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Review

Plant Growth-Promoting Bacteria (PGPB) with Biofilm-Forming Ability: A Multifaceted Agent for Sustainable Agriculture

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Abstract: Plant growth-promoting bacteria (PGPB) enhance plant growth, as well as protect plants from several biotic and abiotic stresses through a variety of mechanisms. Therefore, the exploitation of PGPB in agriculture is feasible as it offers sustainable and eco-friendly approaches to maintaining soil health while increasing crop productivity. The vital key of PGPB application in agriculture is its effectiveness in colonizing plant roots and the phyllosphere, and in developing a protective umbrella through the formation of microcolonies and biofilms. Biofilms offer several benefits to PGPB, such as enhancing resistance to adverse environmental conditions, protecting against pathogens, improving the acquisition of nutrients released in the plant environment, and facilitating beneficial bacteria–plant interactions. Therefore, bacterial biofilms can successfully compete with other microorganisms found on plant surfaces. In addition, plant-associated PGPB biofilms are capable of protecting colonization sites, cycling nutrients, enhancing pathogen defenses, and increasing tolerance to abiotic stresses, thereby increasing agricultural productivity and crop yields. This review highlights the role of biofilms in bacterial colonization of plant surfaces and the strategies used by biofilm-forming PGPB. Moreover, the factors influencing PGPB biofilm formation at plant root and shoot interfaces are critically discussed. This will pave the role of PGPB biofilms in developing bacterial formulations and addressing the challenges related to their efficacy and competence in agriculture for sustainability.

Keywords: abiotic stresses; biofertilizer; biofilm; biocontrol; plant growth-promoting bacteria

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1. Introduction

Elevating food production to feed a growing population, which is projected to increase to 9.15 billion in 2050, under exacerbated climate change is one of the greatest challenges facing the agricultural sector [1]. Intensive use of agrochemicals such as fertilizers and pesticides has successfully increased yield of crop production [2,3]. However, the increase in agricultural production is not proportional to the increase in the mentioned input [4,5]. Moreover, the long-term application of agrochemicals causes water-holding capacity depletion, soil fertility reduction, and disparity in soil nutrients [6–10]. Therefore, this leads to undesirable problems such as increasing pollution, land degradation, depletion of natural resources, loss of biodiversity, and rising production costs [3,10].

Widespread adoption of sustainable agricultural practices is urgently needed to address soil health degradation due to injudicious application of chemical inputs and loss of soil microbial diversity. Such practices ensure an integrated system of crop and livestock production in the long term by producing sufficient quantities of high-quality food, minimizing waste and environmental impacts, and using nonrenewable resources efficiently and profitably [11,12]. This environmentally friendly approach has recently gained considerable attention. The application of sustainable agriculture can help preserve ecosystems,

promote economic stability of farms, and improve the quality of life of farmers [10]. For these reasons, the focus of a sustainable agriculture must be on balancing social, economic, and ecological goals while managing limited resources [3,13].

Soil is not only an essential tool for crop production, but also a complex living medium [14,15], which must be considered holistically. Soil maintains biological productivity, supports the quality of the air and water environment, and sustains the health of plants, animals, and humans [16]. Therefore, healthy soil must be protected and conserved to ensure long-term productivity and stability [17]. Microorganisms, as biological components of soil, are important key players in nutrient cycling, organic matter decomposition, and soil structure maintenance [18]. Hence, they are widely known as "natural soil engineers" [19] and can be an eco-friendly alternative to maintain soil health and improve crop productivity.

Among the plant-associated microbial communities in soil, PGPB can be formulated as biobased organic biofertilizers and biopesticides due to their ability to maintain a nutrient rich soil environment, improve abiotic stress tolerance, and act as antagonists against various pathogens [2]. Moreover, the use of PGPB in agriculture has no negative impact on the ecosystem, ensures food safety, and creates sustainable crop production [12].

This review highlights the importance of biofilm formation as an essential component of plant–PGPB interactions. Understanding the process, mechanisms, and factors influencing biofilm formation by PGPB will lead to its applications and innovative future prospects.

2. PGPB as Multipotent Bioagents

The rhizosphere can be divided into three zones: the endorhizosphere is the interior of the root, the rhizoplane is the surface of the root, and the ectorhizosphere is the zone that extends from the rhizoplane to the bulk soil and consists of soil that adheres to the root [20,21], in addition to the volume of soil that is not part of the rhizosphere and is not influenced by the root is referred to as bulk soil [22]. Plant growth-promoting bacteria are able to colonize plants through different types of plant–microbe interactions and forming associations on root and shoot surfaces as complex, interactive microbial communities [23,24]. These beneficial bacteria can make an important contribution to numerous ecological processes in the soil, including nutrient transformation and fixation, organic matter decomposition, and mitigation of abiotic and biotic stresses [25,26]. Soil in the rhizosphere surrounding plant roots has a microbial population 100 to 1000 times higher than the rest of the soil, which is influenced by substances excreted by the plant roots [21,27]. PGPB colonizing the rhizospheric region interact with other taxa such as fungi, protozoa, nematodes, and plant viruses.

Roots release mainly high-molecular-weight compounds such as enzymes, proteins, and polysaccharides from the root tips, which are called root exudates. This mixture, which consists of polysaccharide-rich secretions, often forms a sheath of slime on the outer surface of the root called mucilage [28]. Other substances such as sugars, amino acids, hormones, vitamins, phenolics, and other secondary metabolites in the form of low-molecular-weight components are also secreted [29]. These various compounds can enrich the rhizosphere with nutrients, make the environment more comfortable for microorganisms, and help maintain stable soil aggregates [6,30]. In addition, the release of compounds by plant roots that affect the physical and chemical properties of the rhizosphere can attract beneficial microbes in the soil, enriching the microbial community [31].

PGPB play an essential role in regulating soil fertility, nutrient cycling, and promoting plant growth [32]. The major regions where plant–microbe interactions occur include the surface and apoplast of leaf tissue (phyllosphere), the rhizosphere, the inner regions of plant tissue (endosphere), and the bulk soil [33]. The microorganisms that originate from the seed are the first to colonize plants. This seed-derived microbiota is eventually supplemented and partially replaced by rhizosphere microbes that enter the plant through the roots. Partnerships between plants and microbes can vary in intricacy. The plant responds to the presence of a microbe and its metabolites; vice versa, the microbe is affected

by the plant environment and reacts to plant metabolism and physiology. Plant exudates attract microbes in the soil toward the root zone. In turn, plant development and health are significantly impacted by the microbiota's activities in the root zone (Figure 1).

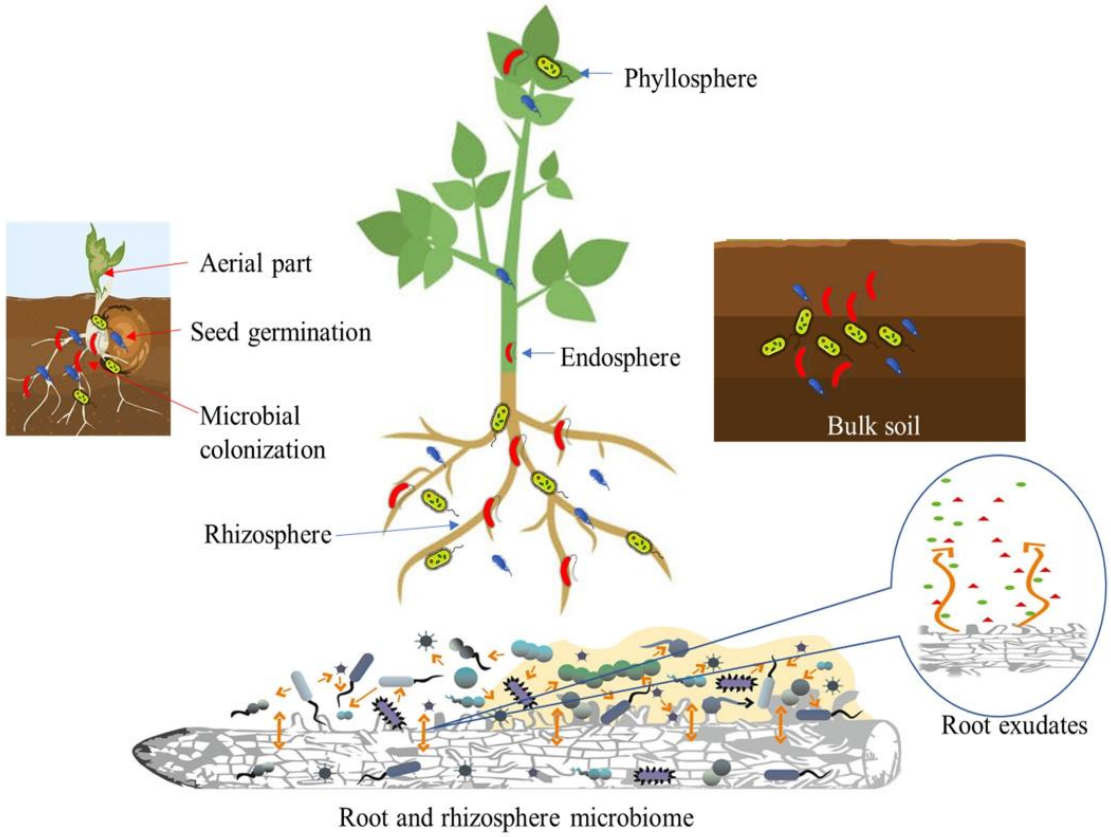

Figure 1. Plant–microbe interaction: regions involved in the development of plant microbiome.

PGPB generally support plant growth through two types of mechanisms: direct and indirect (Figure 2). The direct mechanisms relate to increasing nutrient availability and phytohormone production. Indirect mechanisms of PGPB, on the other hand, include inhibiting various pathogens or preventing negative effects on plant health. Increasing nutrient availability in the soil can occur through various processes such as nitrogen fixation, solubilization of mineral nutrients, and mineralization of organic compounds [27,32,34,35]. One of the limiting and most important factors in agriculture is the supply of plant nutrients, especially nitrogen, phosphorus, and potassium [27]. Nitrogen fixation is considered an essential trait of PGPB to provide nitrogen through symbiotic and nonsymbiotic mechanisms [27,32]. Phosphate solubilization of mineral forms is possible through secretion of organic acid, release of protons, or production of chelating substances [36]. In contrast, mineralization of organic phosphorus occurs through the synthesis of phosphomonoesterase, phosphodiesterase, and phosphotriesterase, which catalyze the hydrolysis of the phosphoric ester [37]. Potassium in soil is usually deficient as it could be in the form of insoluble stones or silicate minerals [20,38]. Furthermore, phytohormone-producing PGPB can stimulate plant growth and development stages, such as cell elongation, cell division, root development, root hair formation, shoot initiation, and tissue differentiation by providing and regulating various plant hormones, including gibberellins (GAs), cytokinins, abscisic acid (ABA), ethylene, and indole-3-acetic acid (IAA) [39,40].

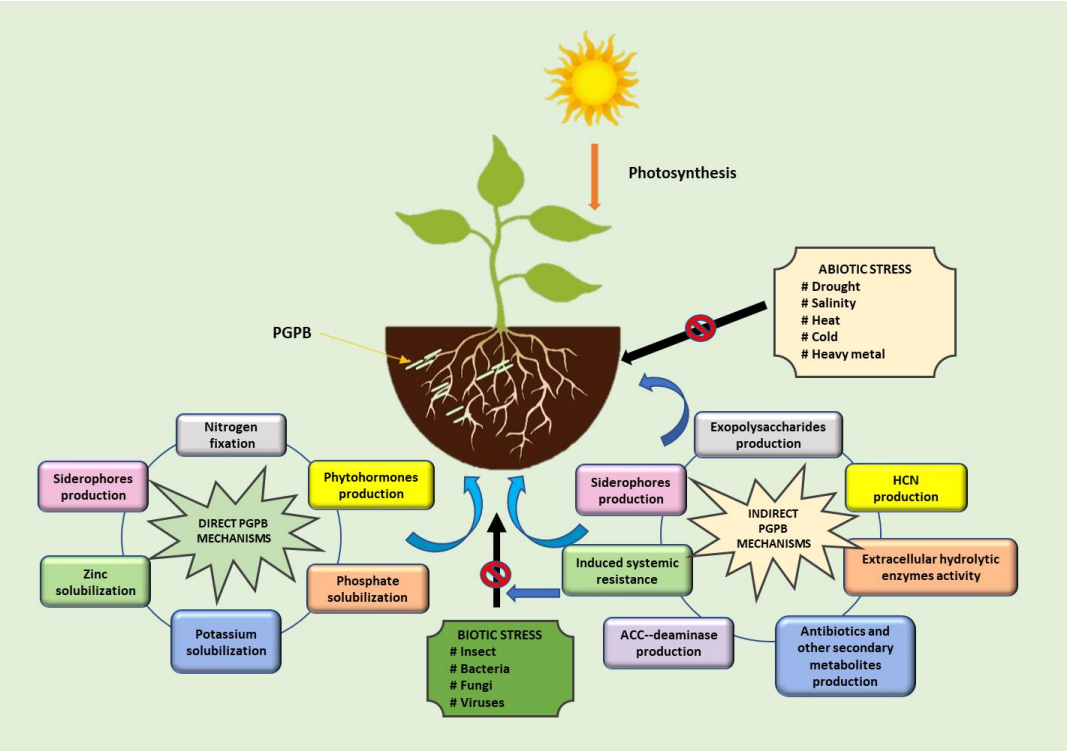

Figure 2. Direct and indirect mechanisms of PGPB to support the plant development.

PGPB can produce various metabolites, such as antibiotics, siderophores, volatile organic compounds (VOCs), hydrolytic enzymes, hydrogen cyanide (HCN), and 1-aminocyclopropane-1-carboxylic acid deaminase (ACC deaminase), that reduce or prevent pathogenic diseases and protect against environmental stress [35,41–43]. Synthesis of antibiotics, which are low-molecular-weight and toxic organic compounds, is a strategy that microorganisms use to compete with other microorganisms. Different microorganisms have the ability to produce different antibiotics. *Bacillus* can produce several antibiotics such as iturins, mycosubtilin, bacillomycin D, surfactin, fengycin, and zwittermicin A [44]. On the other hand, *Pseudomonas protegens* FD6 produces a variety of antibiotics including 2,4-diacetylphloroglucinol, pyoluteorin, and pyrrolnitrin to suppress plant pathogens. Zhang et al. [45] conducted a study on the efficacy of FD6 in controlling gray mold on tomato fruit. The results showed that there were no visible disease lesions at 5 days after inoculation. Siderophores are iron chelators that can sequester iron from the environment. Siderophores not only provide essential metal nutrients for the plants but also inhibit the growth of pathogenic microorganisms and trigger the induction of systemic resistance (ISR) in plants [39,42]. *Pseudomonas putida* B2017 can act negatively against *Fusarium oxysporum*, *Rhizoctonia solani*, and *Sclerotinia sclerotiorum* by secreting siderophores [46]. It has been demonstrated that VOCs produced by microorganisms have antimicrobial effects on plant pathogens by deforming phytopathogenic fungi hyphae and spores [47]. Several VOCs such as 1-undecene, dimethyldisulfide, 2,5-dimethylpyrazine, benzothiazole, 4-chloro-3-methyl, and phenol-2,4-bis(1,1-dimethylethyl) can penetrate the soil and rhizosphere [47,48]. Ossowicki et al. [49] reported that VOCs from *Pseudomonas donghuensis* P482 significantly inhibited the growth of *R. solani* AG2.2IIIB and *F. culmorum* PV. The hydrolytic enzymes, such as chitinases, glucanases, proteases, and lipases are involved in biotic stress mitigation caused by fungi due to their ability to degrade the fungal cell wall [50,51]. Studies by Rasul et al. [52] showed that inoculation of rice seedlings with *Pseudomonas* sp. MR11 and MR34, and *Bacillus* sp. MR42 increased plant seed phosphate content, improved plant root, shoot, and grain weight, and suppressed the causal agent of rice bacterial leaf blight. These bacteria increased the enzymes phenylalanine ammonia lyase, catalase, peroxidase, β, 1–3 glucanase, and polyphenol oxidase. Several PGPB can also protect plants from adverse environmental conditions by

synthesizing ACC deaminase. Lowering ethylene levels is mediated by the conversion of ACC, the precursor of ethylene, into α-ketobutyrate and ammonia [35,53]. Application of two isolates *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp. to French bean seedlings reduced the negative effects of salt stress and increased root length, root fresh weight, shoot length, shoot fresh weight, root and shoot biomass, and total chlorophyll content [54]. These two isolates showed ACC deaminase activity, as well as several plant growth-promoting traits including production of IAA, siderophores, ammonia, and HCN, and solubilization of P and zinc (Zn). Another indirect mechanism is the ability of PGPB to produce exopolysaccharides and form biofilms [6,55]. Exopolysaccharides are responsible for bacterial adhesion to soil particles and root surfaces; therefore, they are important for bacterial biofilm development [55,56]. Plant-associated biofilms are able of support host plant growth, reduce microbial competition, and protect against pathogens and external stresses [57–60].

3. Biofilm Formation by PGPB Communities in Varied Agroecosystems

Biofilm is a structured community of microbial cells in which the cells are often embedded in an extracellular matrix (ECM) composed of extracellular polymeric substances (EPSs) and bound to a surface [61,62]. The ECM is the body of the biofilm and is composed of a conglomerate of different types of EPSs [63]. Microorganisms release EPSs to promote the attachment process on biotic or abiotic surfaces, followed by the formation of the ECM that surrounds and hold cells together [62,64]. Thus, the ECM ensures the structural integrity of a biofilm [65]. Cell density of the biofilm is high, ranging from 10^8 to 10^{11} cells·g^{-1} wet weight [66]. The bacteria can form either a single-layered or multilayered biofilm on the surface with single or multiple bacterial species within the ECM [60]. The ECM in the biofilm provides the mechanical stability of the biofilm, mediates cell–cell communication, and induces the formation of synergistic microconsortia, making the biofilm lifestyle different from the planktonic state [66,67]. Therefore, microbial cells in biofilms provide several advantages over their planktonic counterparts, namely, protection, enhanced cell-to-cell adhesiveness and cohesion between microbial cells, improved nutrient accumulation potential, increased gene change rate, increased tolerance to antimicrobial agents, and better survival in adverse environments [62,66].

3.1. Biofilm Structure

The vast majority of a biofilm is formed by the ECM, while the cells of the microorganisms represent less than 10% of the dry mass [64,68]. The EPS contains mainly polysaccharides, proteins including extracellular enzymes, lipids, and nucleic acids (eDNA and eRNA) [62,66]. The main components of EPSs are exopolysaccharides, long linear or branched chain molecules with a high molecular weight of 500–2000 kDa [69]. There are several types of exopolysaccharides that have been isolated and characterized from a wide variety of bacterial species. Most of them are heteropolysaccharides consisting of two or more different monosaccharides. On the other hand, some of them are homopolysaccharides that are made up of single sugars such as sucrose-derived glucans, fructans, and cellulose [69,70]. Cellulose is one of the most abundant homopolysaccharides in nature, consisting of repeating chains of β-1,4 linked D-glucose that form fibrils [71]. Several bacterial genera such as *Agrobacterium*, *Acetobacter*, *Azotobacter*, *Rhizobium*, *Sarcina*, *Alcaligenes*, and various species from the Enterobacteriaceae and Pseudomonadaceae families can synthesize cellulose [71,72]. One of the best-studied models for biofilm formation is *Pseudomonas aeruginosa*, which produces at least three different exopolysaccharides, including alginate, polysaccharide synthesis locus (Psl) polysaccharide, and pellicle (Pel) [73,74]. Alginate is composed of anionic polymers, such as β-D-mannuronic acid and α-L-guluronic acid [63]. Alginate has multiple functions, including adhesion, scaffold formation, water/nutrient retention, protection from harsh environments, and antimicrobial agents, and it is also responsible for the mechanical stability of mature biofilms [62]. Overproduction of this exopolysaccharide is characteristic of mucoid strains [75]. Psl polysaccharide is a repeating penta-saccharide containing D-mannose, D-glucose, and L-rhamnose [76]. In addition, Psl

polysaccharide plays a role in cell surface attachment and maintenance of biofilm architecture [77]. Pel, on the other hand, is a glucose-rich exopolysaccharide, required for pellicle formation at air–liquid interfaces [71]. Several proteins that constitute the EPS exhibit enzymatic properties, such as protein-degrading enzymes, polysaccharide-degrading enzymes, and lipid-degrading enzymes, are produced in the biofilm mode. The degrading enzymes break down biopolymers into low-molecular-mass products that can be used as carbon and energy sources. Therefore, enzyme proteins have functions in either biofilm reorganization or degradation [78]. In addition, nonenzymatic proteins, such as lectins associated with the cell surface and extracellular carbohydrate-binding proteins involved in the formation and stabilization of the polysaccharide matrix network are also found in the EPS [62].

One component of EPS is extracellular DNA (eDNA), which is either self-secreted or derived from lysed bacteria within the community and serves to strengthen the biofilm infrastructure [74]. The presence of eDNA contributes to the structural integrity of the ECM [79]. It also facilitates the exchange of genetic information between bacterial cells within the biofilm, and can increase the biofilm's tolerance to antimicrobial agents [67,74].

3.2. Biofilm Formation

Development of microbial cells from a free-living planktonic life form into biofilms lifestyle is divided into five main phases. It consists of reversible attachment of bacteria on a surface, irreversible attachment by adhesion to the surface, development of microcolonies, maturation with a three-dimensional structure, and dispersion by the release of bacterial cells to initiate to form a new biofilm [59,80]. Figure 3 shows the phase of biofilm formation.

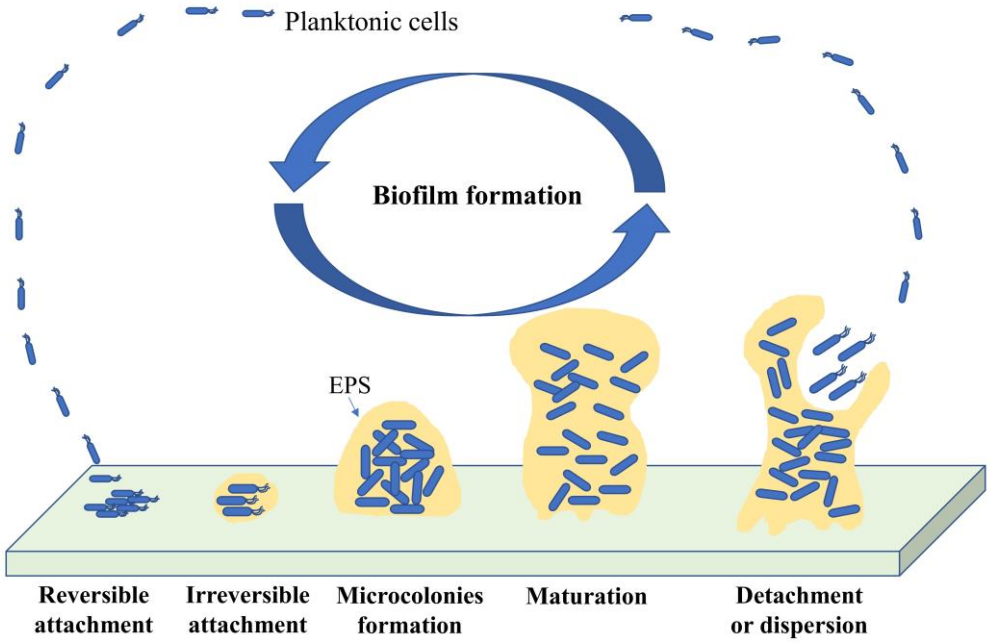

Figure 3. Schematic diagram of different stages in biofilm development.

3.2.1. Bacterial Attachment to a Surface

The first step of biofilm formation is reversible bacterial attachment to the surface. This initial attachment can be easily dislodged and reassembled, either by bacterial mobility or by the action of fluid shear forces [59,81]. Planktonic cells interact with a substrate surface as a result of a random process mediated by Brownian motion and bacterial surface appendages such as pili, fimbriae, and flagella. Another mechanism for surface transport of bacterial cells is sedimentation due to gravitational forces or convection, in which cells are physically transported to the surface by the movement of the bulk fluid [58,59]. Motile bacteria are more competent to overcome hydrodynamic and repulsive forces by utilizing flagella [82]. Flagellum-based motility can be either forward propelling motion in liquids

(swimming) or on solid moist surfaces (swarming) [74,83]. On the other hand, bacteria can exhibit twitching that allows bacterial movement along the surface, driven by type IV pili. Type IV pili play a role in motility, cell–cell adhesion, cell–surface adhesion, and horizontal gene transfer [84,85].

Bacteria constantly change their movement in response to their environment [74]. The ability of motile bacteria to monitor changes in environmental conditions and direct their movement toward a favorable environment in nutrient gradients is called chemotaxis [29,86]. The process of chemotaxis is initiated when a nutrient source or chemoattractants in the environment bind to membrane-anchored receptors and trigger phosphorylation of the associated cytoplasmic histidine kinase CheA. Phosphorylated CheA (CheA-P) interacts with phosphorylated CheY. In addition, CheY-P diffuses through the cytoplasm and then interacts with the flagellar motor, changing the direction of the flagellar motor rotation of the cell toward a favorable environment through a tumble [87,88]. Plants release various complex organic compounds including sugars, amino acids, organic acids, and other small molecules from the roots. Therefore, the chemotaxis response of bacteria to chemical gradients depends on the plant host and root region [29]. O'neal et al. [88] reported that motile cells of *A. brasilense* accumulated in root hairs and elongation zones of wheat but were shed in the root tip. The increased accumulation of *A. brasilense* in the root hairs and elongation zones of wheat was caused by attractant organic acids such as pyruvate, malic acid, and succinate, whereas the low accumulation of *A. brasilense* at the root tips of wheat was due to the production of reactive oxygen species such as hydrogen peroxide.

3.2.2. Adhesion to Surface

The next step in biofilm development is the irreversible attachment of bacterial cells through a permanent bond in the presence of EPSs [80]. The EPSs play an essential role in the host attachment process, acting as a "molecular glue" responsible for the firm anchoring of bacteria to the surface and nurturing contact between cells [59,89,90]. Diazotrophs, such as *Rhizobium leguminosarum*, *Azospirillium brasilense*, and *Gluconacetobacter diazotrophicus* attach to the surface of roots using cellulose microfibrils with agglutinating activity [89]. *P. aeruginosa* produces at least three types of exopolysaccharides, including Psl polysaccharide, Pel, and alginate, which play an important role in biofilm formation [73,74]. Ghafoor et al. [91] reported that *P. aeruginosa* mutants deficient in Psl polysaccharide exhibited decreased crystal violet staining of static biofilms at an initial stage of biofilm development. In contrast, mutants deficient in Pel lacked the formation of pellicle at the air–liquid interphase in inert culture medium. At this stage, it becomes more difficult to break the adhesion of bacterial cells to a surface by treatments such as shear force or chemical treatment with enzymes, detergents, disinfectants, and surfactants [80,92].

3.2.3. Microcolony Formation

The production of EPS matrix leads to the growth and aggregation of microorganisms to form microcolonies [80]. Adhesion of bacterial cells to the substrate and between bacterial cells has a major impact on microcolony formation. Microcolony structures form due to the downregulation of the type IV pili-dependent twitch motility and the production of matrix components that adhere tightly to cells within the biofilm, stopping motility [93,94]. The production of biosurfactants such as rhamnolipids from *P. aeruginosa* plays an additional role in promoting the formation of microcolonies in the initial phase and facilitates the migration of cells to form a mushroom cap in the maturation phase of the biofilm [95]. Several bacteria can form microcolonies on different roots from the tip to the elongation zone [96]. The advantages of forming microcolonies are that they allow substrate exchange between species and remove end products from bacterial cells [59,90].

3.2.4. Biofilm Maturation

After microcolony formation and EPS accumulation, the biofilm community grows by simultaneous cell proliferation [74]. The biofilm expands from a thin layer to up

to 100 layers [97]. Formation of the mushroom shape occurs in a sequential process in which a nonmotile bacterial subpopulation forms the initial microcolonies and the mushroom stalk. The nonmotile bacterial subpopulation may form in a subpopulation due to downregulation of motility [59]. Moreover, mature cells supported by type IV pili and guided by a chemotaxis gradient climb up the mushroom stalk due to nutrients and subsequently form the mushroom caps. As expected, bacteria in the biofilm move toward the nutrient-rich zone to maintain their activity and biofilm growth [93,98,99]. Sheraton et al. [99] revealed that the development of mushroom-shape in *P. aeruginosa* biofilm was influenced by chemotactic motility. Their study showed that chemotaxis-deficient mutants lacking chemotactic motility formed large stalks without caps. In addition, Ghanbari et al. [100] found that the formation of mushroom-shaped structures in the biofilm of *P. aeruginosa* also depends on the nutrient content and initial density of cells on the stalk.

3.2.5. Biofilm Dispersal

During dispersion, the final step of the biofilm life cycle, individual cells leave the biofilm to resume a planktonic lifestyle. Dispersion is the final stage of a biofilm's life cycle, during which individual cells detach from the biofilm and resume a planktonic lifestyle. The detachment process is a strategy used by bacterial cells to leave biofilms and begin a new life cycle under suitable environmental conditions [59]. It is a complex process in response to changes in their environment, such as nutrient starvation, oxygen starvation, production of matrix-degrading enzymes, accumulation of toxic products, and passive behaviors such as detachment and erosion by external forces such as shear forces [77]. In addition, bacterial cells within a mature biofilm can also spread when the number of cells reaches a threshold [74]. During the spreading process, genes responsible for cell motility and EPS degradation are usually upregulated, while genes related to EPS production are often downregulated [59]. Quorum sensing (QS) is the intercellular signaling among bacteria. This process has been shown to play a special role in biofilm spreading in response to cell population density through the cell–cell communication system [59]. Insufficient carbon and nitrogen sources may be the critical factors leading to the bacterial dispersal process. In addition, EPS-degrading enzymes, such as the glycoside hydrolases PelA and PslG in *P. aeruginosa*, also contribute to the detachment of bacteria from the matrix [101]. Another mechanism to escape from mature biofilms is the release of a mixture of D-amino acids, such as D-tyrosine, D-leucine, D-tryptophan, and D-methionine. This mechanism is controlled by racemase enzymes, which catalyze the stereochemical conversion of L- to D-amino acids. Studies by Guilhen et al. [102] have shown that dispersed biofilm cells are more efficient at attaching to plant roots, forming microcolonies, and surviving better than their planktonic counterparts. Dispersion is considered an important stage for biofilm control as the planktonic state becomes more susceptible to immune responses and antimicrobial agents.

3.3. Factors Responsible for Biofilm Formation

Several factors are largely responsible for the formation of biofilms. Abiotic factors are involved in biofilm formation, such as nutrient availability, temperature, pH, oxygen, and surface physicochemical properties. Biotic factors such as microbial cells and metabolites produced by bacteria also influence biofilm formation [89,103]. Nutrient-depleted conditions stress microorganisms but stimulate biofilm formation. However, prolonged nutrient deprivation prevents biofilms from advancing their maturation [104,105]. Savijoki et al. [106] reported that culturing *Lactobacillus rhamnosus* GG in a medium containing 2% fructose increased biofilm formation twofold compared to 2% glucose and that planktonic cells cultured on fructose exhibited higher adherence levels compared to glucose. The concentration of carbon sources also affects biofilm formation. In a study by Zou and Liu [107], different carbon sources such as glucose, maltose, lactose, and sucrose were used at different concentrations (from 0–10 mg/L) to induce biofilm formation. The results showed that the optimal concentration for *Staphylococcus epidermidis* biofilm production

was 2.5 mg/mL for all carbon sources. As mentioned earlier, biofilms are stimulated under stress conditions. Wang et al. [108] demonstrated that *P. stutzeri* A1501 formed a biofilm with the highest biomass in lactate-containing K (LK) medium without added nitrogen, compared to LK medium supplemented with ammonia chloride as a nitrogen source.

Extreme temperatures and pH negatively affect biofilm formation [103]. The optimal growth temperature for *Listeria monocytogenes* was 37 °C. Moreover, biofilm production of 58 isolates of *L. monocytogenes* was five times higher at 37 °C than at 10 °C [104]. *Citrobacter werkmanii* BF-6 has been shown to grow in a wide pH range. Interestingly, biofilm formation increased with decreasing pH at 30 °C in LB medium, although it inhibited bacterial growth [109]. A study by Haque et al. [110] showed that *Enterobacter asburiae* ENSD102, *Enterobacter ludwigii* ENSH201, *Vitreoscilla* sp. ENSG301, *Acinetobacter lwoffii* ENSG302, and *Bacillus thuringiensis* ENSW401 developed thick and robust air–liquid biofilms at pH 7. In addition, *E. asburiae* ENSD102 and *Vitreoscilla* sp. ENSG301 produced optimal solid–air–liquid biofilms at pH 4. Restriction of oxygen availability also affects bacterial biofilm metabolic activity and usually triggers active dispersal [111].

Cell adhesion to the surface is a prerequisite for colonization [103]. However, the physicochemical properties of the surface between the substrate and the bacteria influence each other [59]. For example, surface roughness may promote bacterial attachment and biofilm development due to lower shear forces and greater surface area. However, bacteria prefer to adhere to hydrophobic and nonpolar surfaces rather than hydrophilic surfaces because hydrophobicity reduces the repulsive forces between the surface of the bacteria and the substrate [59,89].

QS is an intercellular signaling in bacteria that regulates gene expression in response to cell population density via a cell–cell communication system. It is mediated by the production and detection of signaling molecules called autoinducers, such as N-acylhomoserine lactones (AHL) in Gram-negative bacteria, oligopeptides in Gram-positive bacteria, and autoinducers-2 (AI-2) in both Gram-negative and Gram-positive bacteria [20,75,112,113]. QS contributes to several key ecological and interdependent properties of bacteria, such as secretion of antibiotics, siderophores, or enzymes, virulence factors of phytopathogens, and communication between plants and microbes [58,114]. QS in *Aeromonas* regulates the expression of biofilm formation, motility, and virulence [96,115].

Lipopeptides such as serawettins and rubiwettins were produced by *Serratia marcescens* and *Serratia rubidaea*, respectively, indicating wetting activity involved in surface colonization [116]. In contrast, *B. subtilis* produced antibacterial agents such as surfactin and bafilomycin L, which are important for swarm motility. Moreover, the inability of *B. subtilis* mutants to produce surfactin, bacillomycin L, or both surfactin and bafilomycin L indicated a significant reduction in biofilm formation [117]. Zhu et al. [118] also reported that the expression of genes encoding the mutants was lower than wildtype *B. pumilus* HR10, affecting swarm motility performance, polysaccharide content, and biofilm formation. Surfactin reduces surface tension and acts as a wetting agent, thereby affecting bacterial swarm motility [117].

EPSs are responsible for facilitating cell-to-surface and cell-to-cell interactions, aggregation or adhesion of cells to the surface, diffusion barrier to protect the cell, and regulation of biofilm formation and structure [60]. EPSs can suppress cell adhesion through electrostatic forces, while large amounts enhance adhesion through interactions between functional groups in EPS [90]. In addition to EPSs, eDNA plays an important role in biofilm formation, including mediating cell–cell interactions, and it is mainly found in the stalk region of microcolonies [74].

Bacteria produce siderophores to chelate iron under low iron availability [119,120]. Under Fe-limiting conditions, microbial surface hydrophobicity and biofilm formation decrease [121]. Guo et al. [122] used *E. coli* UTI89 as a model organism to study the effect of different iron concentrations. They found that biofilm formation increased under an iron concentration of 0 to 10 μM, but was completely inhibited in the presence of 2000 μM iron.

Thus, the iron siderophore plays a role in the formation of structured biofilms. Siderophore-deficient mutants of *P. aeruginosa* showed a decreased ability to form biofilms [123].

4. Role of Biofilm-Forming PGPB in Sustainable Agriculture

PGPB biofilms are found in various niches within agroecosystems. Rhizosphere and plant roots are hotspots for PGPB interactions as significant amounts of nutrients are released from plant roots [29]. Diverse PGPB are able to form microcolonies on different parts of roots, from the tip to the elongation zone. They also grow into large populations and form mature biofilms [124]. Most studies on root colonization patterns have shown that PGPB colonization in the rhizosphere forms microcolonies or aggregates on root surfaces. The distribution of these colonies is patchy and nonuniform [58]. Living in biofilms provides several benefits to PGPB, including facilitating bacterial interactions with plants, improving bacterial resistance to adverse environments, protecting against pathogens, and enhancing uptake of nutrients released in the plant environment [118]. Many beneficial bacterial biofilms associated with various plants have been studied (Table 1).

Table 1. Role of PGPB biofilms associated with various plant species.

Functional Trait	PGPB	Plant Species	Inoculation of PGPB	Enhancement	Reference
Biocontrol	*P. polymyxa* B5	Peanut (Arachis hypogaea L.)	Seed	96.7% biocontrol efficacy 43.5% plant yield	[125]
	B. pumilus HR10	Masson pine (*Pinus massoniana*)	Roots	76.8% biocontrol efficacy	[118]
	P. synxantha, *P. brassicacearum*	*Arabidopsis thaliana*	Roots	81% and 82% biocontrol efficacy, respectively	[126]
	B. subtilis 916	Rice (Oryza sativa L.)	Rice sheaths	60% biocontrol efficacy	[117]
	B. velezensis BBC047	Tomato (*Solanum lycopersicum* L.)	Roots; leaves	±66% and ±53% biocontrol efficacy, respectively	[127]
Plant growth promotion	*B. salmalaya* 139SI	Oil palm (*Elaeis guineensis* Jacq.)	Seedling and soil	55.4% stem height 66.7% stem dry weight	[128]
	Consortium of *Pseudomonas* sp. M45 and *Stenotrophomonas* sp. K96	Tea (*Camellia sinensis*)	Roots	4.85-fold shoot length 4.65-fold root length	[129]
	B. amyloliquefaciens SQR9	Maize (*Zea mays* L.)	Roots	42–60% biomass 32–46% shoot height 33–49% root length	[130]
Plant growth promotion, biocontrol	Consortium of *Microbacterium*, *Stenotrophomonas*, *Xanthomonas*	*Arabidopsis thaliana* L.	Soil	±31% shoot fresh weight ±36% biocontrol efficacy	[131]
Plant growth promotion, drought tolerance	*B. aryabhattai ESB6*, *P. azotoformans ESR4*, *P. cedrina ESR12*, *P. chlororaphis ESR15*, *P. gessardii ESR9*, *P. poae ESR6*, *P. veronii ESR21*, *S. Maltophilia ESR20*	Tomato (*Solanum lycopersicum* L.)	Roots	11%, 14%, 7%, 6%, 8%, 10%, 3%, and 12% plant height, respectively 18%, 33%, 22%, 18%, 3%, 29%, 17%, and 2.5% root dry weight, respectively	[132]
Plant growth promotion, salinity tolerance	*B. licheniformis* QA1, *E. asburiae* QF11	Quinoa (*Chenopodium quinoa* Willd.)	Seeds and soil	±42% and ±46% root length, respectively ±46% and ±13% shoot length, respectively	[133]
Drought tolerance	*B. amyloliquefaciens* 54	Tomato (*Solanum lycopersicum* L.)	Roots	±15% relative water content of leaves	[134]
	P. azotoforman FAP5	Wheat (*Triticum aestivum* L.)	Seeds	9% shoot length 14% root length 10% shoot dry weight 16% root dry weight	[135]
	Consortium of *Microbacterium oxydans*, *Paenibacillus amylolyticus*, *Stenotrophomonas rhizophila*, *Xanthomonas retroflexus*	*Arabidopsis thaliana*	Rhizosphere	2-fold fresh weight 1.5-fold diameter of rosettes 1.5-fold chlorophylls content	[136]
Salinity tolerance	*B. amyloliquifaciens*	Barley (*Hordeum vulgare* L.)	Seeds and soil	23% root dry weight 43% shoot dry weight	[57]

4.1. Biocontrol Activity against Plant Pathogens

Evidence that the survival, persistence, and virulence mechanisms of microorganisms with biocontrol potential are largely related to their biofilm lifestyle has been well established since the early 1980s [137,138]. Various PGPB efficiently occupy, colonize, and form biofilms in/on their rhizospheric or phyllospheric niches as their own survival strategy, as well as to mediate plant control activities [103,139]. Plant-associated biofilms are able to protect plants from pathogenic microorganisms by competing with and inhibiting their colonization, stimulating ISR, and producing antimicrobials [34,45,58,131,134].

Several research groups [140–143] have demonstrated that a lipopeptide "surfactin" triggers bacillus biofilm formation via KinC activation of the Spo0A pathway. Zeriouh et al. [144] demonstrated that surfactin produced by *B. subtilis* strain UMAF6614 triggers biofilm formation on melon phylloplane and contributes to its biocontrol activity against plant pathogens (*Pectobacterium carotovorum*, *Xanthomonas campestris*, and *Podosphaera fusca*). Biofilm formation by biopesticides can be stimulated by plant root exudates or through exposure of the microorganisms to antimicrobial products or stress [125,145–147]. Haggag and Timmusk [125] demonstrated that biofilm formation by *Paenibacillus polymyxa* B5 on peanut plant inhibits colonization of the pathogenic fungus, *Aspergillus niger*, as well as helps in reducing 96.7% crown rot disease and successfully promoting 43.5% of plant yield. Furthermore, Timmusk et al. [148] demonstrated the antagonistic abilities of two *P. polymyxa* strains against *Phytophthora palmivora* and *Pythium aphanidermatum* in an *A. thaliana* model system. Biofilm-forming PGPB significantly protected the plants from various pathogens, resulting in increased plant productivity. However, there were only a few reports that included plant yield information as a consequence of biocontrol agents of biofilm-forming PGPB.

4.1.1. Root Colonization

Colonization of the rhizosphere or roots by PGPB plays essential roles in eliminating pathogenic microorganisms by reducing the availability of root exudates and triggering an innate immune response [139]. As a result, horizontal filtering of soil bacteria occurs, leading to a reduction in bacterial diversity in the soil and greater bacterial specialization on the root. Subsequently, interactions among soil bacteria increase, leading to higher bacterial persistence and colonization of roots through processes such as metabolic exchanges, secretion of antimicrobial substances, and other processes. The ability of PGPB to colonize faster, as well as compete with nutrients and niches, represents the basic mechanisms that protect plants from phytopathogens [149]. Fan et al. [150] reported that the Gram-positive rhizobacterium *Bacillus amyloliquefaciens* FZB42 can colonize different plants with a specific region on the roots. FZB42 preferentially colonized the tips of the primary roots of *Arabidopsis*, along the furrows between the epidermal cells of the roots, and in the concave spaces on the ventral sides of the fronds of *Lemna*. This is dependent on the availability of plant tissue, water, and nutrients [103]. A study by Harting et al. [126] showed that inoculation of *P. synxantha* or *P. brassicacearum* on *A. thaliana* seedlings successfully protected the roots from *Verticillium dahliae* colonization. The roots of *A. thaliana* treated with the bacterial culture were examined under a fluorescence microscope. Fewer fungal hyphae were detected on the roots, and large portions of the root were free of fungal hyphae. This suggests that those *Pseudomonas* isolates may be an effective biocontrol agent. In addition, Haggag and Timmusk [125] used *P. polymyxa* to colonize and form a biofilm on the root of *A. thaliana* to inhibit crown root rot caused by *A. niger*. Their study showed that *P. polymyxa* B5 significantly colonized the root, and the density reached 10^9 bacteria per gram of soil after 30 days. The results may indicate that the higher population densities of strain B5 in the rhizosphere effectively control *A. niger*.

4.1.2. Triggering Induced Systemic Resistance (ISR)

Induced systemic resistance is one of the plant defense strategies initiated by beneficial microbes such as PGPB and mycorrhizal fungi against pathogenic attack [151–153]. The density of PGPB must to reach 10^5–10^7 colony-forming units (CFU) per gram of root to

elicit ISR [151]. Many plants such as bean, cucumber, tobacco, tomato, carnation, radish, and *A. thaliana* can use ISR as a protective mechanism against a variety of plant pathogens, including bacteria, fungi, viruses, and insects [154,155].

Phytohormone signaling pathways such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are required as primary regulators in the plant immune signaling network [131,152,154]. In general, SA is effective against biotrophic pathogens, whereas JA/ET is effective against necrotrophic pathogens and insects [131,153]. *B. cereus* AR156 was involved in both the SA and JA/ET pathways and triggered ISR against the biotrophic pathogen *Pseudomonas syringe* DC3000 on *A. thaliana* [156]. In contrast, *B. cereus* AR156 activated only JA/ET signaling pathways and stimulated ISR against necrotrophic Botrytis cinerea on *Arabidopsis*. Activation of signal transduction pathways during ISR depends on ISR-inducing strains, host plants, and pathogens [154]. According to Zhu et al. [118], the wildtype *B. pumilus* HR10 was able to colonize the roots of *Pinus massoniana* seedlings and inhibit *R. solani* better than the biofilm-deficient mutant MA15. Their study also showed that the expression of PR2, which regulates the salicylic acid-related gene of *B. pumilus* HR10, was higher than that of the biofilm-deficient mutants and the control. This suggests that *B. pumilus* HR10 contributes to the initiation of ISR. Zebelo et al. [157] demonstrated biocontrol activity of *Bacillus* spp. against *Spodoptera exigua* larvae when larvae were fed cotton (*Gossypium hirsutum*) inoculated with *Bacillus* spp.

4.1.3. Antimicrobial-Producing Biofilm

Microbes produce biosurfactants, such as polysaccharide–protein complexes, lipopeptides, glycolipids, phospholipids, fatty acids, and natural lipids. Lipopeptides have high surface activity and antibiotic potential that can be used as biocontrol agents [158]. *Bacillus subtilis* is a recognized biocontrol agent due to the production of lipopeptides such as surfactin, iturin, and fengicin. Hazarika et al. [159] found that *B. subtilis* SCB-1 produces iturin and exhibits strong antagonistic activity against several phytopathogenic fungi belonging to the genera *Alternaria*, *Cochliobolus*, *Curvularia*, *Fusarium*, *Neodeightonia*, *Phomopsis*, and *Saccharicola*. Luo et al. [117] also reported that the surfactin-deficient mutant and bafilomycin-deficient mutant of *B. subtilis* 916 altered swarming motility, reduced biofilm formation, and reduced antagonistic activity of *Rhizoctonia solans*-infected rice scales. Moreover, Stoll et al. [127] concluded that surfactin production by *Bacillus velezensis* is involved in biofilm formation and stable colonization to further activate ISR. The lipopeptide syringomycin produced by *Pseudomonas* spp. was able to inhibit the growth of saprophytic *Aspergillus nidulans* and *Verticillium* spp. Moreover, the inhibitory effect depends on the presence of the gene encoding the transcriptional regulator LuxR or genes involved in the synthesis of syringomycin [126]. In addition to antibiotics, PGPB also produce exoproteases, HCN, or phenazines [27].

4.2. Promoting Plant Growth by Biofilm-Forming PGPB

Beneficial biofilms attached to plant roots aid in nutrient cycling, provide essential macro- and micronutrients, and produce growth-promoting substances, including auxins (indolyl-3-acetic acid), gibberellins, and cytokinins [40]. A study conducted by Haque et al. [132] showed that 26.9% of rhizobacterial strains isolated from drought ecosystems were able to form biofilms in a NaCl-containing liquid culture and exhibit several plant growth-promoting properties such as nitrogen fixation, solubilization of nutrients (P, K, and Zn), and production of IAA, ammonia, siderophores, ACC deaminase, catalases, lipases, cellulases, and proteases. Inoculation of *Xanthomonas*, *Stenotrophomonas*, and *Microbacterium* isolates that formed a biofilm in the soil significantly increased the fresh weight of *Arabidopsis* plants and resulted in systemic resistance to downy mildew [131]. Biofilms of *Rhizobium miluonense* Rm3 and *Burkholderia anthina* Ba8 were able to dissolve inorganic phosphates, lower pH, and release organic acids [160]. In addition, consortium biofilms of PGPB and *Aspergillus* were able to dissolve phosphorus, produce IAA, and exhibit higher nitrogenase activity than their bacterial and fungal counterparts [161]. Further

work by Hazarika et al. [129] found that *Stenotrophomonas* sp. K96 and *Pseudomonas* sp. M45 exhibited strong biofilm formation and colonization on tea roots, as well as synergistic plant growth-promoting properties, resulting in significant increases in several plant growth-promoting vegetative parameters. Bandara et al. [162] reported that the production of indole acetic acid-like substances (IAAS) and the acidity of biofilms composed of endophytic bacteria and fungi were higher than those of mixed cultures, fungi, or bacteria. The acidity was higher because biofilms release H^+, which is reflected in IAA production and solubilization of minerals. In addition, microbial acid production is important for the suppression of plant pathogens [163].

Naturally, biofilm formation in the rhizosphere is composed of several bacterial species [29,164]. Several studies have shown that mixed biofilm-based inoculants form stronger biofilms than single species, suggesting collaboration among strains [29]. A four-species consortium consisting of *Stenotrophomonas rhizophila*, *Xanthomonas retroflexus*, *Microbacterium oxydans*, and *Paenibacillus amylolyticus* produced greater biofilm biomass than individual species, suggesting that all individual strains benefit from inclusion in the multispecies community [164]. A multispecies consortium of *Bacillus* spp. and *Microbacterium* sp. isolated from the rhizosphere showed high synergy in biofilm formation [29]. Biofilm formation of PGPB on plant roots helped to enhance photosynthesis and leaf growth. Co-inoculation of 50% recommended fertilizers with PGPB biofilm biofertilizers helps to increase leaf growth [20]. Conventional application of monocrops or inoculation with mixed crops may not result in the highest microbial effects than application of biofilm consortia [60]. Prasanna et al. [165] showed that inoculation with cyanobacteria induces a plant defense response and increased Zn mobilization in corn hybrids. They also confirmed that cyanobacterial treatment resulted in significant changes in glomalin-related soil proteins and polysaccharides in the soil and the activity of defense enzymes in plant roots and shoots.

4.3. Mitigating Abiotic Stress in Plants by Biofilm-Producing PGPB

Biofilm formation is considered a primary protective strategy against unpredictable and adverse environmental conditions. Therefore, PGPB can survive in biofilms in the rhizosphere and interact with plants better than planktonic cells. Cells within the biofilm matrix have been shown to be more resistant to antimicrobial compounds, desiccation, and UV light [166]. Environmental stresses such as nutrients and osmotic stress lead to increased competition among bacteria for available nutrients. Therefore, planktonic bacteria congregate and form biofilms to protect them in the rhizosphere. In addition, increased production of exopolysaccharides can support biofilms and improve tolerance to abiotic stressors [57].

Studies by Kasim et al. [57], showed that 20 of the PGPB tested had the ability to form a biofilm under 0, 250, 500, and 1000 mM NaCl, which increased with increasing salt concentration. In addition, barley grains coated with nine selected biofilm-forming PGPB isolates showed that they attenuated the deleterious effect of salinity and had higher shoot length by 10–15%, fresh mass of shoots and roots by 64% and 35%, respectively, dry mass of shoots and roots by 41–43% and 8–27%, respectively, and relative water content of shoots and roots by ±7% and 12–15%, respectively, compared to the control. A similar result was also reported by [167]. Inoculation of salt-tolerant strains *Pseudomonas plecoglossicida* PB5 and *Bacillus licheniformis* AP6, which had the ability to form a biofilm, withstood salt stress better than non-inoculated plants, significantly promoted dry mass (89–96%), and improved photosynthetic pigments (10–67%), gas exchange activities (42–67%), and nutrient uptake (9–14%) in sunflower. Some PGPB that form EPS can bind cations such as Na^+, suggesting a role in alleviating salt stress by reducing Na^+ availability, increasing K^+ absorption, and improving water uptake [20,133].

According to Wang et al. [134], biofilms of *Bacillus amyloliquefaciens* 54 improved root colonization and drought tolerance in tomato plants. In addition, plants inoculated with hyper-robust biofilm (ΔabrB and ΔywcC) of mutant *B. amyloliquefaciens* 54 were better able

to withstand drought stress. In another study conducted by Timmusk et al. [168], *Bacillus thuringiensis* AZP2 formed a biofilm and produced an EPS matrix around wheat root hairs, which is an important strategy to improve tolerance to drought stress. Their study also found that AZP2 produced small amounts of alginate, which has the property of retaining water. Thus, it may increase tolerance to drought stress. In addition, Ansari et al. [135] reported that the strain *Pseudomonas azotoforman* FAP5 effectively alleviated drought stress in wheat plants through enhanced biofilm development, photosynthetic pigment efficiency, antioxidant enzymatic activities, and root colonization. Moreover, plant inoculated with strain FAP5 had higher root adhering soil per root tissue (RAS/RT) by 29% compared to the control. Enhancement of RAS/RT indicates an increase in soil aggregation and higher water-holding capacity around the roots, which improves nutrient uptake in plants. A consortium of four species, *Stenotrophomonas rhizophila*, *Paenibacillus amylolyticus*, *Microbacterium oxydans,* and *Xanthomonas retroflexus*, had the strongest synergy in biofilm formation and induced drought tolerance through increased ABA biosynthesis and chlorophyll content [136]. It has also been reported that some soil bacteria form biofilms in response to heavy metal pollution and scavenge heavy-metal ions such as arsenic, lead, mercury, and cadmium, leading to attenuation of heavy-metal contamination of plants in polluted areas [169,170].

5. Conclusions and Future Prospects

PGPB biofilms are considered to have a fundamental role in future agriculture to achieve sustainable development goals. They can provide an alternative to agrochemicals in the agricultural sector as biofertilizers and biocontrol agents. Beneficial biofilms on plant roots help in nutrient cycling, provide inorganic nutrients (N, P, and K), and mitigate abiotic stress. They protect plants from pathogens by competing with and colonizing pathogenic microorganisms, stimulating ISR, and producing antimicrobials. Moreover, the beneficial effects of the interaction between plants and PGPB are enhanced by the formation of a biofilm toward the planktonic form. PGPB as a bioinoculant sometimes fails to competitively colonize plant roots and rhizosphere. Therefore, PGPB biofilm formulation is one of the strategies in bioinoculant development to overcome conflicting in vivo effects. However, significant efforts are still required to develop effective formulations for sustainable agriculture based on biofilms producing PGPB. The most important steps will be (a) the selection of biofilms producing PGPB over planktonic PGPB, (b) crop-specific plant/biofilm-producing PGPB interaction studies before preparing them for commercial scale, (c) the formulation's physical form (e.g., liquid, solid, wettable powder), (d) carrier material selection for the formulation, etc. In addition, it is necessary to understand the communication of bacteria within the biofilm with other microorganisms and plants through a variety of molecular signals. This will help stabilize the effect of biofilm–plant interactions and provide insight into microbial ecology.

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