ANTIMICROBIAL ACTIVITY OF SURFACTANTS OF MICROBIAL ORIGIN

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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, rhamnolipids 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-H20-1 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 lipopeptides 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 trypsin (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 citrus, 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 SCR11043 (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
was seen at the highest studied surfactant concentration [36].

For the action surfactin of \textit{B. amyloliquefaciens} ST34 at concentration 0.26 mg/ml, growth inhibition zones in different strains of \textit{Candida albicans} and \textit{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 \textit{B. amyloliquefaciens} S499 on the phytopathogenic fungus \textit{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 \textit{B. amyloliquefaciens} S499 and \textit{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 \textit{Bacillus amyloliquefaciens} UCMB5113 synthesized 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 \textit{Alternaria brassicicola}, \textit{Alternaria brassicae}, \textit{Botrytis cinerea}, \textit{Sclerotinia sclerotiorum} and \textit{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.

\textbf{Antimicrobial effect of lipopeptides produced by other microorganisms}

Representatives of the genera \textit{Paenibacillus} [16, 39–41], \textit{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. MS1, 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** against strains of the lipopeptide MAC-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-11) 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 amritosarensis* 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** sp. **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 S. epidermidis 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 shown 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 rhamnolipid, one or two rhamnoses are bound to one, two or seldom three molecules of β-hydroxyaliphatic 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>
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<tr>
<th>Test culture</th>
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<td><em>Bacillus laterosporus</em> OSY-I1</td>
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<td>MIC, μg/ml</td>
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<tr>
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<td>[38]</td>
</tr>
<tr>
<td></td>
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<td>32</td>
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<td></td>
<td><em>Paenibacillus thiaminolyticus</em> OSY-SE</td>
<td>64</td>
<td>[38]</td>
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<tr>
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<td><em>Salmonella typhimurium</em> DT 109</td>
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<td>&gt;32</td>
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<td><em>Bacillus laterosporus</em> OSY-I1</td>
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<td>[40]</td>
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<td><em>Streptococcus agalactiae</em></td>
<td><em>Paenibacillus</em> sp. OSY-N (paenipeptin C)</td>
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<td>25 000</td>
<td>[41]</td>
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<tr>
<td><em>Lactobacillus plantarum</em> ATCC 8014†</td>
<td><em>Bacillus laterosporus</em> OSY-I1</td>
<td>1</td>
<td>[40]</td>
</tr>
</tbody>
</table>
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.
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
research showed that surfactants of strain C1501 were more effective antimicrobial agents compared to the chemical analogue. Thus, growth inhibition zones for \textit{S. aureus}, \textit{B. cereus} and \textit{E. coli} with addition of 3\% rhamnolipid solution were 20–22 mm, and that of Tween at similar concentrations was only 5 mm.

\textbf{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 \textit{P. aeruginosa} ZJU-211 on the phytopathogenic fungus \textit{Alternaria alternata}. They found that at 125 \(\mu\)g/ml surfactant, growth of the fungus was inhibited only by 26.6\%, and at 250 \(\mu\)g/ml rhamnolipids, by 40\%. Raising the rhamnolipids concentration to 400–1000 \(\mu\)g/ml was followed by inhibition of the pathogenic spore germination by 64–81.7\%. Treating tomatoes, infected with \textit{A. alternata}, with the mixture of rhamnolipids (500 \(\mu\)g/ml) and laurel oil (500 \(\mu\)g/ml) decreased the degree of infection to 43\%.

At 200 \(\mu\)g/ml, the surfactant complex and fractions of mono- and dirhamnolipids of \textit{P. aeruginosa} KVD-HM52 inhibited the growth of \textit{F. oxysporum} NCIM1072 by 95 and 84\%, respectively [71]. MIC of purified rhamnolipids against the micromycete was only 50 \(\mu\)g/ml.

Another study [72] considered the antifungal activity of rhamnolipids produced by \textit{P. aeruginosa} No. 112 against \textit{Aspergillus niger} MUM 92.13 and \textit{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

<table>
<thead>
<tr>
<th>Strain</th>
<th>Carbon source in the culture medium</th>
<th>Minimum inhibitory concentration ((\mu)g/ml) against</th>
</tr>
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<tr>
<td></td>
<td></td>
<td>\textit{Bacillus subtilis} BT-2 \textit{Enterobacter cloacae} C-8 \textit{Staphylococcus aureus} BMS-1 \textit{Proteus vulgaris} PA-12 \textit{Escherichia coli} IEM-1 \textit{Candida albicans} D-6</td>
</tr>
<tr>
<td>\textit{A. calcoaceticus IMV B-7241} Ethanol</td>
<td>14</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Purified glycerol</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Waste of biodiesel production</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Refined sunflower oil</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>Waste sunflower oil</td>
<td>20</td>
</tr>
<tr>
<td>\textit{N. vacciniii IMV B-7405} Purified glycerol</td>
<td>45</td>
<td>180</td>
</tr>
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<tr>
<td></td>
<td>Refined sunflower oil</td>
<td>20</td>
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<tr>
<td></td>
<td>Waste sunflower oil</td>
<td>18</td>
</tr>
<tr>
<td>\textit{R. erythropolis IMV Ac-5017} Ethanol</td>
<td>60</td>
<td>240</td>
</tr>
<tr>
<td></td>
<td>Purified glycerol</td>
<td>15.6</td>
</tr>
<tr>
<td></td>
<td>Waste of biodiesel production</td>
<td>62.5</td>
</tr>
</tbody>
</table>

\textit{Note.} N.d. — not determined
NaCl fully inhibited growth of test cultures of *A. niger* MUM 92.13, while pure dirhamnolid solution did it only by 40%. Adding salt at the same concentration to monohammolnolid solution was followed by inhibition of test culture only by 40%, and monohammolnolipids 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 \( \beta\)-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. Irrespective 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 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
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 (phosphatidyglycerol, 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 surface-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 metabolically [86, 87] engineering strains, and by implementing physiological approaches described in [88–90].
REFERENCES


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 Actinobacter calcoaceticus IMВ В-7241, Rhodococcus erythropolis IMB Ac-5017 і Nocardia vaccinii IMВ B-7405. Проведений аналіз показав, що ліпопептиди є ефективнішими антимікробними агентами порівняно з гліколіпідами. Мінімальні інгібуючі 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 IMВ В-7241, IMВ Ac-5017 і IMВ B-7405, — у межах, визначених для відомих ліпопептидів та гліколіпідів. Певними гліколіпідами 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.