



Iron oxidizing bacteria: insights on diversity, mechanism of iron oxidation and role in management of metal pollution

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Abstract

In natural ecosystems, diverse iron oxidizing bacteria are of common occurrence. Basically, two different mechanisms have been proposed for catalysis of iron oxidation by bacterial metabolic systems which differ mainly at cytochrome and rusticyanin level. Biological iron oxidizers not only affect the cycling of iron but also efficiently minimize the concentrations of hazardous metals such as lead, nickel, copper, chromium, cadmium and cobalt. The ferric iron generated after biological oxidation forms complexes with metals/metalloids present in their vicinity. Ferric ions produced by biological actions also act as catalyst for oxidation of toxic metalloid such as arsenite (As III) converting it into less toxic form. Most importantly, bacterial iron oxidizers have commercially been employed in industrial bioleaching for the recovery of important elements and remediation of acid mine drainage water. Currently, heavy metal contamination has emerged as one of the prime concerns for the world and is posing serious threats to both environment and human health. Although varieties of physical and chemical techniques are currently being used to manage the metal contamination, treatment using biological iron oxidation approaches are convincing because of their ecofriendly nature and low sludge generation. In the present review we have tried to focus on the diversity of bacterial iron oxidizers, mechanisms of iron oxidation by bacterial species, and role of bacterial iron oxidizers in bioremediation of metal pollutants along with future research possibilities in this area.

Keywords Iron oxidizers · Arsenic · Bioremediation · Metal contamination · Ferric iron · Sludge

Introduction

Iron is one of the abundantly occurring elements on the Earth (Wedepohl 1995) and crucial for multiple biological activities. A number of oxidation states have been proposed for iron, but +2 (ferrous) and +3 (ferric) forms are the most common. The changes in oxidation number are affected by environmental conditions like pH, oxygen content, and oxidation reduction potential. Since conversion of ferrous iron to ferric iron is highly oxygen dependent, we can expect the presence of ferrous iron, and therefore iron oxidizing bacteria, only under anoxic environments such as deep ground water surfaces or under highly acidic condition

where oxidation is negligible to very slow (Bird et al. 2011). Under these oxygen depleted conditions, iron oxidizing bacteria utilize ferrous iron for oxidation to accomplish the energy requirement for carbon assimilation (Schwertmann and Cornell 2000). Among various types of iron oxidizers, bacterial iron oxidizers are widely described. Most of the bacterial iron oxidizers belong to phylum Proteobacteria. The bacterial genera performing the oxidation may be autotrophic, heterotrophic, phototrophic, chemotrophic, aerobic and anaerobic (Bird et al. 2011). Their huge diversity in physiology and phylogeny has made them a good tool for innovative research in the area of pollution management. Iron oxidizers are the important players not only in global iron biogeochemical cycling (Bach and Edwards 2003) but also in cycling of other toxic metals and industrial biomineralizing activities (Rawlings and Johnson 2007). Therefore, there is growing attention amongst researchers on iron oxidation process, genetic regulation of iron oxidation (Bird et al. 2011), industrial application (Zhang et al. 2018), their phylogenetic relationship, and diversity along with their adaptive

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strategies under extreme environmental conditions (Makita 2018).

Rapid human population growth and industrial activities have added considerably hazardous concentrations of metals such as arsenic, nickel cobalt, lead, cadmium, copper, zinc and mercury into the natural environments (Singh and Singh 2018) which need to be removed or transformed in order to maintain the environmental sustainability. A number of physico-chemical methods like coagulation/filtration, adsorption on activated alumina, ion exchange resin, adsorption by hydrous ferric oxides, iron oxide coated sand, iron filings, manganese green sand filtration can minimize the metal contamination (Viraraghavan et al. 1999; Khan et al. 2000) but there is need of a sustainable method which is cost effective, fast and ecofriendly in nature and which can be operated easily. Biological iron oxidation process followed by metal contaminant removal is one of the innovative, reliable, low sludge producing method which may be affordable at micro as well as industrial levels.

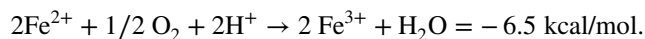
Iron oxidation catalyzed by bacteria

Gallionella ferruginea was recognized as first iron oxidizing bacteria in 1837 (Ehrenberg 1837). Bacterium *Sideroxydans paludicola* is able to oxidize 60% of the iron in a bioreactor under low oxygen concentrations. Bacterium *G. ferruginea* requires Fe(II) for its growth under microaerophilic condition. *Leptothrix ochracea*, *Leptothrix discophora*, *Leptothrix cholodnii* and *Leptothrix mobilis* (van Veen et al. 1978) species also efficiently oxidize iron. These species produce extracellular tubular sheath that is occupied by cell filament. *L. ochracea* is most visible iron oxidizer in fresh water environment (Emerson and Weiss 2004) but it is not able to derive energy from iron oxidation. Its presence in abundance in Fe rich water indicates that it requires iron Fe(II) in higher concentrations for growth (Emerson and Revsbech 1994). It produces oxides of iron which are deposited on the sheaths. Thus, sheath of *Leptothrix* sp. are the site of iron oxide deposition. Sheath plays an important role in protection of cells from becoming encrusted in insoluble iron oxyhydroxide (Ghiorse and Ehrlich 1992). Mixing of Fe(II) and O₂ result in precipitation of the Fe oxide (rust coloured) flocks that cover available surfaces. Aerobic bacteria conserve energy from the oxidation of Fe(II) at neutral pH. Many lithotrophic bacteria are iron oxidizers. At neutral pH, Fe(II) is oxidized to Fe(III) and at the same time Fe(III) hydrolyze H₂O and precipitates as solid iron oxyhydroxide (King et al. 1995).

Microorganisms do the reduction of iron because they need it as a cofactor of many metabolic enzymes and regulatory proteins. However, many of them are also efficient in deriving energy by oxidizing iron. Solubility properties of ferric and ferrous ions are quite different. Under anaerobic

condition, ferric iron is reduced into soluble ferrous form. Presence of aerobic condition and alkaline to neutral pH in aquifers favors the oxidation of ferrous to ferric. Iron oxidizers are known to control the fate of many metals and nutrients like iron, manganese, copper, nickel, chromium, nitrate, phosphate, sulfate and bicarbonate. Ferric iron, generated after bacterial iron oxidation activity, interacts with metals and nutrients to form metal-nutrient-complex which settles down in the aquatic system for very longer duration (Fig. 1). In alkaline environment ferric iron precipitates in the form of ferric hydroxide. Numbers of bacterial species are known to oxidize ferrous iron (Table 1).

Thus, iron forms a variety of oxidized and reduced compounds at different pH and redox potential in aquifer. However, acidic pH and presence of oxygen in aquifer gives the stability to ferrous form of iron. Under such situation acidophilic bacteria like *Thiobacillus ferrooxidans*, *Leptospirillum ferrooxidans* and *Sulfolobus acidocaldarius* are able to oxidize ferrous iron. The reaction is as below:



Bacteria like *Hyphomicrobium*, *Pedomicrobium*, *Planctomyces*, filamentous *Sphaerotilus* and *Leptothrix* derive energy through oxidation of ferrous iron (Jones 1986). Ground water contains ferrous iron and when ground water seeps out to the surface, oxidizes to ferric form and ultimately precipitates as ferric hydroxide. In ground water sulfate reducing bacteria play an important role for the reduction of ferric iron to ferrous iron.

Under well oxygenated conditions, half life of ferrous iron is very low i.e. less than 1 min (Singer and Stumm 1970) while in poorly oxygenated or microaerophilic conditions, half life is enhanced to 300 times (Roden et al. 2004). Iron oxidizing bacteria can oxidize iron at a rate 50×10^3 times faster than the chemical oxidation of iron (Sharmin 2001). Treatment of iron containing drinking water using biological methods is reported by various authors (Mouchet 1992). Most of the iron oxidizing bacterial genera belongs to proteobacteria, the largest bacterial phylum. Hedrich et al. (2011) grouped iron oxidizers into four divisions: (1) acidophilic, aerobic iron oxidizers; (2) neutrophilic, aerobic iron oxidizer; (3) neutrophilic, anaerobic (nitrate dependent) iron oxidizers and (4) anaerobic photosynthetic iron oxidizers. However, some acidophilic species may be well equipped with the property of both oxidation as well as reduction.

Diversity of bacterial iron oxidizers

Acidophilic, aerobic iron oxidizers

Among the most widely studied acidophilic iron oxidizing bacteria are *Acidithiobacillus* which were earlier known as

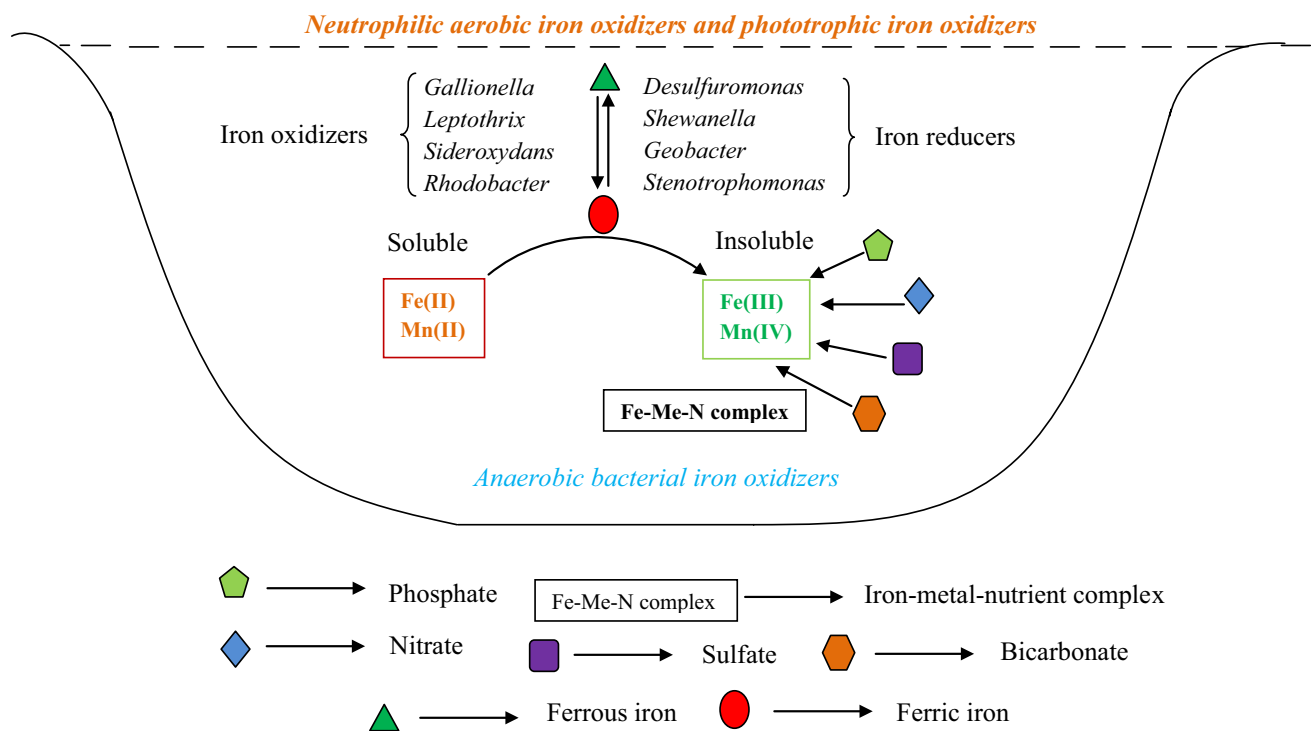


Fig. 1 Iron, metal and nutrient interaction in aquatic ecosystem

Table 1 Ferrous iron oxidation by bacterial species

Oxidizer type	Bacterial species	References
Acidophilic aerobic iron oxidizers	<i>Thiobacillus ferrooxidans</i>	Nemati and Webb (1997)
	<i>Leptospirillum ferriphilum</i>	Ojumua et al. (2009)
	<i>Acidithiobacillus ferrooxidans</i>	Maa and Lin (2012)
	<i>Acidimicrobium</i> sp.	Arroyo et al. (2015)
Neutrophilic, aerobic iron oxidizers	<i>Gallionella ferruginea</i>	Hallbeck et al. (1993)
	<i>Sideroxydans paludicola</i> strain BrT and BR-1, <i>Ferritrophicum radicolica</i>	Weiss et al. (2007)
	<i>Sideroxydans</i> strain CL21	Lüdecke et al. (2010)
	<i>Gallionella</i> sp.	de Vet et al. (2011)
	<i>Pseudomonas</i> species	Liu et al. (2013)
Phototrophic iron oxidizers	<i>Mariprofundus ferrooxydans</i> PV-1	Summers et al. (2013)
	<i>Chromatium</i> strain L7, <i>Rhodobacter</i> strain SW2	Ehrenreich and Widdel (1994)
	<i>Rhodovulum robiginosum</i> , <i>Rhodovulum iodosum</i>	Straub et al. (1999)
	<i>Thiodictyon</i> sp. strain f4	Hegler et al. (2008)
Neutrophilic, iron oxidizers respiring on nitrate	<i>Escherichia coli</i>	Umbriet (1999)
	<i>Nocardioides</i> and <i>Rhodanobacter</i>	Nordhoff et al. (2017)
	<i>Acidovorax</i> (A.) strain BoFeN1, 2AN, A. <i>ebreus</i> strain TPSY, <i>Paracoccus denitrificans</i> Pd 1222, and <i>Pseudogulbenkiania</i> sp. strain 2002	Jamieson et al. (2018)
	<i>Gallionellaceae</i> sp.	Tominski et al. (2018)

Thiobacillus. They oxidize iron and generate electrons which finally go to the terminal electron acceptor through electron transport pathway. This generates energy with the help

of enzyme ATP synthase. *Acidithiobacillus ferrooxidans* is one of the species of *Acidithiobacilli* which was firstly described by Colmer et al. (1950). Based on sequencing

and physiological features, Kelly and Wood (2000) assigned eight *Thiobacillus* species into three genera namely, *Acidithiobacillus*, *Halothiobacillus* and *Thermithiobacillus*. Using two distinct pathways for ferrous iron oxidation, Hallberg et al. (2010) proposed a new species which is different from four species of *Acidithiobacillus*.

A moderately acidophilic species *Thiomonas* was reported by Battaglia-Brunet et al. (2006) possessing the property of both iron as well as arsenite oxidation. Due to their ability to oxidize arsenite into less mobile and more adsorptive form i.e. arsenate, such bacteria are useful for arsenic bioremediation. These bacteria can also grow heterotrophically on yeast extract and with increase in the concentration the growth of bacteria is better.

Neutrophilic, aerobic iron oxidizers

All neutrophilic, aerobic and chemolithoautotrophic iron oxidizers have been grouped together into proteobacteria (Emerson et al. 2010), whereas freshwater and marine forms have been classed, respectively into beta proteobacteria and zeta proteobacteria. Hedrich et al. (2011) have demonstrated that at neutral pH, ferrous iron rapidly oxidizes in aquatic oxygenic environment which causes the neutrophilic iron oxidizers to adapt themselves to grow at the transition zone of aerobic and anaerobic surfaces. They are, thus known as gradient organisms. *G. ferruginea* is the only known species of *Gallionella* which is now the most widely studied neutrophilic iron oxidizing proteobacteria. Earlier Lutters-Czekalla (1990) considered it to be obligate autotroph but subsequent studies proved about its ability to grow autotrophically as well as mixotrophically on ferrous iron (Hallbeck and Pedersen 1991). *Leptothrix* (obligate heterotroph except *L. ochracea*), *Sphaerotilus natans* (heterotroph), *Sideroxydans*, *Ferritrophicum*, *Mariprofundus ferrooxydans* (marine neutrophilic iron oxidizer, Emerson et al. 2007) *Pseudomonas* and *Pseudoalteromonas* (Sudek et al. 2009) are examples of some more species in this group.

Neutrophilic, iron oxidizers respiring on nitrate

Iron oxidizing bacteria coupled to nitrate reduction thrive in fresh water as well as brackish water condition and fall into alpha, beta, gamma and deltaproteobacteria. They are either autotrophic or heterotrophic in nature such as *Acidovorax* (Straub et al. 2004), *Aquabacterium*, *Thiobacillus denitrificans* (Straub et al. 1996), and *Pseudogulbenkiania* (Weber et al. 2006).

Phototrophic iron oxidizers

Ehrenreich and Widdel (1994) have shown the first evidence about the iron oxidizing activity of photosynthetic

bacterium which belongs to the genus *Rhodobacter* species. Strain *Rhodobacter* SW2 uses organic substrates like monocarboxylic acids, glucose and fructose apart from ferrous iron. Most of phototrophic iron oxidizers belong to class alphaproteobacteria except *Thiodictyon* strain L7, which is gammaproteobacterium. The anaerobic iron oxidizing nature of photosynthetic microbes was initially known through purple phototrophic iron oxidizers. They also thrive in freshwater as well as in marine ecosystems. Harmful effects of iron oxidation associated with purple photosynthetic bacteria have also been reported. The ferric iron encrustations around *Rhodomicoccus vannielii* cells hinder the photosynthetic activity because of limited access to light. It is observed that due to inhibitory effect of ferrous iron on photoheterotrophic growth some phototrophic purple bacteria such as *Rhodobacter capsulatus* oxidize iron anaerobically as a defence mechanism (Poulain and Newman 2009).

Oxido-reduction catalysis by iron oxidizers

Some iron oxidizing bacteria also have the property of ferric iron reduction and here ferric iron acts like anaerobic electron acceptor (Lovely 1997; Nealson and Saffarini 1994). These are most important microbiological processes and contribute significantly in iron cycling. The iron reducers normally increase the content of phosphates, trace metals like iron and manganese in groundwater (Lovley et al. 1993). Dissimilatory iron reducing bacteria include both neutrophiles (*Geobacter metallireducens*) as well as acidophiles (*A. ferrooxidans*, *Acidithiobacillus ferrivorans* and *Acidiferribacter thiooxydans* (Lovley 1991). Ehrlich and Newman (2009) have observed that *G. metallireducens* can metabolize variety of organic substrates such as acetate, butyrate, ethanol and propionate to reduce ferric iron. Ohmura et al. (2002) have observed that *A. ferrooxidans*, *A. ferrivorans* and *A. thiooxydans* are capable of oxidizing elemental sulfur for iron reduction whereas *A. ferrooxidans* can also oxidize hydrogen for ferric iron reduction.

Biochemical and molecular mechanisms of iron oxidation in bacteria

Detailed studies have been made on the mechanism of iron oxidation widely in strains of *Acidithiobacillus* species (Sasaki et al. 2003; Ida et al. 2003; Holmes and Bonnefoy 2007; Hallberg et al. 2010). In *Acidithiobacillus* species the oxidation of iron produces electron which have two different fates depending on the requirement of organism. Electron flow reduces oxygen molecule to water and proton counterbalances the downhill flow of electron. It is seen that there is a proton gradient between outside and inside of cell

which due to pH differences (the extracellular pH being 2.0 and intracellular being 6.5–7.0) leads to proton inflow and consequently there is production of ATP by enzymatic activity of ATP synthetases (Quatrini et al. 2009). Culmination of electron flow into reduction of NAD(P) to NAD(P)H is another pathway where electrons move against the redox potential gradient. The uphill flow of electrons requires energy because half redox potential value for $\text{Fe}^{2+}/\text{Fe}^{3+}$ couple at pH 2.0 is more positive as compared to NAD(P)/NAD(P)H couple at pH 6.5–7.0 and this problem is resolved by proton inflow which occurs as a result of pH gradient from outside of cell to inside of cell (Quatrini et al. 2009).

There is change in pathway at rusticyanin level due to the electrons generated by ferrous iron oxidation. Further movement is controlled by the organism's requirement of reducing equivalents in form of NAD(P)H or energy in form of ATP.

Amouric et al. (2011) have proposed four groups to describe iron oxidation pathways in *Acidithiobacillus* species. They have included *A. ferrooxidans* ATCC 23270T in group I and *A. ferrooxidans* ATCC 33020 in group II and both of them utilize proteins encoded by *rus* operon. After oxidation of iron the electrons are received by outer membrane protein cytochrome (Cyc). *A. ferrivorans* represents Group III which uses only *rusB* gene products and *Iro* proteins. Group IV is represented by *Acidithiobacillus* strain JCM 7811 which uses *Iro* and proteins associated therein (Amouric et al. 2011).

The catalysis of Fe(II) to Fe(III) is carried out by a C-type cytochrome (Cyc 2) present in outer membrane of the cells (Fig. 2). Electrons are transferred to the cytoplasmic membrane through a terminal 'aa₃ cytochrome oxidase' and again to the electron transport chain which generates NADH. Molecules which shuttle electrons are rusticyanin and two additional small cytochromes (Cyc-A1 and Cyc-I). *Rhodobacter* sp. are anoxygenic photosynthetic bacteria that utilize Fe(II) as an electron donor. It oxidizes Fe(II) in the periplasm. Thus, there are three possible ways of iron oxidation i.e. (1) the iron oxidation either in the periplasm or at the outer membrane, (2) involvement of cytochrome as primary Fe oxidase for ferric iron formation, and (3) oxidation through electrons transferred by electron shuttles to the cytoplasmic membranes.

The iron oxidation process involves the *rus* operon. The *rusA* and *rusB* genes synthesize the protein rusticyanin A and rusticyanin B. The two different types of iron oxidation described so far differ at the level of rusticyanin. The *pio* operon system present in phototrophic iron oxidizer, *Rhodospirillum rubrum* contains three genes including *pioA*, *pioB*, and *pioC* synthesizing periplasmic cytochrome c-type protein, porin protein, and a periplasmic high-potential iron protein (HiPIP), respectively (Bird et al. 2011). Another operon found in *Rhodobacter* sp. is *Fox* operon responsible for ferrous iron oxidation. The genes encode

proteins named as *FoxE* (cytochrome c), *FoxY* (hypothetic quinone protein) and *FoxZ* (integral protein) (Croal et al. 2007). Quatrini et al. (2009) have extended the information relevant to bacterial iron oxidation by integrating tools of bioinformatics, transcript analysis and RT-PCR. They predicted the novel genes involved in iron oxidation mechanism. The identified genes mediating ferrous iron oxidation were *cup* (copper oxidase-like), *ctaABT* (heme biogenesis and insertion), *nuoI* and *nuoK* (NADH complex subunits), *sdrA1* (a NADH complex accessory protein) and *atpB* and *atpE* (ATP synthetase F₀ subunits). The genes participating in iron oxidation process are described in *Sideroxydans lithotrophicus* ES-1. The genomic analysis revealed the *mto* gene clusters consisting of *cymA*, *mtoA*, *mtoB* and *mtoD* (Shi et al. 2016). The component MtoA has been proposed to help oxidize the ferrous iron as well as their mineral forms whereas MtoD (periplasmic cytochrome) has been expected to participate in electron movement from MtoA (outer membrane protein) to CymA (cytoplasmic membrane protein). However, molecular confirmations are still lacking for the proposed pathway, the currently available information suggests the contribution of MtoA, MtoB, MtoD and CymA mediated electron transfer from ferrous iron to quinone leading to formation of quinol in membrane of iron oxidizing bacterium *S. lithotrophicus* ES-1. Moinier et al. (2017) have described the function of RegB/RegA signal transduction pathway controlling the genes participating in iron oxidation process in *A. ferrooxidans*. They explained that the process of biological iron oxidation in *A. ferrooxidans* happens prior to inorganic sulfur oxidation if the medium is amended with both iron and inorganic sulfur. The four RegA variants consisting of DNA joining region, natural, phosphorylated and non-phosphorylated are specific in binding to upstream parts of genes controlling the biological iron oxidation. Importantly, the phosphorylation was demonstrated to exert no impact on the specificity of RegA. Furthermore, the binding of RegA does not interfere with the binding of RNA polymerase. The mechanism as proposed by Amouric et al. (2011) is presented in Fig. 2a, b.

Applications of bacterial iron oxidizers

Decontamination of metal/metalloid polluted environment

Xiang et al. (2000) evaluated the removal of heavy metals from anaerobically digested sludge using indigenous iron oxidizing bacteria in batch culture experiment. Bacterial inoculation together with the addition of ferrous sulfate in the medium enhanced the solubility of toxic metals like chromium, copper, zinc, nickel and lead. Bacterial growth during bioleaching process lowered the pH of the medium

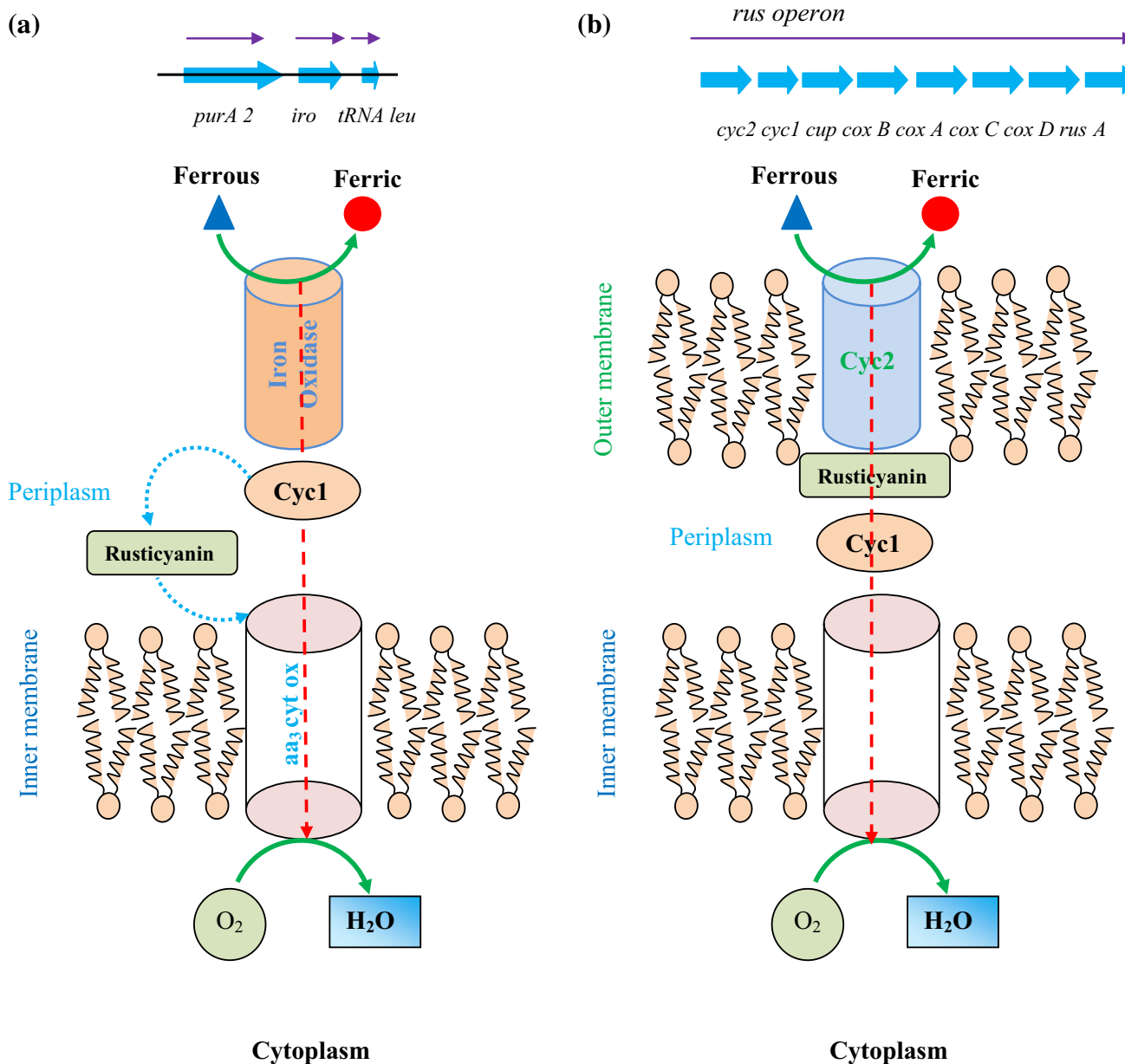


Fig. 2 **a** Iron oxidation in bacteria mediated by iron oxidase (modified from Amouric et al. 2011). **b** Iron oxidation in bacteria catalyzed by rusticyanin (modified from Amouric et al. 2011)

to very acidic (2.0–2.5). Maximum, heavy metal removal by iron oxidizing bacteria was obtained for copper and minimum for lead. The metal content of sludge after treatment was shown to reduce to level which was safe for agricultural application. Katsoyiannis and Zouboulis (2004) employed the iron oxidizing bacteria *G. ferruginea* and *L. ochracea* found in water, for treatment of arsenic contaminated drinking water under fixed-bed upflow filtration unit. Iron oxidation followed by its precipitation promotes the further oxidation of arsenite because ferric iron acts as a catalyst. They reported the efficient recovery of both arsenite as well

as arsenate in the concentration range of 50–200 $\mu\text{g/L}$. The enhanced removal of arsenic was ascribed to the oxidation of arsenite by bacteria and subsequent sorption onto iron oxide. Duquesne et al. (2003) analyzed the arsenic removal performance of *A. ferrooxidans* under acidic condition. Precipitation of dissolved arsenic was observed due to microbiological activities few meters ahead from its discharge site. Under laboratory condition bacterium was able to remove arsenic when grown with ferrous iron. There was efficient precipitation of arsenate with ferric iron and sulfate in form of more or less poorly organized form schwertmannite.

Other precipitated material observed after iron oxidation was jarosite which was not found to be associated with arsenite. Konhauer et al. (1993) reported the mineral formation on the surface of bacteria growing under different solute concentrations in river water system. With time gap changes in bacteria associated mineral phases ranging from poorly ordered to crystalline structures on cell surfaces were observed. They suggested the role of bacterial cell surface deposited minerals in transfer of metals from hydrosphere to sediment phase under natural environmental conditions of river system. Lack et al. (2002) evaluated the efficacy of nitrate dependent anaerobic iron oxidizing bacterium *Dechlorosoma* species for removal of heavy metal cobalt and radionuclide (Uranium) under laboratory conditions. Biooxidation and precipitation of iron resulted into adsorption of 55 μM uranium and 81 μM cobalt. There was significant difference in sorption ability of biogenic iron as compared to synthetic one. Uranium bound to biogenic iron oxide was in the form of U(VI) forming bidentate and tridentate inner sphere complex with Fe(III) precipitates as revealed by X-ray absorption spectroscopy. The study indicated the future application of iron oxidizers as a safe alternative in management of metal and radionuclide polluted systems. Shiratori and Sonta (1993) have used the ability of iron oxidizing bacteria for the treatment of flue gas containing metals like copper, lead, arsenic, and zinc, as well as hydrogen sulfide desulfurization. The bacterial treatment was superior over physicochemical treatment in terms of low cost, efficient metal separation, easy operation, good flexibility and hydrogen sulfide gas recovery. The bacterial treatment was able to remove 90% arsenate and 60% arsenite. Park et al. (2005) demonstrated the feasibility of acidophilic iron oxidizing bacteria in polyurethane based bioreactor system for the metal recovery from electroplating waste. Electroplating industrial effluents are known to possess the higher concentration of toxic heavy metals like nickel and zinc. Biological metal recovery process is advantageous because of low cost, low amount of secondary sludge generation and environment friendly nature. The process also proved beneficial because of easy separation of ferric ions from the mixture of other metals. During three months long operation, bioreactor system exhibited stability and 98% effectiveness in *A. ferrooxidans* mediated ferrous iron oxidation. Effective separation of ferric iron from mixed metals solution was observed at optimum pH 4.0. They suggested the recycling of recovered metals to control the environmental pollution.

Phosphorus has a strong affinity with iron oxyhydroxide (Canfield et al. 2005). Rentz et al. (2009) reported that iron oxides as produced by *L. ochracea* have the capacity of phosphorus retention. Lehimas et al. (2001) were able to bring the concentration of arsenic below permissible limit using *Gallionella* (iron oxidizing bacteria) in arsenic contaminated iron rich ground water. Remediation of arsenic

from ground water with the help of iron oxidizing bacteria like *G. ferruginea* and *L. ochracea* is also reported by several workers (Katsoyiannis and Zouboulis 2004). They observed that As(V) was removed easily in comparison to As(III). Arsenic removal efficiency increased due to oxidation of As(III) to As(V). Arsenic exists in aqueous solution in H_3AsO_3 form and As(V) in H_3AsO_4 . During biological oxidation process of iron in arsenic contaminated water the following reaction occurs:

1. $\text{M-FeOH} + \text{H}_3\text{AsO}_3^- \rightarrow \text{M-Fe-H}_2\text{AsO}_3 + \text{H}_2\text{O}$ (arsenic sorption method),
2. $\text{H}_3\text{AsO}_3 + 1/2 \text{O}_2^- \rightarrow \text{H}_3\text{AsO}_4$ (oxidation through bacteria),
3. $\text{M-FeOH} + \text{H}_3\text{AsO}_4^- \rightarrow \text{M-Fe-H}_2\text{AsO}_4 + \text{H}_2\text{O}$ (arsenic sorption method).

The most common iron oxidizing bacterium *T. ferrooxidans* is able to remove 60–80% arsenic. Thus iron plays a major role in removal of arsenic from arsenic contaminated ground water. Arsenic gets adsorbed on the iron oxide and thus can be filtered out from water for safe drinking purpose.

Iron oxidizers in the environment can control the fate and availability of many metals. Because of ferric iron generation potential iron oxidizers can be utilized for metal remediation from polluted water. After association of ferric iron with metals present in vicinity precipitation happens which can be easily removed by filtration or centrifugation. Bacterial iron oxidizers have been reported to control the pollution caused by metals like arsenic, iron, manganese, nickel, lead, chromium, copper, and zinc. The lists of microorganisms and metals removed from contaminated sites by their application are presented in Table 2.

Industrial applications of bacterial iron oxidizers

Acidithiobacillus ferrooxidans, *G. ferruginea*, *L. ferrooxidans* and *L. ochracea* are the important iron oxidizers present in nature. From industry point of view, acidithiobacilli have immense importance not only in bioleaching but also in treatment and management of acid mine drainage (AMD). To date, *A. ferrooxidans* has been used extensively in mining activities to obtain the metals from respective minerals (Shiratori and Sonta 1993). They used this acidophilic microbe for treatment of flue dust and desulfurization of hydrogen sulfide. The treatment technique is superior over conventional methods due to inexpensiveness, fast extraction of metal contaminants, less amount of sludge formation and sequestration of highly toxic arsenic in arsenate form. Large amount of ferric iron produced by microbiological activity is sufficiently able to oxidize hydrogen sulfide leading to its removal by transformation into elemental sulfur.

Table 2 Iron oxidizing bacteria utilized for metal/metalloid removal

Fe(II) oxidizing bacterial species	Metal of interest	References	Remarks
<i>Acidithiobacillus ferrooxidans</i>	As	Duquesne et al. (2003)	Effluent treatment
<i>Acidithiobacillus ferrooxidans</i>	As	Liao et al. (2011)	Treatment of simulated arsenic contaminated water
<i>Gallionella ferruginea</i>	Fe, As, Mn	Katsoyiannis and Zouboulis (2006)	Treatment of contaminated groundwater
<i>Leptothrix ochracea</i>	Fe, As, Mn	Katsoyiannis and Zouboulis (2006)	Treatment of contaminated groundwater
<i>Thiobacillus ferrooxidans</i>	Ni, Pb, Cr, Cu, Zn	Xiang et al. (2000)	Treatment of sludge
<i>Thiobacillus ferrooxidans</i>	Ni, Pb, Cr, Cu, Zn, Mn	Blais et al. (1993)	Sewage sludge treatment
<i>Acidithiobacillus ferrooxidans</i>	Cu, Cr, Zn	Droguet et al. (2005)	Sewage sludge
<i>Acidithiobacillus ferrooxidans</i> and <i>Acidithiobacillus thiooxidans</i>	Zn, Cu, Pb	Zhou et al. (2017)	Sludge
<i>Acidithiobacillus ferrooxidans</i>	Cu, Cr, Ni, Zn	Li et al. (2018)	Sewage sludge

Bacterial bioleaching has been used at industrial scale for recovery of metals from several low grade ores (Gu et al. 2018; Camargo et al. 2018). In this connection, the exploitation of acidithiobacilli for recovery of metal ions from waste electronic metals can significantly contribute in management of environmental pollution. The acid produced by iron oxidizing bacteria *A. ferrooxidans* has been demonstrated to facilitate the leaching of metals which can be recycled and used for further applications. Wang et al. (2009) reported the leaching efficiency of *A. ferrooxidans* and *A. thiooxidans* individually and in consortium for recovery of metals present in printed wire boards. The mixed culture was able to solubilize 100% copper from the waste after 9 days of treatment while greater than 90% leaching was recorded after 5 days treatment for copper, zinc and lead by individual as well as co-culture conditions. The simultaneous leaching of copper, zinc and lead can be used for recovery of metals from dumped electron materials for industrial application.

Iron oxidation characteristics of bacterial species can be extensively used for human welfare. The death and decay of iron oxidizers on the bottom of sea and rivers give rise to organic material enriched with oxides of iron which in due course develops into thick mat with unique characteristics of metal sorption (Makita 2018). Iron coated mats have been successfully employed to sequester even trace levels of hazardous metals including arsenic, iron and manganese from contaminated water (Katsoyiannis and Zouboulis 2006). Iron oxidation based treatment for removal of iron, manganese and aluminium from groundwater has been used in municipalities of several countries (Yayam 2014). The unique feature of biologically produced iron oxide makes their application in preparation of negative electrodes in lithium based batteries (Hashimoto et al. 2014), as carrier of bioactive molecule for fast release and cancer therapy as well as photocatalytic decomposition of rhodamine B dye (Wang et al. 2016). The special feature of exopolysaccharides produced by iron oxidizing bacteria extends its application in

pharmaceutical and textile industry (Makita 2018). Interestingly, they can be cultivated by utilizing electrical energy for extensive production of specific organic macromolecules. The burning of coal, possessing large amount of sulfur during industrial operations has negative impact on natural environment due to release of large amount of SO₂ into atmosphere. The high sulfur containing coals have been treated by *L. ferriphilum* in order to minimize the content of sulfur (Mishra et al. 2018). The improvement in treatment methodology and bacterial strains employed would give a new dimension for large scale coal biodesulfurization to reduce sulfur emission from industrially used low grade coals.

Future perspectives

So far, significant progress has been made in the direction of understanding the mechanism of iron oxidation and their environmental consequences, yet several issues still need to be dissected in order to employ iron oxidizing bacterial activity for environmental management programs. Several microorganisms are known to use iron for energy production but detailed knowledge is not available. There is lack of information about various genes responsible for iron oxidation which must be searched. Very little information is currently available on role of rusticyanin in oxidation mechanisms. Complete details of electron transfer mechanisms in nitrate dependent iron oxidation are unavailable to date. In addition, physiological details of several uncultured iron oxidizers are not known. Unraveling their physiological details may give new insights into life processes of these ancient microorganisms. Furthermore, iron oxidizing bacteria may help unravel the early life present (biosignature) not only on earth but also on other celestial bodies. The complete genomics is currently unavailable for *A. ferrooxidans*. More information related to genome will help in unraveling of their evolutionary history. The diverse knowledge about the

habitat of iron oxidizing microorganisms thriving under extreme environmental regimes will reveal the novel mechanisms of adaptation. Detailed information regarding the factors affecting their physiological and biochemical activities will give new insights to develop strategies for their industrial scale application in treatment of waste water, sludge and contaminated groundwater. Detailed investigation about the genes and proteins regulating chemotactic movement of iron oxidizers toward a substance would be imperative to adsorb them on specific substratum such as on water filter so as to use them in remediation of contaminated water. Further research on the mechanism as well as regulation of magnetosome synthesis (iron abundant membranous entity) would help us to modify the naturally available iron oxidizers for large amount synthesis. The magnetosome synthesizing microbes are very much helpful in detection of magnetic materials. The magnetic properties can be successfully utilized to recover radionuclides. Knowing the mechanistic details about the survival of iron oxidizers under extreme acidophilic condition will help us to find its applicability in management of acidic soils to enhance the agricultural productivity. Thorough investigations on mechanisms and bioenergetics aspects of microbial iron oxidation process are also required to be researched upon. Research is required to be done on investigation of biological iron oxidizers in ore deposition other than iron. The so called iron oxidizing bacteria which are very efficient in transferring electrons to metals or minerals present outside the cell envelope can produce nanomaterials with novel attributes having significant application in agriculture, human health, and environment. They have also promising future in development of biosensors for detection of hazardous contaminants present in acid mine drainage water.

Conclusions

Currently available physicochemical techniques for purification of contaminated surface and groundwater are not very much beneficial from the environment point of view as well as the associated cost. Biological mechanisms for reducing the concentration of heavy metals are attractive because of lesser sludge generation and being eco-friendly. Iron oxidizing bacteria are important in controlling the fate of many important as well as toxic metals and nutrient ions present in the water. These microorganisms are important in biogeochemistry of important metals including iron and manganese. Currently they are also being applied for the purification of arsenic contaminated drinking water, which has been reported worldwide. Bacterial iron oxidizers are very much diverse as compared to algal and fungal species. Therefore, they have been more widely utilized for the metal remediation under acidic as well as neutral conditions. *G.*

ferruginea, *A. ferrooxidans*, *Sideroxydans*, *Shewanella* and *Geobacter* are of more importance in minimizing concentration of toxic heavy metals in presence of higher concentration of iron as well as manganese. Apart from arsenic, remediation has also been reported for several other heavy metals. They bear the property to control the activity of many nutrients like nitrate, phosphate, sulfate and bicarbonate thus influencing the nutrient availability in aquatic and terrestrial ecosystems. Iron oxidizing bacteria can thus be explored for diverse roles related to remediation of ecosystems affected by anthropogenic activities and for industrial purposes, leading to sustainability of environment.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest in writing the manuscript.

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