



Review

The role of sulfate-reducing prokaryotes in the coupling of element biogeochemical cycling



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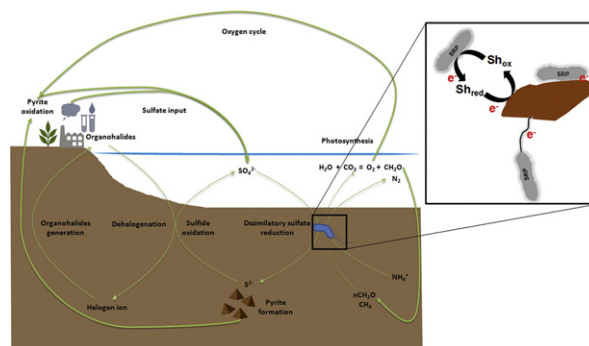
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HIGHLIGHTS

- Present SRP mediated coupled biogeochemical cycling of elements.
- Emphasize anthropogenic contaminations-disturbed sulfur-driven elements biogeochemical cycling
- Summary the mechanism of interaction between SRP and metal(loid)s
- Highlight the SRP studies that focus for some of attractive research

GRAPHICAL ABSTRACT



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ABSTRACT

Sulfate-reducing prokaryotes (SRP) represent a diverse group of heterotrophic and autotrophic microorganisms that are ubiquitous in anoxic habitats. In addition to their important role in both sulfur and carbon cycles, SRP are important biotic and abiotic regulators of a variety of sulfur-driven coupled biogeochemical cycling of elements, including: oxygen, nitrogen, chlorine, bromine, iodine and metal(loid)s. SRP gain energy from most of the coupling of element transformation. Once sulfate-reducing conditions are established, sulfide precipitation becomes the predominant abiotic mechanism of metal(loid)s transformation, followed by co-precipitation between metal(loid)s. Anthropogenic contamination, since the industrial revolution, has dramatically disturbed sulfur-driven biogeochemical cycling; making sulfur coupled elements transformation complicated and unpredictable. We hypothesize that sulfur might be detoxication agent for the organic and inorganic toxic compounds, through the metabolic activity of SRP. This review synthesizes the recent advances in the role of SRP in coupled biogeochemical cycling of diverse elements.

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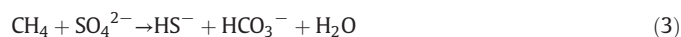
1. Introduction

Sulfate-reducing prokaryotes (SRP) are highly diverse, either heterotrophic or autotrophic, found in many anaerobic environments such as; sediments, wetlands and paddy soils. SRP gain energy from the electron transfer between organic matter/hydrogen/carbon monoxide and electron acceptors (Wang et al., 2017a). SRP are believed to play critical role in coupled biogeochemistry of a range of elements through biotic or abiotic processes, and facilitate more than half of the organic matter oxidation in marine sediments (Meyer-Reil, 1994). SRP can use sulfate as a terminal electron acceptor for the degradation of organic compounds, except for some autotrophic species, resulting in the production of sulfide (Postgate, 1984; Widdel, 1988). The reaction is generally expressed as the following equations (Widdel, 1988; Sheoran et al., 2010):



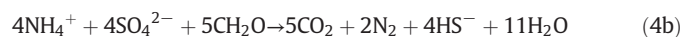
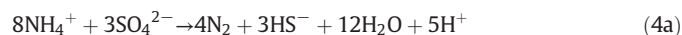
This process, dissimilatory sulfate reduction, involves the key enzymes dissimilatory sulfite reductase DsrAB and adenosine-5'-phosphosulphate reductase AprAB (Rabus et al., 2015). The product of dissimilatory sulfate reduction, sulfide, dominates most of the sulfur pool, combining with Fe(II) as pyrite or pyrrhotite. The oxidative weathering of pyrite/pyrrhotite decreases the proportion of oxygen in the air and freshwater. Thus, SRP play a critical role in the coupling between sulfur, oxygen, and carbon, through sedimentary sulfides formation (Rickard et al., 2017).

Sulfate-driven anaerobic oxidation of methane (AOM) process involves consortia of archaea and SRP (Hoehler et al., 1994; Boetius et al., 2000) (Eq. (3)).



Wherein, archaea are commonly regarded as methane oxidizer that provide reducing equivalents to SRP, although AOM mediated solely by archaea has been recently reported (Basen et al., 2011; Milucka et al., 2012).

The sulfate-reducing ammonium oxidation (SRAO) process was first proposed by Fdz-Polanco et al. (2001). There are many potential reactions or coupled reactions that constitute SRAO, including, (i) direct oxidation of ammonium to dinitrogen (Eq. (4a)); (ii) oxidation of ammonium to nitrite, coupled to nitrite-reducing ammonium oxidation (Eq. (4a)); (iii) oxidation of ammonium to nitrate, coupled to denitrification (Eq. (4b)).



The former two pathways involve lithotrophic sulfate-reducing ammonium oxidation. While, the last pathway involves an organotrophic reaction (Schrum et al., 2009).

SRP play an important role in the dechlorination of organochlorines in natural and controlled environments (El Fantroussi et al., 1998). A previous study showed that a SRP *Clostridium* sp. BXM utilized sulfur species as redox partners and electron shuttles in dechlorination of *p,p'*-DDT (*p,p'*-dichlorodiphenyltrichloroethane) (Bao et al., 2012). Similarly, methyl bromine and methyl iodine was anaerobically degraded in saltmarsh sediments after reaction with sulfide (Oremland et al., 1994). The documented information hint that SRP may fix sulfur and halogen biogeochemistry cycles through abiotic pathway.

SRP are also important regulators of various metal(loid)s transformation coupled with carbon transformation in the ecosystems (Table 1, Fig. 1). Biotic regulation of metal(loid)s by SRP is usually through enzymatic reduction and/or methylation. Cytochrome c and [Fe], [NiFe], and [NiFeSe] hydrogenases play key role in metal(loid)s reduction (Payne et al., 2002; Chardin et al., 2003), with this activity occurring in the periplasm. In particular, thioredoxin reductase was also found to reduce both U(VI) and Cr(VI) (Li and Krumholz, 2009). Field studies have shown that SRP are the key mercury-methylating organisms in nature, utilizing the acetyl-CoA pathway (Compeau and Bartha, 1985; Ekstrom et al., 2003). Moreover, previous studies also imply the underlying importance of SRP in Se and As methylating (Bruschi et al., 2007; Truong et al., 2013; Wang et al., 2014).

The production of sulfide may also be vital in metal(loid) speciation, and has a wider role in metal(loid) removal by abiotic reduction and/or precipitation (Muyzer and Stams, 2008; Sheoran et al., 2010). All

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