Diversity of Sulfur-Oxidizing and Sulfur-Reducing Microbes in Diverse Ecosystems

4

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Abstract

Sulfur (S) is one of the most important elements, of which the organosulfur compounds and/or metal sulfides are considered essential for life. Microbial sulfur oxidation and reduction are the most active and ancient metabolic processes in S cycle that operate in diverse ecosystems. This process is carried out by sulfur-oxidizing (SOB) and sulfur-reducing bacteria (SRB) in all ecosystems and considered as key phenomenon in sulfur biogeochemical cycling. Usually, on the basis of nutrition, SOB and SRB are categorized as lithoautotrophs. SOB oxidize the reduced sulfur compounds such as hydrogen sulfide (H_2S), elemental sulfur (S^0), sulfite (SO_3^{-2}), thiosulfate ($S_2O_3^{2-}$), and various polythionates ($S_nO_6^{2-}$ or -S_nO_6-) into sulfate (SO_4^{-2}). On the contrary, SO_4^{-2} can serve as an electron acceptor of SRB under anaerobic condition, and they reduce the SO_4^{-2} and other oxidized sulfur compounds ($S_2O_3^{2-}$, SO_3^{-2}, S^0) into H_2S. In natural system, SRB reduce the SO_4^{-2} in two different reduction processes, *viz*, dissimilatory and assimilatory reactions. In dissimilatory reaction, SRB utilize three kinds of enzymes (ATP sulfurylase, APS reductase, and sulfite reductase) to reduce the S substrate, whereas the sulfate is assimilated or incorporated into organic compounds under assimilatory process through S substrate reduction. In recent years, molecular methods have emerged as essential tools for a better

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understanding of the microbial role in S transformation under various habitats. Keeping the importance of microbial-mediated S oxidation and reduction in biogeochemical cycle of S, the present chapter describes the role of key functional microbial genes in S transformation such as genes involved in S oxidation (*sox*, *aps*, *asf*, and *sor*) and reduction (*dsr*) and also discusses in detail about the abundance, diversity, and impact of these in diverse ecosystems.

Keywords
Sulfur · Oxidation · Reduction · Functional genes · Microbial diversity

4.1 Introduction

Sulfur (S) is the tenth most copious element in the universe and the sixth most prominent element in microbial biomass (Klotz et al. 2011). It is present throughout the earth's crust as gypsum and pyrite. Sulfur comes from weathered rock, atmosphere (SO_2 and methane sulfonic acid), fertilizers and pesticides, water resources (sulfate, hydrogen sulfide, and elemental sulfur), etc., and these processes are influenced by climate, local vegetation, and topography. The sulfur content of soil varies from 0.002 to 10.0% (Freney et al. 1982), and the highest amount of S is present in tidal flats, saline, acid sulfate, and organic soils. Organic S accounts to >90% of total sulfur present in surface soils, whereas <25% of total S present in agricultural soils are in the form of the inorganic S (Roberts and Bettany 1985; Bettany et al. 1973). The main forms of inorganic sulfur include sulfide, elemental sulfur, sulfite, thiosulfite, tetrathionate, and sulfate (Williams 1972).

Majority of global biogeochemical cycles including that of carbon, nitrogen, phosphorus, iron, and sulfur are driven by microorganisms (Tang et al. 2007). Approximately one-half of the global S cycle represents oxidized form of inorganic S compounds. The bacteria and archaea responsible to form oxidized form of S from reduced S compounds, belonged to either photolithotrophs or chemolithotrophs (Trüper and Fischer 1982; Brune 1989; Takakuwa et al. 1992; Nelson and Fisher 1995; de Zwart et al. 1996; Kelly et al. 1997; Friedrich et al. 2001). Under photolithotrophic growth, green and purple sulfur-oxidizing bacteria (SOB) utilize S compounds as electron donors for reductive carbon dioxide fixation (Brune 1989; Brune et al. 1995), and light energy is used as electrons transfer from S compounds *via* highly reducing electron carriers such as NAD (P) and ferredoxin. This process includes a wide range of enzymes, involved in catalyzing sulfur redox reactions (Trüper and Fischer 1982; Fischer 1989; Brune 1989; Dahl and Truper 1994; Brune et al. 1995). In sulfide oxidation, oxidation of elemental S is catalyzed by sulfide dehydrogenase initially and then catalyzed by flavocytochrome c, other c-type cytochromes, or sulfide/quinone oxidoreductase (Brune 1989; Brune et al. 1995). Another enzyme, siroheme sulfite reductase, oxidized H_2S directly to sulfite, and this enzyme is found in *Chromatium vinosum* D (Schedel et al. 1979). Besides photolithotrophs, reduced sulfur compounds such as hydrogen sulfide (H_2S),

elemental sulfur (S^0), sulfite (SO_3^{-2}), thiosulfate ($S_2O_3^{2-}$), and various polythionates ($S_nO_6^{2-}$ or -S_nO_6-) are utilized by various chemolithotrophs, and they oxidized these forms of S into sulfate (SO_4^{-2}). SO_4^{-2} can serve as an electron acceptor in anaerobic respiration, and S-reducing bacteria (SRB) may reduce the SO_4^{-2} and other oxidized sulfur compounds (S^0, SO_3^{-2}, and $S_2O_3^{2-}$) into H_2S.

Sulfur is essential for the growth and development of living organisms. Plants require it for growth and grain production. Plants generally utilize S in the form of SO_4^{-2}. Due to its existence as several redox states, S is involved in very important biochemical reactions as redox center and carbon carrier (Klotz et al. 2011). Therefore, it is very important to know the nature and amount of S that is present in soil and its transformation process. The main purpose of this chapter is to briefly introduce to researchers how the S cycle is mediated through microbes under different ecosystems and also discuss the kind of functional genes required in S transformation and their abundance, diversity, and impact in diverse ecosystems.

4.2 Biogeochemical of Sulfur Cycle

Sulfur (S) is considered as one of the most important atoms in biological system, and minute amount of this element is mandatory for proper functioning of biological system. Generally, S forms disulfide bridges in biological system, which imparts crucial function to provide specific shapes and properties to other biologically important molecules under that system. The major constituent of S present in the atmosphere is sulfur dioxide (SO_2), coming from burning of fossil fuels and sulfur coal. In the atmosphere, one of the primary components of acid rain is sulfuric acid (H_2SO_4) which is formed when SO_2 is reacted with water vapor and causing many adverse effects in about all regions of the world. Carbonyl sulfide (COS) is another form of S, present in small quantity in the atmosphere. These two forms of S (SO_2 and COS) are highly reactive with oxygen and converted into sulfates (SO_4^{-2}) which is quickly deposited on land and other surfaces. Plant requires S in the form of SO_4^{-2}, and these forms of S mostly come from soil organic S after mineralization by soil microorganisms (Niknahad-Gharmakher et al. 2012). Greater availability of soil S may be immobilized by soil microbes to build their biomass. In soil, the S level in the form of extractable soil S-SO_4 is marginally changed after C addition over time, confirming slow rate of soil S mineralization. Majority (90–95%) of soil S is stored in organic form such as C-S (sulfate bonded with carbon) and/or C-O/N-S (sulfate and sulfamates in the form of ester) (Tabatabai 1984). Plant generally takes sulfates from the ester sulfate fractions (McLaren et al. 1985). In agrosystems, plant residues are the main source of labile carbon (Gentile et al. 2011). The effect of plant residues on S turnover in soils has been studied and found that the net S mineralization was the function of C/S ratio of the crop residue (Jensen et al. 2005). This gives an idea that the S deficiency in cropped soil is functionally correlated with soil microbial biomass and C dynamics (Wu et al. 1995). One of the key factors governing S transformations in soil is availability of C (Knights et al. 2001); probable limiting effect of low S levels on C mineralization has been investigated by few workers

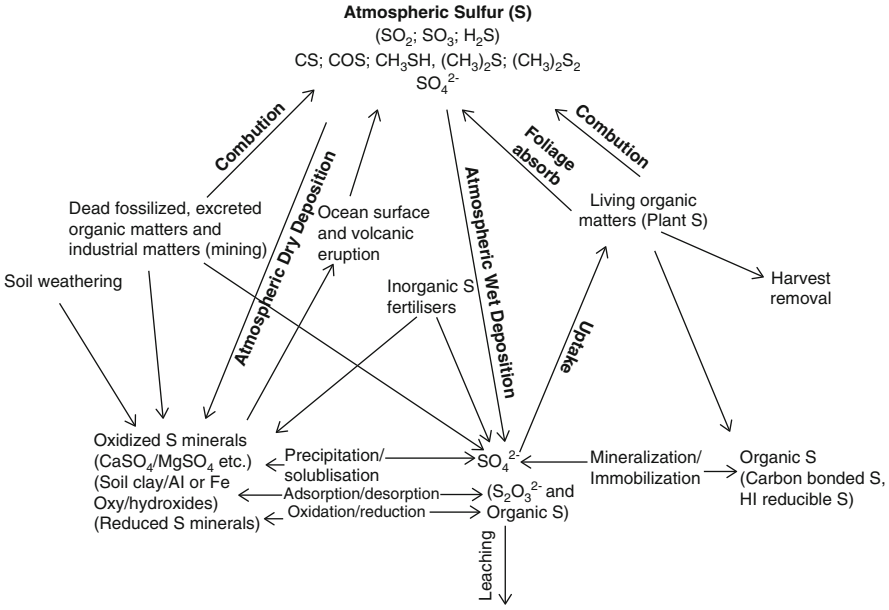

Fig. 4.1 Representative model of biogeochemical cycle of sulfur (Adapted from Germida et al. 1992)

(Chapman 1990). Moreover, Fig. 4.1 presents a representative S cycle which showed the transformation of different forms of S, its compounds, and their metabolic reaction under model system.

4.3 Microbiology of Sulfur Cycling

Biogeochemical cycle of S involves several oxidation and reduction reactions (Tang et al. 2007). The following major pathways involved in S cycle are (1) organic S mineralized into inorganic S form; (2) oxidation of S^0, SO_3^{-2}, and $S_2O_3^{2-}$ into SO_4^{-2}; (3) reduction of SO_4^{-2} into H_2S; and (4) immobilization of S compounds by microbes and subsequent assimilation of S as organic form (http://www4.ncsu.edu). Under S cycling, microorganisms can take part in both oxidation and reduction processes depending on the prevailing environmental conditions in a particular ecosystem.

4.3.1 Sulfur Oxidation by Microbes

Sulfur (S) oxidation is one of the most predominant reactions in environment (Friedrich et al. 2005). It is a very significant process in soil to avoid sulfur deficiencies in crops and also the environmental contamination (Lawrence et al. 1988). The archaea (*Sulfolobus*, *Desulfurococcus*, *Acidianus*, *Metallospora*),

chemolithotrophic bacteria (*Bacillus*, *Acidithiobacillus*), phototrophic bacteria (*Chlorobium*, *Allochromatium*, *Rhodobacter*, *Rhodovulum*), and non-sulfur bacteria (*Rhodopseudomonas*, *Rhodocyclus*) are mainly involved in S oxidation. The majority of them use carbon dioxide as their primary carbon source and sulfur as an electron donor (Brune 1989; Friedrich et al. 2005). The sulfur substrates utilized by the microorganisms include sulfide, thiosulfate, and hydrogen sulfide (Friedrich et al. 2001, 2005). The process of S oxidation occurs through three biochemical pathways: sulfur oxidase pathway, the reverse siroheme sulfite reductase pathway (phototrophic S-oxidizing bacteria), and the archaeal sulfur oxygenase reductase pathway.

4.3.1.1 Phototrophic Sulfur Bacteria

Phototrophic S-oxidizing bacteria use light as energy source and hydrogen sulfide (H_2S) as substrate. They usually oxidized H_2S into elemental sulfur (S^0) and subsequently reduce the carbon dioxide and assimilated as organic compounds. There are several enzymes involved for catalyzing sulfur redox reactions in phototrophic sulfur bacteria (Trüper and Fischer 1982; Fischer 1989; Brune 1989; Dahl and Truper 1994; Brune et al. 1995), which are discussed below with examples.

Green Sulfur Bacteria

Green sulfur bacteria (GSB) are metabolically strict anaerobes and obligately phototrophic and use CO_2 as only carbon source and fixed *via* the reductive tricarbonic acid cycle. Sulfide (H_2S) is used as electron (e^{-1}) donor by all species of GSB except *Chlorobium ferrooxidans* (iron-oxidizing GSB) and subsequently oxidized to sulfate (SO_4^{-2}) with intermediary assimilation of extracellular S. Many are able to grow with elemental S, and even some species also use thiosulfate ($S_2O_3^{2-}$) (Frigaard and Bryant 2008). Tetrathionate may be used as electron donor in some of the GSB like *Chlorobaculum parvum* and *Chlorobium thiosulfatophilum* (Imhoff 2003; Khanna and Nicholas 1982; Larsen 1952). So far, sulfite (SO_3^{-2}) utilization has not yet been discovered in the case of any GSB. Some of the most important GSB are *Chlorobium*, *Ancalochloris*, *Pelodictyon*, *Chloroherpeton*, etc.

Purple Sulfur Bacteria

Purple S-oxidizing bacteria (PSOB) generally use sulfide (H_2S) for their growth and development. They store the sulfur in the form of spherical particles within and outside of the cells and upon oxidation releases sulfates from the cells. They oxidize the sulfide, sulfur, thiosulfate, and sulfite (Imhoff and Hiraishi 2005) to sulfate by different mechanisms. PSOB have two different kinds of pathways for thiosulfate oxidation. In one pathway, two thiosulfate anions were oxidized by enzyme thiosulfate dehydrogenase and produce tetrathionate, whereas another pathway sulfate, was produced after complete oxidation of thiosulfate (Dahl and Friedrich 2008). *Chromatium*, *Allochromatium*, *Thiocystis*, *Thiococcus*, *Thiospirillum*, etc. are the known PSOB in natural environment.

Purple Non-sulfur Bacteria

The occurrence of purple non-sulfur bacteria (PNSB) is wider and heterogeneous, belonging to photoautotrophs which use hydrogen (H_2) or sulfide (H_2S) as electron donor. Some groups of PNSB do not oxidize H_2S completely to sulfate (SO_4^{-2}); instead they form sulfur (S) as an end product. However, SO_4^{-2} is the final end product in the H_2S mediated by many PNSB such as *Rhodovulum*, *Rhodopseudomonas palustris*, *Blastochloris sulfoviridis*, etc. (Brune et al. 1995; Imhoff and Hiraishi 2005). While thiosulfate is oxidized into tetrathionate by *Rhodopila globiformis* (Then and Trüper 1981), *Rhodovulum* species oxidize thiosulfate completely into SO_4^{-2} (Brune et al. 1995; Appia-Ayme et al. 2001; Imhoff and Hiraishi 2005). Most of the PNSB may grow as chemoorganotrophs under microoxic to oxic conditions without presence of light (Smith and Lascelles 1966; Trüper and Pfennig 1966).

4.3.1.2 Chemolithotrophic Sulfur-Oxidizing Bacteria

Chemolithotrophic sulfur-oxidizing bacteria (CSOB) use reduced inorganic sulfur compounds such as sulfite, thiosulfate, hydrogen sulfide, etc. as their energy source. There are two major groups: (1) the obligate chemolithotrophic bacteria, which usually receive energy from the oxidation of S and use main carbon source as CO_2, and (2) the facultative autotrophic bacteria, or mixotrophic bacteria, which can grow autotrophically, mixotrophically, or even heterotrophically. The chemolithotrophic bacteria such as *Thiobacillus ferrooxidans* and *T. thiooxidans* are commonly present bacteria generally responsible for S^0 oxidation in soils and also considered as the most important precursor for S-biogeochemical cycle. *Thiobacillus thiooxidans* is a chemolithotrophic acidophilic bacterium that uses S^0 as an energy source and is important in the microbial catalysis of H_2S. However, the significant number of *Thiobacillus* is not reported in most of the agricultural soils (Chapman 1990; Lawrence et al. 1988; Tourna et al. 2014; Zhao et al. 2017a). *Beggiatoa leptomitiformis* is also a CSOB which uses succinate and thiosulfate or tetrathionate and grows as mixotrophs and oxidized substrate to generate ATP by oxidative phosphorylation. Some of the common CSOB are *Thiobacillus*, *Thiothrix*, *Beggiatoa*, etc.

4.3.1.3 Autotrophic Denitrifying Sulfur-Oxidizing Bacteria

Autotrophic denitrifying sulfur-oxidizing bacteria (ADSOB) generally use various reduced sulfur compounds and produce nitrogen gas by the reduction of nitrate or nitrites. Some of the common ADSOB are *Thiobacillus denitrificans*, *T. versutus*, *Thiosphaera pantotropha*, *Pseudomonas denitrificans*, etc.

4.3.1.4 Heterotrophic Sulfur-Oxidizing Microbes

Heterotrophic sulfur-oxidizing bacteria (HSOB) could oxidize sodium sulfide, tetrathionate, thiosulfate, metabisulfite, and sulfite, but they are unable to gain energy from S oxidation (Tuttle 1980). Starkey (1934) confirmed that HSOB isolated from soil could oxidize $S_2O_3^{2-}$ both in organic and mineral media, with $S_4O_6^{2-}$ being formed as an intermediate. HSOB could also oxidize $S_4O_6^{2-}$ to tri-

and pentathionate, and these oxidations being associated with an initial rise and then a fall in the pH of the culture medium suggest that the growth of some heterotrophic marine bacteria is stimulated when $S_2O_3^{2-}$ is oxidized. A range of hydrogen bacteria (*Xanthobacter autotrophicus*, *Aquaspirillum autotrophicum*, *Pseudomonas pseudoflava*, and *P. pulleronii*) was shown by Friedrich and Mitrenga (1981) to be capable of oxidizing $S_2O_3^{2-}$. Hydrogen sulfide (H_2S)-oxidizing actinomycetes isolated from soil could oxidize S as facultative chemoautotrophs. However, these organisms also act as heterotrophs and are able to scavenge carbon from the atmosphere (Skiba and Wainwright 1984). To date the list of fungi capable of S oxidation contains mainly soil fungi such as *Asteriomyces crucicatus*. Thermophilic fungus *Sporotrichum thermophile* can oxidize SO to $S_2O_3^{2-}$ at 37 to 45 °C. Even ectotrophic mycorrhizae can play a vital role in sulfur oxidation in soils. *Aspergillus niger* and *Mucor fiaous* oxidized elemental sulfur in vitro to form relatively large amounts of sulfate. Some of the examples of HSOB are *Pseudomonas aeruginosa*, *Sphaerotilus natans*, *Xanthobacter autotrophicus*, *Aquaspirillum autotrophicum*, *Pseudomonas pseudoflava*, *P. pulleronii*, *Actinomycetes*, *Alternaria tenuis*, and *Aureobasidium pullulans*. A soil amoeba has been shown to be capable of oxidizing H_2S.

4.4 Sulfur Reduction by Microbes

Microbial sulfur (or sulfate) reduction is governed by two possible pathways, i.e., either assimilatory or dissimilatory process. In the assimilatory reduction pathway, reduced sulfur is generally used for biosynthesis of amino acids and proteins, whereas in dissimilatory reduction, sulfate (or sulfur) is reduced to inorganic sulfide by obligatory anaerobic sulfate reducers. The process of sulfur reduction occurs through dissimilatory sulfur reductase system which is present both in bacterial and archaeal sulfate-reducing species (Wagner et al. 1998). The organisms which are involved in this process draw majority of their metabolic energy from the reduction and use of sulfur compounds as electron acceptors. In this process, carbon substrates such as lactate or ethanol are oxidized, and hydrogen sulfide gas is produced (Jørgensen 1982). The enzyme pathway responsible for the reduction of sulfur is known as the dissimilatory sulfur reductase system. The sulfur-reducing organisms (SRB) are generally found in anaerobic conditions and play vital role in the formation of acid sulfate soils and pyrite. Sulfide can be produced by anaerobic microorganisms while breaking proteins to amino acids. Some of the examples of SRB and archaea are *Desulfurella*, *Desulfuromonas*, *Geobacter*, *Pelobacter*, etc. and *Thermoproteales*, *Thermococcales*, *Sulfolobales*, *Pyrodictales*, *Sulfolobales*, etc., respectively (Schauder and Kröger 1993).

4.5 Microbial Functional Genes Responsible for Sulfur Oxidation

In the recent years, sulfur oxidation pathways have been reported in many S-oxidizing bacteria (SOB), and the biochemistry behind these pathways is quite complicated (Ghosh and Dam 2009). In general, SOB follow two types of S oxidation pathways; one is Sox pathway (*sox* gene) which involves a multienzyme complex catalyzing the complete oxidation of reduced sulfur compounds to sulfate, and another is APS (adenosine-5-phosphosulfate) pathway (*aps* gene) which implements elemental sulfur and sulfite as intermediates (Ghosh and Dam 2009). Other important genes in S oxidation pathway are *asf* and *sor*. *Asf* gene is responsible for aryldesulfonation reaction of sulfonate mostly present in agricultural soils, whereas *sor* gene encodes sulfur oxygenase reductase, which oxidized the elemental sulfur and produced sulfite, thiosulfate, and sulfide. Comprehensive information of function of various key genes associated with biogeochemical cycle of sulfur is presented in Fig. 4.2.

4.5.1 *sox* Gene

The Sox (sulfur oxidase pathway) is currently considered the most widely distributed and the best characterized of the bacterial and archaeal S oxidation pathways. The S*ox* enzyme pathway is responsible for the oxidation of reduced S or S compounds and has been isolated in polythionate-oxidizing bacteria (Bamford et al. 2002). Common sulfur oxidase enzymology in the bacteria was initially illustrated by Trüper and Fischer (1982) in a comparison of chemoautotrophic and phototrophic bacteria. It was noted that a number of enzymes were common to the green, purple, and colorless sulfur bacteria, including the common use of cytochrome C and flavocytochrome C in electron transport (Trüper and Fischer 1982; Friedrich et al. 2001). The Sox enzyme system was originally classified as a number of separate pathways. Each of the pathways was designated principally by function, most

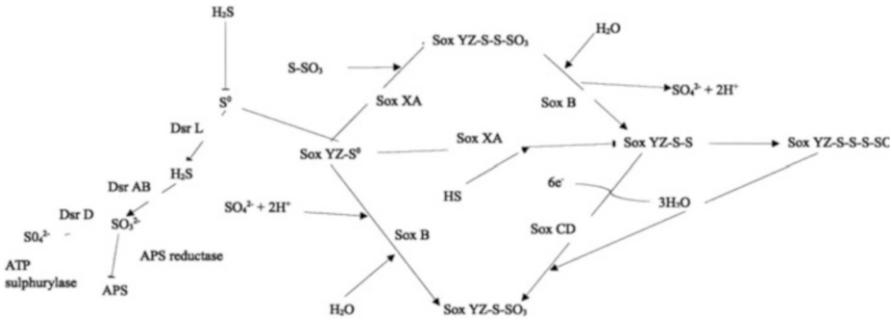

Fig. 4.2 Function of various key genes associated with biogeochemical cycle of sulfur (Adapted from Grabarczyk et al. 2015)

commonly thiosulfate oxidation, due to both the stability of the thiosulfate molecule and the common utilization of thiosulfate by the majority of the bacteria (Petri et al. 2001).

Sox complex has many components such as *soxB*, *soxXA*, *soxYZ*, and *soxCD*. The key constituent among all is *soxB*. The oxidation of thiosulfate ($S_2O_3^{2-}$) to form sulfate (SO_4^{2}) is stringently dependent on the presence of three periplasmic Sox proteins which has been encoded by *soxBXA* and *soxYZ* genes. However, Sox proteins are not necessarily required during oxidation of sulfide (H_2S) process (Hensen et al. 2006). Purple sulfur bacteria comprise 15 different kinds of *sox* genes which have been organized into three transcriptional units such as *soxRS*, *soxVW*, and *sox XYZABCDEFGH*. Out of these, *in vivo* and *in vitro* thiosulfate oxidation are essentially mediated by periplasmic proteins SoxXA, SoxYZ, SoxB, and Sox $(CD)_2$. In green S bacteria (*Chlorobaculum parvum* DSM 263), *soxJ-soxXYZA-soxK-soxBW* genomic arrangement is generally found (Frigaard and Bryant 2008) which forms sulfur (S) during thiosulfate oxidation (Steinmetz and Fischer 1982). Polysulfides may act as intermediates during thiosulfate oxidation in the periplasm of green sulfur bacteria (Frigaard and Bryant 2008; Friedrich et al. 2001). Green S bacteria, *Allochromatium vinosum*, lack the enzyme sulfur dehydrogenase; therefore the sulfane sulfur atom which is linked to *soxY* cannot be oxidized. However, other genes *soxB* and *soxXA* are transcribed divergently in *A. vinosum* (Frigaard and Bryant 2008). Among all *sox* genes, *soxCD* gene is not detected in magnetotactic *Magnetococcus* sp. MC1, *Thiobacillus denitrificans*, thiosulfate-oxidizing green sulfur bacteria, and *A. vinosum* (Frigaard and Bryant 2008).

4.5.2 *aps* Gene

Adenosine-5-phosphosulfate (APS) pathway involves two enzymes such as APS reductase and ATP sulfurylase (Kappler and Dahl 2001). APS reductase is encoded by *aps* gene which forms APS after catalyzing sulfite and adenosyl monophosphate (AMP) during indirect sulfite oxidation. ATP sulfurylase (ATP, sulfate adenyltransferase) and adenylsulfate/phosphate adenyltransferase (APAT) catalyze to transfer AMP moiety of APS to either pyrophosphate or phosphate, respectively. APS reductase also acts as key enzyme in dissimilatory sulfate reduction pathway in sulfur-reducing prokaryotes (Meyer and Kuever 2007). However, this enzyme is involved in the transformation of sulfite to APS in sulfur-oxidizing prokaryotes (Meyer and Kuever 2007). The *aps* gene was first identified in the archaea *Acidianus ambivalens* in which the major enzyme, sulfur oxygenase reductase, catalyzes the oxidation of sulfur (Urich et al. 2005). Recently, this enzyme system has also been detected in multiple members of the bacteria including *Acidithiobacillus* species and *Aquifex aeolicus*.

4.5.3 *asfA* Gene

Assimilation and mobilization sulfonates in agricultural soils are one of the key soil processes in S cycle, and this is mediated by microbial oxidoreductase *asfA* gene. The *asfA* gene was first discovered in *Pseudomonas putida* S-313, which has the ability to desulfurize toluene sulfonate to p-cresol under aryldesulfonation process (Vermeij et al. 1999; Kertesz and Mirleau 2004). Orthologue sequences of *asfA* gene are detected in vast group of cyanobacteria and bacteria including *Cupriavidus* (*Ralstonia*) *metallidurans* which are able to utilize arylsulfonates as sulfur source. A 100-fold increase in the expression of *asfA* gene was detected in *C. metallidurans* or *P. putida* S-313 culture media containing toluene sulfonate as sulfur source, but the expression was largely repressed when sulfate was added. Kertesz and Mirleau (2004) analyzed the *asfA* containing bacterial diversity in barley rhizosphere and indicated the huge diversity of bacteria that were capable to utilize toluene-sulfonate as sulfur source.

4.5.4 *sor* Gene

The sulfur oxygenase reductase (Sor) enzyme is encoded by *sor* gene which oxidizes the elemental sulfur into sulfite and thiosulfate. The Sor enzyme is generally considered as "archaeal-like" enzyme and present in acidophilic leaching bacteria such as *Acidithiobacillus caldus*, *A. thiooxidans*, *A. ferrivorans*, and *Sulfobacillus thermosulfidooxidans* (Janosch et al. 2015). Sor is a thermophilic enzyme, and its oxygenase activity was detected at 75 °C in *Sb. thermosulfidooxidans* DSM 9293T. Besides *sor* genes, oxygenase activity in *Sb. thermosulfidooxidans* DSM 9293T also has another kind of genes which encodes complete heterodisulfide reductase (*hdr* gene), tetrathionate hydrolase (*tth* genes), sulfide/quinone reductase (*sqr gene*), and thiosulfate quinone reductase (*tqo*) gene. Interestingly, no *sox* genes were involved in the oxygenase activity.

4.6 Microbial Genes Involved in Sulfur Reduction

4.6.1 *dsr* Gene

Sulfate-reducing bacteria (SRB) contain *dsr* gene which encodes the dissimilatory sulfite reductase and is able to catalyze the conversion of sulfite to sulfide with reduction of six electrons. Different models have been proposed to explain the exact roles of the *dsr*-encoded proteins in *Allochromatium vinosum* (Dahl et al. 2005). Altogether, 15 open reading frames, designated *dsrABEFHCMKLJOPNRS*, were identified in *A. vinosum* (Hipp et al. 1997; Lübbe et al. 2006). Various studies have been carried out to study the diversity of SRB using a 1.9-kb *dsrAB* gene fragment amplified with DSR1F and DSR4R primers. These primers were used for molecular

characterization of SRB from various habitats including deep sea hydrothermal vents, salt marshes, sediments, etc. (Agrawal and Lal 2009).

4.7 Microbial Association in Sulfur Cycle Under Diverse Ecosystems

The representative microbial groups responsible for sulfur oxidation and reduction in different ecosystems are elucidated in Table 4.1.

4.7.1 Agroecosystems

The impact of sulfur (S) deficiency in agriculture soils has been recognized for more than a century and is becoming increasingly common in many areas of the world as a result of intensive agriculture, high biomass exportation, and reduced S emissions to the atmosphere (Lucheta and Lambais 2012). Among agricultural crops, rice is the dominant and staple food crop of Asia having 90% of the world's total rice grain production. As rice plants can occupy a large volume of the planted soil, oxidized zones can occur which allow the growth and metabolism of aerobic microorganisms, even in flooded conditions (Freney et al. 1982). As a result, sulfur can exist in these soils in all of its oxidation states from +6 of sulfate to −2 of sulfide, and reduced forms of the element are subject to normal oxidation processes, although sulfur oxidation in paddy soils has not been studied extensively. The two microbes, *Thiobacillus thioparus* (Freney et al. 1982) and *T. thiooxidans* (Mouraret and Baldensperger 1977) have been isolated, and other species are likely to be present (Freney et al. 1982). It has already been mentioned that *Beggiatoa* species (Joshi and Hollis 1976) play a dominant role in rice soils, and it is also likely that heterotrophs and purple and green sulfur bacteria are important in the oxidation of reduced S in the rice rhizosphere. It has been reported that the oxidation of sulfide is beneficial for the rice growth and H_2S served as a causal agent in 12 out of the 27 physiological disorders of rice. On the other hand, soluble sulfides are toxic to nematodes and, hence, can be beneficial to rice (Freney et al. 1982).

As sulfur deficiencies are coming up in rice growing, making necessary sulfur fertilization with compounds such as elemental sulfur and sulfur-coated urea, there is a clear need for a better understanding of the sulfur oxidation in rice paddy soils. Reductions of sulfate, under paddy soil, play key roles in the nutrient mineralization process under early flooded rice fields (Yao et al. 1999). Researchers indicated that sulfur concentration is slightly lower in rice field flooded with freshwater than the marine ecosystem. Another study suggested that soil incorporated with rice straw significantly increased sulfate content. The sulfate (SO_4^{2-}) reduction was observed higher in the rice straw-amended slurries due to presence of high *dsrAB* gene copy numbers. Most of the bacteria responsible for SO_4^{2-} reduction in this condition belonged to the genera *Clostridia*, *Desulfobacterium*, *Desulfovibrio*, *Desulfomonile*, and *Syntrophobacter* (He et al. 2010). Recent study by Kumar et al. (2017) revealed

Table 4.1 Association of different sulfur-oxidizing and sulfur-reducing microbes in various ecosystems

Habitat	Microbes	Response (oxidation/ reduction)	References
Agriculture ecosystem	*Beggiatoa sp.* (paddy soil)	Oxidation	Burke et al. (1974) and Joshi and Hollis (1976)
	Thiobacillus denitrificans (cotton and groundnut field)	Oxidation	Yousuf et al. (2014)
	T. thioparus	Oxidation	Wainwright (1984)
	T. neapolitanus	Oxidation	Wainwright (1984)
	T. novellus	Oxidation	Wainwright (1984)
	Rhodovulum sulfidophilum	Oxidation	Yousuf et al. (2014)
	Betaproteobacteria	Oxidation	Yousuf et al. (2014)
	Marichromatium purpuratum	Oxidation	Yousuf et al. (2014)
Aquatic ecosystem	*Beggiatoa sp.*	Oxidation	Wainwright (1984)
Barren terrestrial land ecosystem			
	Rhodothalassium salexigens	Oxidation	Yousuf et al. (2014)
	Thiomicrospira crunogena	Oxidation	Yousuf et al. (2014)
	Paracoccus pantotrophus	Oxidation	Bardischewsky et al. (2005)
Blacks Drain and Cudgen Lake	*Aquifex aeolicus*	Oxidation	Pelletier et al. (2008)
	Paracoccus versutus	Oxidation	Wodara et al. (1997)
	Archaeoglobus profundus	Reduction	Mander et al. (2004)
	Thermodesulforhabdus norvegica	Reduction	Larsen et al. (2001)
	Desulfotomaculum thermocisternum	Reduction	Larsen et al. (2001)
Coastal saline land, hypersaline habitats	*Rhodovulum sulfidophilum*	Oxidation	Tourova et al. (2011)
	Thiomicrospira crunogena	Oxidation	Tourova et al. (2011)
	Spirochaeta sp.	Oxidation	Tourova et al. (2011)
	Rhodovillum adriaticum	Oxidation	Tourova et al. (2011)
Coastal acid sulfate soil under sugarcane cultivation	*Acidithiobacillus ferrooxidans*	Oxidation	Wakai et al. (2004)
Costal ecosystem	*Thiomicrospira sp.*, *Arcobacter sulfidicus*, and *Sulfurimonas denitrificans*	Oxidation	Kuenen and Tuovinen (1981)
Freshwater ecosystem	*Betaproteobacteria*	Oxidation	Wu et al. (2006)

(continued)

Table 4.1 (continued)

Habitat	Microbes	Response (oxidation/ reduction)	References
Hot spring ecosystem	*Proteobacteria*	Reduction	Badhai et al. (2014)
	Thermodesulfovibrio sp.	Reduction	Badhai et al. (2014)
	Thiobacillus ferrooxidans	Oxidation	Wainwright (1984)
	Thiobacillus organoparus	Oxidation	Wainwright (1984)
	Mycorrhizae	Oxidation	Grayston and Wainwright (1988)
Hypersaline habitats	*Thiohalorhabdus denitrificans*	Oxidation	Sorokin et al. (2008)
Lihir Island	*Acidianus sulfidivorans sp. nov.*	Oxidation	Plumb et al. (2007)
Mangrove swamps	*Desulfovibrio desulfuricans*	Reduction	Sahoo and Dhal (2009)
Marine ecosystem	*Asteriomyces crucicatus*	Oxidation	Wainwright (1984)
	Asteriomyces crucicatus	Oxidation	Wainwright (1984)
	Oscillochloris trichoides	Oxidation	Dahl and Friedrich (2008)
Marine sediments	*Gammaproteobacteria*	Oxidation	Yousuf et al. (2014)
	Archaeoglobus fulgidus	Reduction	Mander et al. (2004)
	Thioploca sp.	Oxidation	Jørgensen and Nelson (2004)
	Pseudoxanthomonas mexicana	Oxidation	Krishnani et al. (2010)
Spruce forest ecosystem	*T. thiooxidans*	Oxidation	Wainwright (1984)
	T. thioparus	Oxidation	Wainwright (1984)
Sub-tropical rainforest and back swamps	*Ferrobacillus ferrooxidans*	Oxidation	Brunner et al. (2008)
Swamp ecosystem	*Aspergillus niger*	Oxidation	Grayston et al. (1986)
	Mucor fiaous	Oxidation	Grayston et al. (1986)

that the temporal variation of sulfur-oxidizing bacteria (SOB) was observed under continuous application of chlorpyrifos over seven seasons in paddy soil.

Canola plant (*Brassica napus*) requires high sulfur (S) during its vegetative growth; otherwise, it shows S-deficiency symptoms. Therefore, elemental sulfur (S^o) fertilizer (with or without inoculated sulfur-oxidizing microorganisms) is frequently used to alleviate this problem (Anandham 1991). *Burkholderia* sp. strain ATSB13T, a thiosulfate-oxidizing facultative chemolithoautotrophic, was isolated from tobacco rhizosphere and has ability to serve as a potential inoculant along with elemental sulfur fertilizers (Anandham et al. 2009).

4.7.2 Acid Sulfate Soil

Acid sulfate soils (ASS) are widespread around the globe and are formed by natural accumulation of bacterially formed pyrite in estuarine environments such as mangrove swamps (White and Engelen 1997) worldwide. ASS is the name given to all soils and sedimentary materials that, through pedogenesis, produce sulfuric acid in quantities that affect soil properties. Southeast Asia occupied about half of the area of ASS found in the world (Langenhoff 1986). In India, these soils are mostly located in swampy coastal plains in the Kuttanad tract (kari lands) of Kerala (Mathew et al. 2001). Alteration of soil water regimes has occurred following the increased urban and rural development of coastal regions. The subsequent oxidation of metal sulfide materials in these soils generates sulfuric acid and highly acidic soil conditions (Dent 1986). ASS sites release leachate of low pH metal which is one of the factors responsible for severe contamination and degradation of ecosystem. As such, the oxidation of ASS results in a host of environmental and economic problems that include loss of aquatic habitats and populations, decreased soil productivity, the emission of greenhouse and other gasses into the atmosphere, and the degradation of civil infrastructure. ASS oxidation also reduces the productivity of agricultural land and decreases the ecological health of aquatic ecosystems through the release of acidic leachate. It is proposed that bacterial and archaeal communities play an important role in the oxidation of ASS and the subsequent generation of acid similar to those observed in acid mine drainage environments.

ASS oxidation means oxidation of pyrite which produces a wide range of oxidation products including sulfuric acid. There is a number of oxidation pathways described for the complete oxidation of pyrite. The complete oxidation of pyrite is proposed to proceed via the formation of intermediates including elemental sulfur. A two-step oxidation then produces ferrous iron (Fe^{2+}) and sulfate followed by further oxidation to produce ferric iron (Fe^{3+}). This oxidation process has been referred to as ripening of ASS (Dent 1986). Ferric iron (Fe^{3+}) has the capacity to oxidize pyrite directly in an oxygen-independent reaction. This interaction can further accelerate the oxidation process. Sometimes, ASS oxidation occurs naturally, as a result of drought and increased pressure on groundwater supplies (lower water table elevation) due to evapotranspiration. The oxidation process is often balanced by natural re-flooding events, which reduce the severity and impacts of oxidation products. Biologically mediated pyrite oxidation is attributed exclusively to the activity of bacteria, and acidophilic chemolithotrophic bacteria such as *Acidithiobacillus ferrooxidans* and *Ferrobacillus ferrooxidans* are responsible to catalyze pyrite oxidation at pH below 4 (Rawlings 2001). Fe- oxidizing chemolithotrophs gain energy from the oxidation of acidic ferrous Fe, although S is also used as an alternative electron donor. Sulfate reducers are generally found in the reducing conditions of anoxic environments. The sulfate-reducing bacteria play a vital role in pyrite formation under ASS. Dissimilatory sulfate reducers derive a large proportion of their metabolic energy from the reduction of sulfur and utilization of sulfur compounds as electron acceptors. Sulfate is reduced to sulfite in an eight-electron transfer reaction. In this process, a fixed carbon substrate such as ethanol or lactate is

oxidized, and hydrogen sulfide gas (H_2S) is produced. The enzyme pathway responsible for the reduction of sulfur is known as the dissimilatory sulfur reductase system. Sequence analysis revealed the unique bacterial community assemblage present in the acid sulfate soil environment. A number of novel bacterial genera and species belonging to phyla *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, *Thermomicrobia*, *Verrucomicrobia*, *Firmicutes*, *Acidobacteria*, *Spirochaetes*, *Planctomycetes*, *Chloroflexi*, *Chlamydiae*, *Nitrospira*, *Dictyoglomi*, *Cyanobacteria*, *Deferribacteres*, *Gemmatimonadetes*, *Deinococcus-Thermus*, and *Fusobacteria* and the candidate phyla OP11 and OP10 were identified in the soil profile of a typical coastal acid sulfate soil under sugarcane cultivation. Analysis of the archaeal community composition through cloning-sequencing revealed the primary functions of these organisms in ASS environments were the production of methane and oxidation and reduction reactions of the sulfur cycle (Brunner et al. 2008).

4.7.3 Acid Mine Drainage and Coal Mine Spoils

Colliery spoils of all types contain some sulfur (S). Surface strip mine spoil having a pH <2 was found to contain 3–5% sulfur, which, in decreasing order of importance, was made up of (1) inorganic sulfidic S, (2) water-soluble S, (3) dilute acid-extractable S, (4) reduced S, (5) elemental S, and (6) anion-exchangeable S. Organic S contributed a minor fraction of the overall S content, although organic S may be present in some coal spoils (Harrison 1978). It is not surprising in view of the reduced inorganic S present that S oxidation occurs in colliery spoils. Brock (1978), using the $^{14}CO_2$ technique, showed that chemoautotrophic bacteria were found on the surface of pyritic materials associated with coal, but not below 10 cm depth. They also isolated large populations of heterotrophic bacteria and fungi, notably *Aureobasidium pullulans*, which is interesting considering that this fungus can oxidize sulfur in vitro (Williams and Cloete 2008). Populations of Fe- and S-oxidizing bacteria were also isolated from spoil in southeastern Montana, viz., waste coal (acidic pyrite-rich) and oxidized alkaline materials. S oxidation is generally hampered and decreased during summer and dry months. Not all forms of pyrite encountered in these spoils are subjected for bacterial oxidation. However, large crystals, for example, appeared to present too little surface area for rapid bacterial action. Application of SO_2 to calcareous spoils might improve their quality because *Thiobacillus* oxidize SO_2 to H_2SO_4, thereby lowering the excess alkalinity of the spoils and converting Na-saturated clay to Ca-saturated clay. Lack of sulfur oxidation due to dry spoils is unlikely to be a problem in areas with adequate rainfall. Problems relating to acid drainage from mines are often stressed in the literature (Kleinmann and Crerar 1979). In this respect, the activity of *T. ferrooxidans* has been emphasized. It is worth recalling that *T. ferrooxidans* can oxidize S^0 and $S_2O_3^{2-}$ with the formation of polythionates. For every mole of S oxidized, 180 mol of ferrous ion is oxidized but does not occur simultaneously. Harrison (1978) studied the microbial succession in an artificial coal spoil and showed that heterotrophic bacteria are an important component of the ecology of these habitats. Choline-SO_4^-

utilizing bacteria accounted for 1% of the population. Harrison (1978) suggested that organic sulfur present in coal may first be attacked by heterotrophs and the sulfur released may undergo further oxidation by *Thiobacillus*, particularly *T. ferrooxidans*.

4.7.4 Coastal Sand Dune

Coastal sand dunes are edaphic deserts and usually show nutrient deficiency for plant growth. The plant grown under this condition requires S from SO_4^{2-} deposited in sea spray (Skiba and Wainwright 1984). Coastal dunes tend to be S deficient due to the leaching out of $S0_4^{2-}$ rapidly. In these environments, elemental sulfur might be profitably used for increasing the amount of available sulfur in these environments. It was observed that S^0 was oxidized in sand and soil samples taken at various points along the dune succession, in which intermediates are formed in the form of SO_3 and $S_4O_2^-$. The S oxidation rate is generally enhanced by increasing content of C and N, decreasing in soil pH and vegetation cover. These sands tended to resist the acidification produced as S^0 was oxidized because of their high $CaCO_3$ contents; they might therefore be useful as sinks for waste gaseous S. The most occurring microbes of these ecosystems are *Salicornia* sp., *Puccinellia distans*, *Microcoleus chthonoplastes*, *Lyngbya aestuarii*, and *Leptolyngbya* sp. (Skiba and Wainwright 1984).

4.7.5 Hot Acid Soil

Although hot acid soils occur infrequently, they do provide an interesting habitat for the growth of heterotrophic microorganisms (Brock 1978). Solfatara is found in areas like Yellowstone Park. These are defined as areas where elemental S is precipitating out as a result of the oxidation of H_2S which are raised with steam from within the earth to the surface. They occupy hillsides, plateaus, small ravines, and shallow holes, and here springs are absent, but sulfur-rich soils at various temperatures are found, ranging in temperature from the mid-20 to the mid-30 °C range on the surface to about 75–90 °C at 20 cm depth. High concentrations of SO_2 are present (up to 152 mg g^{-1}), as are high levels of $S0_4^{2-}$ (4 mg g^{-1}), and pH values are as low as 0.7. *Thiobacillus* and *Sulfolobus* are present in these soils at the lower and higher temperatures (70 °C), respectively, and only overlap at 55 °C (Brock 1978).

4.7.6 Hot Spring

Hot springs are sites that release warm groundwater. The main possible reasons of high temperature in hot spring water are geothermal energy, exothermic reactions, and fission in radioactive elements (Mahala et al. 2013). Hot spring water usually

have various kinds of minerals such as sulfates, carbonates, alkali, alkaline metals, and trace elements (Reddy et al. 2013); therefore, this is considered to have medicinal properties. Besides this, it also contains gasses like H_2S, CO_2, and low amount of O_2 (Mahala et al. 2013), and these gasses may be responsible for the sulfurous odor in hot spring water. Indian hot springs generally have moderate temperature (42–58 °C), moderate salinity, and near-neutral pH, whereas hot springs in other countries like the Philippines, China, and Malaysia have high temperature (50–110 °C), low to high salinities, and acidic or alkaline pH. Due to differences in these parameters (temperature, pH, and salinity), significantly dissimilar microbial phyla had been observed across tropical hot springs (Wang et al. 2013).

Moreover, in the hot spring environments, the important decomposers of organic matter under anoxic conditions are sulfate-reducing proteobacteria. Colorless sulfur bacteria can be isolated from sulfidic springs ranging from cold to mesophilic and geothermal hot sulfur springs. *Thiobacillus*, *Thiomonas*, *Beggiatoa*, and *Thiothrix* cells have been observed in the sulfidic springs of Frasassi cave system. *Beggiatoa* populations normally flourish in microaerophilic environment than *Thiothrix* (Macalady et al. 2006). *Themothrix azorensis* an obligately chemolithoautotrophic, thermophile growing in temperature range of 63–86 °C, was isolated from a hot spring (Odintsova et al. 1996). *Thiomicrospira psychrophila*, *Thiobacillus*, and *Halothiobacillus* sp. strain RA13 were reported from Gypsum Hill and Colour Peak sulfur springs; *Thiomicrospira* was dominant in sediment microbial communities as indicated by DNA-based analysis (Perreault et al. 2007). It was observed that few novel microbial species such as *Thiomonas bhubaneswarensis*, *Chelatococcus sambhunathii*, *Comamonas thiooxydans*, and *Gulbenkiania indica* were isolated from the four tropical hot springs of Odisha (India), namely, Taptapani, Tarabalo, Atri, and Athmallik (Jyoti et al. 2010; Narayan et al. 2016). Some of the thermotolerant plant growth-promoting fungi were also isolated from hot springs of Odisha and registered in National Fungal Culture Collection of India (NFCCI), Pune, by Kumar and Dangar (2014). Genus *Sulfolobus* was discovered from hot springs and is a thermophilic, acidophilic, facultative autotroph. *Thermothrix thioparus*, a neutrophilic thermophile, capable of depositing sulfur extracellularly and oxidizing sulfur compounds anaerobically using nitrate, was recovered from a New Mexico hot spring, whereas a sulfur oxidizer bacterium, *Sulfurihydrogenibium yellowstonense*, extremely thermophilic, facultatively heterotrophic, was isolated from Yellowstone National Park. Occurrence of *Sulfurovum-like* spp. with *Thiothrix* and *Thiofaba* spp. was reported from sulfur springs in the USA. Sulfide concentration in the environment also affects diversity of colorless sulfur bacteria. Based on molecular diversity analysis, *Chloroflexus* and *Aquificales* were found dominant in the low-sulfide spring and high-sulfide spring, respectively, at the same temperature (Skirnisdottir et al. 2000).

4.7.7 Marine Water and Sediments

In marine habitats, the initial step of S cycle is the oxidation of hydrogen sulfide (H_2S). However, microbial role of sulfur oxidation under these habitats especially marine sediments is largely unknown, with exception of certain mat-forming and filamentous bacteria (Jørgensen 1982). In marine system, the sulfur-oxidizing prokaryotes generally are able to oxidize H_2S present in sulfidic intertidal sediments which are produced by sulfate-reducing microbes after utilizing oxidized S compounds as substrate (Jørgensen 1982). Other researchers indicated that in freshwater ecosystem (flooded rice field), the sulfur concentration is slightly lower than the marine ecosystem.

4.7.8 Peatland Soil

Peatland ecosystem is formed due to long-term incremental increase of global warming, less precipitation, and atmospheric deposition of reactive nitrogen and sulfur compounds, accompanied by unforeseeable changes in the carbon balance (Dise 2009). It is estimated that peatlands can emit methane which constitutes 10–20% of the total global methane emission (Wuebbles and Hayhoe 2002) and increase global atmospheric sulfur pollution and acid precipitation (Gauci et al. 2004). In peatland soil, anoxic recycling of reduced sulfur compounds accompanied by high sulfate reduction rates resulted in the formation of "thiosulfate shunt" (Blodau et al. 2007). Some of the important factors responsible for this process in peatland ecosystem are vegetation type, drought, and alternating periods of precipitation (Wind and Conrad 1997; Paul et al. 2006; Reiche et al. 2009; Deppe et al. 2010). One representative model (fen system) for peatland system is located at forested Lehstenbach catchment (Bavaria, Germany) which gives the significance of dissimilatory sulfate reduction by microbes in this system (Klemm and Lange 1999; Alewell et al. 2000).

Relatively lower abundance of *Desulfosporosinus* species (only 0.006% of the total bacterial and archaeal 16S rRNA genes) were encountered under peatland system; however substantial capacity of sulfate reduction was catalyzed by them only. On the other hand, a large portion of sulfate reduction under in situ still remains unsolved (Pester et al. 2010). Mostly in peatland, microbial-mediated dissimilatory (bi) sulfite reductase (*dsrAB gene*) is operated that utilizes sulfite or sulfate anaerobically; that is why these genes act as suitable markers to assess molecular diversity studies in peatland (Dhillon et al. 2003; Kjeldsen et al. 2007). *Desulfomonile* and *Syntrophobacter* were occasionally detected by *dsrABFGA* analysis and generally present in lower soil layer than in the deeper soil layers (Steger et al. 2011). In peatlands, usually the position of the water table marks the transition between the oxic and anoxic zones. Novel *dsrAB*-carrying microorganisms are widespread in wetlands, and *dsrB* DGGE bands and a *dsrAB* clone library revealed that these were broadly distributed among different bogs and fens and related to *Syntrophobacter wolinii* (Pester et al. 2010). However, the relatively high abundance of unique

microflora are yet to be discovered under model peatland ecosystem which would be desirable future research to better understand the nutrient cycle including S cycle under this system (Stepanauskas and Sieracki 2007; Wagner 2009; Xie et al. 2005).

4.8 Conclusion and Future Prospects

It has been established that most of the sulfur compounds utilized by plants for their growth is derived from soil organosulfur pool and the mobilization and assimilation of sulfur by plants are mediated by the soil microbial community. The main drivers of sulfur biogeochemical process in different ecosystems are bacteria and archaea. So far, very limited studies have been conducted to prove beneficial effect of inoculation with sulfur-oxidizing bacteria (SOB), and also no commercial product is available elsewhere on SOB-based bioformulations. Recently, researchers attempted to use granular form of elemental S (ES) (Zhao et al. 2017a) and ES-Zn (Mattiello et al. 2017) fertilizers with the help of S-oxidizing microorganisms, and they further indicated that this form of S is slower to oxidize than powdered elemental S mixed through soil (Zhao et al. 2017a). They also suggested that ES oxidation was not affected by short-term changes in bacterial abundance and community composition by temporary increases in soil acidity or ionic strength (Zhao et al. 2017b). Some researchers also revealed for the first time that besides common SOB, two other groups of bacteria (*Comamonadaceae* and *Rhodococcus*) may also play a specialized role in sulfonate cycling in the soil (Schmalenberger et al. 2009). In addition, mycorrhizal fungi and protozoa in association with bacteria are also important in providing sulfur to plants. Till date, researchers have made considerable advances for understanding how soil organosulfur is converted to plant-available sulfur as well as their regulating mechanism of this process. However, further in-depth investigations are required to understand S transformation process under different habitats through integrated molecular ecology approach as sulfur cycling becomes an important component in anthropogenic ecosystem environment.

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