Microbial Cell Factories

REVIEW

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Microbial glycoconjugates in organic pollutant bioremediation: recent advances and applications

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Abstract

The large-scale application of organic pollutants (OPs) has contaminated the air, soil, and water. Persistent OPs enter the food supply chain and create several hazardous effects on living systems. Thus, there is a need to manage the environmental levels of these toxicants. Microbial glycoconjugates pave the way for the enhanced degradation of these toxic pollutants from the environment. Microbial glycoconjugates increase the bioavailability of these OPs by reducing surface tension and creating a solvent interface. To date, very little emphasis has been given to the scope of glycoconjugates in the biodegradation of OPs. Glycoconjugates create a bridge between microbes and OPs, which helps to accelerate degradation through microbial metabolism. This review provides an in-depth overview of glycoconjugates, their role in biofilm formation, and their applications in the bioremediation of OP-contaminated environments.

Keywords: Glycoconjugates, Bioremediation, Biosurfactants, Organic pollutants, Biofilm

Introduction

Organic pollutants (OPs) are used in large quantities in the industrial and agricultural sectors [1]. The rapid industrialization and anthropogenic activities of the present era have increased environmental contamination with various OPs, including compounds like chloroform, benzene, carbon tetrachloride, paints, gasoline, adhesives, plastic compounds, chlorohydrocarbons (CHCs), and pesticides [2]. OPs are presently found in the air, soil, and water and have various adverse effects on living systems, including the flora and fauna present in the ecosystem [3]. These OPs are also reported to be responsible for various toxic effects in humans, including adverse carcinogenic, mutagenic, and teratogenic effects. Thus, remediation strategies for these OPs are essential in the present scenario (Fig. 1). The remediation of OPs usually uses physical and chemical techniques such as soil washing, pumping, aeration, oxidation, incineration, etc. [4]. However, these methods have many disadvantages and usually result in secondary environmental contamination; they are also uneconomical to use. The secondary contaminants are not emitted directly from the source they formed due to degradation reactions of the main pollutants. Therefore, bioremediation strategies utilizing living systems are the only hope for the eco-friendly management of these OPs.

Microbial bioremediation (MB) is usually considered one of the best methods for the treatment of environmental contamination. The rich diversity of metabolizing enzymes participated in the bioremediation processes [3]. The MB of contaminants is possible through enzymatic reactions, which produce different intermediate metabolites through metabolic pathways. Although single microbial cultures have been used as potent contaminant degraders in recent decades, but mixed cultures

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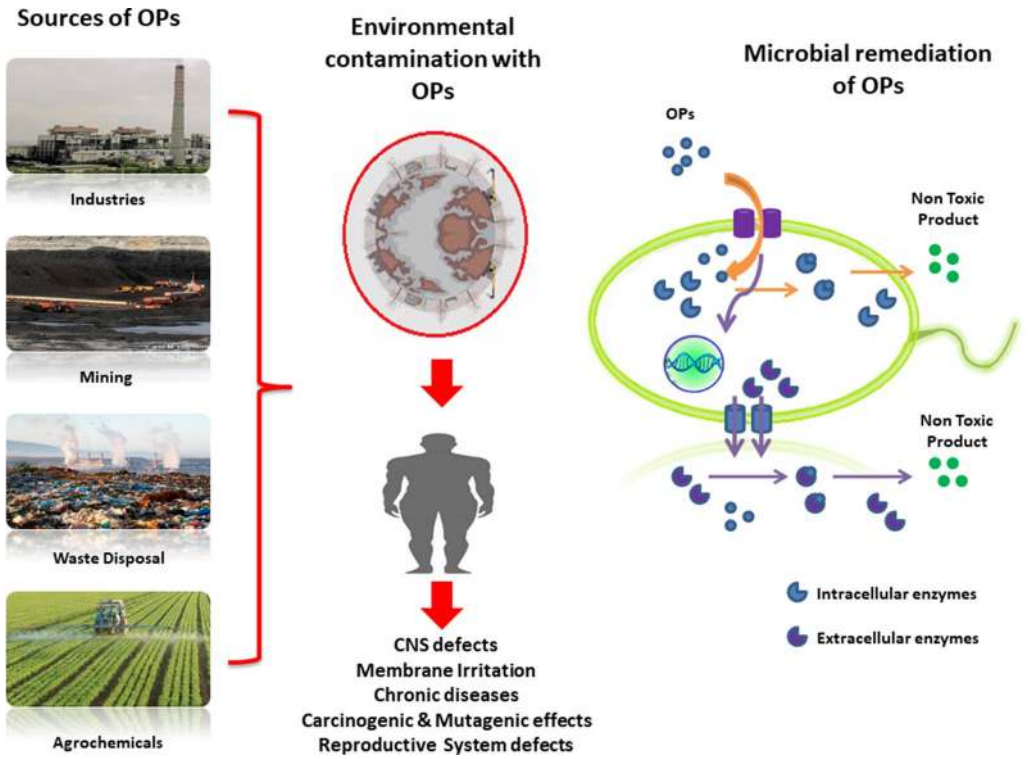

Fig. 1 Microbial remediation of organic pollutants (OPs): sources, adverse effects and micro-remediation mechanisms

perform better in environments [5]. Environmental contamination with OPs can be managed by utilizing microbial metabolic processes that degrade these OPs into non-toxic metabolites in an economical, eco-friendly, and efficient manner [6]. Thus, researchers are involved in the study of microbial biodegradation mechanisms related to OPs to develop low cost and simple techniques for the management of these pollutants. OPs are metabolized by microbial cells using both aerobic and anaerobic metabolism. Anaerobic metabolism is one of the most preferred methods in bioremediation, especially for chlorinated OPs. However, sometimes OPs involve the production of much more toxic compounds, such as trichloroethylene (TCE). Microbial degradation via anaerobic mechanisms results in the production of dichloroethylene (DCE) and vinyl chlorides (VCs), which have higher environmental toxicity than their parent compound, TCE [2]. Thus, at times, aerobes are the best choice for OP bioremediation due to presence of various catabolite enzymes with broad specificity to degrade different types of OPs. These aerobes consist of various oxygenases that play a significant role in the degradation of pollutants from contaminated sites. For example, *Pseudomonas* sp. has oxygenases that can metabolize TCE along with the associated DCE and VCs into CO_2 and Cl^-, where both the final products are non-toxic [4]. However, the efficient degradation of OPs rests in understanding its transportation inside the microbial cell and its assimilation. Studies indicate that microbial glycolipids and other glycoconjugates play a very important role in the mechanism of transport of these OPs across microbial membranes [7]. These microbial glycol compounds act as emulsifiers and are called "biosurfactants", which are located either inside the cell or secreted outside and help in the bioremediation mechanism [8]. This gave rise to the term "microbial glycobiotechnology" (MG), which involves a wide array of methods, with the main goal of decontaminating different types of pollutants.

MG utilizes natural microbial resources for the transformation of the contaminated environment to a safe native natural form. MG involves the microbial production of carbohydrate polymeric compounds with novel applications in the field of bioremediation and waste management. Studies proved that biosurfactant production has a direct correlation to OP degradation. Thus, MG is gaining importance for the management of OPs in the environment [9]. MG interacts with proteins and metabolites and facilitates the degradation of OPs [10]. This review presents an overview of recent advances in MG and its specific applications in the bioremediation of different types of OPs.

Microbial glycoconjugates: types and application in bioremediation

Glycobiotechnology, involves the transfer of the basic knowledge structure and functional relationship of glycoconjugates to practice-related synthetic and applied producers [11]. The term "glycoconjugate" indicates the combination of glycoproteins and glycolipids. Microbial strains are able to produce glycoconjugates and facilitate their metabolism in various ways, such as via the producers of these molecules, uptake of the desirable pollutants, and other substrates (Table 1). Glycoconjugates are an integral part of the bacterial cell membrane, which consists of special types, viz., surface molecules (lipopolysaccharides, capsular polysaccharides, lipo-oligosaccharides, and glycoproteins), cell-wall polymers, and secreted exopolysaccharides [12] (Fig. 2). In addition to this, microbial strains produce extracellular glycoconjugates such as rhamnolipids, sophorolipids and exopolysaccharides, glycoproteins, and glycol-lipopeptides. These glycoconjugates play a crucial role in the bioremediation of the OPs [13].

Table 1 Glycoconjugates in the bioremediation of organic pollutants (OPs)

Microbial strains	Glycoconjugates	Organic pollutants	Mode of action	References
Acinetobacter sp. Y1	Methyl hexadcanoate, methyl octadecanoate	Petroleum hydrocarbon	Reduce surface tension of water, showed strong tolerance with pH, temperature, salinity	[14]
Pseudomonas, *Rhodococcus*	Biosurfactants	Cypermethrin	Emulsion reaction	[15]
Achromobacter sp. A-8	Biosurfactants	Crude oil	Reduce surface tension	[16]
Acinetobacter baumannii BJ5	Glycolipid biosurfactant	Pyrene	Growth linked production	[17]
Burkholderia cenocepacia BSP3	Glucolipid	Methyl parathion, ethyl parathion, trifluralin	Critical micelle formation (CMC) and reducing surface tension	[18]
Pseudomonas aeruginosa WH-1	Biosurfactants	Hexachlorocyclohexane (HCH)	Lower the emulsification with HCH	[19]
Pseudomonas sp.	Rhamnolipids	Chlorpyrifos	Increase the aqueous partition and chlorpyrifos degradation	[20]
Bacillus subtilis MTCC 1427	Biosurfactants	Endosulfan	Increase bioavailability of endosulfan	[21]
Pseudomonas aeruginosa B1, *P. fluorescens* B5, *P. stutzeri* B11 and *P. putida* B15	Exopolysaccharides (EPS)	2,4-D, benzene, toluene, xylene and gasoline	Organic pollutants affect EPS production	[22]
Penicillium simplicissimum	Tea saponin, rhamnolipid	Phenol	CMC, reduce surface tension and increase laccase production	[23]
Pseudomonas aeruginosa CH7	Rhamnolipid	*β*-Cypermethrin	Rhamnolipid promote the dissolution, absorption, adsorption	[24]
Candia, *Pseudomonas*, *Deinococcus*, *Nocardiopsis*, *Serratia*	Rhamnolipids, trehalolipids, mannosylerythritol lipids, cellobiose lipids	Organic pollutants	Bioremediation of the organic pollutants	[25]
Pseudomonas, *Bacillus*, *Candida*	Rhamnolipid	Oil spill	Reduce interfacial tension, disperse oil particles	[26]
Pseudomonas aeruginosa, *Rhodococcus* sp., *Bacillus licheniformis*, *Serratia marcescens*, *P. flourescens*, *B. subtilis*	Rhamnolipid, trehalolipid, sophorolipid, peptide lipid, serrawetin, visconsin, surfactin, emulsan, liposan	Oil pollution	Enhanced degradation	[27]
Serratia marcescens UCP 1549	Lipoprotein, carbohydrate	Organic pollutants	Agricultural and marine bioremediation	[28]
Bacillus subtilis B20	Biosurfactants	Oil rock	Reduced surface and interfacial tension	[29]
Paenibacillus sp. D9	Lipopeptide biosurfactant	Hydrocarbons	Enhanced biodegradation of hydrophobic pollutants	[30]
Bacillus, *Rhodococcus*, *Actinomycetes*, *Pseudomonas*	Lipopeptide, glycolipid, sophorolipds	Organic pollutants	Reduce surface tension with higher degradation	[31]
Bacillus algicola, *Rhodococcus soli*, *Isoptericola chiayiensis*, *Pseudoalteromonas agarivorans*	Rhamnolipids	Crude oil	Low surface tension	[32]

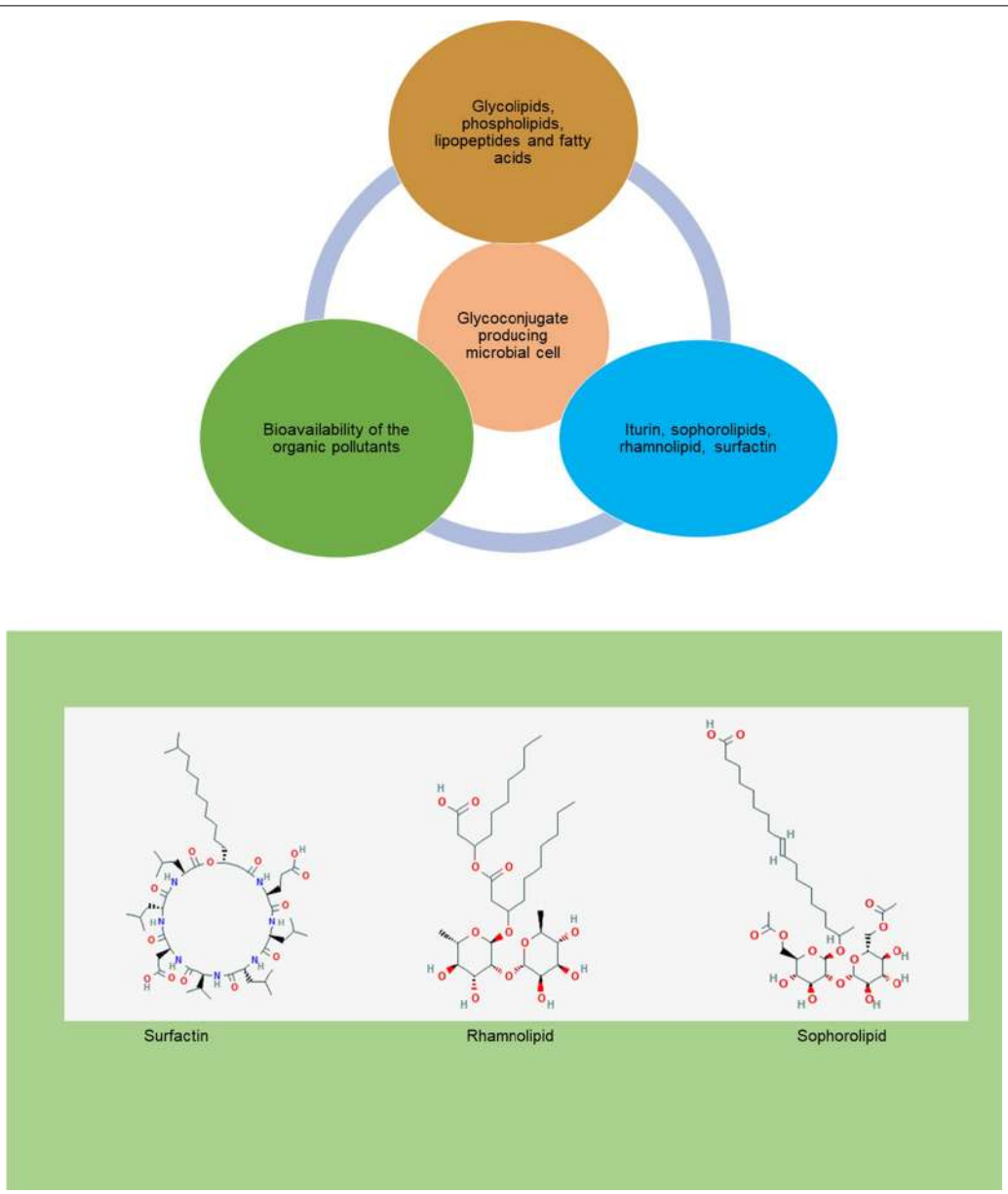

Fig. 2 Microbial glycoconjugates in the bioremediation of organic pollutants (OPs)

Microorganisms produce glycoconjugates with biosurfactant properties during the stationary phase of the microbial growth cycle [33, 34]. Glycoconjugates are amphiphilic compounds synthesized onto the cell surface of the microorganism [35]. These molecules contain hydrophilic and hydrophobic moieties that reduce the surface and interfacial tension. Glycoconjugates can have diverse structures, such as glycoproteins, glycopeptides, peptidoglycans, glycolipids, lipopolysaccharides, and glycosides. The production of the glycoconjugates depends on the producer microorganism, nutritional sources such as carbon and nitrogen, trace elements, and the physicochemical conditions for production. Recently, glycoconjugate rhamnolipids have been the most commonly used in industrial and environmental applications [35, 36]. The glycolipid rhamnolipid is well studied in the *Pseudomonas* and *Burkholderia* species [36]. *Pseudomonas aeruginosa* is considered as the top rhamnolipid producer at over 100 $g \cdot L^{-1}$. In a liquid culture, *Pseudomonas aeruginosa* produces two types of rhamnolipids referred to as mono and dirhamnolipid [35]. These molecules are synthesized by two enzyme-specific rhamnosyl transfer

reactions. The enzyme that catalyzes these reactions is called rhamnosyltransferase [37, 38]. The hydrophobic and hydrophilic parts of the rhamnolipid are synthesized by different biosynthetic reactions in the microbial strains. After their synthesis, both of the portions are linked to each other, forming monorhamnolipids and dirhamnolipids. Yeasts are also reported to produce glycoconjugates such as sophorolipids, mannosylerythritol, cellobiose, and trehalose lipids. These have been explored for their greater potential in the bioremediation of polluted sites [39]. The enhanced bioremediation of pyrene and tetracycline in soil was investigated with the addition of sophorolipid [40].

Hydrophobic pollutants require desorption from the soil and water environment before microbial metabolism. Mineralization of OPs is governed by desorption from the soil. The application of glycoconjugates as biosurfactants for the bioremediation of environmental OPs is also well established; they play a direct role in the desorption of pollutants [41]. In the first step, these glycoconjugates interact with less soluble OPs and improve their transfer into the soil matrix and their subsequent removal [42]. In the second step, glycoconjugates act as a bridge between the microbial strains and soil, due to which the bioavailability of the pollutants increases [43, 44]. The increased concentrations of these surface-active glycoconjugate compounds help in the attachment of microbial cells to pollutants [45]. Biosurfactants increase the surface areas of hydrophobic pollutants through which their solubility increases in the soil and water environment. The use of biosurfactants for the biodegradation of pesticides has gained attention in recent years. Previous reports supported the role of biosurfactants in the bioremediation of hydrocarbon and pesticide-contaminated soil. These reports favor pesticide degradation using glycoconjugated biosurfactant usually synthesized from bacterial species viz., *B. pumilus*, *B. mojavensis*, *B. licheniformis* and *B. amyloliquifaciens* [46]. Biosurfactants of *Lactobacillus pentosus* degrade octane efficiently [47]. In a study, *Burkholderia* species isolated from an oil-contaminated area was able to produce biosurfactant, that plays a critical role in pesticide degradation [18, 48]. Biosurfactants that degrade naturally are ideally suitable for the removal of organic pollutants from the environment and considered ecofriendly to nature [49]. Previous studies indicated that the efficiency of OP degradation was improved in the presence of microbial glycoconjugates. Stimulation in the degradation of OPs was mainly due to the action of the biosurfactants. Enhancement in the degradation of octane was due to the biosurfactants production using *Lactobacillus pentosus* [47]. In addition to mobilization, glycoconjugated biosurfactants increase the degradation rate via other mechanisms [50]. An axenic culture of *Pseudomonas putida* DOT-T1E produced a rhamnolipid that facilitated the bioremediation of chlorinated phenols. The logic behind this mechanism involves entrapment of the chlorophenol in the biosurfactant micelles and the hydrophobic relationship between these two types of compounds [51, 52]. Similarly, *Actinobacteria* produced biosurfactants that enhanced the rate of xenobiotics bioremediation [53]. Rhamnolipids were found to be adequate in the bioremediation of carbendazim with *Rhodococcus* sp. D-1 [54]. The rhamnolipid affected carbendazim degradation in a concentration-dependent manner with maximum bioremediation efficiency. It facilitated carbendazim emulsification and favorable changes on the cell surface, allowing it to enter *Rhodococcus* sp. D1 cells, and degradation subsequently occurred [54]. The glycolipid produced from the *Rhodococcus* sp. strain IITRO3 also makes the greater impact on degradation of 1,1,1-trichloro-2,2-bis (4-chlorophenyl) ethane [55]. The distribution of glycoconjugate-producing bacteria was reported in contaminated arid southwestern soil [56]. Rhizospheric microbes play an important role in the degradation of soil contamination, enhancing the degradation found with production of the glycoconjugates [57].

Another important concern is the effect of glycoconjugate biosurfactants on the candidate microbial strains that degrade OPs. The contrasting strains of *P. aeruginosa* produce glycoconjugate biosurfactants that enhance solubility and metabolism [58]. The purified biosurfactants cause an increase in the solubility of pyrene and higher solubilization of fluorene. The concentration of the biosurfactants is also very important for microbial growth. A higher concentration of these glycoconjugates inhibits the growth of microbial cells and reduces biodegradation potential [59]. These reports are not same for all the microbial strains, however, sometimes, a low concentration of glycoconjugate biosurfactants might also be toxic and show an antimicrobial effect [60, 61]. Most biodegradation of OPs has been reported previously with axenic microbial strains, whereas for the consortium, more biodegradation was achieved. The glycoconjugates increased the rate of OP degradation with a microbial consortium due to cumulative effect of microbial communities [62]. In a study a seawater *B. methylotrophicus* produced glycoconjugate biosurfactants that reduce surface tension, can be used for bioremediation purposes [63]. Microbial rhamnolipids and surfactin are used by researchers for the bioremediation of organic pollutants in last decades [64, 65]. The advantage of biosurfactants over synthetic surfactants is that the former induces low toxicity and stability in the presence of high temperature, high pH, and saline environment [66]. Natural glycoconjugate surfactants play a role in sustainable development and bioremediation [67].

Substrates containing the rich carbohydrates and lipids have been recommended for large-scale microbial glycoconjugate production [65]. The most commonly used substrates viz., corn liquor, glycerol, soybean oil, animal fat, vegetable fat, and molasses [68–72]. The previous study concluded that agro-industrial waste can also be used for microbial glycoconjugate production [73]. These carbohydrate- and lipid-containing compounds are metabolized by microbial metabolic pathways and converted into glycoconjugates such as rhamnolipid. The choice of substrate for microbial growth determines the amount of glycoconjugate production. Microbes are able to produce glycoconjugates from all types of carbon sources, but to achieve higher production, soybeans, corn, canola, and olives can be used (Table 2). Glycoconjugates are considered secondary metabolites due to their production in the stationary phase of microbial growth [37].

Glycoconjugates in action: overview of biofilm formation

In recent years, researchers have taken great interest in the biofilm-based degradation of environmental contaminants. Microbial glycoconjugates also play an important role in biofilm formation and accelerate the bioremediation of the organic pollutants. Generally, under laboratory conditions, a single microbial strain is isolated to test its biodegradation potential for environmental contaminants. However, the basic facts of the environmental interactions between the chosen microbial cell and other microbial communities, or the nature of their habitats, are ignored [100, 101]. Therefore, to harness the potential of microbial cells for glycoconjugate production and impact on biodegradation, it is necessary to consider the behavior of microbial communities and their habitats, even though the experiment was performed under laboratory conditions [5]. In nature, microbes interact with abiotic and biotic factors and produced the glycoconjugates. To maintain their populations via different types of interactions such as synergistic and antagonistic effects that allow microbes to adapt to different environmental conditions at polluted sites. Microbial communities consist of various microbial species that produced the glycoconjugate surfactants which have greater potential than a single culture glycoconjugates because the number of reporting genes and the diversity of metabolic activities work together and provide the maximum output within the shortest period [102]. So, the glycoconjugates produced by various microbial communities showed the cumulative effect on the degradation of the OPs. Importantly, the many microorganisms and microbial species present in microbial "biofilm" can degrade the wide range of contaminants present in the natural environment and engineered systems. Biofilm refers to a group of diverse microbial species attached to any living or nonliving surface and covered by a surrounding self-synthesized glycoconjugates, matrix comprising extracellular DNA, proteins, and water [103, 104]. Biofilm aids in the consumption of nutrients and oxygen, with tolerance against harsh environmental conditions during the bioremediation process. Biofilm based remediation technology is more cost-effective, ecofriendly, and easy for removing pollutants from the natural environment. Due to the production of glycoconjugates microbial biofilm absorbs and immobilizes environmental pollution, and the labor of gene expression divided among the existing microbial communities ultimately works very efficiently as a single unit. The various microbial communities within the biofilm are also responsible for differential gene expression of the substrate, showing a broad range of metabolic pathways for biodegradation. The most important characteristics of biofilm are their chemotaxis and flagellar-based movement. Biofilm can sense the presence of xenobiotics in their proximity and move towards them by swimming, swarming, and twitching, as well as by quorum sensing, which improves biodegradation in presence of glycoconjugates [105, 106]. The composition of microbial biofilm depends on the environmental conditions in which the microbes reside [107–109]. Biofilm provides better environmental conditions and protection from environmental stress, acid stress, antimicrobial stress, UV stress, desiccation, predation, biocides, solvent, toxic chemicals, and other pollutants [110, 111]. Microbial biofilms are increasingly used as indicator systems for monitoring heavy metal contamination in water resources. Changes in the morphology of biofilms and their physiology indicate the occurrence of contaminants in their proximity. Biofilm is frequently found in different geographical locations, such as streambeds, tidal flats, corroded pipes, and sites of infection [112–114].

Microbes are able to communicate with each other in the form of communities and biofilms. The main mechanism behind biofilm formation is quorum sensing. In addition to playing various other roles, glycoconjugates help microbial cells to attach to one another in a biofilm [27]. Glycoconjugates create a favorable environment for the biodegradation of the OPs at the contaminated sites. Microbial cells produce an extracellular matrix that helps the cells attach to each other in communities. Glycoconjugates also help the microbes survive under extreme conditions and protect the microbial cells from the outer environment, especially under water stress conditions. The adhesion of the bacterial cells occurs in both the mobile and stagnant phases. These glycoconjugates are useful for floating the bacterial cells in water bodies as a biofilm, which can be efficiently utilized for bioremediation in water systems.

Table 2 Glycoconjugates producing microorganisms and the associated techniques

Microorganisms	Nature of glycoconjugates	Types of glycoconjugates	Techniques used for identification	References
Pseudomonas aeruginosa MA01	Glycolipid	Monorhamnolipid, dirhamnolipid	Fourier transform infrared spectroscopy (FTIR), thin layer chromatography (TLC)	[74]
Acinetobacter baumannii	Glycolipid	Palmitic and phthalic acid	FTIR, gas chromatography and masss pectrometry (GC-MS), nuclear magnetic resonance (NMR)	[17]
Pseudomonas aeruginosa PG1	Glycolipid	Mono and di rhamnolipid congeners	FTIR, liquid chromatography-mass spectrometry (LC-MS), and scanning electron microscope-energy dispersive spectrometer (SEM-EDS)	[9]
Pseudomonas sp.	Glycolipid	Rhamnolipid	FTIR spectra analysis	[75]
Pseudoxanthomonas sp. G3	Glycolipid	Rhamnolipid type	FTIR spectra analysis	[76]
Lactobacillus casei	Glycoprotein	Glycoprotein	FTIR and NuPAGE method	[77]
Vibrio sp. 3B-2	Glycoprotein	Glycoprotein	Chemical method, spectrometric characterization	[78]
Candida bombicola ATCC 22,214	Glycolipid	Sophorolipid	NMR, high performance thin layer chromatography (HPTLC) and MALDI ToF MS	[79]
Starmerella bombicola	Glycolipid	Sophorolipid	FTIR	[80]
Rhodococcus sp. PML026	Glycolipid	Trehalolipids	LC-MS	[81]
Rhodococcus sp. PML026	Glycolipid	Trehalolipids	Chemical analysis	[82]
Cryptococcus Humicola JCM 1461	Glycolipid	Cellobiose lipid	Chemical analysis	[83]
Streptomyces sp. DPUA 1559	Glycoprotein	Low mol. wt. glycoprotein	Electrophoretic analysis	[84]
Ochrobactrum anthropi HM-1	Glycolipid	Rhamnolipid type	TLC and FTIR spectra analysis	[85]
Citrobacter freundii HM-2	Glycolipid	Rhamnolipid type	TLC and FTIR spectra analysis	[85]
Lactobacillus	Glycoprotein	--	TLC and FTIR	[86]
Pseudomonas isolate DYNA270	Glycolipid	Rhamnolipids	Mass spectrometry	[87]
Streptomyces nocardiopsis A17, *Bacillus subtilis* ICA56	Glycerol	Biosurfactant	TLC and LC-MS	[88]
Bacillus psudomycoides BS6	Lipopeptide	Fatty acid 3-OH and peptide of five amino acid	TLC and FTIR	[89]
Bacillus subtilis B20, *B. subtilis* B30	Glycolipopeptide	Surfactin	Pedant drop method, Lyophilization	[29]
Pseudomonas aeruginosa	Glycolipid	Rhamnolipid		[90]
P. aeruginosa MA01	Glycolipid	Monorhamnolipid	FTIR, electrospray ionization mass spectrometry (ESI-MS)	[74]
Klebsiella pneumonae WME02	Phospholipid	biosurfactant	Biochemical characterization	[91]
Pseudomonas aeruginosa DS10-129	Glycolipid	Rhamnolipid	Mass spectrometry	[92]
Candia lipolytica IA 1055	Glycolipid	Sophorolipid	Emulsification, spectrophotometer	[93]
Pseudomonas aeruginosa	Glycolipid	Rhamnolipid	Spectrophotometer	[94]
Serratia marcescens UCP 1549	Glycolipid	Biosurfactant	Emulsification	[95]
Bacillus subtilis	Glycolipopeptide	Cyclic lipopeptide biosurfactant	High performance liquid chromatography (HPLC), emulsification	[96, 97]
Candia lipolytica UCP0988	Glycolipid	Sophorolipids	TLC, HPLC-ESI-MS	[90]
Marinobacter hydrocarbonoclasticus SdK644	Glycolipid	Biosurfactant	GC-MS, FTIR	[98]
Paenibacillus sp. D9	Glycolipopeptide	Biosurfactant	Emulsification	[31, 97]
Pseudozyma aphidis ZJUDM34	Glycolipid	Mannosylerythritol lipids	TLC, GC-MS	[99]
Bacillus subtilis, *Paenibacillus* sp. D9	Glycolipopeptide	Surface active biosurfactant	Gene cloning and expression, affinity chromatography	[30, 97]

The critical factor of biofilm formation is the production of the glycoconjugate biosurfactant, smoothness at the cell surface, the velocity of flow, and bacterial growth [115]. Biofilm formation is governed by several signaling molecules and glycoconjugates. Naturally, biofilm formation is a complex process that involves many steps. Preliminary bacterial cells produce extracellular polymeric substances (EPSs). These substances act as cementing material on the outer cell membrane and help in the entrapment of nutrients. In addition, EPS also has surfactant properties that help in the mineralization of xenobiotic compounds that are otherwise inaccessible. The production of EPS and water form a slimy layer in biofilms. Microbes also engage in symbiotic relationships with each other at the polluted sites (Fig. 3). The intermediate metabolites produced by primary bacterial colonizers can be used by the secondary colonizers that ultimately form the biofilm. The quorum sensing (QS) mechanisms are well-established for these biofilms and help in regulating EPS production [116]. The QS system can help microbes survive in the presence of stress, such as antimicrobial compounds, nutrient limiting conditions, and OPs. Microbial strains degrade toxic chemicals through the establishment of cellular communications with each other [117].

Glycoconjugates also play an important role in aggregation of the microbial cells in communities. The aggregation of microbial cells is an essential factor in biofilm formation [118, 119]. Bacterial cells from two types of aggregation: auto and coaggregation. In auto-aggregation, genetically identical bacterial cells remain together, whereas coaggregation refers to genetically different cells [120]. The surface factors, extracellular polymeric substances, and diffusible signal molecules are critical factors involved in the auto-aggregation and microbial biofilm at polluted sites [121]. Aggregation also depends on microbial interactions such as antagonism, synergism, mutualism, competition, and commensalism [122].

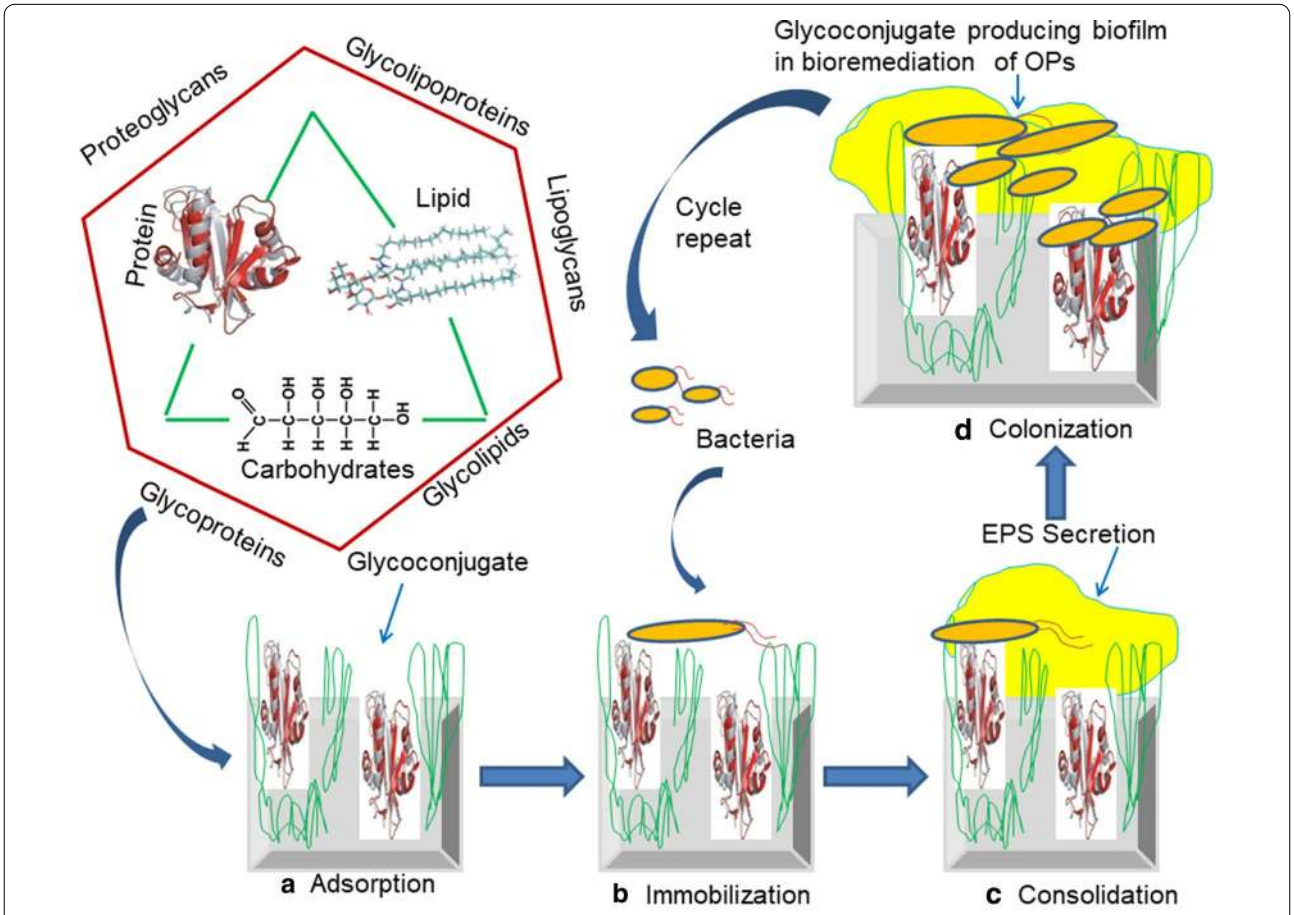

Fig. 3 Role of glycoconjugate in biofilm formation included different steps. Carbohydrate, lipids and protein unite together and form glycoconjugate; **a** adsorption: attachment of carbohydrates and proteins to the surface of substrate; **b** immobilization of microbial cells on the surface of glycoconjugate. **c** consolidation: secretion of extracellular polymeric substance (EPS) by immobilized microbial cells on the cell surface; **d** colonization: microbial cells replicate and secreted large amount of glycoconjugates and forms biofilm which play role in bioremediation of OPs

Several *in-vitro* and *in-situ* studies based on biofilm have been conducted in recent decades in the field of bioremediation with glycoconjugates. *In-situ* biofilm mediated bioremediation can be performed in several ways. In nature, certain contaminants are degraded, transferred, and immobilized under specific environmental conditions without any interference of human activity [123]. Naturally, the biodegradation process requires the availability of the microorganism in the form of biofilm at polluted site and requires a long period of time. The addition of extra nutrients such as carbon, hydrogen, nitrogen, phosphorous, and oxygen to increase the growth rate of the microbial population enhances the degradation rate of pollutants [123, 124].

Biofilm can be used for the treatment of nitrates in wastewater [125] and biodegradation of the organic matter present in nature [126]. This biodegradation effort can be accelerated by designing a barrier material according to the concentration of the contaminant and the composition of the contaminant (mixed contaminant). The biodegradation process can be stimulated by providing added nutrients, electron acceptors and donors, or by providing a biocatalyst [51], which results in the development of biofilm on the surface of the contaminant via the natively present microbial species. If the existence of a required microorganism is lacking at the site of a contaminant, then the contaminant can be placed at a site where biofilm already exists. Alternatively, biofilm can be useful for the remediation of the toxic chemicals. Ultimately, a less harmful product can be formed by microbial biotransformation in nature due to the production of glycoconjugates without engineering the microorganism [113, 127].

Generally, the *ex-situ* bioremediation process is performed in a bioreactor due to the unavailability of suitable microorganisms and the unfavorable conditions at a contaminated site. In bioreactors, biofilms are added as inert support and used for the biochemical conversion of pollutants by sorption, particularly heavy metals, hydrocarbons, industrial waste, and wastewater treatment [128–130]. Biofilm-based bioreactors have many advantages over conventional treatment methods. For example, a high concentration of pollutants can be treated for a longer period of time, the volumetric capacity of biodegradation is enhanced, and the tolerance for highly toxic xenobiotics is increased, thereby supporting anaerobic and aerobic metabolism together and reducing environmental interference. Industrial biofilm reactors are generally set up under special conditions, such as when freely floating microorganisms are unable to produce adequate biomass or the microbial biomass cannot be retained for a long enough time to convert the toxic pollutants to environmentally acceptable forms [130] (Fig. 4).

Bacterial and fungal biofilm is a special type of biofilm where the bacterial cell is attached to fungal hyphae. Fungal hyphae provide nutrients, increase the bioavailability to the bacterial cell, and enhance the rate of consumption of nutrients via competition. This enables the bacteria to search for nutrient by travelling through the fungal hyphae. Phenanthrene, a polyaromatic hydrocarbon of fused benzene rings, is associated with soil contamination. This compound is degraded by *Pseudomonas putida*

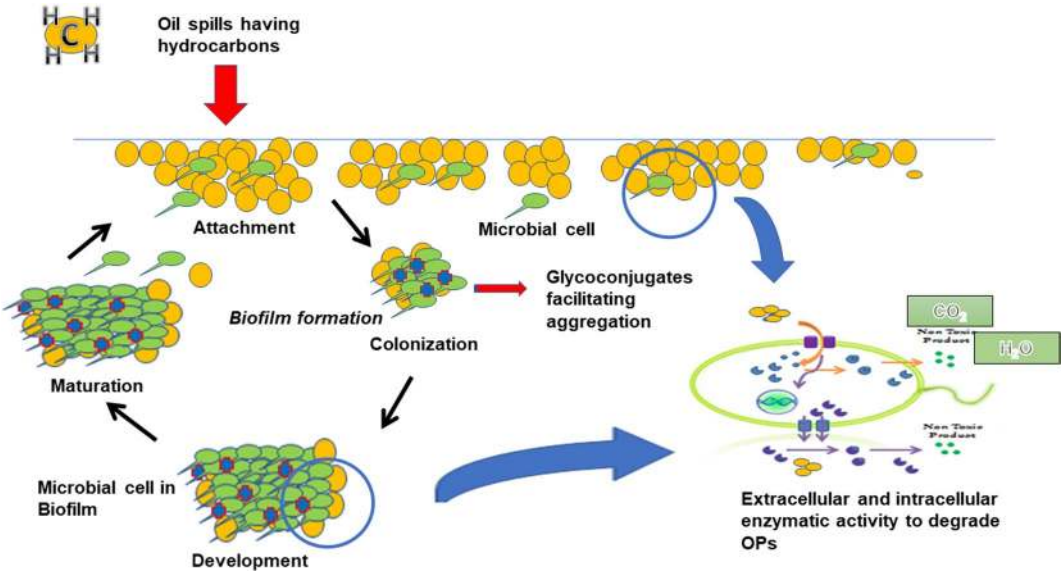

Fig. 4 Mechanism of oil spill hydrocarbon degradation using microbial glycoconjugates

PpG7 in the presence of *Pythium ultimum* fungal mycelia [131]. The previous researcher confirmed the importance of microbial glycoconjugates in biofilm formation and degradation of the OPs.

Glycoconjugates in pesticide degradation

Pesticides are organic compounds used in an enormous quantity in agriculture and homes to control a broad spectrum of pests [132, 133]. Most pesticides are hydrophobic with complex structures. Due to the large amounts of pesticides entering into soil and water systems, these molecules become attached to soil particles and are not available for microbial activities [134–139]. The attachment of pesticides to soil particles is dependent on the physical and chemical properties of the soil and pesticides [140]. Presently, various categories of pesticides are being sold in the market, such as organophosphates, organochlorines, and pyrethroids. The biodegradation of these pesticides is an intricate process due to their low water solubility and poor bioavailability. Microbial glycoconjugates play an important role in the desorption of pesticide molecules from soil particles. These glycoconjugate biosurfactant molecules decrease surface tension and enhance the degradation via microbial metabolism [33, 141]. Such types of microbial glycoconjugates are surface-active amphipathic emulsifying molecules that have the capacity to enhance the partitioning of hydrophobic pesticides to the aqueous phase by producing emulsions at and above their critical micellar concentration (CMC) (Fig. 5). This enhances the bioavailability of pesticides to their potential degraders and can thus play a crucial role in overcoming the above problems [142].

Microorganisms in the soil produce several types of glycoconjugates that induce emulsification of the contaminant and increase water solubility. The water solubility of pesticides is linked to their bioavailable fractions. The bioavailable fraction is used by microbial cells during metabolic activity [143, 144]. The glycoconjugate enhances pesticide degradation by reducing surface tension, modifying hydrophobicity, and enhancing bioavailability [145]. The glycoconjugates are reported to increase the solubility of the pesticides in soil and promote their degradation [146]. Due to the beneficial properties of the glycoconjugate, they are acceptable for use in contaminated sites [147]. Rhamnolipids, fructose lipids, sophorolipids, and glycolipopeptides are commonly investigated for pesticide bioremediation. In the last decade glycoconjugates, have emerged as a facilitator of pesticide degradation under various conditions [46, 148, 149]. We outline the major findings of glycoconjugates in the bioremediation of pesticides in Table 3.

The addition of a glycoconjugate, an increased (30 %) biodegradation of endosulfan isomers by *B. subtilis* MTCC 1427 in both soil and liquids was reported in a previous study [23]. The enhanced mobilization and bioavailability of endosulfan isomers in the presence of the glycoconjugate was also reported and may be attributed to the enhanced solubilization of pesticides or the increased affinity towards microbial cells. The soil spiked with endosulfan showed enhanced degradation after 7 days of the experiment due to the production of rhamnolipids by *P. aeruginosa* [49]. A crude extract of a glycoconjugate (an anionic glycolipid) was produced by the *Pseudomonas* sp. B0406 strain and aided in the solubilization of endosulfan [154]. The *Lysinibacillus sphaericus* strain IITR51 was investigated as a way to produce a thermostable rhamnolipid glycoconjugate with the ability to enhance the solubility of the highly hydrophobic pesticide hexachlorocyclohexane (HCH) and endosulfan [155]. Bioaugmentation with the glycoconjugate-producing bacteria also proved to be an efficient technique for the remediation of pesticides. The α and β isomers of the endosulfan degraded by up to 82 % in the presence of glycocnjugates having biosurfactant properties [151, 152].

The bioavailable fractions of the lindane are poor in the environment, which hinders degradation via microbial actions. Lindane contains six chlorine atoms, which make it more persistent. The *Pseudomonas* Ptm^{+} strain was found to be a potent culture for the degradation of lindane in the environment along with the production of glycoconjugate. The production of the glycoconjugate was monitored in a minimal salt medium during lindane degradation. The produced glycoconjugate emulsified the organochlorine lindane to a greater extent than the other OPs [160]. A 95 % biodegradation rate was reported for lindane isomers by *Sphingomonas* sp. NM05 after the addition of rhamnolipids produced by *Pseudomonas aeruginosa* [156]. The impact of biosurfactants such as rhamnolipid, sophorolipid, and trehalose-containing lipid on the solubilization and biodegradation of HCH, and their isomers in soil were also studied [156]. It was observed that sophorolipids promote a higher degradation of HCH. The increased biodegradation of lindane (700 mg/L) by *Pseudozyma* VITJzN01 was demonstrated by a 3–9-fold increase in the solubilization of lindane isomers and was investigated with the addition of mannosylerythritol lipid bio-microemulsion [158]. Increased solubilization of lindane from 5 to 28 mg L^{-1} was reported under an increasing concentration of rhamnolipids from 0 to 1000 mg L^{-1} [144]. The trehalolipid produced by the *Rhodococcus* sp. strain IITR03 was isolated and characterized from the pesticide-contaminated sites [55]. Similarly, the effect of the rhamnolipid produced by *Arthrobacter globiformis* was investigated in the bioremediation of

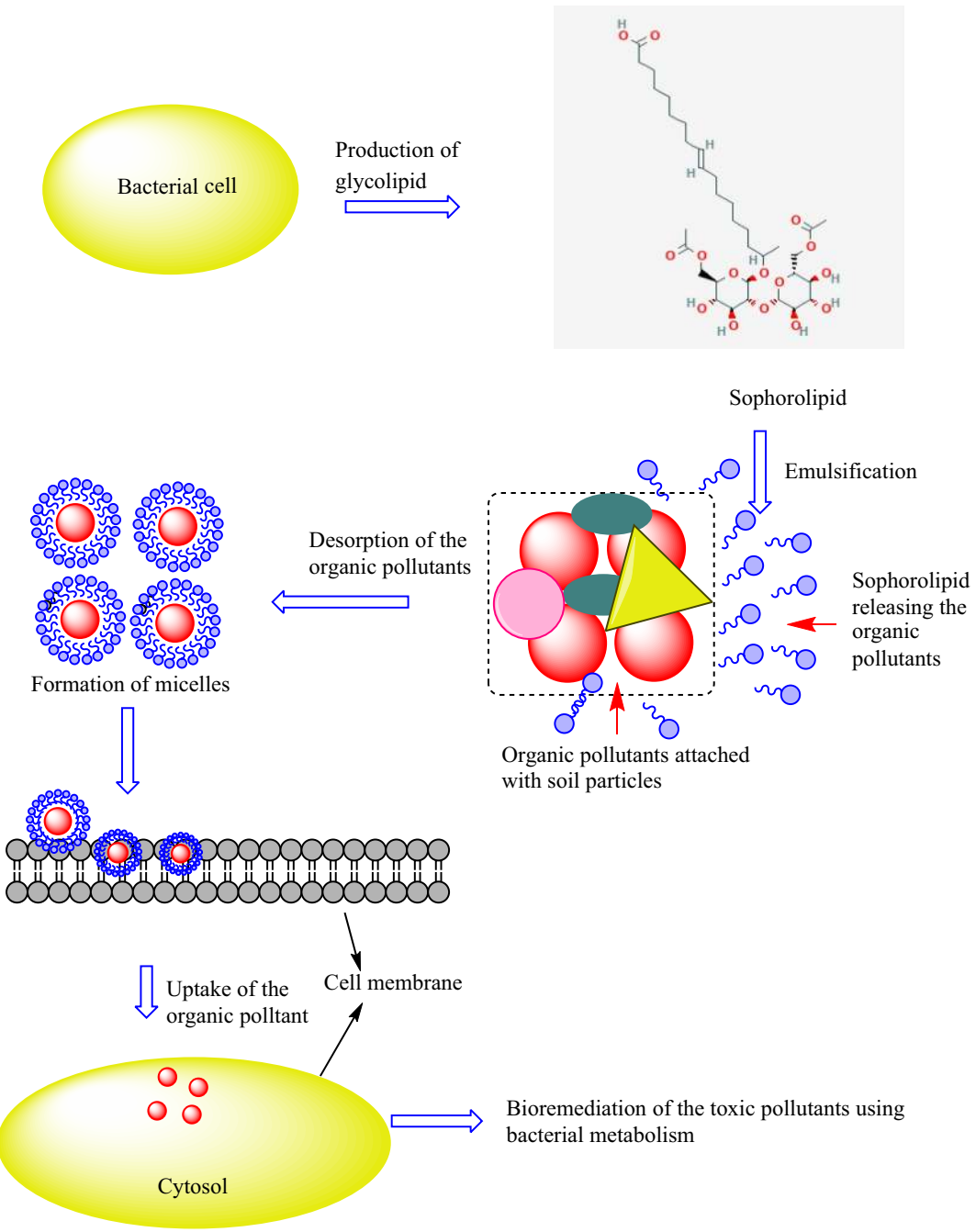

Fig. 5 Microbial glycoconjugates facilitate organic pollutant degradation via micelle formation

dichlorodiphenyl trichloroethane (DDT) [150]. Rhamnolipid enhanced the DDT degradation rate from 52 to 64%. *Pseudomonas* sp. SB was able to produce a biosurfactant that promotes DDT degradation in combination with plant-microbe interactions [152]. The synergistic effects of mixed cultures of the white-rot fungus, *Pleurotus ostreatus*, and the biosurfactant-producing bacteria *Pseudomonas aeruginosa* and *Bacillus subtilis* on DDT biodegradation were investigated and found to enhance DDT degradation [151]. There are many ways to remediate contaminated soil with microbial treatments and other methods. Some of the most commonly applied methods include soil washing, vapor extraction, desorption, microbial consortium, and phytoremediation.

Table 3 Biosurfactant mediated bioremediation of soils contaminated with pesticides

Pesticides	Concentration of pesticide	Biosurfactant/biosurfactant producing microbes	Degradation (%)	References
Organochlorines				
Dichlorodiphenyl trichloroethane (DDT)	282 µM	Trehalolipid from *Rhodococcus* sp. IITR03	50–60	[55]
DDT	1.417 mg/L	*Pseudomonas* sp. SB + *Grass* sp.	65.6	[150]
DDT	0.0474 mg/L	Rhamnolipids from *Arthrobacter globiformis*	64.3	[150]
DDT	0.25 µM	White rot fungi + biosurfactant from *Pseudomonas aeruginosa* and *Bacillus subtilis*	≈86	[151]
α-Endosulfan	200 mg/L	*Bacillus subtilis* MTCC 1427	100	[21]
Endosulfan soil	320 mg/L	*Pseudomonas aeruginosa* + rhamnolipid	> 90	[149]
α- and *β*-endosulfan	50 mg/L	*Arthrobacter* sp. ES-47	76.3–81.8	[152]
α- and *β*-endosulfan	50 mg/L	*Bordetella petrii* I GV 34 & GV36	82–89	[153]
α-Endosulfan	1420–3400 mg/L	Consortium of *Bordetella petrii* I GV 34 and *Bordetella petrii* II GV 36	100	[153]
β-Endosulfan	1280–3100 mg/L	*Achromobacter xylosoxidans* GV 47	100	[153]
Endosulfan	0.92 mg/L	Glycolipid, from *Pseudomonas* sp. B0406	Increased solubility	[154]
Endosulfan and hexachlorocyclohexane (HCH)	50 mg/L (endosulfan), 100 mg/L (HCH)	Rhamnolipid from *Lysinibacillus sphaericus* IITR51	Increased solubility	[155]
HCH	40 mg/L	Rhamnolipid from *Pseudomonas aeruginosa* + *Sphingomonas* sp. NM05	95	[156]
HCH	65 mg/L	*Cytisus striatus* plantation + *Rhodococcus erythropolis* ET54b	33	[157]
HCH	700 mg/L	*Pseudozyma* VITJzN01	3-9-fold increase in solubilization	[158]
HCH	–	Rhamnolipids	Increase solubility	[159]
Organophosphates				
Methyl Parathion	–	Glycolipid from *Pseudomonas* sp. B0406	Increased solubility	[154]
Chlorpyrifos	10 mg/L	*Pseudomonas* sp. ChlD + biosurfactant	> 98	[20, 143]
Methyl parathion and ethyl parathion	500 mg/L	Glycolipid from *Burkholderia cenocepacia* BSP3	Increased solubility	[18]
Quinalphos	10,000 mg/L	Biosurfactant from *Pseudomonas aeruginosa*	94	[159]

Sodium dodecyl sulfate (SDS) and ethylene diamine tetra acetic acid (EDTA) were used to wash the soil with conventional methods. The combination of microbially produced citric acid and rhamnolipids is effective for the remediation of organochlorine pesticides from the soil [144]. Such microbial combinations are environmentally friendly and cost-effective and can help achieve environmental sustainability [160, 161].

The formation of stable emulsions was investigated using glycoconjugate produced by *Bacillus* strains and fenthion [26]. An anionic glycolipid produced by the *Pseudomonas* sp. B0406 strain was reported to aid in the solubilization of methyl parathion [154]. The complete degradation of chlorpyrifos (10 mg/L) was reported within 2 days of using *Pseudomonas* sp. supplemented with a glycoconjugate [21]. A > 10 times increase in the aqueous-phase solubility of chlorpyrifos was reported with the addition of a biosurfactant produced by *Pseudomonas* sp. [143]. The glycolipid from *Burkholderia cenocepacia* BSP3 isolated from oil-contaminated soil was proposed to possess the ability to bioremediate the pesticides methyl parathion and ethyl parathion [18]. It was observed that *Pseudomonas aeruginosa* produces a glycoconjugate that enhances the solubilization of quinalphos [159].

The glycoconjugate from *Pseudomonas cepacia* aided in degrading the hydrophobic herbicide 2,4,5-trichlorophenoxyaceticacid [162]. Similarly, a higher biodegradation of carbendazim was reported by adding rhamnolipid to *Rhodococcus* sp. D-1 [54]. Approximately 24–35 % biodegradation of trifluralin in the soil was reported after the addition of rhamnolipid [163]. The surfactin lipopeptide was produced by marine *Bacillus velezensis* MHNK1 under atrazine biodegradation. The complete degradation of atrazine was observed within 4 days after employing a combination

of *B. velezensis* MHNK1 (2 %) and surfactin (2 CMC) [164].

Glycoconjugates in wastewater treatment

Microbial glycoconjugates have emerged as a tool to clean wastewater contaminated with organic pollutants. Various microbial approaches are used for the bioremediation of wastewater, but glycoconjugates are gaining more attention. The activated sludge process is popular for wastewater treatment. This process is based on the aerobic digestion of the microbial strains that produce flocs (floc-forming microbes) [165]. These flocs are formed by the network of extracellular polymeric substances (EPSs) produced by microbes [166]. Bacterial strains have been reported for glycoconjugate production which consists of carbohydrates, proteins, humic substances, uronic acids, lipid compounds, and nucleic acids. Enzymes play an important role in the hydrolysis of sludge [167]. These enzymes help to release EPSs and identify polysaccharides and glycoconjugates together with a lectin panel [165, 168].

Effective glycoconjugates can reduce the surface tension of water from 72 to 25 mN/m and the interfacial tension between polar and non-polar liquids for water against n-hexadecane from 40 to 1 mN/m [169, 170]. Thus, glycoconjugates can also be used for the treatment of wastewater [171]. In a previous report, the enhanced removal of hydrocarbons was described using rhamnolipids, which was mainly attributed to improved solubility and reduced interfacial tension [172]. Microbial rhamnolipids are also described as efficient candidates for the pretreatment of waste activated sludge and contribute to the process of wastewater treatment [173]. *Rhodococcus* sp. PML026, a marine bacterial strain, was utilized for the production of glycoconjugate characterized as trehalolipids, exerted biosurfactant activity under diverse experimental conditions, and was proven to be an efficient candidate for wastewater treatment and other bioremediation purposes [174]. The various bacterial isolates for glycoconjugates were investigated by their biosurfactant producing abilities. These isolates have the potential to reduce the surface tension in the liquid medium from 71.1 mN/m to 32.1 mN/m. The isolates were mainly belonging to the Aeromonadaceae, Bacillaceae, Enterobacteriaceae, Gordoniaceae, and Pseudomonadaceae families [175]. The wastewater bacterial strains showed antibiotic resistance and biofilm formation due to the production of biosurfactants. Low surface tension values of 28 and 36 mN/m were observed in the bacteria, which were not able to form a biofilm. This study showed that low surface tension can produce a weak biofilm, which can be correlated to the glycoconjugate playing a role in effective biofilm formation at polluted sites [122, 176]. Hollow membranous fibers also developed. These fibers supply the dissolved hydrogen to microbial population that stimulate the biodegradation of the chlorinated solvent present in groundwater [123]. Sophorolipids are another glycoconjugate biosurfactant utilized in oil spill management and the oil biodegradation of contaminated water [124]. Thus, microbial glycoconjugates are utilized in diverse forms for the treatment of wastewater, and the results obtained justify their candidacy for this purpose [97, 177, 178].

Conclusions and future prospects

Microbial glycoconjugates are important for bioremediation purposes, and several investigations have confirmed the degradation-specific role of glycoconjugates. The glycoconjugates can be used for the broad bioremediation of pesticides, hydrocarbons, antibiotics, and several xenobiotics. Microbial glycoconjugates play a key role in the adhesion of cells in biofilms that increase the degradation efficiency for OPs. Thus, recent advances in the field of MG have added to the potential of glycoconjugates in different applications along with the management of OPs, which are an environmental nuisance due to their intense utilization in different anthropogenic activities. MG bears many unexplored horizons to be revealed and utilized in the development of efficient bioremediation procedures. Recent high-throughput omics-based techniques could be applied to explore the molecular basis of the glycoconjugate-based bioremediation of OPs.

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Authors' contributions

PB collected all the relevant publications, arranged the general structure of the review, drafted the text and produced figures. AV, SG and GB revised the review. SC revised and formatted the manuscript. All authors read and approved the final manuscript.

Availability of data and materials

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Declarations

Ethics approval and consent to participate

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Consent for publication

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Competing interests

The authors declare that they have no competing interests.

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