



Review

Role of Plant Growth Promoting Microbes in Plant Growth and Development

Nivethika Ajeethan ^{1,*} , Lord Abbey ¹ and Svetlana N. Yurgel ²

¹ Department of Plant, Food, and Environmental Sciences, Faculty of Agriculture, Dalhousie University, Halifax, NS B2N 5E3, Canada; labbey@dal.ca

² USDA, ARS, Grain Legume Genetics and Physiology Research Unit, Prosser, WA 99350, USA; svetlana.yurgel@usda.gov

* Correspondence: aj634155@dal.ca

Abstract

Plants are sessile organisms and are constantly subjected to varying environmental stressors. However, they can mitigate the effects of these stresses by deploying plant growth-promoting (PGP) microbes for their protection. PGP microbes can boost plant growth and enhance plant protection from biotic and abiotic stresses through a wide variety of mechanisms. PGP mechanisms such as biological fixation of nitrogen in soil and plant roots, phosphate solubilization, siderophore production, ACC (1-aminocyclopropane-1-carboxylic acid) deaminase enzyme activity, and production of plant hormones to promote nutrient acquisition and mitigate stresses. Therefore, this review aims to document studies that reported on the role of PGP microbes in plant growth and development and how PGP traits mentioned above and a novel trait flavins (FLs) secretion help plants against biotic and abiotic stress. Several important PGP functions, and the bacterial strains involved in these functions, that can potentially improve plant growth, development, and plant health are reviewed. This review will help to identify gaps for future studies and guide the development of an alternative strategy to use PGP microbes as biofertilizers and bio-control agents to support eco-friendly agriculture by reducing the indiscriminate use of synthetic agrochemicals.

Keywords: plant growth promotion; flavin secretion; phosphate solubilization; N fixation; siderophores production; ACC deaminase enzyme

1. Introduction

Global warming causes an increase in environmental stress that negatively impacts global food and nutrition security of the rising global population.

The world's population, which is currently around 8.2 billion people, has been projected to increase to around 9.7 billion by 2050, and hence the demand for food is expected to increase anywhere between 59% and 98% by 2050 [1]. Therefore, it is necessary that agricultural food production must be significantly increased within the next few years by expanding the acreage of arable land or by improving agricultural productivity on existing arable lands. Proper agricultural practices such as fertilizer and irrigation applications and adopting new methods like smart farming can help to increase crop yield with the optimization of resource use and minimal environmental impact [2]. However, excessive use of chemical fertilizer harms the environment by polluting soil, water, and air environments [3,4]. The main environmental impacts of indiscriminate usage of synthetic chemical



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fertilizers are ground water pollution by nitrate leaching, surface runoff of nitrogen (N) and phosphorous (P) nutrients leading to aquatic eutrophication, toxic heavy metal pollution, emission of greenhouse gases, and collapse of microbial diversity in soil [5–8].

The use of plant growth-promoting (PGP) microbes as biofertilizers is a promising alternative to reduce the indiscriminate use of chemical fertilizers and to support greener and sustainable agriculture. Moreover, sustainable crop production can be attained through the suppression of pathogenic microorganisms or insect pests [9,10]. Some PGP bacteria (PGPB) act as biocontrol agents, and through this mechanism they can contribute to greener sustainable agricultural production.

An effective long-term solution to provide food for the increased world population must include sustainable and eco-friendly solutions. The use of PGPB in agriculture is an attractive way to address this problem. While our knowledge related to mechanisms employed by PGPB has significantly advanced in the past two decades, in-depth understanding of the fundamental mechanisms behind these bacteria will accelerate their acceptance as suitable and effective agricultural inputs. The efforts to increase field- or commercial-level application of PGPB must start with a better understanding of mechanisms behind these PGPB and how they promote plant growth and development.

2. Role of Microorganisms in Plants

Plant-associated microorganisms play a key role in plant function by influencing their physiology and development [11]. Numerous studies have shown that these plant-associated microorganisms can have significant effects on plants from seed germination to seedling emergence, seedling establishment, and vigor and to whole plant growth and development, as well as nutritional balance, disease prevention, and productivity [12,13]. Microbes can build several types of interaction with host plants, which is a fundamental part of the ecosystem. In general, these interactions can be beneficial or harmful for the host. More specifically, depending on the circumstance, the interaction may be characterized as: (i) commensalism, where one organism benefits and the other organism is neither helped nor harmed; (ii) mutualism, where both species derive a mutual benefit; (iii) competition, where neither benefits, in which the fitness of one is lowered by the presence of another; and (iv) parasitism, where one organism benefits while one is harmed. The parasite lives on or in another living organism (the host) and causes it harm [14]. These interactions are widespread and dependent on the diversity and abundance of both the plant habitat and associated microbes. The most common interactions are commensalism or mutualism [15,16].

Plants harbor various species of microbes and provide a wide diversity of habitats including the phyllosphere (aerial part of plants), the rhizosphere (soil that is directly associated with root or influenced by root secretions), and the endosphere (internal tissues of the plant) [17]. Microbes are classified as epiphytes, rhizophytes, or endophytes, depending on their location within or on the plant [18].

The bulk soil microbial community forms the plant-associated microbiome [19,20]. Living soil is a dynamic environment that consists of a vast selection of microbes including bacteria, fungi, viruses, protozoa, archaea, actinobacteria (formerly known as actinomycetes), cyanobacteria, and microalgae [21,22]. Soil properties such as parent material (the underlying substance from which soil horizons develop), soil organic matter, pH, and soil type are the key determinants of soil microbial community composition [23,24].

Above-ground parts of the plant surfaces (phyllosphere), including leaves, stems, and flowers, are colonized by a variety of microbes, such as filamentous fungi, yeasts, bacteria, and bacteriophages [25]. These phyllospheric bacteria can be endophytic or epiphytic and pathogenic or non-pathogenic [22]. The rhizosphere is the narrow region of soil nearest the plant root system where the plant, soil, and microbes' interactions take place [26]. In

the rhizosphere, rhizophytes (bacteria and other microbes) feed on sloughed-off plant material [27]. The rhizosphere-associated microbes play a vital role in biogeochemical cycling of materials and uptake of nutrients to the plants. Endophytes are bacteria or fungi that live within host plant tissues (at least for part of their life cycle), occupying intercellular spaces, tissue cavities, or vascular bundles without harming the host and often benefiting the host. Bacterial forms generally occur in greater numbers, and many endophytic microbes have been categorized as PGPB [28]. Overall, microorganisms link soil and plant communities and connect the different ecosystems. Many microbes are beneficial to plants since they can promote plant growth and are known as plant growth promoters, while some microbes can harm plants by causing disease and are known as pathogens.

2.1. Negative Plant–Microbe Interaction (Plant Pathogens)

Many plant-associated microbes have a positive role in plant growth, development, and health, and some are pathogenic and can negatively impact plants, leading to crop loss. Disease development in a plant population is determined primarily by the interactions of three major factors such as the presence of (i) a susceptible host plant, (ii) a virulent pathogen, and (iii) a favorable environmental condition [29], commonly referred to as the disease triangle.

Pathogenic fungi, bacteria, mollicutes, protozoa, viruses, viroids, and nematodes contact a site on the plant where infection is possible and penetrate through various mechanisms [30]. Some fungi and nematodes directly penetrate intact plant surfaces, while other fungi, as well as bacteria, mollicutes, viruses, and viroids, require wounds or a vector to enter the plants tissue [31]. The mode of invasion of plant pathogens varies depending on the pathogen [32]. This causes detrimental effects to plant growth and development resulting in economic loss for the farmers. For example, specific replant disease (SRD) is one of the major challenges to orchard owners, which affects orchards and nurseries (Rosaceae family) to replanting the same species plants in a similar site [33,34]. SRD is a soil-borne disease that affects apples, commonly known as apple replant disease (ARD). ARD is caused by complex causal agents such as *Cylindrocarpon*, *Rhizoctonia*, *Phytophthora*, *Phythium*, and in some cases root lesion nematode (*Pratylenchus penetrans*), also reported as a causal agent. Meanwhile, tree roots can select beneficial microbes to prevent the development of pathogens and disease progression [35]. This microbial equilibrium helps maintain the health of fruit trees in old orchards [20].

2.2. Positive Plant–Microbe Interaction (PGP Microbes)

In their natural environments, plants serve as a refuge for many organisms, ranging from mammals and invertebrates to fungi and unicellular bacteria [36,37]. Plants exist in close and complex interactions with numerous microorganisms around, on and within them [38]. Plants provide food, protection, and habitat for microbes, and on the other hand, most microbes help the growth and development of plants and protect them from biotic and abiotic stress.

PGP microbes can enhance plant growth, development, and health by suppressing diseases through various mechanisms. Phosphate solubilization, nitrogen fixation, sulfate solubilization, immune modulation, signal transduction, siderophore production, and disease suppression are some of the mechanisms or functions facilitated by beneficial microbes to promote plant growth and protect plants from pathogenic microbes [39]. Colonization of microorganisms in plants can be influenced by several factors such as the host species, genotype, age of the plant and health status, environmental factors, farming practices, and crop protection strategies [40].

The association between beneficial fungi and plants is common in nature, and such an association helps to improve plant resilience and productivity. Diverse fungal taxonomic groups interact with plants in the phyllosphere and rhizosphere [41]. Mycorrhizal (*Glomus* sp.) and plant-beneficial endophytic fungi persist on or around host plants' root systems as hyphal networks [15]. These kinds of beneficial fungi potentially play a key role in the resistance of host plants against biotic and abiotic stresses, such as infection by pathogens, drought, and excessive salt [42]. Moreover, beneficial fungi associated with the root system can improve the disease resistance of host plants either by stimulating host immune systems [43] or by suppressing soil pathogens through antagonistic effect and antimicrobial metabolites and other chemical compounds [44]. In root systems, mycorrhizal fungi can help plants increase water absorption but also aid in the uptake and utilization of soil nutrients like phosphorus and nitrogen [45]. Therefore, mycorrhizal fungi act as a natural fertilizer factory, an economical and eco-friendly source of plant nutrients compared with synthetic chemical fertilizers. They can enhance agricultural crop production and improve soil fertility in an eco-friendly manner [46]. Likewise, some endophytic fungi have been identified as capable of converting organic sources of nitrogen into inorganic forms, which increases the availability of nitrogen to plants [47]: For example, endophytic fungus, *Phomopsis liquidambaris*, increased crop yield and root nodulation of peanut (*Arachis hypogaea*) and N₂ fixation [48].

Bacteria are omnipresent and successfully occupy all ecological niches [49]. There are many different interactions in which plants benefit either directly or indirectly from their association with bacteria. Bacteria such as *Streptomyces* sp. are active producers of volatile compounds and antibiotics, which have antimicrobial properties and are used as biocontrol agents [46]. Bacteria play a vital role in nutrient uptake in plants. Bacteria enhance nitrogen fixation, phosphorus solubilization, potassium mobilization, siderophores production, plant hormones production, and the production of the enzyme ACC deaminase, which helps to reduce environmental stress on plants (Figure 1) [50,51].

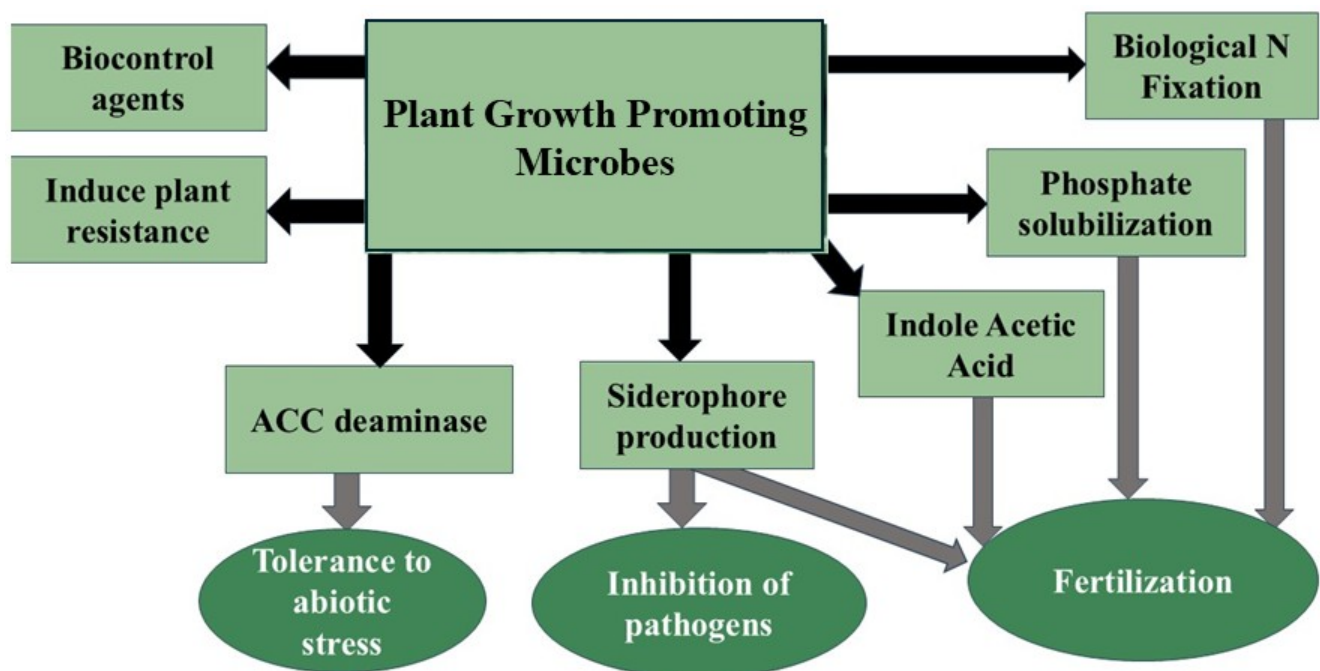


Figure 1. Schematic diagram represents the different plant growth-promoting (PGP) mechanisms and PGP traits of PGP microbes.

3. Importance of the PGP Microbes in Plant Growth and Development

The beneficial interactions between plants and PGP microbes can be either through direct or indirect mechanisms such as nutrient transfer performed by phosphate solubilizing or N-fixing bacteria to provide plants with nutrients. Direct stimulation of growth by bacteria through production of phytohormones, antagonistic activity towards pathogenic microbes, and mitigation of stresses are some other traits of PGP microbes (Figure 1). Therefore, understanding the PGP microbes and plant interaction is an important component in recognizing the role of PGP microbes in greener sustainable agriculture.

3.1. Supporting Plant Growth Under Biotic Stress

3.1.1. Protecting Plants from Pests and Phytopathogens

Conventionally, the management of pests and diseases in agriculture comprised intensive use of synthetic chemical pesticides, leading to pathogen resistance due to persistence application over long time, in addition to increase production costs and serious harmful impacts to the environment and human health [52]. An alternative of crop protection against pests and diseases is biological control using microbes [53]. Fungi, bacteria, viruses, and protozoa can also act as plant protectors, as some of the microbes are parasitic or pathogenic to insects or other organisms that can act as pests or cause disease in plants.

Entomopathogens are microorganisms that are pathogenic to insects, mites, and ticks. The most widely used bacterial insect control agents belong to the genus *Bacillus* and entomopathogenic fungal species; *Beauveria bassiana*, *Verticillium lecanii*, and *Metarhizium anisopliae* are common natural enemies to agricultural pests and cause significant epizootics in aphids [54,55]. These microorganisms are used in the biological control of pests due to their natural insecticidal property.

PGP microbes can induce systemic resistance (ISR) and suppress the growth and fitness of phytopathogens [56]. Certain bacteria, fungi, and nematodes exhibit antagonistic properties and are gaining attention as an alternative for the management of plant diseases with minimal environmental impact and soil pollution. These types of biocontrol of phytopathogens could be possible through antagonism, predation and parasitism, competition, signal interference, induced systemic resistance (ISR), and competition for ferric iron ions, nutrients, and ecological niches [57,58].

3.1.2. Induced Systemic Resistance (ISR)

Induced resistance in plants exists in two ways, namely systemic acquired resistance (SAR) and induced systemic resistance (ISR). In both cases, plant defenses are activated by prior infection or treatment, resulting in increased resistance against the following challenge by a pathogen or parasite. SAR is an enhanced resistance mechanism that accrues after a plant has been infected by a pathogen, enabling it to effectively resist further attack by the same and even different pathogens or, in some cases, insects [59,60]. Depending on the type of plant and the nature of the elicitors, a specific period is required for SAR to be established. During this time, signal molecules like salicylic acid (SA) accumulate, along with pathogenesis-related (PR) proteins [10]. ISR, on the other hand, is a resistant mechanism triggered by PGPB, which stimulates root responses that enhance the plant's defensive capacity against future pathogen infections [61]. Unlike SAR, ISR does not involve the accumulation of SA, but instead, it relies on pathways regulated by jasmonate (JA) and ethylene (ET) [62]. ISR provides protection against soil-borne pathogens and stimulates defenses in the phyllosphere against foliar phytopathogens.

Many studies have shown that PGPBs have the ability to reduce the activity of pathogenic microbes via ISR in the host plant such as bean (*Phaseolus vulgaris*), sugarcane (*Saccharum officinarum*), carnation (*Dianthus caryophyllus*), cucumber (*Cucumis sativus*), rice

(*Oryza sativa*) radish (*Raphanus sativus*), tobacco (*Nicotiana tabacum*), and tomato (*Solanum lycopersicum*) [63–66]. Many PGPB strains such as *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Klebsiella*, and *Paenibacillus* showed ISR of plants against biotic stress [67–70]. ISR responses in plants can be stimulated by volatile organic compounds produced by PGPB [71]. Moreover, different kinds of active molecules like siderophores, cyclic lipopeptides, and bacterial quorum-sensing molecules can provoke the ISR responses of plants by activating JA-/ET-dependent signaling pathways [72,73]. For example, PGPB emitted volatile organic compounds such as acetoin and 2,3-butanediol that induce ISR against pathogens [74]. These properties make ISR-inducing PGPB an effective tool to reduce pathogen or pest attacks that are sensitive to the JA- and ET-dependent signaling pathway. Furthermore, the presence of ISR and SAR can increase protection to plants against a broader spectrum of pathogens than ISR or SAR alone, which are resisted through both mechanisms. Therefore, the biological application of PGPB is an alternative strategy in plant protection when other ways of crop protection are limited or not available, and ISR is one of the mechanisms that may act against plant pathogens in an eco-friendly and durable way.

3.2. Supporting Plant Growth Under Abiotic Stress

Beneficial plant–microbe interactions are vital to plant health, productivity, and soil fertility. PGPB can enhance plant growth and development and protect plants from abiotic stress through the facilitation of resources from the atmosphere and soil by different mechanisms, the production of specific compounds, and support of the plant in minimizing or preventing the adverse effects of environmental changes [75].

PGP microbes support plants by inducing physiological, biochemical, and molecular responses against abiotic stresses. Under drought stress, PGP microbes produce dehydrin proteins, which act as protective biomolecules. They also regulate aquaporin proteins, located in the membranes of root cells, which facilitate water absorption from soil [76]. In addition, the production and regulation of osmolytes, plant hormones, exopolysaccharides, and antioxidants by PGPB contribute to the mitigation of drought and salt stress. PGP microbes can also perform bioleaching or immobilization of heavy metals to reduce the harmful effect of heavy metal stress on plants [77]. During sugar metabolism, these microbes produce organic acids that can bind (chelate) heavy metals, lessening their toxicity to plants [78,79]. Several important bacterial traits, such as phosphate solubilization, biological nitrogen fixation, ACC (1-aminocyclopropane-1-carboxylic acid) deaminase activity, siderophores production, and phytohormone regulation, play a crucial role in enhancing plant tolerance to abiotic stresses [51,80–82].

3.2.1. Nitrogen Fixation

All living organisms require nitrogen (N) to produce biomolecules. For plants, N is a macronutrient vital for the synthesis of chlorophyll, enzymes, amino acids, DNA, and RNA. Nitrogen gas (N₂) is common on earth: it comprises about 78.1% of the molecules in air. N₂ is a very stable molecule because it contains a strong triple bond, which requires a huge amount of energy to break. Consequently, despite its abundance, N₂ is not directly available to most organisms, including eukaryotes. Plants can absorb N in the form of ammonia or nitrate salts. However, plant growth and development can be negatively affected by both N deficiency and excess. N is highly susceptible to loss and often remains unavailable to plants [83], which is why large amounts of nitrogen are supplied through industrial fertilizers. However, production and use of N-based fertilizers are expensive and costly to the environment. The indiscriminate use of these fertilizers can have a negative impact on soil health and water resources due to the run-off (leaching) of excess N. The nitrate

leached from agriculture land can cause acidification of water resources and eutrophication. Eutrophication is a process where a body of water becomes excessively enriched with minerals and nutrients, which induce excessive growth of algae. Massive growth of algae can reduce dissolved oxygen in water bodies that leads to high biological oxygen demand (BOD) level [84].

Biological nitrogen fixation (BNF) is the best approach for the conversion of N_2 to ammonia (NH_3) [85,86]. Prokaryotes occurring as free-living organisms or in symbiosis with plants are involved in BNF for the conversion of atmospheric N_2 into ammonia, which is easily accessible to plants. They perform BNF through enzyme nitrogenase, which is a highly conserved enzyme. The enzyme nitrogenase initiates the reaction with a large quantity of adenosine triphosphate (ATP) and uses a collection of metal ions to accomplish this reaction in nitrogen-fixing bacteria. Nitrogenase contains an atom of molybdenum at its core that is crucial for the reaction [87]. Diazotrophs cannot efficiently fix atmospheric nitrogen when soils are deficient in molybdenum. Symbiotic N-fixing bacteria such as *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium*, and *Allorhizobium* fix N with the symbiotic relationship with the legume root nodule [75]. However free-living bacteria such as *Azospirillum*, *Azotobacter*, *Burkholderia*, *Herbaspirillum*, *Bacillus*, and *Paenibacillus* can also fix nitrogen from the atmosphere for plant use [82].

3.2.2. Phosphate Solubilization

Like N, phosphorus (P) is also one of the vital elements for plant growth and development. P is an essential component of nucleic acids, phospholipids, and ATP and an important element of metabolic and biochemical pathways [88,89]. Like N, P is abundant in soils in both inorganic (primarily in the form of insoluble mineral complexes) and organic forms (incorporated into biomass or soil organic matter) [90]. In soil, phosphates are combined with some cations such as calcium, iron, and aluminum. The reaction between these cations and phosphate ions tends to produce precipitation, and it leads to phosphates becoming inaccessible to plant root uptake [91]. Plants are only capable of absorbing soluble forms of phosphates (mono-, and dibasic-phosphates) [92]. It is a major implication factor for plant growth and productivity. The solubility of P determines its availability to plants, which could be changed by the activity of plant roots and microbes in the soil.

Phosphate solubilizing bacteria (PSB) can resolve this issue of P solubilization through the (i) release of mineral-dissolving compounds like organic acid secretion by sugar metabolism, and organic acids produced by PSB can chelate divalent cations to facilitate the release of phosphates as soluble forms; (ii) release of extracellular enzymes, phytases, and phosphatases, capable of hydrolyzing phytic acid and which also helps in phytate mineralization; and (iii) the release of P during substrate degradation.

Inorganic P solubilization by PSB is possible mainly through organic acid production [93,94]. However, the other mechanisms are the production of H_2S , the release of protons originating from NH_4^+ assimilation, and inorganic acid production [95]. The organic P solubilization process is called mineralization of organic phosphorus. Mineralization of soil organic P is a key mechanism to help P uptake by plants. P from organic sources can be released in soil by enzymatic activities. Phosphatases, phytases, phosphonatases, and C-P lyases are the most abundant and best studied enzymes, which specifically cause the release of P from organic sources [95]. PSB solubilizes inorganic soil phosphates such as $Ca_3(PO_4)_2$, $FePO_4$, and $AlPO_4$ [95–97] into an available form for plant root uptake. Some bacteria solubilize all forms of phosphates while others solubilize more of calcium phosphate [98]. Earlier studies have shown that bacteria belonging to the taxonomy such as *Pseudomonas*, *Rhizobium*, *Achromobacter*, *Streptomyces*, *Agrobacterium*, *Nitrosomonas*, *Enterobacter*, *Escherichia*, *Xanthomonas*, *Flavobacterium*, *Mycobacterium*, *Erwinia*, *Bacillus*, and *Serratia*

are competent PSB that solubilize complex phosphates into plant-available forms [81]. A study showed that 15% of the 40 isolates had P solubilization capacity [99]. Ughamba et al., 2025 alluded that among the total soil microbial population, 1 to 50% of the population is PSB [100].

3.2.3. Siderophores Production

Iron (Fe) is a micronutrient essential for microbes and plants [101]. Fe plays a key role in the synthesis of chlorophyll and in other enzymatic and metabolic processes. Its bioavailability in soil is largely dependent on pH and redox conditions [102]. In soils that are aerobic or of higher pH, Fe is readily oxidized, predominantly in the form of insoluble ferric oxides (Fe^{3+}). Fe^{3+} is not available to consume by living organisms because it is very difficult to dissolve. Due to this reason, Fe bioavailability is a major restricted factor for living things [103]. Microbes have developed active strategies for Fe uptake, which includes the production of siderophores—introduced from a Greek word meaning “iron carrier”. Siderophores are low-molecular-weight molecules in the limit of approximately 400–1500 Da. They have higher attraction for Fe-chelating compounds that are produced by organisms to solubilize Fe^{3+} for uptake from organic or inorganic complexes present in soil [104]. In order to solubilize and make them an available ferric form, many microbes synthesize siderophores [105].

In phytopathogens (bacterial and fungal) control, one of the strategies is biological control, where the competition for Fe nutrition is one of the mechanisms, because most microbes need Fe as a nutrient for growth and development [106]. Some studies have shown that plant pathogens such as fungi and bacterial growth and multiplication were inhibited by some siderophore-producing PGP microbes. The chelating property of siderophores is reducing the Fe availability to other competing microbes and thus negatively affecting pathogenic microbial growth [107]. Based on iron-coordinating functional groups and structural features, siderophores are classified into four different groups such as hydroxamate, catecholate, carboxylates, or mixed [108,109]. The hydroximates type of siderophores are produced by both fungi and bacteria, carboxylates are produced by only a few bacteria (*Staphylococcus* sp. *Rhizobium* sp.), catecholates are produced by bacteria, and fungi belong to Mucorales, while mixed types of siderophores are produced by *Fluorescent pseudomonads*. Siderophores production is neither directly linked to PGP nor to plant protection; rather, they are engaged in the available Fe in soil and in the interaction between plants and microbes in their habitat.

3.2.4. Bacterial ACC Deaminase Enzyme Activity

The hormone ethylene (ET), which is the first identified plant hormone found in all higher plants, is an important regulator of numerous processes in plant growth and development and in plant responses to stress [110]. Plant hormone ET is involved in various aspects of the growth of plant tissues (stems, roots, leaves, flowers, and fruits), and the level of ET is influencing plant developmental process in all stages [111]. ET is well known for its fruit ripening ability.

However, abiotic stresses such as salinity, drought, flooding, cold, heat, heavy metals, and nutrient deficiency as well as biotic stresses like pests and pathogens attack led to an increase in the level of ET from ACC. ACC is secreted by plants as root exudates, which is the immediate precursor of ET [112–114]. This increased level of ET production in plants causes a significant implication in the plant growth and developmental process, and in some cases, it could lead to plant death [115,116]. The key process utilized by PGPB to mitigate stress includes reducing stress ET through conversion of ACC by the ACC deaminase enzyme via hydrolyzation [117]. ACC deaminase is the controller for the

cleavage of ACC into ketobutyrate and ammonia [117]. ACC deaminase-producing PGP organisms are reducing the existence of the immediate precursor of ET (ACC) in plants and lowering the stress ET levels [51] to protect plants from plant growth inhibition or death.

3.2.5. Effect of Bacterial Phytohormone

Indole-3-acetic acid (IAA) is one of the naturally occurring plant growth hormones produced by plants and microbes including bacteria and fungi. IAA plays an important part in plant growth, productivity, and their defense mechanism [118]. In plants, it plays a major function in roots and buds for cell division and elongation, tissue differentiation, fruit development, and senescence. IAA is essential for initiation of roots (primary and lateral), leaves and flowers [119]. Moreover, IAA also regulates plants to respond to light effectively as a signal to reduce shade avoidance syndrome by raising leaves towards the sunlight via apical dominance in plants. Shade avoidance syndrome studies in plants showed that efficient production of IAA in plants improved plant growth compared with deficient IAA-producing plants because IAA-deficient plants lost the ability to avoid shade and accordingly showed symptoms like stunted growth [120]. Plants are associated with many beneficial IAA-producing bacteria such as *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Azospirillum*, *Escherichia*, *Azotobacter*, *Micrococcus*, *Klebsiella*, *Streptomyces*, and *Bradyrhizobium* [121,122]. A study showed that endophytic bacteria *Enterobacter cloacae* (A9G) and *Bacillus* sp. (AMP2) produced considerable amounts of IAA (114 µg/mL and 16 µg/mL, respectively) [123]. Similarly, another study found that *Enterobacter hormaechei* (VR2; 246 µg/mL) and *Bacillus aryabhattai* (MG9; 195.5 µg/mL) produced higher amounts of IAA [124]. Bacterial-derived IAA increases the number, length, and surface area of lateral and primary roots and stimulates root hair development with an optimum level of IAA concentration. Although, a higher concentration of IAA might cause primary root growth inhibition [125].

Many PGPB produce plant growth hormones like cytokinins and gibberellins [66,122,126], but the functions of bacteria-derived hormones in plants, and mechanism of synthesis in bacteria, are not well studied [127]. *Azotobacter*, *Pseudomonas*, and *Bacillus* can produce cytokinin. PGPB-derived gibberellins can help break flowering dormancy and flowering initiation [92,128] and play key roles to enhance shoot growth and spurring germination processes [128]. PGPB-derived cytokinins and auxins together help to enhance root and shoot growth.

3.2.6. Flavin Secretion

Flavins (FLs) are a diverse group of prosthetic compounds involved in various oxidation-reduction (redox) reactions [129]. The flavin group includes riboflavin (RF), flavin mononucleotide (FMN), and flavin adenine dinucleotide (FAD) (Figure 2). RF, also known as vitamin B2, is a 7,8-dimethyl-10-ribitylisoalloxazine compound (Figure 2). It plays a critical role in oxidative metabolism and is essential to all organisms. RF serves as a precursor to the co-enzymes FMN and FAD, both of which are required in various metabolic pathways to redox reactions mediated by flavoproteins [130,131]. RF can be enzymatically or photochemically converted into lumichrome [132], a compound shown to enhance plant growth and development [133].

FLs (RF, FMN, and FAD) are synthesized only by bacteria, fungi, and green plants, but not in humans [134]. Therefore, humans must obtain RF from dietary sources such as milk, cereals, grain, eggs, and green vegetables [135]. FL is vital to all forms of life, as flavoproteins are involved in numerous essential biological processes, including both aerobic and anaerobic metabolism, photosynthesis, bioluminescence, energy production, plant phototropism, protein folding, detoxification, and various biosynthetic pathways [136].

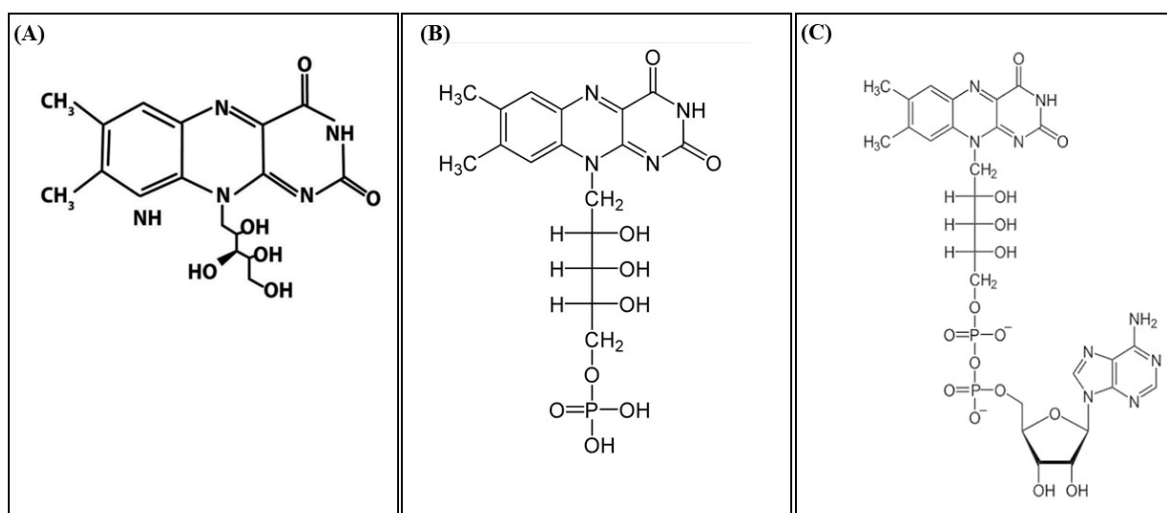


Figure 2. Chemical structure of flavins molecules such as (A) riboflavin (RF); (B) flavin mononucleotide (FMN); and (C) flavin adenine dinucleotide (FAD).

Interestingly, some bacteria have the capability to secrete FLs. For example, FLs are secreted primarily by *Rhizobium* sp., *Shewanella*, and certain methanotrophic bacteria like *Methylocystis* species. Notably, *Sinorhizobium meliloti* strain 1021 secretes a considerable amount of FLs [137,138]. Rhizobia are plant symbionts that provide numerous benefits to both legumes and non-legume plants. Several studies have demonstrated their PGP effect on various plants. For example, *Rhizobia*-associated PGP effects have been observed in rice [139,140], barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*) [141,142], lettuce (*Lactuca sativa*) [143], pepper (*Capsicum annuum*) [144], tomato [144], and sunflower (*Helianthus annuus*) [145].

The specific role of bacteria-derived FLs was studied when an *S. meliloti* 1021 mutant with decreased FL secretion was shown to be less competitive in nodulation [137]. In our recent study, we demonstrated that inoculation with the wild-type strain (secreting higher levels of FLs), compared with the mutant strain 1021, significantly improved plant growth, photosynthetic rate, and phytochemical properties such as chlorophylls *a* and *b*, total carotenoids, total phenolics content, and total flavonoids in lettuce and kale (*Brassica oleracea* var. *acephala*) [146].

4. Introducing PGP Microbes to Soil

Soil resident microorganisms are a component of the soil ecosystem and play many important roles by driving key biogeochemical cycles and improving soil structure and promoting plant growth [147,148]. The introduction of PGP microbes into the soil is currently a common practice; it is used to clean up polluted soil, suppress soil-borne or some plant diseases, promote plant growth, and restore biodiversity [149]. PGP microbes potentially induce shifts in native microbial composition, structure, and function through their synergistic or antagonistic effects on native microbial population, which can be either temporary or transient [150–152]. However, the PGP microbes can stably establish themselves within the native microbiome and alter the microbial community composition [149,153–155]. The efficiency of the PGP microbes in field applications depends on successful survival and colonization. The persistence of PGP microbes in soil is closely associated with microbial competition with native microbes, survival in the soil amidst changing environmental factors, and cell–cell communication via quorum sensing [149,156–160].

5. Application of Molecular-Based Tools for Plant–Microbe Interactions

Plants growing in soil build a close relationship with soil microorganisms. Those microbiomes either support or negatively affect plant health, acting as beneficial symbionts or as pathogens. Soil and root microbiomes represent genetically diverse ecosystems containing complex assemblages of bacteria, archaea, and eukaryotic taxa [161]. To understand and characterize both cultivable and uncultivable communities of microbiomes, the application of molecular-based tools is essential. Metagenomics studies allow for the identification of novel genes, proteins, and even complete genomes of both cultivable and uncultivable microbes with greater accuracy than traditional methods. Advances in metagenomics have improved our understanding of microbial diversity, abundance, and the interactions among microbes within various ecosystems [162,163].

There are two types of metagenomics analysis, namely shotgun metagenomics and marker gene amplicon metagenomics, i.e., 16S/18S rRNA genes and fungal ITS region genes [162,164–166]. Shotgun metagenomics provides more detailed and comprehensive information. However, it is more expensive and resource-intensive [164]. In contrast, marker gene amplicon metagenomics focuses on specific taxonomic markers to characterize the microbial population. Amplicon-based sequencing offers high coverage, enables targeted resequencing, provides flexibility, and reduces sequencing costs and turnaround time [165,166]. The choice between these two approaches depends on the specific objective of the study.

The data obtained from amplicon-based sequencing requires the use of bioinformatic tools to interpret or derive a taxonomic overview of the microbial community [166–168]. Several bioinformatic tools are available to analyze sequence data from 16S rRNA, 18S rRNA, and fungal ITS genes. These include QIIME2 (Quantitative Insights into Microbial Ecology) [169], METAGENassist [170], mothur [171], and MG-RAST (Metagenomics—Rapid Annotation using Subsystems Technology, Argonne National Laboratory, Argonne, Illinois, US) [172]. Among these tools, QIIME (and its updated version, QIIME2) is widely considered the “gold standard” for analyzing amplicon-based microbial community data [173,174]. QIIME2 is a comprehensive bioinformatic pipeline specifically designed to analyze microbial communities using amplicon sequencing. It allows users to process raw sequence data into a range of outputs such as taxonomic bar plots, phylogenetic trees, principal coordinates analyses, and other visualizations of microbial diversity.

Multi-omics synergy will also open up a new direction to study the insights into PGP mechanisms. The use of multi-omic synergy helps to understand in-depth the functional genes related to all PGP functions such as ACC deaminase enzyme activity, phosphate solubilization, nitrogen fixation, and siderophores production. The combined analysis of different “omic” datasets technology can be used to analyze genes that are significantly up- or downregulated by these PGPM in different environments [175,176]. Combined transcriptome and metabolome analyses expose functional genes, clarify the functions of transcription factors, and ultimately screen for functional genes that determine the mechanisms of each PGP function governing metabolites [175,177]. Ding et al. [178] used multi-omic synergy to investigate the mechanism of PSB [178]. Additionally, a multi-omics strategy was used to uncover host–pathogen interactions [179]. These outputs provide powerful tools to study the plant–microbe interaction using a modern, data-driven approach [166,180,181].

6. Conclusions

In recent years, there has been an increasing demand for greener and more sustainable agricultural production systems to reduce the indiscriminate use of synthetic agrochemicals, i.e., pesticides, fertilizers and growth promoters, for soil and environmental sustainability.

It is a timely need to explore alternative approaches to develop new technology that enhances the health and productivity of agriculturally important plants particularly through the association with beneficial PGP microbes. This review highlights that PGP microbes are indispensable microbes with unique abilities to support the well-being of plants directly and indirectly through various mechanisms. Overall, PGP microbes play a pivotal role in achieving sustainable plant production, especially under the rising stressful conditions attributable to abiotic and biotic stresses imposed by global climate change and unsustainable farm management practices. Looking ahead, further research into the molecular mechanisms underlying the PGP functions of microorganisms is essential for a deeper understanding and broader application in agriculture.

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Abbreviations

The following abbreviations are used in this manuscript:

ACC	1-aminocyclopropane-1-carboxylic acid
BNF	Biological nitrogen fixation
BOD	Biological oxygen demand
CO ₂	Carbon dioxide
DNA	Deoxyribonucleic acid
ET	Ethylene
FADs	Flavin adenine dinucleotides
FLs	Flavins
FL+	<i>S. meliloti</i> 1021
FL−	1021ΔribBA
FMNs	Flavin mononucleotides
GTP	Guanosine triphosphate
IAA	Indole-3-acetic acid
N	Nitrogen
N ₂	di-Nitrogen
NO ₃ −	Nitrate
OTUs	Operational taxonomical unit
P	Phosphorus
PGP	Plant growth promoting
PGPB	Plant growth-promoting bacteria
PICRUSt	Phylogenetic investigation of communities by reconstruction of unobserved states
PSB	Phosphate solubilizing bacteria
RF	Riboflavin
RibBA	3,4-Dihydroxy-2-butanone 4-phosphate synthase; GTP cyclohydrolase II
RNA	Ribonucleic acid
rRNA	Ribosomal ribonucleic acid
STAMP	Statistical analysis of taxonomic and functional profiles

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