UDC 759.873.088.5:661.185 **https://doi.org/10.15407/biotech12.01.039**

ANTIMICROBIAL ACTIVITY OF SURFACTANTS OF MICROBIAL ORIGIN

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Received 17.08.2018
Revised 21.12.2018
Accepted 14.01.2019

The recent literature data about the antibacterial and antifungal activity of microbial surfactants (lipopeptides synthesized by representatives of genera *Bacillus*, *Paenibacillus, Pseudomonas, Brevibacillus*, rhamnolipids of bacteria *Pseudomonas, Burkholderia, Lysinibacillus* sp., sophorolipids of yeasts *Candida* (*Starmerella*) and *Rhodotorula*), and our own experiments data concerning antimicrobial activity of surfactants synthesized by *Acinetobacter calcoaceticus* IMB B-7241, *Rhodococcus erythropolis* IMB Ac-5017 and *Nocardia vaccini* IMV B-7405 were presented. The analysis showed that lipopeptides were more effective antimicrobial agents compared to glycolipids. Thus, the minimum inhibitory concentrations (MIC) of lipopeptides, ramnolipids and sophorolipids are on average (μg/ml): 1–32, 50–500, and 10–200, respectively. The MIC of surfactants synthesized by the IMV B-7241, IMV Ac-5017 and IMV B-7405 strains are comparable to those of the known microbial lipopeptides and glycolipids. The advantages of glycolipids as antimicrobial agents compared with lipopeptides were the possibility of their synthesis on industrial waste and the high concentration of synthesized surfactants. The literature data and our own results indicate the need to study the influence of microbes' cultivation conditions on the antimicrobial activity of the final product.

Key words: microbial lipopeptides, rhamnolipids and sophorolipids, antibacterial and antifungal activity.

Biodegradation and non-toxic microbial surfactants are used in many fields due to their surface active and emulsifying properties, antimicrobial and antiadhesive activity. They are a useful alternative to standard chemical surfactants in various industrial, medical and nature conservation technologies [1–3].

Microbial surfactant research has a long history. In 1968 it was found that *Bacillus subtilis* AMS-H2O-1 could produce surfactin [4], in 1977 *B. subtilis* DS-104 was shown to produce iturin [5], and the first reports of rhamnolipids came from as early as 1940's [6], while their bactericidal properties were discovered in early 1970's [7]. However, despite this, the detailed studies of their antimicrobial properties commenced quite recently.

In 1997, Vollenbroich et al. established that the linopeptide produced by *B. subtilis* OKB105 at 0.032 mg/ml inhibits the growth of *Mycoplasma hyorhinis* and *Mycoplasma orale*, which can cause inflectional disease of the urinary tract. This was the first research into the antimicrobial action of that surfactin [8].

In 2001, Abalos et al. revealed antifungal action of seven homologues of rhamnolipids of *Pseudomonas aeruginosa* AT10, which at low concentrations (16–32 μg/ml) inhibited growth of fungi belonging to the genera *Aspergillus, Penicillium, Aureobasidium,* and of the phytopathogens *Botrytis* and *Rhizoctonia* [9].

In 2003, the rhamnolipids of *P. aeruginosa* 47T2 NCBIM 40044 were shown to have antibacterial properties [10]. Thus, minimal inhibiting concentrations (MIC) of these surfactants against some bacteria of the genera *Serratia, Enterobacter, Klebsiella, Staphylococcus* were 0.5–32 μg/ml. Reports [8–10] were the impulse for further research

of the antimicrobial action of microbial surfactants [11–13].

One reason for such interest to microbial surfactants as antimicrobial agents is the pathogen resistance to widespread antibiotics and chemical biocides [11, 13].

Compared to the well-known antimicrobial compounds, microbial surfactants have a number of advantages [1, 2, 11, 13]. They are biodegradable and non-toxic, which prevents environmental pollution and allergies. They can be implemented in a wide range of pH, temperature and other environmental factors, due to their stable physical and chemical properties. Also, their action mechanism is based on the disruption of the cytoplasmic membrane, decreasing the possibility of microorganism resistance [5, 8, 10, 11].

The high interest to the microbial surfactants is evidenced by the many publications about these products of microbial synthesis. A few literature reviews were published in the last five years on the properties and perspectives of the practical implementation of microbial surfactants [1, 3, 14–19]. Those reviews mostly focused on certain surfactant types (rhamnolipids, lipopeptides, sophorolipids etc.) with emphasis on certain properties of these compounds. For example, Zhao et al. [17] pay attention mostly to the anti-inflammatory, antitumour, antiviral, and antiplatelet properties of lipopeptides, their interaction with biofilms, while the antibacterial effect is not considered at all and the antifungal is discussed briefly. The review [15] provides not only the specifics of the chemical composition but also the information about antimicrobial activity of lipopeptides, but the information is of almost a ten years ago. Similarly, Cortés-Sánchez Ade et al. [14], while analyzing antimicrobial properties of glycolipids, largely refer to the data of 2005–2010.

This review aims to summarize literature of the last several years on the antimicrobial potential of various surfactant substances of microbial origin.

Lipopeptides of Bacillus sp. as antimicrobial agents

The bacteria of the genus *Bacillus* are among the most studied sources of lipopeptides. The lipopeptydes are grouped into three families of cyclic compounds: surfactin, iturin and fengicin, differing in the number and sequence of the amino acids they include, as well as in the length of the acyl chain [15, 16]. Differences in the chemical composition and construction determine the range of their biological action. Thus, iturin and fengicin have antifungal properties while surfactin with a shorter acyl chain is characterized by a wider range of antibacterial action [15, 16].

Antibacterial action. In 2015, Torres et al. [20] established antimicrobial activity of the surfactant complex of *Bacillus subtilis* subsp. *subtilis* CBMDC3f, which contains four surfactin homologues and one for each iturin and fengicin. When the complex was added to cell suspension of *Listeria monocytogenes* 01/155 at 0.5 mg/ml, the number of viable cells dropped two orders of magnitude after 25 minutes. A similar effect towards *Bacillus cereus* MBC1 and *Staphylococcus aureus* ATCC 29213 was seen at higher concentrations of lipopeptide complex (1–2 mg/ml). The authors state that surfactants of similar composition produced by other strains of *Bacillus licheniformis* or *B. subtilis* were active only against *B. cereus* and *S. aureus*, without antagonistic activity against the genus *Listeria* [20].

Sharma et al. [21] studied antimicrobial activity of lipopeptides produced by *Bacillus pumilus* DSVP18 on potato peel substrate. Minimum inhibiting concentration against *B. cereus* MTCC 430, *Escherichia coli* MTCC 1687, *Salmonella enteritidis* MTCC 3219, and that against *S. aureus* MTCC 5021 was 30 µg/ml.

Surfactin of *Bacillus amyloliquefaciens* ST34 showed antimicrobial activity against a range of both Gram-negative (*Escherichia coli* ATCC 13706, *Salmonella typhimurium* ATCC 14028, *Klebsiella pneumoniae* ATCC 10031, *Serratia* sp. SM14, *Enterobacter* sp. E11) and Gram-positive (*B. cereus* ST18, *Enterococcus* sp. C513, *Micrococcus* sp. AQ4S2, *S. aureus* C2) bacteria [22]. At the concentration of surfactin 0.26 mg/ml, zones of bacterial growth inhibition were 13–17 mm.

Chen et al. [23] isolated from the sediments of Bohai Sea a strain of *Bacillus licheniformis* MB01 which produces a complex of surfactin and fatty acids showing antibacterial activity against *E. coli, Vibrio cholerae, Vibrio parahaemolyticus, Vibrio harveyi, Pseudomonas aeruginosa, S. aureus, Proteus species.* For example, its MIC against *V. parahaemolyticus* was 50 µg/ml [23].

Strain *B. subtilis* SK.DU4 synthesizes the complex of bacteriocin-like peptide and iturin-like lipopeptide with 15 carbon atoms in the acyl chain [24]. The bacteriocin-like peptide had antimicrobial action against *Micrococcus luteus* MTCC106 and *Listeria monocytogenes*

MTCC839 (growth inhibition zone 12 and 14 mm, respectively). If only the inturin-like lipopeptide was present, the zone of growth inhibition was 11 mm in both test cultures. If the mixture of bacitracin and lipopeptide was used, the zone of *M. luteus* MTCC106 and *L. monocytogenes* MTCC839 growth inhibition increased to 15 and 17 mm, respectively.

The study of Zhou et al. [25] is one of the first concerning dependence of surfactin antimicrobial activity on the carbon source in the culture medium of *B. subtilis* HH2, as well as the stability of antimicrobial action in a wide range of temperature (60–121 °C), pH (1–12), and in the presence of trypcin (100–300 μg/ml, pH 8) and pepsin (100–300 μg/ml, pH 2). It was found that surfactin synthesized on a mixture of glucose (0.33 %) and cellulose (0.67 %) had higher antimicrobial activity (at 0.4 mg/ml surfactin, the growth inhibition zones of *E. coli* CCTCC AB 212358 and *S. aureus* CCTCC AB 91053 were 16 and 14 mm, respectively). Lipopeptide obtained on medium with 1 % glucose, had low antimicrobial effect. Antimicrobial activity of surfactin remained constant at 60–100 °C, pH 2–11, and in the presence of trypsin and pepsin.

Due to synthesis of surfactin, bacteria of the genus *Bacillus* are considered promising in controlling the growth of such phytopathogens as *P. syringae* (causes root infection of arabidopsis), *Xanthomonas axonopodis* pv. *glycines* (bacterial pustule of soybean), and phytopathogen mycoplasms *Spiroplasma citri* and *Acholeplasma laidlawii,* which cause etiolation in citruses, clover phyllody and phytoplasma disease in solanaceous crops, respectively [15, 16].

B. subtilis 9407 synthesizes the complex of lipopeptides, the main one being C13-C16 surfactin A [26]. This complex showed of the antimicrobial effect against *Acidovorax citrulli* MH21 the causative agent of pumpkin bacterial blotch (growth inhibition zone 18 mm). To prove the role of surfactin in inhibition this pathogen, the authors obtained a mutant strain unable of synthesize lipopeptide. The mutant had no antimicrobial activity. Besides *A. citrulli* MH21, lipopeptides of strain 9407 showed antimicrobial effect on other phytopathogenic bacteria: *Pseudomonas syringae* pv. *tomato* DC3000, *Xanthomonas campestris* pv. *campestris* Xcc 8004, *Pectobacterium carotovora* subsp. *carotovora* Ecc 09, *Pectobacterium atrosepticum* SCRI1043 (growth inhibition zones 10–18 mm) [26].

In 2018 [27] was reported about a sea isolate *Bacillus pumilus* SF214 wich produced pumilacidin (the mixture of cyclic heptapeptides linked to fatty acids of different lengths). The lipopeptide inhibited *S. aureus* ATCC 6538 (in the presence of supernatant, growth inhibition zone was 10 mm.

Antifungal activity. In the publications on the antifungal activity pay the most attention to the effect of these surfactants on phytopathogenic fungi. Since we provided the information on antifungal effect of lipopeptides produced by rhizosphere and endophytic bacteria of the genus *Bacillus*, which are promising for control the number of phytopathogenic fungi, what we reported in the review [28], we shall now pay attention to studies which have appeared after then. The lipopeptide antifungal activity is determined by analyzing such parameters as MIC [29–34], degree of the fungal growth inhibition [35, 36], and the diameter of fungal growth inhibition zone [37].

The data on MIC of lipopeptides produced by bacteria of the genus *Bacillus* against fungi and yeast are summarized in Table 1. According to the data, the highest antifungal activity is shown for *B. subtilis* RLID 12.1 lipopeptides. MIC against yeasts of the genera *Cryptococcus* and *Candida* was only 1–20 μg/ml, that orders of magnitude lower than MIC of other lipopeptides against fungi. Notably, the antimicrobial activity of lipopeptides of *Bacillus* sp. AR2 depends on the carbon source in the culture medium [20]. The strain AR2 was found to produce the mixture of homologues of iturin, fengicin and surfactin. If the strain was grown in medium with sucrose, glycerol, sorbitol and maltose the prevailing fraction in the complex was C15 surfactin. However the most active antifungal agents were lipopeptides produced on sucrose. Sarwar et al. [35] studied the degree of growth inhibition of phytopathogenic fungi *Fusarium moniliforme* KJ719445, *Fusarium oxysporum (*the strain was not specified), *Fusarium solani* SAN1077, *Trichoderma atroviride* P150907 for the action of lipopeptides synthesized by bacteria of the genus *Bacillus.*

It was found that lipopeptides of *B. amyloliquefaciens* FZB42, *B. subtilis* NH-100 and *B. subtilis* NH-217 inhibited fungal growth by 83–87, 79–80, and 76–79% respectively.

Lipopeptides synthesized by *Bacillus* XT1 CECT 8661 added at 2–10 mg/ml inhibited the growth of *Botrytis cinerea* by 19–72%, and maximum degree of inhibition

Table 1. **Minimum inhibitory concentrations of *Bacillus* sp. lipopeptides against fungi**

Test culture		Lipopeptide producer	MIC, μg/ml	References
Genus	**Species, strain**			
Alternaria	*Alternaria solani*	*Bacillus subtilis* CU 12	150	[30]
	Alternaria alternata MTCC 2724	*Bacillus* sp. AR2	500–750*	[34]
	Alternaria citri MTCC 4875	*Bacillus* sp. AR2	500–750*	[34]
Fusarium	*Fusarium oxysporum* f. sp. *iridacearum*	*Bacillus subtilis* BBG125	10	[33]
	Fusarium sambucinum	*Bacillus subtilis* CU 12	100	[30]
	Fusarium solani ATCC 36031	*Bacillus* sp. AR2	250–750*	[34]
	Fusarium oxysporum MTCC 7229	*Bacillus* sp. AR2	250–750*	[34]
	Fusarium solani	*Bacillus subtilis* SPB1	3000	[31]
Rhizoctonia	*Rhizoctonia bataticola*	*Bacillus subtilis* SPB1	40	[32]
	Rhizoctonia solani	*Bacillus subtilis* SPB1	4000	[32]
Rhizopus	*Rhizopus stolonifer*	*Bacillus subtilis* CU 12	100	[30]
Verticillium	*Verticillium dahliae*	*Bacillus subtilis* CU 12	100	[30]
Cladosporium	*Cladosporium cladosporioides* ATCC 16022	*Bacillus* sp. AR2	750–2000*	[34]
Scopulariopsis	*Scopulariopsis acremonium* ATCC 58636	*Bacillus* sp. AR2	125–500*	[34]
Microsporum	*Microsporum gypseum* MTCC 4522	*Bacillus* sp. AR2	125–500*	[34]
Trichophyton	*Trichophyton rubrum* MTCC 2961	*Bacillus* sp. AR2	750–2000*	[34]
Botrytis	*Botrytis cinerea*	*Bacillus* XT1 CECT 8661	8000	[36]
Cryptococcus	*Cryptococcus* spp.	*Bacillus subtilis* RLID 12.1	1–16	[29]
Candida	*Candida* spp.	*Bacillus subtilis* RLID 12.1	2–20	[29]

Note.* — different MIC values dependent on the carbon source in the culture medium.

was seen at the highest studied surfactant concentration [36].

For the action surfactin of *B. amyloliquefaciens* ST34 at concentration 0.26 mg/ml, growth inhibition zones in different strains of *Candida albicans* and *Cryptococcus neoformans* were in the range of 13–15 mm [22].

In our review [28] we reported an increased synthesis of antifungal lipopeptides (in particular, fengicin and iturin) in response to the presence of phytopathogenic fungi in the medium of producer cultivation. Zihalirwa Kulimushi et al. [37] studied the effect of a lipopeptide complex (surfactin, fengicin and iturin) produced by *B. amyloliquefaciens* S499 on the phytopathogenic fungus *Rhizomucor variabilis*, and the possibility of inducing the antifungal compounds synthesis in the presence of a pathogen in the culture medium of strain S499. Experiments showed that co-culturing *B. amyloliquefaciens* S499 and *Rhizomucor variabilis* led to an almost three-fold increase in fengicin content and increased the antifungal effect [37].

The another interesting research [38] showed that *Bacillus amyloliquefaciens* UCMB5113 syntesized the mixture of linear fengicins, whereas they commonly occur only in the cyclic form [15, 16]. Linear fengicins were divided into 14 fractions, all fractions showed antagonistic activity against *Alternaria brassicicola*, *Alternaria brassicae*, *Botrytis cinerea*, *Sclerotinia sclerotiorum* and *Verticillium longisporum*; but the fraction 9 had the highest antifungal effect. According to the analysis, it belonged to the family of C15-fengicin. The authors suppose that all other fractions have shorter acyl chains and so are less active.

Antimicrobial effect of lipopeptides produced by other microorganisms

Representatives of the genera *Paenibacillus* [16, 39–41], *Pseudomonas* [42–46],

Brevibacillus [47], *Corynebacterium* [48], *Aneurinibacillus* [49], *Streptomyces* [50], even *Propionibacterium* [51], *Citrobacter* and *Enterobacter* [52] also synthesises lipopeptides.

High antimicrobial activity was revealed for lipopeptide surfactants of strain *Paenibacillus* sp. MSt1, isolated from the peat beds of tropical forests. Thus, its MIC was (μg/ml) 1.5 against *E. coli* ATCC 25922; 25 — methicillin resistant strain *S. aureus* ATCC 700699, and 12.5 — *C. albicans* IMR [39].

Huang et al. [40] established high antimicrobial activity of paenibacterin of *Paenibacillus thiaminolyticus* OSY-SE. MIC of the lipopeptide against strains *E. coli, P. aeruginosa, Acinetobacter baumannii, K. pneumoniae, S. aureus* and *E. faecalis* were fairly low: 8–16 μg/ml, comparable to the MIC of such antibiotics as polymixin B and vancomycin.

In 2017, was reported about strain *Paenibacillus* sp. OSY-N that produce the mixture of lipopeptides BMY-28160, permetin A, a novel cyclic lipopeptide and its linear analogues (paenipeptins A, B and C) [41]. Differences in the compound content underlie their different biological effect. Thus far, the highest antimicrobial effect was seen in paenipeptin C (contains C8-acyl chain and isoamino acid): MIC against Gram-positive (*B. cereus* ATCC 11778, *Listeria innocua* ATCC 33090, *S. aureus* ATCC 25923, *S. aureus* ATCC 6538) and Gram-negative (*E. coli* K-12, *E. coli* ATCC 25922, *Salmonella enterica* ser. Typhimurium LT2, *S. enterica* ser. Typhimurium LT2) bacteriae were 2–4 and 0.5–2 μg/ml, respectively. The authors explain such activity of paenipeptin C, unlike other lipopeptides, by a longer acyl chain, and presence of unusual amino acids and their conformation.

Although bacteria of the genus *Pseudomonas* are more known as sources of glycolipids [1, 2, 7, 9, 10, 12, 14], there are data on their ability to produce lipopeptides, too. As early as 1970's the structure of lipopeptide viscosin was established (the compound was produced by *Pseudomonas fluorescens),* with antimicrobial effect [42] of such magnitude that intensive research of its biological properties lasted until 2000's [43]. Currently, viscosin has been established to have an antimicrobial effect against 94 Gram-negative and 72 Gram-positive bacteria and 95 fungal species [44].

Ma et al. [45] established that *Pseudomonas* sp. CMR5C produced orfamide B and G, with the same amino acid sequence but different acyl chain lenth: C14 for orfamide B and C16 for orfamide G. Irrespectively of the acyl chain length, orfamide had no antifungal effect against *Magnaporthe oryzae* VT5M1, however at 50 μmole/ml the appressorium of *M. oryzae* VT5M1 did not develop.

Pseudomonas aeruginosa MA-1 grown on olive oil (4 %) produced lipopeptides in the high concentration of 12.5 g/l [46] of low antimicrobial effect; the growth inhibition zone of *S. aureus* ATCC 43300 did not exceed 7–9.5 mm at surfactant concentration of 0.5–5 g/l.

The lipopeptide brevibacillin (produced by *Brevibacillus laterosporus* OSY-I1) has high antimicrobial effect on Gram-positive bacteria (MIC 2–4 μg/ml) [47]. Notably, its MIC for Gram-negative bacteriae was higher than 32 μg/ml.

Dalili et al. [48] studied the antimicrobial effect of coryxin, produced by *Corynebacterium xerosis* NS5 [48]. It was found that coryxin had low antimicrobial activity against Gram-negative bacteria (MIC for strains *E. coli* and *P. aeruginosa* were 3120 and 10 000 μg/ml, respectively). However, MIC of this lipopeptides against Gram-positive bacteria *S. aureus* and *Streptococcus mutans* were significantly lower (190 μg/ml).

The aneurinifactin, produced by sea bacteria *Aneurinibacillus aneurinilyticus* SBP-11 A, had significantly higher antimicrobial activity compared to coryxin [49]. Its MIC against strains *E. coli* MTCC 443 and *S. aureus* MTCC 96 was 8 μg/ml, and *P. aeruginosa* MTCC — 16–424 μg/ml.

The study [50] described the lipopeptide produced by *Streptomyces amritsarensis* sp. MTCC 11845T, which at 10 μg/ml showed antibacterial activity to Gram-positive bacteria. The growth inhibition zones for *B. subtilis* MTCC 619, *Staphylococcus epidermidis* MTCC 435 and *Mycobacterium smegmatis* MTCC 6 were 21, 17, 15 mm, respectively. Meanwhile there was no antimicrobial activity to Gram-negative bacteria and fungi, perhaps because of a short (C12) acyl chain of the lipopeptide.

While bacteria of the genus *Propionibacterium* are known sources of organic acids and vitamins, recent research [51] established that *Propionibacterium freudenreichii* subsp. *freudenreichii* PTCC 1674 produces the lipopeptide surfactant inhibiting *Rhodococcus erythropolis* and *B. cereus:* MIC for both was 25 mg/ml.

Strains *Citrobacter* sp. S-3, S-6 and S-7, *Enterobacter* sp. S-4, S-5, S-9 S-10, S-11 and

S-12 were isolated from polluted soil. They [52] produced the complex of lipopeptides with antimicrobial effect to Gram-positive and Gram-negative bacteria. The strains S-3 and S-11 were shown to produce fractions Fr-c and Fr-e with β-hydroxy fatty acids of chain length C14 and C17, respectively. Thus they can be classified as belonging to the fengicin and iturin families. However the antimicrobial effect was seen only in the purified lipopeptide fraction Fr-c with the shorter acyl chain. Its MIC were 12, 15 and 16 μg/ml against Gram-positive test cultures *Micrococcus luteus* MTCC106, *S. aureus* MTCC1430 and *S. epidermidis* MTCC435, and 20 and 32 μg/ml against Gram-negative test cultures *Serratia marcescens* and *P. aeruginosa* ATCC27853, respectively. Notably no of all lipopeptides had an antifungal effect on *C. albicans* MTCC1637.

A summary of lipopeptides antibacterial activity is shows in Table 2, composed to compare MIC of different lipopeptides for the same test cultures. The lipopeptides produced by bacteria of the genus *Paenibacillus* showed the highest antimicrobial activity, a moderate activity — surfactants of the genus *Bacillus*, and lipopeptides of such atypical producer as *Corynebacterium* and *Propionibacterium* were not active enough.

According to recent literature, the antimicrobial activity of lipopeptides depends on their content and on the test culture (species and strain). Usually, higher antifungal activity is seen in lipopeptides with longer (C16–C18) acyl chains, and compounds with fewer carbons atoms (C7–C14) in the fatty acid chain have antibacterial effect. However, currently there is not enough information in the literature, on the basis of which it would be possible to do correct conclusions about the influence of the chemical composition of lipopeptides on their antimicrobial activity. Table 2 contains more higher MIC of lipopeptides than previously described [15, 16], perhaps because the reported data [15, 16] are given for individual substances but not for the complexes analyzed in our review.

Antimicrobial activity of rhamnolipids

A glycolipids has a carbohydrate part which might be rhamnose, trehalose, sophorose etc., and a lipid chain. Accordingly, they are classified into rhamno- trehaloso-, sophorolipids, etc. [1, 2, 14, 18, 53]. Currently, rhamnolipids are the most studied of them. Only in the last few years there were published several reviews [54–60] dedicated to the increasing rhamnolipid biosynthesis, new avenues and problems of their application in various industrial and medical practices.

In a rhamnolipids, one or two rhamnoses are bound to one, two or seldom three molecules of β-hydroxyalyphatic acids. Depending on the number of carbohydrate and fatty acid molecules, the rhamnolipids can be grouped into mono-rhamno-mono-lipids, mono-rhamno-di-lipids, di-rhamno-mono-lipids and di-rhamno-di-lipids [58, 60]. Over sixty rhamnolipid homologues are produced by microorganisms of the genus *Pseudomonas* (*P. chlororaphis, P. alcaligenes, P. putida, P. stutzeri,* etc.), and strains of *P. aeruginosa* are the main rhamnolipid sources. Lately, there were reports of rhamnolipid-synthesizing abilities in bacteria of the genera *Acinetobacter (A. calcoaceticus), Enterobacter, Pantoea, Burkholderia, Myxococcus* [58–60].

The effect of rhamnolipid on bacteria

According to Tedesco et al., rhamnolipids are probably produced by many microorganisms [61]. The rhamnolipid-producing strains of microbiota belonging to *Psychrobacter, Arthrobacter* and *Pseudomonas* were isolated from the Ross Sea (Antarctica). Monorhamnolipids at concentration 1 mg/ml inhibited the growth of pathogenic strains of *Burkholderia (*Table 3). Given the high antimicrobial activity of rhamnolipids of *Pseudomonas* BTN 1, the next step was separation of the rhamnolipid complexes into fractions. This yielded three kinds of monorhamnolipids with different lipid chain length. For each fraction, the researchers were determined the minimum inhibitory and minimum bactericidal concentrations (MBC).

The fractions 1 and 2 of monorhamnolipids with shorter acyl chains were most active. Thus, MIC of these fractions against *B. cenocepacia* LMG 16656, *B. metallica* LMG 24068, *B. seminalis* LMG 24067, *B. latens* LMG 24064 and *S. aureus* 6538P were about 1.56–12.5 μg/ml, and MBC did not exceed 200 μg/ml.

Chebbi et al. [62] isolated from engine oil-polluted soil the strain *P. aeruginosa* W10, which produced 9.7 g/l rhamnolipids on a medium with 2% glycerol. However, the antimicrobial effect of the surfactants turned out to be relatively low. Thus, MIC of rhamnolipid complex of strain W10 against the pathogenic strains *E. coli* ATCC 25922, *S. aureus (*MRSA) ATCC 43300 and *C. albicans* ATCC 10231 were 37.50, 9.37 and 2.34 mg/ml, respectively.

The effect of mono- and dirhamnolipids produced by *Burkholderia thailandensis*

Table 2. **Antibacterial activity of lipopeptides against some microorganisms**

Test culture	Lipopeptide source	MIC, μg/ml	References
Escherichia coli O157:H7 ATCC 43889	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5–1	[39]
Escherichia coli ATCC 25922	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5–1	[39]
	Paenibacillus sp. MSt1	1.5	[37]
	Paenibacillus thiaminolyticus OSY-SE	8	[38]
Escherichia coli O157:H7 EDL 933	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5–1	[39]
	Paenibacillus thiaminolyticus OSY-SE	8	[38]
	Bacillus laterosporus OSY-I1	32	[40]
Escherichia coli 2276	*Paenibacillus thiaminolyticus* OSY-SE	8	[38]
Escherichia coli MTCC 443	*Aneurinibacillus aneurinilyticus* SBP-11	8	[42]
Escherichia coli K-12	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5	[39]
	Bacillus laterosporus OSY-I1	>32	[40]
Escherichia coli MTCC 1687	*Bacillus pumilus* DSVP18	30	[21]
*Escherichia coli**	*Corynebacterium xerosis* NS5	3120	[39]
Staphylococcus aureus (methicillin-resistant)	*Bacillus laterosporus* OSY-I1	1	[40]
Staphylococcus aureus ATCC 6538	*Bacillus laterosporus* OSY-I1	1–2	[40]
Staphylococcus aureus ATCC 25923	*Paenibacillus* sp. OSY-N (paenipeptin C)	2–4	[39]
Staphylococcus aureus ATCC 6538	*Paenibacillus* sp. OSY-N (paenipeptin C)	4–8	[39]
Staphylococcus aureus (methicillin-resistant)	*Paenibacillus* sp. OSY-N (paenipeptin C)	8	[39]
Staphylococcus aureus MTCC 96	*Aneurinibacillus aneurinilyticus* SBP-11	8	[42]
Staphylococcus aureus (methicillin-resistant)	*Enterobacter* sp. S-11	15	[44]
*Staphylococcus epidermidis**	*Enterobacter* sp. S-11	16	[44]
Staphylococcus aureus ATCC 700699	*Paenibacillus* sp. MSt1	25	[37]
Staphylococcus aureus MTCC 5021	*Paenibacillus* sp. OSY-N (paenipeptin C)	16–32	[39]
	Paenibacillus thiaminolyticus OSY-SE	32	[38]
	Bacillus pumilus DSVP18	30–35	[21]
Staphylococcus aureus ATCC 43300	*Paenibacillus thiaminolyticus* OSY-SE	32	[38]
*Staphylococcus aureus**	*Corynebacterium xerosis* NS5	190	[41]
Bacillus cereus ATCC 11778	*Bacillus laterosporus* OSY-I1	2–4	[40]
	Paenibacillus sp. OSY-N (paenipeptin C)	4	[39]
Bacillus cereus ATCC 14579	*Bacillus laterosporus* OSY-I1	1,0	[40]
	Paenibacillus sp. OSY-N (paenipeptin C)	8	[39]
Bacillus cereus MTCC 430	*Bacillus pumilus* DSVP18	30–35	[21]
*Bacillus cereus**	*Propionibacterium freudenreichii* subsp. *freudenreichii* PTCC 1674	25 000	[43]
Bacillus subtilis MTCC 619	*Aneurinibacillus aneurinilyticus* SBP-11	16	[42]
Listeria monocytogenes OSY-8578^{h}	*Bacillus laterosporus* OSY-I1	1–2	[40]

Table 2. Continued

Test culture	Lipopeptide source	MIC, μg/ml	References
Listeria innocua ATCC 33090	*Bacillus laterosporus* OSY-I1	1–2	[40]
	Paenibacillus sp. OSY-N (paenipeptin C)	2–4	[39]
Listeria monocytogenes Scott A	*Bacillus laterosporus* OSY-I1	1	[40]
	Paenibacillus thiaminolyticus OSY-SE	2	[38]
	Paenibacillus sp. OSY-N (paenipeptin C)	4–8	[39]
Pseudomonas aeruginosa ATCC 27853	*Paenibacillus* sp. OSY-N (paenipeptin C)	1–2	[39]
	Paenibacillus thiaminolyticus OSY-SE	8	[38]
	Bacillus laterosporus OSY-I1	>32	[40]
Pseudomonas aeruginosa ATCC 999	*Paenibacillus thiaminolyticus* OSY-SE	8	[38]
Pseudomonas aeruginosa ATCC 2325	*Paenibacillus thiaminolyticus* OSY-SE	8	[38]
Pseudomonas aeruginosa MTCC 424	*Aneurinibacillus aneurinilyticus* SBP-11	16	[42]
*Pseudomonas aeruginosa**	*Enterobacter* sp. S-11	30	[44]
*Pseudomonas aeruginosa**	*Corynebacterium xerosis* NS5	10 000	[41]
Klebsiella. pneumoniae 2461	*Paenibacillus thiaminolyticus* OSY-SE	4	[38]
Klebsiella pneumoniae MTCC 7162	*Aneurinibacillus aneurinilyticus* SBP-11	4	[42]
Klebsiella pneumoniae 2463	*Paenibacillus thiaminolyticus* OSY-SE	8	[38]
Klebsiella pneumoniae ATCC 700603	*Paenibacillus thiaminolyticus* OSY-SE	8	[38]
Klebsiella pneumoniae 2317	*Paenibacillus thiaminolyticus* OSY-SE	64	[38]
Enterococcus faecalis ATCC 51299	*Bacillus laterosporus* OSY-I1	4–8	[40]
Enterococcus faecalis 2731	*Paenibacillus thiaminolyticus* OSY-SE	8	[38]
Enterococcus faecalis ATCC 29212	*Paenibacillus thiaminolyticus* OSY-SE	16	[38]
	Paenibacillus sp. OSY-N (paenipeptin C)	32	[39]
Enterococcus faecalis ATCC 700802	*Paenibacillus thiaminolyticus* OSY-SE	64	[38]
Salmonella enterica ser. Typhimurium LT2	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5–1	[39]
Salmonella enterica ser.Typhimurium DT104	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5–1	[39]
Salmonella enteritidis MTCC 3219	*Bacillus pumilus* DSVP18	30–35	[21]
Salmonella typhimurium DT 109	*Bacillus laterosporus* OSY-I1	>32	[40]
Acinetobacter baumannii ATCC BAA-747	*Paenibacillus thiaminolyticus* OSY-SE	2	[38]
Acinetobacter baumannii 2315	*Paenibacillus thiaminolyticus* OSY-SE	2	[38]
Alicyclobacillus acidoterrestris ATCC 49025	*Bacillus laterosporus* OSY-I1	0.5–1	[40]
Alicyclobacillus acidoterrestris	*Bacillus laterosporus* OSY-I1	1	[40]
*Streptococcus agalactiae**	*Paenibacillus* sp. OSY-N (paenipeptin C)	0.5–1	[39]
*Streptococcus mutans**	*Corynebacterium xerosis NS5*	25 000	[41]
Lactobacillus plantarum ATCC 8014[f]	*Bacillus laterosporus* OSY-I1	1	[40]

Table 2. Continued

Test culture	Lipopeptide source	MIC, μg/ml	References
Lactococcus lactis ATCC 11454[g]	*Bacillus laterosporus* OSY-I1	2	[40]
Clostridium difficile A515[c]	*Bacillus laterosporus* OSY-I1	4–8	[40]
*Rhodococcus erythropolis**	*Propionibacterium freudenreichii* subsp. *freudenreichii* PTCC 1674	25 000	[43]
*Serratia marcescens**	*Enterobacter* sp. S-11	20	[44]
Vibrio cholerae MTCC 3906	*Aneurinibacillus aneurinilyticus* SBP-11	16	[42]
*Vibrio parahaemolyticus**	*Bacillus licheniformis* MB01	50	[23]
*Micrococcus luteus**	*Enterobacter* sp. S-11	12	[44]
*Enterobacter aerogenes**	*Paenibacillus* sp. OSY-N (paenipeptin C)	2–4	[39]
Paenibacillus larvae ATCC 9545	*Bacillus pumilus* DSVP18	30–35	[21]
*Yersinia enterocolitica**	*Paenibacillus* sp. OSY-N (paenipeptin C)	0,5–1	[39]

Note: * — strain number not provided.

Table 3. **Effect of rhamnolipids produced by the Arctic Sea bacteria on strains of *Burkholderia***

Test culture	Inhibition of test cultures (%) in the presence of rhamnolipids, produced by				
	Pseudomonas BTN 1	*Psychrobacter* BTN2	*Psychrobacter* BTN15	*Psychrobacter* BTN5	*Arthrobacter* BTN 4
Burkholderia diffusa LMG 24065	100	75	77	77	63
Burkholderia metallica LMG 24068	92	70	71	77	64
Burkholderia cenocepacia LMG 16656	100	78	87	84	57
Burkholderia latens LMG 24064	100	53	75	58	41
Burkholderia seminalis LMG 24067	100	43	67	40	56

E264 (ATCC 700388) on glycerol, on their antimicrobial activity was studied in [63]. Chemical analysis of the rhamnolipids showed that strain E264 synthesizes the mixture of dirhamnolipids and monorhamnolipids in the ratio 3:1. Further research showed that dirhamnolipids have higher antimicrobial effect than monorhamnolipids. Meanwhile the highest antimicrobial activity was found in supernatant with unpurified rhamnolipid mixture which might be explained by synergy of the fractions or the presence of other compounds besides rhamnolipids with antimicrobial effect.

Aleksic et al. [64] studied antimicrobial activity of both the complex of rhamnolipids produced by *Lysinibacillus* sp. BV152.1 and its separate fractions. It was found that all fractions of strain BV152.1 rhamnolipids had the same weak antimicrobial effect against *P. aeruginosa* PAO1, *P. aeruginosa* DM50, *S. aureus* ATCC 25923, *S. aureus* MRSA and *S. marcescens* ATCC 27117. Their MIC against all test cultures were 500 μg/ml.

The report [65] describes the isolation of a strain identified as *P. aeruginosa LCD12* which synthesizes the complex of mono- and dirhamnolipids, from samples of raw petroleum. The authors studied antimicrobial activity of the surfactant complex and of its constituents. It was found that MIC of all studied rhamnolipids against *Streptococcus epidermidis, B. subtilis, S. aureus* and *E. coli* were close: 4; 4; 16 and 4 μg/ml, respectively.

The data on rhamnolipid antimicrobial activity are summarized in Table 4.

Table 4. **Minimum inhibitory concentrations of rhamnolipids**

Test culture	Producer	MIC, μg/ml	References
Staphylococcus aureus 6538P	*Pseudomonas* BTN 1	1.56–3.12	[61]
Staphylococcus aureus	*Pseudomonas aeruginosa* LCD12	16	[65]
Staphylococcus aureus ATCC 25923	*Lysinibacillus* sp. BV152.1	500	[64]
*Staphylococcus aureus** (methicillin-resistant)	*Lysinibacillus* sp. BV152.1	500	[64]
Staphylococcus aureus ATCC 25923	*Pseudomonas aeruginosa* C2	650	[66]
Staphylococcus aureus ATCC 43300 (methicillin-resistant)	*Pseudomonas aeruginosa* W10	9 370	[62]
Staphylococcus capitis SH6	*Pseudomonas aeruginosa* W10	18 750	[62]
Pseudomonas aeruginosa PAO*1*	*Lysinibacillus* sp. BV152.1	500	[64]
Pseudomonas aeruginosa DM50	*Lysinibacillus* sp. BV152.1	500	[64]
Bacillus subtilis	*Pseudomonas aeruginosa* LCD12	4	[65]
Bacillus licheniformis CAN55	*Pseudomonas aeruginosa* W10	1500	[62]
Escherichia coli	*Pseudomonas aeruginosa* LCD12	4	[65]
Escherichia coli K8813	*Pseudomonas aeruginosa* C2	550	[66]
Esherchia coli ATCC 25922	*Pseudomonas aeruginosa* W10	37 500	[62]
Streptococcus epidermidis	*Pseudomonas aeruginosa* LCD12	4	[65]
Streptococcus oralis	*Burkholderia thailandensis* E264	150	[63]
Streptococcus sanguinis	*Burkholderia thailandensis* E264	150	[63]
Neisseria mucosa	*Burkholderia thailandensis* E264	150	[63]
Actinomyces naeslundii	*Burkholderia thailandensis* E264	300	[63]
Serratia marcescens ATCC 27117	*Lysinibacillus* sp. BV152.1	500	[64]
Candida albicans ATCC 10231	*Pseudomonas aeruginosa* W10	2 340	[62]

Data in Table 5 show that the antibacterial activity of rhamnolipids as well as lipopeptides (Table 2) depends on the test culture (both species and strain) and on the complex of surfactants. Lipopeptides are more efficient antibacterial agents compared to rhamnolipids (Tables 2 and 5).

In a number of recent studies, the antibacterial activity of rhamnolipids was determined by the agar diffusion technique but not the MIC [22, 67–69]. Thus, supernatant (15 μl, with rhamnolipid concentration 0.57 g/l) obtained by culturing *P. aeruginosa* P1R16 on olive oil, the growth inhibition zones were the following: 11 mm for *E. coli* ATCC 25922, 25 mm for *P. aeruginosa* ATCC 27853, 12 mm for *S. aureus* ATCC 25923 and *B. cereus* CCT0198, and 22 mm for *Ralstonia solanacearum* 1226 [67].

In the presence 1.12 mg/ml rhamnolipids of *P. aeruginosa* SARCC 697 the diameters of growth inhibition zones for bacterial test cultures were (mm): 13.5 for *E. coli* ATCC 417373; 29.3 for *E. coli* ATCC 13706; 13.5 for *Klebsiella pneumoniae* ATCC 10031; 8.3 for *K. pneumoniae* P3; 20.3 for *Salmonella typhimurium* ATCC 14028; 14 for *Salmonella enterica* SE19; 14 for *Serratia marcescens* ATCC 13880; 13.7 for *S. aureus* ATCC 25923; and 11.5 for *S. aureus* C2 [22]. Growth inhibition zone for methicillin-resistant strain *S. aureus* ATCC 43300 under the effect of rhamnolipids produced by *P. aeruginosa* 47T2 on the mixture of waste sunflower and olive oil was 10 mm [68].

Oluwaseun et al. [69] compared the antimicrobial activity of rhamnolipids of *P. aeruginosa* C1501 and Tween 80. The

Table 5. **Action of surface-active substances synthesized by *A. calcoaceticus* IMV B-7241, *N. vaccinii* IMV B-7405 and *R. erythropolis* Ac-5017 on some microorganisms**

Strain	Carbon source in the culture medium	Minimum inhibitory concentration (μg/ml) against					
		Bacillus subtilis BT-2	*Enterobacter cloaceae* C-8	*Staphylococcus aureus* BMS-1	*Proteus vulgaris* PA-12	*Escherichia coli* IEM-1	*Candida albicans* D-6
A. calcoaceticus IMV B-7241	Ethanol	14	56	14	14	28	N.d.
	Purified glycerol	4	2	4	N.d.	2	2
	Waste of biodiesel production	16	4	8	N.d.	4	16
	Refined sunflower oil	50	25	14	1.8	0.9	25
	Waste sunflower oil	20	20	2.5	2.5	1.3	40
N. vaccinii IMV B-7405	Purified glycerol	45	180	90	90	45	45
	Waste of biodiesel production	15	120	15	60	30	30
	Refined sunflower oil	20	160	80	80	10	40
	Waste sunflower oil	18	140	70	70	9	35
R. erythropolis IMV Ac-5017	Ethanol	60	240	N.d.	N.d.	15	>480
	Purified glycerol	15.6	N.d.	62.5	62.5	250	N.d.
	Waste of biodiesel production	62.5	N.d.	125	31	125	N.d.

Note. N.d. — not determined

research showed that surfactants of strain C1501 were more effective antimicrobial agents compared to the chemical analogue. Thus, growth inhibition zones for *S. aureus, B. cereus* and *E. coli* with addition of 3 % rhamnolipid solution were 20–22 mm, and that of Tween at similar concentrations was only 5 mm.

Rhamnolipids action on fungi. Our paper [28] provides information on the antifungal activity of rhamnolipids aimed to manage the spread of phytopathogenic fungi, so our current review shall focus on further work.

Yan et al. [70] studied the effect of rhamnolipids of *P. aeruginosa* ZJU-211 on the phytopathogenic fungus *Alternaria alternata.* They found that at 125 μg/ml surfactant, growth of the fungus was inhibited only by 26.6%, and at 250 μg/ml rhamnolipids, by 40%. Raising the rhamnolipids concentration to 400–1000 μg/ml was followed by inhibition of the pathogenic spore germination by 64–81.7%. Treating tomatoes, infected with *A. alternata,* with the mixture of rhamnolipids (500 μg/ml) and laurel oil (500 μg/ml) decreased the degree of infection to 43 %.

At 200 μg/ml, the surfactant complex and fractions of mono- and dirhamnoliipds of *P. aeruginosa* KVD-HM52 inhibited the growth of *F. oxysporum* NCIM1072 by 95 and 84%, respectively [71]. MIC of purified rhamnolipids against the micromycete was only 50 μg/ml.

Another study [72] considered the antifungal activity of rhamnolipids produced by *P. aeruginosa* No. 112 against *Aspergillus niger* MUM 92.13 and *Aspergillus carbonarius* MUM 05.18. It was established that the dirhamnolipids were responsible for the antifungal activity, while monorhamnolipids demonstrated weak inhibiting action. Besides that, the authors showed that adding NaCl to purified mono- and dirhamnolipids increased their antifungal effect. Thus, the mixture of dirhamnolipids of 0.375 g/l and 875 mM

NaCl fully inhibited growth of test cultures of *A. niger* MUM 92.13, while pure dirhamnolipid solution did it only by 40 %. Adding salt at the same concentration to monorhamnolipid solution was followed by inhibition of test culture only by 40 %, and monorhamnolipids without salt did not inhibit the fungal growth at all. The effect of added salt was explained by NaCl repairing structure of rhamnolipids which was disrupted in extraction from the culture medium.

Thus, research of antimicrobial activity of rhamnolipids is still fruitful. Though rhamnolipids are less efficient than lipopeptides in their antimicrobial action, they have a number of some advantages: firstly, the higher productivity of producers, and secondly, the possibility of synthesis on industrial waste, which decreased their cost.

Sophorolipid effect on microorganisms

Main producers of sophorolipids are yeasts of the genera *Candida (Starmerella), Rhodotorula,* and *Wickerhamomyces* [73]. A sophorolipid has a hydrophobic part (fatty acid) and a hydrophilic one (sophorose disaccharide with a β-1,2 bond), and sophorose can be acetylated on the 6' and/or 6'' position. The carboxyl group of the fatty acid can be free forming acid (non-lactone) structure or etherified on the 4'' position forming the lactone variant [73].

Most recent publications focused on the antimicrobial effect of sophorolipids produced by *Candida (Starmerella) bombicola* ATCC 22214 [74–79]. Thus, the authors of [74] studied antimicrobial properties of the glycolipids produced on glucose and lauryl alcohol (10%, v/v). They showed that the yeast culture on the lauryl alcohol produced lactone sophorolipids, which unlike surfactants obtained on glucose fully inhibited the growth of Gram-negative (*E. coli* ATCC 8739, *P. aeruginosa* ATCC 9027) and Gram-positive (*S. aureus* ATCC 6358, *B. subtilis* ATCC 6633) bacteria and of the yeast *C. albicans* ATCC 20910, at concentration 5–10 μg/ml. The data showed that the hydrophobic substrates are more suitable for production of sophorolipids with high antimicrobial activity.

Zhang et al. [75] analysed the antimicrobial activity of sophorolipids produced by *C. bombicola* ATCC 22214 on glucose with added palmitic, stearic and oleic acids as precursors. Irrespectively of the culture conditions, sophorolipids almost did not vary in antimicrobial activity against *Salmonella* spp. and *Listeria* spp.

In the paper [76] it was established that sophorolipids produced by *C. bombicola* ATCC 22214 on coconut oil had higher antimicrobial activity against *E. coli* and *S. aureus,* than if produced on corn oil. Quite probably the different antimicrobial activity of sophorolipids is caused by different length of acyl chain, yet the authors did not stress it.

Elshikh et al. [77] studied the effect of sophorolipids of *C. bombicola* ATCC 2221, on the oral pathogens. MIC of the sophorolipids against *Streptococcus mutans* DSM-20523, *Streptococcus oralis* DSM-20627; *Actinomyces naeslundii* DSM-43013, *Neisseria mucosa* DSM-4631 and *Streptococcus sanguinis* NCTC 7863 were 195, 97.5, 195, 97.5 and 195 μg/ml, respectively.

Solaiman et al. [78] studied the effect of culture condition of *S. bombicola* ATCC 22214 on its sophorolipid antimicrobial action on microbes destroying salt hides. They cultured the microbial source on medium with glucose (10 g/l) with co-substrate (2 g/l) of palmitic, stearic and oleic acids (the sophorolipids were referred to as SL-p, SL-s, SL-o). The experiments showed that MIC of SL-p and SL-o against Gram-positive (*B. licheniformis, B. pumilus, Bacillus mycoides, Enterococcus faecium, Aerococcus viridans, Staphylococcus xylosus, Staphylococcus cohnii)* and Gram-negative (*Pseudomonas luteola, Enterobacter cloacae, Enterobacter sakazakii* and *Vibrio fluvialis)* bacteria were the same (19.5 μg/ml), and MIC of SL-s were lower (4.88–9.76 μg/ml).

Later [79] the same authors studied antimicrobial action of sophorolipids of *S. bombicola* ATCC 22214 on bacteria of the genera *Lactobacillus* and *Streptococcus,* which cause dental caries. The growth of *Lactobacillus acidophilus* ATCC 4356 and *Lactobacillus fermentum* ATCC9338 was fully inhibited at 1.3 and 1.0 mg/ml sophorolipids, respectively. Meanwhile the MIC of the studied compounds against *Streptococcus mutans* ATCC 25175, *Streptococcus salivarius* ATCC 13419 and *Streptococcus sobrinus* ATCC 33478 were only 20–38 μg/ml.

In 2017, sophorolipids produced by *Rhodotorula babjevae* YS3 on a medium with glucose (10 g/l) were shown to have antifungal effect [80]. MIC against *Colletotrichum gloeosporioides* was 62 μg/ml. Comparatively, MIC against *Fusarium verticilliodes, Fusarium oxysporum* f. sp. pisi was 125 μg/ml, while that against *Corynespora cassiicola* and

Table 6. **Advantages and disadvantages of different microbial surfactants as antimicrobial agents**

Surfactant	Advantages	Disadvantages
Rhamnolipids	Possible synthesis on industrial waste; high surfactant content	Producers belong to conditionally pathogenic microorganisms; antimicrobial activity not high enough
Lipopeptides	Low minimum inhibiting concentrations against a wide range of pathogenic microorganisms	Low content of produced surfactants; narrow range of substrates for surfactant synthesis (mostly carbohydrates); antimicrobial activity depends on culture conditions
Sophorolipids	Synthesis on cheap substrates (waste oil, oil production waste); High antimicrobial activity at low surfactant concentrations	Low product yield relative to substrate; sources belong to conditionally pathogenic microorganisms; antimicrobial activity depends on culture conditions
Complex of amino- and glycolipids of strains IMV B-7241, IMV B-7405 and IMV Ac-5017	Synthesis on waste (waste oil, waste of biodiesel production); High antimicrobial activity at low surfactant content	Antimicrobial activity depends on the culture conditions

Trichophyton rubrum was much higher (2000 and 1000 μg/ml, respectively).

Therefore, the antimicrobial activity of sophorolipids is higher than that of rhamnolipids. Sophorolipids have a wide range of antimicrobial action on Gram-negative and Gram-positive bacteria and fungi. Publications of the recent years seldom show that sophorolipid antimicrobial activity depends on the culture conditions, such as the carbon source and the presence of precursors for biosynthesis.

Antimicrobial activity of Acinetobacter calcoaceticus IMV B-7241, Rhodococcus erythropolis IMV Ac-5017 and Nocardia vaccinii IMV B-7405 surfactants

We have already established [81] that chemically the surfactants of *R. erythropolis* IMV Ac-5017 are a complex of glyco- (trehalose mono- and dimycolate), neutral (cetyl alcohol, palmitic acid, methyl ester of n-pentadecane acid, mycolic acids) and phospholipids (phosphatidylglycerol, phosphotidylethanolamine). Glyco- and aminolipids were found in the surfactant of *A. calcoaceticus* IMV B-7241, and *N. vaccinii* IMV B-7405 produces a complex of neutral, glyco- and aminolipids [81].

Table 5 presents the MIC of surface-active substances produced by strains IMV Ac-5017, IMV B-7241 and IMV B-7405 on various carbon substrates against bacteria and yeasts. The data show that the antimicrobial activity of *A. calcoaceticus* IMV B-7241, *N. vaccinii* IMV B-7405 and *R. erythropolis* IMV Ac-5017 surfactants depends on the culture conditions, which agrees with data obtained by other researchers in the recent reports [25, 34, 74, 76, 78]. Notably, the surfactants we studied had no higher MIC then described elsewhere.

* * *

We analysed the recent literature on the antimicrobial properties of suface-active substances produced by different groups of microorganisms as an alternative for antibiotics, chemical biocides and desinfectants. The as-yet few papers and our own results do support the necessity of studying the influence of culture conditions on antimicrobial activity of the synthesized surfactants.

The well-known microbial surfactants are compared in Table 6. It shows that the microbial surfactants have their advantages and disadvantages. A strong advantage is the possibility for culturing on industrial waste, which not only lowers the production cost but helps utilize waste of other industries.

The dependency of the substances' antimicrobial activity on the culture conditions can be regulated by chemical modification [82, 83], by genetically [58, 84, 85] and methabolically [86, 87] engineering strains, and by implementing physiological approaches described in [88–90].

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АНТИМІКРОБНА АКТИВНІСТЬ ПОВЕРХНЕВО-АКТИВНИХ РЕЧОВИН МІКРОБНОГО ПОХОДЖЕННЯ

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Метою роботи було проаналізувати літературу останніх років щодо антибактеріальної та антифунгальної активності мікробних поверхнево-активних речовин (ПАР) (ліпопептидів, синтезованих представниками родів *Bacillus, Paenibacillus, Pseudomonas, Brevibacillus,* рамноліпідів бактерій родів *Pseudomonas, Burkholderia, Lysinibacillus,* софороліпідів дріжджів родів *Candida* (*Starmerella* та *Rhodotorula*), а також дані власних експериментальних досліджень антимікробної активності ПАР, синтезованих *Acinetobacter calcoaceticus* IMB B-7241, *Rhodococcus erythropolis* IMB Ac-5017 і *Nocardia vaccinii* IMB B-7405. Проведений аналіз показав, що ліпопептиди є ефективнішими антимікробними агентами порівняно з гліколіпідами. Мінімальні інгібувальні концентрації (МІК) ліпопептидів, рамноліпідів і софороліпідів становлять у середньому (мкг/мл): 1–32, 50–500 і 10–200 відповідно. МІК поверхнево-активних речовин, синтезованих штамами IMB B-7241, IMB Ac-5017 і IMB B-7405, — у межах, визначених для відомих ліпопептидів та гліколіпідів. Перевагами гліколіпідів як антимікробних агентів порівняно з ліпопептидами є можливість їх синтезу на промислових відходах і висока концентрація синтезованих ПАР. Нечисленні дані літератури і власні результати авторів свідчать про необхідність проведення досліджень щодо впливу умов культивування на антимікробну активність цільового продукту.

Ключові слова: мікробні ліпопептиди, рамноліпіди та софороліпіди, антибактеріальна та антифунгальна активність.

АНТИМИКРОБНАЯ АКТИВНОСТЬ ПОВЕРХНОСТНО-АКТИВНЫХ ВЕЩЕСТВ МИКРОБНОГО ПРОИСХОЖДЕНИЯ

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Целью работы был анализ данных литературы последних лет относительно антибактериальной и антифунгальной активности микробных поверхностно-активных веществ (ПАВ) (липопептидов, синтезированных представителями родов *Bacillus, Paenibacillus, Pseudomonas, Brevibacillus,* рамнолипидов бактерий родов *Pseudomonas, Burkholderia, Lysinibacillus,* софоролипидов дрожжей родов *Candida* (*Starmerella* и *Rhodotorula*), а также собственных экспериментальных исследований антимикробной активности ПАВ, синтезированных *Acinetobacter calcoaceticus* IMB B-7241, *Rhodococcus erythropolis* IMB Ac-5017 и *Nocardia vaccinii* IMB B-7405. Проведенный анализ показал, что липопептиды являются более эффективными антимикробными агентами по сравнению с гликолипидами. Минимальные ингибирующие концентрации (МИК) липопептидов, рамнолипидов и софоролипидов составляют в среднем (мкг/мл): 1–32, 50–500 и 10–200 соответственно. МИК поверхностно-активных веществ, синтезированных штаммами IMB B-7241, IMB Ac-5017 и IMB B-7405, находятся в пределах, установленных для известных липопептидов и гликолипидов. Преимуществами гликолипидов как антимикробных агентов по сравнению с липопептидами являются возможность их синтеза на промышленных отходах и высокая концентрация синтезированных ПАВ. Немногочисленные данные литературы и собственные результаты авторов свидетельствуют о необходимости проведения исследований влияния условий культивирования продуцентов на антимикробную активность целевого продукта.

Ключевые слова: микробные липопептиды, рамнолипиды и софоролипиды, антибактериальная и антифунгальная активность.

The research was performed within the projects of the Ministry of Education and Science of Ukraine "Physiological basis of regulation of microbial synthesis as a basis for creating biotechnologies of complex drugs with stable polyfunctional properties" (2016-2018). State registration 0116U001530 and "Complex microbial drugs for multifunction and properties to the prospects of practical use "(2019-2021), State registration 0119U002575.