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Review

Sulphur oxidising bacteria in mangrove ecosystem: A review

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Mangrove soils are anoxic, sulphidic and variable since their chemistry is regulated by a variety of factors such as texture, tidal range and elevation, redox state, bioturbation intensity, forest type, temperature and rainfall. Sulphur-oxidizing bacteria such as photoautotrophs, chemolithotrophs and heterotrophs play an important role in the mangrove environment for the oxidation of the toxic sulphide produced by sulphur reducing bacteria and act as a key driving force behind all sulphur transformations in the mangrove ecosystem which is most essential to maintain the sulphur cycle as well as eco health. These overviews summarizes the current state of knowledge of diversity and important biotechnological contributions of these microorganisms in agriculture, bio fertility, reduction of environmental pollution, maintenance of the productivity of ecosystems and also highlight areas in which further research is needed to increase our basic understanding of physiology, genomics and proteomics of these microorganisms which is most essential.

Key words: Mangrove habitat, sulphur oxidising bacteria, sulphur cycle, sulphide oxidase.

INTRODUCTION

Mangroves ecosystems occur in the tropical and subtropical intertidal estuarine region and river deltas of the world. They represent highly dynamic and fragile ecosystems. They are the most reproductive and biologically diversified habitats of various life forms including plants, animals and microorganisms (Holguin et al., 2001). These ecosystems are characterized by periodic tidal flooding which makes the environmental factors such as salinity and nutrient availability highly variable. Mangrove sediments are mainly anaerobic with an overlying thin aerobic sediment layer (Sahoo and Dhal, 2009). Degradation of organic matter in the aerobic zone occurs by various microorganisms and among various microorganisms, bacteria play major roles in the chemical and biological redox reactions in this ecosystem that create the biogeochemical cycle. Among the various biogeochemical cycles that takes place in this rich detritus based coastal sediment; the sulphur cycle

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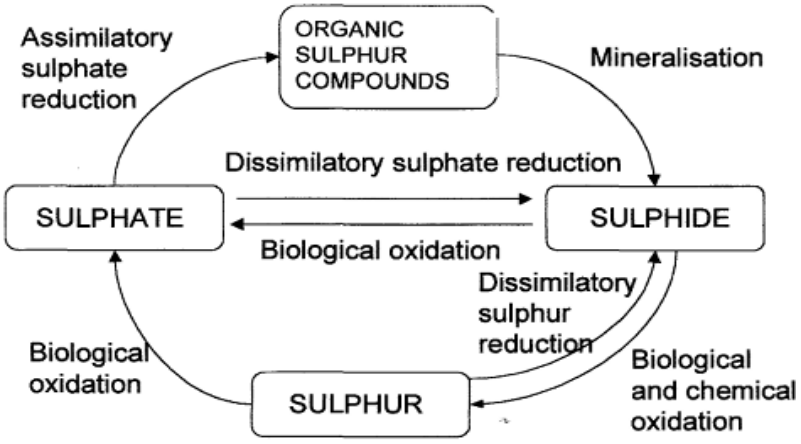

Figure 1. The biological sulphur cycle (Janssen et al., 1999).

(Figure 1) is one of them. Sulphur is biochemically very significant. It is utilized for its structural and functional role in the amino acids cysteine and methionine, and in vitamins such as thiamine, biotin and lipoic acid, as well as in coenzyme A (Madigan et al., 2000).

Sulphur oxidation improves soil fertility. It results in the formation of sulphate, which can be used by the plants, while the acidity produced in sulphur oxidation helps to solubilize plant nutrients and lowers the pH of alkaline soils (Wainwright, 1984). In addition, the sulphur cycle is closely linked to other element cycles, such as the carbon and nitrogen cycles. In the anaerobic layer decomposition occurs mainly through sulphate-reduction (Nedwell et al., 1994). Sulphur-oxidizing bacteria play an important role in the detoxification of reduced sulphide in sediments. The decomposition of organic substance involves various trophic groups of microorganisms acting in a multi-step process. The first step is an enzymatic hydrolysis of polymeric material to soluble monomeric and oligomeric compounds. Under oxic conditions the soluble compounds are directly mineralised to carbon dioxide and water. Under anoxic conditions various physiological groups are involved in the degradation after the initial depolymerisation. Fermentative bacteria convert the products of hydrolysis to a variety of products, mainly short chain fatty acids, carbon dioxide and hydrogen ion (Das et al., 2012). Further conversion through the action of secondary fermenters, sulphate-reducers, acetogens and methanogens produces the end products CO_2, CH_4 and H_2S which may escape into the atmosphere (Das et al., 2012). All three are important greenhouse gases. The extent of the fluxes depends on the penetration of oxygen and the activity of aerobic bacteria in the surface layer, which can oxidize sulphide and methane. Hydrogen sulphide can be oxidised to elemental sulphur, thiosulphate or sulphate (Lyimo et al., 2002). Hydrogen sulphide also precipitates easily with metal ions as the corresponding metal sulphide, for instance FeS, which gives many anoxic types of sediment their black colouration (Lyimo et al., 2002).

The literature shows that mangrove soils are sulphidic and variable, since their chemistry is regulated by a variety of factors such as texture, tidal range and elevation, redox state, bioturbation intensity, forest type, temperature and rainfall (Alongi, 1992). Although several papers on the diversity of sulphur reducing bacteria on the mangrove micro biota have been published, the knowledge of sulphur oxidising bacterial communities and their genomics, metagenomics and proteomics studies with reference to sulphur oxidation in mangrove sediments is sparse. The present review is an attempt to consolidate the latest studies and critical research on diversity of sulphur oxidising bacteria in mangrove and to showcase their important contribution towards the biogeochemical cycle of the ecosystem.

SULPHUR CYCLE IN MANGROVE HABITAT

Sulphur-oxidizing bacteria play an important role in the detoxification of sulphide in water and sediments. Symbiotic sulphur-oxidizers, for example, those within members of the bivalve family Lucinacea, can be commonly found in muddy mangrove areas (Liang et al., 2006). Sulphur reducing bacteria are anaerobic micro-organisms that are wide spread in anoxic habitats like mangrove, where they use sulphate as a terminal electron acceptor for the degradation of organic compounds, resulting in the production of sulphide. Subsequently, the sulphide can be oxidized under oxic conditions by chemolithootrophic sulphur bacteria or under anoxic conditions by phototrophic sulphur bacteria. Sulphur oxidising chemolithotrophs growth is primarily aerobic, that is, using molecular oxygen as terminal

electron acceptor. However, some species (*Beggiatoa* sp., *Thioploca* sp., *Thiobacillus denitrificans*, *Thiomicrospira denitrificans*) oxidize H_2S and aerobically coupling it to nitrate reduction (Brock et al., 2006). In salt marshes, the ecological equivalent of mangroves in temperate areas, sulphate reduction is known to be the major mineralization process. The large inputs of organic matter support high rates of heterotrophic metabolism. Since oxygen is usually depleted below a few millimetre depths, even where the sediment surface is exposed to air, anaerobic metabolism predominates with decomposition mediated primarily by fermentative and sulphate reducing bacteria (King, 1988). Sulphide formed as the product of bacterial sulphate reduction usually undergoes rapid digenetic transformations in coastal sediments. Hence, microbial sulphur transformation is a key process for the biogeochemical sulphur cycle in marine sediments and closely linked to the cycling of other elements like oxygen, nitrogen, and carbon (Bruser et al., 2000).

The major processes of transformation involved in the cycling of sulphur in the environment are:

1. Mineralization of organic sulphur to the inorganic form, hydrogen sulphide, H_2S.
2. Immobilization
3. Oxidation and
4. Reduction

Mineralization

The breakdown/decomposition of large organic sulphur compounds to smaller units and their conversion into inorganic compounds (sulphates) by the microorganisms.

Immobilization

Immobilization involves microbial conversion of inorganic sulphur compounds to organic sulphur compounds. In the process of immobilization, microorganisms absorb inorganic sulphate and convert it into organic form for the synthesis of microbial tissue. If an abundant supply of carbon is available for energy then the entire inorganic sulphate in soil will be converted to organic form, but if little carbon is available then inorganic sulphate will be released from the organic matter. Plant absorbs inorganic sulphate and converts it into organic sulphur compound (Subba Rao, 1999).

Oxidation

Sulphate on the reductive side functions as an electron acceptor in metabolic pathways is used by a wide range of microorganisms and is converted to sulphide. Reduced sulphur compounds such as sulphide serve as electron donors for phototrophic or chemolithothrophic bacteria which convert these compounds to elemental sulphur or sulphate (Robertson and Kuenen, 2006) (Eq^n...1 and 2). When plant and animal proteins are degraded, sulphur is released and accumulates in the soil which is then oxidized to sulphates in the presence of oxygen and under anaerobic condition (water logged soils) organic sulphur is decomposed to produce hydrogen sulphide (H_2S) (Eq^n...3). H_2S can also accumulate during the reduction of sulphates under anaerobic conditions which can be further oxidized to sulphates under aerobic conditions.

$$2S + 3O_2 + 2H_2O \longrightarrow 2H_2SO_4 \longrightarrow 2H(+) + SO_4 \text{ (Aerobic)} \quad (1)$$

$$CO_2 + 2H_2S \xrightarrow{\text{Light}} (CH_2O) + H_2O + 2S \quad (2)$$

$$OR\ H_2 + S + 2CO_2 + 2H_2O \xrightarrow{\text{Light}} H_2SO_4 + 2(CH_2O) \text{ (anaerobic).} \quad (3)$$

The biological oxidation of elemental sulphur and inorganic sulphur compounds (such as H_2S, sulphite and thiosulphate) to sulphate (SO_4) is brought about by direct and indirect methods. In the direct approach photoautotrophic or chemolithotrophic sulphide oxidizing bacteria use sulphide as an electron donor and convert it to sulphur or sulphate. Photoautotrophs use CO_2 as the terminal electron acceptor, while with chemolithotrophs, oxygen (aerobic species) or nitrate and nitrite (anaerobic species) serve as terminal electron acceptors. In the indirect method oxidation of reduced sulphur compound is carried out chemically by ferric iron as the oxidizing agent, and iron oxidizing bacteria are used to regenerate the ferric iron for further use (Pagella and De Faveri, 2000).

Photoautotrophic oxidation of sulphide

The bulk of hydrogen sulphide formed by dissimilatory sulphur reduction is most probably oxidised to sulphate by the respiratory activity of various aerobic sulphur oxidising bacteria and by the direct reaction with oxygen resulting in several intermediary oxidation products such as, sulphur and thiosulphate (Kuenen, 1975). Phototrophic oxidation of sulphide is an anaerobic process which is carried out by green sulphur bacteria such as *Chlorobium,* and purple sulphur bacteria such as *Allochromatium* (Madigan and Martinko, 2006). These bacteria utilize H_2S as an electron donor for CO_2 reduction in a photosynthetic reaction referred to as the vanNiel reaction as described in (Eq^n...4) (Janssen et al.,

1999). Under special condition, however when light has access to the anaerobic, sulphide containing water or the sediment surface, anaerobic phototrophic bacteria may develop which oxidise sulphide and sulphur to sulphate with the concomitant reduction of carbon dioxide to cell substances. The phototrophic green sulphur bacteria, Chlorobiaceae, possess with their chlorosomes, the most efficient light harvesting system, which allows them to grow at lower light intensities or at the lower layer of the water level, adjacent to the sulphide production zone. They oxidise the available sulphide to elemental sulphur outside the cell which is further oxidised to sulphate or reduced to sulphide by sulphur reducing bacteria.

$$2H_2S + CO_2 + \text{Light} \longrightarrow 2S + CH_2O\ (\text{carbohydrate}) + H_2O \quad (4)$$

The purple sulphur bacteria encompass many genera such as *Chromatium*, *Thioalkalicoccus*, *Thiorhodococcus*, *Thiocapsa*, *Thiocystis*, *Thiococcus*, *Thiospirillum*, *Thiodictyon*, and *Thiopedia.* Some of the genera *Ectothiorhodospira*, *Thiorhodospira* and *Halorhodospira* showed special interest because unlike other purple sulphur bacteria, the sulphur produced by these bacteria resides outside the cell (Madigan and Martinko, 2006). Although light seems to be the main source of energy for photoautotrophic sulphide oxidizers, lithoautotrophic growth in the absence of light has been documented for certain purple sulphur bacteria such as *Allochromatium vinosum* and *Thiocapsa roseopersicina* (Friedrich et al., 2001). Green sulphur bacteria, encompassing key genera such as *Chlorobium*, *Prosthecochloris*, *Pelodictyon*, *Ancalochloris, Rhodopseudomonas* and *Chloroherpeton*, use H_2S as an electron donor, oxidizing it first to elemental sulphur and then to sulphate (Tang et al., 2009).

Chemolithotrophic sulphide oxidation

The chemolithotrophic sulphide oxidizers also referred to as colourless sulphur bacteria, do not contain bacteriochlorophyll. In terms of energy and carbon sources, the colourless sulphide oxidizers are classified into four groups. (i) Obligate chemolithotrophs need an inorganic source for energy, and use CO_2 as their carbon source. Despite the classification as "obligate" autotrophs, many species have been shown to benefit from small amount of supplemented carbon compounds (Matin, 1978). Many species of *Thiobacillus*, at least one species of *Sulfolobus*, and all of the known species of *Thiomicrospira* belongs to this category (Tang et al., 2009; Kuenen, 1975). (ii) Facultative chemolithotrophic sulphide oxidizers can grow either chemolitho-autotrophically with carbon dioxide and an inorganic energy source, or heterotrophically with complex organic compounds as carbon and energy source, or mixotrophically using both pathways simultaneously (Tang et al., 2009). Some species of *Thiobacilli*, *Thiosphaera pantotropha*, *Paracoccus denitrificans* (Friedrich and Mitrenga, 1981) and certain *Beggiatoa* (Nelson and Jannasch, 1983) are typical examples of facultative chemolithotrophic sulphide oxidizers. (iii) Chemolithoheterotrophs are characterized by the ability to generate energy from oxidation of reduced sulphur compounds, while being unable to fix CO_2 (Tang et al., 2009). A few species of *Thiobacillus* and some *Beggiatoa* strains fall into this category. (iv) Chemoorgano-heterotrophs such as *Thiobacterium* and *Thiothrix* and some species of *Beggiatoa* can oxidize reduced sulphur compounds without deriving energy from them. These organisms use this reaction as means for detoxifying the metabolically produced hydrogen peroxide (Larkin and Strohl, 1983). They have diverse morphological, physiological and ecological properties and are able to grow chemolithotrophically on reduced inorganic sulphur compounds such as sulphide, sulphur and thiosulphate and in some cases organic sulphur compounds like methanethiol, dimethylsulphide and dimethyldisulphide (Madigan and Martinko, 2006). Many sulphur chemolithotrophs are aerobic as the terminal electron acceptor is primarily oxygen. However, some species can grow anaerobically using nitrate or nitrite as the terminal electron acceptor.

The colourless sulphur bacteria encompass many genera such as *Thiobacillus*, *Acidithiobacillus*, *Achromatium*, *Beggiatoa*, *Thiothrix*, *Thioplaca*, *Thiomicrospira*, *Thiosphaera*, and *Thermothrix* etc. *Achromatium*, a spherical sulphur oxidizer, is common in fresh water sediments containing sulphide. Similar to *Chromatium*, *Achromatium* store elemental sulphur internally as granules which eventually disappear as sulphur is further oxidized to sulphate (Madigan and Martinko, 2006). The genus *Thiobacillus*, one of the most studied groups, consists of several Gram negative and rod shaped species which utilize oxidation of sulphide, sulphur and thiosulphate for generation of energy and growth (Robertson and Kuenen, 2006). The members of genus *Thiobacillus* (obligate chemolithotrophic, non photosynthetic) for example, *T. ferrooxidans* and *T. thiooxidans* are the main organisms involved in the oxidation of elemental sulphur to sulphates. These are aerobic, non-filamentous, chemosynthetic autotrophs. The *thiobacilli* can also oxidize thiosulphate (Eq^n...5).

$$Na_2S_2O_2 + O_2 + HOH \longrightarrow Na_2SO_4 + H_2SO_4 \quad (5)$$

And tetrathionate--(Eq^n...6)

$$2Na_2S_4O_6 + 7O_2 + 6HOH \longrightarrow 2Na_2SO_4 + 6H_2SO_4 \quad (6)$$

Oxidation of reduced sulphur compounds generates significant acidity and thus several species of *Thiobacillus*

are acidophilic. One such species, *Acidithiobacillus ferrooxidans* can also grow chemolithotrophically by the oxidation of ferrous iron (Eq^{n}...7). *Acidithiobacillus ferrooxidans* - an acidophile, very tolerant of low pH (pH between 1 and, at least, pH 5.5) (Quatrini et al., 2003). In addition to oxidizing hydrogen sulphide, this organism can extract iron (Eq^{n}...8) from solid pyrite (FeS_2) in a two-step process in which sulphur atoms are oxidized. First, the organism catalyzes the oxidation of ferrous iron, generating ferric iron

$$Fe^{2+} + 1/2\ O_2 + 2\ H^+ \longrightarrow Fe^{3+} + H_2O \quad (7)$$

Secondly, the ferric iron produced spontaneously reacts with pyrite

$$FeS_2 + 14\ Fe^{3+} + 8\ H_2O \longrightarrow 15\ Fe^{2+} + 2\ SO_4^{2-} + 16\ H^+ \quad (8)$$

The reaction is self-supporting, since the ferrous iron produced in the second reaction can be fed back into the first reaction. Heterotrophic bacteria (*Bacillus*, *Pseudomonas*, and *Arthrobacter*) and fungi (*Aspergillus, Penicillium*) and some actinomycetes were also reported to oxidize sulphur compounds. The important reactions involved in chemolithotrophic oxidation of sulphide, sulphur and thiosulphate under aerobic conditions can be summarized as (Madigan and Martinko, 2006).

$$H_2S + 1/2O_2 \longrightarrow S + H_2O \quad (9)$$

$$S + 3/2O_2 + H_2O \longrightarrow SO_4^{2-} + 2H^+ \quad (10)$$

$$H_2S + 2O_2 \longrightarrow SO_4^{2-} + 2H^+ \quad (11)$$

$$S_2O_3^{2-} + H_2O + 2O_2 \longrightarrow 2SO_4^{2-} + 2H^+ \quad (12)$$

Various colourless sulphur bacteria grow differently under anaerobic conditions, one of the best known pathways is the use of nitrate or nitrite as terminal electron acceptors. Oxidation of sulphide under denitrifying conditions could lead to formation of sulphur, sulphate and nitrite or nitrogen based on the following reactions (Cardoso et al., 2006).

$$S^{2-} + 1.6NO^{3-} + 1.6H^+ \longrightarrow SO_4^{2-} + 0.8N_2 + 0.8H_2O \quad (13)$$

$$S^{2-} + 0.4NO^{3-} + 2.4H^+ \longrightarrow S + 0.2N_2 + 1.2H_2O \quad (14)$$

$$S^{2-} + 4NO^{3-} \longrightarrow SO_4^{2-} + 4NO^{2-} \quad (15)$$

$$S^{2-} + NO^{3-} + 2H^+ \longrightarrow S^- + NO^{2-} + H_2O \quad (16)$$

Oxidation of sulphur and thiosulphate under denitrification can be represented by the following reactions.

$$S + 1.2NO3 - + 0.4H_2O \longrightarrow SO4^{2-} + 0.6N_2 + 0.8H^+ \quad (17)$$

$$S_2O_3^{2-} + 1.6NO_3^- + 0.2H_2O \longrightarrow 2SO4^{2-} + 0.8N_2 + 0.4H^+ \quad (18)$$

Reduction

Two physiological types of sulphate reduction are recognized **(**Peck, 1961**)**. The first is assimilatory or biosynthetic sulphate reduction in which organisms reduces only enough sulphates to meet their nutritional requirements for sulphur. The assimilatory pathway generates reduced sulphur compounds for biosynthesis of amino acids and proteins. This pathway is considered to be in the pathway for the biosynthesis of cysteine and is usually under both coarse and fine metabolic regulation (Roy and Trudinger, 1970)**.**

The second sequence involved in the reduction of sulphate is the dissimilatory or respiratory pathway of sulphate reduction in which sulphate in the absence of oxygen serves as a terminal electron acceptor for anaerobic respiration. Sulphate can be reduced to hydrogen sulphide (H_2S) by sulphate reducing bacteria (for example, *Desulfovibrio* and *Desulfatomaculum*) and may diminish the availability of sulphur for plant nutrition. This is “dissimilatory sulphate reduction” which is not at all desirable from soil fertility and agricultural productivity view point. Dissimilatory sulphate-reduction is favoured by the alkaline and anaerobic conditions of soil and sulphates are reduced to hydrogen sulphide. For example, calcium sulphate is attacked under anaerobic condition by the members of the genus *Desulfovibrio* (Eq^{n}...19).

$$CaSO_4 + 4H_2 \longrightarrow Ca\ (OH)_2 + H_2S + 2\ H_2O \quad (19)$$

Hydrogen sulphide produced by the reduction of sulphate and sulphur containing amino acids decomposition is further oxidized by some species of green and purple phototrophic bacteria (*Chlorobium, chromatium*) to release elemental sulphur (Eq^{n}...20).

$$CO_2 + 2H_2 + H_2S \xrightarrow{\text{Light}} (CH_2O) + H_2O + 2\ S \quad (20)$$

In dissimilative sulphur reduction, sulphate acts as a terminal electron acceptor during the energy-generating oxidation of various materials.

DIVERSITY OF SOB IN DIFFERENT MANGROVE ECOSYSTEM

The knowledge of sulphur oxidising bacterial (SOB)

communities in mangrove sediments is sparse. There are some reports on diversity of SOB from mangrove environment. Sulphur rich mangrove ecosystem, which have mainly anaerobic soil environment, provide favourable condition for the proliferation of photosynthetic anoxygenic bacteria such as purple sulphur bacteria (family *Chromatiaceae*, strain belongs to *Chromatium* sp.) and purple non sulphur bacteria (family *Rhodospirilaceae*, strain belongs to *Rhodopseudomonas* sp.) (Sahoo and Dhal, 2009). Purple sulphur bacteria range in colour from pink to purple and contain bacterio chlorophyll *a* as their major pigment. Purple sulphur bacteria are widely distributed in sulphide rich reducing environment such as mangrove habitat, mud flat and polluted water. These phototrophic anaerobes require sulphide which they oxidise to sulphate for their growth. Physiologically family Chromatiaceae which contain sulphur globules inside their cells are able to oxidise sulphur further to sulphate (Pfenning, 1977). Representatives of the family Chromatiaceae and Rhodospirilaceae were also previously reported from the Indian mangrove habitat (Vethanayagam, 1991; Vethanayagam and Krishnamurthy, 1995) Strains belonging to *Chromatium* sp. *(*Family Chromatiaceae-purple sulphur bacteria) and *Chloroflexux* sp. (family Chloroflexaceae-micro filamentous green photosynthetic bacteria) were also reported to occur in the mangrove habitat (Krishnamurthy et al., 1986). Thatoi et al. (2012) reported the occurance of *Pseudomonas* sp., which oxidised sulphur in the mangrove soil of Bhitarakanika, Odisha, India. The predominant sulphur oxidising bacteria in the mangrove ecosystem of Cochin were identified as members of the genera *Chloronema, Chromatium, Beggiatoa, Thiopedia* and *Leucothiobacteri* (Dhevendaran, 1991). Large population of *chromatium* grew in enrichment culture made of Florida's mangrove sediment (Sahoo and Dhal, 2009). In sediment from the Egyptian coast of the Red Sea on which mangroves grew, 225 isolates of purple non sulphur bacteria belonging to ten species, representing four different genera, were identified. The most common genera were *Rhodobacter* and *Rhodopseudomonas* (Shoreit et al., 1994).

The bacterial diversity present in sediments of a well-preserved mangrove habitat in Ilha do Cardoso, located in the extreme south of Sa˜o Paulo State coastline, Brazil, was assessed using culture independent molecular approaches (denaturing gradient gel electrophoresis (DGGE). The data revealed that the gammaproteobacteria present were 19.28% of the total bacterial community (Dias et al., 2010). The representatives of these Gamaproteobacterial genera were *Acidithiobacillus, Alkalilimnicola, Frateuria, Fulvimonas, Shewanella, Thiorhodospira,* and *Thiobacillus*. *Marichromatium* belonging to the class gammaproteobacteria also reported from a marine Indian aquaculture pond by Kumar et al. (2007). Some of the sulphur oxidising bacteria such as gammaproteobacteria for example, *Chromatiales* were also reported from oil contaminated soil of Brazilian pristine mangrove sediment (Holguin et al., 2001). The Proteobacteria was the most abundant phylum and metabolically highly diverse, widely distributed in marine environments and is an important player in nutrient cycling (Kersters et al., 2006). The potential effect of mangrove roots on sediment proteobacterial populations may influence several environmentally relevant processes in mangrove ecosystems. Gomes et al. (2010) observed that Chromatiales was the second most abundant proteobacterial order and was detected in all samples from an urban mangrove habitat located in Guanabara Bay, Rio de Janeiro, Brazil. This order is represented by anaerobic or microaerophilic microorganisms specialized in sulphur-an oxygenic photosynthesis and are able to oxidize hydrogen sulphide (H_2S) to elemental sulphur (Imhoff, 2006). Campylobacterales were also abundant and mainly detected in the mangrove samples with a marked increased abundance in rhizosphere samples. Members of this order are sulphide-oxidizing denitrifying bacteria (Campbell et al., 2006). *Sulphurovum* belonging to the order Campylobacterales was reported in mangrove rhizosphere samples. This genus is known to be an important player in the process of sulphide-oxidation and denitrification in marine environments (Sievert et al., 2008). The genus *Listonella* includes diazotrophic members with some representative previously detected from mangrove rhizosphere (Gomes et al., 2010). Hart (1958; 1959; 1962) demonstrated that mangrove peat contains large amounts of sulphides and polysulphides. He showed that free sulphur was oxidized to sulphuric acid by *Thiobacillus thio-oxidans* from tidal mangrove soil of Sierra Leone. *Thiobacillus thio-oxidans* was also reported from the mangrove swamp of Keneba (Thornton and Giglioli, 1965). The gammaproteobacteria represented the most abundant proteobacterial subdivision (59% and 77%) among the proteobacterial division reported from Sundarban mangrove habitat, India. The most abundant genera reported are methylophaga, indicating a strong involvement of these bacterial species in the maintenance of the biogeochemical cycle in Sundarban sediment (Ghosh et al., 2010). Kaambo (2006) reported that γ-*Proteobacteria* are the second dominant bacterial group which was observed at the upstream site of the sediments of the Great Berg River estuary of South Africa. They oxidize sulphide to sulphur and are often found in anaerobic sulphur rich regions (Holmer et al., 2001). The gammaproteobacteria such as *Thioalkalivibrio nitratireducens, Thioalkalivibrio denitrificans, Rhabdochromatium marinum*, and *Thiococcus* sp. SZB80 (related (94.9% similarity) to *R. marinum*, a purple sulphur bacterium (Dilling et al., 1995) reported from Futian mangrove swamp) were phylogenetically

associated with cultivated organisms involved in S- or N-cycles (Liang et al., 2006).

Symbiotic association of sulphur-oxidizing bacteria with other organisms has also been reported to occur in mangrove environments. Four tropical lucinids, *Codakia orbiculata, C. pectinella, Linga pensylvanica,* which inhabit sea-grass beds, and *Lucina pectinata*, which inhabits mangrove swamps in Guadeloupe, harbour sulphur-oxidizing endosymbiotic bacteria within bacteriocytes of their gill filaments (Gros et al., 1998). Some of the free-living and symbiotic sulphur oxidising bacteria for example, those within members of the bivalve family Lucinacea were reported from Futian mangrove swamp of China (Liang et al., 2006).

ENZYME RESPONSIBLE FOR SULPHUR OXIDATION

Many published reports address microbial sulphide oxidation. Sulphide oxidase is the key enzyme responsible for sulphide ions oxidation (Mohapatra et al., 2006). Sulfite oxidase contains two identical subunits. The N-terminal domain has a heme cofactor with three adjacent antiparallel beta sheets and five alpha helices. The C-terminal domain hosts a molybdopterin cofactor that is surrounded by thirteen beta sheets and three alpha helices. The molybdopterin cofactor has a Mo (VI) center, which is bonded to sulphur from cysteine, an ene-dithiolate from pyranopterin and two terminal oxygens.

Sulphide oxidase which catalyzes the oxidation of sulphide has been characterized from *Arthrobacter* sp. and *Bacillus* sp. BN53-1 (Mohapatra et al., 2006; Nakada and Ohta, 1999). According to Mohapatra et al. (2006) report, the purified sulphide oxidase was showed to be monomer with a molecular weight of 43 kDa. This molecular weight was found to be higher compared to the purified enzyme from the *Bacillus* sp. BN53-1 which is 37 kDa (Nakada and Ohta, 1999). The sulphide oxidase isolated from *Arthrobacter* sp. was cell-bound and had broad pH activities which are potentially useful in application of the wastewater treatment process (Mohapatra et al., 2006). To our knowledge, in addition to sulphide oxidase there are some other enzyme that are also responsible for sulphur oxidation. Such as, the involvement of *Serratia* regarding sulphate formation from the hydrolysis of organic sulphate by enzymes termed sulphatase (Murooka et al., 1980).

SOX GENE IN SULPHUR OXIDISING BACTERIA

The genes encoding sulphur-oxidizing (Sox) ability is known as *Sox* gene cluster was first described from the alphaproteobacterium *Paracoccus pantotrophus* which is a facultative *chemolithoatotrophs* and grows with thiosulphate (Friedrich et al., 2001). The *sox* gene cluster encoding multienzyme Sox complex of *Pcs. pantotrophus* comprises of at least two transcriptional units of 15 genes (*soxRSVWXYZABCDEFGH*).

SoxR encodes a repressor protein, of ArsR family SoxR which binds to the soxS–V and soxW–X intergenic regions of the gene (Figure 2). SoxS is a periplasmic thioredoxin and essential for the full expression of the *sox* gene cluster (Rother et al., 2005). soxV encodes a membrane protein and soxW encodes a periplasmic thioredoxin. Both are essential for chemotrophic growth with thiosulphate and are probably involved in transfer of reluctant (Bradischewsky and Friedrich, 2001). The subsequent genes *soxXYZABCD* encode four periplasmic proteins, SoxXA, SoxYZ, SoxB and Sox (CD) 2, which reconstitute the core Sox enzyme system. These seven gene *soxXYZABCD,* code for proteins essential for sulphur oxidation *in vitro* (Ghosh et al., 2009) (Figure 2). Sox*EFGH* gene are located downstream of sox*D*. These genes are co expressed with sox structural gene. SoxXA is composed of two *c*-type cytochromes, the diheme SoxX and the monoheme SoxA. SoxYZ is free of cofactors and able to covalently bind sulphur compounds of various oxidation states (Quentmeier and Friedrich, 2001). The SoxB protein, which contains a dinuclear manganese cluster was proposed to function as a sulphate thiohydrolase and has been shown to interact with the SoxYZ complex (Quentmeier et al., 2003). SoxB is believed to act as a sulphate thiol esterase and to be responsible for hydrolytic cleavage of a sulphate group from the bound sulphur substrate. Sox (CD) 2 then oxidize the remaining sulphane sulphur, acting as a sulphur dehydrogenase. Sox (CD) 2 are composed of the molybdoprotein SoxC and the diheme *c*-type cytochrome SoxD (Quentmeier et al., 2000). SoxF gene encodes the monomeric flavoprotein SoxF that has sulphide dehydrogenase activity (Bardischewsky et al., 2005). A novel activity has been discovered for SoxF to activate the thiosulphate- or sulphide-oxidizing Sox enzyme system when reconstituted with a SoxYZ protein separately inactivated by reduction.

Genes homologous to those encoding Sox proteins of *P*. *pantotrophus* (Figure 2) have been identified from partially and completely sequenced genomes of other sulphur oxidising bacteria. For example the sox cluster gene of *Rhodopseudomonas palustris* is similar to that of *P*. *Pantotrophus* and is composed of 16 gene. The Chlorobiaceae are anoxygenic phototrophic green sulphur bacteria that oxidize hydrogen sulphide to sulphuric acid and transiently deposit sulphur globules outside the cell. The genome of *Chlorobium tepidum*, a moderate thermophile, contains a cluster of 13 genes of which soxFXYZAB are homologous to the respective genes of *P. pantotrophus*. *A. Aeolicus* is an obligatory aerobic chemolithotrophic bacterium. This organism requires molecular hydrogen for lithoautotrophic growth and does not grow with thiosulphate alone. The *sox* gene

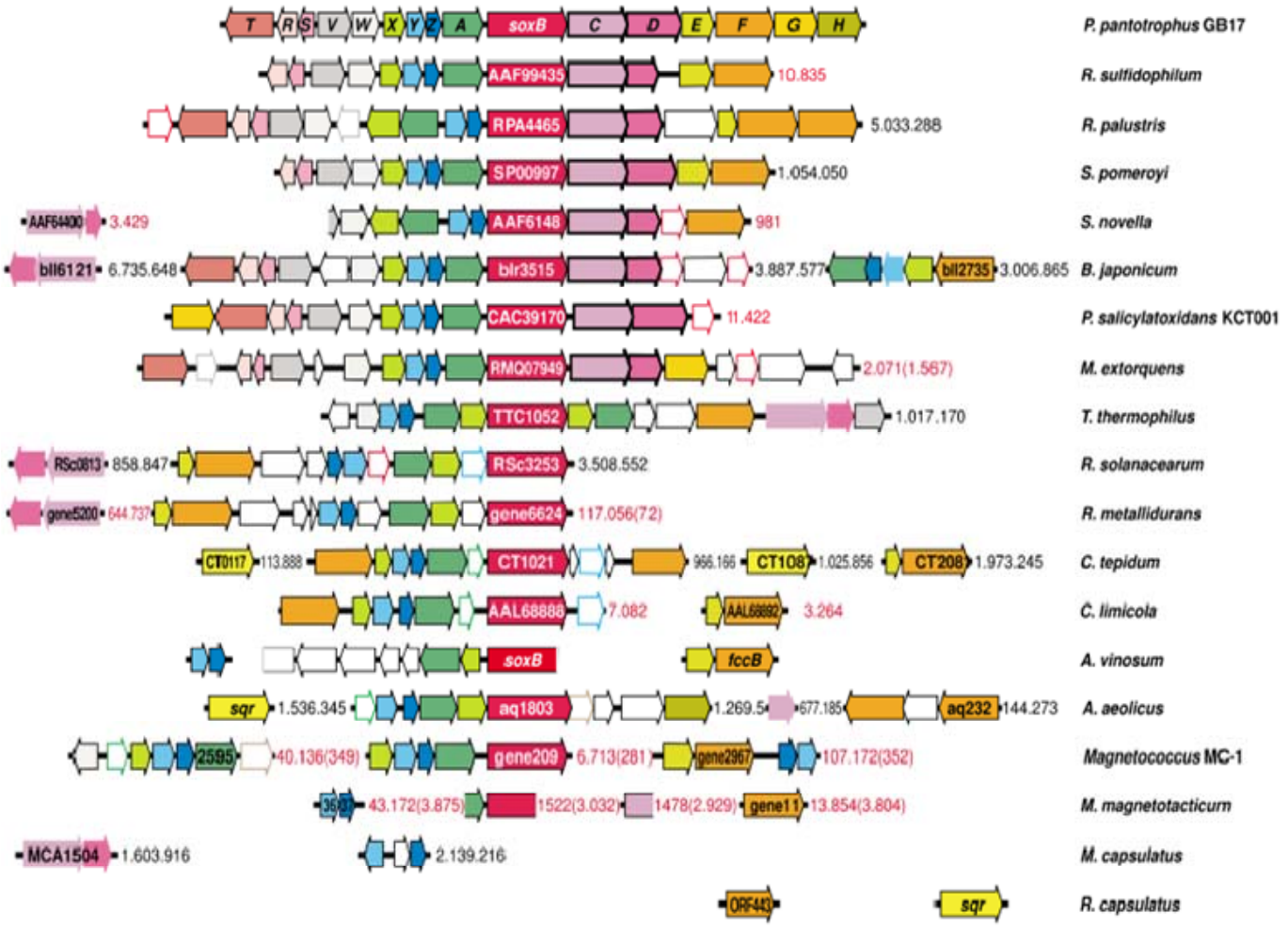

Figure 2. Schematic overview of the sox-locus of *P. Pantotrophus* and related gene of chemolithotrophic and phtotrophic bacteria. (Friedrich et al., 2005).

cluster of *A. Aeolicus* comprises 10 genes. Besides that the complete sox gene clusters encoding essential components of the Sox enzyme system in *P. pantotrophus* are present in partially sequenced genomes of chemotrophic bacteria such as *S. novella*, *Methylobacterium extorquens, Pseudaminobacter salicylatoxidans* and *Bradyrhizobium japonicum*. Also, complete *sox* gene clusters are present in the phototrophs *R. sulfidophilum, Rhodopseudomonas palustris* and the chemolithoheterotroph *Silicibacter pomeroyi*

SOME IMPORTANT BIOLOGICAL APPLICATIONS OF SULPHUR OXIDIZING BACTERIA

Bio leaching

At acid pH, *Thiobacillus ferrooxidans* uses ferrous iron as its energy source and produces ferric iron. This reaction is of great importance in the formation of acid leachate from mining operation and in the microbial leaching of metals from ores. Both processes involve microbiological and chemical reactions. Under aerobic and acidic conditions, *T. ferrooxidans* oxidizes ferrous to ferric iron. Ferric iron chemically oxidizes pyrite to form more ferrous iron and sulphuric acid. The bioleaching, biooxidation of metal sulphides to soluble metal sulphates and sulphuric acid is affected by specialized bacteria. Three species of mesoacidophilic, chemolithotropic bacteria are mainly involved. *Thiobacillus ferroxidants*, *Thiobacillus thiooxidants* and *Leptospirillum ferroaxidans*, *Thiobacillus ferroxidans* oxidizes reduced sulphur compounds to sulphate and iron (II) to iron (III) ions. *Thiobacillus thiooxidants* is able to oxidize only reduced sulphur compounds whereas *L. ferroaxidants* can oxidize only iron (II) ions (Schippers and Sand, 1999).

Biofertiliser

Thiobacilli can also be used in the manufacture of a form of organic fertilizer long favored in Australia. In 'biosuper', a mixture of rock phosphate and sulphur is inoculated with *Thiobacillus thiooxidans.* The biochemical oxidation of the sulphur produces H_2SO_4 which decreases soil pH and solubilizes $CaCO_3$ in alkaline calcareous soils to make soil condition more favourable for plant growth, including the availability of plant nutrients (Linderman et al., 1991), especially phosphorous (Deluca et al., 1989). Applying biofertilizers that is, *mycorrhizae* and *Thiobacillus* that also increased soybean yield has been reported. Symbion-S is a liquid form of “Bio-fertilizer” based on selective strain of sulphur solubilizing bacteria, *Thiobacillus thiooxidans.* These beneficial bacteria are suspended liquid carrier, suspended liquid carrying 10^9 bacterial cells/ml of the product. The bacteria used for the production of this product, namely *Thiobacillus thiooxidants* strain are known for its sulphur solubilizing characters. This bacterial cell converts the non available sulphur and sulphur related compounds to easily assimilable form of sulphur salts through a process of oxidation. During this process, it brings down the high pH of the soil (alkasol soil). Hence, Symbion-S can be utilized in reclaiming the alkaline and saline soil for normal cultivation.

Plant growth promotion

The use of *Rhizobium* inoculant for better crop production is a common practice in agriculture which allows the legume plants to form root nodules within which atmospheric nitrogen is fixed and supplied to the plant. It has also been reported that the synergistic response that occurs when a sulphuroxidizing plant growth promoting rhizobacteria (PGPR) *Delftia acidovorans* RAY209 is added to some *Rhizobium* inoculants, the plants showed enhanced seed emergence, increased biomass, and increased nodule numbers (Yesmin et al., 2004). A number of sulphur oxidizing plant growth promoting rhizobacteria: RAY12, identified as *Achromobacter piechaudii*; RAY28, identified as *Agrobacterium tumefaciens*, RAY132, identified as *Stenotrophomonas maltophilia*; and RAY209, identified as *Delftia acidovorans*. The PGPR act to oxidize elemental sulphur which in turn provides sulphate for the plants. As a result of this arrangement, plants are able to grow more efficiently and effectively and have enhanced growth characteristics, for example (Banerjee and Yesmin, 2002). Hence we can use these bacteria as a bioinoculant for plant growth promotion.

Biocontroling agent

The role of *Thiobacillus* in controlling plant diseases in sulphur amended soils has been demonstrated with regard to potato scab caused by *Streptomyces scabies* and the rot of sweet potatoes caused by *S. ipomoea*.

Under acidic soil conditions (below pH 5.0), inoculation of soil with *thiobacilli* after addition of sulphur effectively minimizes losses due to these pathogens (http://www.western4marketing.com/thiobacillus.php).

Deodorization

Sulphur-oxidizing micro-organisms play a key role in biological deodorization processes. In the prior studies, a number of bacteria capable of oxidizing H_2S were exploited for biological deodorization processes. These bacteria include phototrophic *Chlorobium limicola*, *F. Thiosulfatophilum* (Cork et al., 1986) heterotrophic *Xanthomonas* spp. (Cho et al., 1992) *Pseudomonas putida* (Chung et al., 1996a) and chemoautotrophic *thiobacilli* (Jensen and Webb, 1995). Use of chemo-autotrophic *thiobacilli* for H_2S removal is particularly advantageous because of their simple nutritional requirement, high affinity and removal rate for H_2S and low microbial cell yield (Jensen and Webb, 1995). *Thiobacilli* strains within the species *Acidithiobacillus thiooxidans* (Cho et al., 2000), *Acidithiobacillus ferrooxidans* (Neumann et al., 1990), *Thiobacillus thioparus* (Chung et al., 1996b) and *Thiobacillus denitrificans* (Sublette and Sylvester, 1987) have been reported for their application to H_2S removal in the biological deodorization processes. Removal of H_2S from any effluent, would greatly improve the economics of the process, particularly if this could be achieved micro-biologically. It is therefore of importance to select a microbe that can grow well at ambient temperatures and neutral pH and oxidize sulphide to sulphur in wastewater.

Rubber recycling

Worldwide deposition of waste rubber materials, for example vehicle tyres, constitutes environmental threats and a source of unutilized raw material. The problem with rubber recycling resides in the sulphur cross-links created between the rubber polymers during vulcanization. These cross-links give the material its excellent and characteristic properties but also make it impossible to melt and reshape, as one can do with, for example, glass and plastics. The sulphur-oxidizing bacteria *Acidithiobacillus* and the sulphur-reducing *archaeon Pyrococcus furiosus* have been used to break the sulphur cross-links in vulcanized rubber materials which improved the physical properties of the recycled rubber (Katarina, 2003).

CONCLUSION

The present review highlights the ecology and diversity of

sulphur oxidizing bacteria in different mangrove habitats. Genes and enzyme involved in the sulphur oxidizing process via SOB were exhibited. Finally, the biotechnological potential of such bacteria was treated.

SOB is an important group of microorganisms and widely distributed in all habitats. Though there are much information available on ecology and diversity of SOB, they were only restricted to aerobic enviroemnt. The anaerobic environment like mangroves was sparsely studied by the microbiologists and how SOB sustaining to mangrove ecology is not yet clear. So this review is a collection of recent studies on SOB in different mangrove habitats and their biotechnological application. These microorganisms are not only versatile in their metabolism but also in the environmental conditions in which they thrive. Apart from their importance in nature, SOB, together with sulphur-reducing microorganisms can be successfully exploited in various biotechnological applications such as waste treatment, bioremediation, agriculture, biocontrol etc. Although we have tried to generate information on the diversity and biotechnological application of SOB, we think that we have only scratched the surface and our knowledge of SOB in mangrove ecosystem is still in base line which is one of the greatest challenges in microbial ecology. Therefore, future research is necessary by using innovative technologies to study their ecophysiology, behaviour and interactions with other organisms which will generate enormous opportunities for microbiologists to obtain detailed insights into the diversity, ecology and biotechnology of these important microorganisms.

Conflict of Interests

The author(s) have not declared any conflict of interest.

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