

ACTIVITY CHARACTERISTICS OF SULFATE REDUCING BACTERIA AND FORMATION MECHANISM OF HYDROGEN SULFIDE

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(Received 31st May 2018; accepted 13th Sep 2018)

Abstract. Various anaerobic environments exist in the Earth's ecosystem, which can produce a great deal of organic matter each year. In anaerobic habitats, bacterial sulfate reduction may occur due to the action of sulfate-reducing bacteria. As a result, hydrogen sulfide (H₂S) is formed. This paper focuses on sulfate-reducing bacteria and the revision of the activity characteristics of these bacteria in the reducing environment. It discusses the metabolic process of sulfate-reducing bacteria using sulphate and organo-sulfur compounds as sulfur source, the mechanism of bacterial sulfate reduction and H₂S formation mechanism. There are two main ways of H₂S formation in sulfate-reducing bacteria, the production of metabolic sulphate and the metabolic organo-sulfur compounds (mainly cysteine). The paper, combined with the activity characteristics of sulfate-reducing bacteria and the pathway of metabolic formation of H₂S, also discusses the circulation of sulfur in the environmental system of the Earth due to the action of sulfate-reducing bacteria, concerning the redox zone division in submarine sedimentary strata and landfills, the biogas formation phase of sulfate-reducing bacteria metabolism in sedimentary formations, and the bacterial sulfate reduction action in salt lakes (seawater) systems. Moreover, the production of hydrogen sulfide and the formation model of dolomite are both presented here. The findings support that sulfate-reducing bacteria are the most important biological source of H₂S production. The study of the physiological characteristics of sulfate-reducing bacteria and the formation mechanism of H₂S due to bacterial sulfate reduction can provide useful reference for the exploration of the laws of sulfur geochemical cycle and the rules of the ecological environment, which is essential for the protection of the natural environment and the restoration of polluted ecosystems, and can also provide a useful reference for the control of aerobic microorganisms.

Keywords: *microorganism, hydrogen sulfide (H₂S), bacterial sulfate reduction, formation mechanism*

Introduction

Hydrogen sulfide is mostly the product of the decomposition of organic matter under the microorganisms' action, the action of bacterial sulfate reduction (BSR), or the chemical process byproducts (Deng, 2017). The sulfate-reducing bacteria absorbs sulfate without the participation of oxygen, obtains energy from the oxidation of organic compound and discharges H₂S produced by the reduction of sulfate, which metabolic process is defined as bacterial sulfate reduction (Machel, 2001; Orr, 1974). The gaseous pollutant of H₂S mainly comes from man-made pollution and natural pollution. Man-made pollution mainly includes exploitation of petroleum, coal-bed methane, shale gas

etc, mining and non-ferrous metal smelting, low-temperature coking of coal, extraction of sulfur-containing substances, rubber, leather, dyes and other industrial production. Natural pollution often exists in many anaerobic environments in the Earth's ecosystems, such as underground pipeline, rice fields, industrial effluent, mud, swamps, lake bottom sediments, oil and gas wells, hot springs, landfills, and farm excretion, deposits and other venues (Martins et al., 2009).

The hazards of H₂S are mainly manifested in the following two aspects:

(1) Hazards to health. H₂S, a polar molecule, is highly toxic and flammable. It is colorless, smelly and prone to explosion. A small amount of H₂S in high concentration inhaled can be fatal to a person in a short time (Wei et al., 2014; Deng et al., 2018). And H₂S in low concentration affects the eye, respiratory and central nervous system badly. The physiological effects of H₂S concentration and contact time on human body are shown in *Figure 1* (Wei et al., 2014).

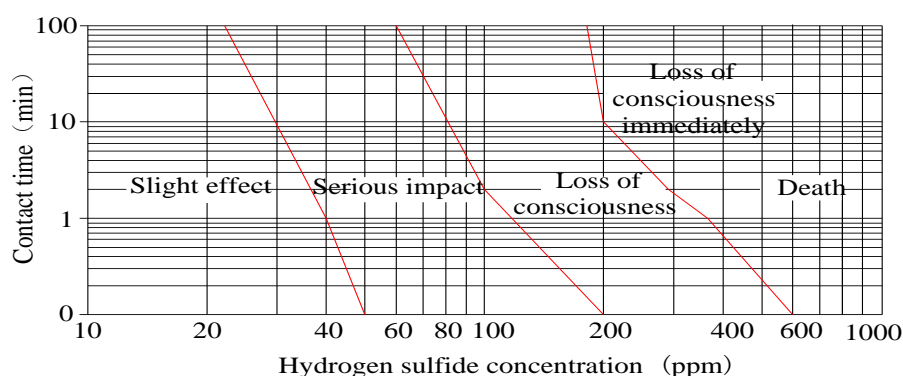


Figure 1. Physiological influence to human of H₂S

(2) Pollution to the environment. In the combustion process or in the atmosphere, H₂S will be quickly oxidized to sulfur dioxide, which will increase the concentration of SO₂ in the atmosphere to damage the plants and animals. Furthermore, it is also the main reason for the formation of acid rain (smog). Sulfate-reducing bacteria (SRB) is considered to be one of the main causes of corrosion of industrial equipment (Wei et al., 2014). H₂S in the water and air has a strong corrosion effect on concrete, electrical equipment, pipe networks, metals and plastics. When the H₂S content in the water exceeds 0.5 to 1.0 mg/L, it will cause great harm to the aquaculture (Ren et al., 2009).

H₂S is estimated to account for 100 million tons into the atmosphere per year in the world, of which about 3 million tons are produced annually by humans. The majority of the remaining H₂S produce naturally, mainly derived from the metabolic activities of producing H₂S sulfate-reducing bacteria. Therefore, SRB is the most important biological source for H₂S production. Therefore, the study on the physiological characteristics of SRB and the formation mechanism of H₂S under BSR can provide reference for revealing the laws of sulfur geochemical cycling and ecological environment.

Activity characteristics of SRB

The group SRB is heterotrophic and mixed that can utilise sulfates, sulfites, thiosulfates, sulfur, or other oxidized sulfides as electron acceptors to catabolize organic

materials and form H₂S (Gibson, 1990; Xiao et al., 2011). 18 genera and more than 40 species of SRB have been studied respectively. The names and characteristics of some genera are shown in *Table 1* (Ren et al., 2009; Liao, 2004). The common 9 genera mainly involve *Desulfovibrio* which does not produce spores and *Desulfotomaculum* which produce spores. The former is generally medium or low temperature, and it is likely to die when the temperature exceeds 43 °C. The latter is generally medium temperature or high temperature (Luptakova et al., 2005).

Table 1. Characteristics of SRB

Name	Features	Exercisability	Growth T (°C)
<i>Desulfovibrio</i>	No spores, curved rods	+	25-40
<i>Desulfomicrobium</i>	Rod-shaped, no spores	+/-	25-40
<i>Desulfobollus</i>	curved	+/-	
<i>Desulfotomaculum</i>	Straight or curved rod	+	25-40, 40-65
<i>Desulfobacter</i>	Round, rod-shaped, without spores	+/-	20-23
<i>Desulfococcus</i>	Spheroidal, no spores	-/+	28-35
<i>Desulfosarcina</i>	Stacking, without spores	+/-	33
<i>Desulfoarculus</i>	curved	+/-	
<i>Desulfomonile</i>	Rod-shaped, spheroidal	-	37
<i>Desulfobulbus</i>	Oval, shape of Lemon, No spores	-/+	25-40
<i>Desulfacinum</i>	Spheroidal or oval type		
<i>Thermodesulfobacterium</i>	Small shape, arc, rod		65-70
<i>Desulfobacula</i>	Oval		
<i>Desulfonema</i>	Screw shape, no spores	slide	28-32
<i>Desulfobacterium</i>	Round, rod-shaped	+/-	20-35

The group SRB is heterotrophic and mixed, and it survives in facultative anaerobic environment. The suitable grow temperature is between -5 and 75 °C. Some strains can grow below -5 °C, and some with spore species can withstand high temperatures of 80 °C. The optimum growth temperature for most mesophilic SRB is 28 ~ 38 °C, and some can grow in the condition of 45 °C (Larry, 1995). The surviving pH value of SRB is 4 to 9.5. Most SRBs are neutrophils. The most suitable pH is 6.5 ~ 7.8 (Vallero et al., 2005). SRB can survive in salinity greater than 1 g/L water. The best growth salinity is 100 g/L, and the upper limit reaches to 240 g/L. Some SRBs are halophilic, and they can be detected in some high-salt (such as salt lakes, the Dead Sea) ecosystems. Most of the halophilic bacteria isolated in the laboratory are mild halophilic bacteria (suitable salinity ranged from 1 to 4%), and rarely isolated moderately halophilic bacteria (Zhao et al., 1995). The growth of SRB is generally lower than -150 mV in Eh (Barton et al., 1995). Fe²⁺ is the active component of various enzymes in SRB cells. Decreasing the concentration of Fe²⁺ ions can reduce the growth rate of SRB.

The carbon sources used by different strains of SRB are different. The carbon source not only increases the amount of bioenergy required, but also acts as an electron donor to reduction and dissimilation sulfates. The most common source is the use of C₃, C₄ fatty acids. In addition, the sources as some volatile fatty acids and easily fermented substances are also applied. Stephenson et al. (Stephensonl et al., 1931) presented that

hydrogenases contained in SRBs and (Jannasch, 1988) illustrated that 33 out of 39 SRBs can absorb hydrogen at 28 °C.

Formation mechanism of H₂S by SRB

SRB can produce H₂S by assimilation of sulfates, or degradation of sulfur-containing organics (mainly cysteine). The former has a small yield and is quickly assimilated into organic sulfur compounds. The latter, with a larger yield, is the main formation of H₂S (Luhachack et al., 2014).

The metabolic mechanism of sulfate as a sulfur source

The metabolic process of SRB with sulfate as sulfur source can be divided into three stages. Decomposition, electron transfer, and oxidation, as shown in *Figure 2* (Xu et al., 2009).

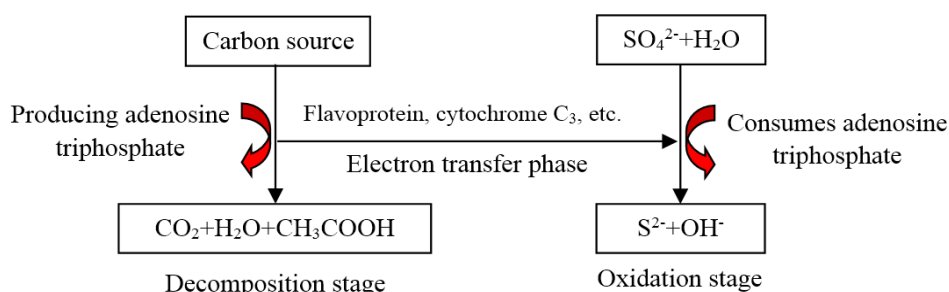
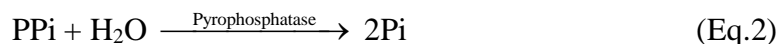
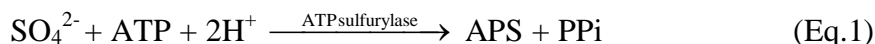


Figure 2. The metabolic process of SRB with sulfate as a sulfur source

(1) Decomposition stage. Sulfates are highly thermostable. Under anaerobic conditions, the sulfate ion (SO₄²⁻) first accumulates out of cell and then enters the cell of SRB, while organics produce adenosine triphosphate (ATP) and energetic electrons through substrate level phosphorylation. Thereafter, SO₄²⁻ is activated by ATP sulfurylase to produce pyrophosphoric acid (PPi) and adenosine-5'-phosphosulfate (APS), PPi quickly decomposed into inorganic phosphate (Pi) (Zhao et al., 1997), stepwise reaction formulas are shown *Equation 1* and *2*, and total reaction formula is shown in *Equation 3*.



(2) Electron transfer stage. In the previous stage, the energetic electrons released by energy are transferred step by step through SRB-specific electron transport chains (such as flavoprotein, cytochrome C₃, etc.). Affected by APS reductase, APS is continuously decomposed to sulfite and adenosine monophosphate (AMP). Sulfite is dehydrated into pyrosulfite (S₂O₅²⁻). S₂O₅²⁻ is extremely unstable and then would be converted to the intermediate dithionite (S₂O₄²⁻). Afterwards, S₂O₄²⁻ is rapidly reduced to trithionate

($S_3O_6^{2-}$), and $S_3O_6^{2-}$ is broken down to thiosulfate ($S_2O_3^{2-}$) and sulphite (SO_3^{2-}). The reaction formula is shown in *Equations 4–6*, and the electron transfer is shown in *Figure 3* (Bradley et al., 2011).

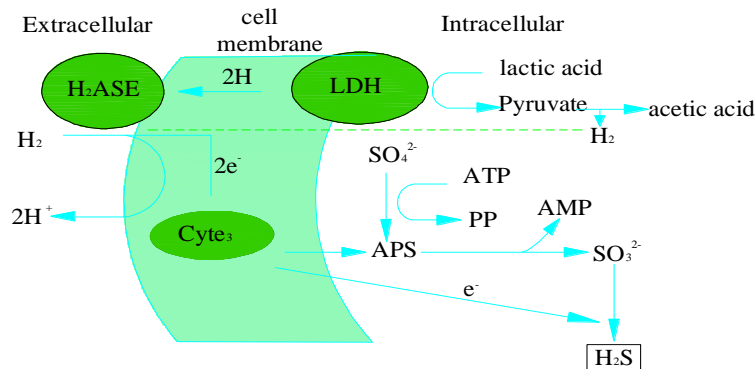
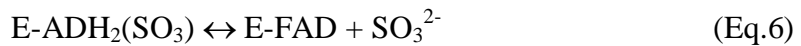
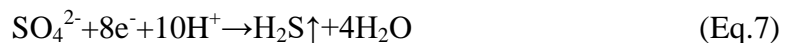
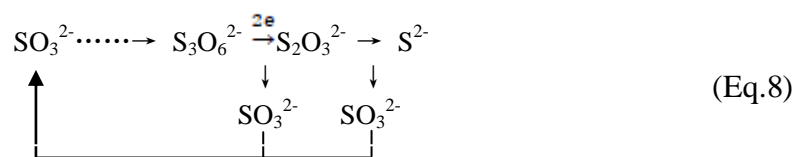


Figure 3. Electron transfer process of SRB. ATP - adenosine triphosphate; PP - Polypyrrrole; APS - adenosine-5'-phosphosulfate; AMP - adenosine monophosphate; LDH-lactate dehydrogenase

(3) Oxidation stage. The electrons are transferred to the oxidized sulfur elements ($S_2O_3^{2-}$, SO_4^{2-} , SO_3^{2-}), which consume a lot of ATP. From SO_4^{2-} to S^{2-} , there are 8 electron transfers. ATP thiokinase catalyzes the adsorption of SO_4^{2-} to ATP phosphatase, which in turn forms APS. The sulfated portion of APS is directly reduced to sulfite and releases AMP. The initial product of sulfate reduction is sulfite. Once the sulfite is formed, the reaction process shown in *Figure 4* can be proceed (Bradley et al., 2011), finally producing H_2S , H_2S and the reaction formula is shown in *Equation 7*.



The followings may be the reaction pathway from SO_3^{2-} to H_2S formation (Cai et al., 2009). (1) 3 consecutive two-electron transfer, forming $S_3O_6^{2-}$ and thiosulfate ($SO_3^{2-} \rightarrow S_3O_6^{2-} \rightarrow S_2O_3^{2-} \rightarrow S^{2-} \rightarrow H_2S$). (2) SO_3^{2-} directly lose 6 electrons, the above-mentioned intermediate product is not formed and is referred to as coordinated 6-electron reaction, namely $SO_3^{2-} + 6e^- + 8H^+ \rightarrow H_2S + 3H_2O$. (3) In the continuous two-electron transfer process, the reverse reaction may also occur. The reaction formula is shown in *Equation 8*.



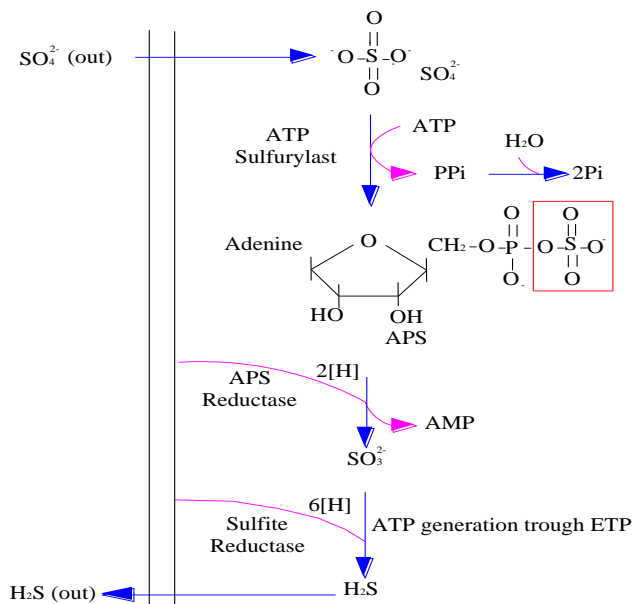


Figure 4. Diagram of dissimilatory sulfate reduction. ATP - adenosine triphosphate; PPI - pyrophosphoric acid; Pi - inorganic phosphate; APS - adenosine-5'-phosphosulfate; AMP - adenosine monophosphate; ETP - electron transport particles

SRB utilizes lactate as an electron donor and SO_4^{2-} as an electron acceptor for BSR action. There are three enzymes involved in the sulfite reduction process during the reduction of SO_3^{2-} to S^{2-} , namely $\text{S}_3\text{O}_6^{2-}$ forming enzyme, $\text{S}_3\text{O}_6^{2-}$ reductase or thiosulfate-forming enzyme and thiosulfate reductase. In BSR, SRB produces and accumulates large amounts of S^{2-} or HS^- in the cells. When the concentration of S^{2-} or HS^- in the cell reaches to a certain value, it will be released into the solution through the cell membrane, increasing the concentration of S^{2-} in the surroundings, which leads to the change in the redox potential of the environment and the concentration of related ions (Ren et al., 2009; Pérez et al., 2001). SRB metabolic H_2S formation process is shown in Figure 5 (Peck et al., 1982).

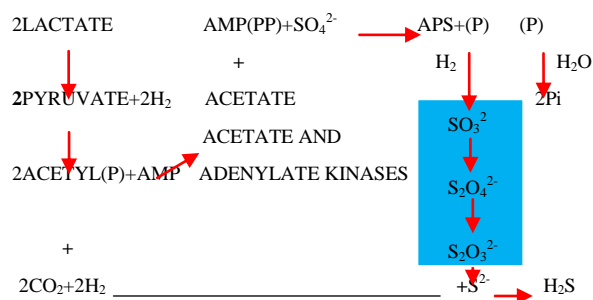


Figure 5. Flowchart of SRB metabolism forming H_2S . Pi - inorganic phosphate; APS - adenosine-5'-phosphosulfate; P - Phosphorum

The carbon of dibenzothiophene (DBT) as metabolic material is reacted with SRB to decompose the aromatic ring structure and form a sulfur-containing compound. The Kodama pathway is shown in Figure 6 (Kodama et al., 2008).

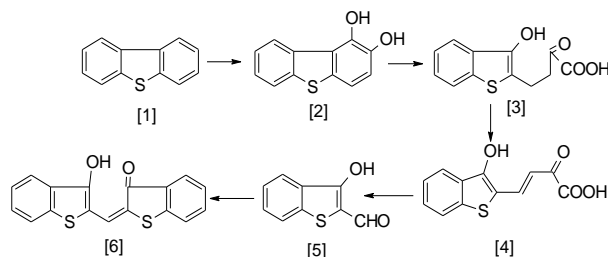
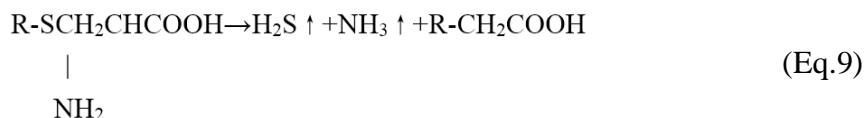


Figure 6. Kodama pathway of metabolic mechanism of SRB use the carbon

The metabolic mechanism of organo-sulfur compounds as a sulfur source

SRB is degraded by sulfur-containing organic substances (such as sulfur amino acids, cysteine, cysteine, sulfanilic acid, methionine, sulfonate, glutathione, etc.) as sulfur sources to produce H₂S. The degradation process differs depending on the types of SRB. Usually some SRBs will completely degrade some polymer-containing organic compounds to produce H₂S. Some will only degrade them into relatively low-molecular-weight sulfur-containing organic compounds such as mercaptans, and then other species. The SRB degrades it to the end product such as H₂S (Ren et al., 2001). The sulphur-containing organic degradation reaction can be summarized as shown in Equation 9.



The 4S pathway of sulfur metabolism (sulphoxide/sulphone/sulponate/sulphate) (Isbister et al., 1998). For different strains, the 4S pathway is not exactly the same, all of which have a common role in the C-S bond. For example, Rhodococcus sp. strain IGTS8 bacteria are considered to have two desulfurization pathways (Ma et al., 2000), as shown in Figure 7.

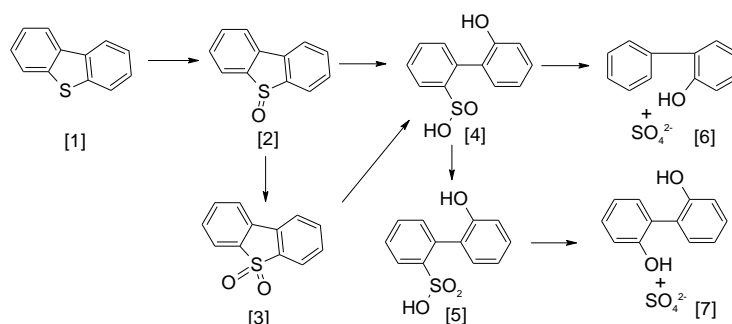


Figure 7. The 4S pathway of Rhodococcus sp. strain IGTS8 bacterium

The sulfur in DBT will generate SO₄²⁻, SO₃²⁻ and 2, 2'- Dihydroxybiphenyl or 2-hydroxybiphenyl and sulphur containing compounds after 4 steps.

Metabolic pathway of SRB

The sulfur cycle is an important geochemical cycle in the Earth's environmental system, and SRB plays an indispensable role in this system. The basic process can be described as the following (Rasch et al., 2000): when the onshore volcanic eruptions, sulfur in the earth's crust and magma is released into the atmosphere in the form of H_2S , sulfate and SO_2 . Some of the sulfur emitted from the volcanic eruption of the submarine is dissolved in sea water and some of it is released into the atmosphere by gaseous sulfides. Sulfur in the atmosphere circulates through sulfuric acid or sulphate aerosols into the biosphere, pedosphere and hydrospheres. These sulphur compounds are then passively absorbed and assimilated by plants and animals. The absorbed sulfur forms the body of plants and animals. Animal and plant residues are decomposed by microorganisms, and sulfur becomes H_2S escaped into the atmosphere or deposited into peat. The reduction of sulphate in water is accomplished by reverse sulfidation of various sulfate-reducing bacteria. In the absence of oxygen, sulfates are produced into H_2S as hydrogen acceptors. Sulfate, H_2S and sulfur is mineralized under the common action of aqueous medium and organic matter to generate organic sulfide or inorganic sulfide. The sulfur cycle in global ecosystem is shown in *Figure 8* (Deng et al., 2013).

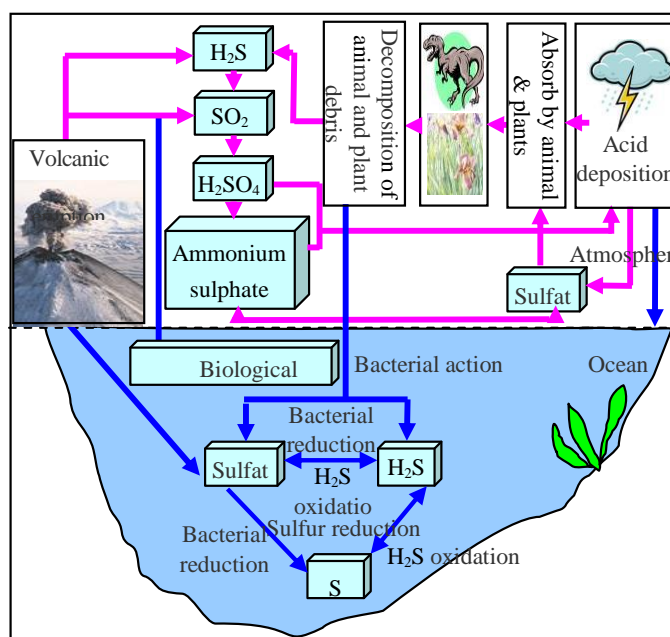


Figure 8. Sulfur cycle in the Earth's environmental systems

It has been known that due to the action of microorganisms, there are obvious redox zone from the top down of shallow sediment layers in the seabed, which can be divided into oxidation zone, weak oxidation zone, reduction zone and methanogenic zone in turn. The SRB is mainly distributed in the reduction zone in *Figure 9*, where it plays a dominant role and produces H_2S (Berner, 1981; Froelich et al., 1979).

There are also four sequential redox zones in the sulfate reduction zone, iron reduction zone, nitrate reduction zone and oxidation zone in landfill leachate sites, as shown in *Figure 10* (Zhou et al., 2008). The biocenosis structure in each zone has obvious bacterial species properties. Accordingly, sulfate-reducing bacteria, iron-

reducing bacteria (IRB) and denitrifying bacteria (NRB) are the dominant bacterial groups. The distribution of redox zone and microbial flora indicates that there is a certain overlap between the redox zones, where the sulfate reduction zone is the main zone where malodorous gas (H_2S) is generated.

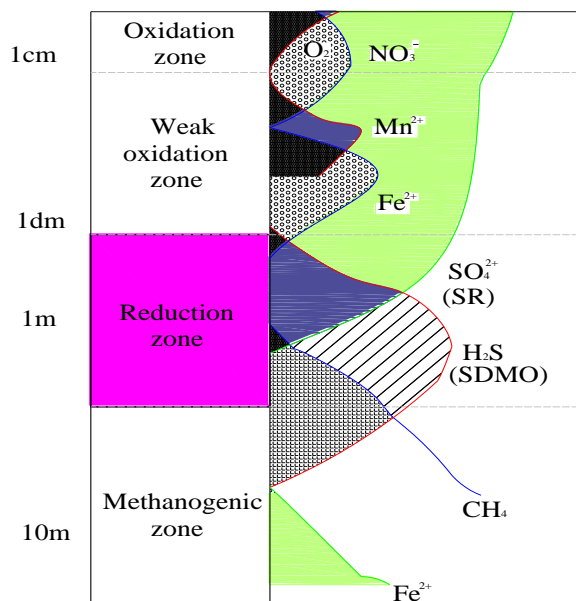


Figure 9. SRB and redox zone division in submarine deposits

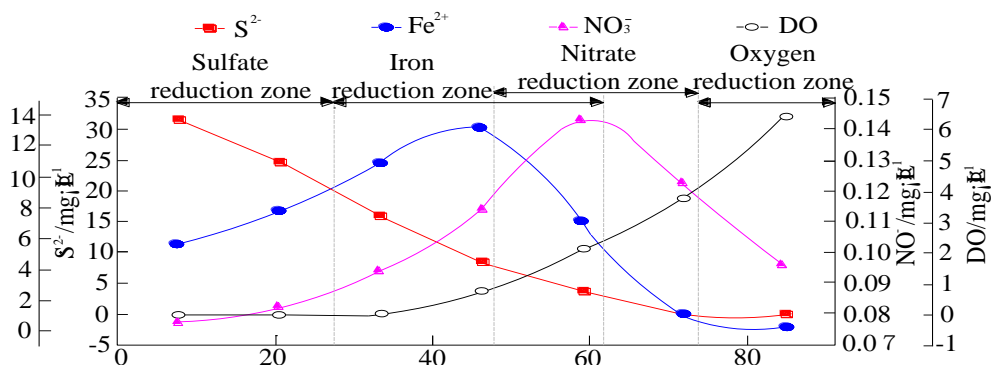


Figure 10. Distribution of redox zones in landfills

Organic sulfur compounds are produced mainly in humification stage. H_2S , CH_3SH , and $(CH_3)_2S$, S^0 , or polysulfide compounds generated by the bacteria dissociation are oxidized to sulfates in an oxygen-rich environment. When the interface between the aqueous medium and the sediment exists in anoxic environment and the sulphate solubility reaches a certain value, SRB is metabolized by SO_4^{2-} as a sulphur source, and BSR works after decomposition, electron transfer and oxidation. The metabolic activity of SRB reduces the solubility of SO_4^{2-} and releases H_2S , HS^- , or S^0 . HS^- or S^0 can react with organic matter to form organic sulfur, which can also react with iron ions to form pyrite. If the active iron ion is absent in the system and the SO_4^{2-} content is relatively

sufficient, a large amount of secondary organic sulfur compounds may be produced under suitable conditions, which is shown in *Figure 11* (Dai et al., 1996).

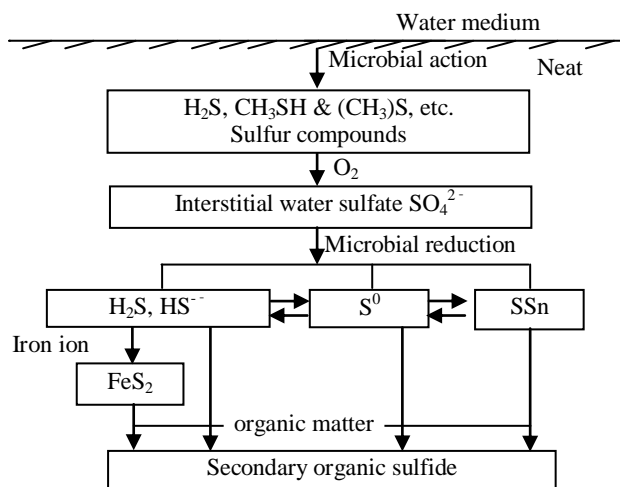


Figure 11. The evolution of organic sulfur

In sedimentary formations, due to the interaction between sedimentary factors and ecological factors, three different biological systems are formed, each of which is dominated by different microbial populations, namely the Aerobic microbial zones, sulfate reduction zones and organisms Methane generation zone. In the sulfate reduction zone, H₂S may be generated as shown in *Figure 12* (Lin et al., 2015).

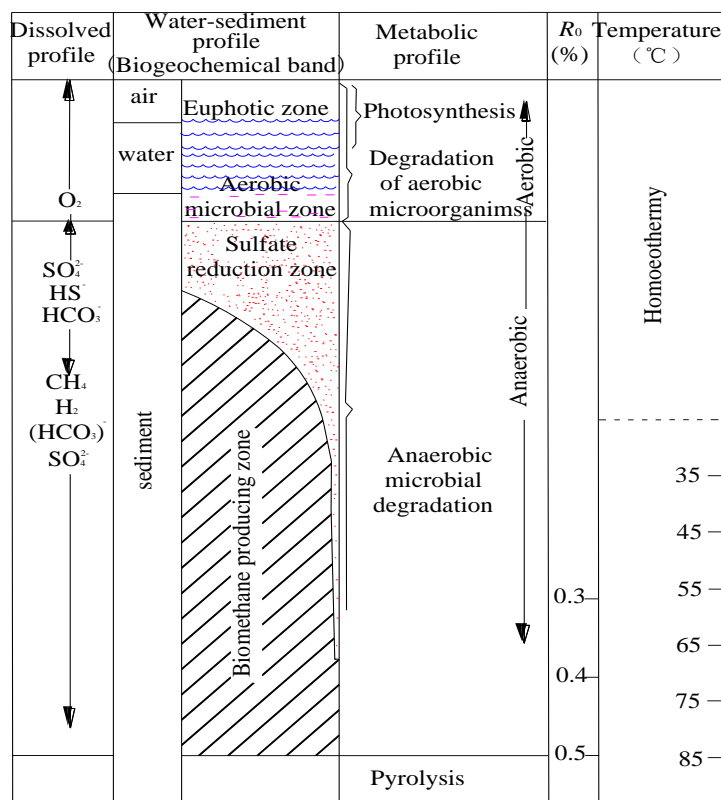


Figure 12. Schematic diagram of biogenic gas phase in sedimentary strata

(1) In a reducing environment, anaerobic sulfate-reducing bacteria reduce the sulfate in the water to form H₂S (Eq. 10).



(2) In the oxygen-enriched oxidizing environment, biosulfur and sulfuric acid are formed under the action of sulfur oxidizing bacteria (Eq. 11).



(3) If the solution contains Fe²⁺, native pyrite framboids and microbial dolomite will be appeared. The principle is that Fe²⁺ reacts with H₂S to produce pyrite (Eq. 12).



SRB has become an active participant in the early diagenesis process (Brüchert et al., 2001; Krause et al., 2012). Krause et al. found that in anoxic, low-temperature (21 °C) modern seawater (normal salinity and Mg²⁺/Ca²⁺ values), BSR action occurs under the action of SRB, which can lead to the formation of H₂S and precipitation of dolomite. Its formation model is shown in Figure 13. The possible reaction formulas are shown in Equations 13 and 14 (Glud et al., 1998).

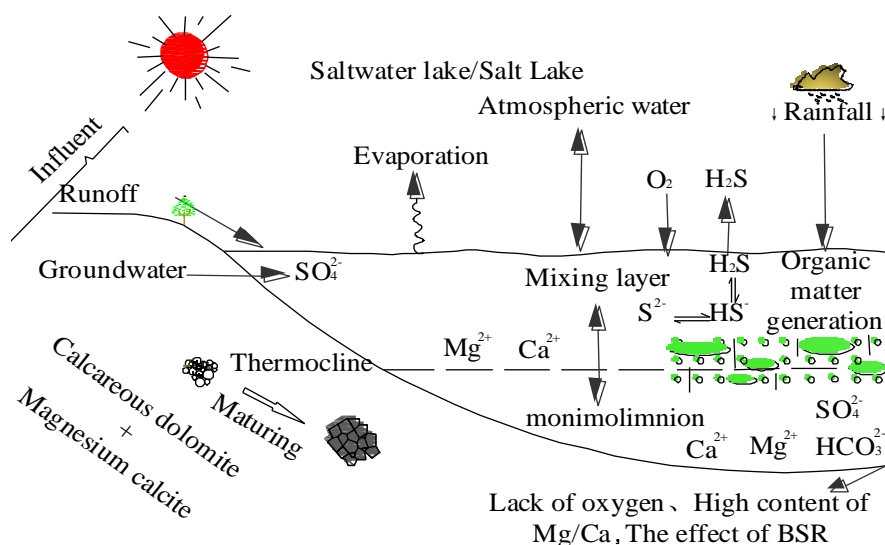
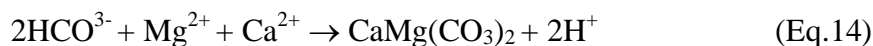


Figure 13. Microbial mechanism model of primary dolomite in lake system



In the formation of dolomite and H₂S under the action of BSR in the salt lake (seawater) system, the SRB metabolic activity and intracellular reaction processes can be described as shown in Figure 14 and Equations 15–18 (Corzo et al., 2005).

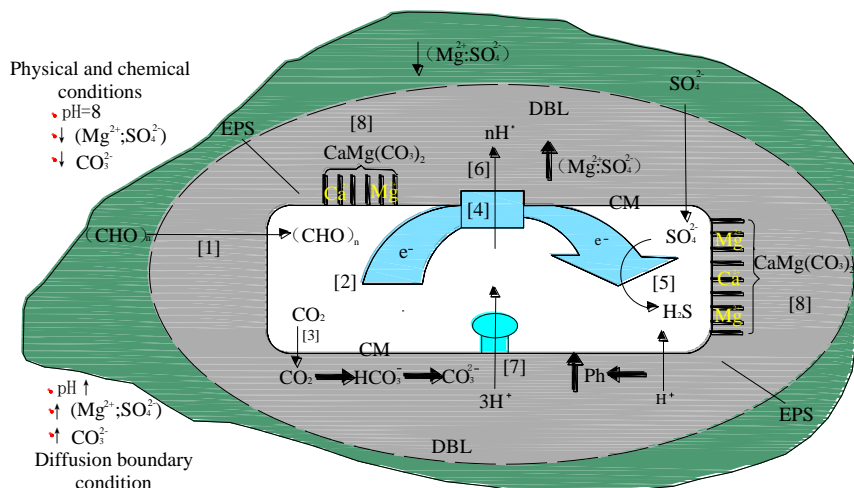
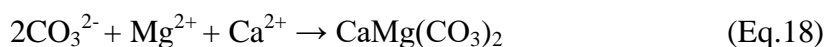
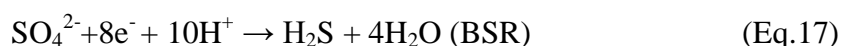
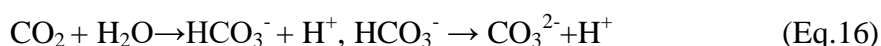
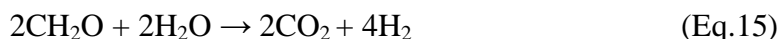


Figure 14. SRB metabolic activity and intracellular reaction process. DBL - diffusion boundary layer; EPS - cell membrane and outer polymer matrix; CM - cell membranes



In the process of degrading organic matter, SRB in solution can reduce the SO_4^{2-} solubility, increase the concentration of $\text{Mg}^{2+}/\text{SO}_4^{2-}$, pH value, HCO_3^- concentration and dolomite saturation, and generate H_2S , which will produce a micro-environment conducive to the precipitation of dolomite. SRB cells, which are in the dark green area, are surrounded by the effective diffusion boundary layer (DBL) in the colour of the dark gray. The low-molecular-weight organic compounds in surroundings enter the cells [1], which are oxidized to CO_2 [2, e.g. (Eq. 16)] and released to DBL [3, e.g. (Eq. 16)]. The ions formed by the oxidation of organic matter pass through cell-electron-transporting cell membranes (CM) [4] to SO_4^{2-} and undergo a reduction to generate H_2S [5, e.g. (Eq. 17)]. The electron flow (H^+) migrates to the DBL [6] through the anaerobic respiratory chain, forming an electrochemical gradient across the cell membrane and stimulating H^+ entry via ATP synthetase. Hence, under fully constrained stoichiometry ($3\text{H}^+ \cdot \text{ATP}$), the H^+ ion flux in these cells is coupled to ATP synthase [7]. Since these processes cause the cells to be negatively charged, Ca^{2+} and Mg^{2+} are adsorbed to the cell membrane and outer polymer matrix [8, e.g. (Eq. 18)] (Lith et al., 2010, 2003). Therefore, near the cell membrane and DBL, H_2S is formed and dolomite is produced and precipitated [8, e.g. (Eq. 18)].

Conclusion

In anaerobic (reduced) habitats, sulfate-reducing bacteria have a unique sulfate-reducing activity. The physiological characteristics and mechanism of H_2S formation not only provide a basis for revealing the biogeochemical cycle of sulfur elements,

which is conducive to the protection of the natural environment and the restoration of polluted ecosystems, and also provide a useful reference for the control of aerobic microorganisms.

The metabolic reduction process of SRB, using sulfate and sulfur-containing organic material as sulfur source, is not only related to sulfate-reducing bacteria, but also closely related to non-sulfate-reducing microorganisms. A large number of sulfur sources metabolized by SRB are converted into soluble intermediate organic products that can be used by non-SRBs in the metabolic system.

In the earth system, there are many places of metabolism of sulfate-reducing bacteria. And under the metabolism of SRB, BSR may occur to form H₂S. The metabolites in various places are closely related to their micro-environment.

It finds that SRB is the most important biological source for H₂S production. The study on the formation mechanism of H₂S under BSR can provide meaningful reference for the disclosure of the geochemical cycle law of sulfur and the rules of the ecological environment, and supply with a helpful reference for the control of aerobic microorganisms.

Acknowledgements. This work was supported by “National Natural Science Foundation of China (51774116, U1504403)”, “Scientific and Technological Project of Department of Science & Technology of Henan Province (182102210320)” and “Postdoctoral Research Fund of Henan Province (2017)”. In the study process, the authors are also grateful to Professor Mingju Liu of Henan Polytechnic University for his ardent guidance and help.

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