



REVIEW ARTICLE

Mechanism of biofilm formation and development on plant roots under environmental stress condition

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Abstract

Biofilm formation on plant roots represents a critical adaptive strategy that enhances plant-microbe interactions and improves plant resilience under environmental stress conditions. Root-associated biofilms, primarily formed by plant growth-promoting rhizobacteria (PGPR), are structured microbial communities embedded in extracellular polymeric substances (EPS), which provide mechanical stability, facilitate nutrient exchange and protect against environmental fluctuations. This review synthesises current knowledge on the mechanisms governing biofilm formation on plant roots, with particular emphasis on microbial attachment, EPS production and quorum sensing-mediated regulation. The integration of these mechanisms enables the transition from planktonic to sessile microbial lifestyles and supports the development of functionally efficient biofilms. Environmental stressors such as drought, salinity, nutrient limitation, temperature extremes and heavy metal contamination significantly influence biofilm formation by modulating microbial physiology and plant root processes. Biofilm-mediated responses enhance water retention, regulate ion balance, improve nutrient acquisition and protect plants from toxic compounds and pathogens. Furthermore, biofilms play a key role in modulating root architecture, phytohormone balance and microbial persistence in the rhizosphere, thereby contributing to improved plant growth and productivity. Despite these advantages, challenges remain in understanding the molecular regulatory networks and ensuring consistent field-level performance of biofilm-based applications. Overall, root-associated biofilms represent a promising tool for sustainable agriculture, offering potential strategies to enhance crop resilience and reduce dependence on chemical inputs. Future research should focus on integrating mechanistic insights with field-based approaches to optimise the application of biofilm-forming microorganisms in diverse agro-ecosystems.

Keywords: biofilm formation; environmental stress; extracellular polymeric substances; plant growth-promoting rhizobacteria; quorum sensing; rhizosphere

Introduction

Microorganisms in natural environments predominantly exist as structured, surface-associated communities known as biofilms rather than as free-living planktonic cells (1, 2). These biofilms are embedded within a self-produced matrix of extracellular polymeric substances (EPS), which provides structural stability, facilitates intercellular communication and enhances microbial survival under fluctuating environmental conditions (1, 3). In terrestrial ecosystems, particularly within the rhizosphere, biofilm formation represents a dominant microbial lifestyle that governs plant-microbe interactions and influences soil ecological processes (4, 5).

The rhizosphere constitutes a highly dynamic interface where plant roots, soil physicochemical properties and diverse microbial populations interact continuously (4, 6). Root exudates, including sugars, amino acids, organic acids and secondary metabolites, create nutrient-rich microenvironments that selectively recruit and sustain microbial communities (7, 8). Within this niche, biofilm-forming microorganisms, especially plant growth-promoting rhizobacteria (PGPR), establish stable associations with plant roots, enabling efficient colonisation and long-term persistence (9, 10).

Biofilm formation on plant roots has emerged as a critical adaptive strategy that enhances plant performance under a wide range of abiotic stress conditions, including drought, salinity, nutrient limitation, temperature extremes and heavy metal contamination (11, 12). The EPS matrix plays a central role in mediating these interactions by maintaining hydration, facilitating nutrient retention, buffering osmotic stress and immobilising toxic ions (1, 13). Compared to planktonic cells, biofilm-associated microbes exhibit increased resistance to environmental stressors and improved functional efficiency in supporting plant growth (14).

In addition to stress mitigation, root-associated biofilms contribute significantly to plant nutrition and health through mechanisms such as biological nitrogen fixation, phosphate solubilisation, siderophore production and modulation of phytohormone levels (10, 15). These processes collectively enhance nutrient acquisition, root system architecture and overall plant productivity. Furthermore, biofilms provide a protective barrier against soil-borne pathogens by promoting competitive exclusion, producing antimicrobial compounds and inducing systemic resistance in host plants (4, 9).

Despite substantial advances in understanding the ecological significance of biofilms, the mechanistic basis underlying their formation, regulation and functional dynamics on plant roots remains incompletely resolved (16, 17). In particular, the integration of microbial attachment processes, EPS biosynthesis, quorum sensing and environmental signal transduction requires further elucidation at molecular and systems levels.

Therefore, the present review aims to synthesise current knowledge on the mechanisms governing biofilm formation and development on plant roots under environmental stress conditions. Emphasis is placed on (i) the sequential stages of biofilm development, (ii) key molecular and physiological mechanisms, including microbial attachment, EPS production and quorum sensing and (iii) the modulation of these processes under diverse abiotic stresses. Additionally, the implications of root-associated biofilms for plant growth, stress resilience and sustainable agricultural practices are critically examined.

Biofilm formation on plant roots: conceptual overview

Biofilm composition and structural organisation

Biofilms are structured microbial communities embedded within a self-produced EPS matrix that anchors cells to biotic or abiotic surfaces (1–3). In the rhizosphere, biofilms formed on plant roots represent highly organised and dynamic systems in which bacteria, fungi and other microorganisms coexist and interact within a hydrated microenvironment (4, 5).

The EPS matrix constitutes the fundamental structural framework of biofilms and is primarily composed of polysaccharides, proteins, extracellular DNA (eDNA) and lipids (1). This matrix performs multiple functions, including facilitating cell-cell adhesion, anchoring microbial cells to root surfaces and creating a protective barrier against environmental fluctuations (1, 3). The physicochemical properties of EPS, such as viscosity, charge and water-holding capacity, influence biofilm architecture and functionality (1, 2).

In addition to microbial EPS, plant-derived compounds such as root mucilage contribute significantly to the structural complexity of rhizosphere biofilms (5). Root mucilage, rich in polysaccharides and glycoproteins, shares functional similarities with microbial EPS and enhances the formation of a cohesive biofilm matrix (4, 5). This synergistic interaction between plant-secreted polymers and microbial exopolymers promotes the establishment of a stable and interactive microenvironment at the root-soil interface.

Biofilm architecture is inherently heterogeneous, characterised by microcolonies, water channels and gradients of nutrients and oxygen (14, 16). These structural features enable efficient nutrient diffusion, waste removal and spatial organisation of microbial populations (15). Such organisation supports metabolic cooperation and functional specialisation within the biofilm, thereby enhancing the resilience and adaptability of microbial communities associated with plant roots.

Stages of biofilm development on plant roots

Biofilm formation on plant roots is a dynamic and sequential process involving distinct developmental stages that collectively determine the stability and functionality of the microbial community (14) (Fig. 1).

Initial attachment represents the first stage, wherein motile microbial cells approach the root surface and establish reversible interactions mediated by physicochemical forces such as van der Waals interactions, electrostatic forces and hydrophobic interactions (3). Root exudates act as chemoattractants, guiding microbial cells toward the rhizoplane and facilitating initial contact (7, 8).

Following reversible attachment, microorganisms transition to irreversible adhesion, characterised by the production of adhesins, extracellular polysaccharides and surface-associated proteins that strengthen attachment to the root surface (18). This transition marks the commitment of microbial cells to a sessile lifestyle. This transition is tightly regulated by intracellular signalling molecules such as cyclic di-guanosine monophosphate (c-di-GMP) (17, 19).

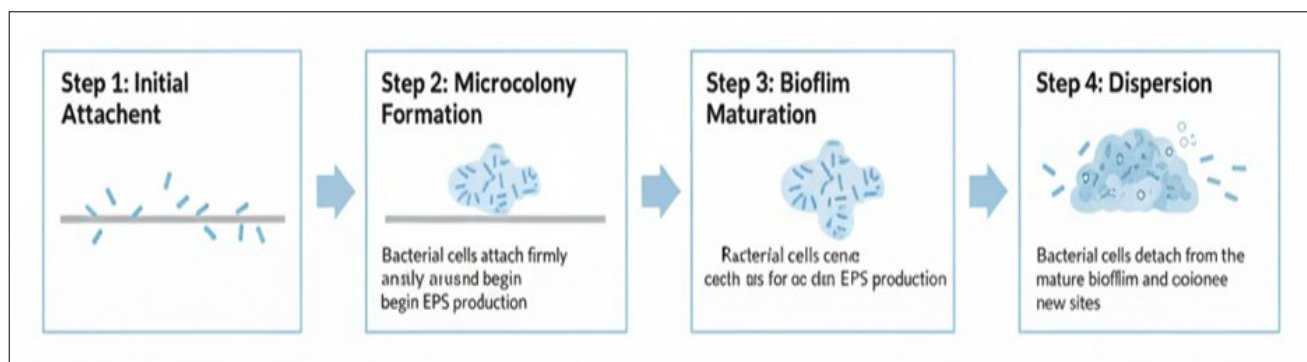


Fig. 1. Stages of biofilm formation on plant roots, illustrating initial reversible attachment, irreversible adhesion, microcolony formation, maturation with extracellular polymeric substance (EPS) production and dispersion.

Subsequently, attached cells proliferate and form microcolonies, which serve as the foundational units of biofilm structure. During this stage, increased EPS production promotes cell aggregation and stabilisation of the developing biofilm matrix (3, 15).

As the biofilm matures, it develops into a complex three-dimensional structure through the process of biofilm maturation. This stage involves extensive EPS accumulation, formation of structured microenvironments and establishment of nutrients and signalling gradients (14). Mature biofilms exhibit enhanced resistance to environmental stressors and improved functional capabilities.

Finally, the dispersion stage enables the release of microbial cells from the biofilm into the surrounding environment. Dispersed cells can colonise new root surfaces or niches, thereby facilitating the spread and persistence of biofilm-forming populations in the rhizosphere (14).

These stages are not strictly linear but are regulated by environmental conditions, plant-derived signals and microbial regulatory networks (4, 11). Understanding this developmental continuum is essential for elucidating the mechanistic basis of biofilm formation and its role in plant-microbe interactions (Table 1).

Microbial attachment and root colonisation

Microbial attachment to plant root surfaces represents a critical initial step in biofilm formation, governing the transition from a free-living (planktonic) to a surface-associated (sessile) lifestyle (3, 20). This process is highly regulated and involves a combination of physicochemical interactions, microbial structural components, plant-derived signals and regulatory networks.

The initial phase of attachment is mediated by weak and reversible physicochemical forces, including van der Waals interactions, electrostatic forces and hydrophobic interactions (3, 16). These forces enable microbial cells to approach and transiently associate with the rhizoplane. The physicochemical properties of the root surface, influenced by root exudates and mucilage, play a significant role in modulating these interactions by altering surface charge, wettability and nutrient availability (5, 7).

Microbial motility and surface sensing are essential for effective root colonisation. Flagella-driven motility facilitates chemotactic movement toward root exudates, while type IV pili contributes to surface exploration and attachment through twitching motility (3, 20). Upon sensing a suitable surface, microbial cells undergo physiological changes that reduce motility and promote adhesion (17, 19). This transition is tightly regulated by intracellular signalling molecules, particularly cyclic di-guanosine monophosphate (c-di-GMP), which acts as a key regulator of the switch between motile and sessile states (17, 19).

Irreversible attachment is established through the production of cell surface-associated adhesins, including fimbriae, pili and large extracellular adhesion proteins (18, 21). These structures mediate strong binding to root surfaces and facilitate stable colonisation. In addition, the initiation of extracellular polymeric substance (EPS) production reinforces attachment by embedding microbial cells within a cohesive matrix that anchors them to the root surface and to neighboring cells (1, 3).

Root exudates play a central role in shaping microbial attachment and colonisation patterns. These exudates, composed of sugars, amino acids, organic acids and secondary metabolites, function as chemoattractants and nutrient sources that selectively recruit beneficial microorganisms (7, 8). Moreover, specific exudate components can induce the expression of genes associated with adhesion and biofilm formation, thereby enhancing colonisation efficiency (7, 8).

Plant immune responses further influence microbial attachment dynamics. Root cells possess pattern recognition receptors capable of detecting microbe-associated molecular patterns (MAMPs), triggering defence responses that can restrict microbial colonisation (22). However, successful biofilm-forming microorganisms employ strategies to evade or modulate host immunity, including the secretion of effector molecules, alteration of cell surface properties and colonisation of immune-privileged niches such as root tips and elongation zones (4, 9).

Environmental factors, including soil moisture, salinity, temperature and the presence of toxic compounds, significantly affect attachment efficiency (11, 12). For instance, drought conditions enhance mucilage production, creating a hydrated microenvironment that facilitates microbial retention on root surfaces (5, 6), whereas high salinity may alter ionic interactions and influence adhesion dynamics (23). Microorganisms often respond to such conditions by modifying surface properties and increasing EPS production to maintain stable attachment.

Overall, microbial attachment to plant roots is a dynamic and multifactorial process that integrates physical interactions, biological signalling and environmental cues (3, 14). The successful establishment of stable root colonisation sets the foundation for subsequent biofilm development and functional interactions between plants and microbial communities.

Extracellular polymeric substances (EPS) in biofilm formation

Extracellular polymeric substances (EPS) constitute the principal structural and functional component of microbial biofilms, playing a central role in the establishment, stabilisation and persistence of root-associated microbial communities (1, 2). The EPS are high-

Table 1. Mechanisms involved in initial microbial attachment to plant roots

Process	Key mechanisms	Plant example	Reference
Reversible attachment	Weak physicochemical forces (van der Waals, electrostatic, hydrophobic), motility (flagella, pili)	Rice roots under drought; recruitment of <i>Bacillus</i> and <i>Streptomyces</i>	(18)
Irreversible adhesion	Adhesins, EPS production, quorum sensing regulation	<i>Bacillus velezensis</i> SQR9 on cucumber roots	(21)
Stress-mediated modulation	Altered root exudates, mucilage secretion, osmotic adjustment	Rhizosheath formation in drought-stressed rice	(5)
Host-mediated selection	Root immune recognition, MAMP signalling, microbial evasion strategies	<i>Rhizobium</i> spp. on legume root hairs	(31)
Regulatory coordination	Cyclic-di-GMP signalling, quorum sensing	<i>Pseudomonas fluorescens</i> surface sensing	(17, 19, 24)

EPS: extracellular polymeric substances; MAMP: microbe-associated molecular pattern; GMP: guanosine monophosphate.

molecular-weight polymers predominantly composed of polysaccharides, proteins, extracellular DNA (eDNA) and lipids, which collectively form a hydrated and viscoelastic matrix surrounding microbial cells (1).

During the transition from reversible to irreversible attachment, EPS production is a defining event that facilitates the consolidation of microbial cells on the root surface (3, 18). The adhesive properties of EPS enhance cell surface and cell-cell interactions, enabling the formation of microcolonies and the development of a cohesive biofilm structure (1, 3). The biochemical composition of EPS influences its functional properties, including surface affinity, hydrophobicity, porosity and water retention capacity, which are critical for stable root colonisation (1, 2).

Beyond its structural role, EPS functions as a protective barrier that shields microbial communities from environmental stressors (11, 12). The hydrated matrix maintains local moisture conditions, buffers osmotic fluctuations and restricts the diffusion of toxic compounds, thereby enhancing microbial survival under adverse conditions. In the rhizosphere, EPS also contributes to soil aggregation and the formation of a rhizosheath, improving root-soil contact and facilitating resource exchange (5, 6).

The biosynthesis of EPS is tightly regulated by complex microbial signalling networks. Intracellular secondary messengers, particularly cyclic di-guanosine monophosphate (c-di-GMP), play a central role in activating EPS production while repressing motility-related genes, thereby promoting the transition to a sessile biofilm lifestyle (17, 19). In addition, quorum sensing (QS) systems coordinate EPS synthesis at the population level by regulating gene expression in response to cell density (3, 24). These regulatory mechanisms ensure that EPS production is synchronised with biofilm developmental stages and environmental conditions.

Extracellular polymeric substances also plays a critical role in mediating interactions between microorganisms and host plants. By forming a physical interface at the root surface, EPS facilitates close association between microbial cells and plant tissues, enabling efficient exchange of nutrients and signalling molecules (4, 9). Furthermore, EPS contributes to plant protection by limiting the accessibility of root surfaces to pathogenic organisms (9, 13) and by immobilising toxic ions such as sodium and heavy metals through biosorption and chelation processes (12, 13).

Environmental factors strongly influence EPS production and composition. Under drought conditions, increased EPS synthesis enhances water retention and creates a hydrated microenvironment that mitigates desiccation stress (5, 11). In saline soils, EPS binds and sequesters sodium ions, thereby reducing ionic toxicity and maintaining osmotic balance (13, 23). Similarly, in metal-contaminated environments, EPS acts as a sink for heavy metals, decreasing their bioavailability and limiting their uptake by plant roots (13, 25).

Collectively, EPS represents a multifunctional component of root-associated biofilms that integrates structural integrity, environmental protection and plant-microbe interactions (1, 12). Its regulated production and adaptive properties are fundamental to the successful establishment and resilience of microbial biofilms in the rhizosphere.

Quorum sensing and regulatory networks in biofilm formation

Quorum sensing (QS) is a cell density-dependent communication mechanism that enables microorganisms to coordinate collective behaviours, including biofilm formation, through the production, release and detection of signalling molecules known as autoinducers (3, 24). In root-associated microbial communities, QS plays a central role in regulating the transition from individual cellular activity to coordinated, multicellular biofilm development.

QS systems operate through the accumulation of autoinducers in the local environment as microbial population density increases (24). In Gram-negative bacteria, N-acyl homoserine lactones (AHLs) serve as the primary signalling molecules, whereas Gram-positive bacteria typically utilise oligopeptides (24). Once a threshold concentration is reached, these signalling molecules bind to specific regulatory proteins, triggering the activation or repression of target genes associated with biofilm formation (3, 24).

A key function of QS in biofilm development is the regulation of genes involved in microbial adhesion, EPS biosynthesis and structural organisation of the biofilm matrix (1, 3). During the early stages of biofilm formation, QS enhances the expression of adhesins and surface-associated proteins, facilitating stable attachment to plant roots (3, 20). As the biofilm develops, QS regulates the production of EPS components, ensuring coordinated matrix formation and structural integrity of the microbial community.

Quorum sensing also plays a critical role in biofilm maturation by controlling the spatial organisation and functional differentiation of microbial populations. It regulates the formation of microcolonies, development of nutrient channels and establishment of metabolic gradients within the biofilm (14, 16). These processes enhance resource utilisation efficiency and contribute to the resilience of the biofilm under fluctuating environmental conditions (14).

In addition to structural regulation, QS modulates the expression of genes involved in stress responses, antimicrobial compound production and competitive interactions (11, 12). This enables biofilm-forming microorganisms to adapt to environmental challenges and suppress competing or pathogenic species within the rhizosphere.

Plant-derived compounds further influence QS-mediated regulation. Root exudates, including flavonoids and other secondary metabolites, can modulate QS activity by either enhancing or inhibiting signal perception and gene expression (4, 7, 22). This interaction allows plants to indirectly shape microbial behaviour and selectively promote beneficial biofilm-forming populations.

QS systems are also integrated with intracellular regulatory networks, particularly those involving c-di-GMP, which coordinates the transition between motile and sessile states (17, 19). The interplay between QS signalling and intracellular second messengers ensure precise temporal and spatial regulation of biofilm development.

Overall, QS serves as a central regulatory mechanism that synchronises microbial activities during biofilm formation on plant roots. By integrating population density signals, environmental cues and plant-derived factors, QS enables the development of structured, functional and adaptive biofilm communities in the rhizosphere (3, 14).

Integration of mechanisms governing biofilm formation

Biofilm formation on plant roots is not governed by isolated processes but rather by a highly coordinated network of interacting mechanisms that collectively regulate the transition from planktonic to sessile microbial lifestyles (3, 14). Microbial attachment, EPS production and QS function as interconnected components of a dynamic regulatory system, integrating environmental signals and host-derived cues to control biofilm development (1, 3).

The initial stages of biofilm formation involve reversible attachment mediated by physicochemical interactions and microbial motility (3, 20). Upon successful surface sensing, intracellular signalling pathways particularly those involving c-di-GMP trigger a regulatory switch that suppresses motility and activates genes associated with adhesion and EPS biosynthesis (17, 19). This transition marks the onset of irreversible attachment and commitment to biofilm formation (18).

Extracellular polymeric substances production reinforces this transition by stabilising microbial cells on the root surface and promoting cell-cell aggregation (1, 3). Simultaneously, QS systems monitor population density and synchronise gene expression across the microbial community (3, 24). As autoinducer concentrations reach threshold levels, QS amplifies the expression of genes involved in adhesion, matrix production and biofilm maturation, ensuring coordinated development of the biofilm structure (14).

These regulatory processes are further modulated by plant-derived signals, particularly root exudates, which influence microbial behaviour at multiple levels (4, 7). Exudates act as chemoattractants during initial colonisation, induce gene expression related to adhesion and EPS production and can modulate QS signalling pathways (7, 22). This bidirectional communication enables plants to shape the composition and activity of root-associated microbial communities.

Environmental conditions provide an additional layer of regulation, influencing each stage of biofilm development (11, 12). Factors such as soil moisture, salinity, temperature and nutrient availability affect microbial physiology, signal transduction pathways and EPS composition (11, 13). For example, stress conditions often enhance EPS production and QS activity, promoting the formation of more resilient biofilm structures (12). Thus, biofilm formation represents an adaptive response that integrates environmental stress signals with microbial regulatory networks.

At the systems level, biofilm development can be conceptualised as a coordinated sequence of transitions governed by feedback loops between intracellular signalling molecules (e.g., c-di-GMP), extracellular communication systems (QS) and environmental and host-derived inputs (14, 16). These interactions ensure that biofilm formation occurs only under conditions favourable for stable colonisation and long-term survival.

Overall, the integration of attachment processes, EPS biosynthesis and QS establishes a robust regulatory framework that enables microorganisms to form structured, adaptive and functionally efficient biofilms on plant roots (3, 12). Understanding this integrated network is essential for manipulating biofilm formation in agricultural systems to enhance plant resilience and productivity (15).

Environmental stress-mediated modulation of biofilm formation

Biofilm formation on plant roots is strongly influenced by environmental conditions, particularly abiotic stress factors that alter both microbial physiology and plant root dynamics (4, 11). In the rhizosphere, stresses such as drought, salinity, nutrient limitation, temperature extremes and heavy metal contamination not only challenge microbial survival but also actively promote biofilm formation as an adaptive response (12). These conditions modulate key processes including microbial attachment, EPS production, QS and community composition, thereby shaping the structure and function of root-associated biofilms (3, 12).

Drought stress

Drought stress reduces soil water potential, limits nutrient diffusion and imposes osmotic constraints on microbial cells (6, 11). In response, many rhizosphere microorganisms enhance EPS production, which contributes to the formation of a hydrated microenvironment surrounding plant roots (1, 5). This leads to the development of a rhizosheath, wherein soil particles adhere to roots through mucilage and microbial polymers, improving water retention and protecting roots from desiccation (5).

Microorganisms also accumulate compatible solutes such as trehalose and glycine betaine to maintain cellular integrity under osmotic stress (6). Drought conditions frequently select stress-tolerant microbial taxa, including members of Actinobacteria and Firmicutes, which can form resilient biofilms (6, 11). These adaptations collectively enhance plant water status, maintain root functionality and promote survival under water-limited conditions (11, 12).

Salinity stress

Salinity stress imposes both osmotic and ionic challenges due to elevated concentrations of sodium and chloride ions (23). Biofilm-forming microorganisms mitigate these effects primarily through EPS-mediated sequestration of sodium ions, reducing their availability and toxicity to plant roots (1, 13). The polyanionic nature of EPS facilitates the binding of cations, thereby contributing to ionic homeostasis within the rhizosphere (1).

In addition, microorganisms synthesise osmoprotectants such as proline and ectoine to counteract osmotic imbalance (23). Salinity has also been shown to upregulate genes associated with EPS production and QS, indicating that biofilm formation is an actively regulated adaptive strategy under saline conditions (12). However, extreme salinity may reduce microbial diversity, leading to dominance of specialised halotolerant biofilm-forming populations (23).

Nutrient deficiency

Nutrient limitation significantly influences biofilm dynamics by altering both microbial metabolism and plant root exudation patterns (4, 10). Under conditions of carbon or nitrogen limitation, microorganisms often increase surface attachment and EPS production as a survival strategy to conserve resources and enhance nutrient capture (10).

Phosphorus deficiency can stimulate the recruitment of phosphate-solubilising microorganisms through the release of organic acids and secondary metabolites by plant roots (4, 10). Biofilms enhance nutrient acquisition by concentrating enzymes such as phosphatases and siderophores within the EPS matrix,

thereby improving nutrient availability and uptake by plants (10, 15). However, under severe nutrient deprivation, biofilm stability may be compromised, leading to dispersal of microbial cells in search of alternative nutrient sources (14).

Temperature extremes

Temperature fluctuations influence microbial growth rates, metabolic activity and biofilm architecture (11). Moderate increases in temperature can enhance biofilm formation by accelerating microbial metabolism and EPS production (12). In contrast, heat stress may destabilise biofilm structures, induce dispersal or select for thermotolerant microbial populations (12).

Cold stress generally slows biofilm development but favours the proliferation of psychrotolerant microorganisms capable of producing cryoprotective EPS with altered physicochemical properties (11). These adaptations help maintain cellular integrity and biofilm stability under low-temperature conditions. Overall, temperature acts as a key determinant of biofilm composition, structure and functional efficiency in the rhizosphere.

Heavy metal contamination

Heavy metals such as cadmium, lead and chromium exert strong selective pressure on microbial communities due to their toxicity (13). Biofilm formation enhances microbial tolerance to these contaminants through multiple mechanisms, including biosorption, chelation and precipitation of metal ions within the EPS matrix (1, 13). This reduces metal mobility and limits their uptake by plant roots (13).

Certain microorganisms possess additional detoxification mechanisms, such as efflux pumps and metal-binding proteins (e.g., metallothioneins), which further enhance resistance (12). Biofilm-mediated immobilisation of heavy metals contributes to phytostabilisation and can improve plant growth in contaminated soils (12, 13). However, in some cases, microbial activity may increase metal mobility, highlighting the need for careful management in agricultural applications (13).

Cross-stress mechanisms and integrated responses

Despite the diversity of environmental stressors, several conserved mechanisms underpin biofilm-mediated adaptation in the rhizosphere (11, 12). Extracellular polymeric substances production represents a central and universal response, contributing to water retention under drought, ion sequestration under salinity and metal immobilisation under contamination (1, 13). Similarly, quorum sensing integrates environmental signals with population-level responses, regulating gene expression associated with biofilm formation and stress tolerance (12, 24).

The accumulation of compatible solutes, modulation of membrane composition and activation of stress-responsive genes are additional common strategies employed by biofilm-forming microorganisms across multiple stress conditions (6, 12). These responses are often accompanied by shifts in microbial community

composition, favoring stress-tolerant taxa capable of maintaining biofilm integrity under adverse conditions (4, 11).

Collectively, these cross-cutting mechanisms highlight biofilm formation as a versatile and adaptive strategy that enables microorganisms to withstand diverse environmental challenges while simultaneously enhancing plant resilience (Fig. 2).

Understanding these integrated responses is essential for developing targeted approaches to manipulate biofilm formation for improved agricultural sustainability (12, 15) (Table 2).

Functional implications of root-associated biofilms in plant systems

Root-associated biofilms play a pivotal role in enhancing plant performance by integrating microbial metabolic activities with plant physiological processes (2, 9, 10). Through coordinated interactions within the rhizosphere, biofilm-forming microorganisms contribute to improved nutrient acquisition, enhanced stress tolerance, modulation of plant development and protection against soil-borne pathogens. These functional outcomes collectively underpin the importance of biofilms in sustainable plant production systems.

Enhancement of nutrient acquisition

Biofilm-forming microorganisms significantly improve nutrient availability and uptake in plants through multiple mechanisms (10, 15). Within the biofilm matrix, enzymes and metabolites are concentrated, increasing the efficiency of nutrient transformations in the rhizosphere (2, 3). For instance, phosphate-solubilising bacteria release organic acids and phosphatases that convert insoluble phosphorus into plant-available forms, while nitrogen-fixing bacteria contributes to the biological conversion of atmospheric nitrogen into ammonia (4, 9).

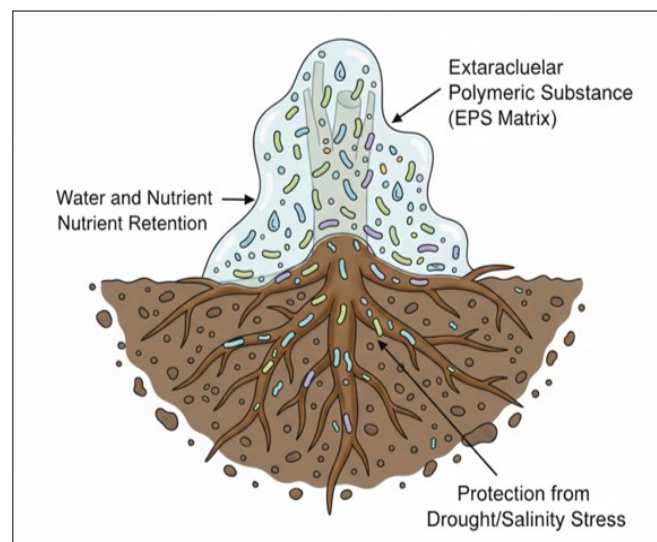


Fig. 2. Schematic representation of root-associated biofilms under environmental stress conditions, illustrating extracellular polymeric substances (EPS)-mediated microbial attachment, water retention, ion sequestration under salinity and heavy metal immobilisation, contributing to enhanced plant stress tolerance.

Table 2. Environmental stresses and biofilm-mediated mechanisms in plant roots

Environmental stress	Biofilm mechanism	Benefit to plant	Reference
Drought	EPS production, rhizosheath formation	Water retention, reduced desiccation	5, 11
Salinity	EPS-mediated Na^+ sequestration	Reduced ionic toxicity, osmotic balance	1, 13, 23
Heavy metals	Biosorption and chelation by EPS	Reduced metal uptake	13, 25
Nutrient deficiency	Enzyme concentration, siderophore production	Improved nutrient availability	10, 15

EPS: extracellular polymeric substances.

In addition, the production of siderophores enhances the mobilisation and uptake of micronutrients such as iron by chelating and transporting them to plant roots (4, 10). The close spatial association between microbial cells and root surfaces within biofilms further facilitates efficient nutrient exchange, thereby improving nutrient use efficiency and promoting plant growth under both optimal and nutrient-limited conditions (2, 3).

Enhancement of stress tolerance

Biofilms contribute to plant resilience against abiotic stresses by creating a protective microenvironment around roots (11, 12). The EPS matrix maintains hydration, buffers osmotic stress and regulates the availability of toxic ions, thereby protecting both microbial communities and plant tissues (1, 5). Under drought conditions, biofilms enhance water retention and stabilise soil aggregates, while under salinity stress, EPS-mediated ion sequestration reduces sodium toxicity (13, 23).

Biofilm-forming microorganisms also induce physiological responses in plants, including the activation of antioxidant systems and stress-responsive pathways, which further enhance tolerance to environmental stresses (11, 26). These combined effects improve plant survival, growth and productivity under adverse conditions.

Modulation of root architecture and morphological adaptations

The presence of biofilm-forming plant growth-promoting rhizobacteria (PGPR) influences root system architecture, leading to increased root length, branching and surface area (9, 27). These changes enhance the plant's ability to explore soil resources and improve the uptake of water and nutrients.

Biofilms also promote the formation of root-associated structures such as rhizosheaths, which improve soil adhesion and root stability (5, 6). These morphological adaptations are particularly beneficial under stress conditions, where efficient resource acquisition is critical for plant survival.

Regulation of plant hormonal balance

Biofilm-associated microorganisms play a significant role in modulating plant hormone levels, thereby influencing plant growth and development (9, 10). Many PGPR produce phytohormones such as indole-3-acetic acid (IAA), gibberellins and cytokinins, which regulate cell division, elongation and differentiation in plant roots (9, 10).

In addition to hormone production, biofilm-forming microorganisms can modulate plant endogenous hormone signalling pathways, enhancing stress tolerance and promoting adaptive growth responses (28). This hormonal regulation contributes to improved root system development and overall plant vigour.

Suppression of soil-borne pathogens

Biofilms provide an effective biological barrier against pathogenic microorganisms through multiple mechanisms (4, 9). Beneficial microbes within biofilms compete with pathogens for space and nutrients, thereby limiting pathogen establishment on root surfaces (4, 9). Additionally, biofilm-forming microorganisms produce antimicrobial compounds that inhibit the growth of pathogenic bacteria and fungi (11, 29).

Quorum sensing-mediated coordination within biofilms further enhances the production of these bioactive compounds and strengthens collective defence responses (24, 30). Moreover, biofilms can induce systemic resistance in plants, priming host defence mechanisms against subsequent pathogen attacks (22). These protective effects contribute to reduced disease incidence and improved plant health.

Collectively, the functional implications of root-associated biofilms highlight their integral role in promoting plant growth, enhancing resilience to environmental stresses and protecting against pathogens (2, 9). These multifaceted benefits position biofilm-forming microorganisms as key components of sustainable agricultural systems (Table 3).

Plant-microbe interactions in biofilm development

Plant-microbe interactions in the rhizosphere are fundamental to the establishment and functioning of root-associated biofilms (4, 6). These interactions are mediated through complex biochemical signalling, nutrient exchange and ecological dynamics that collectively determine microbial community structure and functionality (2, 3). Biofilms provide a structured platform that enhances these interactions, enabling stable and long-term associations between plants and microorganisms (2, 14).

Symbiotic and commensal relationships

Microorganisms associated with plant roots engage in a range of interactions, including symbiotic and commensal relationships, which are facilitated by biofilm formation (4, 10). In symbiotic associations, such as those between rhizobia and leguminous plants, microorganisms colonise root surfaces and subsequently form specialised structures (nodules) where biological nitrogen fixation occurs (31). These interactions are mutually beneficial, with plants supplying carbon sources to microbes and receiving essential nutrients in return.

In commensal relationships, microorganisms inhabit the rhizosphere or root surfaces without directly affecting plant growth. However, the formation of biofilms enhances the persistence and stability of these microbial populations by providing protection against environmental fluctuations such as desiccation, pH variation and nutrient limitation (1, 11). This stability contributes to the maintenance of a balanced microbial ecosystem around plant roots.

Table 3. Biofilm-forming plant growth-promoting rhizobacteria (PGPR) and their role in enhancing plant stress tolerance

PGPR organism	Plant	Stress	Biofilm function	Plant response	Reference
<i>Bacillus amyloliquefaciens</i>	Tomato	Drought	EPS production, antioxidant activation	Increased biomass, water use efficiency	11
<i>Pseudomonas fluorescens</i>	Wheat	Salinity	Biofilm stability, Na ⁺ sequestration	Improved root growth, chlorophyll	29
<i>Bacillus velezensis</i> SQR9	Cucumber	Nutrient stress	Adhesin-mediated colonisation	Enhanced root colonisation	21
<i>Rhizobium</i> spp.	Legumes	Drought	Root hair biofilm formation	Improved nitrogen fixation	31
PGPR consortium (<i>Bacillus</i> + <i>Pseudomonas</i>)	Wheat	Drought	QS-regulated biofilm	Increased yield, stress tolerance	9, 10

PGPR: plant growth-promoting rhizobacteria; EPS: extracellular polymeric substances; QS: quorum sensing.

Biofilm formation also promotes metabolic cooperation and resource sharing among microbial populations, enabling efficient utilisation of available nutrients (2, 14). These interactions contribute to the establishment of a resilient and functionally diverse microbial community that supports plant health.

Role of root exudates in biofilm formation

Root exudates are key drivers of microbial recruitment and biofilm formation in the rhizosphere (4, 7). Plants release a diverse array of compounds, including sugars, amino acids, organic acids, fatty acids and secondary metabolites, which serve as chemoattractants and signalling molecules for microorganisms.

These exudates influence microbial behaviour by stimulating motility, adhesion and EPS production, thereby facilitating biofilm establishment on root surfaces (3, 20). Specific compounds, such as flavonoids, play a crucial role in initiating symbiotic interactions by activating gene expression in rhizobia and other beneficial microorganisms (31).

Root exudates also shape the composition of microbial communities by selectively enriching microorganisms capable of utilising these compounds (7, 8). This selective recruitment enhances the colonisation of beneficial microbes while limiting the establishment of less competitive or potentially harmful species.

Furthermore, the interaction between root exudates and microbial signalling systems, including QS, enables plants to indirectly regulate microbial activities within biofilms (17, 30). This dynamic interplay ensures the formation of functionally efficient microbial communities that support plant growth and adaptation.

Influence of biofilms on plant growth-promoting rhizobacteria (PGPR)

Biofilm formation significantly enhances the functional efficiency of PGPR (9, 10). Within the biofilm matrix, PGPR exhibit increased stability, metabolic activity and resistance to environmental stress compared to their planktonic counterparts (2, 11).

Biofilms facilitate the expression of genes associated with nutrient acquisition, stress tolerance and phytohormone production, thereby amplifying the plant growth-promoting effects of these microorganisms (12, 15). For example, biofilm-forming PGPR demonstrates improved capabilities in phosphate solubilisation, siderophore production and nitrogen fixation, contributing to enhanced nutrient availability for plants (4, 10).

In addition, the protective environment of the biofilm matrix enables PGPR to maintain consistent interactions with plant roots, ensuring sustained delivery of beneficial metabolites and signalling molecules (1, 14). This stability is particularly important under stress conditions, where biofilm-associated PGPR can maintain their functional activity and support plant resilience.

Biofilm-mediated interactions also enhance the ability of PGPR to participate in phytoremediation processes by improving the immobilisation or transformation of toxic compounds in the rhizosphere (25, 32). These properties highlight the importance of biofilm formation in maximising the effectiveness of PGPR in agricultural systems.

Overall, plant microbe interactions within biofilms represent a highly coordinated system that integrates chemical signalling, ecological interactions and functional cooperation (2, 14). These interactions are essential for the establishment of stable microbial communities that contribute to plant growth, stress tolerance and overall ecosystem sustainability.

Applications of root-associated biofilms in agriculture

The understanding of biofilm formation on plant roots has opened new avenues for improving agricultural productivity and sustainability (9, 10). Root-associated biofilms, particularly those formed by PGPR, offer innovative strategies to enhance crop performance under both optimal and stress conditions (11, 12). These applications are increasingly relevant in the context of climate change, soil degradation and the need to reduce dependence on chemical inputs.

Enhancement of crop resilience under abiotic stress

Biofilm-forming microorganisms play a significant role in improving plant tolerance to abiotic stresses such as drought, salinity and heavy metal contamination (11, 13). Through EPS production, biofilms enhance water retention, regulate ion balance and reduce the bioavailability of toxic compounds in the rhizosphere (1, 5).

Inoculation with biofilm-forming PGPR has been shown to improve plant physiological parameters, including water use efficiency, antioxidant activity and osmotic regulation (23, 26). These effects contribute to improved plant growth and yield under stress conditions. The use of stress-adapted microbial strains capable of forming robust biofilms represents a promising approach for developing climate-resilient cropping systems (15, 27).

Biofilm-based microbial inoculants

Biofilm-based inoculants represent an advancement over conventional single-strain microbial formulations (9, 12). In these systems, microorganisms are applied in pre-formed or induced biofilm states, which enhances their survival, colonisation efficiency and functional performance in the rhizosphere (3, 14).

Such inoculants often consist of multispecies consortia that exhibit synergistic interactions, including nutrient cycling, hormone production and pathogen suppression (4, 10). The biofilm mode of growth provides protection against environmental stress and improves the persistence of microorganisms introduced in soil (2, 11). This results in more consistent and reliable plant growth-promoting effects compared to planktonic inoculants.

Bioengineering and synthetic approaches

Advances in microbial biotechnology and synthetic biology offer opportunities to engineer microorganisms with enhanced biofilm-forming capabilities (17, 19). Strategies include the modification of genes involved in EPS production, QS and stress tolerance to improve biofilm stability and functionality (24, 30).

In addition, the design of synthetic microbial consortia allows for the combination of complementary traits, enabling the development of customised biofilms tailored to specific crops or environmental conditions (9, 10). Emerging approaches also involve the use of nanomaterials and polymer-based carriers to improve the delivery, stability and performance of biofilm-forming inoculants in agricultural systems (29).

Integration with sustainable agricultural practices

Biofilm-based technologies can be integrated into sustainable agricultural systems to reduce reliance on chemical fertilisers and pesticides (4, 11). By enhancing nutrient use efficiency and promoting natural disease suppression, biofilm-forming microorganisms contribute to environmentally friendly crop production (9, 10).

These approaches align with principles of sustainable agriculture, including soil health management, biodiversity

conservation and resource efficiency (12, 13). The use of biofilm-forming PGPR as biofertilisers and biocontrol agents supports the development of low-input agricultural systems while maintaining or improving crop productivity (15, 23).

Overall, the application of root-associated biofilms represents a promising strategy for advancing sustainable agriculture (2, 9). Continued research and technological development are essential to optimise these approaches and facilitate their large-scale adoption in diverse agro-ecosystems.

Challenges and future perspectives

Despite significant advances in understanding root-associated biofilms and their functional roles in plant systems, several challenges limit their effective application and broader scientific interpretation (2, 14). Addressing these limitations requires integrated research approaches that combine molecular biology, ecology and field-based validation.

Knowledge gaps in mechanistic understanding

Although considerable progress has been made in elucidating the processes involved in biofilm formation, the molecular mechanisms underlying plant-biofilm interactions remain incompletely understood (17, 19). In particular, the regulatory networks governing the coordination between microbial signalling pathways, EPS biosynthesis and plant responses require further investigation (24, 30).

Current knowledge is largely derived from model organisms under controlled laboratory conditions, which may not fully represent the complexity of natural rhizosphere environments (3, 4). There is a need for advanced omics-based approaches, including genomics, transcriptomics, proteomics and metabolomics, to unravel the functional dynamics of multispecies biofilm communities and their interactions with plant hosts under varying environmental conditions (8, 11).

Variability in field performance

One of the major challenges in applying biofilm-based technologies in agriculture is the inconsistency of their performance under field conditions (13, 15). Factors such as soil type, pH, temperature, moisture and native microbial communities can significantly influence the establishment and stability of introduced biofilm-forming microorganisms (4, 6).

The effectiveness of microbial inoculants observed in laboratory or greenhouse studies often does not translate directly to field environments due to these complex interactions (9, 10). Therefore, extensive field trials across diverse agro-ecological regions are necessary to evaluate the robustness and scalability of biofilm-based interventions.

Stability and compatibility of microbial consortia

The use of multispecies biofilm-forming consortia offers advantages in terms of functional diversity and resilience; however, maintaining the stability and compatibility of these consortia remains a significant challenge (10, 12). Interactions among microbial species, including competition and antagonism, can affect community structure and functional performance (2, 14).

Designing stable and effective microbial consortia requires a deeper understanding of microbial interactions, ecological compatibility and functional complementarity (4, 11). Synthetic biology and systems biology approaches may provide valuable tools for constructing and optimising such consortia (17, 19).

Environmental and biosafety considerations

The introduction of biofilm-forming microorganisms into agricultural systems raises important environmental and biosafety concerns (4, 25). Potential risks include unintended effects on native microbial communities, horizontal gene transfer and ecological imbalances (2, 12).

Careful assessment of these risks is essential to ensure the safe and sustainable use of biofilm-based technologies. Regulatory frameworks and guidelines must be developed and implemented to evaluate the environmental impact and biosafety of microbial inoculants before large-scale application.

Future directions

Future research should focus on bridging the gap between mechanistic understanding and practical application (14, 17). Integrating omics technologies with advanced imaging techniques will provide deeper insights into biofilm dynamics and plant-microbe interactions at multiple scales (8, 11).

The development of crop-specific and stress-adapted microbial consortia represents a promising avenue for enhancing agricultural productivity under changing environmental conditions (15, 23). Additionally, the incorporation of nanotechnology and novel delivery systems may improve the stability, efficiency and field performance of biofilm-based inoculants (29).

Long-term field studies and multidisciplinary approaches will be critical for translating laboratory findings into viable agricultural solutions. Ultimately, a comprehensive understanding of biofilm-mediated processes will enable the design of targeted strategies for sustainable crop production and soil health management (2, 9).

Conclusion

Root-associated biofilms represent a fundamental strategy by which microorganisms establish stable and functional associations with plant roots in the rhizosphere. This review highlights that biofilm formation is governed by an integrated network of mechanisms involving microbial attachment, extracellular polymeric substance (EPS) production and quorum sensing (QS)-mediated regulation. These processes are dynamically modulated by plant-derived signals and environmental conditions, enabling the development of structured and adaptive microbial communities.

Environmental stresses such as drought, salinity, nutrient limitation, temperature extremes and heavy metal contamination act not only as constraints but also as drivers of biofilm formation. Through coordinated physiological and molecular responses, biofilm-forming microorganisms enhance plant resilience by improving water retention, nutrient acquisition, ion homeostasis and protection against toxic compounds and pathogens.

The functional implications of root-associated biofilms extend to multiple aspects of plant growth and development, including modulation of root architecture, regulation of phytohormone balance and enhancement of microbial persistence in the rhizosphere. These attributes underscore the potential of biofilm-forming plant growth-promoting rhizobacteria (PGPR) as key components of sustainable agricultural systems.

Despite these advances, significant challenges remain in translating mechanistic understanding into consistent field-level applications. Future research should focus on elucidating molecular regulatory networks, optimising microbial consortia and developing robust delivery systems tailored to diverse agro-ecosystems.

In conclusion, biofilm-mediated plant-microbe interactions offer a promising framework for improving crop productivity and resilience under changing environmental conditions. Harnessing these interactions through integrative and multidisciplinary approaches will be essential for advancing sustainable agriculture and ensuring long-term soil and ecosystem health.

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Authors' contributions

MRR conceptualised the review, conducted the literature survey and prepared the original draft. GSR provided conceptual guidance, refined the manuscript structure and critically reviewed the content. SD and SS contributed to literature collection, analysis and drafting sections related to plant-microbe interactions, stress responses and microbial stress mitigation. AKP assisted in data interpretation and improvement of scientific content. PVB supervised the study, contributed to the interpretation of soil-root-microbial processes and critically revised the manuscript. CR assisted in literature compilation, editing and integration of soil biological aspects, while RM contributed to manuscript refinement and critical review. All authors read and approved the final manuscript.

Compliance with ethical standards

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