

Microbial exopolysaccharides: Nature's solution to environmental challenges

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Microbial exopolysaccharides (EPS) are high molecular weight, complex biopolymers secreted by microorganisms such as bacteria, fungi, and algae. These highly hydrated macromolecules form protective extracellular matrices that confer resistance to desiccation, osmotic shock, and predation. EPS have a wide range of bioactivities, including antibacterial, antiviral, immunomodulatory, and anticancer characteristics, and their intrinsic biodegradability, biocompatibility, and low toxicity are driving increased interest in environmental biotechnology. Microbial EPS are chemically composed of polysaccharide backbones that are frequently functioning with protein, lipids, uronic acids, and phenolic moieties, allowing for multifunctional interactions with soil matrix, aquatic systems, and biological interfaces. In this article, we discuss analysis of major EPS-production, and their functional properties, discussion of the principal biosynthetic pathways (Wzx/Wzy-dependent, ABC-transporter-dependent, and synthase-dependent) and the fermentation parameters that govern EPS yield, and an evaluation of emerging genomic, metabolic engineering, synthetic biology, and CRISPR-based strategies for tailoring EPS production. Use of EPS is a flexible, environmentally friendly technology for the next-generation environmental management that combines sustainable engineering and microbial physiology.

Keywords: Bioremediation, Circular bioeconomy, EPS biosynthesis, Green nanotechnology, Sustainable biopolymers, Waste water treatment

INTRODUCTION

Exopolysaccharides (EPS) are high-molecular-weight and structurally varied carbohydrate polymers released by microorganisms such as bacteria, fungus, and algae to increase resilience against environmental stressors¹. These macromolecules are made up of repeating monosaccharide units, mostly pentoses and hexoses, linked by glycosidic bonds. Variations in sugar composition, linking patterns, branching, and functional group modifications cause structural variety². This structural variation strengthens

the extensive spectrum of biological and physicochemical capabilities that EPS exhibits, such as biofilm stabilization, gelation, emulsification, and metal chelation³.

EPS are often divided into two main categories: heteropolysaccharides and homopolysaccharides. Homopolysaccharides are made up of a single kind of monosaccharide residue, which includes glucose or fructose, and can have either linear or branching structures. Heteropolysaccharides, on the other hand, contain two or more different sugar units, which are often supported by non-carbohydrate sub-

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Received 06 June 2026 | Revised 17 July 2026 | Accepted 30 July 2026



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tituents like acetyl, pyruvyl, or sulphate groups, resulting in higher structural complexities and functional adaptability⁴. Microbial EPS have drawn a lot of interest as sustainable biomaterials used for agricultural, industrial, and biomedical applications since they are non-toxic, biodegradable, and biocompatible⁵. Recent studies demonstrate its importance in sustainable nanotechnology, where EPS allow the renewable synthesis and stabilization of metallic nanoparticles, providing healthier substitutes compared to standard chemical-based reductants and capping agents⁶. Beyond their applications in industry, EPS have significant biological roles in the microbial ecology, including as mediating cell-cell signaling, assisting in the uptake of nutrients, and enabling colonization of hostile or nutrient-limited environments⁷. In agroecosystems, EPS assist in soil structure stabilization, retaining moisture, and plant stress mitigation, whereas in engineered systems, they increase pollution elimination via biofilm-induced coagulation and biosorption⁸. In order to retain cellular integrity in the high salinity, temperature, or pH, marine and extremophilic microorganisms further utilize EPS to modify their microenvironments⁹. This review thoroughly addresses recent developments in EPS structural characterization, microbial production methods, and mechanistic applications in green nanotechnology, wastewater treatment, bioremediation and soil health¹⁰. In addition, we also addressed current issues with standardization, scalability, and regulatory translation, offering a unified framework to hasten the implementation of EPS-based solutions in circular bioeconomy models^{11,38}. Using this groundwork, the current review then tackles recent developments (2023-2026) in microbial EPS systems, creates useful tables (Tables 1-4) of quantitative features such as EPS composition, adsorption capacities and efficiency of pollutant removal, presents a section on the biosynthetic processes of EPS with emphasis on fermentation conditions determining EPS output in addition to innovations in gene editing and biomanufacturing methods for modifying EPS features.

STRUCTURAL AND FUNCTIONAL ATTRIBUTES OF EPS

The physicochemical characteristics of microbial exopolysaccharides (EPS) are inherently linked to the producing strains and cultivation conditions¹². The degree of branching, glycosidic linking patterns, monosaccharide content, and substrate-dependent metabolic changes all contribute to structural variability. In this regard, ethapolan, synthesized by *Acinetobacter* spp., demonstrates altered fatty acid incorporation when cultured on ethanol-glucose mixes, although uronic acid, carbohydrate, and mineral profiles remain relatively consistent¹². These structural characteristics directly determine functional properties, including molecular weight, viscosity, solubility, and charge density which determines industrial application. EPS is

made up of repeated glycosidic-associated sugar units that can be synthesized persistently or inducible during regular microbial metabolism. These units can combine into flexible or rigid supramolecular structures^{6,7}. These polymers play vital ecological functions, such as protecting cells from desiccation and predators, mediating surface adhesion, cleaning up ambient pollutants, and promoting intercellular communication mediated by quorum sensing^{6,7,39}.

Beyond ecological roles, microbial EPS are widely used in biotechnology due to their excellent rheological and surface-active characteristics. They are used as natural emulsifiers, stabilizers, immune-modulators, and viscosity enhancers in food, cosmetics, and pharmaceutical formulations¹³. Microbial-derived biopolymers generally exhibit superior or equivalent bioactivity to plant- or algal-derived substitutes, placing them as ideal choices for sustainable industrial application. Both Gram-positive and Gram-negative bacterial lineages are involved in EPS production. Commercially useful polymers including cellulose, xanthan, and levan are produced in large quantities by gram-negative species like, *Pseudomonas*, *Xanthomonas*, *Agrobacterium*, *Rhizobium*, *Acetobacter*, and *Gluconobacter*⁴⁰. On the other hand, probiotic formulations, food fermentation, and dairy texture modification are all facilitated by Gram-positive microbes such as *Leuconostoc*, *Bacillus*, *Lactobacillus*, and *Streptococcus*⁴. EPS facilitates robust biofilm formation by facilitating cellular aggregation and surface colonization, which provides significant cellular survival properties³. In addition to improving microbial persistence, these three-dimensional matrices work as localized bioreactors for the breakdown of resistant substrates and foreign substances⁴¹. Because EPS is amphiphilic, it may effectively scavenge nutrients and emulsify hydrophobic molecules, increasing metabolic flexibility. Moreover, the polymer matrix's anionic functional groups have a potent metal-chelating ability that successfully sequesters harmful cations like (Pb²⁺) and (Cd²⁺)^{5,8}. Collectively, these features improve competitive viability against pathogens and preserve microbial activity under food scarcity or osmotic stress³. EPS secretion is increased in response to abiotic stresses, such as excessive pH, temperature changes, and osmotic shock, in order to stabilize the cellular envelope structure and reduce oxidative or chemical damage^{4,9}.

EPS are divided into two spatial categories: slime polysaccharides (SPS), which freely diffuse into the extracellular environment, and capsular polysaccharides (CPS), that stay firmly linked to the cell envelope^{4,7,42}. Their environment-friendly degradation characteristics, low toxicity, and biodegradability highlight their potential for sustainable biotechnological applications. Branched architecture, glycosidic linking arrangement, overall charge, and molecular weight are all structural characteristics that have a direct impact on solubility, rheological behavior, and interfacial activity⁴. Dextran, for

instance, shows molecular weight-dependent functionality; high-molecular-weight variations significantly enhance bread texture and dough rheology in comparison to low-molecular-weight fractions^{5,8}. Their hydrocolloid nature, which is determined by hydration dynamics and molecular weight, supports the effectiveness of thickening, stabilization, and pollutant removal^{10,11}. With regard to their versatile profile, microbial EPS are widely used in the agricultural, culinary, pharmaceutical, and environmental industries as natural thickeners, stabilizers, emulsifiers, and biosorbents¹⁴. Their incorporation into biologic processes and remediation procedures demonstrates a scalable, environmental-friendly approach towards sustainable resource management. Table 1 consolidates representative EPS-producing microbes together with their chemical composition, principal physicochemical properties, and documented environmental applications, providing a comparative reference point for the sections that follow. Fig. 1 shows the applications of microbial EPS in diverse fields, which shows their potential in coming years to maintain a clean and green environment.

EPS BIOSYNTHESIS AND FACTORS AFFECTING PRODUCTION

The importance of microbial EPS in ecology and applied science is extensively researched, but understanding how these polymers are produced and exported can be beneficial for developing effective bioprocesses and innovating in polymer materials⁴³. There are three basic types of pathways used by bacterium for the EPS production: Wzx/Wzy type, ABC transporter dependent pathway, and the synthase-dependent pathway. Each one of the pathways has its own constraints with respect to the chemical composition of EPS polymers, their length and the efficiency of the exporting process^{33,34}. Fig. 2 summarizes the key steps of these three pathways.

Wzx/Wzy-dependent pathway

The Wzx/Wzy-dependent pathway is responsible for most heteropolysaccharide exopolysaccharides as well as the polysaccharides found in capsules and O-antigens. In this pathway, glycosyltransferases first create a repeat unit of lipid-linked oligosaccharide on an undecaprenyl phosphate (Und-P) carrier in the cytoplasmic part of the inner membrane. The flippase Wzx transports this repeat unit through the inner membrane, which is then added in a sequential manner to the growing chain at the reducing end by the polymerase Wzy carrying out polymerisation. The co-polymerase Wzz is responsible for controlling the chain length^{33,34}. The finished polymer is then transferred across the outer membrane by an outer membrane polysaccharide export (OPX) translocon like Wza. Because the repeat units are produced in advance prior to polymerisation, the

pathway is capable of producing heteropolysaccharides with a varying composition of sugars⁴.

ABC transporter-dependent pathway

While the ABC-transporter-dependent pathway shares various early processes within the cytoplasm with Wzx/Wzy. This pathway differs from these in the point that all of the polysaccharide chain is polymerized at the cytoplasmic side of the inner membrane before it is exported. After that, the complete and lipid-associated polymer is transported through the membrane by means of ATP-binding cassette (ABC) transporter during a single step dependent on ATP utilization. The surface deposition is ensured thanks to a periplasmic co-polymerase as well as an OPX translocon. This pathway is mostly characteristic of capsular polysaccharide (CPS) synthesis which does not spread freely in the environment but is firmly connected to the cell^{33,34}, which is consistent with CPS/RPS distinction mentioned before.

Synthase-dependent pathway

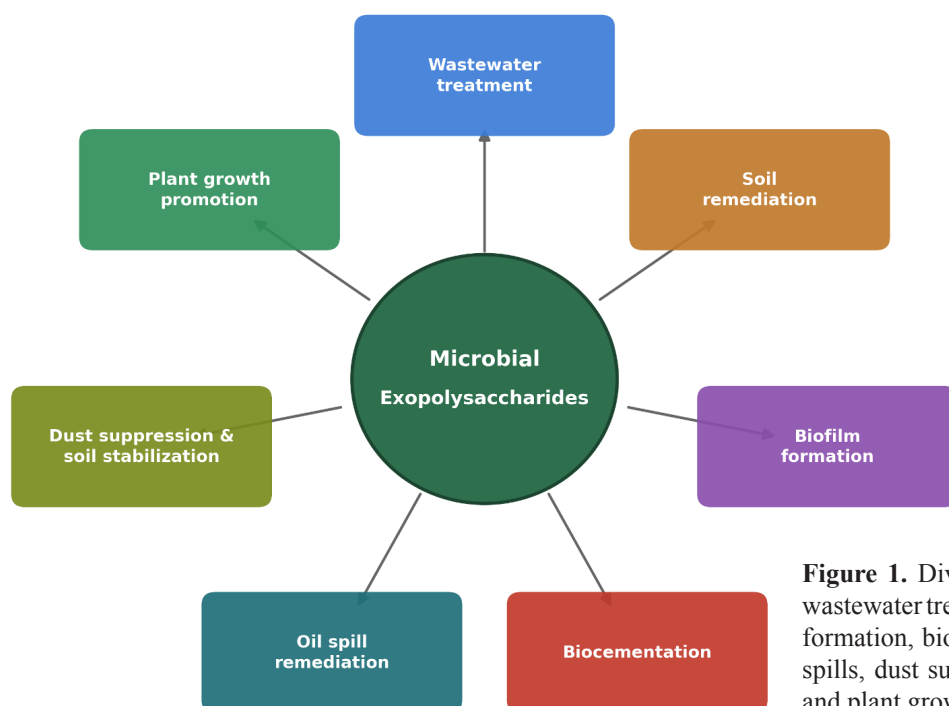
The synthase-dependent route is primarily used for homopolysaccharides like bacterial cellulose and alginate. A singular membrane-embedded synthase system connects polymerization and translocation as one process which is often allosterically triggered by cyclic-di-GMP. The chain that is still being built is pushed through a dedicated channel in the outer membrane directly without the need for a separate lipid-bound exported intermediate^{33,34}. Since polymerization and export are closely connected, this approach has fewer points of interference in structural modification

Factors influencing EPS biosynthesis and yield

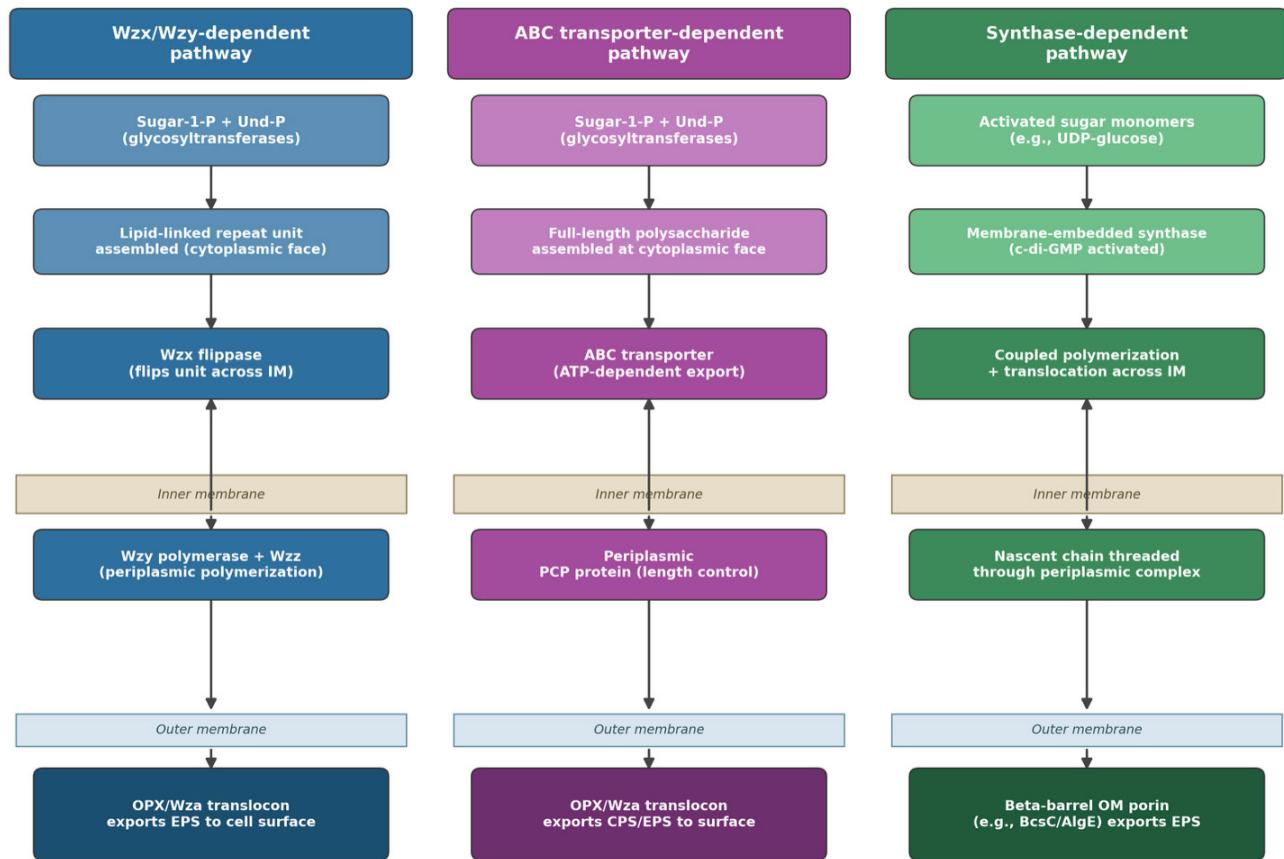
Apart from the genetically determined processes of production of EPS, yield and structure of EPS is influenced by cultivation conditions. Source of carbon and its concentration affect the accumulation of precursor sugars. For example, ethapolan produced by *Acinetobacter* spp. is incorporated into the composition of fatty acids during production from mixture of ethanol/glucose rather than from single carbon source⁴³. Also, carbon-to-nitrogen ratio is significant, as nitrogen shortage under carbon excess will shift the metabolic flux from the biomass production to the synthesis of EPS¹⁷. Optimization of C/N ratio can help to enhance the efficiency of sludge sedimentation by additional 30% in activated sludge process²⁷. pH of culture and temperature influence activity of glycosyltransferases and ionization of carboxylic functional groups making alterations in configuration of the polymer chain and viscosity of the solution as well as oxygen content in the environment which determines whether the metabolic flux is directed to EPS secretion or biomass growth^{4,9}. These variables interact rather than act independently, that is why

Table 1. Comparative overview of representative EPS-producing microorganisms, chemical composition, physicochemical properties, and environmental/industrial applications

Microorganism	EPS / Polymer	Chemical composition	Key physicochemical properties	Environmental / industrial application
<i>Xanthomonas campestris</i>	Xanthan	Glucose, mannose, glucuronic acid backbone with acetyl/pyruvyl substituents	High viscosity, pseudoplastic, shear-thinning, stable over a wide pH/temperature range	Bioflocculant, soil conditioner, viscosifier ^{4,5}
<i>Leuconostoc mesenteroides</i>	Dextran	α -1,6-linked glucose homopolymer with occasional α -1,3 branching	Molecular-weight-dependent viscosity; highly water-soluble	Food texturiser, pharmaceutical excipient, biosorbent ^{5,8}
<i>Acinetobacter</i> spp.	Ethapolan	Carbohydrate–protein–lipid complex with uronic acids	Fatty-acid content varies with carbon source; mineral profile stable	Emulsifier; hydrocarbon bioremediation ^{1,2}
<i>Pseudomonas</i> spp.	Alginate-type EPS	Mannuronic/guluronic acid heteropolymer	Strongly anionic, metal-chelating, gel-forming	Heavy-metal bio-sorption, biofilm-based bioremediation ^{17,21}
<i>Bacillus</i> spp.	Levan-/ γ -PGA-associated EPS	Fructose-based homopolymer or glutamic-acid polymer	High water-holding capacity; thermostable	Soil aggregation, biofertiliser carrier, metal biosorption ^{4,14}
<i>Rhizobium</i> / <i>Azotobacter</i> spp.	Succinoglycan-type EPS	Glucose/galactose with succinyl, acetyl substituents	Anionic, high molecular weight	Rhizosphere nutrient cycling, phosphate/iron solubilisation ^{1,2}
Cyanobacteria (e.g., <i>Nostoc</i>)	Sheath/capsular EPS	Heteropolysaccharide rich in uronic acids and sulfated sugars	UV-protective, highly hydrated, cohesive	Biological soil crust formation, erosion control ^{14,15}
<i>Zoogloea ramigera</i>	Zoogloean EPS	Heteropolysaccharide with protein components	Strong flocculating capacity	Activated-sludge bioflocculation ^{17,20}

**Figure 1.** Diverse roles of microbial EPS in wastewater treatment, soil remediation, biofilm formation, biocementation, remediation of oil spills, dust suppression and soil stabilization, and plant growth promotion

Major Biosynthetic Pathways of Microbial Exopolysaccharides



IM = inner membrane; OM = outer membrane; PCP = polysaccharide co-polymerase; Und-P = undecaprenyl phosphate

Figure 2. Schematic overview of the three principal biosynthetic pathways of microbial EPS Wzx/Wzy-dependent, ABC-transporter-dependent, and synthase-dependent, showing key steps from precursor synthesis at the inner membrane (IM) to extracellular export across the outer membrane (OM)^{33,34}

refined approaches of fermentation process improvement are used to find the most optimal conditions for production of EPS.

EPS IN SOIL HEALTH AND AGROECOSYSTEM MANAGEMENT

Extracellular polysaccharides (EPS) produced by microalgae and cyanobacteria are critical for maintaining soil health and stability. These microorganisms facilitate the formation of biological soil crusts, which act as natural protective layers that mitigate erosion, retain water, and support the proliferation of other living organisms^{14,15}. Consequently, they contribute to enhanced soil structure and fertility, thereby improving the overall health of the agroecosystem. The synthesis and structural organization of these polysaccharides vary according to the producing photosynthetic microorganism. In certain taxa, EPS is entirely secreted into the extracellular environment, where

it actively interacts with soil particles and other microbial communities. In contrast, some EPS remains associated with the cell surface, forming a protective sheath around the microbial cells. Owing to these structural and functional distinctions, researchers employ distinct terminologies to classify these polymers⁴⁴.

When the polysaccharides remain closely attached to the cell, they are termed capsular polysaccharides (CPSs) or bound polysaccharides (BPSs), and are sometimes referred to as slime layers or sheaths. However, when freely released into the environment, they are designated as exopolysaccharides (EPS) or released exopolysaccharides (RPS). These secreted EPS polymers are critical for biofilms, soil particles aggregation, and protecting microorganisms from desiccation and other environmental stresses⁴⁵. As a result, EPSs produced by microalgae and cyanobacteria are key components of soil stability and ecosystem balance. Whether attached to cells or freely secreted, they facilitate microbial survival, pedogenesis, and maintenance of the

overall health of terrestrial ecosystem¹⁴.

Microbial (EPS) also plays a pivot role in the cycling and translocation of nutrients in soil. They facilitate the retention and controlled release of essential elements such as nitrogen (N), phosphorus (P), iron (Fe), and other minerals required for plant growth. The sticky, negatively charged EPS layer traps these nutrients from the soil and makes them available to plants over time⁴⁶. This process mitigates nutrient loss through leaching and helps maintain the soil fertility over extended period⁴. EPS-producing microorganisms, especially those inhabiting the rhizosphere, support plant-microbe interactions that enhance nutrient uptake. The EPS layer surrounding bacterial cells provides a specialized microenvironment for enzymatic activities involved in the solubilization of insoluble phosphates and iron compounds¹. For example, EPS-producing *Pseudomonas* and *Rhizobium* species can solubilize phosphate and chelate iron, which directly improving plant nutrition¹. Additionally, by capturing and gradually releasing necessary cations, EPS improves the soil's capacity for cation exchange. This mechanism enhances nutrient cycling and microbial development, which eventually improves soil fertility and crop productivity². Thus, EPS-producing microorganisms not only improve nutrient retention, but also stimulate the synthesis and bioavailability of crucial components in agricultural soils, facilitating effective and sustainable nutrient management. Additionally, microbial EPS helps plants to withstand harsh environments such as salt, drought, and heavy metal pollution. These polymers create a sticky covering around soil particles and plant roots that traps water, allowing plants to use moisture more efficiently under water scarcity⁵. The EPS layer in saline soils traps sodium ions, keeping them from getting into plant roots. In addition to protecting the plant against salt toxicity, this mechanism makes it easier for the plant to absorb nutrients including potassium (K⁺), calcium (Ca²⁺), and magnesium (Mg²⁺), that are essential for healthy growth⁶.

Additionally, EPS is essential to climate-smart agriculture, which prioritizes environmentally beneficial and sustainable farming practices. By binding particles together, reducing erosion, and boosting water retention, EPS-producing bacteria enhance soil structure¹⁵. This capacity helps crops withstand drought and abrupt temperature changes by preserving high soil moisture and stability levels⁴. Furthermore, EPS-producing bacteria aid in the sequestration of soil organic carbon (SOC), which promotes fertility and lowers greenhouse gas emissions¹⁶. These bacteria reduce the need for chemical fertilizers and promote root development and nutrient cycling when used as soil conditioners or biofertilizers. This improves farming's ability to withstand harsh environmental conditions like heat waves, droughts, and salt⁷. Finally, EPS-producing microorganisms

are increasingly seen as valuable collaborators in the development of climate-smart agriculture. These helpful microbes naturally improve soil quality, raise SOC levels, and strengthen the land's tolerance to extreme weather. Their application promotes more sustainable farming methods and helps reduce greenhouse gas emissions by lowering the demand for artificial fertilizers and excessive watering. In order to create robust and climate-ready agricultural systems, this environmentally beneficial technique makes use of microbial EPS as a smart and natural tool¹⁷.

EPS IN WASTEWATER MANAGEMENT AND ENVIRONMENTAL BIOREMEDIATION

Microbial exopolysaccharides (EPS) are hydrated, high-molecular-weight polymers released by fungi, bacteria, and algae that bind cells and colloidal particles together in a structural matrix. This matrix greatly improves the efficiency of pollutant removal in wastewater ecosystems and contaminated environments by stabilizing microbial aggregation and mediating biological, chemical, and physical processes^{17,45}. EPS are the perfect, sustainable agents for clean-water treatment techniques and ecological remediation since they have biocompatibility, non-toxicity, and biodegradability¹⁷.

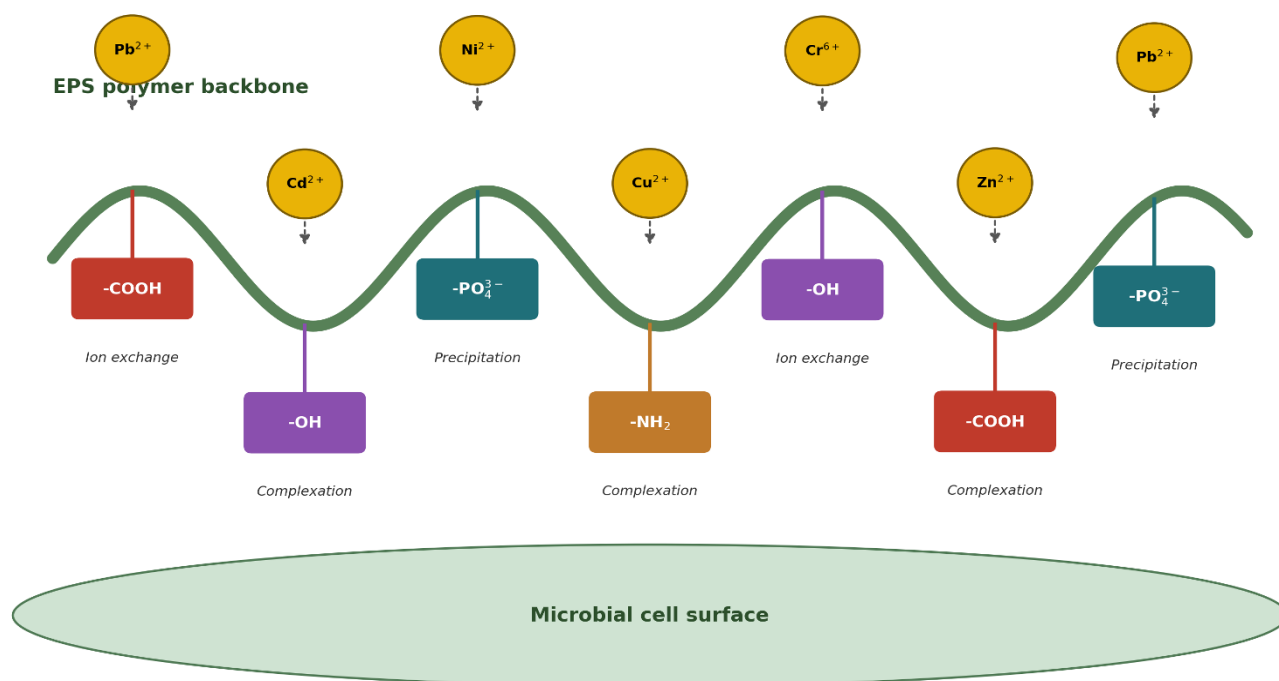
Heavy metal biosorption and sequestration

Microbial EPS are essential for detoxifying and removing heavy metals from contaminated environments. Functional groups like phosphate (-PO₄³⁻), amino (-NH₂), hydroxyl (-OH), and carboxyl (-COOH) moieties are abundant in the polymeric matrix and have a strong affinity for positively charged metal ions, such as Lead (Pb²⁺), nickel (Ni²⁺), copper (Cu²⁺), hexavalent chromium (Cr²⁺), and cadmium (Cd²⁺)^{17,21}. By immobilizing heavy metals via precipitation processes, ion exchange, or complexation, these charged sites function as organic biosorbents. *Pseudomonas*, *Bacillus*, and *Azotobacter* are examples of EPS-producing bacteria that have a notable ability to sequester metal ions; isolated EPS has adsorption capabilities of 150-250 mg/g³⁷. These composite biosorbents provide affordable, reusable substitutes for synthetic chemical coagulants like polyacrylamide, which frequently produce hazardous byproducts, when immobilized on carrier materials like alginate or charcoal²¹. This method provides an ecologically sustainable approach to manage metal pollution by lowering metal toxicity and increasing the possibility of recovering valuable metals¹⁷.

Table 2 compares reported heavy-metal biosorption capacities and dominant sequestration mechanisms across representative EPS-producing bacterial genera, and Fig. 3 illustrates the underlying mechanism at the level of individual EPS functional groups.

Table 2. Comparative heavy-metal biosorption capacities and dominant mechanisms of representative EPS-producing bacteria

EPS-producing organism	Target metal ion(s)	Reported adsorption capacity	Dominant mechanism	References
<i>Pseudomonas</i> spp.	Pb ²⁺ , Cu ²⁺	150-250 mg/g	Ion exchange, surface complexation	17, 21
<i>Bacillus</i> spp.	Cd ²⁺ , Ni ²⁺	150-250 mg/g	Complexation via carboxyl/phosphate groups	17, 21
<i>Azotobacter</i> spp.	Hexavalent chromium (Cr ⁶⁺)	150-250 mg/g	Reduction-coupled complexation	17, 21
EPS immobilized on alginate/charcoal carriers	Mixed heavy-metal effluents	Enhanced reusability vs. free EPS	Combined ion exchange + precipitation	21



Anionic functional groups on the EPS matrix immobilize metal cations via ion exchange, complexation, and surface precipitation

Figure 3. Proposed mechanism of heavy-metal biosorption by anionic functional groups (-COOH, -OH, -PO₄³⁻, -NH₂) present on the microbial EPS matrix, illustrating ion exchange, complexation, and precipitation as the principal sequestration mechanisms^{7,21}

Decomposition of biofilm consortia and organic pollutants

EPS are highly efficient in the biological remediation of organic contaminants such as hydrocarbons, synthetic colours, and pesticides. The sticky and porous structure of EPS allows for the adsorption of hydrophobic, organic compounds, which are then concentrated adjacent to microbial cells containing breakdown enzymes¹⁷. For instance, by capturing oil droplets and boosting their bioavailability, EPS matrices made by *Rhodococcus* species and *Pseudomonas aeruginosa* improve hydrocarbon decomposition. Similarly, by stabilising enzymes and

shielding microorganisms from harmful shocks, EPS-forming bacterial consortia can break down pesticide residues and decolourise textile colours¹⁸.

The functional and structural support that EPS gives microbial biofilms is a major factor that causes this increased deterioration. EPS serves as a 3-D matrix that envelops many microbial species in biofilm consortia, promoting cooperative degradation and metabolic cross-feeding. Polyaromatic hydrocarbons (PAHs) and other complex pollutant combinations can be completely broken down because to this division of metabolic activity. Furthermore, EPS improves the long-term stability of

biofilm communities by protecting them from adverse environmental circumstances. As compared with planktonic (free-living) microbial cells, engineered EPS-containing biofilms in bioreactors exhibit greater removal efficiency and flexibility¹⁹.

Sludge settling, nutrient recovery, and bioflocculation

EPS is crucial for bioflocculation in wastewater treatment systems, which improves the segregation of treated water from biomass by allowing microbial cells and colloidal components to group together to create stable flocs that settle readily. Through hydrogen bonds, hydrophobic forces and ionic interactions the polysaccharide chains in EPS function as organic bridging agents, establishing connections between cells¹⁷. A firm adherence of EPS to the microbial cell surfaces in activated-sludge systems promotes floc density and strength, improving sedimentation rates while minimizing sludge thickening. Additionally, protein-rich EPS increases the compressibility and flexibility of flocs, thereby enhancing the dewaterability of sludge. According to recent studies, sludge stability and settling efficiency can be increased by up to 30% via varying the carbon/nitrogen (C/N) ratio¹⁷.

In addition to solid-liquid separation, EPS targets suspended solids, organic debris, and nutrients including phosphorus (P) and nitrogen (N) in multistage pollutant removal. The EPS matrix provides a specialized micro-niche for nitrifying and denitrifying bacteria, resulting to efficient nitrogen removal. In order to achieve steady sludge performance, EPS-producing bacteria like *Pseudomonas putida* and *Zoogloea ramigera* are essential. Further research has shown that EPS based biofilms could immobilize up to 70% of the organic pollutants and heavy metals found in influents²⁰.

Uses in advanced bioreactors and constructed wetlands

EPS provides the structural support for the microbial biofilms that cover root systems and filter media in artificial wetlands and bioreactors. This biofilm matrix facilitates nutrition exchange, improves microbial adhesion, and provides defense against mechanical stress. The EPS layer sustains anaerobic niches and microaerophilic that sustain a variety of microbial communities by retaining moisture, oxygen, and substrates⁴⁶. For instance, EPS enhances nitrogen cycling by encouraging the cohabitation of denitrifying bacteria (*Pseudomonas*, *Paracoccus*) and nitrifying bacteria (*Nitrosomonas*, *Nitrobacter*)²¹. Additionally, EPS helps sedimentation and lessens blockage in subsurface-flow wetlands by trapping suspended materials. When compared to control wetlands, EPS-rich biofilms have been demonstrated to increase both hydraulic retention period and organic matter clearance by as much as 40%²². Additionally, it has been observed that

the EPS matrix protects microbial consortia and improves the longevity of bioreactors by acting as a barrier to diffusion that retains heavy metals²³. Table 3 summarises quantitative performance improvements reported for EPS-mediated processes across different wastewater treatment configurations, providing a comparative overview of the mechanisms discussed above.

GENOMICS, METABOLIC ENGINEERING, SYNTHETIC BIOLOGY, AND CRISPR-BASED STRATEGIES FOR TAILORING EPS PRODUCTION

Due to developments in whole genome sequencing and comparative genomics, it has now become possible to reveal and describe the so-called EPS biosynthesis gene clusters across a wide range of bacteria, fungi, and algae. Despite the proximity of taxonomic groups, very different glycosyltransferase complexes, regulatory operons, and excretion mechanisms can be detected. This knowledge opens two paths to engineering the amount and properties of EPS via rational metabolic engineering and combinatorial synthetic biology techniques⁴⁷.

In general, metabolic engineering is aimed at modifying precursor supply, thus affecting the carbon flux used for the synthesis of nucleotides and sugars, such as UDP-glucose and GDP-mannose. The necessary modification is achieved through either the overproduction of key enzymes or slight modifications of the cyclic di-GMP levels. The essence of synthetic biology is the possibility of assembling heterologous glycosyltransferases and modifying the functioning of flippase-polymerase pair, which allows for designing chimeric repeat units in order to produce desired physical and chemical properties of resulting EPS⁴⁸.

Genome-editing technologies based on CRISPR/Cas, which have already found enormous application in the precise design of technological microorganisms, could be applied also for the improvement of EPS production by means of knockout of any alternative exopolymer or storage carbohydrate pathway, promoter substitution aimed at deregulating the expression of EPS operon, and tuning of regulatory genes through the use of CRISPR interference without any permanent genome alterations⁴⁹. The implementation of CRISPR/Cas technology in EPS producers is still rather limited compared with other organisms such as *Escherichia coli* and *Saccharomyces cerevisiae*, but the experience with CRISPR-assisted engineering of metabolic pathways indicates a promising perspective with regard to the possibility of improving EPS yield, molecular weight and the density of functional groups in EPS-version strains. In order to realize this promising potential, the distance between annotation of the entire genome pathways and validated approaches to strain-specific editing should be minimized⁵⁰.

Table 3. Comparative performance improvements reported for EPS-mediated wastewater treatment processes

Process / system	Reported performance improvement	Key EPS contribution	References
Activated sludge (C/N ratio optimisation)	Sludge settling/stability improved by up to 30%	Floc bridging, dewaterability	17
Biofilm-based bioreactors	Immobilisation of up to 70% of influent organic pollutants and heavy metals	3-D matrix concentrating pollutants near degrading cells	20
Constructed wetlands (EPS-rich biofilms)	Hydraulic retention time and organic-matter clearance increased by up to 40% vs. control wetlands	Sedimentation of suspended solids, extended microbial contact time	22
Engineered EPS-containing bioreactor biofilms	Greater removal efficiency and operational flexibility than planktonic cultures	Metabolic cross-feeding within biofilm consortia	19

EPS AS GREEN ALTERNATIVES IN ENVIRONMENTAL BIOTECHNOLOGY

EPS as eco-friendly substitutes for synthetic polymers

EPS are natural polymers produced by microorganisms such as bacteria, fungi, and algae. Owing to their biodegradable, non-toxic, and derivation from renewable sources, EPS are considered safe and eco-friendly alternatives to synthetic polymers. These microbial EPSs possess distinct physicochemical properties including the ability to increase viscosity, form gels, and promote bioflocculation. Due to these properties, they can effectively replace petroleum-based materials in various environmental and industrial applications⁵. In environmental biotechnology, EPS are widely studied as eco-friendly bioflocculants because they can replace harmful synthetic chemicals used in wastewater treatment. They facilitate the removal of dyes, heavy metals, and other pollutants without generating toxic by-products. EPS also functions as a biosorbents and stabilizing agents, rendering them highly useful in soil remediation and erosion control. This capability reduces the need for chemical additives and supports enhanced environmental sustainability⁵¹. Furthermore, EPS are being explored for use in biodegradable packaging materials and functional biofilms in the food and material industries, where their natural origin and safety are major advantages. Since EPS are produced through biological processes and can be obtained from renewable biomass via microbial fermentation, they strongly support green and sustainable biotechnological practices¹⁰.

Application in green nanotechnology

Microbial EPS can naturally reduce metal ions and stabilize nanoparticles, enabling the biosynthesis of metal nanoparticles without the use of harmful chemical reagents. EPS-based synthesis of silver and gold nanoparticles is environmentally friendly because it relies on renewable biological sources and is carried out under mild, safe reaction conditions²⁴. EPS-coated nanoparticles are more

biocompatible and less toxic, enhancing their suitability for biomedical and environmental applications. In green nanotechnology, EPS also acts as natural capping agents that control the size and shape of nanoparticles, resulting in stable and uniformly formed particles. EPS-based nanoparticles are widely used in wastewater treatment because they can strongly bind and remove heavy metals and organic pollutants from contaminated water²⁵. Furthermore, because EPS are biodegradable, nanomaterials derived from EPS are environmentally safe and well suited for sustainable nanotechnology development. In addition, green synthesis using EPS supports the circular bioeconomy by utilizing microbial biomass and helping to reduce industrial waste production²⁶.

The ability of EPS to produce nanoparticles is based on the way polyanionic functional groups work. Hydroxyl group, carboxyl group, phosphate group and sulfate group, along the polymer backbone donate electrons, thus reducing metals in the dissolved state, including gold ions (Au^{3+}), silver ions (Ag^+), and zinc ions (Zn^{2+}), to their zero-valent or oxide states, followed by adsorption of these groups on the surface of nanoparticles being formed, thus stopping the process of growth and aggregation. Both functions are fulfilled here: reducing agent and capper^{24,35}.

Representative examples reveal the extent of this approach. EPS from bacteria has been used in the production of antimicrobial AgNP, with polyanionic hydroxyl, carboxylic, sulfate, and phosphate groups acting as both reducing and stabilizing agents. Thus, antibacterial and antifungal activity can be attained. EPS produced by thermophilic marine bacteria has also had similar success in the synthesis of gold and silver/silver-chloride nanoparticles, since the resulting bionanocomposites still exhibit antimicrobial properties, even in the absence of toxic agents. For ZnO nanoparticles, EPS such as dextran complex Zn^{2+} ions via the carboxylate and hydroxyl interactions on the growing oxide lattice, thereby improving both the antibacterial performance and biocompatibility of the EPS-ZnO composites for various applications⁵². A summary regarding the EPS-mediated nanoparticle systems is found in Table 4.

CHALLENGES AND LIMITATIONS

Variability in EPS composition and properties

Microbial EPS differ widely in their chemical makeup and physiochemical behavior because they are produced by different microorganisms under varying environmental conditions. As a result, various microbes generate EPS with different types of sugars, molecular weights, and functional groups, leading to noticeable differences in properties such as viscosity, stability, and their ability to chelate metals²⁴. Environmental factors such as temperature, pH, and the availability of nutrients greatly affect both the structure and the yield of EPS produced, which makes it challenging to obtain products with uniform quality. This variation can reduce the efficiency and reliability of EPS when they are used in applications like bioremediation, wastewater treatment, and green nanotechnology. Therefore, careful analysis and standardization of EPS production methods are necessary to achieve consistent and dependable performance in industrial and environmental uses²⁷.

High production cost and scalability issue

Producing microbial EPS on a large scale is costly because it involves carefully controlled fermentation conditions, specialized nutrient media, and additional processing steps such as purification and drying. The need for high energy input and sterile equipment further adds to the overall production cost at the industrial level. Moreover, expanding EPS production from the laboratory scale to an industrial scale is challenging, since microbial growth and EPS yield can vary greatly in large fermentation systems²⁸. Variations in EPS yield and quality during scale-up can lower production efficiency and restrict their use in commercial environmental and biotechnological applications. Therefore, it is important to develop low-cost raw materials, optimize fermentation methods, and implement advanced bioprocess technologies to make large-scale EPS production more practical and economically feasible²⁹.

Stability and performance in field conditions

EPS-based materials can lose their structural integrity and functional effectiveness when exposed to harsh environmental conditions such as extreme pH, fluctuating temperatures, and high salt levels. Factors like ultraviolet (UV) radiation and natural microbial degradation can further decrease the durability and performance of EPS in real field conditions. In addition, interactions between EPS and other organic or inorganic substances present in soil and water may alter their binding ability and overall efficiency²⁵.

Regulatory and environment safety concerns

The widespread use of EPS and EPS-based nanomaterials requires thorough evaluation to ensure their safety for both humans and the environment³⁰. Obtaining regulatory approval for EPS-based products is difficult because clear and standardized guidelines for their production, quality control, and practical use are still lacking³¹. In addition, there is a risk of contamination with microbial residues or toxins during EPS production, which raises safety concerns, especially for biomedical and food-related applications³². Moreover, the long-term environmental impacts of EPS-based nanomaterials are not yet fully known, necessitating more toxicological and ecological studies²⁴.

Downstream processing and economic feasibility

The recovery and purification of microbial EPS not only constitute the main cost factor in most studies at the laboratory level but also complicate the issue of the economic feasibility of the implementation of EPS as bioproducts. The steps involved in the downstream process of EPS comprise separation of cells, precipitation with either solution or salt, deproteinization, dialysis or ultrafiltration, as well as drying. Each of them contributes to the prolongation of the process and requires further optimization when scaling up the process^{28,29,31}. This means that besides the minimal fermentation titers, which were

Table 4. Representative examples of EPS-mediated green synthesis of metal and metal-oxide nanoparticles

Nanoparticle	EPS source	Functional groups implicated	Reported application	References
Silver (Ag)	Bacterial EPS (various Gram-positive/negative producers)	-OH, -COOH, -SO ₄ , -PO ₄ (reduction + capping)	Broad-spectrum antimicrobial coatings/materials	35
Gold / Ag-AgCl	Marine thermophilic bacterial exopolymers	Polyanionic reducing/capping groups	Antimicrobial bionanocomposites	24
ZnO	Probiotic / dextran-type EPS	Carboxylate and hydroxyl coordination at Zn ²⁺ / oxygen-vacancy sites	Antimicrobial food packaging, biomedical composites	30
EPS-coated NPs (general)	Various bacterial EPS	Surface capping limiting aggregation	Heavy-metal and organic pollutant removal in wastewater	25

already discussed, the feasibility of the application of EPS also depends on the entire downstream process.

FUTURE PERSPECTIVES

In order to turn the scientific advancements described previously into practical, commercial EPS-based technologies, certain steps need to be taken, which are discussed below and presented in a schematic format in Fig. 4.

Scale-up and bioprocess intensification

Moving EPS production from laboratory shake flasks into industrial-scale bioreactor systems requires bioprocess intensification methods like fed-batch or continuous fermentation, using low-cost agro-industrial waste streams as carbon source, and using integrated process design that simultaneously optimizes fermentation and downstream processing instead of considering them separately.

AI-assisted bioprocess optimization

Various artificial intelligence techniques such as supervised models to predict yield, reinforcement learning to control feed rate, and digital twins are employed in fermentation processes in order to reduce time and expenses associated with applying trial-and-error optimization techniques and ensure real-time control of fermentation processes³⁶.

Moreover, the application of these techniques for EPS fermentation can help identify all needed combinations of carbon source, C/N ratio, pH, temperature, and aeration parameters as well as provide quality control of EPS production process when scaling it up.

Circular bioeconomy integration

The process of creating EPS using waste streams from agriculture and food processing provides an opportunity to recycle waste materials, which allows for the production of EPS to conform to the principles of a circular economy (Fig. 4). However, the success of the process is dependent upon the uniformity of the waste streams, as a low-cost supply of raw materials is sought for the creation of EPS^{10,26}.

Commercialization challenges

In addition to the technical aspects of producing EPS products, commercialisation of EPS will also require the presence of regulations governing their use. Moreover, there has to be a preliminary agreement upon the protocol that will allow quality assessment of EPS to ensure uniformity of its characteristics from one batch to another in terms of costs as compared to synthetic materials, which gets more complex if the EPS products should be used for sensitive applications such as medical drugs or food^{27,31}.

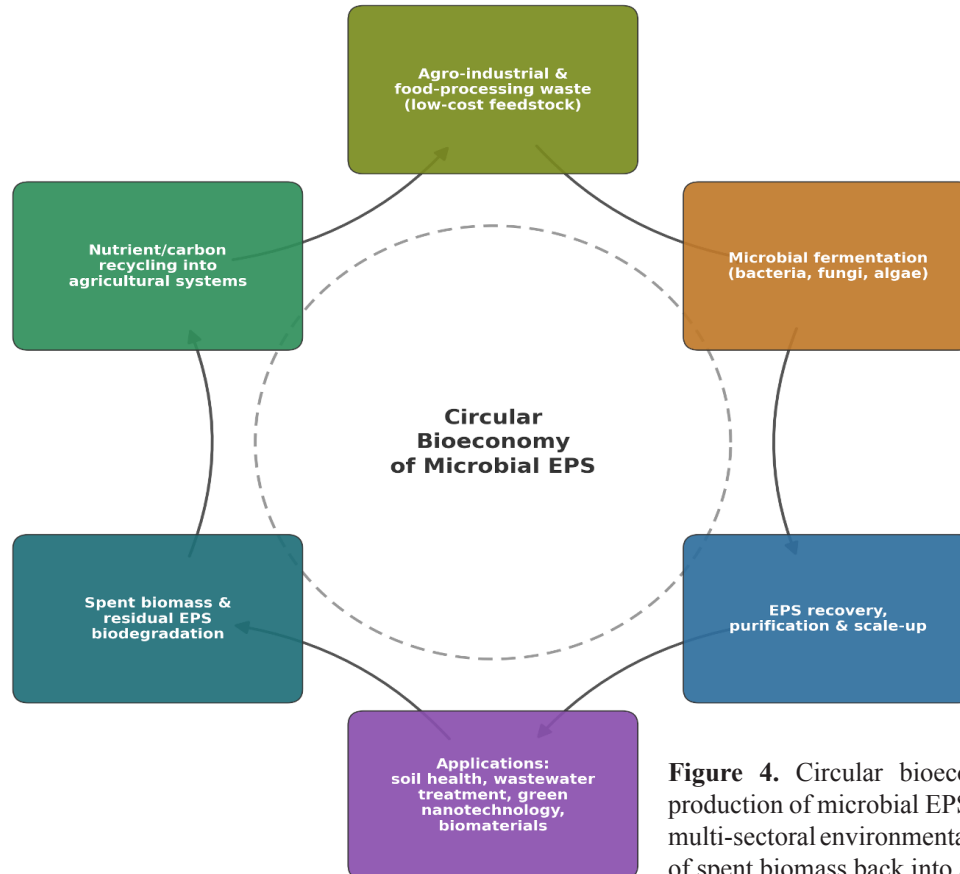


Figure 4. Circular bioeconomy model illustrating the production of microbial EPS from agro-industrial waste, its multi-sectoral environmental applications, and the recycling of spent biomass back into agricultural systems^{10,26, 53}

Hybrid EPS-based materials

Combining EPS with other materials adds a new feature to EPS making it more efficient in terms of its mechanical stability, reuse ability and ability to bind pollutants. Such hybrid materials along with EPS-nanoparticles composites discussed in Section 7.2 are the next step in developing EPS based environmental technologies. Fig. 4 illustrates the circular bioeconomy of EPS, showing applications in low-cost feed stock, nutrients recycling, and other fields.

CONCLUSIONS

Microbial EPS play an indispensable role in environmental management due to their natural, biodegradable, and highly versatile nature. They help improve soil structure by increasing soil aggregation, water-holding capacity, and nutrient availability, which in turn supports healthier plant growth and overall soil quality. In wastewater treatment and polluted environments, EPS act as effective biosorbents that can capture heavy metals, pesticides, and other organic pollutants, facilitating their removal easier through processes such as bioflocculation and biofilm formation. In addition, EPS protect microorganisms from environmental stresses like high salinity, drought, and toxic substances, allowing them to survive and function efficiently in harsh conditions. Their role in biofilm formation also improves the stability and performance of microbial communities involved in wastewater treatment and bioremediation of contaminated sites. Because EPS are environmentally friendly and can be produced from renewable resources, they provide a sustainable alternative to synthetic polymers used in environmental technologies.

It should be noted that significant developments in studying basic EPS biosynthetic pathways and employing different methods such as the use of the genome, and bioengineering, have perfectly combined with AI-based agri-tech applications and developments in the area of circular economy.

Overall, microbial exopolysaccharides offer a promising eco-friendly approach for pollution control, soil rehabilitation, and sustainable environmental management. Further research aimed at improving EPS production efficiency and expanding their practical applications will strengthen their contribution to solving major environmental challenges.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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