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REVIEW

A review of the role of biosurfactants in the biodegradation of hydrophobic organopollutants: production, mode of action, biosynthesis and applications

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Abstract
The increasing influence of human activity and industrialization has adversely impacted the environment via pollution with organic contaminants, which are minimally soluble in water. These hydrophobic organopollutants may be present in sediment, water or biota and have created concern due to their toxic effects in mammals. The ability of microorganisms to degrade pollutants makes their use the most effective, inexpensive and ecofriendly method for environmental remediation. Microorganisms have the ability to produce natural surfactants (biosurfactants) that increase the bioavailability of hydrophobic organopollutants, which enables their use as carbon and energy sources. Due to microbial diversity in production, and the biodegradability, nontoxicity, stability and specific activity of the surfactants, the use of microbial surfactants has the potential to overcome problems associated with contamination by hydrophobic organopollutants.
This review provides an overview of the current state of knowledge regarding microbial surfactant production, mode of action in the biodegradation of hydrophobic organopollutants and biosynthetic pathways as well as their applications using emergent strategy tools to remove organopollutants from the environment. It is also specified for the first time that biosurfactants are produced either as growth-associated products or secondary metabolites, and are produced in different amounts by a wide range of microorganisms.

Keywords Biodegradation · Biosurfactant synthesis · Hydrophobic organopollutants · Microbial surfactants

Introduction

Increasing anthropogenic activity and industrialization have considerably increased environmental pollution from organic contaminants. Organic pollutants include a wide range of organic xenobiotic chemicals, which are minimally soluble in water and may be present in water, sediment or biota. They include compounds such as plastics, gasoline, paints, adhesives, polycyclic aromatic hydrocarbons (PAHs), benzene, polychlorinated biphenyls, toluene, ethylbenzene and pesticides, among others (Semple et al. 2003; Rasheed et al. 2019; Bhatt et al. 2021). The presence of these hydrophobic organic pollutants in the environment has caused concern due to their toxic effects in mammals, which include mutagenic, carcinogenic and teratogenic effects (Dsikowitzky and Schwarzbauer 2014; Sánchez 2021). In this context, a bioremediation approach using living systems represents an efficient and environmentally friendly strategy to manage pollutants. Microbes are present in diverse habitats, and some have developed extraordinary strategies that allow them to grow and adapt to extreme environments (Sarmiento et al. 2015; Sánchez et al. 2020). Microbial strategies include a powerful enzymatic system composed of stable enzymes produced under extreme conditions and an ability to produce natural surfactants as a means to increase the bioavailability of hydrophobic organopollutants (Kaczorek et al. 2018). These microbial strategies allow microbes to use complex substrates (i.e. hydrophobic organopollutants) as carbon and energy sources. Microbial surfactants (biosurfactants) can be found on the cell surface or are released into the extracellular space (Ward 2010). Biosurfactants provide increased hydrophobicity on the cell surface of the producing microorganisms, which facilitates the access and use of

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hydrophobic substrates by microbial cells (Perfumo et al. 2009; Satpute et al. 2010; Uzoigwe et al. 2015).

Some microbes secrete biosurfactants only when growing on hydrophobic substrates, whereas others produce these compounds during growth on both hydrophobic and hydrophilic substrates (Gautam and Tyagi 2006). The production of biosurfactants can be affected by growing substrate, temperature, pH, nitrogen and carbon sources (Sanches et al. 2021).

Biosurfactants have advantages in relation to their chemical analogs. Microbial surfactants are biodegradable, have high activity, are nontoxic and are stable under extreme conditions (i.e. pH, temperature and salinity) (Abdel-Mawgoud et al. 2010; Jahan et al. 2020). Therefore, biosurfactants have enormous potential in the development of significant biotechnological processes due to their unique properties (Santos et al. 2016). In addition to bioremediation, biosurfactants are employed in cosmetic formulations, food, biomedicine, pharmaceuticals, and nanotechnology (Jahan et al. 2020; Sanches et al. 2021). Biosurfactants are considered important biomolecules, and their production represents a key technology for development in the current century (Santos et al. 2016).

This review provides, for the first time, an overview of the current state of knowledge about microbial surfactant production, the mode of action in the biodegradation of hydrophobic organopollutants and the biosynthetic pathways of surfactants as well as their applications to hydrophobic organopollutant remediation using emergent strategy tools in a single document. It is also specified that biosurfactants are produced either as a growth-associated or secondary metabolites, and are produced in different amounts by a wide range of microorganisms.

Characteristics and mode of action of microbial surfactants

Microbial surface-active or microbial surfactant compounds are a structurally diverse group of molecules produced by many microorganisms. These compounds contain a hydrophobic component of saturated or unsaturated hydrocarbon chains or fatty acids and a hydrophilic component that includes an acid, peptide anions, cations, or mono-, di- or polysaccharides (Banat et al. 2010). The majority of these compounds are either neutral or anionic; only a few are cationic (e.g. those containing amine groups). In solutions, the shape of the micelles depends on the structure of the component molecules as previously reported (Israelachvili 1992). The size of the hydrophilic moiety in relation to the hydrophobic component has an impact on packing into cylindrical micelles, spherical micelles, inverted micelles or bilayers (Linder et al. 2005). An important chemical-physical parameter of surfactants is the critical micelle concentration (CMC), which refers to the minimum concentration of surfactant necessary to give the minimum surface tension in water and form micelles (Wijaya et al. 2016). The ability to decrease the surface and interfacial tensions is facilitated via the adsorption of the surfactant in different phases, allowing dissimilar phases to mix and interact more easily (Uzoigwe et al. 2015). Therefore, an efficient surfactant has a low CMC, requiring less surfactant to decrease surface tension (Rufino et al. 2014).

Microbial surfactants can be grouped into low molecular mass compounds, known as biosurfactants (glycolipids, lipopeptides) and high molecular mass compounds (lipopolysaccharides, lipoproteins, hydrophobic proteins), known as bioemulsifiers or bioemulsans (Fig. 1) (Rosenberg and Ron 1997; Smyth et al. 2010a, 2010b). Biosurfactants are able to reduce the surface and interfacial tensions between different phases (liquid–liquid, liquid–air, and liquid–solid) until the interface is saturated and micelles begin to form. In contrast, bioemulsifiers or bioemulsans are amphiphilic or polyphilic polymers that are able to efficiently stabilize oil-in-water emulsions; however, they do not substantially reduce surface tension (Smyth et al. 2010b).

Several studies have reported that microorganisms produce their own surfactant (which can be induced) during the degradation of hydrophobic organopollutants (Table 1) or can be produced intrinsically on conventional substrates (e.g. glucose and sucrose), organic materials or organic wastes (Tables 2 and 3). Biosurfactants are generally composed of sugars, fatty acids, amino acids and functional groups such as carboxylic acids (Uzoigwe et al. 2015) and generally have a molecular weight of approximately 0.5–1.5 kDa (Santos et al. 2016). It has been reported that particular class of biosurfactants called hydrophobins, which are produced exclusively by fungi, have a molecular weight of approximately 10–17 kDa (Dąbrowska et al. 2021; Puspitasari et al. 2020; Pothiratana et al. 2020). However, some studies have shown that hydrophobins can have a higher molecular weight (i.e. 19–70 kDa) than those previously reported (Table 4). Several hydrophobins have been isolated from different fungi. These biomolecules are composed of some hydrophobic amino acids and also possess eight Cys residues (Shuren and Wessels 1990; Santacruz-Juarez et al. 2021). Based on their differences in hydrophobic properties, morphology and solubility, hydrophobins are divided in class I and class II. Class I hydrophobins are highly insoluble, while those of class II hydrophobins easily can be dissolved in a variety of solvents (Wessels, 1994) (Table 4).

Most natural surfactants reduce surface tension to approximately 30 mN/m (Table 2). It has been reported that synthetic surfactants such as modified heterogeneous alcohol ether, fatty alcohol methyl esters of ethoxylate and Tween 80 have surface tension values of 29.5, 33.6 and 37.8 mN/m,

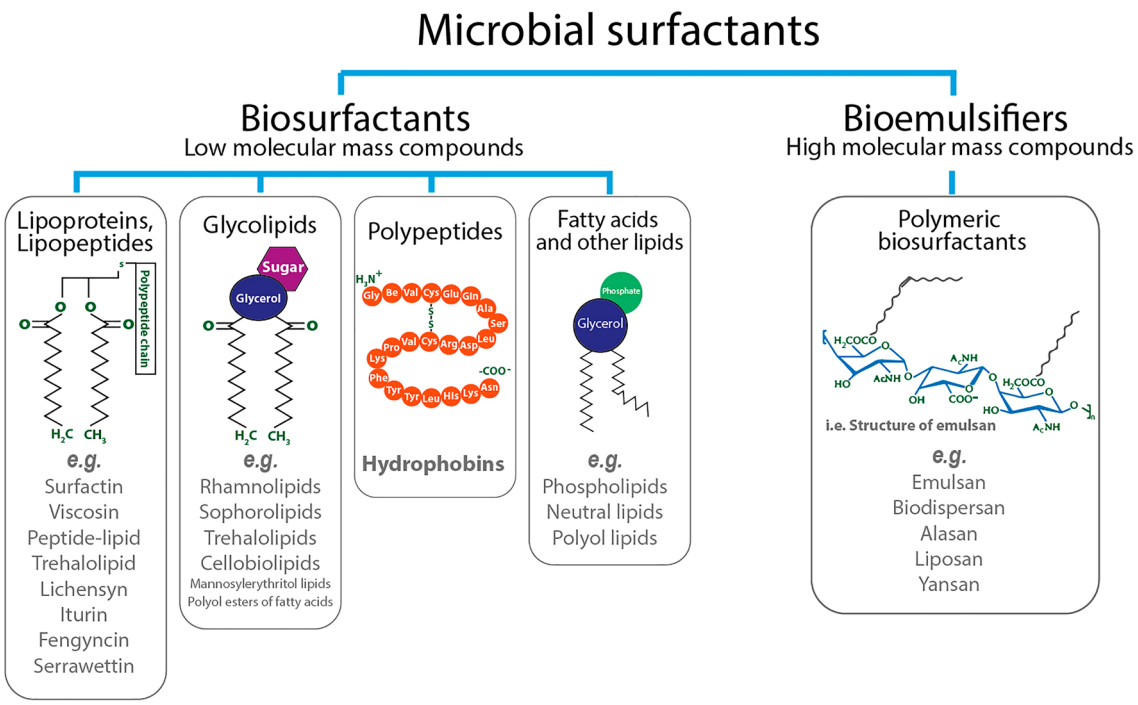


Fig. 1 Some types of microbial surfactants, which can be grouped into low molecular mass compounds, known as biosurfactants (e.g. glycolipids, lipopeptides, proteins), and high molecular mass compounds, known as bioemulsifiers or bioemulsans (i.e. polymers of lipopolysaccharide proteins or lipoproteins and polysaccharides) (Mondal et al. 2015; Mnif and Ghribi 2015; Dhanya 2021)

respectively, at their respective CMC values of 14, 80 and 14 mg/L (Li et al. 2017). Some microbial surfactants have a low CMC and are able to form stable emulsions. It has been reported that the CMCs of biosurfactants generally vary from 1 to 200 mg/L (Mulligan, 2005; Singh et al. 2018); however, recent studies have found higher CMC values for biosurfactants (Tables 1, 2). For example, CMCs of 1200, 1500 and 1700 mg/L have been reported for glycolipids, anionic surfactants, and glycoproteins produced during the degradation of pyrene, burned motor oil and diesel oil by *Acinetobacter baumannii* (Gupta et al. 2020), *Serratia marcescens* (Araújo et al. 2017, 2019) and *Rhizopus arrhizus* (Pele et al. 2019), respectively. However, the CMCs of a hydrophobin and a lipopeptide were 10 mg/L and 12.5 mg/L during the degradation of crude oil by *Trichoderma harzianum* and *Bacillus subtilis*, respectively (Nogueira-Felix et al. 2019; Pitocchi et al. 2020).

As shown in Fig. 2, the biodegradation of hydrophobic organopollutants occurs via the formation of a micellar structure with biosurfactants, in which the hydrophilic heads are oriented to the aqueous water stage, and the hydrophobic tails are attached to hydrophobic pollutants, facilitating pollutant adsorption into the microbial cell followed by intracellular enzymatic degradation of the pollutant (Sun et al. 2016; Zhong et al. 2016; Shao et al. 2017) (Fig. 2a). Alternatively, some studies have reported that the biodegradation of hydrophobic compounds takes place once the biosurfactants have surrounded the substrate, allowing microbial attachment and increased substrate availability, and microbial growth and specific enzyme secretion would then allow microbial colonization of the substrate and its degradation (Fig. 2b) (Sánchez 2020, 2021; Dąbrowska et al. 2021).

Microbial surfactant production for organopollutant biodegradation

Various levels of biodegradation of organopollutants by biosurfactant producers have been reported, mainly by bacteria from genera such as *Pseudomonas*, *Klebsiella*, *Meyerozyma*, *Bacillus*, *Rhodococcus*, *Acinetobacter*, *Staphylococcus*, and *Achromobacter* and from fungal genera such as *Trichoderma*, *Aspergillus*, *Agrocybe*, and *Candida* (Table 1).

Producers of microbial surfactants have been found in every habitat, including marine environments (psychrotolerant and halotolerant microorganisms) (Zakaria et al. 2019; Trudgeon et al. 2020; Pourfadakari et al. 2021; Cheffi et al. 2020), hydrophobic pollutant-contaminated soils (Ahmadi et al. 2021), wastewater (Nogueira-Felix et al. 2019; Cheffi et al. 2020), freshwater lake ecosystems (Phulpoto et al. 2021), lichens (Santos et al. 2019), and plants (Marchut-Mikolajczyk et al. 2018) (Table 2).

Some studies have reported that biosurfactants are microbial growth-associated products. Sharma and Pandey (2020) reported that *B. subtilis* RSL2 produced a lipopeptide

Table 1 Selected studies on the type of microbial surfactants produced during the biodegradation of hydrophobic organopollutants reporting biosurfactant CMC values and mode of action

Organism	Biosurfactant produced during the degradation	Chemical class	Organopollutant as substrate	Analytical methods for surfactant detection	CMC (mg/L)	Mode of action	Biodegradation	Reference
Bacteria								
Klebsiella sp. KOD36	Mono-rhamnolipid	Glycolipid	Phenanthrene (PHE)	FTIR; X-ray diffractometry, SEM–EDS	124	Reduce surface tension to 38 mN/m	56% of total PHE (100 mg/L) after 168 h	Ahmad et al. (2021)
Pseudomonas aeruginosa MF069166	Mono-/di-rhamnolipids	Glycolipid	Crude oil	RP-HPLC	40	Reduce surface tension to 29 mN/m	91% of the petroleum hydrocarbons	Rehman et al. (2021)
Meyerozyma sp. MF138126	Acidic and lactonic forms of sophorolipids congeners	Glycolipid	Crude oil	RP-HPLC	50	Reduce surface tension to 33 mN/m	87% biodegradation efficiency	Rehman et al. (2021)
Vibrio sp. LQ2	Phospholipid	Other lipids	Diesel oil	TLC, FTIR	200	Reduce surface tension from 72 to 39.6 mN/m	94.7%, reduction from 169.2 mg to 8.91 mg	Zhou et al. (2021)
Bacillus subtilis RSL-2	Surfactant contains amine group and fatty acid log chains	Lipopeptide	Crude oil	FTIR	500	Reduce surface tension to 38 mN/m	72% (Ci = 1000 mg/L)	Sharma and Pandey, (2020)
Rhodococcus sp. ADL36	Trehalolipid (possibly)	Glycolipids	Hydrocarbons (diesel oil and used motor oil)	TLC, FTIR	NR	Ability to reduce water surface tension to < 30 mN/m	NR	Habib et al. (2020)
Acinetobacter sp. Y2	Peptide and lipid moieties (i.e. hexadecanoic and octadecenoic acids)	Lipopeptide	n-alkanes and PAHs	TLC, FTIR and GC–MS	187.5	Reduce surface tension from 72.2 mN/m to 30.2 mN/m	Reduction from 2635.4 mg/L to 159.7 mg/L (n-alkanes), reduction from 918.6 µg/L to 209.6 µg/L (PAH) in 7 d	Zhou et al. (2020)
Acinetobacter baumannii BJ5	Palmitic and phthalic acid as main lipids, polysaccharides and long aliphatic chain	Glycolipid	Pyrene	FTIR, NMR and GC–MS	1200	Reduce surface tension from 72.3 to 38.3 mN/m	56% of total pyrene (Ci = 600 mg/L) after 14 d	Gupta et al. (2020)
Staphylococcus sp. CO100	Lichenysin and iturine members	Lipopeptide	Crude oil	ESI–MS	Varying between 65 and 750	Reduce surface tension to 27 mN/m	72% of the aliphatic hydrocarbons (crude oil, 1%, v/v), after 20 d	Hentati et al. (2021)

Table 1 (continued)

Organism	Biosurfactant produced during the degradation	Chemical class	Organopollutant as substrate	Analytical methods for surfactant detection	CMC (mg/L)	Mode of action	Biodegradation	Reference
Achromobacter species strain AC15	A long-chain C16 fatty acid and peptide comprised of four amino acid residues	Lipopeptide	Pyrene	GC–MS,, amino acid analysis, and LTQ 42 Orbitrap Elite mass spectrometry	NR	Reduce surface tension from 67.2 to 33.2 mN/m after 14 d	40% (Ci = 300 mg/L) after 14 d	Li et al. (2020)
Pseudomonas sp. KZ1 strain	Saturated unbranched fatty acids (lauric and palmitic)	Glycolipids	Diesel oil	FTIR and GC–MS	120	Reduce surface tension to 31.7mN/m	50% (Ci = 0.33 mL)	Zdarta et al. (2019)
P. aeruginosa, and other bacteria	Rhamnolipid	Glycolipid	Crude oil from contaminated cotton cloth	ATR-FTIR	NR	Reduce surface tension from 72 to 29 mN/m	Removed 3.8-fold increase in comparison to the control (Ci = 0.3 mg/L)	Tripathi et al. (2020)
P. aeruginosa S5	Surfactant contains functional groups of sugar and lipids	Glycolipid	high weight molecular PAHs	FTIR	96.5	Reduced surface tension from 72.2 to 29.6 mN/m	Reduction from 9141 to 5117 µg/L in 15 d	Sun et al. (2019)
Bacillus velezensis MHNK1	Surfactin	Lipopeptide	Atrazine	TLC, HPLC, FTIR, ^{1}H and ^{13}C NMR and LC–MS-ESI	40	Reduced surface tension from 72 to 33 mN/m	87% (Ci = 200 mg/L) within 5 d	Jakinala et al. (2019)
P. aeruginosa PG1	Rhamnolipid comprising of both mono- and di-rhamnolipid congeners	Glycolipid	Crude oil components	FTIR, LC–MS, and SEM–EDS	56	Biosurfactant promotes the reduction of surface tension	81.8% of total crude oil (Ci = 2%) after 5 weeks	Patowary et al. (2017)
Achromobacter PS1	Di-rhamnolipid and mono-rhamnolipid moieties	Glycolipid	Crude oil	TLC, FTIR and GC–MS	NR	Lowering of surface tension from 59.27 mN/m to 32.43 mN/m in 7 d	46.32% of 2% (w/v) crude oil with 70.77% and 77.17% reduction in peak area of aliphatic and aromatic fractions respectively	Joy et al. (2017)
P. aeruginosa CH7	Two compounds of rhamnolipid	Glycolipids	Beta-cypermethrin (synthetic pyrethroid insecticide)	TLC, HPLC, GC-FID, GC–MS	NR	The surface tension of the culture decreased from 61.3 to 37.4 mN/m	67% of the beta-cypermethrin (Ci = 100 mg/L) within 4 days	Zhang et al. (2011)

Table 1 (continued)

Organism	Biosurfactant produced during the degradation	Chemical class	Organopollutant as substrate	Analytical methods for surfactant detection	CMC (mg/L)	Mode of action	Biodegradation	Reference
Pseudomonas sp. ChlD	A partially purified rhamnolipid	Glycolipid	Chlorpyrifos (organophosphate pesticides)	GC, HPLC	200	Enhance aqueous phase partitioning and degradation of chlorpyrifos	98% of total chlorpyrifos (Ci = 100 mg/L) after 120 h incubation	Singh et al. (2009)
Fungi								
Trichoderma viride GZ1	Hydrophobin	Protein (17 kDa)	PET	Atomic force microscopy	NR	Formation of hydrophobin film on the plastic surface	Modifications of the surface of PET	Dąbrowska et al. (2021)
Aspergillus oryzae	Hydrophobin RolA	Polypeptide (11 kDa; hydrophobin, class 1)	PET	SDS-PAGE, atomic force microscopy	NR	High surface-active substance and can spontaneously self-assemble at hydrophilic-hydrophobic interfaces	Weight loss of 26% in 4 days	Puspitasari et al. (2020)
Agrocybe cylindracea (mycelia)	Hydrophobin	Structurally similar to class I hydrophobin (9.6 kDa),	Hexane,	LC–MS/MS,	NR	Displayed emulsifying activity Reduce the surface tension	NR	Pothiratana et al. (2020)
Aspergillus terreus MUT271	Hydrophobin	Cerato-platanins, small, conserved, hydrophobic proteins	Crude oil	SDS-PAGE (A proteomic approach)	120	Reduce the surface tension to 56.3 mN/m	NR	Pitocchi et al. (2020)
Trichoderma harzianum MUT290	Hydrophobin	Cerato-platanins, small, conserved, hydrophobic proteins	Crude oil	SDS- PAGE (A proteomic approach)	10	Reduce the surface tension to 36.4 mN/m	NR	Pitocchi et al. (2020)
Candida tropicalis NN4	Sophorolipid	Glycolipids	Indeno(1,2,3-cd) pyrene	TLC, FTIR	NR	NR	90% (Ci = 1 mg/L) (using biosynthesized iron nanoparticles)	Ojha et al. (2019)
A. oryzae (cutinase, CutL1*)*	Hydrophobin RolA	Polypeptide	Polybutylene succinate-coadipate	Imunofluorescence method using a confocal laser scanning microscope	NR	RolA adsorbed to the hydrophobic surface of PBSA recruits CutL1, stimulation of PBSA hydrolysis	NR	Takahashi et al. (2005)

NR Not reported, *Ci* Initial concentration, *FTIR* Fourier Transform Infrared; *LC–MS* Liquid Chromatography-Mass Spectrometry; *SEM–EDS* Scanning Electron Microscopy with Energy Dispersive Spectroscopy; *RP-HPLC* Reversed-Phase-HPLC; *ATR-FTIR* Attenuated Total Reflectance-Fourier Transform Infrared Spectroscopy; *ESI–MS* Electrospray Ionization-Mass Spectrometry; *TLC* Thin Layer Chromatography; *NMR* Nuclear Magnetic Resonance; *GC-FID* Gas Chromatography with Flame Ionization Detection

Table 2 Selected reports on the production of microbial surfactants using conventional substrates that reported the physicochemical properties of biosurfactants and biodegradation findings

Microorganism	Source	Growth substrate	Type of biosurfactant produced	CMC (mg/L)	Surface tension (mN/m)	Findings	Reference
Bacteria							
P. aeruginosa R4	Synthetically and naturally hydrocarbon-contaminated soil	Glucose	Glycolipid	50	32.5	Pyrene desorption rate of 82% (Ci = 200 mg/L)	Ahmadi et al. (2021)
Stenotrophomonas sp. S1VKR-26	Polluted river	Olive oil	Rhamnolipid	30	30.5	Different PAHs were significantly remediated from petroleum refinery wastewater	Patel and Patel., (2020)
Halomonas pacifica Cnaph3	Contaminated seawater	Glycerol	Lipopeptide	500	27.6	98.8% of naphthalene (200 mg/L) was degraded after 7 d	Cheffi et al. (2020)
B. subtilis	Wastewater treatment plant (from a chlorination tank)	Cashew apple juice	Cyclic lipopeptide with molecular structure similar to that of surfactin	12.5	31.8	Oil-contaminated soil could be significantly improved	Nogueira-Felix et al. (2019)
B. cereus UCP 1615	Culture collection (Catholic University of Pernambuco, Brazil)	Molasses and corn steep liquor	Lipopeptide	900	26.2	Remove motor oil adsorbed to marine rock	Ostendorf et al. (2019)
Serratia marcescens UCP 1549	Soil	Cassava flour wastewater, supplemented with lactose and corn oil	An anionic and polymeric structure	1500	25.92	Remove burned motor oil from sand	Araújo et al. (2017; 2019)
B. subtilis MG495086	From formation water of Assam oil reservoir	Light-paraffin oil	Lipopeptide (surfactin)	40	29.85	Oil degradation capability (91%)	Datta et al. (2018)
Fungi							
Rhodotorula sp.	Oilfield	Wastewater from olive oil mills	Peptides, carbohydrates and lipids in its structure	180	30.16	Remobilization of hydrocarbons from polluted soil with a removal rate of greater than 95%	Derguine-Mecheri et al. (2021)
Candida lipolytica	Culture collection of the Catholic University of Pernambuco, Brazil	Molasses, corn steep liquor and waste frying oil	NR	50	28	Showed efficiency in removing 57%-70% of the motor oil in contaminated soil under static conditions	dos Santos et al. (2021)
Rhizopus arrhizus UCP 1607	Soil	Crude glycerol and corn steep liquor	Glycoprotein	1700	28.8	Removed the pollutant diesel oil from marine soil (79.4%)	Pele et al. (2019)
Aureobasidium thailandense LB01	Cashew (*Anacardium occidentale* L.) apple peduncle	Yeast extract, olive oil mill wastewater and glucose	Molecular structure similar to a lauric acid ester	550	31.2	Able to disperse crude oil	Meneses et al. (2017)

Table 3 Selected studies on the production of microbial surfactants reporting the amount of biosurfactants produced, culture conditions and incubation period

Microorganism	Growth substrate	Biosurfactant	Temperature (°C)/pH	Biosurfactant production (g/L)	Fermentation system	Incubation period (h)	Reference
Bacteria							
B. subtilis 309	Waste glycerol derived from soap production	Surfactin analogs (mainly C13, C14 and C15 surfactin)	37/7	2.8	Submerged	96	Janek et al. (2021)
P. aeruginosa R4	Glucose	Glycolipid	31/7	0.09	Submerged	168	Ahmadi et al. (2021)
P. aeruginosa PU1	Molasses	Rhamnolipid	37/NR	8.9	Submerged	48	Domdi et al. (2020)
Stenotrophomonas sp. S1VKR-26	Olive oil and glucose	Rhamnolipids	37/NR	5.15	Submerged	120	Patel and Patel, (2020)
Bacillus nealsonii S2MT	Glycerol	Cyclic lipopeptides relating to surfactin-like isoforms (C13–C15)	30/8	1.3	Submerged	72	Phulpoto et al. (2020)
P. aeruginosa NJ2	Glucose, and fried oil	Rhamnolipids	30/7	4.28	Submerged (fed-batch)	96	Pathania and Jana, (2020)
B. subtilis RSL 2	Crude oil	Lipopeptide	25/4	3.5	Submerged	168	Sharma and Pandey, (2020)
Pseudomonas sp. TMB2	Glucose	Mono-rhamnolipids and di-rhamnolipids congeners	30/7.2	NR	Submerged	96	Haloi et al. (2020)
P. aeruginosa	Sunflower oil	Rhamnolipid	25/8.5	240	Submerged (fed-batch)	260	Bazsefidpar et al. (2019)
P. aeruginosa	Soybean oil	Rhamnolipid	32/5.5–5.7	42	Submerged	217	Sodagari et al. (2018)
Paenibacillus sp. D9	Diesel fuel	Lipopeptide	30/7	4.11	Submerged	168	Jimoh and Lin, (2019)
B. subtilis M2 (mutant strain)	Glucose	Lipopeptide	37/7	4.5	Submerged	72	Bouassida et al. (2018)
B. subtilis MG495086	The optimum light-paraffin oil	Lipopeptide (surfactin)	62.4/7.7	6.3	Submerged	96	Datta et al. (2018)
B. subtilis A1	Sucrose	Lipopeptide	40/7.0	4.85	Submerged	120	Parthipan et al. (2017)
P. aeruginosa	Mineral medium containing olive oil	Rhamnolipids	37/8	0.56	Submerged	72	Leite et al. (2016)
Bacillus megaterium	Food waste	Lipopeptide	33.3/6.7	6.58	Submerged	44	Dhanarajan et al. (2014)
Bacillus pumilus UFPEDA 448	Okara with sugarcane bagasse	Surfactin	37/7	0.8	Solid-state	48	Slivinski et al. (2012)
Fungi							
Aspergillus niger M3 (Mutated strain)	Banana stalks powder	Presence of amine, amide, fatty acids and triglycerides functional groups	35/7.0	5.5	Solid-state	168	Asgher et al. (2020)

Table 3 (continued)

Microorganism	Growth substrate	Biosurfactant	Temperature (°C)/pH	Biosurfactant production (g/L)	Fermentation system	Incubation period (h)	Reference
Mucor hiemalis UCP 0039	Post-frying soybean oil Post-frying soybean oil	Biosurfactants (glycolipid nature; cationic charge), Bioemulsifiers (glycolipid nature; anionic charge)	28/NR 28/NR	7.73 1.17	Submerged (shaking conditions) Submerged (static conditions)	96 96	Silva-Ferreira et al. (2020) Silva-Ferreira et al. (2020)
Starmerella bombicola	Sunflower acid oil with glucose	Sophorolipid	30/3.5	51.5	Submerged	192	Jadhav et al. (2019)
Starmerella bombicola ATCC 22214	Corn steep liquor, rapeseed oil and glucose	Sophorolipids	25/3.5	342	Submerged	221	Liu et al. (2019)
Aureobasidium pullulans	Sucrose	Liamocins (glycolipids)	30/6.5	10	Submerged		Saur et al. (2019)
Cunninghamella echinulata	Corn steep liquor, and soybean oil waste	Anionic profile	28/5.5	5.18	Submerged	120	Mendes-de Souza et al. (2018)
Pseudozyma tsukubaensis	Cassava wastewater	Mannosylerythritol lipids-B	30/NR	1.26	Submerged	84	de Andrade et al. (2017)
A. thailandense LB01	Yeast extract; olive oil mill wastewater and glucose	Similar structure to a lauric acid ester	28/5.5	0.14	Submerged	48	Meneses et al. (2017)
C. tropicalis	Waste frying oil, corn steep liquor, molasses	NR	28/5.5	4.19	Submerged	120	Almeida et al. (2017))
Rhodotorula aff. *paludigena* *Rhodotorula babjevae*	Glucose Glucose	Triacylglycerols (TG) and polyol esters of fatty acids (PEFA) TG, PEFA	27/6.5 27/6.5	8.8 (TG) and 21 (PEFA) 18.5 (TG) and 11.2 (PEFA)	Submerged Submerged	168 168	Garay et al. (2017) Garay et al. (2017)
Candida sphaerica UCP	Ground-nut oil refinery residue, corn steep liquor	Glycolipid	27/NR	21	Submerged	144	Luna et al. (2015)
Fusarium sp. BS-8	Sucrose	Lipopeptide	30/7	1.21	Submerged	360	Qazi et al. (2014)

NR Not reported

Table 4 Some hydrophobins produced by fungi and their characteristics

Hydrophobin	Protein-encoding gene	Molecular mass (kDa)	Class	Fungal group	Organism	Reference
HFBII	*hjb2*	7.2	II	Ascomycete	*T. reesei*	Nakari-Setälä, et al., (1997)
SRHI	*srh1*	7.5	II	Ascomycete	*T. harzianum*	Muñoz et al., (1997)
HYPA	*hypA*	8–9	I	Basidiomycete	*Agaricus bisporus*	De Groot et al., (1996)
Vmh1, Vmh2	*vmh1 and vmh2*	9	Nd	Basidiomycete	*Pleurotus ostreatus* var. *florida*	Peñas et al., (2002)
POH1	*POH1*	9	I	Basidiomycete	*P. ostreatus*	Asgeirsddttir et al., (1998)
XEH1	*XEH1, XPH1*	8.4	I	Ascomycete (symbiotic phenotype of the lichen-forming ascomycetes)	*Xanthoria parietina and X. ectaneoides*, (a conglutinate)	Scherrer et al. (2000)
CoH1	*coH1*	10	I	Basidiomycete	*Coprinus cinereus*	Asgeirsdóttir et al. (1997)
POH3	*POH3*	10	I	Basidiomycete	*P. ostreatus*	Asgeirsddttir et al. (1998)
CmHYD1 CmHYD2 CmHYD4	*Cmhyd1* *Cmhyd2* *Cmhyd4*	10.57 10.32 10.45	II II I	Ascomycete	*Cordyceps militaris*	Li et al. (2021)
Fbh-1	*fbh1*	12	II	Basidiomycete	*P. ostreatus* var. *florida*	Peñas et al. (1998)
Hum3	*Hum3*	13	I	Basidiomycete	*U. maydis*	Müller et al. (2008)
HYDPt-1	*hydPt-1*	13	I	Basidiomycete	*Pisolithus tinctorius*	Tagu et al. (2001)
SC1	*Sc1*	13.5	I	Basidiomycete	*Schizophyllum commune*	Schuren and Wessels (1990); Wessels et al. (1991); Wessels (1997)
CmHYD3	*Cmhyd3*	13.48	I	Ascomycete	*C. militaris*	Li et al. (2021)
DGH2	*DGH2*	14	I	Basidiomycete	*Dictyonema glabratum*	Trembley et al. (2002)
SC4	*Sc4*	14.5	I	Basidiomycete	*S. commune*	Schuren and Wessels(1990); Wessels (1997)
SC3	*Sc3*	15	I	Basidiomycete	*S. commune*	Schuren and Wessels, 1990; Wessels, 1997
POH1	*POH1*	15	I	Basidiomycete	*P. ostreatus*	Asgeirsddttir et al., 1998
MPG1	*MPG1*	15	1	Ascomycete	*Magnaporthe grisea*	Talbot et al., 1996
Rod A	*RODA*	16	I	Ascomycete	*Aspergillus fumigatus*	Paris et al., 2003
ABH1	*ABH1*	16	I	Basidiomycete	*A. bisporus*	Lugones et al., 1996
Vmh3	*vmh3*	17	nd	Basidiomycete	*P. ostreatus* var. *florida*	Peñas et al., 2002
ABH3	*ABH3*	19	I	Basidiomycete	*A. bisporus*	Lugones et al., 1998
POH2	*POH2*	20	I	Basidiomycete	*P. ostreatus*	Asgeirsddttir et al., 1998
Hyd 1	*hyd1*	23	II	Basidiomycete	*Tricholoma terreum*	Mankel et al., 2002
CFTH1	*cfth1*	36.5	II	Ascomycete	*Claviceps fusiformis*	de Vries et al., 1999
CPPH1	*cpph1*	70	II	Ascomycete	*Claviceps purpurea*	Mey et al., 2003

biosurfactant that was released primarily within the exponential phase when grown on crude oil as a carbon source. Similarly, Datta et al. (2018) found that a lipopeptide (surfactin) produced by *B. subtilis* MG 495,086 as the primary metabolite reached maximum yield during the exponential phase using light paraffin oil as the carbon source. Moreover, *B. subtilis* A1 and *Bacillus licheniformis* AL 1.1 also produced a lipopeptide as a growth-associated metabolite, using sucrose and glucose as carbon sources, respectively (Coronel-León et al. 2015; Parthipan et al. 2017).

However, other biosurfactants such as glycolipids (i.e. rhamnolipids, trehalolipids) have been reported as compounds produced by microorganisms as secondary metabolites. Bacteria such as *Acinetobacter calcoaceticus*, *Enterobacter asburiae* and *Pseudomonas aeruginosa* produced rhamnolipids during their growth on medium containing sodium citrate as a carbon source, enhancing biosurfactant production during the late stationary phase (Hošková et al. 2015). Furthermore, *Marinobacter* sp. MCTG107b produced a mixture of different rhamnolipids

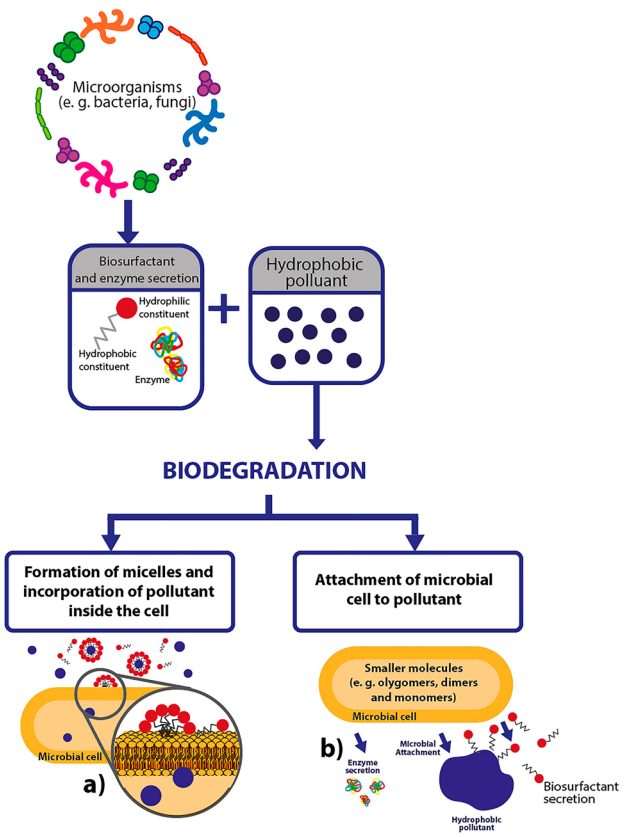


Fig. 2 Schematic illustration of the mechanisms of microbial degradation of hydrophobic organopollutants using biosurfactants: **a** formation of micelles and incorporation of pollutants inside the microbial cell and **b** microbial attachment of hydrophobic pollutants

when grown on glucose as a carbon source and were suggested to be secondary metabolites (Tripathi et al. 2019). Moreover, *P. aeruginosa* was able to produce rhamnolipids as secondary metabolites in a mineral medium containing olive oil (Leite et al. 2016). In addition, *Fusarium fujikuroi* produced α,β-trehalose containing glycolipid after 7 days of growth in a glucose medium and was reported as a secondary metabolite biosurfactant (Loureiro-Dos Reis et al. 2018). Additionally, *Ustilago maydis*, *Schizonella melanogramma*, *Candida antarctica*, and *Geotrichum candidum* have been reported to produce mannosylerythritol lipids (glycolipid biosurfactants) as secondary metabolites (Das et al. 2008).

In comparison, hydrophobins are produced by filamentous fungi and have been described as the most effective surface-active proteins (Cicatiello et al. 2016). It has been shown that these biomolecules are expressed at different developmental stages of fungal life, having a role as structural components in fungal growth and in environment-fungal interactions. Therefore, hydrophobins are found in vegetative hyphae, the fruit bodies of mushrooms and spores (Linder et al. 2005).

Biosurfactants can be produced by different microorganisms in different amounts using different substrates. As shown in Table 3, some species such as *Aureobasidium thailandense*, strains of *Pseudomonas aeruginosa* and *Bacillus pumilus* produced surfactants in amounts of approximately 0.09–0.8 g/L using glucose and/or other substrates (Slivinski et al. 2012; Leite et al. 2016; Meneses et al. 2017; Ahmadi et al. 2021). However, some *Bacillus* species, *Stenotrophomonas sp Mucor hiemalis*, *Aspergillus niger*, *Rhizopus arrhizus*, *Fusarium* sp, *Candida tropicalis, Aureobasidium pullulans* and others have been reported to produce between 1 and 10 g/L biosurfactant on a variety of substrates (Table 3) (Qazi et al. 2014; Dhanarajan et al. 2014; Bouassida et al. 2018; Datta et al. 2018; Mendes-de Souza et al. 2018; Saur et al. 2019; Silva-Ferreira et al. 2020; Asgher et al. 2020; Domdi et al. 2020; Patel and Patel, 2020; Phulpoto et al. 2020; Janek et al. 2021). Other studies have shown that bacteria such as *Candida sphaerica*, *Pseudomonas aeruginosa* and *Starmerella bombicola* were able to produce 21, 42 and 51.5 g/L of surfactant, respectively, using organic materials or organic wastes as substrates (Luna et al. 2015; Sodagari et al. 2018; Jadhav et al. 2019). It has been reported that *P. aeruginosa* produces 240 g/L of rhamnolipids under optimal production conditions using sunflower oil as the substrate (Bazsefidpar et al. 2019). A strain of *Starmerella bombicola* (strain ATCC 22214) produced 342 g/L surfactant (sophorolipids) using an efficient technology for biosurfactant separation and using corn steep liquor, rapeseed oil and glucose as substrates (Liu et al. 2019).

Studies on hydrophobin production have shown that *Aspergillus oryzae* produced a hydrophobin, which was extracted from the mycelium pellet using malt extract as the substrate (Puspitasari et al. 2020). Furthermore, Kulkarni et al. (2020) found that *Pleurotus ostreatus* produced higher amounts of hydrophobin in solid-state fermentation (3.8 mg/g biomass) than in submerged fermentation (1.86 mg/g biomass) using agro-industrial waste oil cakes of coconut and sesame vs. yeast maltose and glucose media, respectively. In addition, hydrophobin was extracted (9.4 mg/g of dry weight) from the fungal biomass of *Trichoderma reesei* grown on glucose using an improved extraction and production method (Vereman et al. 2021). These studies have shown that the type of biosurfactant and its production depend on the strain, the formulation of the culture medium (substrate) and the culture conditions in which the organism grows. As shown in Fig. 3, to optimize microbial surfactant production, it is necessary to use microorganisms with high production capabilities growing in optimal conditions on low-cost substrates employing an adequate system for fermentation (i.e. optimization of the fermentation process). The use of novel technological developments is also necessary to efficiently enhance biosurfactant production. In this context, the use of metabolomic and metagenomics

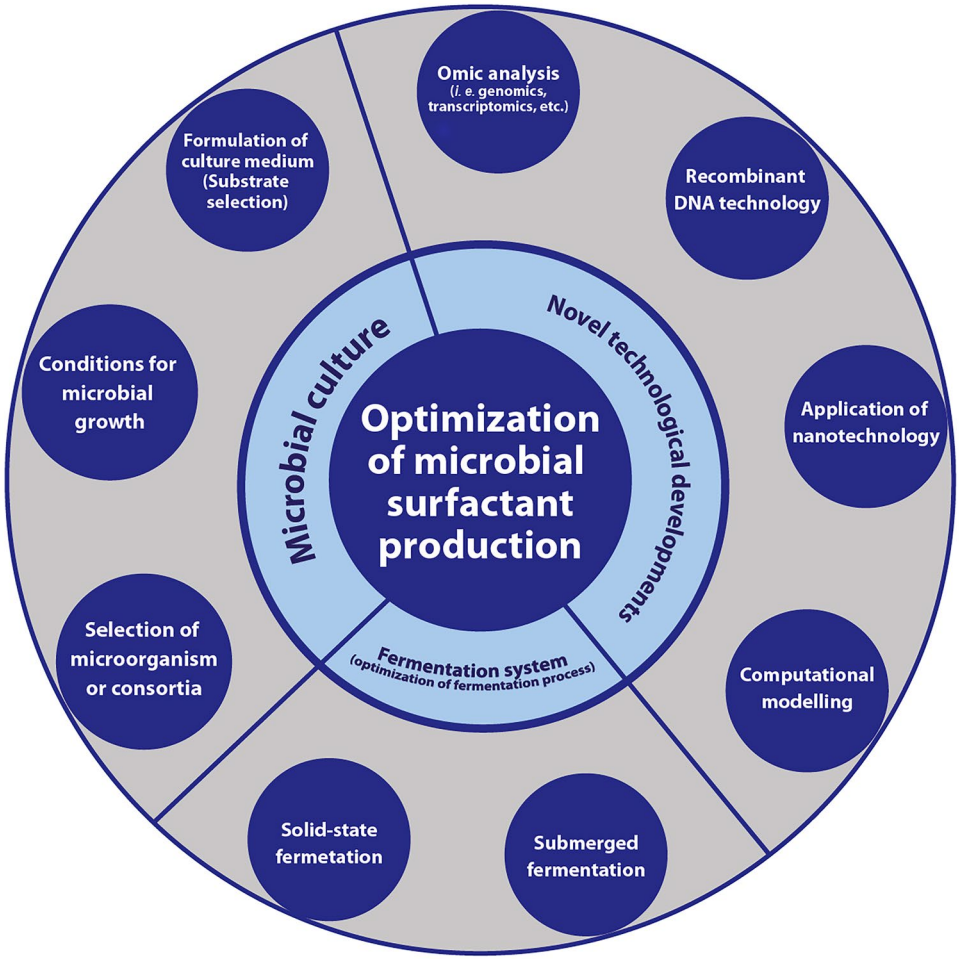


Fig. 3 An overview of factors influencing biosurfactant production. The selection of microbial culture as well as the use of adequate fermentation systems and novel technological developments are important for the optimization of microbial surfactant production

approaches may allow identifying efficient biosurfactant producers as well as novel microbial surfactants. In addition, in silico analysis provides a versatile methodology for integrating multi-omics information to enhance the biosurfactant production (Occhipinti et al. 2018). Recombinant DNA technology also enables overproduction of microbial surfactants (Gaur et al. 2022). Furthermore, nanotechnology is a promising tool in the development of biosurfactant-based nanostructures (nano-adsorbent structures), which are efficient nanoparticles for environmental application (Kundu et al. 2016; Nitschke et al. 2022).

Biosynthetic pathways of microbial surfactants

It has been reported that microorganisms use independent pathways to synthesize the hydrophobic and hydrophilic portions of biosurfactants, which are subsequently combined (Théatre et al. 2021). The biosynthetic pathway to be used depends on the carbon source in which the microorganism grows. For example, for glycolipid biosynthesis in the presence of carbohydrates as the sole carbon source, carbon flow is used in both the lipogenic and glycolytic pathways for lipid moiety and hydrophilic portion synthesis, respectively (Fig. 4). As illustrated in Fig. 4, when glucose is present in the growth medium, glucose-6 phosphate is the first intermediate of glucose metabolism, which is one of the principal precursors of carbohydrates that constitute the hydrophilic part of a biosurfactant (e.g. sophorose, trehalose, and mannose). The hydrophobic part of the surfactant is synthesized by the oxidation of glucose to pyruvate, which is then converted into acetyl-CoA. Acetyl-CoA is converted to malonyl-CoA, and then a series of reactions occurs to convert malonyl-CoA to fatty acids, which are then channeled into the lipid biosynthetic pathway (Parsons and Rock 2013; Fakas 2016). For example, for the sophorolipid biosynthesis, oleic acid is synthesized via de novo fatty acid biosynthesis, which is converted to ω-hydroxy fatty acid. UDP-glucose enters into the biosynthesis to form glucolipid and then a non-acetylated acid sophorolipid is formed. Subsequently, a series of reactions occur to convert this last compound to lactones both in monomeric or in dimeric structures, since sophorolipid exists in two forms acidic and lactonic (Van Bogaert et al 2011; Saerens et al 2015; Wongsirichot,

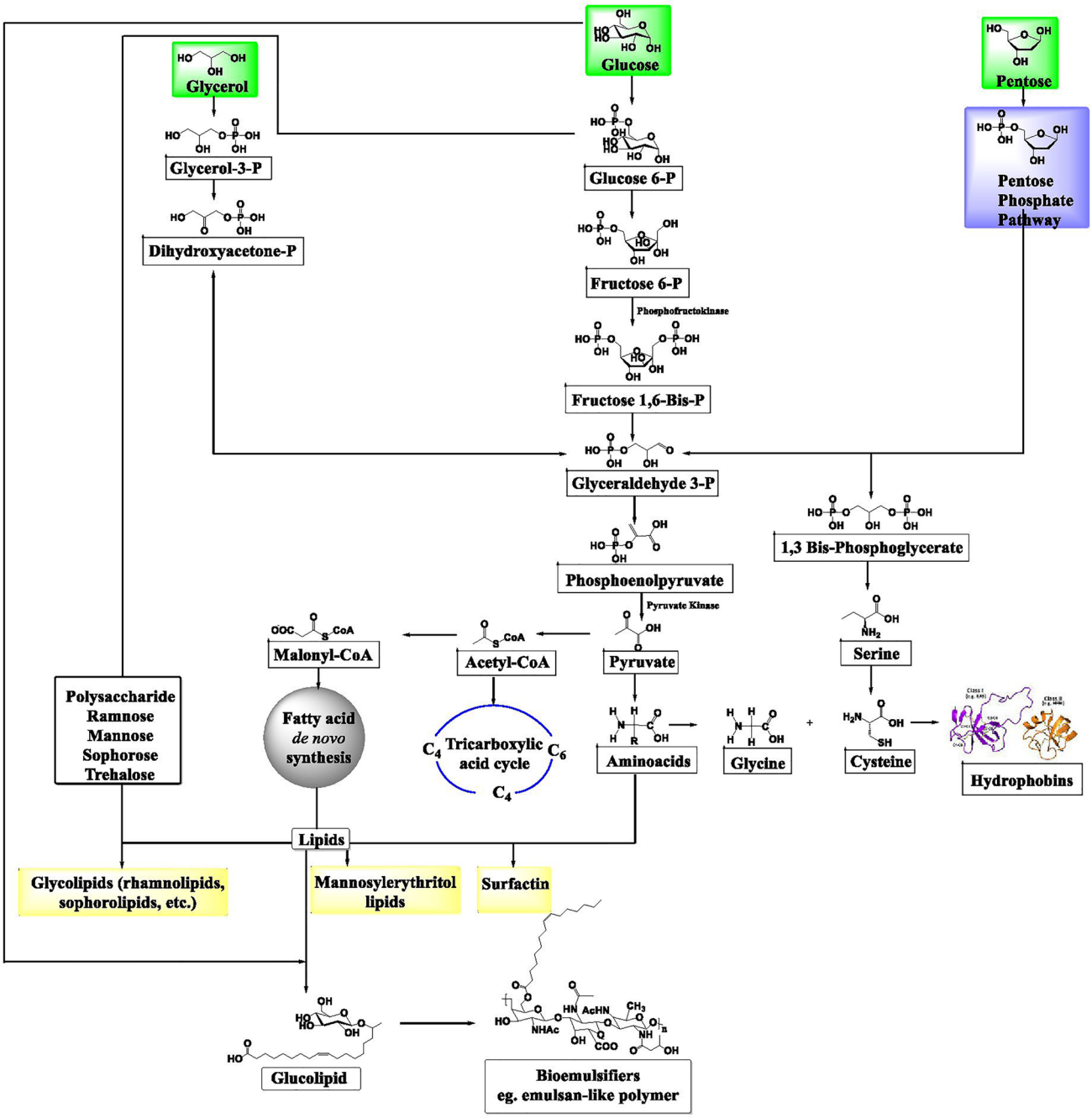
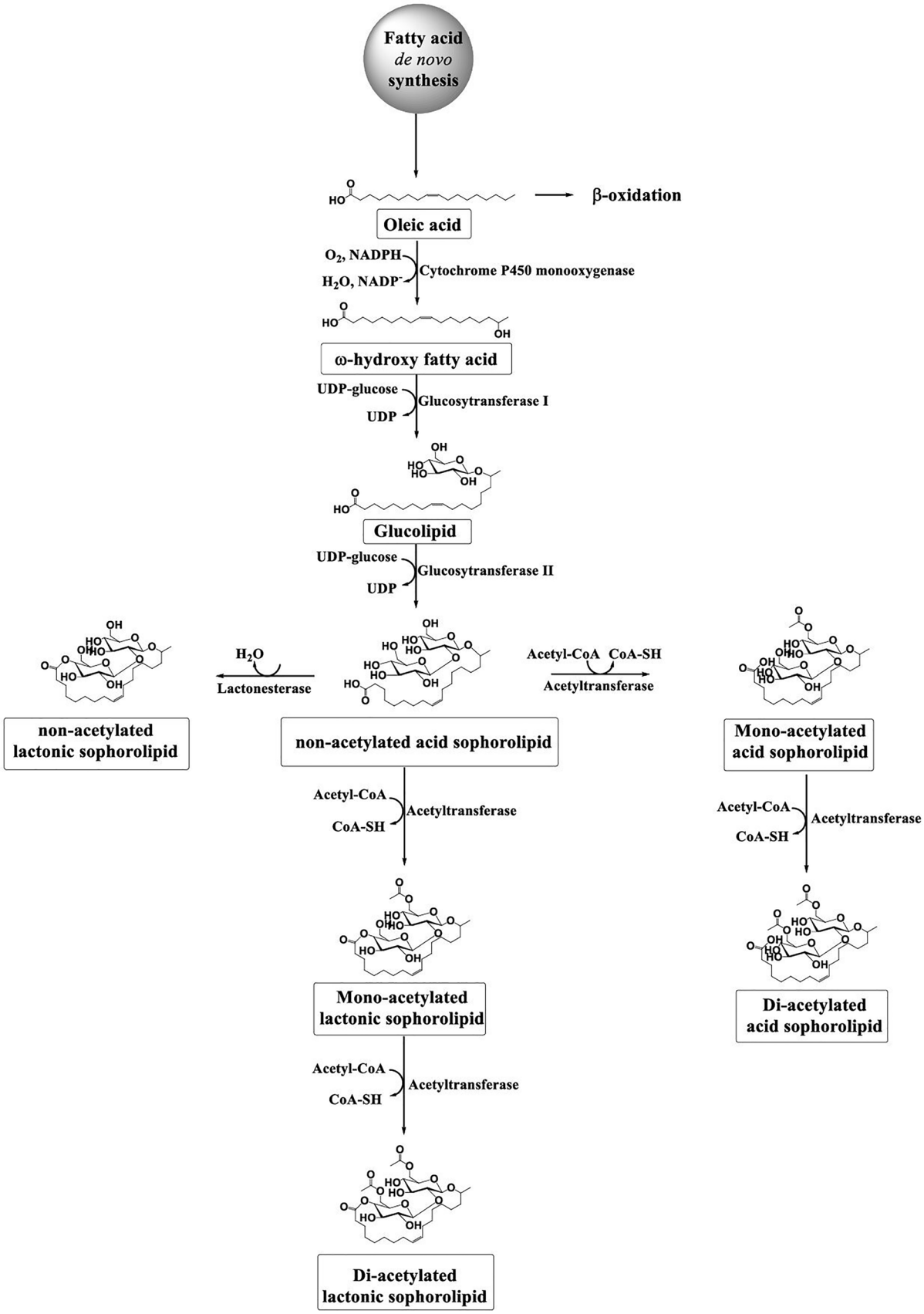


Fig. 4 Biosynthetic pathways for the production of different types of glycolipids (i.e. rhamnolipids, sophorolipds, etc.), lipopeptide (i.e. surfactin), hydrophobins and bioemulsifiers using carbohydrate substrates (redrawn and extended from Luft et al. 2020; Jimoh et al. 2021; Fernandes-Moutinho et al. 2021). Carbon flow is used in both the lipogenic and glycolytic pathways for lipid moiety and hydrophilic portion synthesis, respectively

et al 2021) (Fig. 5). Emulsan and hydrophobins can also be synthetized through de novo fatty acid biosynthesis and amino acid formation pathways, respectively (Fig. 4). The biosynthetic pathways of bioemulsifiers also have been proposed. For example, for emulsan biosynthesis, fructuose 6-P would be transformed into UDP-N-acetyl-D-glucosamine, which after a series of reactions would be converted to UDP-N-acetyl-L-galactosaminuronic acid and then to UDP-N-acetyl-D-galactosamine uronic acid. This last compound would undergo sequential transfer of sugars, acetylation, trans-amidation and trans-esterification of fatty acids, translocation and polymerization of repeat units to form emulsan (Singh et al 1990; Nakar and Gutnick, 2001) (Fig. 6).


Fatty acid
de novo
synthesis
β-oxidation
Oleic acid
O2, NADPH
H2O, NADP-
Cytochrome P450 monooxygenase
ω-hydroxy fatty acid
UDP-glucose
UDP
Glucosytransferase I
Glucolipid
UDP-glucose
UDP
Glucosytransferase II
H2O
Lactonesterase
Acetyl-CoA CoA-SH
Acetyltransferase
non-acetylated
lactonic sophorolipid
non-acetylated acid sophorolipid
Mono-acetylated
acid sophorolipid
Acetyl-CoA
CoA-SH
Acetyltransferase
Acetyl-CoA
CoA-SH
Acetyltransferase
Mono-acetylated
lactonic sophorolipid
Di-acetylated
acid sophorolipid
Acetyl-CoA
CoA-SH
Acetyltransferase
Di-acetylated
lactonic sophorolipid

◂**Fig. 5** Biosynthetic pathway for the production of sophorolipids. A series of reactions occur to convert non-acetylated acid sophorolipid to lactones both in monomeric or in dimeric structures. Sophorolipid exists in two forms acidic and lactonic (redrawn from Van Bogaert et al 2011; Saerens et al 2015; Wongsirichot, et al 2021)

In contrast, when hydrocarbons are employed as a carbon source for biosurfactant biosynthesis, microorganisms employ the gluconeogenic pathway (the formation of glucose from nonhexose precursors) and the lipolytic pathway for the production of the hydrophilic part (saccharides) and the hydrophobic part (fatty acids), respectively (Fig. 7). The gluconeogenic pathway is activated for the production of saccharides, which begins with fatty acid β-oxidation to acetyl-CoA (or propionyl-CoA, for odd-chain fatty acids). Acetyl-CoA undergoes reactions inverse to those performed in glycolysis. Acetyl-CoA is converted to oxaloacetate, which is decarboxylated and then phosphorylated to form phosphoenolpyruvate. This compound is eventually converted into glyceraldehyde 3-phosphate. Glyceraldehyde 3-phosphate then transforms into fructose 1,6-bisphosphate via either direct conversion or through the intermediate dihydroxyacetone phosphate. Fructose 1,6-bisphosphate transforms into fructose 6-phosphate, which forms glucose-6-phosphate. This compound is the precursor of the carbohydrates (the hydrophilic moiety) in the biosurfactant (Fig. 7) (Karmakar, 2017; Park et al. 2020; Luft et al. 2020; Jimoh et al. 2021).

Microbial biosurfactants are synthesized intracellularly or extracellularly, and their synthesis requires specific genes or enzymes to be activated in the presence of a particular substrate (Jimoh et al. 2021). For example, in *P. aeruginosa*, three enzymes (rhamnosyltransferase chain A, chain B and chain C) that catalyze rhamnolipid production in this bacterium are encoded by the *rhlAB* operon and the *rhlC* gene. The expression patterns of these genes have suggested that the synthesis of monorhamnolipids initially occurs early in the stationary phase followed by the conversion of some into dirhamnolipids (Wagner et al. 2003; Suh et al. 2019). In the fungus *U. maydis*, mannosylerythritol biosynthesis requires the enzymes mannosyltransferase, acetyltransferase and acyltransferase, which are encoded by the *emt1*, *mat1* and *mac1* genes, respectively (Hewald et al. 2006). Several studies have reported that surfactin is produced by *Bacillus* species (Tables 1, 2 and 3). The biosynthesis of this surfactant is catalyzed by surfactin synthase, which involves joining amino acids into the surfactin peptide component through a thiotemplate mechanism. This process includes the assembly of amino acids into a peptide chain. The lipopeptide is then formed by linking the hydroxyl fatty acid to a peptide using an acyltransferase (Jimoh et al. 2021). Specifically, it has been shown that in *B. subtillis*, surfactin biosynthesis involves *srfA* gene expression, which is regulated by repressor proteins and other transcriptional regulators (Sullivan, 1998; Roongsawang et al. 2010; Jimoh et al. 2021). In comparison, in the fungus *T. reesei,* the biosynthesis of hydrophobins depends on the *hfb1* and *hfb2* genes (Askolin et al. 2005), whereas *Fusarium graminearum* possesses five genes encoding hydrophobins (i.e. *FgHyd1-5*) (Quarantin et al. 2019). An increase in the expression of hydrophobin coding genes has been detected in studies on polyethylene terephthalate degradation by *Trichoderma viride* GZ1 (Dąbrowska et al. 2021).

Emergent strategy tools for biosurfactant applications in the biodegradation of hydrophobic organopollutants

Biosurfactants possess practical and efficient applications in the environmental biodegradation of hydrophobic organopollutants. Studies on the use of partially purified biosurfactant or biosurfactant producers for hydrophobic organopollutant biodegradation have been conducted ex situ (*e.g.* in the laboratory). In this context, investigations on benzo(a)pyrene biodegradation were performed in contaminated water and soil by adding a surfactant produced by *Pseudomonas frederiksbergensis* (Guo and Wen 2021). It was observed that the benzo(a)pyrene in contaminated water decreased by 66% (2 mg/L, initial concentration) when the dosed biosurfactant was 3 mg/L, whereas 84.8% of this pollutant was biodegraded in contaminated soil by adding 0.5% (w/w) biosurfactant (Guo and Wen 2021). Furthermore, the cell-free broth containing surfactants produced by *Bacillus algicola*, *Rhodococcus soli*, *Isoptericola chiayiensis*, and *Pseudoalteromonas agarivorans* was able to desorb crude oil in oil-polluted marine sediment (Lee et al. 2018). Moreover, the addition of a crude lipopeptide biosurfactant produced by *Bacillus methylotrophicus* to biodiesel-contaminated clayey soil at a low concentration (0.5% w/w) enhanced biodiesel removal by approximately 16% after 90 days (Decesaro et al. 2021). In addition, research on PAH biodegradation revealed that the addition of phenol (which frequently coexists with PAHs) and a biosurfactant extracted from the production of *P. aeruginosa* were able to enhance PAH bioavailability in sludge and improve biodegradation (Zang et al. 2021). Furthermore, the application of rhamnolipids in a fungal-cultured biotrickling filter for toluene removal showed significantly improved biodegradation of this hydrocarbon (> 96%) (Dewidar and Sorial 2022).

Additionally, a study on the biodegradation of petroleum wastewater was performed using an anoxic packed bed biofilm reactor that was inoculated with in situ biosurfactant-producing bacteria (Molaei et al. 2022). Biosurfactant (rhamnolipid and surfactin) production and dehydrogenase activity increased during biodegradation, showing efficient biodegradation of cyclic aliphatic, aliphatic, and aromatic

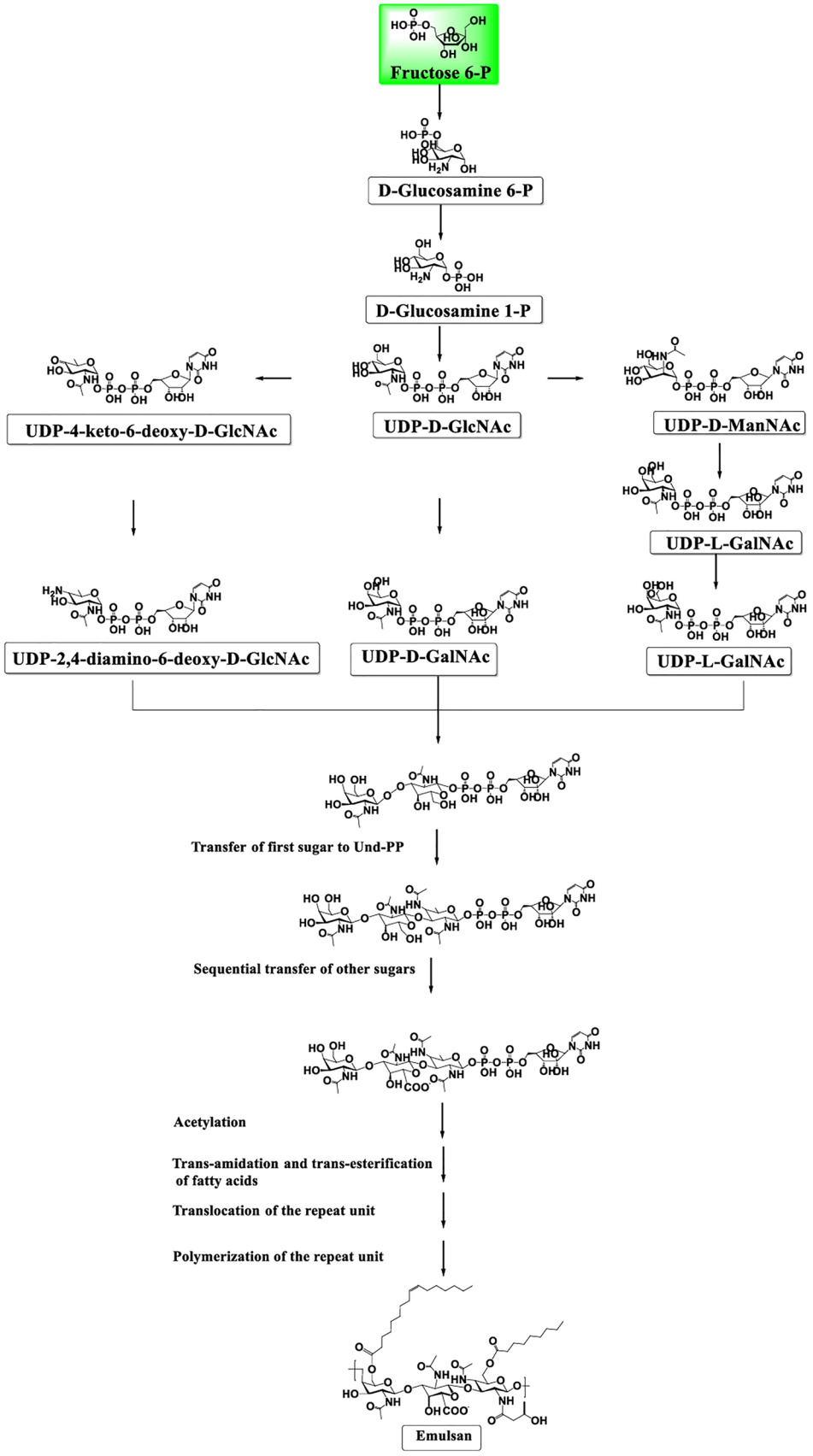


Fig. 6 Proposed biosynthetic pathway for the production of emulsan. Fructuose 6-P would be transformed into UDP-D-GlcNAc, which after a series of reactions would be converted to UDP-D-GalNAc. This last compound would undergo sequential reactions to form emulsan (redrawn from Singh et al 1990; Nakar and Gutnick, 2001). GlcNAc, N-acetylglucosamine; ManNAc, N-acetylmannosamine; GalNAc, N-acetylgalactosamine; GalNAc, N-acetylgalactosamine uronic acid

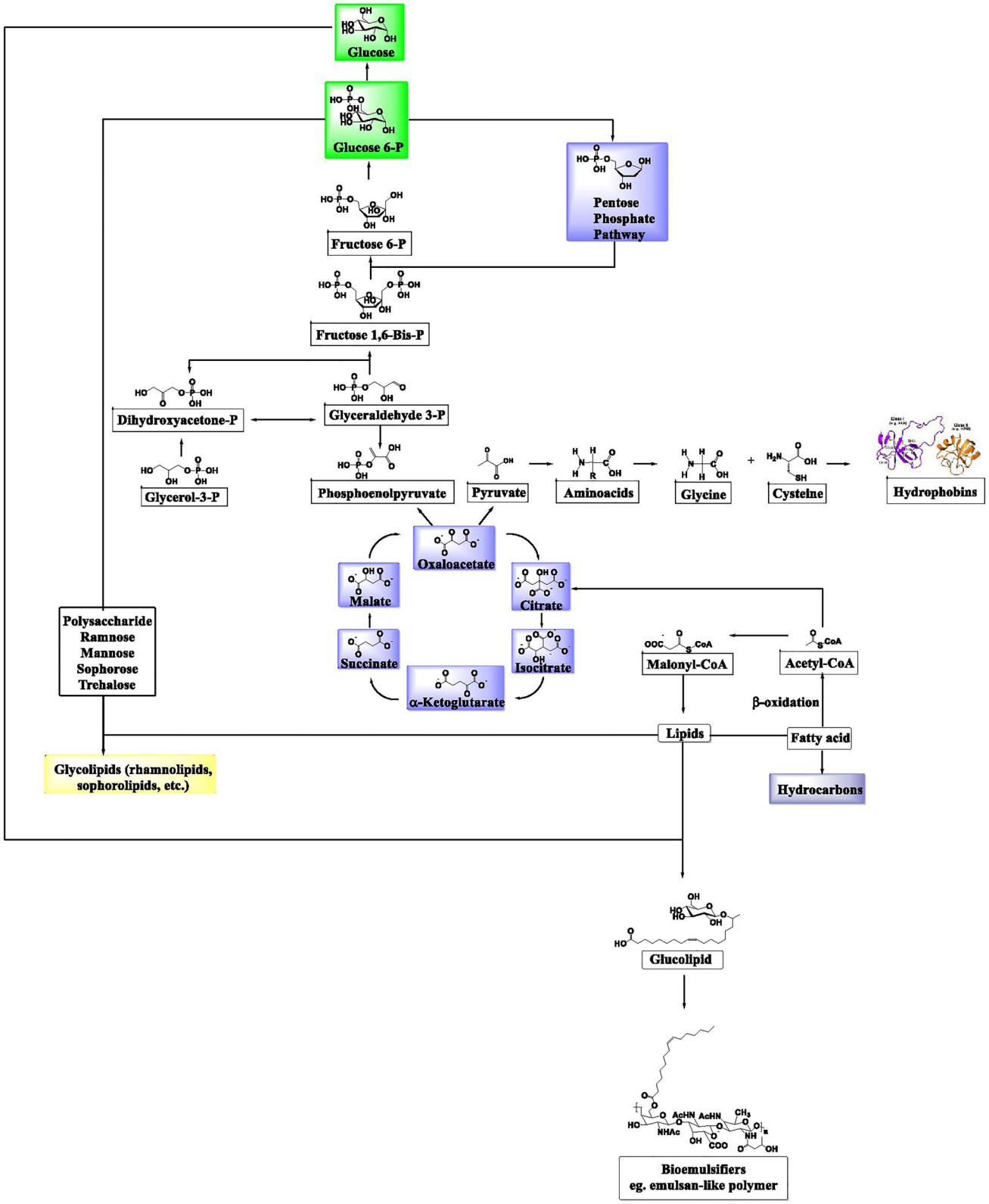


Fig. 7 Metabolic pathways for the synthesis of different types of glycolipids (i.e. rhamnolipids, sophorolipds, etc.), hydrophobins, bioemulsifiers, etc., using a hydrocarbon substrate (redrawn and extended from Luft et al. 2020; Jimoh et al. 2021). Microorganisms employ the gluconeogenic pathway (the formation of glucose from nonhexose precursors) and the lipolytic pathway for the production of the hydrophilic part (saccharides) and the hydrophobic part (fatty acids), respectively

hydrocarbons (Molaei et al. 2022). Moreover, the biosurfactant producers *Bacillus* sp. AKS2 and *P. aeruginosa* AKS1 isolated from refinery sediments were used in biodegradation experiments performed in microcosm sediments (125 mg crude oil/10 g sand) (Chettri et al. 2021). The half-lives for hydrocarbon biodegradation were 50 and 61 days for *P. aeruginosa* and *Bacillus* sp respectively (Chettri et al. 2021).

A study using immobilized *Vibrio* sp. LQ2, a biosurfactant (phospholipid) producer in the bioremediation of diesel oil-contaminated seawater, was conducted (Zhou et al. 2021). It was shown that the inoculation of biochar-immobilized LQ2 resulted in 94.7% diesel oil removal (reduction from 169.2 mg to 8.91 mg) after 7 days. This investigation also revealed an increase in the degradation-related genes *alkB* and *CYP450-1*, which were 3.8 and 15.2 times higher in the immobilized LQ2 experiment than those in the free-cell experiment (Zhou et al. 2021).

An analysis of the utilization of biosurfactants or microbial producers of biosurfactants in combination with other methods to improve organopollutant degradation has also been undertaken. In this context, a study on the use of a bacterial surfactant (lipopeptide) in electrokinetic remediation increased the degradation rate of crude oil-contaminated soil by approximately 92% (Prakash et al. 2020). In addition, an enhanced method for the treatment of oil-contaminated soil has also been reported using a biosurfactant (rhamnolipid and surfactin)-assisted washing mechanism coupled with hydrogen peroxide-stimulated microbial degradation (Fanaei et al. 2020). Furthermore, an effective remediation (84%) method for diesel-contaminated soil was reported by integrating electrokinetics with bioremediation using the biosurfactant-producing bacterium *Staphylococcus epidermidis EVR4* (Vaishnavi et al. 2021). Moreover, a process in which aromatic hydrocarbons were removed from contaminated soil from industrial sites using a surface-modified lipopeptide biosurfactant (with enhancement of polar amino acids) produced by *Bacillus malacitensis* and an activated functionalized carbon matrix was investigated; a 62% total petroleum hydrocarbon removal efficiency was found after 28 days (Christopher et al. 2021).

Furthermore, studies using biosurfactants in situ (i.e. in polluted areas) have also shown biodegradation of hydrophobic organopollutants. For example, a field trial on LaTouche Island (in Alaska) demonstrated the effectiveness of the microbial surfactant PES-51, which was able to remove weathered crude oil from beach material. Hydrocarbons (semivolatile petroleum) were reduced by approximately 70% (Tumeo et al. 1994). In addition, a biodegradation experiment on crude oil-contaminated soil was undertaken near an oil production company, demonstrating that 77% of crude oil was degraded using a combination of rhamnolipids, nutrients and hydrocarbon-degrading bacteria (Tahseen et al. 2016). Furthermore, it was found that *Enterobacter xiangfangensis* STP-3 was capable of degrading 82% of petroleum hydrocarbons in 14 days during the biotreatment of real field petroleum oil sludge with the simultaneous production of metabolic enzymes and biosurfactants (Muneeswari et al. 2021).

Concluding remarks

Biosurfactants are produced either as growth-associated products or secondary metabolites with diverse chemical structures and in varying amounts by a wide range of microorganisms. Microbial surfactant production can be induced by the presence of hydrophobic substrates or they can be produced intrinsically using conventional organic materials or organic wastes as substrates. Biosurfactants are biodegradable and ecofriendly, and their microbial diversity in production, high stability and specific activity make them a promising technology to clean up polluted environments in a green manner. The use of microbial surfactants offers a promising strategy to overcome the problems associated with contamination by hydrophobic organopollutants. However, biosurfactant production must be optimized to increase yield and decrease production costs. For this reason, it is necessary to use microbial producers with high biosurfactant production capabilities on low cost substrates. Additionally, the use of novel technological developments (e.g. omic analysis, recombinant DNA technology, nanotechnology, computational modeling, efficient separation technology) in multidisciplinary research would enhance the efficient production of biosurfactants. Further studies are needed to fully understand the mechanisms of biosurfactant biosynthesis, in which the use of bioinformatics analysis is a promising tool. In addition, more research is required to understand the interaction of biosurfactants with cells in order to improve our knowledge of their mechanism of action for the organopollutants degradation. The development of integrated strategies that combine techniques and biosurfactants is an interesting approach to explore the most effective treatment technology for the remediation of hydrophobic organopollutant contamination.

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Author contribution CS conceived, designed, wrote, read and approved the manuscript.

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Declarations

Competing Interest The author has no conflicts of interest to declare.

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