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Biosurfactants: Structure, Function and Their Properties

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ABSTRACT:
Biosurfactants are microbial derived amphiphilic surface active molecules having immense industrial applications. These are produced on living surfaces, mostly on microbial cell surfaces or sometimes excreted extracellularly. The amphiphatic nature of biosurfactants confer them the ability to accumulate between fluid phases reducing surface and interfacial tensions. Most biosurfactants are either anionic or neutral and the hydrophilic moiety can be a carbohydrate, an amino acid, a phosphate group, or some other compounds and the hydrophobic moiety is a fatty acid chain.
This article describes the biosurfactant molecule in detail. Composition and characteristics of biosurfactants, their producers, classification and physiology of biosurfactant production are illustrated completely in this article. Advantages and disadvantages of using biosurfactants are also incorporated in the article. It also deals with genetic regulation of biosurfactant production giving emphasis on the production of rhamnolipid biosurfactant.

INTRODUCTION:

Biosurfactants: Definition, composition and characteristics
Biosurfactants are diverse groups of surface active molecules/chemical compounds synthesized by microorganisms (Desai and Banat 1997). These amphiphilic compounds are produced on living surfaces, mostly on microbial cell surfaces, or excreted extracellularly. These are amphipathic molecules having both hydrophilic and hydrophobic domains that confer the ability to accumulate between fluid phases. This in turn reduces surface and interfacial tensions at the surface and interface respectively (Karanth et al. 1999). This property of biosurfactant makes them potential candidates for enhancing oil recovery (Sarkar et al. 1989). Most biosurfactants are either anionic or neutral and the hydrophilic moiety can be a carbohydrate, an amino acid, a phosphate group, or some other compounds. The hydrophobic moiety is mostly a long carbon chain fatty acid. Because of surface active property of biosurfactants, micro emulsions are created where hydrocarbons can solubilize in water or water in hydrocarbons (Banat 1995). Biosurfactants enhance the emulsification of hydrocarbons, have the potential to solubilize hydrocarbon contaminants and increase their availability for microbial degradation. The use of chemicals for the treatment of a hydrocarbon polluted site may contaminate the environment with their by-products, whereas biological treatment may efficiently destroy pollutants, while being biodegradable themselves.

PRODUCERS OF BIOSURFACTANTS:

Quite a lot of microorganisms have been reported to produce several classes of biosurfactants such as glycolipids, lipopeptides, phospholipids, neutral lipids or fatty acids and polymeric biosurfactants

(Cooper 1986; Kosaric 1993). These compounds are produced during the growth of microorganisms on water soluble and water insoluble substrates (Sheppard and Mulligan 1987; Desai et al. 1988; Ron and Rosenberg 2001). Microorganisms utilize a variety of organic compounds as the source of carbon and energy for their growth. When the carbon source is an insoluble substrate like a hydrocarbon (C_nH_n), microorganisms facilitate their diffusion into the cell by producing a variety of biosurfactants. Some

bacteria and yeasts excrete ionic surfactants which emulsify the C_nH_n substrates in the growth medium. Some examples of this group of biosurfactants are rhamnolipids which are produced by different *Pseudomonas* sp. (Guerra-Santos et al. 1984; Guerra-Santos et al. 1986), or the sophorolipids which are produced by several *Torulopsis* sp. (Cooper and Paddock 1983). Some other microorganisms are capable of changing the structure of their cell wall, which they achieve by synthesizing lipopolysaccharides or nonionic surfactants in their cell wall. Examples of this group are: *Candida lipolytica* and *Candida tropicalis* which produce cell wall-bound lipopolysaccharides when growing on *n*-alkanes (Osumi et al. 1975) and *Rhodococcus erythropolis*, many *Mycobacterium* sp. and *Arthrobacter* sp. which synthesize nonionic trehalose corynomycolates (Kretschmer et al. 1982; Ristau and Wagner 1983). There are lipopolysaccharides, such as emulsan, synthesized by *Acinetobacter* sp. (Rubinowitz et al. 1982) and lipoproteins or lipopeptides, such as surfactin and subtilisin, produced by *Bacillus subtilis* (Cooper et al. 1981). Other effective biosurfactants are mycolates and corynomycolates which are produced by *Rhodococcus* sp., *Corynebacteria* sp., *Mycobacteria* sp. and *Nocardia* sp. (MacDonald et al. 1981; Kretshmer et al. 1982) and ornithinlipids, which are produced by *Pseudomonas rubescens*, *Gluconobacter cerinus*, and *Thiobacillus ferroxidans* (Knoche and Shively 1972; Tahara et al. 1976). Till now, the most commonly isolated and the best studied groups of biosurfactants are mainly glycolipids and phospholipids in nature.

CLASSIFICATION AND CHEMICAL NATURE OF BIOSURFACTANTS:

Chemically synthesized surfactants are usually classified according to the nature of their polar groups but biosurfactants are generally categorized mainly by their chemical composition. The hydrophilic moiety may consist of amino acids, peptides, mono-, di- or polysaccharides. The hydrophobic moiety may consist of saturated or unsaturated fatty acids (Desai and Banat 1997). Rosenberg et al. (1999) suggested that biosurfactants can be divided into low-molecular-mass molecules, which efficiently lower surface and interfacial tension, and high molecular-mass polymers, which are more effective as emulsifiers. The major classes of low mass surfactants include glycolipids, lipopeptides and phospholipids, whereas high mass surfactants include polymeric and particulate surfactants like polyanionic heteropolysaccharides containing both polysaccharides and proteins. The yield of microbial surfactants varies with the nutritional environment of the growing microorganism. The most important groups of biosurfactants and some of their classes are described below.

Glycolipids

Glycolipds are the most known biosurfactants. They are conjugates of carbohydrates and fatty acids. The linkage is by means of either ether or an ester group. Among the glycolipids, the best known are rhamnolipids, trehalolipids and sophorolipids (Muthusamy et al. 2008).

RHAMNOLIPIDS:

Rhamnolipids are the best studied glycolipids in which one or two molecules of rhamnose are linked to one or two molecules of β-hydroxydecanoic acid. While the -OH group of one of the acids is involved in glycosidic linkage with the reducing end of the rhamnose disaccharide, the -OH group of the second acid is involved in ester formation (Karanth et al. 1999). Jarvis and Johnson (1949) first described production of rhamnose containing glycolipids in *Pseudomonas aeruginosa*. Because of their excellent surface activity, the physicochemical properties of RLs have received considerable interest (Abdel-Mawgoud et al. 2009; Hansen et al. 2008; Pornsunthorntawee et al. 2009). L-Rhamnosyl-L-rhamnosyl-β-hydroxydecanoyl–β-hydroxydecanoate and L-rhamnosyl-β-hydroxydecanoyl-β-hydroxy- decanoate, referred to as di- and mono-rhamnolipids respectively. They are the principal glycolipids produced by *Pseudomonas aeruginosa* (Edward and Hayashi 1965).

TREHALOLIPIDS:

Several structural types of microbial trehalolipid biosurfactants have been reported. These trehalose lipids are mainly produced by rhodococci have interesting physicochemical and biological properties (Lang et al. 1998). Disaccharide trehalose linked at C-6 and C-6′ to mycolic acid is associated with most species of *Mycobacterium*, *Nocardia* and *Corynebacterium*. Mycolic acids are long chain, α-branched-β-hydroxy

fatty acids. Trehalolipids from different organisms differ in the size and structure of mycolic acid, the number of carbon atoms and the degree of unsaturation (Asselineau and Asselineau 1978). A number of possible applications have been proposed for these compounds. In addition, succinoyl trehalose lipids have been found to induce differentiation of leukemia cell lines (Sudo et al. 2000) and to inhibit protein kinase activity (Isoda et al. 1997).

SOPHOROLIPIDS:

These glycolipids are mainly produced by yeast such as *Torulopsis bombicola* (Cooper and Paddock 1984; Hommel et al. 1987*), Torulopsis petrophilum* and *Torulopsis apicola.* They consist of a dimeric carbohydrate sophorose linked to a long-chain hydroxyl fatty acid by glycosidic linkage. Generally, sophorolipids occur as a mixture of macrolactones and free acid form. It has been shown that the lactone form of the sophorolipid is necessary, or at least preferable, for many applications (Hu and Ju 2001).

Lipopeptides and lipoproteins

A large number of cyclic lipopetides, including decapeptide antibiotics (gramicidins) and lipopeptide antibiotics (polymyxins) are produced. These consist of a lipid attached to a polypeptide chain. Two of them are described below-

SURFACTIN:

Surfactin is an important biosurfactant with superior surface activity and belongs to a group of cyclic lipoheptapeptides containing beta-hydroxyl fatty acids and D−/L- amino acid residues (Haddad et al. 2008; Tang et al. 2007). The cyclic lipopeptide surfactin is produced by *Bacillus* sp. It is composed of a seven amino-acid ring structure coupled to a fatty-acid chain via lactone linkage (Arima et al. 1968).

LICHENYSIN:

Bacillus licheniformis produces several biosurfacants which act synergistically and exhibit excellent temperature, pH and salt stability. These are also similar in structural and physio-chemical properties to the surfactin (McInerney et al. 1990). The surfactants produced by *Bacillus licheniformis* are capable of lowering the surface tension of water to 27mN/m and the interfacial tension between water and *n*-hexadecane to 0.36 mN/m.

FATTY ACIDS, PHOSPHOLIPIDS, AND NEUTRAL LIPIDS:

Several bacteria and yeast produce large quantities of fatty acids and phospholipid surfactants during growth on *n*-alkanes (Cirigliano and Carman 1985). The hydrophilic and lipophilic balance (HLB) is directly related to the length of the hydrocarbon chain in their structures. In *Acinetobacter* sp. strain HO1-N, phosphatidylethanolamine rich vesicles are produced (Kappeli and Finnerty 1979), which form optically clear micro emulsions of alkanes in water. Phosphatidylethanolamine produced by *Rhodococcus erythropolis* grown on *n*-alkane causes a lowering of interfacial tension between water and hexadecane to less than 1mN/m and a critical micelle concentration (CMC) of 30 mg/l (Kretschmer et al. 1982).

CORYNOMYCOLIC ACID:

Corynomycolic acids, (R^1-CH (OH)-CH (R^2)-COOH) are a group of surface active compounds with varying number of carbon atoms. Substrate in the growth media influencs a lot in synthesizing biosurfactans with varying chain length. A mixture of corynomycolic acids with excellent surfactant properties has been isolated from *Corynebacterium lepus*. It caused significant lowering of surface tension in aqueous solution and the interfacial tension between water and hexadecane at all values of pH between 2 and 10 (Cooper et al. 1981).

POLYMERIC BIOSURFACTANTS:

Polymeric biosurfactants are high molecular weight biosurfactants. Most polymeric biosurfactants has a backbone of three or four repeating sugars with fatty acids attached to the sugars (Rosenberg and Ron 1997). The best studied polymeric biosurfactants are emulsan, liposan, alasan, lipomanan and other polysaccharide-protein complexes. Liposan is an extracellular water soluble emulsifier synthesized by

Candida lipolytica and is composed of 83% carbohydrate and 17% protein (Cirigliano and Carman 1984).

EMULSAN:
Emulsan is a complex extracellular acylated polysacharide synthesized by the gram-negative bacterium *Acinetobacter calcoaceticus* with an average molecular weight of about 1000 KD (Kim et al. 1997) and has been extensively researched for its industrial applications as an emulsifier (Gorkovenko et al. 1999). This molecule is composed of an unbranched polysaccharide backbone with O-acyl and N-acyl bound fatty acid side chains. The polysaccharide backbone consists of three aminosugers, D-galactosamine, D-galactosaminouronic acid and a dideoxydiaminohexose in the ratio of 1:1:1 (Panilaitis et al. 2002). The fatty acid side chains range in length from 10 to 22 carbon atoms with the amino groups either acetylated or covalently linked by an amide group bound to 3-hydroxybutyric acid and can represent from 5 to 23% (w /w) of the polymer. It is is an effective emulsifying agent for hydrocarbons in water (Zosim et al. 1982), even at a concentration as low as 0.001 to 0.01%.

PARTICULATE BIOSURFACTANTS:
Particulate biosurfactants are of two types, extracellular vesicles and whole microbial cell. Extracellular membrane vesicles partition hydrocarbons to form micro-emulsions, which play an important role in hydrocarbon uptake by microbial cells. Sometimes the whole bacterial cell itself can work as surfactant.

VESICLES:
Acinetobacter sp. when grown on hexadecane accumulated extracellular vesicles of 20 to 50 mm diameter with a buoyant density of 1.158 g/cm^3. These vesicles appear to play a role in the uptake of alkanes by *Acinetobacter* sp. HO1-N. These vesicles with a diameter of 20-50 nm and a buoyant density of 1.158 cubic g/cm are composed of protein, phospholipids and lipopolysaccharide (Kappeli and Finnerty 1979). Like *Acinetobacter* sp., *Pseudomonas marginalis* also form vesicles to work as surfactants

WHOLE MICROBIAL CELLS:
Most hydrocarbon-degrading microorganisms, many nonhydrocarbon degraders, some species of *Cyanobacteria*, and some pathogens have a strong affinity for hydrocarbon-water and air-water interfaces. In such cases, the microbial cell itself is a surfactant (Karanth et al. 1999).

PHYSIOLOGY OF BIOSURFACTANT PRODUCTION
The common view attributes only one role for microbial surfactants, i.e., the growth of microorganisms on hydrocarbons. Most publications in this field discuss biosurfactants with respect to the growth of bacteria on water insoluble carbon sources. The models for uptake of hydrocarbons consider the roles of dissolved molecules, contact of the cells with large oil droplets, or contact with fine oil droplets (Hommel 1990). In addition to the role of bacterial surfactants for growth on hydrocarbons as a carbon source, some other functions are mentioned in two review articles.
Rosenberg (1986) suggested that the diversity of structures and functions is a general property of microbial surfactants and clearly stated that ‘‘It is unlikely that they all serve the same function.’’ He discussed adhesion of biosurfactants to hydrocarbons as a special case, a function in the emulsification of water-insoluble compounds as substrates, and a function in de-adhesion from interfaces. Furthermore, he mentioned a role in gliding and cell-cell interaction. Haferburg et al. (1986) also made clear that the exact physiological functions of most microbial surfactants remain unclear. They discussed microbial
Surfactants mainly in terms of hydrocarbon assimilation and biocide activity. The biocidal activity of microbial surfactants is closely related to the lipid moiety of the molecules. However, they also suggested a possible role in gliding of bacteria and in wetting of interfaces. In addition, biosurfactants have been shown to be involved in cell adherence which imparts greater stability under hostile environmental conditions and virulence (Rosenberg and Rosenberg 1981), in cell desorption to find new habitats for

survival (Rosenberg and Rosenberg 1981), in antagonistic effects toward other microbes in the environment (Lang et al. 1989; Kitamoto et al. 1993) etc.

BIOSYNTHESIS AND GENETIC REGULATION OF BIOSURFACTANT PRODUCTION:

Biosurfactants display a range of different amphiphilic structures. Biosurfactants are made up of hydrophobic and hydrophilic moieties. For synthesis of these two moieties two different synthetic pathways must be used: one leading to the hydrophobic and one to the hydrophilic moiety. The hydrophobic fatty acid components- which may be a long chain fatty acid, a hydroxyl fatty acid or alpha-alkyl-beta-hydroxy fatty acid are synthesized by rather common pathway of lipid metabolism. The hydrophilic moieties however exhibit a greater degree of structural complexity. This explains the wide variety of biosynthetic pathways involved in their synthesis (Muller 2011).

Among all the biosurfactants reported till date, the molecular biosynthetic regulation of rhamnolipid, a glycolipid type biosurfactant produced by *Pseudomonas aeruginosa* and a lipopeptide biosurfactant called surfactin produced by *Bacillus subtilis* were the first to be deciphered. Other biosurfactants whose molecular genetics have been delineated in the recent years include arthrofactin from *Pseudomonas* sp., iturin and lichenysin from *Bacillus* species, mannosylerythritol lipids (MEL) from *Candida* and emulsan from *Acinetobacter* species (Das et al. 2008).

A putative rhamnolipid biosynthesis pathway is summarized in Fig. 1. (Rahim et al. 2001; Soberón-Chávez et al. 2005; Winsor et al. 2009; Müller 2011). The biosynthetic pathway can be divided into three major steps; synthesis of the hydrophilic part, synthesis of the hydrophobic part and synthesis of rhamnolipid from these two parts. The precursors, dTDP-L-rhamnose and activated 3-(3-hydroxyalkanoyloxy) alkanoate (HAA) respectively for hydrophilic and hydrophobic parts are synthesized de novo (Burger et al. 1963). Altogether the biosynthesis can be separated into three major parts. Finally, the rhamnolipid is produced by the reaction of two special rhamnosyltransferases catalyzing the sequential rhamnosyl transfer reactions from the precursors over mono- toward di-rhamnolipids.

In *Pseudomonas aeruginosa*, several genes have been found to be involved in rhamnolipid biosynthesis. Ochsner et al. (1994a) discovered a 2-kb fragment capable of restoring rhamnolipid biosynthesis while tested in a rhamnolipid deficient mutant strain of *Pseudomonas aeruginosa*. The 2-kb fragment contains a single open reading frame (rhlR) of 723 bp specifying a putative 28- kDa protein (RhlR). Disruption of the *Pseudomonas aeruginosa* wild-type rhlR locus led to rhamnolipid-deficiency, thus confirming directly that this gene is necessary for rhamnolipid biosynthesis. The rhlAB genes encode a rhamnosyltransferase, RhlAB, which catalyzes the transfer of rhamnose from TDP-rhamnose to β- hydroxydecanoyl-β-hydroxydecanoate (Ochsner et al. 1994b). The transcriptional activation of rhlAB appears to depend on a functional RhlR regulatory protein. The sequence upstream of the rhlA promoter contains two inverted repeats that define putative binding sites for the RhlR regulator. Another gene, rhlI, which is also required for rhamnolipid synthesis, has been identified downstream of the rhlABR gene culster. The rhlI gene production, RhlI, has been proved to be a bacterial autoinducer (usually belongs to homoserine lactone family) synthase. The *Pseudomonas aeruginosa* rhlA promoter is actived only when both the rhlR and rhlI genes are present or when the rhlR gene alone is supplied together with synthetic autoinducers (Ochsner and Reiser 1995). The RhlR-RhlI regulatory mechanism is known as quorum sensing (QC). QC describes population density dependent cell to cell communication in bacteria using diffusible signal molecules. These signal molecules produced by bacterial cells, regulate various physiological processes important for social behavior and pathogenesis like synthesis of rhamnolipid in *Pseudomonas aeruginosa* (Dusane et al. 2010).

ENVIRONMENTAL FACTORS INFLUENCE THE SYNTHESIS OF BIOSURFACTANT:

Synthesis of biosurfactant like any other chemical reaction is influenced by a number of environmental factors that either increase its productivity or inhibit it (Rahman and Gakpe 2008). Literature shows that different environmental factors are required for synthesis of biosurfactant by different microbial sp. same conditions are not suitable for all the microbes. For example, some bacteria synthesize maximum biosurfactant in n-hexadecane whereas some others can not tolerate n-hexadecane. Environmental factors

such as pH, temperature, salinity, agitation and oxygen supply affect biosurfactant production (Raza et al. 2007). The type, quality and quantity of biosurfactant produced are influenced by the nature of the carbon substrate (Lang et al. 1984), the concentration of N, P, Mg, Fe, and Mn ions in the medium, and the culture conditions (Kretschmer et al. 1982). However, it was reported that biosurfactant production from *Pseudomonas* strains MEOR 171 and MEOR 172 are not affected by temperature, pH, and Ca, Mg, concentration in the ranges found in many oil reservoirs (Karanth et al. 1999). Interestingly, Sabra et al. (2002) recently proposed that *P. aeruginosa* is producing rhamnolipids to reduce oxygen transfer rate as a means to protect itself from oxidative stress, and it appears that this mechanism is activated by iron deficiency (Kim et al. 2003). However, excellent rhamnolipid production is also obtained in the absence of oxygen (Chayabutra et al. 2001). The nitrogen source can be an important key to the regulation of biosurfactant synthesis. The nitrogen source can be an important key to the regulation of biosurfactants synthesis. *Arthobacter paraffineus* ATCC 19558 preferred ammonium to nitrate as inorganic nitrogen source for biosurfactants production. A change in growth rate of the concerned microorganisms is often sufficient to result in over production of biosurfactants (Kretschmer et al. 1982). A change in growth rate of the concerned microorganisms is often sufficient to result in over production of biosurfactant. Salt concentrations also affect biosurfactant production depending on its effect on cellular activity. Production of biosurfactant by a few microbes however was not affected by salt concentrations up to 10% (w/v), although slight reductions in the CMCs were detected (Abu-Ruwaida et al. 1991). Raza et al. (2007) reported that biosurfactant production is fully affected and influenced by the nature of the carbon substrate. Diesel and crude oil were identified to be good sources of carbon for biosurfactant production by many organisms (Hori et al. 2005). *Torulopsis petrophilum* did not produce any glycolipids when grown on a single-phase medium that contained water-soluble carbon source (Cooper et al. 1983). However, there have been examples of the use of a water-soluble substrate for biosurfactant production by microorganisms (Mata-sandoval et al. 2001).

ADVANTAGES OF BIOSURFACTANTS:

When compared to synthetic surfactants, biosurfactants have several advantages including high biodegradability, low toxicity, low irritancy and compatibility with human skin (Cameotra and Makkar 2004).Therefore they are superior to the synthetic ones. Some of the advantages of biosurfactants are discussed below:

BIODEGRADABILITY:

Biosurfactants are biodegradable in nature. Biodegradability is a very important issue concerning environmental pollution. Being able to be broken down by natural processes by bacteria, fungi or other simple organisms into more basic components, they do not create much problem to the environment and particularly suited for environmental applications such as bioremediation (Mulligan et al. 2005) and dispersion of oil spills.

LOW TOXICITY:

Biosurfactants do not cause serious damage/harm of the biotic ecosystem since their toxicity level is low. Many chemical surfactants are toxic to the living beings making them less useful for being used in different industries. Very little data are available in the literature regarding the toxicity of microbial surfactants. They are generally considered as low or non-toxic products and therefore, appropriate for pharmaceutical, cosmetic and food uses. A report suggested that a synthetic anionic surfactant (Corexit) displayed an LC50 (concentration lethal to 50% of test species) against *Photobacterium phosphoreum* ten

times lower than rhamnolipids. This demonstrated higher toxicity of the chemically derived surfactant. When comparing the toxicity of six biosurfactants, four synthetic surfactants and two commercial dispersants, it was found that most biosurfactants degraded faster, except for a synthetic sucrose-stearate that showed structure homology to glycolipids and was degraded more rapidly than the biogenic glycolipids. It was also reported that biosurfactants showed higher EC50 (effective concentration to

decrease 50% of test population) values than synthetic dispersants (Poremba et al. 1991). A biosurfactant from *Pseudomonas aeruginosa* was compared with a synthetic surfactant (Marlon A-350) widely used in the industry, in terms of toxicity and mutagenic properties. Both assays indicated higher toxicity and mutagenic effect of the chemical-derived surfactant, whereas the biosurfactant was considered slightly non-toxic and nonmutagenic (Flasz et al. 1998).

Biocompatability and digestibility

Biosurfactants are biocompatible in nature (Rosenberg et al. 1999) which means they are well tolerated by living organisms. These when interact with living organisms do not change bioactivity of the organisms. This property allows their application in cosmetics, pharmaceuticals and as functional food additives.

AVAILABILITY OF RAW MATERIALS:

Biosurfactants can be produced from cheap raw materials like rapeseed oil, potato process effluents, oil refinery waste, cassava flour wastewater, curd whey and distillery waste, sunflower oil etc. (Muthusamy et al. 2008) which are available in large quantities. The carbon source may come from hydrocarbons, carbohydrates and/or lipids, which may be used separately or in combination with each other.

ACCEPTABLE PRODUCTION ECONOMICS:

Depending on the application, biosurfactants can also be produced from industrial wastes and by products. This is of particular interest for bulk production (e.g. for use in petroleum related technologies) of biosurfactant which is economically acceptable. In addition to that, a lot of biosurfactants

Use in environmental control

Biosurfactants can be efficiently used in handling industrial emulsions, control of oil spills, biodegradation and detoxification of industrial effluents and in bioremediation of contaminated soil.

Specificity

Biosurfactants, being complex organic molecules with specific functional groups, are often specific in their action. This would be of particular interest in detoxification of specific pollutants, de-emulsification of industrial emulsions, specific cosmetic, pharmaceutical and food applications.

DISADVANTAGES OF BIOSURFACTANTS:

Concerning disadvantages, one of the problems is related to large scale and cheap production of biosurfactants. Large quantities are particularly needed in petroleum and environmental applications, which, due to the bulk use, may be expensive. To overcome this problem, processes should be coupled to utilization of waste substrates combating at the same time their polluting effect, which balances the overall costs. Another problem may be encountered in obtaining pure substances which is of particular importance in pharmaceutical, food and cosmetic applications. Downstream processing is involved with multiple consecutive steps. Therefore, high yields and biosurfactant concentrations in bioreactors are essential for their facilitated recovery and purification.

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TABLE 1. MAJOR CLASSES OF BIOSURFACTANT, MICROORGANISMS INVOLVED IN PRODUCTION AND ECONOMIC IMPORTANCE

Biosurfactant		**Microorganism**	**Economic importance**	**References**
Group	**Class**			
Glycolipids	Rhamnolipids	*Pseudomonas aeruginosa*, *Pseudomonas* sp., *Burkholderia glumae*, *Burkholderia plantarii*, *Burkholderia thailandensis*	antimicrobial activity against *Mycobacterium tuberculosis*, anti-adhesive activity against several bacterial and yeast strains isolated from voice prostheses, enhancement of the degradation and dispersion of different	Hörmann et al. 2010

			classes of hydrocarbons; emulsification of hydrocarbons and vegetable oils; removal of metals from soil	
	Trehalose lipids	*Rhodococcus erythropolis, Nocardia erythropolis, Mycobacterium* sp., *Arthobacter* sp.	Enhancement of the bioavailability of hydrocarbons, antiviral activity against HSV and influenza virus	Franzetti et al. 2010
	Sophorolipids	*Torulopsis bombicola, Torulopsis apicola, Torulopsis petrophilum*	Recovery of hydrocarbons from dregs and muds; removal of heavy metals from sediments; enhancement of oil recovery,	Whang et al. 2008
	Mannosylerythritol lipid	*Candida antartica*	antimicrobial, immunological and neurological properties	Wakamatsu et al. 2001
	Cellobiolipids	*Ustilago zeae, Ustilago maydis*	–	Desai and Banat 1997
Lipopeptides and lipoproteins	Surfactin/ iturin/fengycin	*Bacillus subtilis, Bacillus licheniformis*	Enhancement of the biodegradation of hydrocarbons and chlorinated pesticides; removal of heavy metals from a contaminated soil, sediment and water; increasing the effectiveness of phytoextraction, antimicrobial and antifungal activities inhibition of fibrin clot formation haemolysis and formation of ion channels in lipid membranes antitumour activity against Ehrlich's ascite carcinoma cells antiviral activity against human immunodeficiency virus 1 (HIV-1), antimicrobial	Awashti et al. 1999;

			activity and antifungal activity against profound mycosis effect on the morphology and membrane structure of yeast cells increase in the electrical conductance of biomolecular lipid membranes non-toxic and non-pyrogenic immunological adjuvant	
	Viscosin	*Pseudomonas fluorescens*	Antimicrobial activity	Saini et al. 2008
	Lichenysin	*Bacillus licheniformis*	Enhancement of oil recovery, antibacterial activity chelating properties that might explain the membrane-disrupting effect of lipopeptides	Sen 2008
	Serrawettin	*Serratia marcescens*	Chemorepellent	Pradel et al. 2007
	Subtilism	*Bacillus subtilis*	Antimicrobial activity	Ghribi et al. 2012
	Gramicidin	*Brevibacterium brevis*	Antibiotic, disease control	Elad and Stewart 2007
	Polymixin	*Bacillus polymyxa*	Bactericidal and fungicidal activity	www.cyberlipid.org/simple/simp0005.htm
	Antibiotic TA	*Myxococcus xanthus*	Bactericidal activity, chemotherapeutic applications	Karanth et al. 1999;
Fatty acids/neutral lipids/ phospholipids	Corynomycolic acid	*Corynebacterium lepus*	Enhancement of bitumen recovery	Gerson et al.1978
	Spiculisporic acid	*Penicillium spiculisporum*	Removal of metal ions from aqueous solution; dispersion action for hydrophilic pigments; preparation of new emulsion-type organogels, superfine microcapsules (vesicles or liposomes), heavy metal sequestrants	Ishigami et al. 2000

	Phosphati-dylethanolamine	*Acinetobacter* sp., *Rhodococcus erythropolis Mycococcus* sp.	Increasing the tolerance of bacteria to heavy metals	Appanna et al. 1995
Polymeric surfactants	Emulsan	*Acinetobacter calcoaceticus*	Stabilization of the hydrocarbon-in water emulsions	Zosim et al. 1982
	Alasan	*Acinetobacter radioresistens*	Stabilization of the hydrocarbon-in water emulsions	Toren et al. 2001
	Biodispersan	*Acinetobacter calcoaceticus* A2	Dispersion of limestone in water	Rosenberg et al. 1988
	polysaccharide protein complex	*Acinebacter calcoaceticus*	Bioemulsifier	Kaplan et al. 1987
	Liposan	*Candida lipolytica*	Stabilization of hydrocarbon-in-water emulsions	Cirigliano and Carman 1985
	Mannoprotein	*Saccharomyces cerevisiae*		
	Protein PA	*Pseudomonas aeruginosa*	Bioemulsifier	Karanth et al. 1999
Particulate biosurfactants	Vesicles	*Acinetobacter calcoaceticus, Pseudomonas marginalis*	Degradation and removal of hydrocarbons	Karanth et al. 1999; Rosenberg et al. 1999
	Whole microbial cells	*Cyanobacteria*		

Figure legend

Fig. 1. Rhamnolipid
Fig. 2. Trehalolipid
Fig. 3 Sophorolipid
Fig. 4. Surfactin
Fig. 5. Lichenysin
Fig. 6. Corynomycolic
Fig. 7. Emulsan
Fig. 8. Putative rhamnolipid biosynthesis pathway according to Müller (2011), LPS, lipopolysaccharides; PHA, polyhydroxyalkanoates; HAQ, 4-hydroxy-2- alkylquinolines; ACP, acyl carrier protein; CoA, coenzyme A; dTDP, deoxythymidine 5'-diphosphate; NADPH/NADP+, nicotinamide adenine dinucleotide phosphate; HAA, 3-(3- hydroxyalkanoyloxy)alkanoate; EC, enzyme commission number; *m*, *n* = 4–8.

Fig. 1.

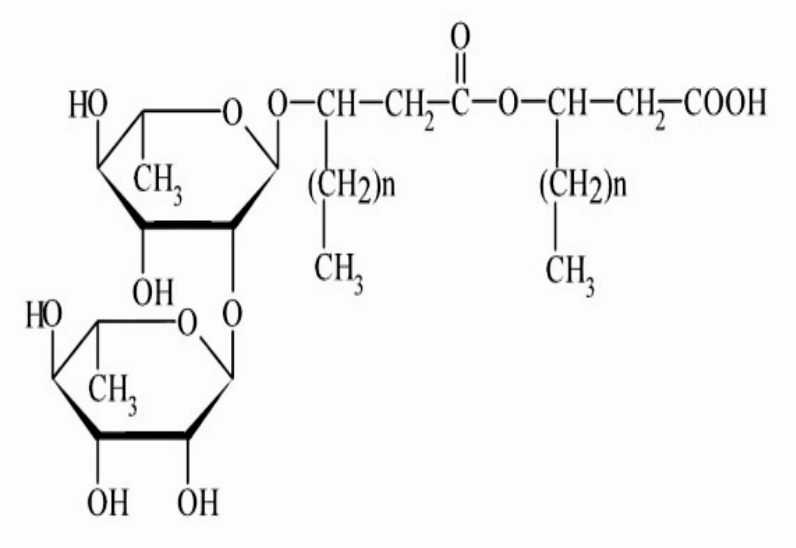
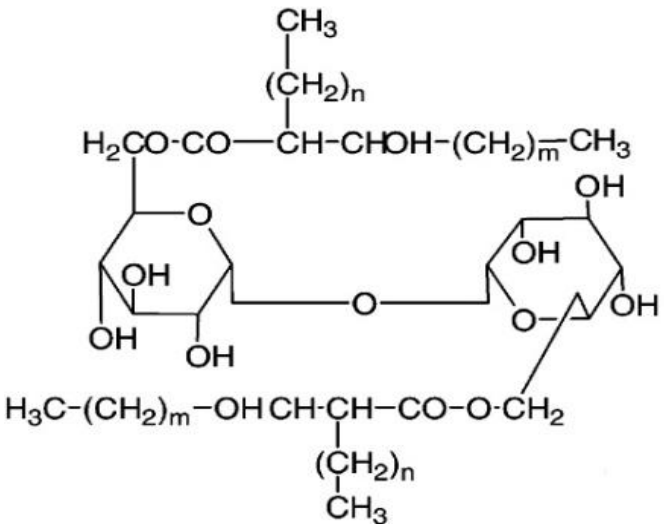


Fig. 2.



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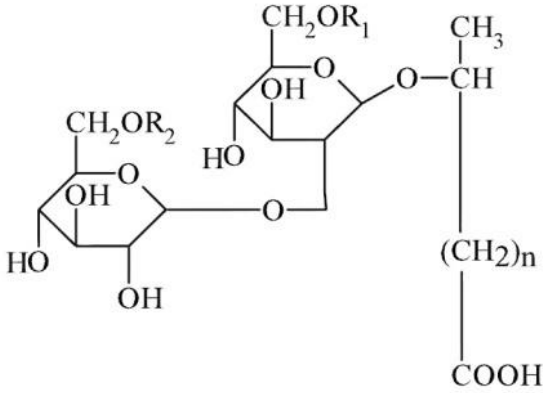

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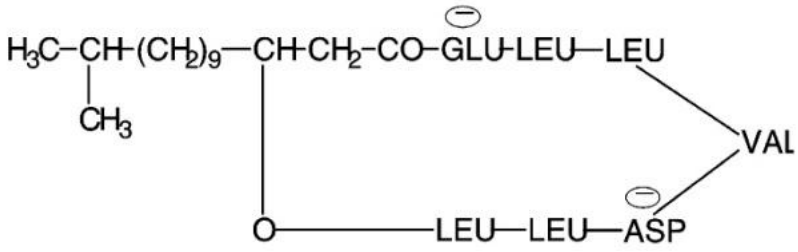

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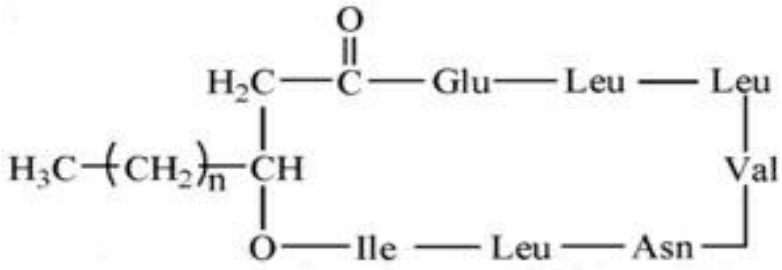

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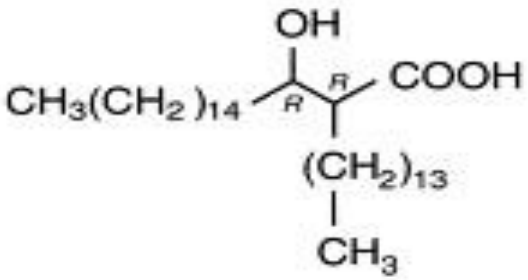

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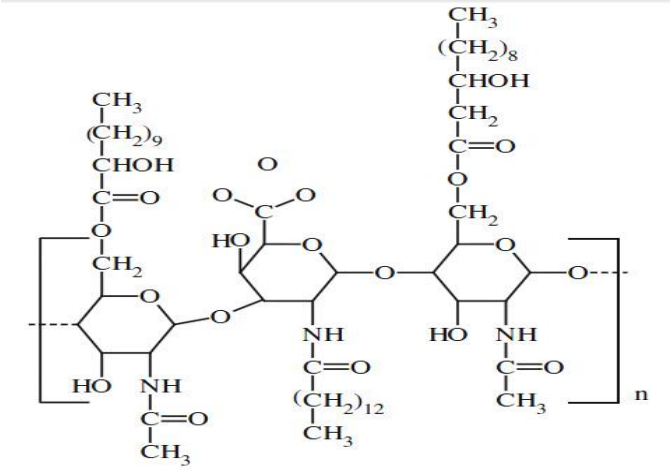

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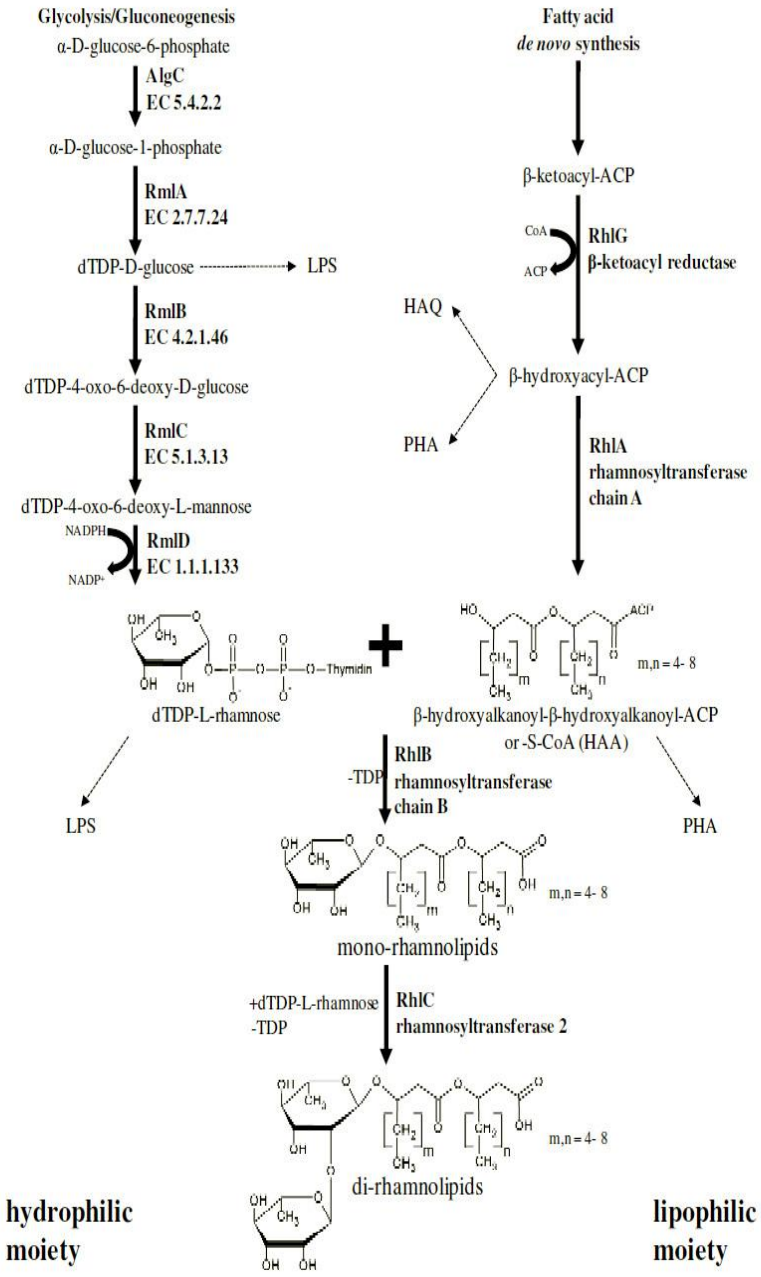
Glycolysis/Gluconeogenesis
α-D-glucose-6-phosphate
AlgC
EC 5.4.2.2
α-D-glucose-1-phosphate
RmlA
EC 2.7.7.24
dTDP-D-glucose
LPS
RmlB
EC 4.2.1.46
dTDP-4-oxo-6-deoxy-D-glucose
RmlC
EC 5.1.3.13
dTDP-4-oxo-6-deoxy-L-mannose
NADPH
NADP+
RmlD
EC 1.1.1.133
dTDP-L-rhamnose
Fatty acid
de novo synthesis
β-ketoacyl-ACP
CoA
ACP
RhlG
β-ketoacyl reductase
HAQ
PHA
β-hydroxyacyl-ACP
RhlA
rhamnosyltransferase
chain A
m,n = 4- 8
β-hydroxyalkanoyl-β-hydroxyalkanoyl-ACP
or -S-CoA (HAA)
LPS
PHA
-TDP
RhlB
rhamnosyltransferase
chain B
mono-rhamnolipids
+dTDP-L-rhamnose
-TDP
RhlC
rhamnosyltransferase 2
di-rhamnolipids
hydrophilic
moiety
lipophilic
moiety