

Plant Growth-Promoting Bacteria; A Review on Mechanisms and Sustainable Crop Production

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Abstract: *The ability of agricultural systems to provide food globally may be limited by growing environmental concerns. The biggest issue the world is now dealing with is climate change. By 2050, food production will need to quadruple to fulfill the world's food demand. In the field of sustainable agriculture, plant growth-promoting bacteria (PGPB) have been shown to have a significant impact. Increasing agricultural yield while using less synthetic chemical fertilizers and pesticides is a major issue in today's world. It has been demonstrated that using PGPB to promote plant development through direct or indirect means is a sustainable method of raising agricultural yields. Among PGPB's processes are the control of hormonal and nutritional balance, the development of resistance against plant diseases, and the solubilization of minerals to facilitate their simple absorption by plants. Moreover, PGPB interact both antagonistically and synergistically with microorganisms in bulk soil and the rhizosphere, which indirectly accelerates plant development. Numerous bacterial species have been reported in the literature to function as PGPR and to effectively enhance plant development. There is a difference, nevertheless, between the PGPR's function as a biofertilizer and its method of action (mechanism) for plant development. Therefore, this analysis fills in the aforementioned void and provides an overview of PGPR's mechanism as a biofertilizer for sustainable agriculture*

Keywords: agricultural systems

I. INTRODUCTION

The world's population, which is now estimated to be about 8 billion, is predicted to rise to almost 8 billion by 2020. It is evident that feeding everyone on the planet will become increasingly difficult in the next ten to twenty years due to the combined effects of the predicted rise in global population and the growing environmental harm caused by ever-increasing levels of industrialization. There is no time to waste; in order to feed the world's expanding population, agriculture output must be significantly increased in a sustainable and ecologically acceptable manner. Reexamining many of the current agricultural practices, which involve the use of chemical fertilizers, herbicides, fungicides, and insecticides, is needed in order to feed the world's expanding population. Rather, transgenic plants (for instance, go to <http://www.isaaa.org/inbrief/default.asp>) and plant growth promoting bacteria, or PGPB, will probably be used far more in sustainable agriculture [1]. According to estimates, "environmental degradation, coupled with the growth in world population, are (considered to be) major causes behind the rapid (global) increase in human disease" (<http://www.sciencedaily.com/releases/2007/08/070813162438.htm>) and "water, air, and soil pollution cause about 40% of deaths worldwide." That is to say, the earth's atmospheric, terrestrial, and aquatic systems are no longer enough to absorb and decompose the growing quantity of garbage that humans create as a result of both population growth and industrialization. As a result, a variety of hazardous metals and organic chemicals are finding their way into the environment [2, 4]. Understanding the scope and nature of the issue is a crucial first step. But even if there was no more environmental contamination tomorrow, remediation of all damaged lands and seas would still be necessary. Using phytoremediation-the deliberate use of plants to absorb, concentrate, or degrade a variety of environmental pollutants-as a solution to this issue is one possibility [5-8]. Furthermore, adding PGPB to plants employed in phytoremediation techniques usually results in a considerably more effective remediation process overall [3, 9, 10].

II. PLANT GROWTH-PROMOTING BACTERIA (PGPB)

Microorganisms such as bacteria, fungus, actinomycetes, protozoa, and algae are abundant in soil. Approximately 95% of these various microorganisms are bacteria, making them the most prevalent kind. It has long been known that soil has a high concentration of bacteria (usually 10⁸–10⁹ cells per gram of soil) and that the proportion of culturable bacteria to total cells in soil is typically only 1% [11]. However, the quantity of culturable bacteria in stressed-out environments might be as low as 10⁴ cells per gram of soil [12]. Furthermore, microorganisms in soil are typically not dispersed equally. That is, compared to the rest of the soil, the rhizosphere—the area around a plant's roots—generally has a significantly higher concentration of bacteria. This is due to the nutrients found in plant root exudates, which include sugars, amino acids, organic acids, and other tiny molecules and may make up as much as one-third of the carbon fixed by a plant [14–17].

There are three possible ways that bacteria might impact plants, depending on how many are present in a given soil sample. From the plant's point of view, the relationship between soil bacteria and plants might be advantageous, detrimental, or neutral [18]. But if circumstances alter, a given bacterium's impact on a plant may also alter. For instance, when significant amounts of artificial fertilizer are applied to the soil, a bacterium that promotes plant development by supplying either fixed nitrogen or phosphorus—compounds that are frequently present in only limited levels in many soils—is unlikely to assist plants in any way. Furthermore, it is feasible for a single bacteria to have varying effects on several plants. For instance, a mutant of the bacteria *Pseudomonas fluorescens* BSP53a that produces an excess of IAA enhanced the growth of roots in blackcurrant cuttings but inhibited the same process in cherry cuttings [19]. It is possible to explain this data by supposing that the bacteria increased the inadequate amount of IAA present in the blackcurrant cuttings. However, with the cherry cuttings, the extra IAA that the bacterium delivered became inhibitory since the IAA level was already at its peak when the bacterium was added. With these exceptions, it is typically simple to determine whether a bacteria encourages or hinders plant development.

The term "plant growth-promoting bacteria," or "PGPB," refers to a variety of bacteria that can coexist with plants, form particular symbiotic relationships with them (such as *Rhizobia* and *Frankia* species), colonize some or all of the internal tissues of plants, and are known as cyanobacteria (formerly known as blue-green algae). Despite their diversity, these bacteria all make use of the same processes. PGPB can either directly or indirectly stimulate plant growth by reducing the inhibitory effects of different pathogenic agents on plant growth and development, i.e., by functioning as biocontrol bacteria, or by enabling resource acquisition or modifying plant hormone levels [20]. In the past, a great deal of research was done on *Rhizobia* species from physiological, biochemical, and molecular biological viewpoints before there was a lot of interest in figuring out how to use or comprehend additional PGPB to promote plant development [21–23]. As a result, the conceptual foundation for mechanistic research on PGPB was established by these early investigations. However, research to better understand some of the processes utilized by PGPB have addressed a wide variety of alternative mechanisms since, in contrast to *Rhizobia* spp., most PGPB fix no nitrogen or only a small quantity of it [13, 20, 24].

2.1. Commercialization

Even while our knowledge of PGPB-plant interactions is currently restricted, some of these bacteria are still employed in the agricultural industry as supplements [1, 25]. PGPB strains that have been commercialized include *Agrobacterium radiobacter*, *Bacillus licheniformis*, *Bacillus firmus*, *Bacillus megaterium*, *Bacillus mucilaginosus*, *Bacillus pumilus*, *Bacillus spp.*, *Bacillus subtilis*, *Bacillus subtilis* var. *amyloliquefaciens*, *Burkholderia cepacia*, *Delftia acidovorans*, *Paenobacillus macerans*, and *Pantoea agglomerans*. *Serratia entomophila*, *Streptomyces griseoviridis*, *Streptomyces spp.*, *Streptomyces lydicus*, and many *Rhizobia* spp. are among the *pseudomonas* that include *Pseudomonas aureofaciens*, *Pseudomonas chlororaphis*, *Pseudomonas fluorescens*, *Pseudomonas solanaceum*, *Pseudomonas spp.*, and *Pseudomonas syringae*. But PGPB-inoculated crops only make up a tiny portion of agricultural practices used now in the globe.

Many challenges must be resolved in order to commercialize PGPB strains more widely. These include: (i) identifying the characteristics that are most crucial for effective functioning and then choosing PGPB strains with the right biological activities; (ii) uniformity among regulatory bodies in various nations regarding which strains can be released into the environment and what circumstances make genetically modified strains suitable for environmental use; (iii) a

better comprehension of the benefits and drawbacks of using rhizospheric versus endophytic bacteria; (iv) choosing PGPB strains that function optimally under particular environmental conditions (e.g., those that perform well in warm and sandy soils versus organisms better suited to cool and moist environments); (v) the creation of more efficient methods for delivering PGPB to plants in different environments (such as the field as opposed to a greenhouse); (vi) an improved comprehension of the possible interactions between PGPB and other soil fungi, such as mycorrhizae.

III. DIRECT MECHANISMS

3.1. Facilitating Resource Acquisition

The most well-researched methods of bacterial plant growth promotion involve giving plants nutrients and resources that they don't already have, including fixed nitrogen, iron, and phosphorus. Plant development is sometimes subpar in agricultural soils because of a lack of one or more of these chemicals in appropriate amounts. In order to avoid this issue and achieve greater plant yields, farmers have relied more and more on artificial supplies of phosphate and nitrogen. In addition to being expensive, the manufacture of chemical fertilizers puts human and environmental health at risk and uses up nonrenewable resources like natural gas and oil. Clearly, it would be beneficial if at least some of the artificial nitrogen and phosphorus that are presently utilized could be replaced by effective biological methods of giving plants these nutrients.

3.1.1. Nitrogen Fixation

Many free-living bacteria, such as *Azospirillum* spp., may fix nitrogen and supply it to plants in addition to *Rhizobia* spp. [26]. Nonetheless, the general consensus is that free-living bacteria only supply a tiny portion of the fixed nitrogen needed by the host plant linked with the bacteria [27]. Genes related to iron molybdenum cofactor biosynthesis, electron donation, structural genes involved in Fe protein activation, and regulatory genes necessary for the manufacture and operation of the enzyme are among the nitrogenase (*nif*) genes needed for nitrogen fixation. The *nif* genes, which encode 20 distinct proteins through seven operons, are normally found in a cluster of 20–24 kb in diazotrophic (nitrogen-fixing) bacteria. Genetic techniques to enhance nitrogen fixing have been difficult to implement due to the intricate nature of this system. It was originally thought by some scientists that nitrogen fixation might be genetically engineered to enhance if genes were extracted and described. Furthermore, some people asserted that it could be able to genetically modify plants so they can fix nitrogen on their own. These concepts appear a little naive now.

It would be preferable if bacterial carbon resources were directed toward oxidative phosphorylation, which results in the synthesis of ATP, rather than glycogen synthesis, which results in the storage of energy in the form of glycogen, since the process of nitrogen fixation requires a significant amount of energy in the form of ATP. In one study, a strain of *Rhizobium tropici* was created with the glycogen synthase gene deleted [28]. Compared to treatment with the wild-type strain, treatment of bean plants with this modified bacteria led to a considerable increase in the number of nodules that developed as well as an increase in the dry weight of the plant. This is one of the extremely few instances when researchers have genetically altered a bacterium's nitrogen fixation system to produce higher amounts of fixed nitrogen. Regrettably, despite the fact that this mutant enhanced plant biomass and nodule number in the field, it is not very resilient in the soil.

Oxygen is necessary for *Rhizobium* spp. bacteroid respiration, but it also inhibits the enzyme nitrogenase and is a negative regulator of *nif* gene expression. Bacterial hemoglobin, which binds free oxygen, can be added to the environment to prevent oxygen from impeding nitrogen fixation while yet supplying enough oxygen for the bacteroides inside the nodule to breathe. After *Rhizobium etli* was transformed with a hemoglobin gene from *Vitreoscilla* sp., a gram-negative bacteria, the respiratory rate of the rhizobial cells was two to three times greater than that of the nontransformed strain at low concentrations of dissolved oxygen. After being injected with hemoglobin-containing *R. etli*, bean plants in the greenhouse exhibited 68% higher nitrogenase activity than plants injected with wild-type *R. etli*. The nitrogen content of the resulting seeds increased by 16% and the nitrogen content of the leaves by 25–30% as a result of this variation [29]. Plant ethylene levels frequently rise slightly and locally when legumes become infected with *Rhizobium* species. This elevated ethylene content has the potential to prevent nodulation and subsequent rhizobial infection [30]. By producing a tiny molecule known as rhizobitoxine [31], which chemically inhibits the activity of the

enzyme ACC synthase, one of the ethylene biosynthesis enzymes, certain rhizobial strains can limit the rise in ethylene and increase the number of nodules that form on the roots of a host legume. After being injected with hemoglobin-containing *R. etli*, bean plants in the greenhouse exhibited 68% higher nitrogenase activity than plants injected with wild-type *R. etli*. The nitrogen content of the resulting seeds increased by 16% and the nitrogen content of the leaves by 25–30% as a result of this variation [29]. Plant ethylene levels frequently rise slightly and locally when legumes become infected with *Rhizobium* species. This elevated ethylene content has the potential to prevent nodulation and subsequent rhizobial infection [30]. By producing a tiny molecule known as rhizobitoxine [31], which chemically inhibits the activity of the enzyme ACC synthase, one of the ethylene biosynthesis enzymes, certain rhizobial strains can limit the rise in ethylene and increase the number of nodules that form on the roots of a host legume. On the other hand, certain rhizobial strains generate the enzyme ACC deaminase, which eliminates a portion of ACC, the plant's direct precursor to ethylene, before it can be converted to ethylene [30]. Reducing the ethylene concentration in legume hosts can lead to a 25–40% increase in nodule number and plant biomass [32, 33]. Since 1–10% of rhizobial strains found in the field naturally have ACC deaminase [34], it is feasible to engineer *Rhizobium* strains lacking ACC deaminase with genes (and regulatory regions) isolated from other strains in order to boost their nodulation efficiency. In one case, the number of nodules and biomass of host alfalfa plants were significantly enhanced when an ACC deaminase gene from *R. leguminosarum* bv. *viciae* was inserted into the chromosomal DNA of a strain of *Sinorhizobium meliloti* that did not have this enzyme [33]. However, most governments presently do not allow genetically modified strains of *Rhizobium* to be used in the field due to political and regulatory reasons. Several commercial inoculant manufacturers have started screening/testing their more recently obtained *Rhizobium* strains for active ACC deaminase, despite this political/regulatory limitation.

3.1.2. Phosphate Solubilization

Even while the average soil contains a significant quantity of phosphorus (typically 400–1,200 mg kg⁻¹ of soil), the majority of this phosphorus is insoluble and thus not accessible to promote plant development. It can be found as an inorganic mineral like apatite or as one of various organic forms including phosphomonesters, phosphotriesters, and inositol phosphate (soil phytate) [35]. Furthermore, a large portion of the soluble inorganic phosphorus used in chemical fertilizers quickly gets immobilized after application, making it inaccessible to plants and thus lost. The inability to absorb enough phosphorus frequently restricts plant growth because of the element's poor bioavailability from the soil and its need for plant growth [36]. Therefore, phosphate-solubilizing bacteria's ability to solubilize and mineralize phosphorus is a crucial characteristic of both PGPB and fungi that promote plant development, including mycorrhizae [37, 38].

Generally, low molecular weight organic acids like citric and gluconic acid—both of which are produced by different soil bacteria—are responsible for the solubilization of inorganic phosphorus [38–40]. Conversely, the process of mineralizing organic phosphorus is brought about by the creation of several phosphatases, which catalyze the hydrolysis of phosphoric esters [38]. It's noteworthy that a single bacterial strain may exhibit both mineralization and phosphate solubilization [41]. Unfortunately, there hasn't been much commercial usage of phosphate-solubilizing PGPB due to inconsistent findings. In particular, when phosphate-solubilizing bacteria are coinoculated with other physiological capacities like N fixation or with mycorrhizal or nonmycorrhizal fungi, the most consistent favorable impacts of the application of these bacteria are observed [42].

3.1.3. Sequestering Iron

Iron is the fourth most abundant element in the universe, but in aerobic soils, neither bacteria nor plants can easily assimilate it because the predominant form of iron, ferric ion or Fe⁺³, is only very sparingly soluble, leaving very little iron available for assimilation by living things [43]. High levels of iron are necessary for both microorganisms and plants, and getting enough iron becomes increasingly difficult in the rhizosphere where fungus, bacteria, and plants fight with one another for iron [44, 45]. Bacteria create low-molecular mass siderophores (approximately 400–1500 Da) to survive on such a limited iron supply. These molecules have a very high affinity for Fe⁺³ (Fe⁺³ ranging from 10²³ to 10⁵²) and membrane receptors that can bind the Fe-siderophore complex, which helps microorganisms absorb iron

[46, 47]. Currently, approximately 500 siderophores are identified; 270 of these compounds have had their chemical structures elucidated [46].

Multiple types of tests have revealed the direct advantages of bacterial siderophores on plant development. For instance, (i) a number of studies using radiolabeled ferric-siderophores as the only source of iron revealed that plants can absorb the labeled iron [48–55]; (ii) mung bean plants grown under iron limiting conditions and inoculated with the siderophore-producing *Pseudomonas* strain GRP3 showed reduced chlorotic symptoms and an enhanced chlorophyll level compared to uninoculated plants [56]; (iii) *Arabidopsis thaliana* plants absorbed the Fe-pyoverdine complex synthesized by *Pseudomonas fluorescens* C7, increasing the amount of iron inside plant tissues and improving plant growth [57].

It is much more crucial for soil bacteria to provide plants with iron when the plants are under environmental stress, such as heavy metal contamination. In this instance, siderophores aid in reducing the stressors that high soil concentrations of heavy metals place on plants [58–62].

Bacterial communities' organizational structure in the rhizosphere can be impacted by plant iron feeding. For instance, transgenic tobacco has less accessible iron in the rhizosphere than nontransformed tobacco because it overexpresses ferritin and accumulates more iron [63]. Consequently, the bacterial community's composition in the rhizosphere was much different from that of tobacco lines that had not undergone transformation.

3.2. Plant hormone Level Modulation

Plant hormones are essential for both the growth and development of plants as well as how they react to their surroundings [64]. Furthermore, a plant is frequently exposed to a variety of nonlethal stressors during its life that may restrict its development until the stress is eliminated or the plant is able to modify its metabolism to withstand the effects of the stress [65]. Plants frequently try to modify the amounts of their endogenous phytohormones in response to growth-limiting environmental circumstances, with the goal of lessening the detrimental impacts of the stressors [66]. While this tactic can occasionally work, rhizosphere microorganisms can also manufacture or modify phytohormones in vitro [66], allowing numerous phytohormone-producing bacteria (PGPB) to change phytohormone levels and impact the plant's hormonal balance and stress response [65].

3.2.1. Cytokinins and Gibberellins

Numerous investigations have demonstrated that PGPB in particular, as well as many other soil bacteria, are capable of producing gibberellins, cytokinins, or both [67–72]. For instance, several strains of *Azotobacter* spp., *Rhizobium* spp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Paenibacillus polymyxa* have been shown to have cytokinins in their cell-free media. Furthermore, it has been documented that some PGPB that produce gibberellin or cytokinin can promote plant development [73–77]. Nevertheless, a thorough knowledge of the function of hormones produced by bacteria as well as the regulation of the bacterial synthesis of these plant hormones is now lacking. Therefore, a large portion of our understanding of the function of gibberellins and cytokinins generated by bacteria is derived from investigations on plant physiological responses to exogenous administration of pure hormones to developing plants.

Lastly, certain phytopathogen strains have the ability to produce cytokinins. On the other hand, it seems that PGPB create less cytokinins than phytopathogens, which explains why PGPB has a stimulatory impact on plant development whereas pathogen-produced cytokines have an inhibitory effect.

3.2.2: Indoleacetic Acid

Although a number of naturally occurring auxins have been reported in the literature, indole-3-acetic acid, or indoleacetic acid, IAA, is by far the most widely used and researched auxin. In fact, a large portion of the scientific literature regards auxin and IAA as synonymous names [78, 79]. IAA influences photosynthesis, pigment formation, the biosynthesis of various metabolites, resistance to stressful conditions, and lateral and adventitious root formation. It also affects plant cell division, extension, and differentiation, stimulates seed and tuber germination, increases the rate of xylem and root development, controls vegetative growth processes, and initiates lateral and adventitious root formation [80, 81].

For over seven decades, it has been shown that the physiology of plants is significantly impacted by varying IAA concentrations. Plant responses to IAA differ depending on the type of plant; some plants are more or less sensitive to IAA than others; depending on the specific tissue involved, such as roots versus shoots (the ideal level of IAA for supporting plant growth is approximately five orders of magnitude lower for roots than for shoots); and depending on the stage at which the plant is developing. On the other hand, the uptake of IAA released by soil bacteria may modify the endogenous pool of plant IAA. In this sense, whether bacterial IAA promotes or inhibits plant development depends on the amount of IAA that the plant synthesizes. Endogenous IAA in plant roots may be either inadequate or ideal for growth [82], and extra IAA absorbed from bacteria may change the IAA level to either optimal or supraoptimal, promoting or inhibiting plant development, respectively.

Plant-bacterial interactions may entail IAA synthesised by bacteria at various stages. IAA specifically affects root nodulation and plant growth promotion. After this strain's IAA-deficient mutant was created, researchers looked into the function of IAA, which was produced by the PGPB *Pseudomonas putida* GR12-2, in the growth of canola roots [83]. When wild-type *P. putida* GR12-2 was injected into seeds, the result was the production of roots that were 35–50% longer than those from seeds treated with the IAA-deficient mutant and uninoculated seeds. However, compared to controls [85], mung bean cuttings inoculated with a mutant of the same strain [84] that overproduces IAA resulted in a much higher number of shorter roots.

The combined effects of auxin on growth promotion and ethylene's suppression of root elongation were shown to be responsible for this outcome [86]. The plant's incorporation of bacterial IAA enhanced the activity of ACC synthase, leading to a rise in ACC synthesis [86], which in turn caused an increase in ethylene, which hindered root growth [87]. Overall, bacterial IAA lengthens and increases the surface area of the roots, giving the plant better access to nutrients in the soil. Furthermore, bacterial IAA breaks down the cell walls of plants, which allows for more root exudation and the subsequent supply of extra nutrients that promote the development of rhizosphere bacteria.

The majority of *Rhizobium* strains that have been studied have been shown to generate IAA [88], and a number of investigations have revealed that auxin levels in the host plant must rise in order for nodules to grow [89]. *Bradyrhizobium elkanii* mutants with reduced IAA production levels therefore produced fewer nodules on soybean roots than the wild-type strain [90]. Furthermore, it was discovered that the IAA content of nodules produced by low IAA-producing *Rhizobium* sp. NGR234 mutants was lower than that of nodules induced by the wild-type strain. This finding lends credence to the theory that some of the IAA present in nodules is of prokaryotic origin and that it aids in nodulation [91].

3.2.3. Ethylene

One of the most basic chemicals with biological action is ethylene, the hormone found in plants. The prophet Amos was a “herdsman and a nipper of figs,” according to the Hebrew Bible. This remark suggests that people knew as early as the ninth century BCE that piercing or nipping figs released ethylene gas, which accelerated the ripening process and increased the figs' sweetness. The plant hormone ethylene is active at concentrations as low as 0.05 $\mu\text{L/L}$ and has a wide variety of biological actions; yet, ripening fruit can have ethylene levels as high as around 200 $\mu\text{L/L}$ [92].

Promoting root initiation, inhibiting root elongation, fruit ripening, flower wilting, stimulating seed germination, encouraging leaf abscission, activating the synthesis of other plant hormones, preventing *Rhizobia* spp. nodule formation, reducing mycorrhizae-plant interaction, and reacting to biotic and abiotic stresses are just a few of the numerous ways that ethylene can influence plant growth and development [92]. The term “stress ethylene” [92] refers to the synthesis of ethylene that occurs in response to a variety of environmental stresses. These include temperature extremes, intense light, flooding, droughts, the presence of organic pollutants and toxic metals, radiation, wounding, insect predation, high salt, and various pathogens, such as bacteria, viruses, and fungi [93]. Under response to a variety of environmental challenges, a greater quantity of ethylene is produced. This increased ethylene can either worsen the symptoms of the stress or cause reactions that improve plant survival under challenging circumstances. A theory that explains this seemingly paradoxical behavior is that when plants are stressed, they swiftly react by releasing a brief peak of ethylene, which starts the plant's protective reaction, such as the transcription of genes encoding defensive proteins [65, 94]. A second, significantly greater peak of ethylene appears, usually a few days later, if the stress is

severe or continues. Plant growth and survival may be significantly inhibited by the processes that this second ethylene peak triggers, including senescence, chlorosis, and abscission.

After the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase was found in soil bacteria [95], a number of investigations revealed that this enzyme was a common characteristic of numerous PGPB [96, 97]. Furthermore, a model was developed that detailed this enzyme's function in PGPB-induced plant growth facilitation [98]. According to this hypothesis, PGPB invade a developing plant's seed or root, and in response to tryptophan and other small molecules found in exudates from the seed or root, the bacteria produce and exude IAA [78, 83]. In conjunction with endogenous plant IAA, this bacterial IAA has the ability to either promote plant development or trigger the production of the plant enzyme ACC synthase, which transforms the chemical S-adenosyl methionine into ACC, the direct precursor of ethylene in all higher plants. A part of the freshly generated ACC is removed from seeds or plant roots [99], absorbed by the PGPB, and transformed into easily digested chemicals like ammonia and α -ketobutyrate by the enzyme ACC deaminase. The activity of this enzyme directly results in a decrease in the quantity of ethylene that the plant produces. Thus, PGPB that produce ACC deaminase colonize roots or seeds to stop plant ethylene levels from becoming growth inhibitory [20, 98].

Enhancement of plant root elongation is the primary short-term observable result of seed or root inoculation with ACC deaminase-producing bacteria; longer-term investigations often show encouragement of shoot growth [13, 100–107]. Local increases in ethylene levels are also brought about by other processes including the nodulation of legumes and the formation of mycorrhizae in the host plant. Therefore, in a variety of legumes, including pea, alfalfa, mung bean, and chickpea [32, 33, 107, 108] and cucumber [109], ACC deaminase-producing bacteria can increase the extent of both rhizobial nodulation and mycorrhizal colonization by lowering the local ethylene content in these plants.

IV. INDIRECT MECHANISMS

There has been a lot of interest in the capacity of biocontrol bacteria to indirectly stimulate plant growth, with two goals in mind: (i) understanding some of the underlying mechanisms by which the bacteria function, and (ii) using these bacteria commercially to replace chemical pesticides. In actuality, these two goals work best together. In other words, knowing the strategies used by biocontrol bacteria should make it easier to use certain strains of bacteria effectively in the future.

4.1. Lytic Enzymes and Antibiotics

The PGPB property that is most frequently linked to the bacterium's capacity to stop plant pathogens—typically fungi—from proliferating is the production of a variety of different antibiotics [110–115]. A number of these antibiotics, as well as their mechanism of action and specificity, have been thoroughly investigated; some of these biocontrol strains have even gone on sale. An issue with overly relying on bacteria that produce antibiotics as biocontrol agents is that some phytopathogens may become resistant to particular antibiotics as a result of the increased usage of these strains. To prevent this from happening, some researchers have deployed biocontrol strains that synthesize hydrogen cyanide as well as one or more antibiotics. Although hydrogen cyanide may not have much biocontrol action on its own, this strategy works well because it seems to work in concert with antibiotics that are encoded in bacteria. Enzymes such as chitinases, cellulases, β -1,3 glucanases, proteases, and lipases are produced by some biocontrol bacteria and have the ability to partially break down the cell walls of certain dangerous fungus. It has been discovered that PGPB that produce one or more of these enzymes have biocontrol action against a variety of pathogenic fungus, such as *Sclerotium rolfsii*, *Botrytis cinerea*, *Fusarium oxysporum*, *Phytophthora* spp., *Rhizoctonia solani*, and *Pythium ultimum* [116–119].

4.2. Siderophores

Some bacterial strains can function as biocontrol agents by producing siderophores, even if they don't use any other kind of biocontrol. In this instance, siderophores from PGPB may inhibit the capacity of some phytopathogens to multiply by preventing them from obtaining an adequate supply of iron [120, 121]. According to some theories, the reason this mechanism works is that the biocontrol agent, PGPB, produces siderophores with a far higher affinity for iron than do fungal pathogens [122], which prevents the pathogens from proliferating due to a shortage of iron in the

rhizosphere of the host plant's roots [123]. Fungal pathogens are efficiently outcompeted for available iron in this model by the biocontrol PGPB.

However, because most plants can grow at far lower iron concentrations than most microbes, the depletion of iron in the rhizosphere induced by the siderophores generated by biocontrol PGPB typically has little effect on plant growth [123]. Furthermore, a variety of plants have the ability to bind, absorb, and subsequently use the biocontrol PGPB siderophore complex [124, 125]. Numerous studies provide experimental data that supports the role of biocontrol PGPB siderophores in the reduction of plant diseases caused by fungal pathogens. For instance, some research using mutants deficient in siderophore synthesis discovered that these strains were less successful than wild type strains in defending plants against fungus infections [126–128]. However, one study found that plants were better protected against fungal infections by siderophore overproducing mutants [129].

4.3. Ethylene

In response to phytopathogens, plants usually produce ethylene under stress, which intensifies the effects of the stress on the plant [92]. Therefore, reducing the plant's ethylene response is one strategy to lessen the harm that a variety of phytopathogens may do to plants [131]. The easiest method for doing this is to apply PGPB that contains ACC deaminase to plants (usually the roots or seeds) [98]. Thus far, studies conducted in growth chambers and greenhouses have demonstrated that this approach reduces the harm inflicted upon castor bean, tomato, carrot, cucumber, and soybean plants [132–136]. Significantly, a variety of phytopathogens, including *Pythium ultimum*, *Fusarium oxysporum*, *Erwinia carotovora*, *Agrobacterium tumefaciens*, *Agrobacterium vitis*, *Sclerotium rolfsii*, and *Rhizoctonia solani*, have been evaluated in these investigations. Furthermore, transgenic plants expressing a bacterial ACC deaminase exhibit a notable degree of protection against different phytopathogen-induced damage [137, 138]. Despite these potentially promising findings, it has not been investigated if PGPB that contains ACC deaminase may lessen pathogen-induced plant damage in the field. This probably indicates that many people are reluctant to cope with the possibly challenging regulatory permission procedure that is involved in doing this kind of field testing.

4.4. Induced Systemic Resistance

Plants can experience a phenomena called induced systemic resistance (ISR) in response to infection by a pathogenic agent. This event is phenotypically comparable to systemic acquired resistance (SAR) [139]. It is suggested that ISR-positive plants are "primed" in order to trigger defensive systems more quickly and potently in response to pathogen assault. ISR doesn't focus on any particular infections. Instead, it could be useful in managing illnesses brought on by certain viruses. ISR is mediated by plant hormones called jasmonate and ethylene, which activate the host plant's defensive mechanisms against several pathogens [140]. The virus and the resistance-inducing PGPB do not need to interact directly for ISR to occur [141]. In addition to ethylene and jasmonate, other bacterial molecules have also been shown to function as indicators for the induction of systemic resistance. These include salicylic acid, pyoverdine, chitin, β -glucans, flagellar proteins, the O-antigenic side chain of the bacterial outer membrane protein lipopolysaccharide, and chitin.

V. REDUCING THE IMPACT OF ENVIRONMENTAL STRESS

In perfect conditions, a lot of a plant's growth and development may be seen as happening in a roughly linear form over time [65]. On the other hand, a variety of biotic and abiotic stressors might impede plant development in the field. Extremes in temperature, bright light, flooding, drought, the presence of hazardous metals and organic pollutants in the environment, radiation, wounding, insect predation, nematodes, excessive salt content, and a variety of pathogens, such as bacteria, fungus, and viruses, are some of these stressors. Plant development is thus always less than it would be in their absence as a result of these numerous diverse environmental pressures.

Throughout addition, a plant may encounter several nonlethal stressors throughout its lifetime that restrict its development until the stress is eliminated or the plant is able to modify its metabolism to withstand the stress. As a result, in real life, plant development usually consists of intervals of peak growth separated by different intensities of growth inhibition. PGPB may use any one or more of a number of distinct mechanistic techniques when they are introduced to plants in an effort to get around this growth inhibition.

5.1. Ethylene

The majority of the environmental stressors indicated above cause the formation of ethylene stress inhibitory levels. Using PGPB that contains ACC deaminase can help prevent high amounts of ethylene and the harm it causes, as was previously discussed when talking about the stress ethylene produced as a result of phytopathogen infection [142]. Extremes in temperature [143], floods [144], drought [145, 146], metals and metalloids [60, 61, 147–152], hypoxia [153], salt [154–165], and organic pollutants [150, 151, 166–168] are a few abiotic stressors whose impacts can be lessened in this way. According to the aforementioned reports from around the globe, a variety of ACC deaminase-containing PGPB can significantly protect plants from a variety of abiotic stresses. This suggests that the technology is ready for commercial application in the field and that the approach could have a big impact on agricultural practices. ACC deaminase-containing bacteria, however, are probably more likely to find their first large-scale commercial uses as parts of phytoremediation protocols, which use bacteria and plants simultaneously to remove organic contaminants and metals from the environment, given the reluctance in many jurisdictions to use bacteria in agriculture on a large scale [3, 9].

5.2. IAA

A number of findings show that some PGPB, even in the absence of ACC deaminase, can shield plants from the harmful effects of abiotic stressors. According to more recent research, PGPB may aid plants in overcoming abiotic challenges by giving them IAA, which directly promotes plant development even in the presence of substances that would otherwise hinder it [169–176].

Together with the results already stated, several other research have revealed that the bacteria that shield plants from a variety of stressors are also those that generate both ACC and IAA deaminase [65, 177–179]. Tryptophan is an amino acid that is rejected by plant roots and then taken up by PGPB attached to the roots, where it is transformed into IAA. This is one hypothesis that explains how IAA and ACC deaminase work together to promote plant development [20, 65, 178]. Together with the plant's own supply of IAA, the bacterially generated IAA is released, absorbed by plant cells, and initiates an auxin signal transduction pathway that includes a number of auxin response proteins. Plant cells multiply and grow as a result. Meanwhile, some of the IAA stimulates transcription of the gene encoding the enzyme ACC synthase, increasing the concentration of ACC and ultimately ethylene (which is catalyzed by the enzyme ACC oxidase since ACC is the direct precursor of ethylene).

Different biotic and abiotic stressors can also either promote the transcription of the ACC synthase gene or enhance the synthesis of IAA. When a bacterium with the ACC deaminase enzyme is present, some ACC may be taken up by the plant-bound PGPB and broken down into ammonia and N-ketobutyrate. As a result, an ACC deaminase-containing PGPB functions as a sink for ACC, which has the effect of reducing the amount of ethylene that the plant produces and its stress response to an environmental stress. Auxin response factor transcription is suppressed in plants with elevated ethylene levels [65, 180–182]. When bacterial ACC deaminase is absent, ethylene inhibits the transcription of auxin response factors, which in turn restricts cell development and proliferation. Furthermore, ethylene decreases IAA stimulation of ethylene production, which is crucial for plant survival. Less ethylene is produced when ACC deaminase is present. Therefore, the presence of ACC deaminase prevents the inhibition of auxin response factor transcription, allowing IAA to promote cell growth and proliferation without also contributing to the accumulation of ethylene. As a result, in the presence or absence of plant stress, ACC deaminase both reduces the ethylene-induced restriction of plant development and permits IAA to optimally enhance plant growth.

5.3. Cytokinin

Named for its capacity to stimulate plant cell division, or cytokinesis, cytokinins are substances with an adenine-like structure (Sakakibara 2006). Plants, several yeast strains, and certain soil bacteria, including PGPB, all generate them [66, 68]. Transgenic plants that overproduce cytokinins are considerably shielded against the harmful consequences of abiotic stress, particularly when such stressors occur [183]. Regrettably, no conclusive research has been done to determine if cytokinins generated by bacteria may also shield plants from abiotic stressors. This would include a thorough analysis of the biological activities of PGPB-producing cytokinin-minus mutants and cytokinin-producing PGPB.

5.4. Trehalose

Trehalose is a nonreducing disaccharide found in many forms in nature. It is a α -1,1-glucoside made up of two molecules of α -glucose. Bacteria, yeast, fungus, plants, insects, and invertebrates all contain it. Elevated trehalose levels can serve as a buffer against a variety of abiotic stressors, such as excessive salinity, drought, and temperature fluctuations. Trehalose is a very stable molecule that may form a gel phase when cells dry, replenishing water and reducing the harm caused by salt and dehydration. Trehalose is resistant to both acid and high temperatures. Trehalose can also stop some of the aggregation and degradation of proteins that frequently happen in response to stressors from hot and low temperatures. Treating plants with PGPB that have been modified to overproduce trehalose is one method of giving them resistance to drought and other stresses [184, 185]. Therefore, compared to plants inoculated with wild-type *Rhizobium etli*, plants treated with the symbiotic bacterium that had been genetically modified to overproduce trehalose had more nodules, fixed more nitrogen, had more biomass, and recovered from drought stress to a greater extent [185]. Similarly, plants treated with PGPB *Azospirillum brasilense*, which had been genetically engineered to overproduce trehalose, were shown to be more resistant to drought and to yield higher biomass than plants treated with wild-type *A. brasilense* [184]. While it is feasible to genetically modify plants such that they generate excessive amounts of trehalose, using genetically modified PGPB is a far easier way to accomplish the same goal. Furthermore, a variety of agricultural plants may be successfully protected by a single modified bacterial strain.

List of plant growth promotion rhizobacteria

PGPR	PGPR Mechanisms	Crops	Application Mode	Observation/Findings	Ref.
<i>Azoarcus</i>	Nitrogen fixation	rice	Plants were grown gnotobiotically with a mutant of strain BH72 expressing the b-glucuronidase gene constitutively.	The presence of <i>Azoarcus</i> in the stele, especially in the stelar tissue of culms, suggests that these bacteria might spread systemically <i>in situ</i> , and underline their endophytic life style.	[195]
<i>Azobacter</i>	Cytokinin synthesis	Cucumber	-	-	[196]
<i>Azorhizobium</i>	Nitrogen fixation	Wheat	2 mL of rhizobial culture were added four times to each wheat plant, once during the planting of the seeds, and subsequently three times at one-week intervals.	Five weeks after inoculation with <i>A. caulinodans</i> IRBG314, there were approximately five times more short lateral roots, each up to 3 mm in length, present on inoculated wheat.	[197]
<i>Azospirillum</i>	Nitrogen fixation	sugar cane	-	-	[198,199,200,201]
<i>Azotobacter</i>	Nitrogen fixation	Wheat, barley, oats,	-	-	[202]

PGPR	PGPR Mechanisms	Crops	Application Mode	Observation/Findings	Ref.
		rice, sunflowers, maize, line, beetroot, tobacco, tea, coffee and coconuts			
<i>Bacillus</i>	Auxin synthesis	Potato	Seed-dipping (108 mL ⁻¹ cfu)	Both the strains enhanced the auxin content of inoculated plants up to 71.4% and 433%, respectively, as compared to non-inoculated plants.	[203]
<i>Bacillus</i>	Cytokinin synthesis	Cucumber	Seed-dipping 106 cells/mL (106 CFU/mL)	Cucumber seedlings subjected to bacterization had well developed lateral roots.	[204]
<i>Bacillus</i>	Gibberelin synthesis	Pepper	-	-	[205]
<i>Bacillus</i>	Potassium solubilization	pepper, cucumber	Seedling was inoculated with 1 mL of inoculum containing around 108 cells.	The results showed that there was a relatively higher availability of P and K in soils planted with pepper than with cucumber.	[206,207]
<i>Bacillus</i>	Induction of plant stress resistance	Peanuts Maize	Plants were inoculated with 1 mL of a 108 cfu suspension Seed-dipping for 30 min	Increasing salt concentrations, biological N fixation may be competitive, becoming a more economic and sustainable alternative to chemical fertilization. The bacterial inoculants increased the total N, P, and K contents of the shoot and root of maize in calcisol soil from 16% to 85% significantly as	[208,209]

PGPR	PGPR Mechanisms	Crops	Application Mode	Observation/Findings	Ref.
				compared to the control counterpart.	
<i>Bacillus</i>	Antibiotic production	Alfalfa	Seedling was inoculated	Filtrates of cultures suppressed alfalfa disease caused by <i>P. medicaginis</i> and inhibited the growth of the pathogen in an agar plate assay.	[210]
<i>Bacillus</i>	Siderophore production	Maize, pepper	-	-	[211]
<i>Beijerinckia</i>	Nitrogen fixation	Sugar cane	-	-	[198,212]
<i>Burkholderia</i>	Nitrogen fixation	Rice	-	-	[213,214]
<i>Chryseobacterium</i>	Siderophore production	Tomato	Soil drenched	Siderophore production increased as bacterial biomass increased after 16 h of culture	[215]
<i>Frankia</i>	Nitrogen fixation	<i>Alnus</i>	-	-	[216]
<i>Gluconacetobacter</i>	Nitrogen fixation	Sugar cane	Root-dipping of seedlings for 1 h	The endophytic establishment of <i>G. diazotrophicus</i> within stems of sugarcane was confirmed by the scanning electron microscopy.	[217]
<i>Herbaspirillum</i>	Nitrogen fixation	rice	Seed was inoculated	GFP-tagged cells of <i>Herbaspirillum</i> sp. strain B501gfp1 were apparently localized in intercellular spaces of shoot tissues of 7-day-old seedlings of <i>O. officinalis</i> W0012.	[218]
<i>Mycobacterium</i>	Induction of plant stress resistance	Maize	-	-	[208]
<i>Paenibacillus</i>	Indole acetic acid	Lodgepole pine	-	-	[219]

PGPR	PGPR Mechanisms	Crops	Application Mode	Observation/Findings	Ref.
	synthesis				
<i>Paenibacillus</i>	Potassium solubilization	Black pepper	-	-	[220]
<i>Phyllobacterium</i>	Phosphate solubilization	Strawberries	The strawberry seedlings were inoculated with 1 mL of 108 CFU/mL suspensions.	Strain PEPV15 was able to solubilize moderate amounts of phosphate (5mm radius around the colonies).	[221]
<i>Phyllobacterium</i>	Siderophore production	Strawberries	The strawberry seedlings were inoculated with 1 mL of 108 CFU/mL suspensions.	The strain grew on the CAS indicator medium where the colonies were surrounded by a yellow-orange halo (3.5 mm radius around colonies) indicative of the siderophore production.	[221]
<i>Pseudomonas</i>	Chitinase and β -glucanases production	Several crops	-	-	[222]
<i>Pseudomonas</i>	ACC deaminase synthesis	Mung beans, wheat	-	-	[223,224]
<i>Pseudomonas</i>	Induction of plant stress resistance	Cotton, Maize	-	-	[208,225]
<i>Pseudomonas</i>	Antibiotic production	Wheat	-	-	[226]
<i>Pseudomonas</i>	Chitinase and β -glucanases production	Pigeon pea	The method of Weller and Cook (1983) was adopted for seed bacterization	<i>P. fluorescens</i> LPK2 and <i>S. fredii</i> KCC5 showed chitinase activity on chitinase minimal medium. b-1,3-glucanase activity was more pronounced in the fluorescent pseudomonads strains.	[227]
<i>Pseudomonas</i>	Siderophore production	Potato, maize	-	-	[211]
<i>Rhizobia</i>	Nitrogen	Legumes	-	-	[228]

PGPR	PGPR Mechanisms	Crops	Application Mode	Observation/Findings	Ref.
	fixation				
<i>Rhizobia</i>	Induction of plant stress resistance	Peanuts	-	-	[209]
<i>Rhizobia</i>	Hydrogen Cyanide Production	Legumes	-	-	[229]
<i>Rhizobium</i>	Nitrogen fixation	Rice	-	-	[230]
<i>Rhizobium</i>	Indole acetic acid synthesis	Pepper, tomato, lettuce, carrot	Seed Inoculation Seedlings were inoculated with 250 μL plant ⁻¹ of a bacterial suspension with a turbidity of 5 in McFarland standards (1.5×10^9 CFU mL ⁻¹).	The dry weight of the inoculated seedlings (shoots and roots) was more than twice with respect to the uninoculated seedlings. Concentrations of N, P, and Ca were significantly higher in inoculated plants, indicating that they had higher potential for nutrient uptake than control plants.	[231,232]
<i>Rhizobium</i>	ACC deaminase synthesis	Pepper, tomato, mung beans,	-	-	[223,231]
<i>Rhizobium</i>	Siderophore production	Tomato, pepper, Carrot, lettuce,	Seed Inoculation Seedlings were inoculated with 250 μL plant ⁻¹ of a bacterial suspension with a turbidity of 5 in McFarland standards (1.5×10^9 CFU/mL ⁻¹).	The colonies of strain TPV08 were surrounded by a yellow-orange halo (3.5 mm radius around colonies) indicative of siderophore production.	[231,232]
<i>Sinorhizobium</i>	Chitinase and β -glucanases production	Pigeon pea	-	-	[222]
<i>Sphingomonas</i>	Gibberelin synthesis	Tomato	-	-	[233]

PGPR	PGPR Mechanisms	Crops	Application Mode	Observation/Findings	Ref.
<i>Streptomyces</i>	Indole acetic acid synthesis	Indian lilac	-	-	[234]
<i>Streptomyces</i>	Siderophore production	Indian lilac	-	-	[234]

VI. CONCLUSION

The technology whose time has come is the incorporation of PGPB as a fundamental aspect of agricultural operations. Many underdeveloped nations now effectively employ these microorganisms, and it is anticipated that this practice will spread. The application of PGPB fills a little but expanding niche in the advancement of organic agriculture in the more industrialized countries, where agricultural chemicals are still comparatively affordable. Furthermore, it seems sense to anticipate seeing PGPB used in a greater number of phytoremediation techniques.

Encouragement should be provided to the application of PGPB in agriculture because of its favorable effects on biofertilization, biocontrol, and bioremediation—all of which have a positive impact on crop yield and ecosystem functioning. With luck, technology will advance to the point where successful research and development is possible. PGPB utilization will then become a reality and play a key role in the vital processes that guarantee the productivity and stability of agro-ecosystems, guiding us in the direction of the perfect agricultural system.

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