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SULFUR REDUCING ACTIVITY OF THE *DESULFUROMONAS ACETOXIDANS* IMV B-7384 UNDER DIFFERENT CULTIVATION CONDITIONS

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The main goal of the work was to study sulfur reducing activity of *Desulfuromonas acetoxidans* IMV B-7384 under different cultivation conditions. Sulfur-reducing bacteria *Desulfuromona acetoxidans* IMV B-7384 and *Desulfuromonas* sp., isolated from water and soil in Yazivske sulfur deposit were used during the reasearch. Bacteria were grown in a medium Postgate C without sulfates. The sulfur reducing activity was determined by the amount of formed hydrogen sulfide, which was synthesed during the reaction. One unit of enzyme activity is defined as the 1 μM of H_2S per min. Bacteria *D. acetoxidans* IMV B-7384 carry out the dissimilatory sulfur reduction using elemental sulfur and polysulfide as electron acceptors. Bacteria accumulated up to 2.6 mM hydrogen sulfide in the medium with sulfur and 0.93 mM of hydrogen sulfide in the medium with polysulfide. Sulfur reducing activity of bacteria *D. acetoxidans* IMV B-7384 is 1.5 times higher than sulfur reducing activity of *Desulfuromonas* sp. Maximal sulfur reducing activity occurs on the seventh day during the stationary phase of growth and can be 23.6 units/mg. Sulfur reductase of bacteria *D. acetoxidans* IMV B-7384 is sensitive to oxygen. It was established that sulfur reductase of *D. acetoxidans* IMV B-7384 is inducible enzyme, which synthesed under the presence of elemental sulfur in the media. It was also established that the maximal sulfur reducing activity of the bacteria *D. acetoxidans* IMV B-7384 was observed at a temperature of 30 °C and pH 7.5. The donor of reducing equivalents for sulfur reductase is $NADH^+$ and $NADPH^+$. Km sulfur reductase was 0.65±0.08 mM, Vmax – 3.48±0.12 units/mg.

Keywords: sulfur reducing activity, sulfur reductase, hydrogenase.

Sulphur as one of the biogenic elements is a nutrient component in the metabolism of all living organisms. It is a part of amino acids (0.8–2.4 %), vitamins, nucleotides and herbal essential oils. Therefore the sulfur cycle plays a significant role for sustaining life on Earth. Sulfur is an element of variable valence, so it can involved in a variety redox reactions. The majority of these reactions occurs in nature involving living organisms. The significance of these reactions for different organisms varies – for some organisms oxidation of recovered sulfur compound is an energy source for other the oxidation products of these reactions are used in the processes of catabolism [6]. And the microorganisms utilize different organic compounds and molecular hydrogen using them as terminal acceptors of electrons in the process of anaerobic respiration various sulfur compounds (sulphate, sulphite, thiosulphate, organic sulphoxides, elemental sulfur, polysulfides, organic disulfides, etc.) and reduce them primarily to hydrogen sulfide [10].

The oxidation and reduction of sulfur compounds is an important part of the natural sulfur cycle [8]. The ability to reduce an elemental sulfur to hydrogen sulfide was found in different typies of microorganisms that inhabit the anoxic areas of freshwater and sea, rich in sulfur soil and hydrothermal streams (wellsprings) [1, 20].The representatives of mesophilic δ-Proteobacteria (*Desulfovibrio vulgaris*, *Pelobacter carbinolicus*, *Geobacter sulfurreducens*), thermophilic δ-Proteobacteria (*Desulfurella acetivorans*), γ-Proteobacteria (*Shewanella putrefaciens*), ε-*Proteobacteria* (*Wolinella succinogenes*), and also the representatives of cyanobacteria

(«*Oscillatoria limnetica*») and heperthermophilic archaea (*Pyrococcus furiosus*, *Acidianus ambivalens*) are able to reduce an elemental sulfur [1, 7, 16, 24].

Animals and plants use sulfur in the form of ions SO_4^{2-} [15, 18]. Microorganisms use various organic and inorganic compounds of sulfur, therefore microorganisms provide the most processes of the sulfur cycle [6].

Sulfur cycle, which is carried out by microorganisms, is divided into following stages: 1) oxidation of reduced forms of sulfur; 2) reducing of oxidized form of sulfur 3) conversion of sulfur without changing the degree of its oxidation [10].

The abundance of sulfur in the earth's crust is 0,05 % [12, 18]. In nature it can occure in free and chemically bound condition. Sulfur ores contain the natural free sulfur. The part of free sulfur in its amount in the earth´ crust is very small. It can be in colloidal and crystalline states and its solubility in water is very low [10, 25]. The significant amount of sulfur is chemically bound and occurs in form of sulfide – ions (sulfide sulfur) and sulphate – ions (sulphate sulfur) contained in natural minerals and different kinds of fuels [10].

Reducing of elemental sulfur is provided by involvement of two enzymes – sulfur reductase (EC 1.97.1.3) and polysulfide reductase (EC 1.12.98.4), which are located in the cytoplasmic membrane and bounded with hydrogenase by cytochromes or quinines [2, 7, 11, 18, 24].

The ways of reduction of elemental sulfur to hydrogen sulfide by mesophilic and thermophilic microorganisms haven't been explored in detail. The sulfur reductase and polysulfide reductase were found in the most described types of sulfur reducing bacteria [9, 14, 24]. Polysulfide reductase from *Wolinella succinogenes* includes hydrophilic and hydrophobic subunits, which help the transfer of electrons from hydrogenase through cytochromes *b* and quinone, creating an electrochemical gradient [7, 19, 24].

Similar multienzyme sulfur-reducing complexes were found in thermophilic bacterias *Pyrococcus furiosus* and *Pyrodictium abyssi* [3, 14, 19].

The goal of the work is to research the sulfur reducing activity of the *Desulfuromonas acetoxidans* IMV B-7384 under different cultivation conditions.

Materials and methods

Sulfur-reducing bacteria *Desulfuromonas acetoxidans* IMV B-7384 and *Desulfuromonas* sp. isolated from water and soil in Yazivske sulfur deposit, were used during the research [4]. These bacteria were grown in the medium Postgate C [17] without sulfates with such ingredients (g/l): KH_2PO_4 – 0.5; NH_4CL – 1.0; $CaCL_2$ x $6H_2O$ – 0.06; $MgCL_2$ x 6 H_2O – 0.05; sodium lactate (40 %) – 12 ml; yeast extract – 1.0; sodium citrate – 0.3; ascorbic acid – 1.0; elemental sulfur – 1.0, distilled water to 1 liter; pH 7.5 [17]. The medium was sterilized at 1 atm for 30 minutes and poured into the tubes (25 ml), closed with sterile rubber stoppers, so that they had no air. A medium was seeded with cell suspension (0.3 g/l) and cultured at 30 °C during 5 days. For the research of enzyme activity under various culture conditions, sodium acetate instead of sodium lactate, fumarate in an amount of 6 g/l, was added in the medium. Polysulfide solution was prepared in such way: 24 g Na_2S x $9H_2O$ and 7.2 g flowers of sulfur was added to water to yield a final volume of 100 ml. The suspension was heated in a boiling water bath and stirred until the sulfur has dissolved. The polysulfide solution was sterilized at 1 atm for 30 minutes in the closed bottle [23].

To determine sulfur reducing activity in culture liquid, cells were separated from the medium by centrifugation at 4000 g for 30 min. The cells were washed twice with 10 mM potassium phosphate buffer, pH 7.5, and destroyed by ultrasound homogenizer UZDN-2T at frequency of 22 kHz for 5 minutes. The supernatant was separated by centrifugation from cell extract at 9.000 g for 30 minutes, free-cellular extract was resuspended in extracted buffer (50 mM potassium phosphate buffer, pH 7.5; 10^{-5} M EDTA (ethylenediaminetetraacetate) 10^{-5} M PMSF (phenyl-

methylsulfonyl fluoride). The activity of enzyme was determined by the amount of formed hydrogen sulfide that was synthesed during the reaction [21]. The reaction mixture, in which sulfur reducing activity was measured, had the following composition: 3.7 mM potassium phosphate buffer (pH 7.5), 1 mM $NADH^+$, 1 mM EDTA, and 1 mM glycerol; elemental sulfur – 0.04 g, culture liquid – 400 ml in a total volume1.2 ml. For studying the sulfur reducing activity in free-cellular extracts and supernatant, potassium phosphate buffer (pH 7.5) in an amount of 720 ml and free-cellular extracts and supernatant in an amount of 120 ml were added in the reaction mixture. Sulfur reducing activity was determined under anaerobic conditions. The reaction mixture was transferred to a test tubes, filled with argon. The incubation time was 10 min. The reaction was started by adding $NADH^+$ and was stopped by adding 2 M NaOH (0.4 ml). The content of hydrogen sulfide was determined by formation of methylene blue [22]. One unit of enzyme activity is defined as the 1 μM of H_2S per min. For observing the effect of pH on the activity of the enzyme, different buffers were used: 0.1 M glycine-HCL buffer, pH 2.2 – 3; 0.1 M sodium acetate buffer, pH 4 – 5; 0.1 M potassium phosphate buffer, pH 6 – 8; 0.1 M glycine-NaOH buffer, pH 9 – 10. The enzyme activity was determined by the temperature of 30 °C after the incubation of culture liquid in buffer for 20 minutes.

Protein concentration was determined by Lowry method [13].

The results are represented as mean adjusted with standard error (M±m). Statistical analysis of the results was performed using the programme "Microsoft Excel 2010", "Origin 6.1".

Results and discussion

The solubility of elemental sulfur in water at 25 °C is very low. In an aqueous sulfide solution sulfur turns into a hydrophilic form – polysulfide [7]. These polysulfides are used by sulfur-reducing bacteria involving key enzyme of the sulfur respiration – sulfur reductase. Therefore the accumulation of biomass and hydrogen sulfide of bacteria *D. acetoxidans* IMV B-7384 in the presence of elemental sulfur and polysulfide were explored.

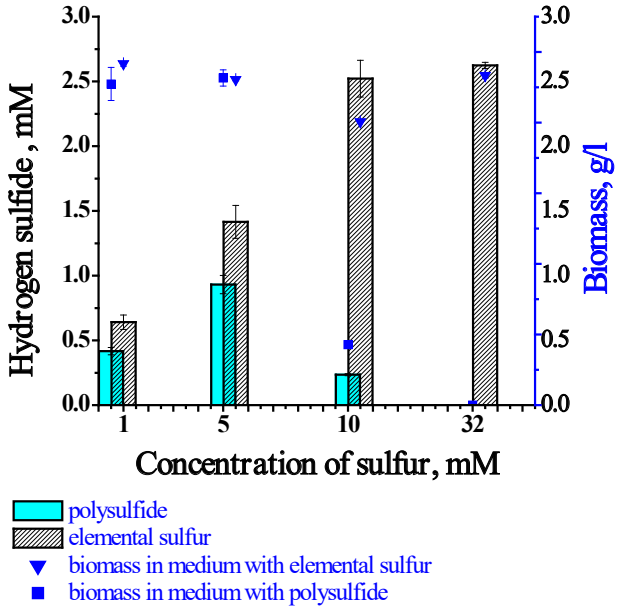


Fig. 1. The accumulation of biomass and hydrogen sulfide by bacteria *D. acetoxidans* IMV B-7384 in the presence of elemental sulfur and polysulfide

The results showed that in the medium with elemental sulfur bacteria produce 1.5 times more hydrogen sulfide than in the medium with polysulfide. At increasing concentration of hydrogen sulfide the concentration of sulfur increases (Fig. 1). The maximal concentration of hydrogen sulfide was 2.6 mM. The accumulation of biomass at growth on sulfur with concentration from 1 mM to 32 mM remains unchanged. Maximal accumulation of biomass and hydrogen sulfide in the medium were observed at concentrations of 5 mM polysulfide. Accumulation of hydrogen sulfide and biomass were not observed at the concentration of polysulfide 10 mM and higher.

In subsequent experiments sulfur reducing activity of *D. acetoxidans* IMV B-7384 and *Desulfuromonas* sp. at the presence of elemental sulfur was researched. It is known that in cells of *Wolinella succinogenes* and *Aquifex aeolicus* polysulfide reductase and sulfur reductase are localized in the cytoplasmic membrane bound with hydrogenase by cytochromes or quinones [5, 7]. In *W. succinogenes* polysulfide reducing occurs in the periplasm, because polysulfide reductase is localised on the exterior side of the membrane [7, 18, 24]. Hyperthermophilic chemolithoautotrophic bacteria *A. aeolicus* occurs the reducing of sulfur in the cytoplasm [5].

To determine the localisation of the enzyme in *D. acetoxidans* IMV B-7384 and *Desulfuromonas* sp., sulfur reducing activity in the culture liquid and soluble sedimentary fractions (Fig. 2) was determined. The results of investigation show that the highest sulfur reducing activity was found in both bacteria in the culture liquid. In sedimentary fraction sulfur reducing activity was 40 times lower and in the soluble fraction it was not detected (Fig. 2). That is why the bacterial sulfur reductase of *D. acetoxidans* IMV B-7384 and *Desulfuromonas* sp. are localized in the cytoplasmic membrane and excreted by bacteria in the extracellular environment. Sulfur reducing activity of *D. acetoxidans* IMV B-7384 was detected in the culture liquid and sedimentary fraction in 1.5 times higher than sulfur reducing activity of *Desulfuromonas* sp. and was equaled to 70 and 1.7 units/mg, respectively. In further experiments sulfur reducing activity in the culture liquid in *D. acetoxidans* IMV B-7384 was researched.

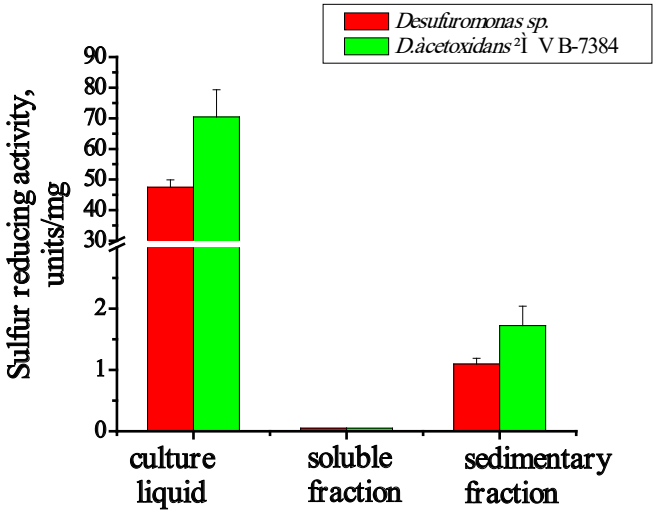


Fig. 2. Sulfur reducing activity of *Desulfuromonas* sp. and *D. acetoxidans* IMV B-7384 in various fractions

The growth and sulfur reducing activity of *D. acetoxidans* IMV B-7384 depending on the time of cultivation were studied. Maximal sulfur reducing activity was observed in the fourth-sixth days of cultivation and the transition of culture in the stationary phase decreases rapidly (Fig. 3).

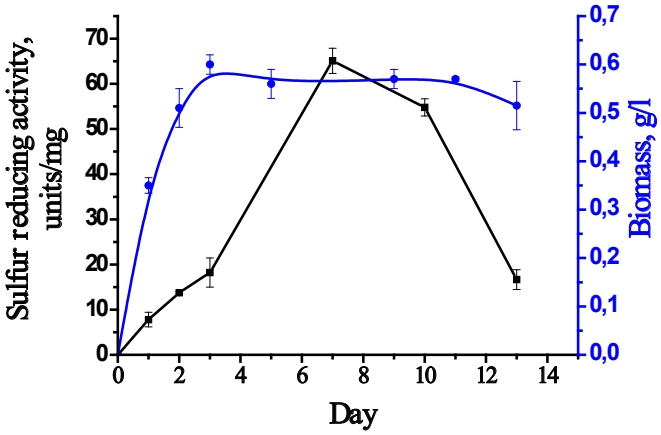
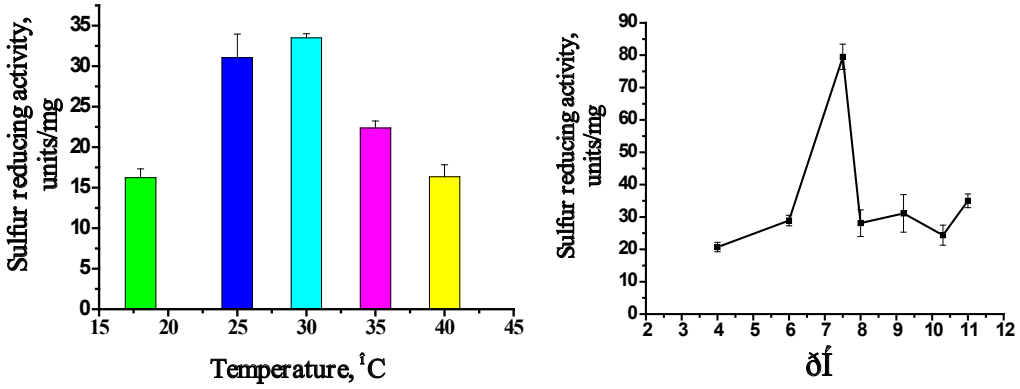


Fig. 3. The accumulation of biomass (- ● -) and sulfur reducing activity (- ■ -) in the culture liquid *D. acetoxidans* IMV B-7384

The effect of pH and temperature on sulfur reducing activity in the culture liquid were studied. It was established that the maximal sulfur reducing activity was at a temperature of 30 °C and pH 7.5 (Fig. 4, 5).



a b

Fig. 4. The effect of temperature (a) and pH (b) on sulfur reducing activity of bacteria *D. acetoxidans* IMV B-7384

To understand the properties of sulfur reducing activity of *D. acetoxidans* IMV B-7384, the influence of various abiotic factors on enzyme activity was examined. It was also established that under anaerobic conditions sulfur reducing activity was 12.36 units/mg. After exposure of the culture liquid by air on circular shaker during one hour the activity decreased twice. Sulfur reducing activity was not detected, when culture liquid have been heated to 80 °C for 10 minutes in atmosphere of argon (Table 2).

The almost double decrease of sulfur reducing activity under aerobic condition indicates its sensitivity to oxygen. *Yong K*. and others showed that sulfur reducing activity of iron-oxidizing bacteria *Thiobacillus ferrooxidans* NASF-1 was not stable under aerobic conditions, but relatively stable in the presence of sodium and hydrogen sulfide under anaerobic conditions [26].

Data presented in the table 3 show that the sulfur reducing activity of *D. acetoxidans* IMV B-7384 in the presence of various reducing equivalents donors in medium. The data showed that

sulfur reducing activity in the presence of $NADPH^+$ was higher (24.5±4.2 units/mg), and about two times lower in the presence of $NADH^+$. In the presence $FADH_2$ sulfur reducing activity was not detected (Table 3).

Table 1

Sulfur reducing activity of bacteria *D. acetoxidans* IMV B-7384 under different conditions incubation

Conditions of incubation	Sulfur reducing activity	
	units	units/mg
Control (anaerobic)	4.45±0.32	12.36±0.89
Aeration for one hour	2.29±0.8	6.36±1.04
Heating to 80 °C under anaerobic conditions	–*	–*

Note: * No enzyme activity.

Table 2

Sulfur reducing activity of bacteria *D. acetoxidans* IMV B-7384 in the presence of various reducing equivalents donors

Electron acceptor	Donors reducing equivalents	Sulfur reducing activity units/mg
S^0	$NADH^+$	11.2±0.26
	$NADH^+$	24.5±4.2
	$FADH_2$	–*

Note: * No enzyme activity.

D. acetoxidans IMV B-7384 used acetate and lactate as electron donor and S^0 and fumarate as acceptor [4]. To determine, whether sulfur reductase is inducible enzyme, bacteria were grown in different mediums with acetate, lactate, fumarate and S^0. In the media with acetate and fumarate and fumarate alone, sulfur reducing activity was absent (tab. 4). Enzyme activity was detected in bacteria *D. acetoxidans* IMV B-7384 cultivated in media with lactate, acetate and sulfur. Thus, the obtained results indicate that sulfur reductase was synthesed in the presence of elemental sulfur in the media. This observation confirmed that is inducible enzyme.

Table 3

Sulfur reducing activity of bacteria *D. acetoxidans* IMV B-7384 under different culture conditions

Electron donor	Electron acceptor	Sulfur reducing activity, units/mg
lactate	S^o	16.76±1.4
acetate	S^o	64.74±0.86
acetate	fumarate	–*
fumarate	fumarate	–*

Note: * No enzyme activity.

The research of the major kinetic parameters of sulfur reductase of *D. acetoxidans* IMV B-7384 in the sedimentary fraction shows that at the temperature 30 °C and pH of 7.5 Km was 0.65±0.078 μM, Vmax – 3.48±0.12 units/mg.

Research of the optimal conditions for sulfur reducing activity of *D. acetoxidans* IMV B-7384 might be prospective for further research and practical applications

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СУЛЬФУРРЕДУКТАЗНА АКТИВНІСТЬ *DESULFUROMONAS ACETOXIDANS* ІМВ В-7384 ЗА РІЗНИХ УМОВ КУЛЬТИВУВАННЯ

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Метою роботи було дослідити сульфурредуктазну активність у бактерій *Desulfuromonas acetoxidans* ІМВ В-7384 залежно від умов культивування. У роботі використовували сірковідновлювальні бактерії *Desulfuromonas acetoxidans* ІМВ В-7384 і *Desulfuromonas* sp., виділені з водойм Язівського сіркового родовища. Бактерії вирощували у середовищі Постгейта С без сульфатів. Активність ферменту визначали за кількістю утвореного гідроген сульфіду, що синтезувався в ході реакції. Активність ферменту виражали в мкМ H_2S/ хв. Досліджено сульфурредуктазну активність *D. acetoxidans* ІМВ В-7384 та *Desulfuromonas* sp. Бактерії *D. acetoxidans* ІМВ В-7384 здійснюють дисиміляційну сіркоредукцію, використовуючи елементну та полісульфідну форми сірки. У середовищі з елементною сіркою бактерії нагромаджують до 2,6 мМ гідроген сульфіду, а з полісульфідом – 0,93 мМ. Сульфурредуктазна активність бактерій *D. acetoxidans* ІМВ В-7384 у 1,5 разу вища за сульфурредуктазну активність *Desulfuromonas* sp. Максимальна, сульфурредуктазна активність припадає на сьому добу в період стаціонарної фази росту і становить 23,6 од/мг білка. Сульфурредуктаза бактерій *D. acetoxidans* ІМВ В-7384 чутлива до кисню. Досліджено, що сульфурредуктаза бактерій *D. acetoxidans* ІМВ В-7384 є індуцибельним ферментом, синтезується за наявності у середовищі елементної сірки. Оптимальною для сульфурредуктазної активності бактерій *D. acetoxidans* ІМВ В-7384 є температура 30 °С і pH 7,5, донором відновних еквівалентів – $НАДН^+$ і $НАДФН^+$. Km ферменту становить 0,65±0,08 мкМ, Vmax 3,48±0,12 од/мг білка.

Ключові слова: сульфурредуктазна активність, сульфурредуктаза, гідрогеназа.