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REVIEW

Microbial exopolymeric substances and biosurfactants as 'bioavailability enhancers' for polycyclic aromatic hydrocarbons biodegradation

P. J. Yesankar[1,2] · M. Pal[1,2] · A. Patil[1] · A. Qureshi[1,2]

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Abstract

Bacterial cells dwelling in the Polycyclic Aromatic Hydrocarbons (PAH) contaminated ecosystem occur as an eco-community or biofilms having biosurfactants and exopolymeric substances (EPS) producing capacity. Bacteria have developed several mechanisms to utilize the low accessible PAH compounds by modifying their structural and physiological process. EPS provides an adsorption site for PAH binding and acts as an emulsifier, enhancing PAH uptake in bacterial cells. Biosurfactants aid in the solubilization of the low-bioavailable carbon sources by reducing the interfacial surface tension between the aqueous phase and PAH-sorbent matrix, solubilizing PAHs thus making them bioavailable. Mining of exopolysaccharides synthesizing key genes (priming Glycosyltransferase) and biosurfactant producing genes (synthetases) in PAH degrading bacteriomes established their concomitant involvement in PAH solubilization and uptake. The transcriptional and translational regulators (secondary messenger cyclic-di-GMP, quorum sensing molecules, small ribosomal RNAs, two-component signaling molecules) control the synthesis of these 'bioavailability enhancers' towards PAH utilization and have been elucidated explicitly in the current review.

Keywords Biofilms · Exopolysaccharides · Quorum sensing · Solubilization · Emulsification · Uptake of hydrophobic compounds

Introduction

For decades, contamination with toxic and recalcitrant pollutants has increased drastically due to anthropogenic interventions. Industrial processes add waste comprising all sorts of hydrophobic organic compounds, ultimately contaminating soil, aquatic environment, and atmosphere (Beolchini et al. 2021; Lai et al. 2015). Polycyclic aromatic hydrocarbons (PAHs) include a wide range of hydrophobic organic compounds consisting of two or more fused benzene rings arranged in diverse spatial configurations**.** These are widespread in the environment, and most of them are persistent due to their high hydrophobicity leading to poor aqueous solubility (Abdel-Shafy and Mansour 2016). Several PAH compounds cause mutagenic and toxic effects on humans and other planetary organisms. The indiscriminate and alarming use of these PAH compounds also deteriorates the existing environment, necessitating efficient removal methods (Patel et al. 2020). Many chemical and physical processes, including chemical washing, precipitation, electrochemical decomposition, activated carbon/additives adsorption, have been devised to treat these polluted systems (Kuppusamy et al. 2017). However, the conventional techniques involving these processes have numerous disadvantages, such as high treatment cost and partial degradation of the pollutant resulting in harmful secondary products. Many of these drawbacks can be surmounted by using the biological means of remediation termed 'bioremediation' (Azubuike et al. 2016).

Bioremediation is an ecological, cost-effective, and efficient method for detoxifying and mineralizing toxic pollutants, including organic and inorganic harmful xenobiotic

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✉ A. Qureshi
a_qureshi@neeri.res.in

[1] Environmental Biotechnology and Genomics Division, CSIR-National Environmental Engineering Research Institute (NEERI), Nehru Marg, Nagpur 440 020, India

[2] Academy of Scientific and Innovative Research (AcSIR), Ghaziabad 201 002, India

pollutants. The results of natural treatment methods utilizing microbes, microbial associations, and their products are promising and are in *La mode* (Bhandari et al. 2021; Singh and Haritash 2019). Bioremediation using bacterial consortium having degrading potential seems practical in the appliance, as cell–cell communication among different bacterial species helps improve the overall efficiency of remediation (Kuppusamy et al. 2016; Sharma et al. 2016). It has been well characterized that several bacteria can degrade PAHs via aerobic and anaerobic processes (Moayed et al. 2021); however, the viability of the augmented bacteria often decreases due to encountered unfavorable environmental stresses such as temperature, nutrient availability, and pH fluctuations (Mishra et al. 2021).

In nature, microbes spend their lifecycle in a microclimatic condition, where they develop an adaptive response to survive under multiple stress conditions. Practically, most bacterial species are known to form biofilms adhered to every possible biotic and abiotic surface, and within it lays a spatially organized metabolic connection between species (O'Toole et al. 2000). These are structured eco-community where microbes are embedded in a self-secreted matrix of polysaccharides, which has been well studied to provide protection and resistance against several environmental cues, including physical and chemical stress (Berlanga and Guerrero 2016). Various physiological interactions occur within the complex network of microbial biofilms, which bestows the cells with enhanced nutrient availability, beneficial for utilizing less bioavailable and potent toxic compounds such as PAHs. The significance of facilitating biofilm-forming bacteria to enhance degradation in polluted environments has been well appreciated. Indeed, various reports suggest the proficiency of biofilms over planktonic microorganisms for bioremediation (Ghosh et al. 2017). Various species belonging to different genera are now known to possess PAH degradation potential, such as *Pseudomonas, Bacillus, Serratia, Burkholderia,* and *Sphingomonas* (Kotoky et al. 2017a, b; Shukla et al. 2014). It is well known that EPS mediates the uptake of low-accessible hydrophobic compounds in the biofilm community (Shukla et al. 2019). In recent years, biosurfactants are also explored as solubilizers improving the uptake and degradation of organic compounds earlier limited by the aromatic carbon accessibility (Bezza and Chirwa 2017). Bacteria harboring EPS and biosurfactants biosynthesis potential can provide a platform for the enzymatic metabolism of PAHs. Their concomitant involvement can be projected as excellent players in pollutant biodegradation strategies. Comprehensive knowledge of these biopolymers secreted by potential PAH degraders would provide essential information to assess the bacterial community utilizing PAHs. The phylogenetic coincidence of PAH degradation potential with EPS and biosurfactants synthesizing attribute would prove helpful in designing the bioremediation strategies.

Many studies described the individual role of these bioavailability enhancers (Mishra et al. 2021; Shukla et al. 2019); however, surprisingly little has been reported on their cohort action towards solubilization of difficult to degrade PAHs. The interaction of these microbial bioactive agents with PAHs would help in the explicit exploration of their solubilization mechanisms leading to enhanced hydrocarbon biodegradation. In this review, an elucidation has been made to exemplify the interaction and mechanism of uptake of PAH compounds by bacterial cells through biosurfactants and EPS biopolymer. In silico mining of the genomic treasure for specific genes could help explore the multi-potent nature of bacterial cells. With this view, the genes for biosurfactants and the priming glycosyltransferase genes of exopolysaccharide biosynthesis (a major EPS component) are reviewed in thirty-five bacterial genera (reported for PAH degradation). Quorum sensing, small RNAs, cyclic diguanosine-5'-monophosphate (c-diGMP), and two-component signal transduction pathway control the synthesis and release of these emulsifiers and the PAH degradation process (Wolska et al. 2016; Schmid et al. 2015). This review provides an exemplary description of these regulators to lighten up the regulatory mechanism of bacterial cells towards PAH utilization.

Polycyclic aromatic hydrocarbons: a less bioavailable hydrocarbon

The bioavailable fraction of any chemical compound towards degradation by microbial cells is defined as its 'bioavailability'. This fraction varies greatly with mass-transfer parameters and is controlled by the experimental parameters set in-vitro (Semple et al. 2007). Hydrophobicity and bioaccumulation property of PAHs increases with molecular size and structural angularity. As the molecular mass of PAH increases, its aqueous solubility decreases significantly, affecting the bioavailable fraction of PAHs to microbes (Abdel-Shafy and Mansour 2016). Biodegradation of PAHs is dependent mainly on their bioavailability and limited due to their strong tendency to remain bound tightly to the sorbent matrix particles, including clays and other organic matter (Garcia-Delgado et al. 2019; Ren et al. 2018). Several studies reported unsuccessful degradation of PAH compounds due to its sorption on coal tar, black carbon that significantly affected its bioavailability (Benhabib et al. 2010; Ren et al. 2018).

Microbial sequestration of PAH molecules is dependent mainly on the amount of organic carbon present in the soil (Lu et al. 2011). The organic matter content and soil particle size affect the availability of PAH congeners to the

microbial cells by sorption and sequestration mechanisms. It was demonstrated that high organic content renders a low rate of PAH degradation by indigenous microorganisms. The diffusion of contaminants in the hydrophobic pockets of the soil matrix and the time interval of PAH contact decide the bioavailable fraction of the compound to the thriving microbes (El-Maradny et al. 2021; Ossai et al. 2020). The time interval for which the PAH compound interacts with the sorbent matrix is crucial; it has been noted that the longer the contact time of PAH with soil, the lesser is the bioavailability towards degradation (Luo et al. 2012). The process is known as 'aging' and has been reported to limit the bioremediation rate significantly. The degradability of PAH compounds is also dependent on the presence of co-metabolic substrates and the abundance of the hydrocarbon-degrading microbial population (Ghosal et al. 2016).

PAHs fate and transport into the bacterial cell are also dependent on the cell surface hydrophobicity (CSH) of the interacting bacterial cell. It is relevant when PAHs are more portioned within the residual soil matrix and are firmly bound to minerals and organic matter (Sun et al. 2014; Ren et al. 2018). The hydrophobicity of PAH compounds is directly related to their molecular mass, which renders its low aqueous solubility. This physiochemical characteristic affects its uptake and subsequent degradation by bacterial cells. PAHs generally depict high water-octanol partition value (i.e., high K_{ow}) and remain firmly adhered to the sorbent of non-aqueous polar liquids (NAPL) and organic matter, thus limiting its uptake (Wang et al. 2020). However, many factors determine CSH; it largely depends on hydrophobic proteins on the cell surface. High CSH stimulates PAH adsorption and partition from the soil/sediment surface onto the cell to encourage PAH uptake and utilization. Tribedi and Sil 2014 reported the direct correlation of CSH and PAH degradation in *Pseudomonas sp*.

Metabolic enzymes remain useless if the substrate is unable to enter the cell. Due to their low solubility, many microbes have evolved their systems to mineralize them more readily. Microorganisms develop upgraded systems that efficiently degrade, enhancing the diffusive flux, thereby reducing the concentration of PAH proximal to the cell surface. Some microbes thrive on the mineral matrix and form a biofilm to adsorb the PAHs reducing the diffusion time and the distance between PAH and cell surface (Johnsen and Karlson 2004; Zhang et al. 2012). Hence, bioavailability is regarded as the most significant hurdle restricting the biodegradation of PAH compounds by microbial cells (Johnsen et al. 2005). Bioavailability, therefore, decides the fate of the hydrophobic compounds to remain sorbed to the sorbent matrix or get dissolved in the NAPL like oil or utilized by the microbial community.

Sustainable adaptations under PAH stress

Along with several other hydrophobic organic contaminants, PAH represents a carbon reservoir; however, its low bioavailability becomes the dead-end for microbial cells to use as carbon and energy. A dynamic and complex microenvironment surrounds the cells under stress and communicates to respond and thrive under extreme environments. During carbon limiting conditions, the ecological flora devises internal modifications to utilize these compounds as substrate by secreting various polymers and molecules (Bezza and Chirwa, 2017; Zhang et al. 2013; Zhang et al. 2016; Zhang et al. 2015).

Microenvironment for PAH biodegradation

Bacterial species preferred to live in a community by forming biofilms, and almost all bacterial species encompass the tendency of biofilm formation when triggered by an environmental cue. Biofilms are structured eco-communities where microbes get attached to abiotic/biotic surfaces embedded in a matrix of self-secreted polysaccharides (O'Toole et al. 2000). The organic and inorganic substances present in the surrounding environment reflect any microbial community physicochemical and structural behavior. Bacterial biofilms can be effectively used for the remediation process as the bacterial community is encased within the sticky glue of 'exopolymeric substances' (EPS), protecting the underlying bacteria from several environmental threats (Flemming 1993). Additionally, it endows an environment that encourages intercellular communication and gene transfer through quorum sensing ability, metabolite diffusion, and bacterial chemotaxis (Yesankar et al. 2022). Compared with their planktonic counterparts, bacterial biofilms show greater tolerance to toxic pollutants, higher survival chances, and improved transformation potential through catabolic pathways (Ghosh et al. 2017). It can harbor varied aerobic and anaerobic bacteria that combine these PAH pollutants as an energy source using electron acceptors such as oxygen, nitrate, or sulfate. Biofilm-mediated remediation demonstrates enhanced transforming potential and adaptability towards toxic wastes due to improved bioavailability of toxic pollutants to organisms (Yesankar et al. 2022). Bacterial species may utilize PAH as a carbon and energy source within this complex community developing bioavailability enhancement strategies like biosynthesis of biosurfactants or EPS (Schmid et al. 2015; de Gannes and Hickey 2017). It dates back to the twenty-first century when in an *in-vitro* study by (Johnsen et al. 2005), most strains degrading PAH in pure culture state were tested to be biofilm formers.

Sphingomonas polysaccharides used in the study showed a further increase in the solubility of hydrophobic PAHs. Thus, it was confirmed that biofilms forming on the PAH crystal might favor the degradation of PAHs from crystals to the bacterial cells.

Bacterial uptake and solubilization of PAHs

In a study on microbial genetic adaptations, (de Gannes and Hickey 2017) proposed three bacterial survival methods to sustain in PAH stress environment. Bacteria can adapt to the stress environment by synthesizing the carbon assimilating enzymes and regulating the expression of modifying enzymes bringing structural modifications in cells to adsorb compounds. Biofilms provide a natural platform for accessing hydrophobic PAH adsorbed in EPS, making them available for enzymatic degradation. It has been well documented that degradation of PAH becomes feasible as they get solubilized in biofilms allowing them to overcome their mass-transfer limitation (Shukla et al. 2014). Biofilms provide an enlarged substratum for binding of PAHs, making them available for degradation due to the multi-ionic nature of EPS.

PAHs are distributed disparately in soil and sediments. It has been known that chemotaxis plays a vital role in making the compound accessible for degradation, as the movement of microbes towards a chemical stimulus is favorable in the stress of organic chemicals (Ahmad et al. 2020). Microbes adapt to chemotactic behavior steepening the chemical gradient in response to a carbon deprivation state, enabling hydrophobic PAHs bioavailability, and improving biodegradation efficiency. The bacterial movement towards pollutants helps direct adhesion to adsorbed PAHs and subsequent secretion of extracellular enzymes or biosurfactants for accessing adsorbed PAHs for microbial uptake (Krell et al. 2013).

PAHs transport and degradation in bacterial cells

PAH transportation across the bacterial membrane is the initial step before metabolic enzymes act upon them. Bacterial cells tend to facilitate the PAH transport by narrowing the expanse of the substrate through various physiological changes (Zhang et al. 2012). Bacteria may employ their existing non-specific transport systems to transport PAHs into cells instead of developing specific transporters for particular PAHs. The uptake system of any carbon is classified as active and passive. The dynamic system for carbon transport includes phosphoenolpyruvate (PEP): a carbohydrate-phosphotransferase system (PTS) requiring ATP (Jeckelmann and Erni 2019). However, the study by (Yan and Wu 2020) describes the passive transportation system for PAHs as highly likely to be symporters, not consuming ATP. The PTS is likely to transport phosphorylated molecules, and PAHs do not contain a hydroxyl group for phosphorylation and cannot be transported through the same. PAHs cannot create a chemiosmotic gradient and therefore cannot lead through uniporters, leaving behind the last substitute of antiporters, but only when sufficient protons have been generated through low molecular weight (LMW)-PAH metabolism. Consequently, the central mechanism for PAH uptake remains through symporters only when a proton (H^+) gradient is generated inside the cell through the metabolism of LMW PAHs as they are partially soluble in an aqueous medium, and their transportation is favored through H^+ symporters (Yan and Wu 2020).

Microbes biologically degrade PAHs and, through mineralization, they can be further utilized to meet carbon and energy needs. Detoxification of these PAHs makes them water-soluble intracellularly, which can also be used to synthesize secondary metabolites. This detoxification seems to be the priming step in ring cleavage and carbon assimilation in microbial cells. Researchers have studied and characterized various bacterial species dealing with PAH degradation genomes for decades. Many studies mention the use of bacterial and fungal isolates to degrade LMW and high molecular weight (HMW) PAHs through in-situ and ex-situ approaches, as reviewed by Haritash and Kaushik (2009). Extensive studies have reported the isolation of PAH degraders from the aerobic system, besides many potential PAH-degraders being isolated from the anaerobic environment. Indigenous microbial communities can utilize PAHs pollutants; still, its low abundance and lack of accessibility to microbes become a delimiting factor for remediation (Krell et al. 2013). Researchers propose to augment bacterial consortia enriched with differential PAH degradation potential. It is noteworthy that consortia of bacterial species are generally utilized for degradation studies as a mixed population provides a cooperative and improved degradation rate (Guo et al. 2017). The biofilm synthesized by *Stenotrophomonas acidaminiphila* NCW-702 was more efficient in degrading PAHs than its planktonic counterparts (Mangwani et al. 2016). Biofilms have been employed for on-site remediation of contaminated environmental systems in contaminated soil and groundwater. Several reports mention the bacterial species forming biofilms applied for degrading PAHs such as *Pseudomonas, Bacillus, Rhodococcus, Acinetobacter, Burkholderia sp.* (Gupta et al. 2020; Mahto and Das 2020). In a study, *Sphingobium xenophagum* D43FB was reported to degrade 95% phenanthrene in the presence of cadmium, and its microscopic studies (Scanning Electron Microscopy) revealed the direct adherence of biofilms to phenanthrene crystals. Its genome sequencing analysis reveals several PAH degrading genes (Gran-Scheuch et al. 2017).

EPS–Crucial player enhancing uptake and degradation of polycyclic aromatic hydrocarbons

The limited carbon reserve, the chemotactic ability of bacterial species, the uptake and subsequent degradation of PAHs by cytoplasmic enzymes all form the synchronous cycle of bacterial PAH metabolism. Microbes in soil pose several nutrient assimilation challenges, primarily carbon compounds for maintaining their metabolic state. For this, microbes secrete structurally diverse biopolymers and surface-active agents to utilize difficult to degrade hydrophobic compounds making their sustenance feasible (Costa et al. 2018; Tripathi et al. 2020). Many hydrophobic organic substrates exist in a contaminated environment. Co-metabolism enables the synthesis of biopolymers and surface-active agents, making the degradation process feasible (Perfumo et al. 2010). EPS secreted provides a quasi-liquid environment (containing carbohydrates, proteins, and lipids) to bind PAHs and other hydrophobic compounds. Various functional moieties, including phosphate, sulfhydryl, carboxylate, amino, and phenolic groups, impart multi-ionic character to EPS (Salama et al. 2016). PAH degradation must be therefore characterized by a natural tendency of bacteria acquiring PAH degradative genes in oligotrophic environments.

EPS are either synthesized as a capsular material or attached to the cell as a dispersed slime layer (Flemming et al. 2016). Many bacteria (Gram-positive and Gram-negative) algae, fungi, and archaea produce EPS. The ecological niche of any bacteria determines the physiological function of the EPS secreted. Although a larger pool of energy sources is needed for EPS formation during adverse conditions, the advantages offered are credited with more enormous proportions of profit like protection against extreme temperatures, salt stress, and carbon limitation conditions (Green and Mecsas 2016). Its layer indubitably provides a multi-ionic uptake pool of nutrients and carbon sources. The function of EPS is to give physical infrastructure delivering nutrition and adhesion, cellular communication, water retention, adsorption of organic and inorganic constituents, and notably a protective barrier against environmental cues (Flemming et al. 2016).

Exopolysaccharides- as bioemulsifiers

Synthesis of EPS is clocked during the late logarithmic growth phase of the microbe, and different environmental factors regulate its synthesis. EPS synthesis is enhanced when a surplus carbon source is available, serving as a carbohydrate reserve for metabolism. (Turakhia and Characklis, 1989) have validated a direct correlation between EPS synthesis and microbial growth. Contrastingly it was reported that EPS synthesis is enhanced when cells are metabolically slow-acting, in conjunction with the notion that few bacteria synthesize less EPS when growing in carbon-rich sources (Evans et al. 1994). Thus, the EPS synthesis rate depends on the microbe and the environmental system in which they are blooming.

Exopolysaccharides are the main structural component of EPS and coagulative homopolymers or hetero-polymers of hexose sugars D-glucose, D-mannose, D-galactose, and pentose sugars like xylose and arabinose secreted in the surrounding environment with customary shielding mechanisms. The degree of polymerization and the length of the polysaccharide chain is precise and vary within species (More et al. 2014). The monomer units, their length, and rate of recurrence of branching decide the exemplary role of EPS. In addition, amino sugar derivatives of hexoses and pentoses have also been a part of EPS. Non-carbohydrate substituents are found at the end of the polymerized carbohydrate chain, giving a specific charge to the polysaccharide (Hussain et al. 2017). The examples of homopolysaccharides produced by microorganisms are dextran, Curdlan, and cellulose. Heteropolysaccharides include alginate, xanthan, gellan, hyaluronic acid. Table 1 summarises the homo-exopolysaccharides and hetero-exopolysaccharides produced by different bacterial species, their composition, and modifications in the form of charge moieties determining the charge on exopolysaccharides. Apart from carbohydrate residues, EPS is constituted of proteins and extracellular DNA having individual roles. Lipids and their derivatives in conjunction with methyl/acetyl-linked polysaccharides attribute to the hydrophobic nature of EPS, while hydrated forms of monomers, proteins, and extracellular DNA add to the hydrophilic nature of EPS. The overall surface chemistry of EPS is determined by the amount and number of non-sugar components like acetate, succinate, pyruvate, and inorganic modifiers such as sulfate and phosphate. Also, uronic acids add a negative charge to the EPS (More et al. 2014; Hussain et al. 2017). These components can bring the anionic, cationic or neutral charge to the concerned EPS. The consequences of charged species substituted on the homopolymer and heteropolymer of exopolysaccharide of EPS are significant for PAH adsorption and solubilization. Structural composition studies on EPS hydrolysis reveal that nearly 24% of amino acids were hydrophobic, and 25% had a negative charge (Dignac et al. 1998). It demonstrates the significance of EPS as a sorption surface for binding hydrophobic organic compounds. The multi-ionic charges depicted by the EPS matrix thus provide the difference in the hydrophobicity and hydrophilicity for the effective partitioning of PAH molecules from the sorbent or NAPLs.

Table 1 Bacterial exopolysaccharides with their components and charge imparting enzyme of exopolysaccharide biosynthetic pathway

Bacterial source	EPS produced	Polysaccharide composition	Synthesis pathway	Charge modifications	Extracellular enzyme/ Charge imparting enzyme	Reference
Bacillus subtilis	Levan -1	β-(2→6) linked Fructose and occasional branch chain Frutose β -(2→1)	Synthase	NA[1]	Levan sucrase	Dogsa et al. (2013)
Lactobacillus gasseri	Inulin	β -(2→1) linked Fructose branch chain β -(2→6) attached to the fructosyl moiety of sucrose	Synthase	NA	Inulosucrase	Shoaib et al. (2016)
Agrobacterium sp.	Curdlan	β-(1→3) linked D-Glucose	Synthase	NA	crdS -glucan synthase	Ruffing and Chen (2012)
Leuconostoc mesenteroides BD1710	Dextran	α-(1→6) linked D-Glucose	Synthase	NA	Dextran sucrase	Nácher-Vázquez et al. (2017)
Bacillus subtilis strain RB14	Cellulose	β-(1→4) linked D-Glucose	Synthase	NA	*bcs*ABCD operon	Romling and Galperin (2015)
Staphylococcus sp.	Polysaccharide intercellular adhesin	β-(1→6) linked N-acetyl-glucosamine	Synthase	Partially deacetylated	*icaADBC locus icaB*	Arciola et al. (2015)
Pseudomonas aeruginosa	Alginate	β-(1→4) linked acetylated D-Mannose with its C5 epimer (L-GuluronicA)	Synthase	Acetate	*Alginate operon algI*, *algJ*, and *algF*	Chanasit et al. (2020)
Pseudomonas aeruginosa	Pel	Linear polymer of N-acetyl hexosamine linked via β-(1→4) linkage	Synthase	De-acetylated	Pel operon/pelA	Colvin et al. (2013)
E.coli members	Colanic acid	Glucose, (2)Fucose, (2) Galactose, Glucoronic acid	Wzx/Wzy	Acetate, pyruvate	wcaF, wcaB:Acetyl transferase pyruvyltransferase (*wcaK)*	Scott et al. (2019)
Burkholderia cepacia	Cepacian	Glucose, Guluronic acid, Mannose, Rhamnose, and Galactose (1:1:1:1:3)	Wzx/Wzy	Acylation	Bce complex *bce*O/*bce*S/*bce*U	Sousa et al. (2013)
Bacterial source	EPS produced	Polysaccharide composition	Synthesis pathway	Charge Modifications	Extracellular enzyme/ Charge imparting enzyme	References
Sphingomonas sp	Gellan	L-Rhamnose- α-(1→3)-D-Glucose-β-(1→4) D-Glcoronic acid-β-(1→4) D-Glucose	Wzx/Wzy	Acetate, Glycerol	*Gel operon (Not known)*	Scott et al. (2019)
Sphingomonas sp	Welan	L-Mannose- β -(1→3)-D-Glucose-β-(1→4) D-Glcoronic acid-β-(1→4) D-Glucose	Wzx/Wzy	Acetate	*Wel operon (Not known)*	Kaur et al. (2014)
Sinorhizobium melloti	Succinoglycan	β-linked Glucose and Galactose (7:1)	Wzx/Wzy	succinate, pyruvate and acetate	*Exo operon/exoH: succinate exoV:pyruvyl*	Hawkins et al. (2017)

Table 1 (continued)

Bacterial source	EPS produced	Polysaccharide composition	Synthesis pathway	Charge Modifications	Extracellular enzyme/ Charge imparting enzyme	References
Xanthomonas campestris	Xanthan	Repeated pentasaccharide units of Linear β-(1–4)-linked glucose units; attached to trisaccharide side chains via (α-1,3) linkage Trisaccharide-{D-mannose-(β-1,4)-glucuronic acid-(β-1,2)-D-mannose}	Wzx/Wzy	Acetate, pyruvate on D-Mannose	*Gum operon (genes gumB-gum M) gum F and gum G:Acetate gumL: Pyruvate*	da Silva et al. (2018)
Streptococcus pyrogenes	Hyaluronic acid	Linear polymer of Glucuronic acid and N-acetylglucoronic acid with alternate β-(1→3) and β-(1→4) linkage	Synthase	Acetate	*Has ABC operon*/glu M	de Oliveira et al. 2016

[1]*NA* Not Applicable

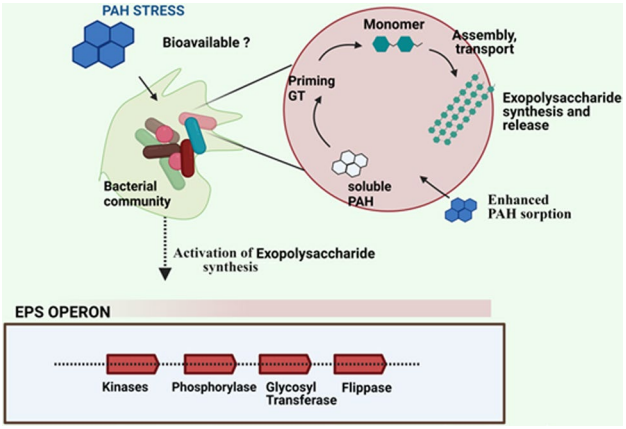

Fig. 1 Schematic representation of biofilms towards PAH stress through exopolysaccharide synthesis. Stages of exopolysaccharide synthesis comprise four steps catalyzed by four classes of enzymes. First, kinases and phosphorylase prepare activated sugars, and priming glycosyltransferase (Priming GT) initiates the glycan biosynthesis by transferring phosphosugar onto the isoprene lipid carrier, followed by the sequential action of substrate-specific glycosyltransferases. Polysaccharides with modified charged moieties are then secreted by the hydrophobic group of enzymes like flippases bringing about the excretion of completely synthesized exopolysaccharides across the membrane. These exopolysaccharides, along with other components of EPS, further provide the adsorption site for PAHs enhancing their sorption and uptake

Late in the twentieth century, the biosynthetic pathway of exopolysaccharide was studied. Now fully explained mechanisms are known that are dependent on the following broad classes of proteins-Wzx/Wzy proteins, ATP-binding cassette (ABC) transporter, and the synthases. Exopolysaccharide synthesis occurs in four phases controlled by four different enzymes (Kumar et al. 2007). A synchronous cycle of exopolysaccharide synthetic machinery involved in EPS production in the presence of less bioavailable PAH compound has been drawn in Fig. 1. Firstly, the carbon source is taken up and phosphorylated by the first group of kinases. Then, priming glycosyltransferase (PGT) initiates the glycan biosynthesis by transferring phosphosugar onto an isoprene lipid carrier with a long chain of 55-carbon-undecaprenyl phosphate (Van Kranenburg et al. 1999). This lipid moiety allows the segregation of traffic of glycan components towards the periplasm where exopolysaccharides polymerization occurs. The phosphorylated sugar linked to lipid carrier may then be used for polysaccharide synthesis followed by the action of substrate-specific glycosyltransferases. Polysaccharides are generally released with modified charged moieties like acetyl, acyl, sulfate, methyl, or phosphate, affecting the function of EPS secreted (Mishra and Jha 2013). Modified polysaccharide chain is then secreted by the hydrophobic group of enzymes like flippases bringing about the excretion of completely synthesized exopolysaccharides across the membrane.

EPSs imperative and diverse role is dependent on the biotope of the producing organism and the selective environmental pressure, which influences the biosynthesis of exopolysaccharides.

EPS implications in the environmental sector

The genetic manipulation of EPS genes for more significant production could prove helpful in systems depicting the uncontrolled existence of multiple hydrophobic compounds in the ecosystem. The bioremediation technique using microbial products is effective, especially with the treatment of PAH-contaminated systems. Bacterial EPS has shown multi-ionic charge property that aids in binding/adsorption and ion uptake characteristics useful in bioremediation processes. These EPS immobilize the hydrophobic compounds, which are otherwise less accessible, and enhance their microbial cellular uptake (More et al. 2014). Some exopolysaccharide acts as emulsifying agents, such as *emulsan*, a hetero-polysaccharide, that shows emulsification property towards hydrocarbons even at low concentrations, justifying its use in different applications (Kumar et al. 2007; Sałek and Euston 2019). EPS polymer known as biodispersion produced by *A.Calcoaceticus A2* species is long known to have dispersing characteristics for water-insoluble compounds (Rosenberg and Ron 1997). The enhancement of pyrene-dissipation in contaminated soils by rhamnolipids secreted by *P.aeruginosa* was significantly improved from 59.8% to 86.4% (Jorfi et al. 2014).

PAH degraders synthesize and secrete EPSs for various essential physiological processes like biofilm formation, adherence to hydrophobic substrates, cell aggregation, and intoxication of inorganic ions, like heavy metals. EPS also possesses surfactant properties in surfactin, emulsion, and viscosin, enabling them to disperse hydrophobic substances from the medium, making them available to the bacterial population (Shukla et al. 2019). In addition, EPSs are involved in the remediation of hydrophobic compounds as in *Halomonas* sp. strain TG39 among the indigenous microbial community (obtained from Deepwater Horizon oil spill) (Gutierrez et al. 2013). In a degradation study, *Enterobacter cloacae* TU was reported to utilize PAHs and n-hexadecane by secretion of EPS composed of repeating glucose and galactose units confirmed by NMR studies (Hua et al. 2010).

Notably, the EPS secreted by the Gram-negative bacteria increased the CSH and neutralized the cell surface charges, contributing to enhanced bioavailability of the pollutant and its degradation efficiency. Research studies claim that bacterial EPS secretion helps biofilm formation utilizing organic compounds as energy substrate (Chakraborty and Das 2014). A study on *P.aeruginosa* biofilms shows enhanced EPS synthesis, altering cell surface property towards the PAHs biosorption, followed by entry into the bacterial cell for catabolic enzyme degradation (Chakraborty and Das, 2014). An example can be cited where mycolic acids, a component of *Mycobacterium sp*. capsule, enhance its CSH, which serves the passive uptake of PAH into the cell (Kim et al. 2005). Thus, it can be summarised that the microbial attachment-directed bioavailability depends on the ionic nature of the secreted EPS.

EPS applications in oil recovery other than remediations are gaining interest among the scientific community. The oil contains several aliphatic and aromatic compounds, including PAHs. Oil recovery has been carried out using microbes and their EPS in the petroleum industry called Microbial Enhanced Oil Recovery (MEOR) (Ke et al. 2018). MEOR utilizes the immobilization property of EPS for treating the residual oil following extraction using conventional methods. Thermally stable EPS with high viscosity obtained from *Enterobacter cloacae* and *Volcaniellaeurihalina F2-7* has been applied for MEOR (Calvo et al. 1995; Chandran and Das 2011). Another polymer, xanthan, secreted mainly by *Xanthomonas* spp., is used for enhanced oil recovery; its use is restricted to low-temperature recovery procedures due to its temperature sensitivity (Shukla et al. 2019). An alternative to this is welan gum produced by *Alcaligenes* spp., which is used as an excellent oil displacement agent due to its high excellent rheological traits in terms of viscoelasticity and high-temperature resistance. Their rheological properties are durable and less affected by pH changes, making them apparent for oil recovery.

EPSs are now more explored for their autem applications in diverse healthcare, pharmaceutics, agriculture, and food industry as thickeners, stabilizers, and emulsifying agents (Barcelos et al. 2020). In addition, several bacteria are studied for their EPS composition, structure, and biosynthesis mechanism, and it is now considered as an industrially important product with varied applications in food, oil recovery, and cosmetic industries (Jindal and Singh Khattar 2018; Moscovici 2015; Roca et al. 2015; Freitas et al. 2011). Besides these, the essential role of these chemical compounds lies in the protective and adsorption advantages it offers to bacterial cells in adverse environments.

Transcriptional and post-transcriptional regulation of EPS synthesis

Regulators of EPS biosynthesis and biofilms are overlapping and are well-coordinated processes regulated at different levels requiring an understanding of each facet meticulously. Various reports suggest quorum sensing (QS), regulation by cyclic diguanosine monophosphate (c-di-GMP), two-component signal transduction pathways, small RNAs (sRNAs), alternative RNA polymerase σ-factors and anti-σ-factors are the central core regulators of EPS synthesis.

Quorum sensing

Quorum sensing (QS) is a unique language used by microorganisms for intercellular signaling and communication, mediated by self-generated signal molecules termed autoinducers. Depending on the bacterial population density and the autoinducer concentration, the bacterium answers the sensor call of critical mass by activating or repressing the target genes (Tabassum 2021). QS signaling is indirectly involved in glycoconjugate polymer biosynthesis in EPS and biosurfactants production affecting PAH bioremediation (Bhatt et al. 2021).

QS mediated through acylated homoserine lactone (AHL) is well studied and conserved in *P. aeruginosa* and consists of two inducer/regulator complexes viz., *lasI/R rhlI/R* genes coding for the Lux family transcriptional activators (Acet et al. 2021). The role of and also in the bioremediation of phenanthrene and pyrene. The expression studies of *lasI* and *rhlI* coding for AHL synthase of *P. aeruginosa* N6P6 found elevated expression in the presence of phenanthrene (3- ring PAH) and pyrene (4-ring PAH) and is reported to be essential in the synthesis of pel polysaccharide (Mangwani et al. 2015).

Two-component signal transduction system and small Ribosomal RNAs

Two-component signal transduction system (TCSs) comprises the predominant method through which bacteria responds to changing environments and plays significant roles in modulating bacterial fitness in the environmental niche. GacS-GacA plays a significant role as a TCS protein involved in alginate and pel polysaccharides in *Pseudomonas* species (Fata Moradali and Rehm 2021). KinB and FimS are the sensor kinases that regulate AlgB and AlgR proteins, respectively activating the expression of alginate biosynthesis machinery by binding to *algD* promoter (Hay et al. 2014). Succinoglycan synthesis is another example where the *exoS* sensor gene with its product *chvI* negatively regulates the transcription of *exo* genes resulting in lowered EPS yields. The role of *mucR* encoded regulatory protein controlling EPS biosynthesis in *Rhizobium* was studied in the late twentieth century (Janczarek 2011). The elevated expression of *exoF, exoK,* and *exoY* genes, mainly *exoY* gene products, acts as a priming glycosyltransferase in the exopolysaccharide biosynthesis in these rhizobial strains. Two-component regulatory proteins also control hyaluronic acid biosynthesis- CovR/CovS binding the AT-rich region of the *has* operon (Federle and Scott 2002). In Xanthomonas strains, EPS synthesis and virulence genes are closely related and controlled via cell–cell signaling controlled by signal factors under the regulation of two-component signal transduction factors RpfC/RpfG. The RpfC/RpfG signaling is mediated and sensed by the concentrations of c-di-GMP (Yin et al. 2013).

Small non-coding RNA molecules (sRNAs) are also known to regulate and involve the post-transcriptional regulation of metabolic genes, stress response genes, virulence-associated genes, and quorum sensing (Ghaz-Jahanian et al. 2013). These RNAs are transcriptionally regulated by two-component system proteins and are involved in post-transcriptional control of EPS biosynthesis. (Falaleeva et al. 2014) identified promoters for transcription of sRNAs and an intrinsic terminator limiting EPS synthesis at transcriptional levels in *Streptococcus pyogenes* for hyaluronic acid capsule biosynthesis.

Chambers and Sauer (2013) demonstrated the dependency of the initial attachment of planktonic cells to the surface to the levels of sRNAs. *In P. aeruginosa, rsmY* and *rsmZ* are the best-known regulatory units that regulate the activity of biofilm matrix polysaccharide Psl. Three sensor kinases, namely *RetS, LadS*, and *GacS*, phosphorylate the effector proteins and activate their transcription. The expression of another transcription regulator, RpoS, causing expression of the *psl* gene, is also essential for EPS synthesis (Yu et al. 2016). The Csr (carbon storage regulator) is a multi-component regulatory system that acts as a repressor of secondary metabolites in bacterial cells. Csr controls gene expression of many critical cellular functions like repression of glycogen metabolism, gluconeogenesis, and biofilm formation; simultaneously, it activates glycolysis, cell motility, and pathogenesis as demonstrated in several γ-Proteobacteria genera (*Pseudomonas, Escherichia, Salmonella, and Vibrio)* (Sobrero and Valverde 2020; Romeo et al. 2013). An example can be cited as RsmA that can activate and upregulate motility apparatus (flagella and pili associated genes) and negatively regulate the expression of *las* and *rhl* transcripts involved in synthesizing *alginate* and *pel* polysaccharide in *Pseudomonas sp* (Sobrero and Valverde 2020).

cyclic-di-GMP signaling

Another vital regulator during EPS biosynthesis and determining PAH degradation is bis-(3'-5')-cyclic dimeric guanosine monophosphate (c-diGMP). c-di-GMP signaling molecule synthesized by bacteria controlling several biological processes and plays a significant role in regulating EPS synthesis. When c-di-GMP concentrations rise, it induces conformational changes in flagellar synthesis, negatively regulating it and promoting EPS synthesis genes during biofilm mode (Hengge 2009). Reports on biofilm of *Pseudomonas sp*. validate the role of c-di-GMP in the synthesis of alginate and *pel* polysaccharides and their transport across the cell envelope (Matsuyama et al. 2016). Effector targets, *Alg44* and *FleQ*, activated by c-di-GMP, control alginate synthesis while *PelD* and *FimX* regulate *Pel* polysaccharide synthesis.

Another group of biofilm-associated proteins is type IV pili that bind the c-di-GMP regulator and regulate EPS synthesis. The pili filaments are polar and responsible for the twitching motility of bacteria and are essential in early biofilm initiation phases (Hay et al. 2014). Several EPS synthases/copolymerases contain *PilZ* domains, which bind c-di-GMP and bring about post-translational conformational changes in the glycosyltransferase enzyme responsible for bringing the nucleotide sugar at a proximal distance to the active site. Activation of the *PilZ* domains of *Alg44* and *BscA* protein regulates alginate and cellulose biosynthesis expression, respectively (Morgan et al., 2014).

Reviewing biosurfactants for PAH solubilization

Biosurfactants synthesis is also a physiological response to carbon and nutrient stress stimuli. These act as solubilizers synthesized by several microorganisms, including bacteria, fungi, and yeasts (Shekhar et al. 2015), and are produced as secondary metabolites or membrane components showing remarkable surface properties, bringing about solubilization of poorly-available hydrophobic PAHs (Perfumo et al. 2010). The secretion of biosurfactants aids in reducing the surface tension of substrate at the matrix boundary leading to the availability of PAHs in a soluble form, which is a pre-requisite for the microbial uptake of a low bioavailable compound that may then be metabolized by microbial metabolic machinery (Chirwa et al. 2021). Biosurfactants are amphiphilic molecules secreted by intrinsic microbial communities in the surrounding environment or remain part of the cell membrane. These small biological active surface agents increase the bioavailability of PAHs that can serve as a carbon source in nutrient-limiting conditions (Bezza and Chirwa 2017). The primary hurdle for PAH entry into the cell is the outer-membrane permeability to various PAHs and their degree of hydrophobicity, which varies across taxa (Leech et al. 2020). The selective partitioning of PAH compounds by surfactant micelles occurs during micellar solubilization at critical micelle concentration (CMC). At this CMC, the rate of desorption of solute is maximum between PAH and aqueous phase, and at sub-CMC levels, the surfactant monomers assemble at the interface of PAH-soil soil-aqueous junctions. It increases the contact angle between the soil matrix and PAH, resulting in severance of PAH from the soil matrix. Biosurfactants thus partition at the polar-apolar interface and cause a reduction of the surface tension, enhancing the desorption of PAHs from the soil/sediment matrix into the aqueous medium (Souza et al. 2014). Biosurfactants are bestowed with multi-potential properties of high foaming, higher selective surface tension reducing potential, low CMC values, and higher emulsification index, making them better than the chemically derived surfactants (Jimoh and Lin 2019). Bacterial cells producing biosurfactants interact interfacially and alter the microbe's surface characteristics (Kaczorek et al. 2018). It builds up a microenvironment where the emulsification of compounds occurs through the secretion of other inducers via various quorum-sensing processes.

Biosurfactants mode of action

Several cellular activities are involved in the solubilization and uptake of PAH compounds by bacterial cells. There are many ways to access PAH compounds by bacterial cells, where biosurfactants play a significant role. Figure 2a illustrates the bacterial uptake of PAH compounds following biosurfactants-mediated solubilization. The pathway involves the binding of PAHs to microbial cells followed by activation of biosurfactants synthetases resulting in the release of biosurfactants monomers. The nature of biosurfactants is amphiphilic due to the hydrophobic attribute of saturated and unsaturated fatty alcohols or hydroxylated fatty acids bonded to the hydrophilic head of phosphorylated glycerol moiety (Karlapudi et al. 2018). The structure of (di)-rhamnolipid as a model biosurfactant depicting the amphiphilic nature is schematically shown in Fig. 2b. The biosurfactants molecule bind to the PAH compound via hydrophobic tails and forms hydrophilic bonds with surrounding water molecules (Fig. 2c). The emulsification characteristics of biosurfactants enable an increase in the surface area of the substrate, thus improving solubility in the aqueous environment. At critical micellar concentration (CMC), the biosurfactants monomers form micelles encapsulating the PAH compound where emulsification and pseudo- solubilization of the PAH compound may occur. The solubilized compound is now bioavailable and transported to the microbial cell. Following PAH uptake, metabolic enzymes for PAH degradation are activated, subsequently hydrolyzing the hydrophobic substrate.

Bacterial cells mostly directly adhere to PAHs for acquisition from sorbent surface (soil), involving direct modification of the contaminant matrix. It consists of the biosynthesis of EPS and biosurfactants, relieving the hurdle of bioavailability. It is relevant, as the growth of microbes on the substrate in biofilms is the most common mode of development where concomitant involvement of EPS and biosurfactants can occur (Hall-Stoodley et al. 2004). The substratum on which biofilm develops during PAH adsorption may be an organic mineral lattice or NAPL like oil containing dissolved PAH. Direct uptake on these matrices depends on several complex processes affected by the bacterial cell characteristics and environmental factors (Johnsen and Karlson 2004). The substratum condition enables the cell surface to reach the least diffusion distance for a sorbed

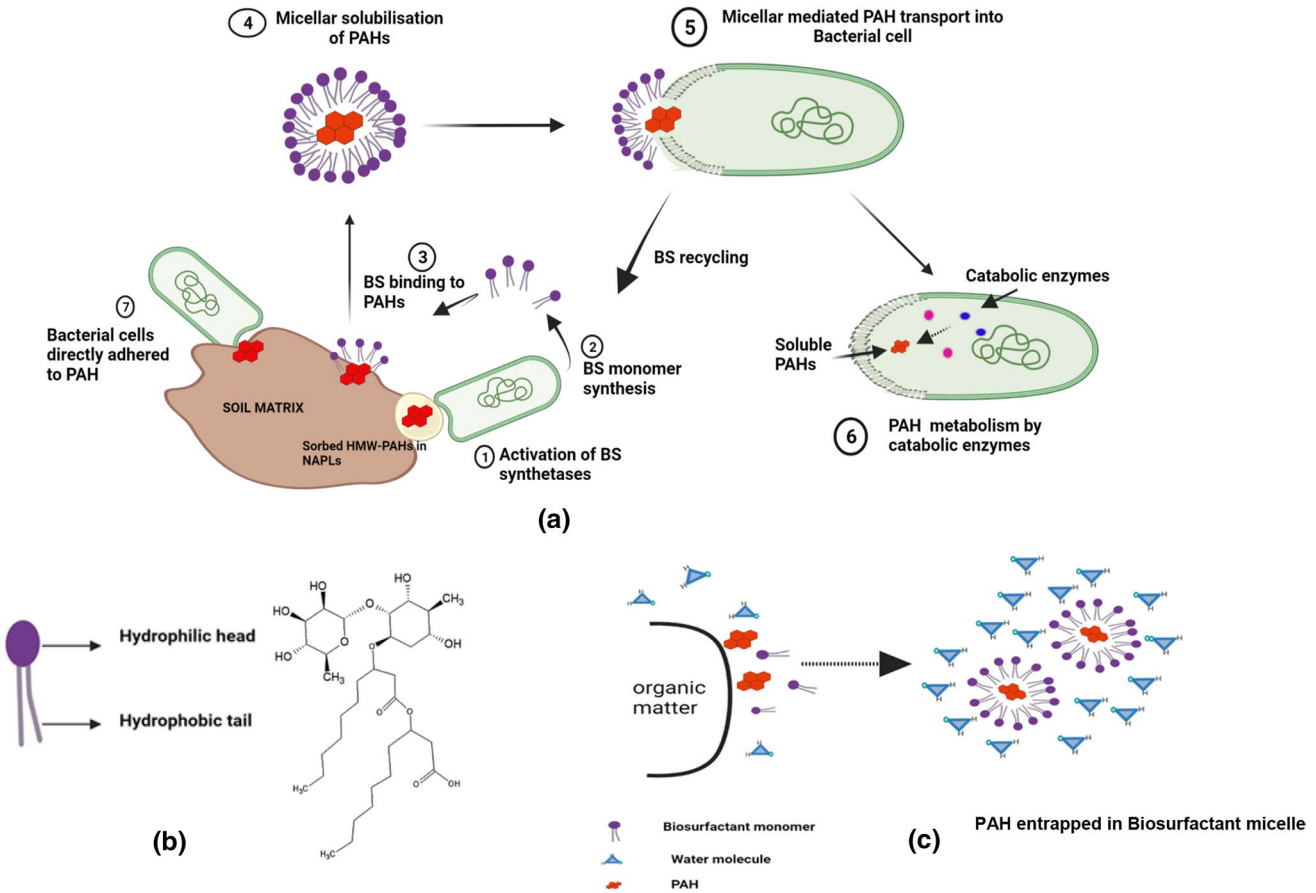

Fig. 2 Mechanism of action of biosurfactants in the solubilization and uptake of PAH compounds. **a** The mechanism through which PAHs are accessed by bacterial cells via biosurfactants is drawn. The pathway involves the binding of PAHs to microbial cells followed by activation of biosurfactants monomers. The monomers bind to the PAH via hydrophobic tails and forms micelles reaching a critical micellar concentration (CMC) involving solubilization of PAH pollutant and then transport to a microbial cell (1–5). Following PAH uptake, metabolic enzymes for PAH degradation get activated. A bacterial cell can directly adhere to PAHs for direct acquisition from sorbent surface (soil) involving direct modification of the contaminant matrix. It involves the biosynthesis of EPS and biosurfactants, relieving the hurdle of bioavailability (7). **b** Structure of model glycolipid biosurfactant- Structure of (di) Rhamnolipid depicting amphibolic nature of biosurfactants (hydrophilic head and hydrophobic tails). **c** Emulsification mechanism of Biosurfactants- Biosurfactants monomers secreted by bacterial cells form micelles around PAH molecule (at CMC) via hydrophobic tails and to water molecules via hydrophilic heads, making PAH compounds water-soluble

PAH, diffusing through the bacterial membrane (Johnsen et al. 2005). PAH uptake is therefore determined by the release of soluble PAH into the aqueous cellular environment. Biosurfactants monomers aggregate to form colloids, i.e., micelles with a hydrophobic core and hydrophilic heads outside. LMW PAHs tend to be encased in the hydrophobic core and are transported to the cell via micelles (Karlapudi et al. 2018). The apparent water solubility of PAH increases with solubilization and leads to subsequent emulsification of the hydrophobic structure. The PAHs are then uptaken by these solubilizing agents, then transported in NAPL dissolved state towards the degrading bacteria.

Biosurfactants may alter the cellular membrane properties, resulting in improved bacterial adherence to PAH compounds, improving biodegradation efficiency. It has been well studied that biosurfactants enhance the bacterial CSH, resulting in the enhanced uptake and degradation of pyrene and other HMW PAHs (Lu et al. 2019). However, the biosurfactant role is not exclusively dependent on the microbial growth of PAH compounds. For example, the study by (Johnsen and Karlson 2004) reports no evidence of biosurfactant secretion by the *Proteobacteria* and *Actinobacteria* cells adhered to PAH. Conversely, a strong correlation has been found in the synthesis of rhamnolipids secreted by *P.aeruginosa* N6P6 utilizing phenanthrene and pyrene as a carbon and energy source (Mangwani et al. 2016). Here the quorum-sensing (QS) systems *lasI* are *rhlI* positively correlated to the biofilm formation and PAH degradation.

Solubilization capacity of PAHs by multiple biosurfactants

Biosurfactants are classified according to their microbial origin and chemical nature. Two groups are categorized based on ionic group molecular size and presence. Based on molecular weight, biosurfactants with lower interfacial surface tension are divided into low molecular mass and high molecular weight polymers. Glycolipids, lipopeptides, and glycoproteins constitute low-mass biosurfactants, and particulate and polymeric surfactants come under the sizeable polymeric category (Sobrinho et al. 2014). Biosurfactants are mostly anionic with some neutral exceptions, based on the charge of the hydrophilic moiety resulting from a carbohydrate part, amino acid, phosphate group, or a cyclic peptide.

Advancement in biochemistry and molecular genetics revealed different biosurfactants operons, and the metabolic enzymes associated with these pathways can thus be elucidated. A multienzyme peptide synthetase complex called non-ribosomal peptide synthetases (NRPSs) generally catalyzes the synthesis of lipopeptide biosurfactants (Challis and Naismith 2004). Synthesis pathways of lipopeptides such as surfactin, lichenysin, iturin, and arthrofactin are mediated by NRPSs, in different bacterial species depicting the conserved nature of this enzyme complex (Esmaeel et al. 2016; Ibrahim 2018). The biosynthetic regulation pathway of surfactin (a lipopeptide biosurfactant) produced mainly by *B.subtilis* and rhamnolipids (a glycolipid biosurfactant) by *P.aeruginosa* is widely explored (Das et al. 2008). Other biosurfactants include viscosin, putisolvin, amphisin– all lipopeptides secreted by *Pseudomonas* species and emulsan produced by *Acinetobacter* species. Different strains *of Serratia* produce cyclopeptide biosurfactants known as serrawettin W1, W2, and W3 by a single gene *psw*P sharing homology with the NRPSs family genes. Rhamnolipids are the widely studied glycolipid biosurfactants produced by *Pseudomonas* species and are regulated by a plasmid-encoded *rhl* QS system (Soberón-Chávez et al. 2021). Other glycolipids include trehalolipids and sophorolipids with good solubilization properties; however, they are less explored.

Several studies report the culturing and isolation of biosurfactants producing bacterial strains from PAH contaminated sites (Ibrahim 2018) and have been enlisted in Table 2. A scientific work demonstrates it as a consortial process serving other non-biosurfactant producing members providing a substrate in a solubilized (Ibrar and Zhang 2020). Mineralization of crude oil by *A. borkumensis*; resulted in the secretion of biosurfactants that enhanced the uptake of alkanes by other consortial members (McKew et al. 2007). Enhanced biodegradation of crude oil was obtained in a salt-tolerant bacterial consortium with biosurfactant potential capacity (Chen et al. 2020). The synergistic role of multiple biosurfactants has been long known and studied in an eight-strain microbial consortium where only the biosurfactants released by the whole community and not by a single member achieve rapid degradation of hydrocarbon (Rambeloarisoa et al. 1984).

Biosurfactants influence the microbial growth on PAH, overcoming the barrier of poor availability and improving its uptake rate (Bezza and Chirwa 2016). Lipopeptides and glycolipids ensembles remarkable rheological properties helpful in crude oil recovery, proficient removal of heavy metals and hydrocarbons from contaminated soils in the complete bioremediation process (Carolin et al. 2021). *Bacillus* species are well known for biosurfactants synthesis. *B. circulans* has been shown to improve the bioavailability of anthracene compound by emulsifying it and enhancing its growth, improving the PAH degradation rate by nearly 30% (Bezza and Chirwa 2015).In addition, the use of lipopeptides enhanced the solubility of various PAHs viz., phenanthrene, fluoranthene, and pyrene and increased their uptake rate up to three folds (Bezza and Chirwa 2016).

Rhamnolipids, as stated earlier, are well-studied glycolipids, and their increased concentration in contaminated soil resulted in a proportional increase in phenanthrene desorption from the soil particles. The phenanthrene desorption was more profound in the presence of rhamnolipid and soluble substrates such as citric acid, oxalic acid, acetic acid, and tartaric acid. Among the different combinations, rhamnolipid and citric acid significantly affected the desorption (Liu et al. 2018). Earlier, Xiao-Hong et al. (2010) studied a high degradation rate of 99.5% of phenanthrene in *Sphingomonas* species GF2B using rhamnolipids. Peng et al. (2015) report an increase in the degradation rate of 37.52% and 25.58% of anthracene and pyrene using 0.065 mM and 0.075 mM concentrations of rhamnolipids, respectively. The solubility of PAH is affected by the increasing number of fused benzene rings. The fact is well proven while using an increasing concentration of rhamnolipids above its CMC, linearly increasing the solubility of naphthalene (2-ring), phenanthrene (3-ring), and pyrene(4-ring). The molar solubilization ratios of respective PAHs were 7.44, 2.83, and 1.34. Liquid chromatography coupled to mass spectroscopic analysis (LC–MS) of the purified polymeric substance secreted by *B. subtilis* strains reported two groups of ionic isoforms differing in their m/z range eluting at different retention times. The larger group represented fengycins, while the smaller fraction represented a mixture of surfactins and iturins (Li et al. 2015). It thus illustrates the synthesis of multiple biosurfactants by a single organism under a set of growth conditions.

Xia et al. (2014) reported concomitant degradation of PAHs (fluorene, pyrene) and alkanes like n-Dodecane by a mixture of lipopeptide surfactants. The purified lipopeptides were revealed to be surfactin, fengycin, and lichenysin

Table 2 Biosurfactant-assisted remediation of PAHs reported in different bacterial species

Bacterial species	Bacterial isolation source	Substrate for Biosurfactant production	Remarks	CMC values	Biosurfactants Functional groups (FTIR characterisation)	Predicted Biosurfactant	References
Achromobacter sp. strain AC15	Mangrove soil	Pyrene	pyrene solubility increased 1.5–1.9 times	ND[a]	ND	Linear peptide BS-15	Li et al. (2020)
Pseudomonas strain W10	Used motor oil-contaminated soil	Phenanthrene	80% Phenanthrene degradation	400 mgL^{-1}	CH_3, CH_2, and CH stretches aldehyde group carbonyl (C=O) stretching, C–O ester stretch	Rhamnolipid BSW10 (glycolipid)	Chebbi et al. (2017)
Bacillus cereus SPL-4	PAHs contaminated plant soil	3% (v/v) sunflower oil	51.2–55% 64.1–79% Degradation	90.5 mgL^{-1}	ND	Lipopeptide	Bezza and Chirwa (2017)
Bacillus stratospheric-us, Bacillus subtilis, Bacillus megaterium, and *Pseudomonas aeruginosa*	Wood treatment plant soil rich in Cresote	Mixture of 15 PAHs	Total removal rate 79 ± 2.5% on reactor scale	ND	(–CH_3, CH_2–), –NH–, and –CO–N, amine groups	Lipopeptide	Bezza and Chirwa (2016)
Bacillus subtilis CN2	Coal tar creosote contaminated soil	Motor oil and HMW PAHs	84.6 ± 7.1 recovery of used motor oil	185 ± 10 mgL^{-1}	N–H stretching (peptide group) C–H stretching in aliphatic group C–O stretching in the peptide bond C–O–C in ester groups	Lipopeptide	Bezza and Chirwa (2015)
Brevibacillus sp. PDM-3	Hydrocarbon contaminated sludge	Phenanthrene	ND	ND	C=O, OH, C–H stretching in CH_3, CH bending and C–O stretching in esters	Glycolipid	Reddy et al. (2010)

[a]*ND* not determined

present in all the biodegradation setups. Marine sediments act as a sink for various hydrophobic pollutants. Li et al. (2020) revealed biosurfactant-assisted pyrene degradation (300 mg L^{-1}) by *Achromobacter* AC15 strain, isolated from mangrove sediments. The purified biosurfactant BS15 is a linear lipopeptide with four aminoacids and C16 fatty acid constituents. These studies indicate the potential significance of biosurfactants towards bacterial degradation of HMW PAHs. Biosurfactants also play a significant role in the remediation of crude oil and residues. In a recent study, a salt-tolerant and biosurfactant-producing *Achromobacter* sp. A-8 bacterium was screened from petroleum-contaminated wastewater that decreased the petroleum viscosity by 45%, designating application in MEOR (Deng et al. 2020).

Regulation of biosurfactant biosynthesis

Because of its high emulsification index, rhamnolipids are the mainly studied glycolipid biosurfactant produced by *P.aeruginosa*. It is associated with the uptake of poorly bioavailable hydrocarbon compounds such as PAHs and acts as a bacterial response to nutrient limiting conditions (Ahmad et al. 2021). Rhamnolipid synthesis is directly dependent on the population density and expressed at lower rates even in the exponential phase of planktonic cells. Its biosynthesis is linked to three QS systems:*lasI/lasR*, *rhlI/rhlR,* and *PQS* (*Pseudomonas* Quinolone Signal) system. AHLs including N-3-oxododecanoylhomoserine lactones (3-oxo-C12-HSLs) and N-butyryl-homoserine lactones (C4-HSLs) involved in lasI/lasR and rhlI/rhlR directly control rhamnolipid biosynthesis in *P. aeruginosa*. PQS autoinducer regulates rhamnolipid synthesis via the direct or indirect method via C4-HSLs (Dusane et al. 2010). GidA is a post-transcriptional regulator of the *rhlI/rhlR* system, modulating the expression of Rhl-associated genes. This fact is well proven in *gidA* deficient mutants, where the expression of *rhlR* mRNA is significantly reduced.

The report also suggests the regulation of rhamnolipid biosynthesis via the QS system in *Burkholderia* species; however, these species have low production capacity. Studies on the mutant strain of *Burkholderia glumae* (deficient in C8-HSL) showed reduced rhamnolipid synthesis controlled by a single QS system (Nickzad et al. 2015), while Chandler et al. (2009) earlier characterized the presence of three QS systems in *B. thailandensis* that is comprised of three pairs of synthase/receptors.

Several environmental factors control the production and efficiency of rhamnolipids, such as temperature, pH, and salt concentrations. Ilori et al. (2005) reported that the chemical structure of biosurfactants is disrupted in extremes of pH conditions that alter the hydrocarbon degradation potential of surfactant molecules. *PQS* system in *P.aeruginosa* is related to stress responses like UV irradiation resistance, oxidative stress, and antimicrobial agents; therefore, *PQS* acts as a transcriptional regulator of rhamnolipid synthesis. Colanic acid polysaccharide biosynthesis is mainly induced by osmotic stress on cell envelope structure and regulated by several *Rcs* proteins, including *RcsA, RcsB, and RcsD*, as exemplified by Majdalani and Gottesman (2005). Whitfield (2006) optimized the colanic acid biosynthesis in bacterial cultures and found its temperature-dependent synthesis in wild-type strains at 37 °C affected the EPS synthesis while lower temperature induced the polymer synthesis. This altered growth and expression of the operon to be co-related to the *Rcs* machinery. The sigma factor *rpo*S in biofilms plays a crucial role in stress conditions, and its level increases in response to the onset of nutrient deprivation state. In addition, *rpo*S regulon has overlapping regions with *las* and *rhl* systems and is essential for swarming motility, a bacterial phenotypic characteristic related to rhamnolipids and hyaluronic acid synthesis. Besides these, several environmental factors also play a critical role in biosurfactant synthesis and therefore affect their solubilization property towards hydrophobic compounds. Elevated temperatures and salinity alters microbial growth and affects their biodegradation potential for hydrophobic compounds (Varjani et al. 2017). Besides carbon and energy requirements, other macronutrients like nitrogen, potassium, phosphorous are required for microbial growth that needs to be added during biodegradation applications. The substrate and microbe type influence the type and yield of the produced biosurfactant (Ilori et al. 2005). Biosurfactant production was highest in medium containing glucose as a carbon source compared to medium with diesel and acetate. The nitrogen source was also reported to get optimum biosurfactant production at 5% NaCl concentration in pH 8.0 and 40 °C temperature (Ilori et al. 2005). Aeration and agitation are also prime factors that affect and facilitate the oxygen transfer from gaseous to aqueous form and may be linked to the functional property of emulsification influencing hydrocarbon degradation. Adamczak and Bednarski (2000) studied and reported the maximum surfactant production when the airflow rate was maintained to 1vvm with 50% dissolved oxygen saturation.

Bacterial genomes mined for biosurfactants and EPS genes

In silico analysis of a genome can provide us with hidden knowledge behind a microorganism's degradative catabolic capacity (Tikariha et al. 2016) and helps in designing waste management bioprocesses (Purohit et al. 2016). Several genomes are now known, bestowed with functional potential for various persistent organic pollutants (Sagarkar et al. 2014; Qureshi et al. 2007). The development of tracking tools for degradative genes would provide a fast and reliable

method for detecting potential environmental degraders (Qureshi et al. 2009; Nazirkar et al. 2020).

To screen biosurfactant-producing traits in PAH degrading bacterial strains, bacteria with PAH degradation potential were retrieved from the *National Center for Biotechnology Information (NCBI) database* (NCBI Resource Coordinators 2018). The bacterial genomes were confirmed for the presence of PAH hydroxylating genes such as ring hydroxylating dioxygenases and aromatic ring hydroxylating dioxygenase (Online Resource 1). Ring cleaving dioxygenases, namely PAH ring hydroxylating dioxygenases (RHDs), can be considered biomarkers for depicting the microbial PAH-degrading potential in an environmental niche. These genomes (35) belonging to different genera were annotated for biosurfactant-associated genes using the *BioSurfDB database* (Oliveira et al. 2015). The genomes sequence was pairwise aligned to surfactant genes on the available database classified under the BLAST category using default parameters. The absolute abundance of biosurfactants in these genomes is depicted in Fig. 3. Given absolute abundance, most PAH degraders are predicted to contain iturin operon ($n = 30$). *P.aeruginosa* strain DN1 includes the maximum number of biosurfactant-associated genes regarding the abundance of surfactant genes. Well-characterized surfactant synthesis genes for surfactin, rhamnolipids, and serrawettin W1 were present in *B.subtilis*, *P.aeruginosa,* and *Serratia marcescens,* respectively.

EPS synthesized by different bacteria depicts varied composition and chemical bonding of the monosaccharide sugars (Table 1). Notably, the mechanism of EPS synthesis, however, is conserved. The PGTs catalyze the initial step of glycan synthesis and are highly homologous compared to other glycosyltransferases across Gram-positive and Gram-negative bacteria. PGT is selected as a marker gene for screening the ability of EPS production trait in PAH degrading bacteria (Online Resource 2). Gene sequences coding for PGT were retrieved for the same set of bacterial genomes used for biosurfactants gene mining. The strategy of mining this

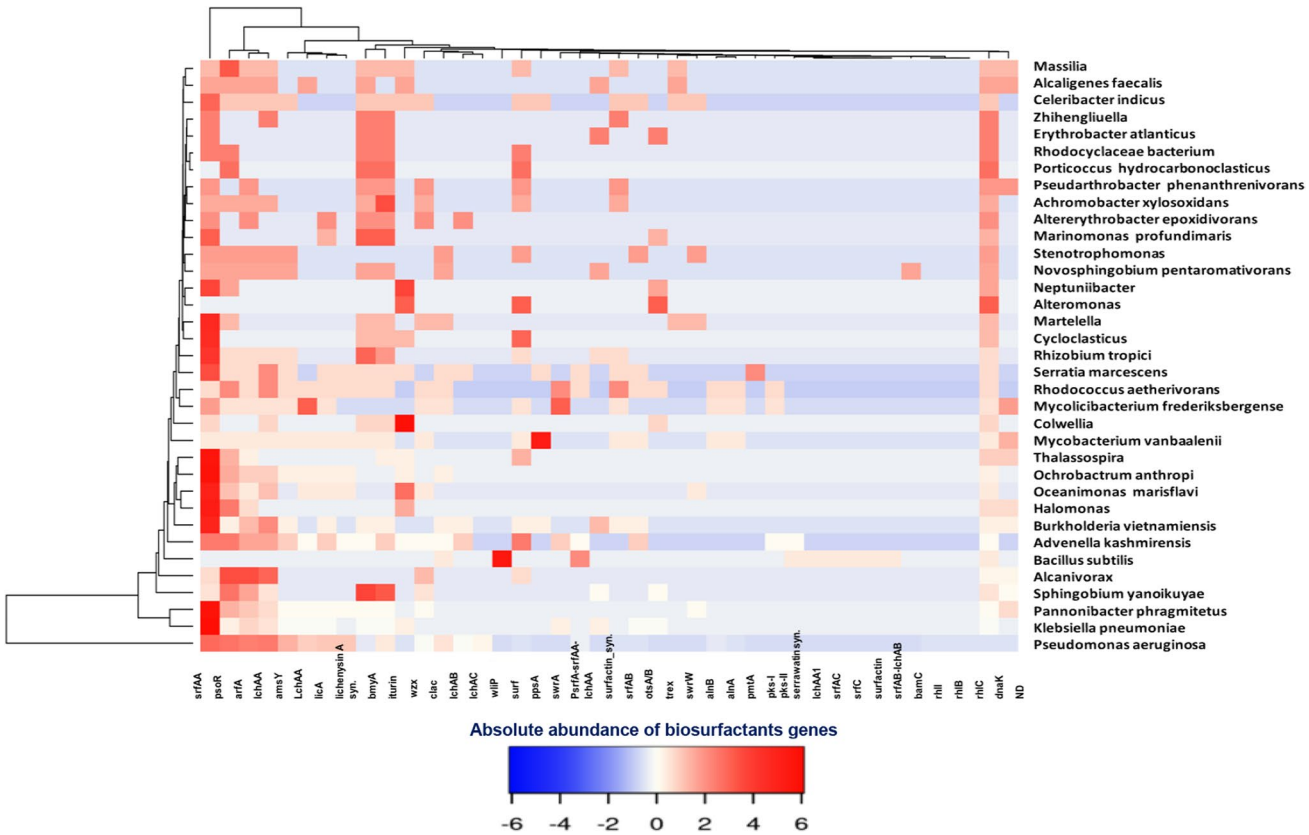

Fig. 3 Absolute abundance of Biosurfactant genes among PAH degrading genomes. Heat map shows quantitative abundances of biosurfactants genes associated with 35 PAH degrading bacteria. The genes retrieved from the BiosurfDB database (https://www.biosurfdb.org) are shown along the X-axis while PAH degrading bacteriomes along Y-axis. The heatmap plot depicts the absolute values of each biosurfactant-associated gene (variables clustering on the X-axis) within each genus (Y-axis clustering). The values for gene abundance are depicted by color intensity according to the legend provided below the figure. Hierarchical clustering based on the distances of the groups along the X-axis and the bacterial genera along the Y-axis is indicated in the upper part and on the left side of the figure, respectively. The white color indicates that no biosurfactants associated genes were found in bacteria

unique protein in hydrocarbon utilizing bacteria could hint to find EPS synthesizers among the bacterial population. The phylogenetic relationship among diverse bacteria for EPS synthesis potential (presence of PGTs) in PAH degrading bacterial genomes (Fig. 4). Mining PGTs tested the hypothesis that EPS could enhance biodegradation of polycyclic aromatic hydrocarbons in bacteria.

In a consortium study in a laboratory or a natural state as in biofilms, bioavailability enhancers (biosurfactants or EPS) produced by one bacterium may be helpful to other members, constituting a cooperative network metabolizing the otherwise inaccessible PAH substrate. The genome survey of PAH degrading bacteria suggests that not all PAH degrading members carry both EPS and biosurfactants production genes; it seems not essential for PAH degradation but likely benefits PAH-degrading bacteria in contaminated environments where microbes live in a community. This polymer synthesis trait might also be strain-specific but, if present together, allows improved PAH assimilation and subsequent degradation by microbial cells. The review studies the abundance of biosurfactants genes and EPS priming GTs; however, restricted to a small set of bacterial genomes varying across the genus, it brings the concomitant presence of these bioavailability enhancers in PAH degrading bacteriomes.

Conclusion

The abundance of biosurfactants genes (*srf, rhl, itu, lic*) and EPS marker gene (priming glycosyltransferase) in the PAH degrading bacterial community substantiates those diverse bacteria imbibe both the properties of biosurfactants and EPS synthesis during PAH biodegradation. Based on genomic analysis, it is envisaged that bacteria producing EPS may not necessarily produce biosurfactants and vice-versa. Hence, concomitant development of consortia encompassing compatible biosurfactants (like rhamnolipids) and EPS producers as associates may mutually benefit the enhanced uptake of PAH for the bioremediation process. The review hypothesizes the use of EPS and biosurfactants in combination to enhance the uptake of PAHs, especially heavy molecular weight (HMW) PAHs, which are otherwise inaccessible to the microbial system. However, the future promise for using these 'bioavailability enhancers' relies on extensive knowledge of pollutant-sorbent-microbial interactions studies using HMW PAHs as substrates.

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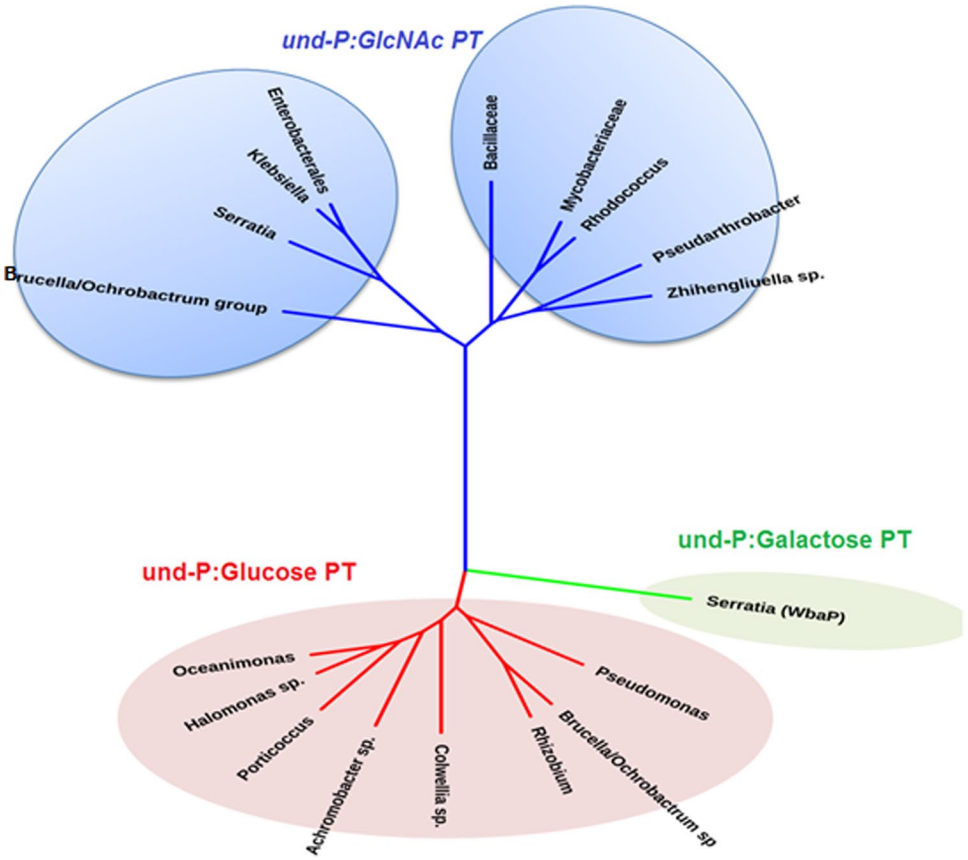

Fig. 4 Phylogenetic analysis of priming glycosyltransferase (PGTs) from 16 different PAH degrading bacteriomes. Different clades correspond to the divergence of priming glycosyltransferase based on their substrate, phosphorylated to lipid carrier undecaprenyl phosphate (und-P). und-P: Glucose PT; und-P: Galactose PT; und-P: N-acetylglucosamine PT corresponds to the enzyme catalyzing the transfer of monomeric units of sugars (glucose, galactose, and N-acetyl glucosamine) onto undecaprenyl phosphate, respectively

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Declarations

Conflict of interest The authors declare no conflict of interest.

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