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REVIEW ARTICLE

Microbial biofilms and their role in sustainable agriculture and climate-smart farming

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Abstract

Microbial biofilms are organised populations of microbes covered with a self-made extracellular polymeric matrix and are at the core of climate-smart farming and sustainable agriculture. Biofilms enhance soil health by stabilising soil structures, enhancing microbial diversity and promoting nutrient cycling and thereby naturally supporting plant growth and resilience. One way biofilm-forming plant growth-promoting rhizobacteria (PGPR) might be helping plants is by making them better able to take up nutrients through the solubilization of elements such as nitrogen, phosphorus and potassium; at the same time, they release phytohormones and compounds that alleviate stress to make plants resistant to abiotic stresses like salinity and drought. Root colonisation becomes more durable and pathogen biocontrol can be done more efficiently by biofilm matrices, which protect microorganisms from environmental stresses. Rhizospheric interactions exemplified by cross-kingdom biofilms with fungi are the most effective ways to exchange nutrients and enhance ecosystem resilience. The growth of stable biofilm communities and their microbial diversity can be supported by agricultural techniques such as the use of organic additives and conservation tillage. Recent developments emphasise the use of biofilm-based inoculants as biofertilizers, bio-stimulants and biocontrol agents in an effort to lower chemical inputs and greenhouse gas emissions in agroecosystems. More research and innovative applications like multi-strain consortia and biofilm-enhanced seed coating provide promising ways of harnessing microbial biofilms for increased agricultural productivity and soil quality, as well as environmental sustainability in the face of climate change.

Keywords: biocontrol; climate-smart farming; microbial biofilms; plant growth-promoting rhizobacteria; soil health; sustainable agriculture

Introduction

Significant challenges are presented to agricultural systems around the world, ranging from soil deterioration to climate change. These difficulties are a significant obstacle that must be removed to boost food production without exacerbating environmental damage. Various strategies and technologies have been developed and employed in view of achieving enhanced productivity along with improved soil health, increased nutrient use efficiency and reduced greenhouse gas emissions, which include sustainable and climate-smart agricultural practices. Biological inputs such as microbial biofilms consisting of a structured consortia of microorganisms encapsulated in a self-produced extracellular polymer are gaining attention for their ability to improve the stability and robustness of soil and plant environments (1-3). A plant root or a soil particle serves as a point of attachment for the formation of microbial biofilm, where these adhered cells produce a matrix of extracellular polymeric substances (EPS), which results in the development of a functioning multispecies community. These communities are more stable, resilient and functional than their free-living counterparts. In addition to protecting plants from biotic and abiotic stressors and maintaining positive interactions between microbes and plants, such resilient microbial systems can help improve plant nutrient uptake (4). Non-EPS-producing plant growth-promoting bacteria (PGPB) are less competitive and less effective in promoting plant growth and soil health due to their limited ability to form biofilms, tolerate stress and improve soil structure. Extracellular polymeric substances production is a key trait for maximising the benefits of PGPB in sustainable agriculture (5, 6). These PGPB can survive longer, exhibit higher colonisation of plant roots and ultimately result in better plant effects, such as nutrient mineralisation (7). These bacterial biofilms can also enhance the stability of soil aggregates, along with offering protection to resident microbes against abiotic stress.

In order to reduce the dependency on synthetic fertilisers and pesticides and thereby to achieve a reduction in the associated greenhouse gas emissions through climate-smart agriculture, microbial biofilms could play a vital role. They could promote soil carbon sequestration through increased soil microbial biomass and improved soil aggregation, hence offering an eco-friendly solution for the existing hindrances to achieve sustainable soil and plant health (8).

This review discusses the current and future roles microbial biofilms play in climate-smart agriculture to promote plant health, maximise resource use efficiency and mitigate environmental stresses. Continued research and innovative applications of biofilm-forming microbes would lead to unlocking their full potential, which would yield resilient and sustainable agroecosystems amidst changing climates.

Composition and Structure of Biofilms

Microbial biofilms are not just random clumps of cells; rather, they are structural communities of microorganisms embedded inside a self-secreted matrix, arranged in three-dimensional structures on surfaces such as plant roots or soil particles (9). Biofilms are made up of colonies of microorganisms enclosed in a self-produced extracellular matrix that consists of EPS, like polysaccharides, proteins, extracellular deoxyribonucleic acid (eDNA) and extracellular ribonucleic acid (e-RNA), water, lipids and other biomolecules (10). The major constituent of the biofilm matrix is the EPS, which comprises around 50-90 % of the total organic matter in many biofilms. This matrix primarily comprises water, supplemented by polysaccharides, proteins and eDNA. Water is the essential constituent, maintaining the biofilms' hydration and promoting nutrient transport within it. Polysaccharides serve as an adhesive framework that facilitates cellular adhesion to the surface and to each other, thereby imparting strength and protective properties to the biofilm. Proteins and eDNA also support the architecture of the biofilm and contribute to its overall functions (11).

Biofilm formation occurs in several distinct stages. It starts when free-floating (planktonic) microorganisms make initial, reversible contact with a surface, gradually leading to a more permanent attachment. Once anchored, the cells begin to cluster together and release EPS, creating tiny microcolonies (10). As this matrix expands, the biofilm grows into a mature, three-dimensional structure that can take on species-dependent structures such as towers or mushroom-like formations. Fully grown biofilms often display a complex structure, with a regulatory zone at the base, a dense microbial layer in the middle and an outer region that contains cells poised to detach and spread to new environments (8, 9).

Biofilms are not static; their composition and structure vary in response to physical, chemical and biological factors. Under hydrodynamic stress or shear (which parallel movement around the root or in soil pores), microorganisms have been found to boost the matrix formation and modify the chemical composition of EPS (like richer in carbohydrates) to retain the mechanical integrity (12).

Formation and Development of Microbial Biofilms/Biofilm Development Phase

Root-associated bacteria in agricultural systems form biofilms through a four-stage developmental sequence: (i) initial attachment, (ii) irreversible attachment and microcolony formation, (iii) maturation into structured biofilms and (iv) dispersion.

Initial attachment (Reversible adhesion)

Planktonic cells use flagella-based motility and chemotaxis to move toward root exudate gradients, eventually making initial contact with the root surface or a soil particle (13). Transcriptome analysis of the plant growth-promoting rhizobacteria (PGPR) *Bacillus amyloliquefaciens* SQR9 under biofilm-forming conditions in the presence of maize root exudates revealed that chemotaxis and flagellar genes (*cheA, cheB, cheW, mcpB/C, fli, flg, flh, hag*) were very strongly upregulated at the early time points. This indicates that motility and surface recognition are indispensable for the attachment stage (14). Likewise, the study also found that the motility genes and transcriptional start sites of *Bacillus amyloliquefaciens* FZB42, which were differentially regulated based on the condition, were changed significantly when the bacteria were grown in the medium supplemented with soil extract and maize root exudates under rhizosphere-mimicking conditions. This further supports that cells actively migrate towards plant-derived compounds (15).

Irreversible attachment and microcolony formation

After reversible adhesion, they move to irreversible attachment by fabricating adhesins and EPS. Out of 78 rhizobacterial isolates from drought-prone soils that were screened, 21 isolates produced robust air–liquid interface biofilms in test tubes. Fourier transform infrared spectroscopy identified that the matrices of these strains had proteins, polysaccharides, lipids and nucleic acids, which pointed to active-matrix production during the early stages of colonisation (16).

Maturation of biofilm

Microcolonies develop into 3D architectures with channels and different cell subpopulations as they mature (17). The plant-associated strain *Pseudomonas donghuensis* P482, when grown on glass in the presence of glycerol, produces highly structured biofilms. Confocal laser scanning microscopy and crystal violet assays revealed dense, three-dimensional clusters with prominent microcolonies, thus indicating that the development of complex architectures from the very first attachment sites is time and nutrient regime-dependent (18). In particular, the two organic acids - fumaric and citric - which are parts of the root exudate of maize, were able to boost the transcription of the genes *epsD* and *tapA* for matrix production in the biofilm of SQR9 by more than tenfold, thus linking the completion of the matrix with some exudate-derived molecular signals (14).

Dispersion

Some subpopulations of cells might regain their motility and depart from the biofilm, thus being able to travel and colonise new soil microhabitats or root zones (19). Comparative transcriptome analysis of *Bacillus amyloliquefaciens* SQR9 and FZB42 in rhizosphere-like conditions shows that the expression of genes involved in motility and chemotaxis is very flexible and different between the early and later time points, thus indicating functionally different stages that transition from attachment through biofilm development to dispersal. This is the case even though there is still very little direct visualisation of dispersal in the field (14, 15).

Functional Role of Microbial Biofilms for Sustainable Agriculture

The self-produced EPS of bacteria form complex 3D structures that serve multiple purposes in agricultural ecosystems. The majority of soil microorganisms (98 %) exist within biofilm structures, which display three-dimensional arrangements that function as essential microstructures for maintaining ecosystem stability and operational efficiency (20). The complex microbial communities perform essential agricultural functions, which include nutrient cycling and disease management and stress mitigation for sustainable farming practices.

Nutrient recycling and biofortification

Biofilms formed by plant growth-promoting microorganisms (PGPM) significantly contribute to raising soil fertility and improving the bioavailability of essential nutrients (21). Through various mechanisms such as solubilisation, fixation, and retention, these microbial consortia directly impact the cycling of essential nutrients, including nitrogen (N), phosphorus (P) and potassium (K). A recent meta-analysis study highlighted the importance of microbial activity in transforming N, P and K into plant-available forms, a crucial process for supporting crop nutrition (22). Biofilm-forming bacteria, such as *Brucella* sp. (BF10) and *Lysinibacillus macroides* (BF15) in wheat, provide a clear physiological benefit, according to data from a recent field trial. Inoculation with certain PGPR strains resulted in grain N and P levels that were significantly enhanced by as much as 58.5 and 63 % compared to non-inoculated plants (23). Research has demonstrated the functional relationship between enhanced plant nutrient uptake and root colonisation by biofilm-forming consortia.

Plant growth promotion mechanism

Biofilm-associated microbes not only contribute to nutrient cycling but also aid in plant growth promotion using various mechanisms. This includes root colonisation and persistence, improved phytohormone synthesis such as indole-3-acetic acid (IAA), gibberellic acid, etc., modifications in the root system architecture and enhanced acquisition of micro-nutrients (24). These traits were evident when the biofilm-producing *Bacillus aryabhattai* ESB6, when inoculated in the tomato plants grown in drought-prone areas, produced a higher quantity of antioxidant enzyme activity, which reduced the oxidative tissue damage over the control (16). When wheat was pretreated with biofilm-forming PGPR, namely *Brucella* sp. (BF10) and *Lysinibacillus macroides* (BF15), increased root biomass, shoot length and number of tillers (23). These observed growth parameters are testimony to the concept of successful root occupancy by beneficial microbes leading to a synergistic plant-microbe partnership.

Disease suppression and biocontrol

Through various processes, including competitive exclusion, antibiosis and elicitation of plant defensive responses, microbial biofilms significantly improve disease resistance in crops. By filling niches and generating antimicrobials like phenazines, iturins and surfactins, beneficial biofilm-forming microbes may be able to lower the number of phytopathogens. Further, biofilms protect beneficial bacteria from both biotic and abiotic environment stresses, are well as antimicrobial substances (25).

Competition and antagonism

On root surfaces, rhizoplane bacteria, including *Azospirillum*, *Pseudomonas* and *Bacillus,* create biofilms that act as a barrier against pathogens that cause disease (26). Studies have demonstrated that *Bacillus subtilis* can protect plants depending on the conserved genes required for biofilm formation. Therefore, this is crucial for bacteria to colonise plant root surfaces (27). Rhizobacteria linked to plant root surfaces that promote plant growth aid in the competition for the conserved genes required for biofilm formation. Rhizobacteria linked to plant root surfaces that promote plant growth aid in the competitive suppression of infections by the production of antibiotics and secondary metabolite -mediated systemic resistance (28).

Rhizosphere engineering and plant-microbe interaction

A tripartite relationship exists among plant roots, arbuscular mycorrhizal fungi and their associated bacteria. In this system, bacterial biofilms form a continuous cell layer that interacts closely with fungal structures, which are held together within the matrix of self-secreted exopolysaccharides (29). These intricate partnerships improve the efficiency of nutrient transfer and generate combined benefits that support overall plant development. Growing in a biofilm state also enhances the quorum-sensing communication, enabling the microbes to synchronise the expression of necessary traits that promote plant health (30).

Soil structure and quality enhancement

Microbial biofilms stabilise soil aggregates, strengthening the soil structure and improving its capacity to absorb and retain water (31). Biofilms are crucial for preserving soil stability, which is necessary for adequate aeration and moisture retention, by encouraging the production of these aggregates. The EPS that biofilm-forming microorganisms create has adhesive qualities that aid in binding individual soil particles into long-lasting clusters, improving soil porosity, airflow and erosion resistance (20). This enhanced structure promotes microbial activity and healthier root development, initiating a positive feedback loop that enhances the general health and quality of the soil.

Salt tolerance

By attaching sodium (Na) ions to the matrix and lowering the toxicity, biofilm-producing microorganisms that colonise plant roots help defend against salt stress. It has been demonstrated that in salinity circumstances, biofilm-forming halotolerant PGPR boost the uptake of K, calcium (Ca) and magnesium (Mg) and decrease the accumulation of Na. For instance, biofilm–producing isolates decreased electrolyte leakage, decreased Na^+ concentration and increased the K^+/ Na^+ ratio in tomato plants subjected to seawater-induced salinity (16). Rhizobacteria that produce biofilms have the potential to improve food absorption, stabilise cell membranes and increase antioxidant activity (32). Additionally, they generate growth-promoting substances that lessen ionic and osmotic stress, including IAA, 1-aminocyclopropane-1-carboxylate deaminase (ACCD), siderophores and osmo protectants. A sustainable method of controlling soil salinity, inoculating plants with halotolerant, biofilm-producing bacteria increases chlorophyll levels, biomass and overall plant vigour under salt stress conditions (16).

Role in soil microbial diversity and ecosystem resilience

Biofilms act as small-scale ecological hubs that promote high microbial diversity by offering protection, maintaining stable microhabitats and enabling coordinated metabolic interactions (Fig. 1). Microorganisms cooperate, share metabolites and create ordered communities that can withstand stress and changes in their surroundings inside these structured matrices. In soil ecosystems, their cooperative framework improves microbial populations' resilience and functional stability (33).

The cross-kingdom microhabitats created by the bacterial biofilms growing on ectomycorrhizal hyphae facilitate close fungal-bacterial coexistence. Because they encourage resource exchange and boost functional diversity within the soil microbiome, these hybrid biofilms are essential for structuring complex below-ground microbial communities (34). Furthermore, important microbial

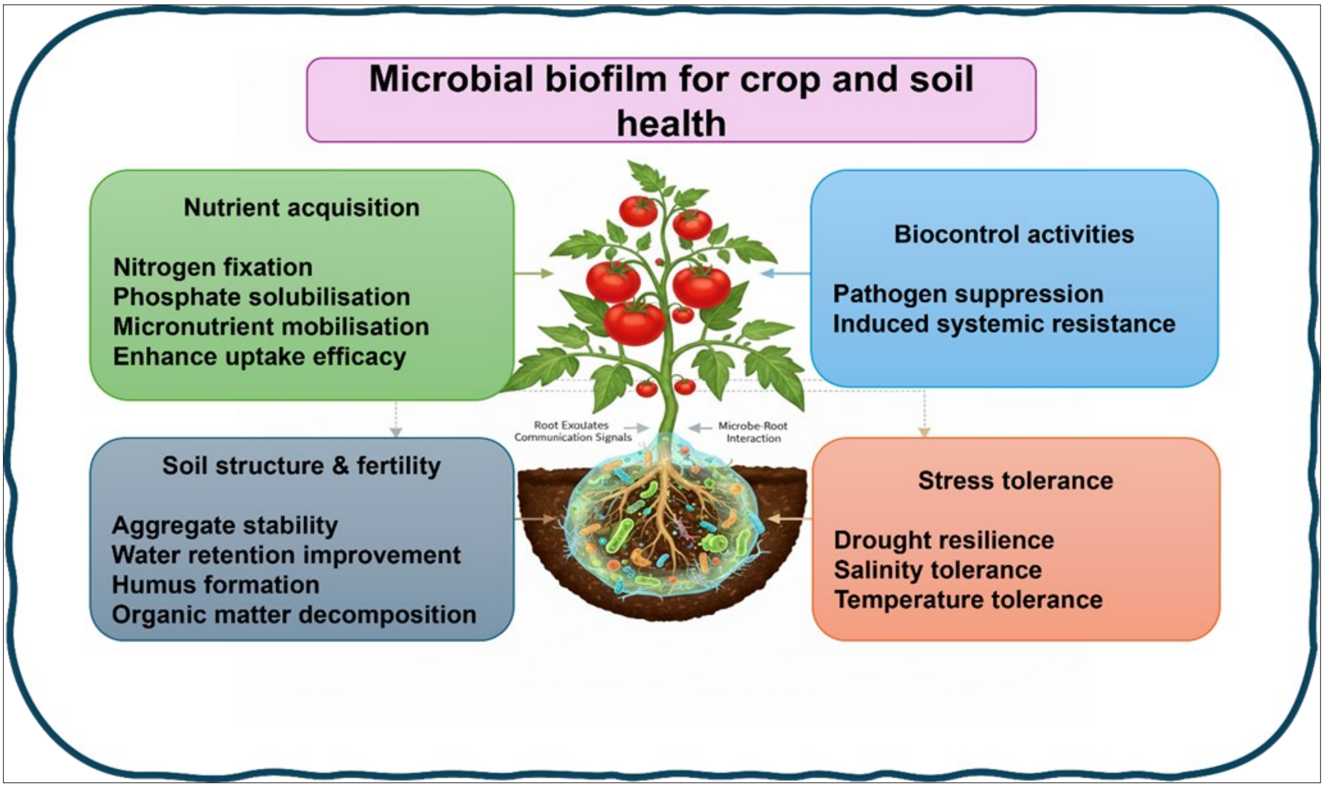

Fig. 1. Microbial biofilms contribute to soil rejuvenation and plant growth by performing beneficial functions.

reservoirs are root surface microbial biofilms. Numerous bacterial species that can create antibiotic chemicals, nutrients cycle and transform heavy metals which present in these biofilms. It has been demonstrated that the rich and adaptable microbial populations found in rhizosphere soil microbial biomass improve the rhizospheres' ecological resilience, especially in situations involving soil contamination or environmental stress (35).

The PGPR that form biofilms are essential for boosting microbial resistance to abiotic stressors such as salinity, drought and temperature changes. Biofilm-forming bacterial strains have been demonstrated to stabilise microbial populations in the rhizosphere and increase plant resistance to drought in wheat farming (36). These findings underscore the protective functions of biofilms, which serve as a physical and physiological barrier, allowing microbial populations to withstand environmental stress and continue supporting key soil processes in Table 1.

Bacterial and Fungal Strains Exhibiting Biofilm-Mediated Plant Growth Promotion

The microbial biofilms that develop on plant roots or along fungal hyphae provide a protective, sticky microenvironment that keeps the beneficial microbes in proximity to the plant. The exopolysaccharide eDNA and protein coating of the biofilm assist the microbes to adhere firmly to the root surface, as well as to survive longer within the soil. These matrix components also enhance nutrient availability by promoting processes such as phosphate solubilization and iron uptake with the help of siderophores. Plant growth-promoting compounds like IAA and ACCD also build within the biofilm, providing plants with easier access to growth regulators. The osmotic stress and drought tolerance of roots in the hydrated system also prevent the biofilm from forming, since the biofilm holds water and enhances soil aggregates around the root zone. Microbial communities that form biofilms also protect plants against pathogenic microbes: they generate antimicrobial or antifungal molecules and physically impede the access of the pathogenic microbes to the root colonisation areas Table 2.

Role of epiphytic and endophytic microbial biofilms for agriculture

Epiphytic biofilms grow on the external surfaces of the plant, including leaves, stems and fruits, whereas endophytic biofilms grow within plant tissues, typically in intercellular spaces or within vascular systems (44). They both use EPS to adhere and survive on surfaces and to resist stress, but operate in different conditions: epiphytic biofilms experience variable environmental conditions and endophytic ones are under a more protective internal environment (45). Previous microscopic observations revealed that epiphytic communities on leaf surfaces could accumulate to a multi-layered structure of about 20 µm, which is concentrated in a nutrient-rich region on the surface of the leaf (46). Leaf-FISH imaging shows that leaf-associated bacteria do not disperse uniformly; rather, some species favour niches like small cuticular depressions or subcuticular areas, indicating functional roles linked with particular microhabitats (47).

The epiphytic yeast *Saccharomyces cerevisiae* on fruit surfaces serves as an example of how naturally forming biofilm-like communities can be advantageous to agriculture. Diverse yeast groups whose composition changed with location and plant conditions were discovered in studies on wild grape berries (*Vitis vinifera* spp. *sylvestris*), indicating that these communities are shaped by the environment rather than being generated at random (48). Native epiphytic yeasts that successfully inhibited the principal grape disease, *Botrytis cinerea*, *Aspergillus* spp. and *Fusarium oxysporum in vitro* were found in research on Malaysian grapevines. These yeasts also show excellent antifungal activity under berry-like surface conditions (49).

Strong plant-beneficial characteristics, such as auxin production, siderophores release and the capacity to solubilise phosphate, K and zinc (Zn) were demonstrated by endophytic *Bacillus* strains from pearl millet (*Pennisetum glaucum*). Additionally, they released several hydrolytic enzymes such as amylase, cellulase, lipase and proteases that improved nutritional absorption and aided

Table 1. Role of microbial biofilms in soil health components

Soil health component	**Mechanistic role of microbial biofilms**	**Experimental outcomes**	**References**
Stress-protected microbial community	The EPS matrix protects microbes from desiccation and osmotic stress	Mixed biofilm-producing PGPR from drought-prone soil improved soil microhabitat stability and enhanced plant growth	(16)
Nutrient retention	The EPS matrix traps nutrients; bacteria solubilise P and micronutrients and improve uptake	Biofilm-forming wheat PGPR increased soil N, P and K availability and improved nutrient uptake and yield	(23)
Ecosystem resilience to stress	Biofilms buffer microbes against drought, salinity and temperature extremes	In wheat, biofilm-forming PGPR increased antioxidant activity, improved RWC and stabilised rhizosphere microbial populations under drought	(36)
Microbial diversity enhancement	Biofilms act as microhabitats supporting multispecies communities	Bacteria formed biofilms on *Laccaria bicolor* hyphae; increased coexistence and cross-kingdom interactions	(34)
Soil structure and aggregation	The EPS binds soil particles, increases aggregate stability and creates a cohesive rhizospheric matrix	The EPS-producing PGPR increased soil aggregation, root-adhering soil and soil moisture retention in wheat soils	(37)
Rhizosphere soil stability	Biofilms form a protective coating on root surfaces, stabilising root–soil contacts	Root surface microbial biofilms (RSMB) improved soil particle adhesion around roots and created a stable nutrient-rich microenvironment	(38)
Mineral binding & reduced leaching	The EPS chelates minerals (Ca^{2+}, Mg^{2+}, Fe^{3+}), reducing nutrient loss	Biofilms concentrated nutrient ions near root zones, leading to higher nutrient-use efficiency	(38)
Functional diversity and metabolic cooperation	Sharing metabolites, enzymes and signals within biofilms increases functional redundancy	Biofilm-associated communities near roots contained diverse nutrient-cycling and contaminant-transforming bacteria	(38)

Table 2. Microbial strains for exhibiting biofilm for crop growth

Strain (bacterial/ fungal)	**Experimental host**	**Functional traits**	**Experimental outcome**	**References**
Bacillus amyloliquefaciens SQR9	Maize roots	Biofilm stimulation by root exudates; matrix genes upregulate; chemotaxis and motility genes are activated	Strong biofilm architecture on roots; enhanced rhizosphere colonisation; increased expression of PGPR genes	(14)
Bacillus velezensis FZB42	Root-associated PGPR (biofilm regulatory assays)	c-di-GMP regulated biofilm formation and dispersal; EPS and matrix dynamics	Controlled biofilm dispersal; enhanced stability of root-associated population	(15)
Mixed biofilm-producing rhizobacteria (*Bacillus, Arthrobacter, Lysinibacillus*)	Tomato under drought	Biofilm production ACC deaminase; IAA; siderophores; P and Zn solubilization	Improved shoot/root biomass, chlorophyll content relative water content under drought	(16)
Biofilm-forming *Brucella* sp (BF10) and *Lysinibacillus macroides* (BF15)	Wheat (filed + green house	Biofilm formation; P solubilization; IAA and siderophore production	Increased grain yield, root mass, NPK uptake; strong positive correlation between biofilm biomass and yield traits	(23)
Pseudomonas donghuensis P482	Tomato and maize roots	Strong biofilm formation; EPS production; carbon-source dependent and root colonisation traits	Dense root-surface microcolonies; improved colonisation on both hosts; glycerol significantly enhanced biofilm biomass	(18)
Bacteria forming biofilm on the ectomycorrhizal fungus *Laccaria bicolor*	*Laccaria bicolor* hyphae	eDNA-mediated adhesion; cross-kingdom biofilm formation	Dense bacterial films on hyphae; increased hyphal stability and potential nutrient exchange	(34)
Pseudomonas rhodesiae HAI-0804	Cucumber roots	Strong biofilm-mediated root colonisation; antifungal metabolites	Significant reduction of Pythium damping-off; high root colonisation density enhanced by glutamate amendment	(39)
Bacillus subtilis (root-associated isolates)	*Arabidopsis thaliana*	Strong biofilm formation: antibiotic biosynthesis (surfactin, plipastatin)	Forming dense biofilm on roots significantly increased expression of antibiotic gene clusters when colonising the root, improving root protection	(40)
Pseudomonas simiae PICF7	Olive (*Olea europaea)*	Biofilm formation; root colonisation; biocontrol of *Verticillium dahliae*	Reduced verticillium wilt incidence; colonised root epidermis &cortical tissues; suppressed pathogen colonisation in planta	(41)
Paenibacillus polymyxa A26	Wheat	The EPS-rich biofilms antifungal polysaccharides	Reduced induced thick structured biofilms showed strong inhibition of fungal pathogen, improved root colonisation patterns	(42)
Pseudomonas fluorescens SBW25	Barley and *Arabidopsis* (root colonisation assays)	Biofilm formation, cyclic lipopeptide (viscosin) production and root colonisation	CLP-deficient mutant showed reduced biofilm stability& smaller root colonising population; wild type formed thick, structured biofilms	(43)

in the suppression of infection (50). Altogether, the existing evidence indicates that both epiphytic and endophytic biofilms serve the initial protective purposes to the plant in terms of the external surfaces and deeper internally stable roles on the nutrition, stress resistance and general health, respectively. A viable strategy to reduce chemical inputs and enhance crop resilience to changing climatic conditions is to develop microbial inoculants that also incorporate strong surface colonisers, e.g., antagonistic yeasts or phyllosphere bacteria with biofilm-forming endophytes, e.g., *Bacillus, Pseudomonas* or *Stenotrophomonas*.

Techniques Used for Studying PGPR Biofilms

The PGPR with biofilm formation are distinct in comparison with those that do not or have low biofilm-forming PGPR. The biofilm-forming PGPR generate a protective matrix which increases their survival, nutrient uptake and defence against unfavourable conditions like drought, salinity and pathogen attack (51, 52). This results in improved root colonisation, growth in plant biomass and better physiological values when compared to no biofilm-forming strains that tend to have lesser persistence and less significant plant growth advantages (4). Some of the most common methods used to study these differences include crystal violet staining in microtiter plates to determine biofilm biomass, scanning electron microscopy (SEM) and confocal laser scanning microscopy to determine biofilm morphology of roots and colony-forming unit (CFU) counts to determine root colonisation. Direct comparison of the functional effects of biofilm formation is also done using genetic approaches, such as the utilisation of biofilm-deficient mutants, as shown in Table 3.

Factors Involved in Microbial Biofilm Formation in Agriculture

The growth of microbial biofilms in agricultural soils is influenced by a wide variety of related biological and environmental factors. Soil temperature, moisture availability and pH are some of the factors that have significant influences on dictating the behaviours of microbes in the rhizosphere. Moreover, the chemical composition of root exudates, essential minerals concentration and the general microbial biodiversity of the soil have a strong impact on the way the rhizobacteria treat plant roots, adhere to them and eventually form stable biofilm communities. A combination of these factors leads to a dynamic environment that controls the effectiveness of microbial colonisation and positive interactions with plants (23). Knowledge of such determinants is necessary to utilise the biofilm-producing microorganisms to improve crop productivity and resistance in sustainable agriculture.

Root exudate composition and plant species

Carbon and signalling chemicals that control the transition between planktonic and biofilm life forms can be produced by root exudates. In *Bacillus amyloliquefaciens* SQR9, maize root exudates enhanced biofilm formation and altered the expression of genes encoding matrix production (*epsD, tapA*) and chemotaxis/flagellar motility. This suggests that glucose, citric acid and fumaric acids specifically promote matrix gene expression and growth during biofilm formation (14). The idea that combined exudate-soil signals drive biofilm formation patterns observed near the root is supported by genome-wide differential ribonucleic acid (RNA) sequencing of *Bacillus amyloliquefaciens* FZB42 grown in media supplemented with maize root exudates, soil extract or both, which showed that rhizosphere-like conditions induce distinct sets of genes, including those related to surface structures and EPS (15). Colonisation patterns are further influenced by the type of root tissue and plant species. Confocal imaging revealed that *Pseudomonas donghuensis* P482 produced comparatively large dispersed microcolonies on tomato roots but more frequent fine colonies on maize roots, suggesting that host and root surface characteristics have a significant impact on the spatial organisation of biofilms (18).

Quorum sensing (QS) and cell-to-cell communication

One important regulatory route that controls several phases of biofilm growth is QS. According to recent research, biochar can improve microbial aggregation and cell survival, strengthening intercellular communication mediated by QS signalling networks. Bacteria may coordinate a variety of cooperative physiological processes and synchronise biofilm formation by synthesising and sensing particular signalling molecules through this density-dependent communication system (11).

Carbon source and nutrient regime

Under ideal conditions (37 °C and pH 7.0), biofilm development was enhanced when cultures were incubated with 0.025 % glucose, but biofilm formation was suppressed by a higher glucose content of 0.4 % (58). This pattern suggests that glucose affects biofilm physiology in a biphasic concentration-dependent manner. Glucose promotes cellular proliferation and EPS synthesis at lower to moderate levels, which aid in the formation of biofilms. However, too much glucose can inhibit the production of biofilms, most likely as a result of osmotic stress or the build-up of metabolic waste products linked to overflow metabolism (18). Similarly, in *Bacillus amyloliquefaciens*, SQR9 showed that sugar, sugar alcohols, glycosylamines, carboxylic acids, phenolic acid and amino acid made up the majority of the exudates from maize roots. The most common carbohydrate was determined to be glucose and xylose (14) plays an important role in biofilm formation and PGPR activity.

Environmental and abiotic factors

Biofilm-forming rhizobacteria such as *Pseudomonas fluorescence,*

Table 3. Analytical techniques used to study biofilm formation

Methods	Uses	Robustness/limitations	References
Crystal violet staining (Microtiter plate)	Quantifies biofilm biomass on polystyrene well	High throughput, reproducible; may not reflect *in situ* conditions	(51, 53)
Scanning Electron Microscopy (SEM)	Visualises biofilm structure in roots/ surfaces	High resolution, direct evidence and labour-intensive	(54, 55)
Confocal Laser Scanning Microscopy	3D imaging of biofilms, often with fluorescent markers	Detailed spatial information requires labelling	(54)
Colony counts/ CFU on roots	Measures viable colonisation in the rhizosphere/ rhizoplane attached with microbes	Quantitative; it may miss non-culturable cells	(34)
Genetic/ mutant analysis	Compares wild type with biofilm-deficient mutants for functional studies	Mechanistic insights; need genetic tools	(56, 57)

Bacillus cereus, Paenibacillus polymyxa and *Enterobacter* sp. are isolated from drought-prone agricultural soils, often exhibiting significant levels of EPS synthesis together with good tolerance to various abiotic stimuli (59-62). After screening the bacterial isolates from water-limited habitats, it was shown that several strains could form strong biofilms at the air–liquid interface despite drought, high salinity, severe pH and high temperatures. The authors hypothesised that these microbes have a unique ecological advantage due to their capacity to form biofilms and produce a protective EPS matrix, which allows them to endure and perform well in field environments with variable moisture conditions and osmotic stress (16). Because the EPS matrix protects cells from temperature fluctuations, reactive oxygen species and ultraviolet (UV) light by limiting the penetration of harmful agents and facilitating collective stress responses (antioxidant enzymes, suitable solute exchange), stressful abiotic environments favour biofilm lifestyles. Strong biofilms are often produced by multi-stress-tolerant strains, according to screening of isolates from stressed environments; transcriptomic and phenotypic data show that stress responses are integrated into biofilm regulatory circuits so that exposure to heat, salinity, or oxidative stress increases EPS production and shifts population structure toward protected microcolonies (63).

Microbe-microbe and cross-kingdom interactions

Biofilms are often multispecies assemblies in which communities are maintained through physical scaffolding (fungal hyphae), signalling (quorum sensing) and cooperative metabolic exchange (cross-feeding). Bacteria that build biofilms on fungal hyphae use eDNA and EPS filaments to bind and construct filamentous networks that solidify bacterial–fungal consortia. By combining complementary tasks (such as nutrient mobilisation by bacteria and soil exploration by fungi), these cross-kingdom biofilms expand the spatial reach of bacteria (through fungal hyphal networks); these benefits do not occur when single strains are used. Molecular studies and experimental microscopy demonstrate that eDNA filaments and bacterial clustering on ectomycorrhizal hyphae represent a shared mechanism (34).

Soil organic matter (SOM) and external inputs (manures, fertilisers)

Slow-releasing carbon and particulate surfaces for microbial attachment are provided by SOM; particles and humic components can adsorb EPS and encourage cell-mineral bridging. Higher labile carbon soils or amendments have been shown in experiments to increase microbial activity and EPS synthesis, which improves soil aggregate formation and biofilm persistence. Mechanistically, SOM provides physical anchor points that stabilise microcolonies against shear and desiccation and enhance the local availability of substrates for polymer production (3).

Hydrophobicity, surface topology and micro-niche architecture (soil pores, grooves and root hairs)

The effective contact area between cells and surfaces is increased by micro-roughness, hydrophobic patches and crevices (root hairs, junctions). These features also create protected microhabitats with stable diffusional gradients and low shear forces. Confocal imaging of root colonisation reveals that microcolonies preferentially form in grooves and at the bases of root hairs; on soil particles, pore geometry controls nutrition and oxygen micro gradients that, when combined with EPS trapping, promote localised biofilm maturation. Therefore, the location of biofilm initiation and the structural development of biofilms are determined by physical surface features (18, 23).

Extracellular polymeric substances chemistry and matrix components (lipids, proteins, polysaccharides and eDNA)

The biological makeup of EPS affects the viscosity of matrices, the holding capacity of water, cation binding and mechanical strength. Recent analyses of composition show that the major part of EPS is polysaccharides and proteins, followed by eDNA, lipids and amino sugars. The differences in these proportions (depending on species and environment) influence the rates of diffusion, the sorption of nutrients and contaminants and the mechanical strength of the biofilm. Mechanistically, proteins provide adhesin and enzyme capabilities, eDNA forms filamentous cross-linkages that enhance cohesion and carbohydrate polymers form a scaffold, which undergoes hydration to provide structure to biofilm functions in soil and on roots (63).

Agricultural management practices

It has been demonstrated that the conservation tillage methods, including strip tillage and no-tillage, have a serious impact on the diversity and composition of soil bacterial and fungal communities (64). Bacterial communities are highly reactive to changes brought about by tillage compared to fungal communities and such systems normally promote greater microbial diversity. Less intensive methods of tilling are usually advantageous in promoting the development of more stable, resilient and diversified biofilm-forming communities of microbes because over-tilling breaks the soil structure and destroys any existing biofilm and microbial network (20). Research has demonstrated that the incorporation of biofilm-based biofertilizers with regular chemical fertilisers is capable of raising organic carbon in the soil to a large extent, lowering the rate of leaf transpiration and improving plant performance overall. Along with these, the duo treatments are also good for soil moisture conservation and support the rhizoremediation process. Additionally, healthy microbial communities and readily available carbon sources supplied by organics such as compost and manure, which in turn, become a fertile ground for the formation and growth of microbial biofilms in the soil, are two inseparable facts (65). The biofilm formation in farming soils is not influenced by one single factor, but rather is a consequence of the interplay of abiotic stresses, strain-specific regulatory networks, nutrient availability and carbon sources and plant-derived signals (root exudates, host species). Creating climate-smart applications that effectively steer biofilm generation to beneficial functions in the rhizosphere requires knowledge of these factors.

Application of Microbial Biofilm in Agriculture

Microbial biofilms are being recognised extensively as flexible biological tools for climate-smart and sustainable agriculture. They outcompete traditional planktonic inoculants due to their firm root attachment, resistance to a changing environment and capacity to deliver several plant-beneficial effects at the same time (66). Biofilm-forming PGPR typically achieve greater root colonisation and thus enhanced rhizosphere persistence in crops such as wheat, maize and tomatoes, leading to improved plant performance under both controlled and open-field conditions (23). One of the ways to maintain a steady presence in the rhizosphere is through strong biofilms, which, in turn, help bacteria like *Pseudomonas entomophila* FAP1 to better absorb nutrients, to make the growth of the plant faster and to increase the vitality of the seedlings (54) .

Biofilm-based inoculants are highly potent next-generation biofertilizers and bio stimulants because they more efficiently provide key plant growth-promoting processes such as phosphate solubilization, siderophore release, IAA synthesis and ACCD activity. By their EPS-rich biofilms, they not only enhance rhizo-sheath formation but also retain water in the root zone of rainfed or drought areas, thus giving a biological means of reducing water demand for irrigation (67). Similarly, PGPR inoculants that produce EPS enhance soil aggregation and aid in carbon retention, enhancing long-term soil health while reducing nutrient losses (68). A primary mechanism by which biofilm-forming rhizobacteria exert biocontrol is by filling root niches, producing antimicrobial chemicals and supporting long-lasting colonisation, thus outcompeting pathogens effectively. Research on tomato and wheat shows that these biofilm-producing strains are more effective in reducing disease symptoms under stress because they stay closely associated with roots and continue to release protective compounds for a longer time (16). This persistence highlights the potential for the use of biofilm-based microbial consortia as a part of integrated pest and disease management systems.

As biofilm-producing PGPR raise the resistance of plants to heat, salt and drought, they are also very promising for climate-smart agriculture. They raise plant tolerance to abiotic stress by modifying osmolyte accumulation, water retention and antioxidant activity (36). Besides that, biofilms help slow down the climate change process by improving carbon use efficiency, strengthening soil aggregation and getting rid of the microbes that emit nitrous oxide (N_2O), thus becoming very efficient agents for cutting down greenhouse gas releases in agricultural systems (69).

Future Prospects

One of the future opportunities could be the development of biofilm-based microbial products, biofilm-coated seeds and formulations that combine biofilms with organic materials to improve the survival of inoculants and their effectiveness in the field. This is because research on EPS-rich strains such as *Agrobacterium pusense* JAS1 and various *Bacillus* species has demonstrated that choosing or genetically modifying microbes to produce more EPS results in stronger biofilms and improved plant benefits, which in turn means that targeted biofilm can be used to speed up the process of commercialisation (70). The use of multi-strain consortia that are able to form coordinated, cross-kingdom biofilms on roots or mycorrhizal hyphae is another way to look at the future, as it can help in improving nutrient cycling and stress resilience. Thus, microbial biofilms hold almost limitless potential across the spectrum of applications - from biofertilization and biocontrol to stress tolerance, soil improvement and climate-friendly farming. Numerous greenhouse and field experiments that have been conducted so far and whose results have been published indicate that biofilm-based technologies may become the core components of future sustainable agriculture systems.

Conclusion

Microbial biofilms are vital biological frameworks that support plant productivity and soil wellness in climatic-cognizant and sustainable agriculture. They have a wet matrix that prevents the harm of beneficial microbes and can maintain colonisation of roots even during environmental stress. The culture of biofilm-forming PGPR/PGPM promotes nutrient mobilisation and uptake, resulting in improved crop nutrition and yield at reduced external inputs. They activate root growth, balance phytohormones and enhance antioxidative defence, thus leading to performance in drought and salinity. The soil aggregation mediated by EPS also enhances porosity, water retention and stability. Competitive exclusion, antimicrobial activity and the activation of host immunity are other disease management functions that are played by biofilms. Mycorrhizal relationships widen nutrient procurement and create stable micro ecosystems. The phyllo sphere provides a multidimensional protection of internal tissues by epiphytic and endophytic biofilms. Root exudates, soil characteristics and management practices are the driving forces of their formation, which offer chances to rhizosphere engineering. New biofilm-based inoculate, consortia and coated seeds are better established and persistent compared to traditional products. Microbial biofilms enhance the nutrient-use efficiency, the stress resilience of soil and the ability to retain carbon in the soil, offering a nature-based approach to increasing regenerative agriculture as well as long-term climate resilience.

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Authors' contributions

VK conceptualised the review, led the literature collection and critical analysis and prepared the initial and final drafts of the manuscript. RP and KA provided guidance on content structuring, supervised the overall work and critically revised the manuscript. MS and KR contributed to the literature synthesis, organisation and assisted in manuscript writing. TSJR, MV and SAK supported in reviewing and refining the content. All authors read and approved the final manuscript.

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