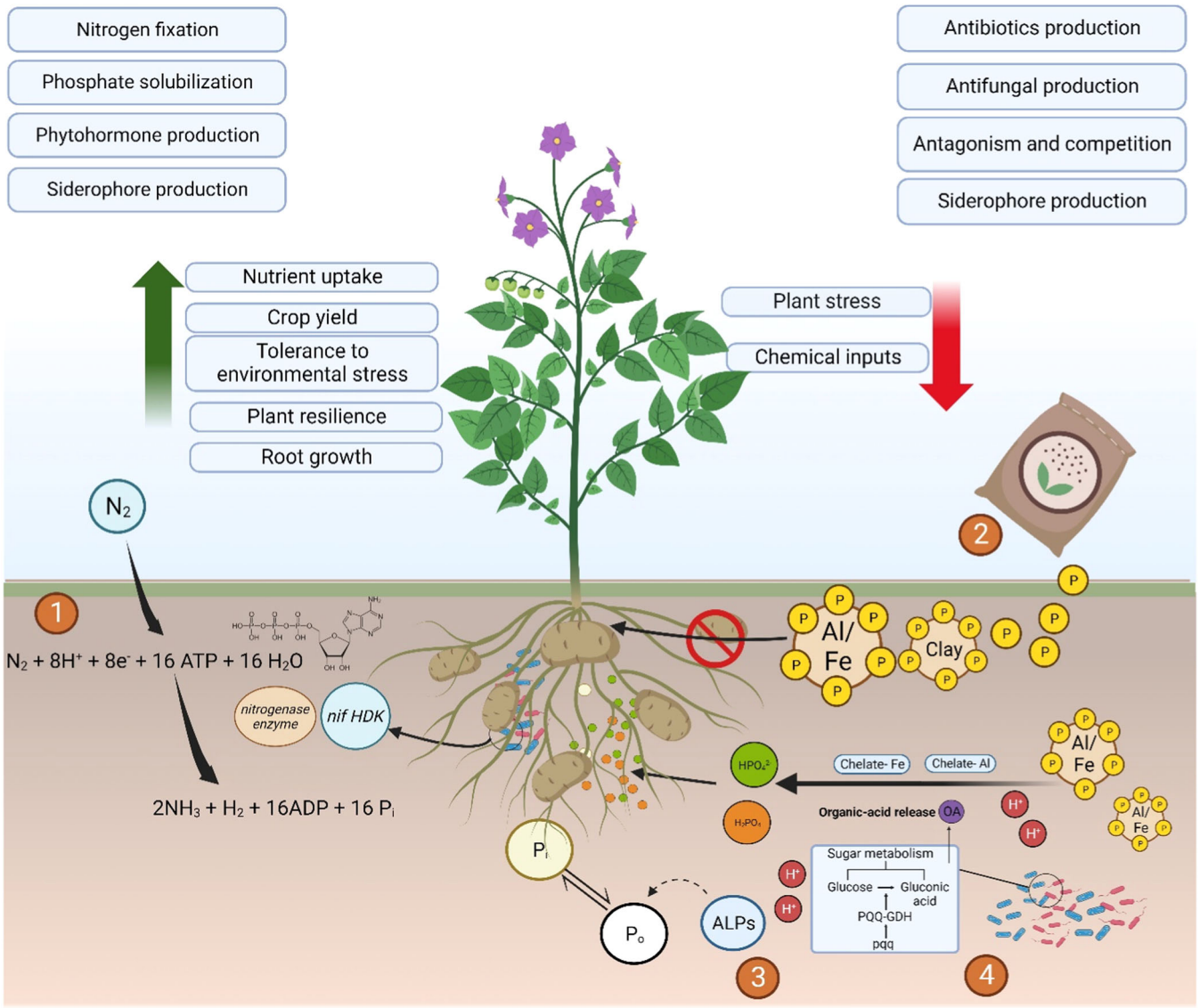

FIGURE 1 The interaction between plant growth-promoting rhizobacterias and plants, highlighting their profound impact on plant growth and development. (1) Atmospheric nitrogen (N) fixation, promoting N uptake by plants. (2) Phosphorus (P) from fertilizer forming chelates with soil particles, thereby making P less accessible to plants. (3) Synthesize acid phosphatases (alkaline phosphatase, ALPs), which play a crucial role in converting organic phosphate (Po) into an inorganic form (Pi) that plants can readily absorb. (4) Chemical messengers activate Pyrrolo quinoline quinine (pqq), which leads to the production of various organic acids.

PGPR as individual strains or commercial PGPR-based biostimulants to highlight their practical applications in real-world agricultural contexts, emphasizing their potential as cost-effective inputs for optimizing nutrient-use efficiency and maximizing crop productivity. Furthermore, the review explores the roadmap for commercializing PGPR-based biostimulant products. Addressing the challenges and limitations associated with PGPR utilization, we will provide a balanced perspective on their practical implementation in modern agriculture. In addition to the current applications, the review will also offer insights into future prospects, identifying research gaps and unexplored avenues for fully harnessing the potential of PGPRs in sustainable agricultural practices.

2 | MODE OF ACTION OF PGPRS

2.1 | Direct mechanisms

2.1.1 | Increased nutrient availability

Nitrogen is a critical and often limiting nutrient essential for plant growth. It serves as a building block for vital biomolecules such as proteins and nucleic acids (Singh et al., 2023). Despite the abundance of N in the atmosphere in the form of dinitrogen (N_2), its triple covalent bond renders it unreactive and unavailable for direct plant uptake (Raza et al., 2020). Although some natural N fixation exists, it cannot meet the increasing demand for higher crop yields and quality.

The revolutionary Haber-Bosch reaction has provided a groundbreaking solution by converting atmospheric N into reactive forms that can be transformed into N fertilizers (Kissel, 2014). With the increasing population, N fertilizer has become indispensable for meeting global food demand. However, the excessive use of N fertilizers contributes to environmental challenges, including climate change through greenhouse gas emissions (Singh et al., 2020) and eutrophication (Withers et al., 2014). Approximately one-third of the applied N fertilizer is effectively utilized by plants, while the remainder is lost to the environment, exacerbating these environmental issues (Raun & Johnson, 1999). As a result, there is a need to explore alternative approaches to reduce N fertilizer use while ensuring optimal crop productivity.

Certain friendly members of the phytomicrobiome exhibit the remarkable ability to fix atmospheric N and thus can partially fulfill the N demand of crops (Sible et al., 2021). These friendly bacteria can reduce the need for N fertilizer in the soil through direct or indirect mechanisms. In the direct approach, symbiotic interactions with legume plants, such as rhizobium–legume interactions, enable these bacteria to fix atmospheric N. In the indirect approach, these bacteria support N fixers by secreting substances that aid in the N fixation process (Kabiraj et al., 2020)

These friendly bacteria can be categorized into two groups based on their association with plants: symbiotic and nonsymbiotic free-living bacteria. Symbiotic species derive their energy from root exudates and fix atmospheric N, making it accessible for plant uptake. Genera such as *Rhizobium*, *Azoarcus*, *Burkholderia*, *Mesorhizobium*, *Sinorhizobium*, *Frankia*, *Allorhizobium*, *Bradyrhizobium*, *Azorhizobium* and some *Achromobacter* strains fall into this category (Gupta et al., 2015; Tajini et al., 2012; Toukabri et al., 2021).

The process of atmospheric N fixation is energetically demanding, requiring 16 moles of adenosine triphosphate to fix 1 mol of N. This considerable energy is obtained through the oxidation of organic molecules. Photoautotrophs utilize sugars produced through photosynthesis as a rich energy source, whereas nonphotosynthetic N fixers rely on various organisms for these energy-rich molecules. Among the most studied N fixers, the group of PGPRs often obtain these essential molecules from their host plants in exchange for the N they fix (Wagner, 2011). Additionally, PGPRs need nitrogenase enzyme, which is highly vulnerable to oxygen and needs anaerobic conditions to maintain its functionality (Fay, 1992).

In the symbiotic relationship of the host plant and N fixer bacteria, both bacteria and host plant undergo several changes. Host plants develop specialized root structures called nodules to house the bacteria, while the bacteria transform from rod-shaped cells into branched N-fixing bacteroids (Gully et al., 2016). Nodules provide a protected, anaerobic environment and offer reduced carbon compounds as an energy source to the bacteria. In return, the bacteria supply the host plant with N in an available form by reducing atmospheric N (Fisher & Newton, 2002). The amount of N fixation in leguminous crops can range up to 200 kg N ha^{-1}, and on a global scale, this symbiotic relationship contributes ~20–40 Tg N per year to agricultural systems (Herridge et al., 2008). The utilization of rhizobial bacteria in commercial products for inoculating leguminous crops represents one of the earliest examples of biostimulants in the market and remains a popular choice for enhancing the growth of leguminous crops.

In recent decades, there has been a growing interest in developing commercial biostimulants from free-living N-fixing bacteria to inoculate nonleguminous crops. Prominent examples of these free-living N-fixing species include *Azospirillum*, *Azoarcus* sp., *Azotobacter* sp., *Gluconacetobacter diazotrophicus*, *Herbaspirillium* sp., *Achromobacter*, *Acetobacter*, *Alcaligenes*, *Arthrobacter*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Rhodospirillum*, *Rhodopseudomonas* and *Xanthobacter* (Katiyar et al., 2022; Preininger et al., 1997; Rohela & Saini, 2022; Turan et al., 2016).

Unlike symbiotic N-fixing bacteria, these free-living species do not establish a symbiotic relationship with plants but rather inhabit the roots (rhizosphere) or on the roots (rhizoplane) of the plants (Haghighi et al., 2011). They derive the energy required for N fixation from the root exudates of plants (Backer et al., 2018). To prevent the irreversible inactivation of the nitrogenase enzyme by oxygen, various oxygen protection mechanisms have been identified in free-living N-fixing bacteria. These include increased respiration, the production of extracellular polymers as a barrier to oxygen diffusion and cell enlargement (Inomura et al., 2017). Some of these bacterial species do not always fix atmospheric N, but they enhance N availability to the plant. For instance, they stimulate root growth, enabling roots to explore the soil for available N (Beattie, 2015).

Following N, P is the second most limiting nutrient for plant growth, playing a crucial role in various physiological and metabolic activities such as photosynthesis, cell division and biological oxidation (Singh, 2022). Although most agricultural soils contain abundant P, their availability for plant uptake is often limited due to fixation by Al and Fe in acidic soils and by Ca in alkaline soils (Hemwall, 1957). Consequently, only a small fraction of P is accessible to plants. To circumvent this constraint, crops are commonly fertilized with rock phosphate extracted from a handful of major deposits, with a significant portion concentrated in Morocco and Western Sahara (Cooper et al., 2011). Under specific circumstances, growers apply more P fertilizer than recommended in an attempt to counteract P fixation.

Moreover, ~90% of the applied fertilizer P becomes insoluble in soil, making it unavailable for plant uptake due to fixation by other metal cations, leading to P buildup in the soil (Dhillon et al., 2017). This approach proves costly for farmers and poses various climate change effects. The excessive P may run off from farms into nearby water resources, causing eutrophication and polluting aquatic environments (Zhang et al., 2018). Therefore, an imperative challenge is to liberate P from its bound forms and make it plant available, enabling efficient utilization of P fertilizers and reducing the environmental impact of nutrient runoff.

Researchers and agricultural experts are exploring innovative strategies, including the use of PGPRs as biostimulant, to enhance P availability and uptake by plants. Several species of PGPRs possess

the capability to enhance plant-available P by solubilizing insoluble P or mineralizing organic P. Notable examples include *Agrobacterium* spp, *Pseudomonas* spp, *Bacillus*, *Rhizobium*, *Paenibacillus*, *Burkholderia*, *Azotobacter*, *Enterobacter* and *Erwinia* (Adeleke et al., 2021; Ahemad & Khan, 2010; Alori et al., 2017; Goswami et al., 2014; Liu et al., 2015).

The mechanism of insoluble P solubilization involves the secretion of metabolites such as gluconic and 2-keto gluconic acids by PGPRs. These organic acids, with their hydroxyl and carboxyl groups, chelate cations bound to phosphate, leading to the solubilization of insoluble P and making it accessible for plant uptake (Riaz et al., 2021; Sharma et al., 2011). These PGPRs oxidize glucose to gluconic acid, which chelates cations bound with phosphate, making phosphate more accessible to plants (Tariq & Ahmed, 2022). Another strategy PGPRs use to increase soil-available P is the hydrolysis of organic phosphates through extracellular enzymes (Singh & Satyanarayana, 2011). The PGPRs secrete various enzymes to facilitate organic P mineralization. Notably, two important enzymes in this process are phosphatases and phytases. The PGPRs have shown promising results in reducing P fertilizer requirements by up to 25% (Sundara et al., 2002). Many of these species have been commercialized, presenting opportunities to enhance P availability for crops and subsequently decrease P fertilizer needs.

Certain PGPRs have the remarkable ability to enhance the uptake of other essential nutrients like potassium (K), Fe and zinc (Zn) by their plant hosts (Rana et al., 2012). Some bacterial species can release K from their immobile forms in the soil, thereby increasing its availability for plant uptake (Etesami et al., 2017). Additionally, they can facilitate the availability of Fe by producing organic acids or siderophores, which helps in the solubilization of Fe in the soil (Kartik et al., 2023). The mechanisms of Zn mobilization by these bacteria are likely similar to those involved in P and Fe mobilization, which include chelation, acidification, exchange reaction mechanisms and dissolution processes through the secretion of organic acids into the soil. Overall, the role of PGPRs in improving nutrient availability and uptake holds significant potential for sustainable agriculture by reducing the need for excessive fertilizer application and minimizing environmental impacts.

2.1.2 | Phytohormone production

Phytohormones are essential chemical compounds synthesized in plant cells and are important in regulating plant growth, development and nutrient distribution. Although 10 different chemical groups of phytohormones are reported, the most prominent include indole-3 acetic acid (IAA)—a type of auxin, gibberellins (GAs) and cytokinins (CKs). Many PGPRs can synthesize these phytohormones and control plant growth and development. Table 1 presents a comprehensive compilation of studies, each providing evidence supporting the notion that the phytohormones secreted by PGPRs play a pivotal role in enhancing plant growth.

Auxin plays multifaceted roles, including regulating cell elongation, cell division, tissue differentiation and facilitating apical dominance. Moreover, auxin is crucial for processes like gravitropism (response to gravity) and phototropism (response to light) in both roots and shoots (Retzer et al., 2014). The PGPR, however, does produce IAA, a type of auxin. The IAA is essential for the extension of primary roots and the proliferation of lateral and adventitious roots (Ali et al., 2008). Approximately 80% of rhizospheric bacteria possess the ability to synthesize IAA. Consequently, this presents a promising avenue for identifying and harnessing such bacterial species to increase plant growth. The IAA produced by rhizobacteria influences the root system by increasing root size, biomass and soil contact area. Cumulatively, all these changes lead to a better root system that allows plants to explore more soil for nutrients and can result in better nutrient-use efficiency (Solano et al., 2008).

Additionally, a better root system offers a tangible advantage in terms of plant establishment, rendering plants more resilient and better equipped to withstand adverse weather conditions. Furthermore, PGPRs, capable of synthesizing IAA, have been demonstrated to induce transcriptional modifications in hormone, defence and cell wall-related genes (Spaepen et al., 2014). Additionally, PGPR-mediated IAA production has been linked to a reduction in stomatal size and density (Llorente et al., 2016) and activation of IAA response genes (Ruzzi & Aroca, 2015).

Beneficial microbes can influence IAA concentration through direct synthesis. Several studies have demonstrated that certain PGPRs can produce IAA in culture settings (Ahmed & Hasnain, 2014; Ali, 2015; Ali et al., 2009). The PGPRs exhibit a capacity to synthesize and liberate IAA as secondary metabolites, primarily fuelled by the abundant substrates from root exudates. The microbial biosynthesis of IAA can occur in different pathways. It is not limited solely to the L-tryptophan-dependent pathway; it can also transpire via an alternative, tryptophan-independent route. However, in the presence of L-tryptophan, these microbial entities are inclined to release significantly greater quantities of IAA (Normanly, 1997). Table 1 presents a comprehensive compilation of studies, each providing evidence supporting the notion that the phytohormones secreted by PGPRs play a pivotal role in enhancing plant growth.

In contrast to auxins, the roles of less explored phytohormones, such as GAs and CKs, which are synthesized by bacteria, remain incompletely understood (Kang et al., 2009). The GAs constitutes a class of phytohormones pivotal in seed germination, flower initiation, leaf expansion, stem elongation and the development of flowers and fruits. Several PGPRs, including *Bacillus* and *Acinetobacter*, have been documented as capable of producing multiple types of GAs, thereby fostering plant growth (Jha & Saraf, 2015). *Bacillus pumilus* and *Bacillus licheniformis*, isolated from the rhizosphere of alder (*Alnus glutinosa* [L.] Gaertn.), have demonstrated the ability to synthesize substantial quantities of biologically active GAs (Gutiérrez-Mañero et al., 2001). Numerous other bacterial species, known for promoting plant growth through GAs production, are also summarized in Table 1.

TABLE 1 Effects of phytohormone production by PGPRs on plant growth in various crops.

PGPRs	Phytohormone	Host plant	Results	References
Pseudomonas putida GR 12-2	IAA	Canola	35%–50% longer primary roots compared to IAA-deficient mutant and uninoculated seeds	Patten and Glick (2002)
Bacillus subtilis PRBS-1	IAA	Soybean	Stimulated lateral root outgrowth	Araujo et al. (2005)
Bacillus amyloliquefaciens KPS46	IAA	Soybean	Increased root, shoot length and biomass	Buensanteai et al. (2008)
Bacillus pumilus *Bacillus licheniformis*	IAA	Alder	Promotes stem elongation	Gutiérrez-Mañero et al. (2001)
B. subtilis 26D	IAA	Potato	Increased root mass	Sorokan et al. (2021)
Pseudomonas sp., *Bacillus* sp., *Azospirillum* sp.	IAA and CK	Wheat	Increased spike length, tillers, seed weight	Hussain and Hasnain (2011)
Acinetobacter calcoaceticus SE370	GA	Cucumber, Chinese cabbage, Crown daisy	Increased shoot height and biomass	Kang et al. (2009)
B. amyloliquefaciens RWL-1	GA	Rice	Increased shoot and root length	Shahzad et al. (2016)
Bacillus cereus MJ-1, *Bacillus macroides* CJ-29, *B. pumilus* CJ-69	GA	Red pepper	Increased shoot and root fresh weight	Joo et al. (2005)
B. subtilis JW1	GA	Chinese cabbage	Enhanced growth attributes	Kang et al. (2019)
Bacillus methylotrophicus KE2	GAs and IAA	Lettuce	Improved germination, increased biomass, nutrient and pigment content	Radhakrishnan and Lee (2016)
Bacillus megaterium	CKs	Thale cress	Threefold increase in shoot and root weight	Ortíz-Castro et al. (2008)

Abbreviations: CK, cytokinin; GA, gibberellin; IAA, indole acetic acid; PGPR, plant growth-promoting rhizobacteria.

CKs constitute another category of phytohormones that influence cell division, shoot differentiation and photomorphogenic development. Similar to IAA and GAs, exogenously applied CKs induce an array of physiological responses in plants, including enhanced cell division, root development, root hair formation, inhibition of root elongation, shoot initiation and more, as described by numerous studies (Hussain & Hasnain, 2011; Ortíz-Castro et al., 2008; Ruzzi & Aroca, 2015). Furthermore, the production of CKs by PGPRs can stimulate greater root exudate production by the host plant, further promoting the plant–microbes relationship. Veselov et al. (1998), isolated a high-molecular-weight complex of polysaccharides and biologically active Cks in liquid cultures of *Bacillus* species. Other PGPRs, such as *Pseudomonas* and *Azospirillum*, have also been documented to enhance plant growth by secreting CKs (Alexandre et al., 1996; Hussain & Hasnain, 2011).

2.2 | Indirect mechanisms

2.2.1 | Abiotic stresses

Crop production relies on a complex interaction between the genetic potential of plants and their performance during critical growth and developmental stages. However, many environmental stressors can significantly impede this potential, including abiotic stresses (such as drought, salinity, extreme temperatures, heavy metal toxicity and nutrient deficiencies) and biotic stresses (such as pest infestations and diseases). Effective management of these stressors is imperative for achieving sustainable crop production.

In recent years, the challenges posed by climate change have become increasingly apparent, with more frequent occurrences of extreme environmental conditions like drought, intense rainfall, salinity, temperature extremes, heavy metal contamination and nutrient deficiencies. These climatic shifts have substantially reduced crop yields and overall quality globally. For example, a recent heat wave and drought event resulted in decreased crop yields and a fodder shortage across European countries (Mazumdaru, 2018). Annually, abiotic stresses cause significant losses in food and cash crop production worldwide, with abiotic stressors accounting for more than 30% of total crop loss.

Traditional breeding methods for stress tolerance are time-consuming and resource-intensive, whereas genetic engineering approaches often face ethical and social acceptance challenges. Consequently, there is a growing recognition of the vital role played by beneficial microorganisms in stress management and the development of agriculture resilient to the challenges posed by climate change (Table 2). These microorganisms hold promise as a sustainable and environmentally friendly means of improving crop resilience and ensuring food security in a changing world.

Salinity is widely recognized as one of the primary abiotic stressors among these various stresses. Photosynthesis, respiration and protein synthesis are hampered by salinity stress, which impacts crop yields. It leads to oxidative stress through the generation of harmful reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2) and superoxide ions (O^{2-}), causing damage to vital biomolecules (Bano et al., 2021). To combat this oxidative stress, plants have developed efficient antioxidant defence systems comprising enzymes such as peroxidase, superoxide dismutase, catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR), primarily found in chloroplasts and mitochondria (Gill & Tuteja, 2010). During salt stress, plants increase ROS production and activate antioxidant enzymes to mitigate damage. Applying halophilic/halotolerant microorganisms is one of the most influential and environmentally friendly methods to sustain productivity under salt stress conditions (Alexander et al., 2020). They improve tolerance in several ways, including increasing plant immunity (induced systematic resistance, ISR), and increasing plant antioxidant enzymes, such as APX, CAT and GR. The N-fixing ability of legumes is also affected by salinity conditions that hinder nodule formation and low bacterial count in the root vicinity. PGPRs improved the growth of eggplant (*Solanum melongena* L.), wheat (*Triticum aestivum* L.) and quinoa (*Chenopodium quinoa*) under salt stress conditions (Fu et al., 2010; Orhan, 2016; Yang et al., 2016). Nadeem et al. (2007) reported that some biostimulants improve the chlorophyll content and photosynthetic

TABLE 2 A summary of PGPRs amelioration of abiotic stresses.

PGPRs	Crop	Stress	References
Achromobacter piechaudii ARV8	Tomato	Water	Mayak et al. (2004a)
A. piechaudii ARV8	Tomato	Salinity	Mayak et al. (2004b)
Microbacterium oleivorans KNUC7074, *Brevibacterium iodinum* KNUC7183 and *Rhizobium massiliae* KNUC7586	Pepper	Salinity	Hahm et al. (2017)
Bacillus licheniformis TRQ65	Wheat	Salinity	Ibarra-Villarreal et al. (2021)
Bacillus amyloliquefaciens NBRI-SN13	Rice	Salinity	Tiwari et al. (2017)
Pseudomonas psychrotolerans CS51	Corn	Salinity	Kubi et al. (2021)
B. amyloliquefaciens, *B. licheniformis*, *Bacillus thuringiensis*, *Paenibacillus favisporus*, *Bacillus subtilis*	Corn	Drought	Vardharajula et al. (2011)
B. subtilis	Chickpea	Drought	Abd_Allah et al. (2018)

Abbreviation: PGPR, plant growth-promoting rhizobacteria.

ability of corn (*Zea mays*) and rice (*Oryza sativa*) when applied under salt-stress conditions. Rhizopheric bacteria-based biostimulant protects the photosynthetic pigments of common bean (*Phaseolus vulgaris*) under salt stress conditions (Alexander et al., 2020).

Gram-positive rhizobacteria, which are easily handled and capable of endospore formation, are said to improve colonization under water-scarce conditions. The exact mechanism of plant drought stress tolerance is unknown, but some possible explanations include: the production of hormones such as abscisic acid, GAs, auxin and CKs; the production of essential enzymes, 1-aminocyclopropyl-1-carboxylate deaminase to reduce ethylene in the roots of developing plants; inducing systematic resistance, production of exopolysaccharides and so on.

Extreme temperatures can significantly reduce crop yields, whether cold or warm. Beneficial microbes have the potential to mitigate crop stress caused by temperature. *Pseudomonas* sp., for instance, has been found to promote the growth of wheat plants under low-temperature stress conditions (Mishra et al., 2011). *Acinetobacter oleivorans* IRS14 mitigates cold stress in wheat by regulating key physiological and biochemical factors. It modulates biochemical and metabolic pathways in wheat plants, decreasing chilling stress and increasing plant growth rate and biomass (Ali et al., 2023).

2.2.2 | Biotic stresses

Meeting the ever-growing food demand of our global population while simultaneously enhancing agricultural productivity on limited arable land presents a formidable challenge for both researchers and farmers. Among the numerous challenges faced in agriculture, biotic factors, such as pests and diseases, significantly impact crop yield. Although chemical solutions have yielded successful results, their indiscriminate usage has raised significant environmental concerns due to their adverse effects (He et al., 2016). PGPRs act as biocontrol agentsand protect the plants against various pathogens, including fungi, bacteria, viruses and insects. PGPRs offer numerous advantages over chemical pesticides. They are human and environmentally safe, readily degrade in soil and are less likely to lead to the development of pathogen resistance (Saeed et al., 2021).

The PGPRs effectively mitigate or prevent the detrimental impacts of one or more phytopathogenic species. Remarkably, a single PGPR species can utilize multiple mechanisms simultaneously to shield plants from biotic stress and improve plant's growth (Saeed et al., 2021). These mechanisms encompass the creation of competence for nutrients and space, cell wall degradation enzymes, production of antagonistic compounds and/or inducing pathogen resistance (Gupta et al., 2015).

Every plant possesses inherent defence mechanisms against pathogen attacks (Avis et al., 2008). Significantly, the occurrence of diseases can be mitigated when these defence mechanisms are effectively induced before pathogen's attack. This phenomenon is termed induced resistance, representing a defensive capability that plants develop in response to specific biotic or chemical stimuli (Choudhary et al., 2016). Induced systemic response (ISR) emerges as a product of pathogen-specific recognition by plant receptors (Pieterse et al., 2014). The PGPRs have the remarkable ability to trigger ISR within plants, thereby activating the expression of pathogenesis-related genes. This activation occurs through phytohormone signalling pathways and defense regulatory proteins (Avis et al., 2008; Pieterse et al., 2014). The ISR phytohormone signalling pathway includes the signalling molecules jasmonic acid and ethylene (Glick, 2012). The key determinants responsible for PGPRs-mediated ISR are siderophores, pyocyanin, lipopolysaccharides, homoserine lactones, the volatile 2,3-butanediol, lipopeptides, antibiotics 2,4-diacetylphoroglucinol, iron-regulated compounds and N-alkylated benzylamine (Doornbos et al., 2012). Among PGPRs, *Pseudomonas* and *Bacillus* sp. have garnered considerable attention for their ability to induce ISR, as summarized in Table 3.

Another mechanism used by many PGPRs involves the production of cell wall-degrading enzymes. Chitinase and β-1,3-glucanase play pivotal roles by degrading chitin, a soluble linear polymer composed of β-1,4-N-acetylglucosamine, which serves as a major constituent of fungal cell walls. For instance, *Paenibacillus* and *Streptomyces* produce β-1,3-glucanase enzymes, which lyse the cell wall of *Fusarium oxysporum* (Kumar et al., 2015).

Another mechanism includes the production of antibiotics, one of the most powerful biocontrol mechanisms employed by PGPRs against phytopathogen (Gupta et al., 2015). Antibiotics refer to a diverse group of organic compounds characterized by their low molecular weight (Duffy et al., 2003). These antibiotics encompass six distinct classes, including hydrogen cyanide, cyclic lipopeptides, pyoluteorin, phenazines, pyrrolnitrin and phloroglucinols are the six classes of antibiotic compounds (Haas & Défago, 2005). Among the various PGPRs, *Bacillus subtilis* can produce a variety of antibiotics and can suppress the growth of 23 diverse types of plant pathogens (Stein, 2005). Furthermore, PGPRs may also play a role in attracting the natural enemies of pathogens, thus indirectly contributing to the control of biotic stress (Alizadeh et al., 2013).

Although research has identified several promising PGPRs for use in pathogen biocontrol (as summarized in Table 3), some challenges and shortcomings are still associated with their practical application. One significant drawback relates to the inconsistencies observed under field conditions. A major contributing factor to this inconsistency is the inadequate colonization of plant roots by introduced bacteria. Effective root colonization is widely recognized as a prerequisite for a biocontrol agent to be successful (Handelsman & Stabb, 1996). The PGPR species must colonize both the rhizosphere and the plant's surface to provide effective protection against root diseases. Furthermore, consortia of PGPR strains are believed to be more effective at controlling biotic stress than single inoculants (Alizadeh et al., 2013). Consortia offers certain advantages over single strains, primarily due to the potential for bacterial species to synergistically interact and benefit each other (Shah et al., 2021). Addressing these shortcomings in biocontrol strategies, particularly through the utilization of phytomicrobiome, holds promise for

TABLE 3 A summary of PGPRs action against biotic stresses in various crops.

PGPRs	Crop	Common name of stress	Plant pathogens	Action or results	References
Pseudomonas sp. 23S	Tomato	Bacterial canker disease	*Clavibacter michiganensis*	Enhanced the defense capacity of the plants	Takishita et al. (2018)
Bacillus cereus AR156	Tomato	Bacterial speck disease	*Pseudomonas syringae* pv. *tomato* DC3000	Production of induced systemic resistance	Niu et al. (2012)
Bacillus amyloliquefaciens strain S1	Tomato	Bacterial canker disease	*C. michiganensis*	Efficient in reducing disease	Gautam et al. (2019)
Paenibacillus xylanilyticus YUPP-1, *Paenibacillus polymyxa* YUPP-8 and *Bacillus subtilis* YUPP-2	Cotton	Verticillium wilt	*Verticillium dahlia*	Reduction in disease by 38.1%	Yang et al. (2013)
B. amyloliquefaciens (SN13)	Rice	Sheath blight	*Rhizoctonia solani*	Enhanced immune response	Srivastava et al. (2016)
Bacillus mycoides	Sugar beet	Cercospora leaf spot	*Cercospora beticola* Sacc.	Reduces the disease by 38%–91%	Bargabus et al. (2002)
Bacillus pumilus INR7	Cucumber	Bacterial wilt	*Erwinia tracheiphila*	Disease incidence was significantly lower	Zehnder et al. (2001)
B. amyloliquefaciens 937a, *B. subtilis* 937b and *B. pumilus* SE34	Tomato	Tomato mottle virus	ToMoV	Disease severity was significantly reduced	Murphy et al. (2000)
Pseudomonas fluorescens HC1-07	Wheat	Rhizoctonia root rot	*R. solani* AG-8	Production of a cyclic lipopeptide	Yang et al. (2014)
B. pumilus strain SE34, *Kluyvera cryocrescens* strain IN114, *B. amyloliquefaciens* strain IN937a and *Bacillus subtilus* strain IN937b	Tomato	Cucumber mosaic	Cucumber mosaic virus	PGPR-mediated induced resistance against CMV	Zehnder et al. (2000)
Pseudomonas putida, *P. fluorescens*, *Pseudomonas aureofaciens*, *Serratia plymuthica*	Cucumber	Anthracnose	*Colletotrichum orbiculare*	Induced systemic resistance	Kloepper et al. (1992)
P. polymyxa	Peanut	Crown rot	*Apergillus niger*	99% reduction in disease	Haggag (2007)
P. fluorescens (S 97	Common bean	*Halo blight*	*P. syringae* pv. *phaseolicola*	Induced systemic resistance	Alström (1991)
Burkholderia cepacia BRB 21	Black pepper	Root rot	*Phytophthora capsici*	Promote chemical regulatory system	Dinesh et al. (2014)
P. fluorescens strain 4	Chickpea	Collar rot	*Sclerotium rolfsii*	phenolic acid synthesis	Maurya et al. (2008)
Bacillus megaterium WL-3	Potato	Late Blight	*Phytophthora infestans*	Production of lipopeptide	Wang et al. (2020)
B. amyloliquefaciens and *B. subtilis*	Potato	Bacterial wilt	*Ralstonia solanacearum*	84.6% reduction in disease	Ding et al. (2013)
P. fluorescens PF15	Tomato	Fusarium wilt	*Fusarium oxysporum f.*sp. *lycopersici*	Induced systemic resistance	Boukerma et al. (2017)
Bacillus halotolerans QTH8	Wheat	Crown rot	*Fusarium pseudograminearum*	Reduced conidial germination of *F. pseudograminearum*	Li et al. (2022)

Abbreviations: CMV, cytomegalovirus; PGPR, plant growth-promoting rhizobacteria.

mitigating biotic stress, especially in the context of the ongoing threat of climate change.

3 | PGPR STRAINS OR COMMERCIAL PGRP-BASED BIOSTIMULANTS AFFECT ON PLANT GROWTH PROMOTION

Among the numerous benefits that PGPRs confer to host plant crop growth and yield enhancement are the primary roles of enhancing the plant's N uptake, resulting in better seed germination and seedling emergence (Table 4). Atmospheric N fixation, enhancing P availability to plants through solubilization of inorganic P and mineralization of organic P, and the release of organic acids, which aid in making available forms of nutrients like Zn and others, are some of the mechanisms involved (Tilak et al., 2005). The PGPRs play a pivotal role in enhancing agricultural productivity. Their symbiotic relationship with plant roots unlocks the hidden potential of soil, resulting in remarkable growth and amplified yield. Mishra et al. (2020) observed that a combination of *Pseudomonas putida* BSP9 and rhamnolipid BS maximum 2% BS in bioinoculant showed the maximum enhancement in growth parameters, total oil and flavonoid content in *Bacillus juncea*. Application of PGPRs to different vegetables may improve their quality (protein and vitamins) and shelf life, along with improving soil health (Song et al., 2015). According to the results of net photosynthesis, leaf N content and total N content in soil have a positive correlation. N is the main ingredient of proteins, especially chlorophyll. This strong correlation results from a large amount of leaf N in chloroplasts. Therefore, leaf N was distributed to photosynthetic organs and activities. Jang et al. (2017) observed that rhizobacteria inoculation with some additional charcoal application ($300\ kg\ ha^{-1}$) resulted in the highest survivability (94.2%), total biomass production, net photosynthetic rate ($24.52\ \mu mol\ m^{-2}\ s^{-1}$). *Stentrophomonas maltophilia* BJ01 enhances the growth of peanut

TABLE 4 PGPRs benefits on plant growth and development.

Role or benefits of PGPR strains	PGPR strain(s)	Crops	References
Growth and yield	*Pseudomonas putida BSP9*, *Bacillus mucilaginosus*, *Bacillus subtilis* SM21, *Bacillus cereus* AR156, *Serratis* sp. XY21	Mustard	Mishra et al. (2020); Song et al. (2015); Zhang et al. (2019)
N and P uptake	*Pseudomonas culture*,	Rice	Yadav and colleagues (2014)
Soil fertility improvement	*B. subtilis*, *B. cereus*, *Rhizobium* sp.	Mung bean, *Vigna mungo*, Populus,	Jang et al. (2017); Islam et al. (2016); Ahmad et al. (2011)
Salinity tolerance	*Stenotrophomonas maltophilia* BJ01, *Bacillus pumilus*, *Bacillus megaterium*, *Azospirillum* sp., *Achromobacter piechaudii*, *Eneterobacter* sp., *Exiguobacterium oxidotolerans*	Peanut, corn, tomato, rice, sorghum, finger millet	Alexander et al. (2020); Mayak et al. (2004a, 2004b); Bharti et al. (2013); Marulanda et al. (2010); Fasciglione et al. (2015); Sagar et al. (2015)
Disease tolerance or biocontrol	*B. subtilis* strain PFMRI, *Pseudomonas macerans* strain BS-DFS and PF9, *Pseudomonas fluorescens* PF20, *B. subtilis* SM21, *Paenibacillus xylanexedens*, *Bacillus amyloliquefaciens*, *Streptomyces* sp., *Pseudomonas* sp., *Ochrobacttrum intermedium*, *Paenibacillus lentimorbus*	Wheat, rice, tomato,	Aliye et al. (2008); Zhang et al. (2019); Verma et al. (2016); Srivastava et al. (2016); De Vasconcellos et al. (2009); Gowtham et al. (2016); Khan et al. (2012); Reshma et al. (2018)
Drought tolerance	*Azospirillum brasilense*, *Enterobacter hormaechei*, *P. fluorescens* DR11, *Pseudomonas migulae* DR35, *B. subtilis*, *A. piechaudii* ARV8, *Phyllobacterium brassicacearum*, *Paenibacillus polymyxa*, *Rhizobium tropici*	Corn, wheat, foxtail millet, common bean, thale cress, tomato, chilli pepper	Timmusk et al. (2014); Niu et al. (2018); De Lima et al. (2019); Bresson et al. (2013); Figueiredo (2008); Yang et al. (2009); Ilyas et al. (2020)
Increased nutrition absorption	*P. polymyxa*, *Pantoea sp.* S32	Rice, habanero-type pepper	Chen and Liu (2019); Pii et al. (2015); Castillo-Aguilar et al. (2017)
Seed germination	*P. fluorescens*, *Azospirillum lipoferum*, *P. putida*, *B. subtilis*, *Serratia marcences*	Corn, Wheat	Almaghrabi et al. (2011); Rana et al. (2011)
Bioremediation of heavy metals	*B. cereus*, *P. fluorescens*, *Pseudomonas aeruginosa* RZS3, *Enterobacter* sp.	Rice, peanut, corn, ashwagandha	Pandey et al. (2013); Khan and Bano (2016); Das and Kumar (2016); Kalam et al. (2017); Patel et al. (2016); Sayyed et al. (2015)
Secondary metabolites	*B. subtilis*, *B. pumilus*, *P. putida*, *Azotobacter chroococcum*	Basil, waterhyssop	Banchio et al. (2009); Ordookhani et al. (2011)

Abbreviation: PGPR, plant growth-promoting rhizobacteria.

plants and protects the photosynthetic pigments under salt-stress conditions. Total amino acid content and growth hormone auxin were improved in plants cultivated with *S. maltophilia* (Alexander et al., 2020).

Corn seeds treated with *Serratia marcences* had the highest germination rate. It increased seed germination from 7% to 13% in comparison with the control (no inoculation). This is because the rhizosphere is a microorganism-rich environment that enhances the soil's physical and chemical properties, as well as nutrient availability in the upper soil zone. These conditions are more favourable for seed germination (Almaghrabi et al., 2011). This may also be the result of an increase in the production of hormones such as GAs, which stimulate the activity of specific enzymes that promote early germination, such as amylase. This enzyme increases the assimilation of starch. Increased auxin synthesis can boost seedling vitality.

4 | ROADMAP TO COMMERCIALIZE A PGPR-BASED BIOSTIMULANTS

The successful commercialization of PGPRs as a bacterial biostimulant involves a series of crucial steps (Figure 2). The first crucial step entails isolating and selecting PGPR strains through extensive soil and plant sampling from diverse growing environments. The isolation of these strains typically involves collecting samples from the rhizosphere of plants. Subsequently, these strains undergo rigorous screening in controlled environments, such as laboratories and greenhouses, either as single strains or in combination with others (Vasseur-Coronado et al., 2021). This meticulous screening process allows for the identification of PGPRs strains that exhibit promising plant growth-promoting properties. In the context of selecting beneficial strains, the following key factors should be considered:

a. Plant beneficial and environmentally friendly: The chosen strains should improve plant growth and health through a broad mode of action. Moreover, it should be environmentally friendly, displaying no harmful effects on the surrounding ecosystem.
b. Rapid proliferation in soil: The selected strains should be able to proliferate rapidly in the soil upon inoculation and colonizing plant roots, ensuring timely and efficient integration within the soil ecosystem.
c. Nonantagonistic towards friendly soil microbes: The strains should not possess antagonistic properties against other beneficial soil microbes already present in the soil. Instead, it should foster a harmonious relationship with the existing friendly microbial communities, contributing to a diverse and resilient soil microbiome.

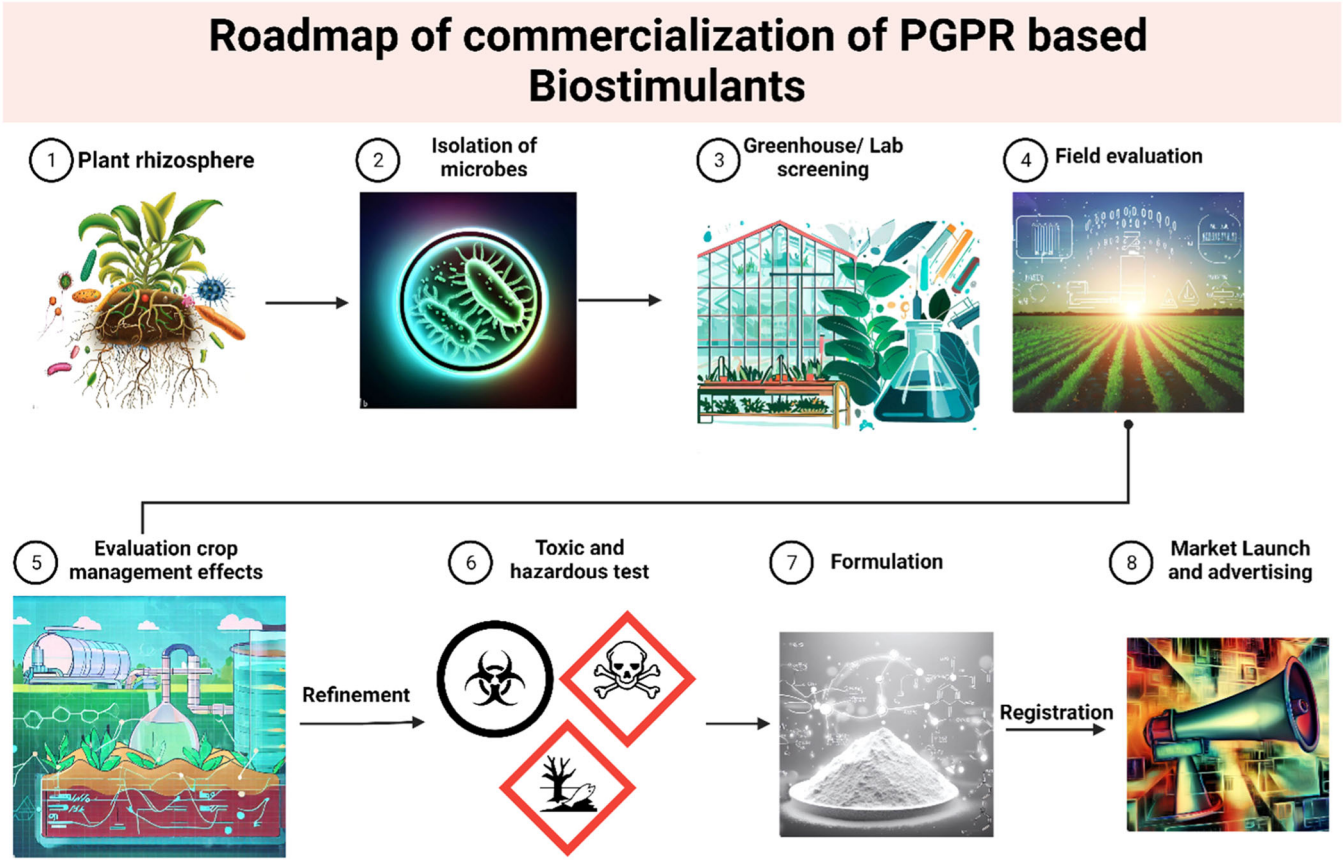

FIGURE 2 Steps involved in the commercialization of plant growth-promoting rhizobacteria (PGPR)-based biostimulants.

d. Competitive advantage: The chosen strains should outcompete other microbes present in the rhizosphere.
e. Adaptability to harsh climatic conditions: The chosen strains should exhibit robust performance even under challenging environmental conditions, ensuring consistent and reliable benefits for plant growth and productivity.

Following the selection of the most promising PGPR strains, further evaluations are conducted under complex and realistic conditions. Field trials are conducted on different crops and under various crop environments to evaluate the efficacy of the selected PGPR strains comprehensively. Factors such as irrigation practices, soil types and chemical inputs are considered during these evaluations to understand how these field management practices may impact the performance and proliferation of the PGPR strains in the soil environment. By conducting these field trials, researchers can identify potential challenges or limitations that may arise due to specific agricultural inputs or field conditions. Additionally, conducting toxicity and hazardous tests on the most promising strains is vital to ensure their safety for the environment and human health.

Once the best PGPR strains are selected, choosing a suitable carrier material becomes crucial for their successful transition from the laboratory to the field. The success or failure of PGPRs inoculation hinges on the quality of the carrier material utilized. A good carrier material ensures the successful inoculation and sustained performance of PGPRs. The carrier material serves as a shelter and source of nutrition for the PGPRs, ensuring their population and viability are maintained before inoculation in the field. Even distribution of the carrier material over the field is essential to ensure uniform coverage. Furthermore, the carrier material should exhibit high water-holding and retention capacities to ensure an adequate moisture supply for the PGPRs. It should also maintain a nearly sterile, chemically and physically uniform, and nontoxic composition. Ensuring the carrier material is easily biodegradable and nonpolluting minimizes potential environmental impact. Finally, once the product formulation is complete, it undergoes registration before being launched in the market. The registration process ensures compliance with regulatory standards, confirming the safety and efficacy of the PGPR-based biostimulant for commercial use. A diverse array of biostimulants is currently available in the market and a summary of some examples is presented in Table 5.

5 | CHALLENGES AND LIMITATIONS

Although PGPRs use numerous strategies to promote plant growth through direct and indirect mechanisms. However, many challenges still exist that must be addressed further to enhance their efficiency and adaptability in agricultural systems. The first challenge is to find

TABLE 5 Commercially available biostimulants.

Action	Commercial product and company	PGPR strain	References
N fixing	PGPR Agents (Huawei Biotech Company, Guangzhou, China)	*Bacillus subtilis* and *Bacillus mucilaginosus*	Song et al. (2015); García-Fraile et al. (2017); Aloo et al. (2020); MAcik et al. (2020); Mehnaz (2016)
	Nitragin Gold, Cell tech for pulses, Tagteam, (Novozymes, US), Custom N2 (Custom Biologicals, US), Nodulator Duo SCG (BASF, Canada)	*Sinorhizobium meliloti*, *Rhizobium leguminosarum*, *Rhizobium* sp., *Penicillium bilaiae*, *Paenibacillus polymyxa*, *Bradyrhizobium japonicum*	
	Agrilife Nitrofix (AGrilife, India), Ajay Azospirillum (Biofix, India), Symbion N (Stanes, India)	*Rhizobium japonicum*, *Azospirillum* sp., *Rhizobium* sp.	
P solubilizer	Rhizosum PK (Spain), Phosphobacterin (Russia), CataPult (Mabiotec, Australia), Symbion Van Plus (Stanes, India), P Sol B (Agrilife, India)	*Bacillus megatrium*, *Frateuria aurantia*, *Rhizophagus irregularia*, *Bacillus* sp. *Glomus intraradices*, *Pseudomonas striata*, *Bacillus polymyxa*	
K solubilizer	Rhizosum K (Spain), K Sol B (Agrilife, India)	*F. aurantia*	
Zn solubilizer	BioZink, Zn Sol B (Agrilife, India)	PGPR *Consortia*, *Thiobacillus thiooxidans*	
Phytostimulator	EVL Coating (Canada), Amase (UK), Biogold (Srilanka), Bioactivo (UK)	PGPR Consortia, *Pseudomonas azotoformans*, *Azotobacter chroooccum*, *Pseudomonas fluorescens*	
Biocontrol	Cedomon (lantmannen, Swedan), Cedress (lantmannen, Swedan), Cerall (lantmannen, Swedan), Biotilis (Agrilife, India), SoilFix (South Africa), Novozymes Actinovate (USA)	*Pseudomonas chlororaphis*, *B. subtilis*, *Brevibacillus laterosporus*, *Paenibacillus chitinoyticus*	

Abbreviation: PGPR, plant growth-promoting rhizobacteria.

appropriate PGPR strains, which starts with isolating the strain from the rhizosphere and conducting primary in vitro assays in the laboratory (Figure 2). This initial screening involves extensive evaluation of their ability to promote plant growth. However, screening isolates based solely on these mechanisms may not always result in effective plant growth promotion in the field. Conversely, some pure culture isolates may possess alternative and yet undiscovered plant growth promotion strategies in the soil but have limited in vitro growth-promoting functions. The lack of comprehensive understanding of these mechanisms complicates their screening and, thus, beneficial strains utilizing these mechanisms might be discarded due to perceived poor performance in conventional in vitro PGPR screening methods (Cardinale et al., 2015).

Achieving the maximum benefits of inoculation depends on establishing a suitable population density of the inoculant within the host plant's rhizosphere (McNear, 2013). However, several challenges hinder efficient rhizosphere colonization. Foremost among these is the concept of plant–microbe specificity, implying that although PGPRs may perform well in controlled environments, their performance under field conditions can be poor (Tabassum et al., 2017). Furthermore, the unpredictable nature of PGPRs also poses considerable hurdles. PGPRs showing optimal performance in a specific environment and under certain management practices may not necessarily exhibit the same performance in another context (Tabassum et al., 2017). Undoubtedly, the field screening of PGPRs is conducted with great care, considering various soil environments and crop management practices. However, the complexity of plant environments presents challenges in comprehensively accounting for every variable. Crop environment variables, such as soil type, properties, climatic conditions, water availability and more, influence the interactions between PGPRs and their host plants. Developing PGPR-based biostimulants tailor-made for every crop under a specific environment remains impractical.

Additionally, many growers often fumigate their soil using broad-spectrum biocidal fumigants to address various soil-borne pests and diseases. However, the extensive use of these fumigants alters the bio-community structure of the soil, causing significant disruptions to the soil microbial community. Prolonged fumigation can have detrimental effects on soil health, affecting the beneficial interactions between microbes and plants that aid in nutrient acquisition and mobilization. Consequently, the rhizosphere colonization by PGPR inoculants may be adversely impacted, presenting a challenge to effective PGPRs establishment and function in such soils (Dangi et al., 2017).

Another challenge is the limited shelf life of biostimulant products containing live inoculum, requiring protection during transportation and storage (Tabassum et al., 2017). Ensuring protection against extreme conditions during transportation and storage is important. Moreover, the possibility of genetic mutations arising during storage or transportation further complicates matters. In such instances, there is a risk that farmers might unknowingly apply biostimulant with compromised efficacy directly from the packaging. This scenario could lead to financial losses for growers, as the diminished performance of PGPR-based products could result in inadequate benefits.

The deeply rooted preference for chemical inputs among farmers poses a significant challenge in adopting PGPR-based products to reduce the chemical input rate. Growers believe that chemical fertilizers are the optimal solution for enhancing crop production. Thus far, we have not introduced any technologies capable of entirely replacing chemical fertilizers without compromising yield and production quality (Moser et al., 2008). However, PGPR-based products could contribute to addressing climate change by curbing the reliance on chemical inputs. The shift toward novel and environmentally friendly techniques encounters obstacles due to several factors. Primarily, the lack of comprehensive field research encompassing diverse crop growth conditions leaves farmers uncertain about the efficacy of these alternatives. Moreover, the economic considerations of adopting PGPR-based biostimulant products often deter farmers from transitioning away from chemical fertilizers. Farmers are more inclined to adopt technology when it increases their profit despite being environmentally beneficial.

6 | CONCLUSION AND FUTURE DIRECTIONS

The application of PGPR-based biostimulant in agriculture is a bandwagon in agricultural research due to their potential to provide environmentally sound solutions to improve crop productivity. However, a thorough understanding of their mechanisms and addressing the challenges associated with their performance under field conditions remains imperative.

Strategies for enhancing PGPRs efficacy could involve combining multiple strains with distinct growth-promoting properties to ensure a more comprehensive and balanced nutrient uptake while providing pathogen protection. Such an approach could potentially incentivize farmers to adopt this technology by offering multi-dimensional benefits.

Oxygen-sensitive nitrogenase enzyme activity needs strategies for preserving anaerobic conditions when considering N fixing. Understanding how free-living bacteria protect nitrogenase from oxygen could increase the use of these microbes in cereal crops. Moreover, N fixation is an energy-consuming process, so bacteria fixing atmospheric N stops working whenever N is present in the soil. Furthermore, nutrient-deficient plants secrete exudates that modify certain bacterial strain's transcriptomes, enhancing their functionality (Carvalhais et al., 2013). The dilemma of bacterial N fixation in the presence of soil N could be resolved through gene modifications, allowing fixation to continue even under N-rich conditions. Gene editing and biotechnology developments play a crucial role in optimizing N-fixing microbes for crop supply potential, offering opportunities to increase efficiency (Farrar et al., 2014).

Furthermore, upon identification of a promising strain, it becomes imperative to ascertain the boundaries of its N production in terms of its capacity to fulfill crop nutrient demands.

Understanding its established crop partners, the nuances of its N-fixing genes and avenues for genetic refinement is pivotal in shaping a more potent and effective strain (Sible et al., 2021).

The evolution of screening techniques for PGPR inoculants is a crucial path ahead. The unpredictable field behaviour of PGPRs necessitates field-based screening and subsequent controlled-environment analyses to understand their action mechanisms. An effective strategy involves the initial screening of microbes in actual field conditions, followed by their assessment within controlled environments using small-to-medium-sized phenotyping platforms (Rouphael et al., 2018). A crucial aspect during screening is their performance within a diverse range of environments, especially diverse crops and soil conditions. Additionally, the adoption of more intricate technological methodologies, such as the multi-omics approach, holds promise in comprehending plant-microbe interactions. As suggested by Paul et al. (2019), the amalgamation of high-throughput phenotyping and metabolomics could provide a robust framework for screening, offering insights into the biochemical, metabolomic and morpho-physiological dimensions of their mode of action.

Moreover, most microorganisms cannot be cultured in the lab. Approximately 99% of the microbes on the planet earth cannot be grown or cultured in the lab. Considering this, utilizing metagenomics could help to address this challenge. This approach holds the potential to provide valuable insights into their mechanisms, thereby contributing to a deeper understanding of their roles and functionalities (Arora et al., 2011; Berg et al., 2020).

Additionally, while screening microbes for P solubilizing capacity, several studies have employed tricalcium phosphate as an insoluble P source despite numerous microbes being able to solubilize it. Therefore, utilizing multiple P sources for screening offers a more accurate assessment of P solubilizing capabilities (Bashan et al., 2013). This involves the use of Ca-phosphates for alkaline soils, Fe- or Al-phosphates for acidic soils and phytates for soils enriched with organic P reservoirs.

Developing improved carrier materials for inoculants is another avenue to explore. Biochar integration shows promise in enhancing the soil's root colonization and survivability of PGPRs. Incorporating PGPR inoculation with biochar creates a conducive environment that offers essential nutrients and shelter, thus facilitating the growth and rhizosphere colonization of microbes. Research findings have indicated the beneficial outcomes of this integration. Studies such as those by Yang et al. (2023) and Kumar et al. (2017) have demonstrated that biochar increases the survival rates of PGPRs within the soil environment, while enhancing their growth-promoting activities.

Although plant biostimulants show promise as a novel agricultural input alongside synthetic fertilizers, a pressing need exists within the research community and fertilizer industries to uncover the molecular and physiological mechanisms governing their effectiveness. A deeper understanding of these mechanisms is crucial for the widespread adoption and integration of these bio-based products into the agricultural sector. Lastly, harnessing PGPR-based biostimulant's complete advantage requires collaboration among stakeholders, farmers, public research institutions and regulatory bodies. By working together, we can pave the way for profitable and sustainable agricultural practices that effectively address the challenges posed by climate change.

AUTHOR CONTRIBUTIONS

Ravinder Singh: Conceptualization; literature review; software; visualization; writing—original draft; writing—review and editing. **Sehijpreet Kaur**: Writing—original draft; writing—review and editing. **Sukhveer S. Bhullar**: Writing—review and editing. **Hardeep Singh**: Supervision; writing—review and editing. **Lakesh K. Sharma**: Supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable—no new data generated.

ETHICS STATEMENT

Not applicable.

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