Iron-Degrading Bacteria in the Aquatic Environment: Current Trends and Future Directions

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Abstract

Iron (Fe) is an abundant element found in the earth's crust and is required by organisms to perform their metabolic activity. However, its toxicity in excess amounts in the aquatic environment can negatively impact the organism's habitat. Therefore, the extra amount of iron in the aquatic environment needs to be checked or converted into a nontoxic form to sustain the well-being of the organisms. Biologically, this can be achieved by targeting iron-degrading microbes that can degrade iron in the environment. In this chapter, we present the role of various iron-degrading bacteria and their importance in the environment. Moreover, we highlight some essential mechanisms involved in the degradation of iron through microbes. *Gallionellaceae* sp. in the KS culture, for example, could oxidize iron in such a way that an electron is gained through iron oxidation and transmitted through the electron transport chain (ETC) where nitrate (NO_2) is reduced step by step to nitric oxide (NO). Thus, this chapter explores the possibility of key microbial groups in remediating iron-toxic environments and the underlying mechanisms involved in the process to benefit the degrading environment.

Keywords

Anaerobic photosynthetic · Acidophilic · Aquatic environment · Iron-degrading microbes · Neutrophilic · *Gallionellaceae*

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17.1   Introduction

Iron is one of the fourth most abundant key elements and also the redox-active metal in the earth's crust. The iron requirement in the organisms is also remarkable; without it, the microorganisms cannot conduct their metabolic activity significantly. For instance, it is involved in cellular respiration and oxygen transport (Bury et al. 2001). Although it is imperative for organisms, excess of it affects the organisms. Most countries face the problem of excess iron in their environment, such as water bodies and sediment, which subsequently lead to iron toxicity to the organism. The ability of microbes to oxidize iron may convert the negative impact of iron to the positive impact in the environment that ultimately utilized by the microbes. Therefore, in this chapter, we discuss the key role of iron-degrading bacteria in nature and their importance in the aquatic environment. In addition, we also highlight some important mechanisms concerned in the degradation of iron by using microbes.

17.2   Toxicity of Iron

The toxicity of iron to organisms, particularly fish, can be broadly classified as acute or chronic depending on the time and strength of the toxic substance that the organisms are exposed to. While the first addresses a brief duration with a greater concentration of the toxic substance that causes adverse effects and leads to mortality in organisms, and the second addresses a prolonged exposure with a lower concentration of the agent that causes gradual adverse effects in the organism. Many researchers have studied iron toxicity to organisms, including fishes. For instance, according to Bury et al. (2001), the ferrous form (Fe^{2+}) is more harmful to European plaice (*Platichthys flesus*) than the ferric form (Fe^{3+}), and iron intake occurs largely in the latter section of the gut. The iron toxicity in the fish mainly affects the fish's gills, subsequently causing respiratory problems (Zahedi et al. 2014). In addition, animals on iron-rich diets may experience stunted development, low feed conversion, food refusal, death, and histopathological injury in the liver cells, which retain excessive iron (Bury and Grosell 2003). Fish can be employed as ecological indicators, displaying physiological changes including opercular beating, abnormal swimming, gill modifications, and feeding changes or problems responding to changes in the aquatic ecosystem (Hundley et al. 2018). According to Gemaque et al. (2019), both the forms of iron ions (Fe^{2+} and Fe^{3+}) are detrimental to the "piau" (*Leporinus friderici*), with Fe^{2+} being the most toxic.

17.3   Classification

Iron-degrading bacteria may be classified broadly into two groups: iron-reducing bacteria (IRB) and iron-oxidizing bacteria (IOB), based on their potential to reduce and oxidize iron, respectively, in the nature. While the first one applies to the ability of the bacteria to convert ferric (Fe^{3+}) ions to ferrous (Fe^{2+}) ions under both aerobic

and anaerobic environments, the latter one is the ability of the bacteria to transform ferrous ions to ferric (Fe^{3+}) ions under anaerobic and/or microaerobic conditions (Ebrahiminezhad et al. 2017). The majority of IOB are found in a variety of phyla within the bacteria domain, along with Firmicutes and Nitrospirae, the lion's share being Proteobacteria (Hedrich et al. 2011). Moreover, IOB may be classified into four classes based on their physiological diversity: (a) acidophilic, aerobic iron oxidizers; (b) neutrophilic, aerobic iron oxidizers; (c) aerobic iron oxidizers; and (d) anaerobic photosynthetic iron oxidizers. With the exception of nitrate-dependent iron oxidizers, the majority of the species in this phylum belong to one of the Proteobacteria classes. Furthermore, the Zetaproteobacteria are iron-oxidizing neutrophilic chemolithoautotrophs found in estuarine and marine settings all over the world.

17.3.1 Acidophilic, Aerobic Iron-Oxidizing Proteobacteria

These groups play an essential role in creating acidic and metal-fortified mine drainage waters. Acidophilic prokaryotes utilize the pH gradient across their cell membranes to drive ATP synthesis through F_1F_0 ATP synthase, but the accompanying proton influx is balanced by gaining electrons from the oxidation of ferrous iron (Hedrich et al. 2011). For example, *Acidithiobacillus ferrooxidans*, *Acidithiobacillus ferrivorans*, *Acidiferrobacter thiooxydans*, *Thiobacillus prosperus*, *Mariprofundus ferrooxydans*, *Ferrovum myxofaciens*, and *Thiomonas* spp are included in this group of proteobacteria (Colmer et al. 1950; Hallberg et al. 2010; Hedrich et al. 2011).

17.3.2 Neutrophilic, Aerobic Iron-Oxidizing Proteobacteria

These are the stalk-forming organisms where they divide at a limited partial pressure of oxygen in anti-gradients of oxygen and Fe^{2+}, viz. *Crenothrix*, Ferritrophicales, *Ferritrophicum radicicola*, *Gallionella*, *Leptothrix cholodnii*, *Leptothrix discophora*, *Leptothrix mobilis*, *Metallogenium*, *Siderocapsa*, *Sideroxydans* spp., *Sideroxydans*, *Sideroxydans* sp. ES-1, *Sideroxydans paludicola*, and *Sphaerotilus natans* (Emerson and Moyer 1997). Transmission electron microscopy of *Gallionella ferruginea* or *Mariprofundus ferrooxydans* revealed that stalks are made up of certain fibrils, which accommodate few millimicrometer-sized iron oxyhydroxide crystals (Chan et al. 2011). In 1838, *Gallionella ferruginea* was first proclaimed by Ehrenberg as a leading neutrophilic iron oxidizer, where it can grow mixotrophically or autotrophically utilizing an electron donor (ferrous iron) (Hallbeck and Pedersen 1991). *Mariprofundus ferrooxydans* is an autotrophic, mesophilic, marine iron oxidizer, which has an immediate morphological resemblance to *G. ferruginea*, although phylogenetically it is amazingly isolated from the freshwater bacterium and is related to Zetaproteobacteria (Emerson et al. 2010). In addition, it was announced that such heterotrophic *Pseudomonas* or
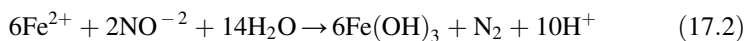
Pseudoalteromonas-like gammaproteobacteria separated from a seamount of volcanic sands under microaerobic conditions could catalyze ferrous iron oxidation and consequently lead to the development of iron mats in the deep seas (Sudek et al. 2009).

17.3.3 Neutrophilic, Anaerobic Iron Oxidizers

These groups have been created in freshwater, brackish, marine, and anaerobic sediments. Microbes that have a characteristic to oxidize iron and reduce nitrate under anaerobic conditions are classified as autotrophic and heterotrophic. These unique bacteria may thrive in organic acids when nitrate or oxygen served as an electron acceptor (Straub et al. 1996) such as *Acidovorax* sp., *Aquabacterium*, *Dechlorosoma suillum* strain PS, *Dechloromonas* spp., and *Geobacter* (Chaudhuri et al. 2001). In the presence of nitrate, *Thiobacillus denitrificans* also oxidized iron sulfide (FeS) (Straub et al. 1996). Comprehensive research is still being done to convert nitrate to nitrogen gas under anoxic conditions, in a process known as "nitrate-dependent anaerobic ferrous oxidization (NAFO)" with the help of ferrous iron as the electron donor (Su et al. 2017; Zhang et al. 2015). This is because iron is the most redox-active metal in organisms, sediment, and soil (Li et al. 2014).

Pseudogulbenkiania strain 2002, an isolate from a sediment of a freshwater lake, could reduce nitrate and oxidize ferrous iron during the time of growing as an autotroph (Weber et al. 2006), but it can also grow under heterotrophic conditions on a variety of organic substances. 16S rRNA gene sequence analysis disclosed that this isolate was nearly linked to the beta proteobacterium, *Pseudogulbenkiania subflava* (99.3% sequence similarity) (Weber et al. 2009). Surprisingly, the discovery of iron-oxidizing proteobacteria explained nitrate-dependent iron (Fe^{2+}, ferrous) oxidation by the stringent anaerobe *Geobacter metallireducens* (Finneran et al. 2002). Moreover, Raiswell and Canfield (2012) proposed that, anaerobically, ferrous form Fe^{2+} is oxidized with nitrate in the nitrate-containing oxygen minimum zones (OMZs) of present sea.

Anaerobic iron oxidation with nitrate (NO_3) produces nitrite (NO_2^-), nitrogenous gases (nitrogen [N_2] or nitrous oxide [N_2O]), or ammonium (NH_4^+) (Carlson et al. 2013), and a range of authigenic Fe minerals, based on surrounding water chemistry and pH (Carlson et al. 2013), for example,

$$2Fe^{2+} + NO^{-3} + 5H_2O \rightarrow 2Fe(OH)_3 + NO^{-2} + 4H^+ \tag{17.1}$$

$$6Fe^{2+} + 2NO^{-2} + 14H_2O \rightarrow 6Fe(OH)_3 + N_2 + 10H^+ \tag{17.2}$$

In the presence of nitrite, such as via heterotrophic nitrate reduction, iron oxidation accompanied by nitrite in Eq. (17.2) has been demonstrated to occur abiotically at around neutral pH, peculiarly when reactive Fe oxyhydroxide mineral surfaces are accessible to catalyze the process (Picardal 2012). The phrase "nitrate-dependent iron oxidation" refers to the microbial and partially abiotic mechanisms with the aid

of ferrous iron oxidized using nitrate as the terminal electron acceptor (Picardal 2012; Klueglein et al. 2014).

Nitrate-dependent iron oxidation has been occurred in a diverse freshwater and marine sediments and also shown in laboratory cultures (Straub et al. 1996; Scholz et al. 2016). This might be a crucial mechanism in biogeochemical cycling, especially in OMZs. Despite the fact that sediments under the Peru OMZ discharge large quantities of iron into the anoxic column of water (Noffke et al. 2012), primary production in the eastern equatorial Pacific high-nitrate-low-chlorophyll (HNLC) zone off Peru has been demonstrated to be iron-restricted (Hutchins et al. 2002). Furthermore, ample of iron liberated from the sediments of Peru margin is restored and buried adjacent to its origin rather than being moved offshore within the OMZ (Scholz et al. 2014). Both of these surprising data might be explained by nitrate-dependent iron oxidation inside the anoxic column of water (Scholz et al. 2016).

17.3.4 Anaerobic Photosynthetic Iron (Fe) Oxidizers

The first proof that microbes might oxidize ferrous iron (Fe^{2+}) in anaerobic settings came from phototrophic purple proteobacteria. The class Alphaproteobacteria is placed in the majority of iron-oxidizing phototrophs that have been discovered. *Thiodictyon* strain L7, a gammaproteobacterium, is the striking exception. This type of bacterium uses ferrous iron as a cause of carbon dioxide reductant, as revealed in the following equation, where CH_2O represents fixed biomass carbon:

$$4Fe^{2+} + CO_2 + 11H_2O + hv \rightarrow CH_2O + 4Fe(OH)_3 + 8H^+ \qquad (17.3)$$
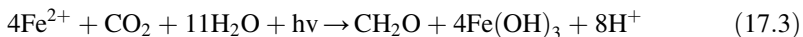
At the same time, the majority of photosynthetic microbes that oxidize ferrous iron consume such a reaction for the assimilation of carbon; it can further be utilized as a detoxification mode of action. Moreover, phototrophic iron oxidizers can employ soluble ferrous iron and other minerals, namely FeS or ferrous carbonate ($FeCO_3$), as origins of reductants although they are not allowed to access ferrous iron in more crystalline minerals like magnetite (Fe_3O_4) or pyrite (FeS_2) (Kappler and Newman 2004). So far, most of the identified and validated phototrophic iron oxidizers have been placed under the thoroughly varied family of Rhodobacteraceae within the class of Alphaproteobacteria including aerobic and anaerobic facultative heterotrophs, facultative methylotrophs, fermentative bacteria, and photoheterotrophs (Imhoff 2005).

Rhodobacter sp. strain SW2, the foremost iron-oxidizing phototroph identified, oxidizes ferrous iron exclusively when supplied with an organic carbon origin and also uses hydrogen (H_2) and organic molecules (Ehrenreich and Widdel 1994). Additional iron-oxidizing photosynthetic purple bacteria in the Rhodobacteraceae family comprise *Rhodovulum iodosum* and *Rhodovulum robiginosum*; both of them are found in marine environments and oxidize sulfide and ferrous iron when fed an organic cosubstrate like acetic acid (Hedrich et al. 2011). Heising and Schink (1998) revealed that a phototrophic isolate of *Rhodomicrobium vannielii*, a heterotrophic

nonsulfur purple bacterium from the Hyphomicrobiaceae family, can oxidize ferrous iron, a trait that was later validated in the species' type strain. Tentatively, Widdel et al. (1993) had already identified *Rm. vannielii* as the sole of the iron-oxidizing phototrophic isolates from freshwaters they had collected. Acetate or succinate was introduced to strain BS-1 as cosubstrates to promote growth when ferrous iron was present. According to Heising and Schink (1998), ferrous Fe oxidation is just a small act for *Rm. Vannielii* strain BS-1. Alternatively, the Hyphomicrobiaceae species, *Rhodopseudomonas palustris* strain TIE-1, segregated from an iron-rich mat was utilized as a model species for a genetic research by Jiao et al. (2005). The two photosynthetic iron-oxidizing gammaproteobacteria of *Thiodictyon* strains have been reported. One of the two, strain L7, was desegregated from the identical origin as *Rhodobacter* sp. SW2 (Ehrenreich and Widdel 1994), while the other *Thiodictyon* sp. strain f4 was from a marsh (Croal et al. 2004). In addition, among all the isolated phototrophic iron-oxidizing bacteria, *Thiodictyon* sp. strain f4 shows iron oxidation at elevated rates (Hegler et al. 2008). However, Widdel et al. (1993) observed no one at all of the confirmed *Thiodictyon* spp. they experimented with which could oxidize ferrous iron, implying that such a feature is unusual in this genus.

17.4   Iron-Reducing Bacteria's Role

In the sediment column, the presence of anaerobic dissimilatory Fe(III) iron-reducing bacteria makes distinguishing the type of reactive iron challenging (Lovley and Phillips 1986). These organisms seem to be present in both bacteria and archaea and have a broad phylogenetic range (Kashefi and Lovley 2003). The Geobacteraceae, a wide phylogenetically coherent group that oxidizes acetate to carbon dioxide (CO_2) using Fe(III) as the only electron acceptor (Lonergan et al. 1996), and also H_2-oxidizing Fe(III) reducers including *Shewanella putrefaciens* and *S. alga*, are among them (Lonergan et al. 1996). It was proved that Fe(III) reducers may decrease Fe(III) sheet silicates and magnetite (Kostka et al. 1999). Because Fe sheet silicates and magnetite are resistant to inorganic acid leaching, they are normally allocated as unreactive or weakly reactive iron phases in sequential leaching systems. Numerous sulfate-reducing bacteria (SRB) are linked to Fe(III)-reducing bacteria (FeRB) on a phylogenetic level, and many Geobacteraceae species reduce S(0). The sulfate and iron reducers may be an element of a compact ecosystem as the FeRB uses acetate, which is a typical by-product of SRB metabolism. As a result, these organisms are expected to have a big influence on the iron in the sediment's oxic and transition zones. The proportion of Fe(III) that is reduced by iron-reducing bacteria and reacting with the Fe(II) produced will be determined by the relative rates of the bacterial reduction reactions and sulfidation and the time spent by Fe(III) before being exposed to S(-II) in the bacterial iron-reducing subenvironment. Sequentially, this will change depending on sedimentation characteristics such as the degree of advection in the column of water, sediment grain size, the concentration of organic matter, and the velocity of sedimentation (Rickard 2012).

Moreover, the Fe-reducing bacteria may play a vital role in oil degradation. For instance, ferric iron is used by the hyperthermophile *Ferroglobus placidus* to consume benzene at 85 °C (Holmes et al. 2011; Waikhom et al. 2020). In oil field brine enrichment cultures, iron-reducing bacteria have been detected (Magot 2005); nevertheless, the availability of iron oxide surfaces may restrict the degree of oil biodegradation in the deep below. In sandstones, Fe(III) is found in the range of 0.4–4.0 oxide weight percent on pore filling or grain coating material (Pettijohn 1963). Although the energy gained by Fe(III) reduction is equivalent to aerobic respiration or NO_3 reduction, the oxidant amount required is significantly more. According to the volume, around 10 L of hematite would be required to biodegrade 1 L of hydrocarbon approximately. Due to the inadequate biological availability of ferric iron in hematite, such a procedure would be extremely slow, made even more difficult by the fact that hematite is frequently destroyed in course of diagenesis, and the majority of the iron in sedimentary reservoir rocks is constrained in surprisingly less reactive silicates and sulfides (Prince and Walters 2016).

17.5   Mechanism of Iron Oxidation

17.5.1 Mechanisms

Mechanisms utilized by anaerobically nitrate-reducing iron oxidation (NRFeOx) bacteria to oxidize Fe(II) are yet to be more explored, even though it appears to have different mechanisms, even if the bacteria are autotrophs, chemodenitrifiers, or mixotrophs.

For autotrophic NRFeOx bacteria, three mechanisms have been put forward for Fe(II) oxidation (Fig. 17.1) such as (a) a devoted Fe(II) oxidoreductase, (b) a nonspecific performance of the nitrate reductase, or (c) the *bc1* complex that receives electrons from Fe(II) and passages down the quinone pool (Bryce et al. 2018). The first scenario has dominated research in the recent years, intending to discover a particular outermost membrane Fe(II) oxidoreductase seen in these bacteria (Beller et al. 2013). Metagenomics investigation of the NRFeOx in the KS culture revealed homologs of the cytochrome c putative Fe(II) oxidase *Cyc2*, which have been detected in other identified and validated Fe(II) oxidizers in the draft genomes of *Gallionellaceae sp.* and *Rhodanobacter* sp. observed in KS culture (He et al. 2016).

Furthermore, the *Gallionellaceae* sp. and *Dryobalanops aromatica* RCB in the KS culture, which was suspected to be autotrophic but was not confirmed, both include homologs of the porin cytochrome c porin complex MtoAB (He et al. 2017). Figure 17.1a depicts a possible process for the autotrophic Fe(II) oxidizer to oxidize Fe(II) in the KS culture, in which an electron is gathered through Fe(II) oxidation and transmitted through the ETC, where nitrate is reduced step by step to nitric oxide (NO). NO has the ability to be absorbed by the surrounding population or to react with aqueous Fe(II) outside the cell.

Some NRFeOx bacteria may undergo an enzymatic process to oxidize Fe(II), but whether or not these organisms are real mixotrophs is still up for debate. Many
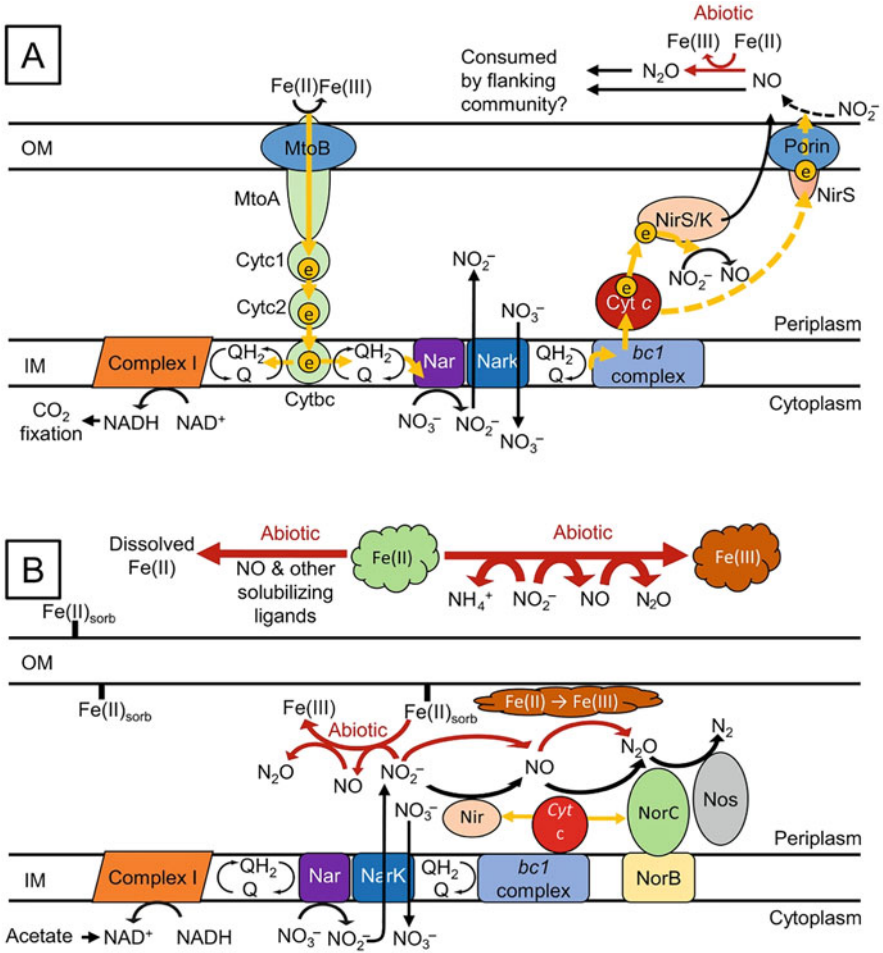
Fig 17.1 The existing hypotheses on the mechanism of iron oxidation in (**a**) *Gallionellaceae* species, considered autotrophic nitrate reducers and Fe(II) oxidizers in the KS culture and (**b**) the reduction of nitrate might be mediated by *Nap* in place of *Nar*, and the reduction of nitric oxide could be aided by *NorZ* instead of *NorC*. Notably, *NorZ* utilizes electrons from quinols as opposed to cytochrome c (Reprinted from Bryce et al. (2018), copyright 2022 Society for Applied Microbiology, with permission from John Wiley and Sons). Abbreviations: OM, outer membrane; IM, inner membrane; Cyt c, cytochrome c; NO, nitric oxide; N2O, nitrous oxide; NAD, Nicotinamide adenine dinucleotide

people assume that Fe(II) oxidation is powered by denitrification (Brons et al. 1991). It has been hypothesized by Carlson et al. (2013) that all heterotrophic denitrifiers can increase nitrate-dependent Fe(II) oxidation. Several nitrate reducers, including *Escherichia coli*, can oxidize an organic molecule when it is combined with Fe (II) (Brons et al. 1991).

Although the rate of dissolved Fe(II)-mediated abiotic nitrate reduction by nitrite to N_2O is a slow process, the rate of Fe(II)-mediated nitrite reduction to N_2O is kinetically advantageous under environmental conditions if reactive chemical substrates act as catalysts (Colman et al. 2008). Heterogeneous surface catalysis, for instance, can decrease nitrogen species by Fe(II) on viable surfaces such as cell surfaces, green rust, crystalline Fe(III) oxyhydroxides, and pyrite (Bryce et al. 2018). Many researchers have shown that microbially driven NRFeOx, heterotrophic nitrate reduction, and Fe(III)-coupled ammonium oxidation, that is, iron-ammox can result in the development of reactive nitrogen species (nitrite, NO_2^-, or nitric oxide [NO]) as a metabolic intermediate (Picardal 2012), providing a sufficient stock of compounds that could react rapidly with Fe(II) (Bryce et al. 2018).

17.5.2 Mechanisms of Ferrous Iron Oxidation by Photoferrotrophs

The insight mechanisms engaged in Fe(II) oxidation by phototrophic anoxygenic Fe (II)-oxidizing bacteria are yet a mystery. However, *Rp. palustris* TIE-1 has been the subject of the most scientific research for the process of phototrophic bacterial Fe (II) oxidation. Besides, the *pioABC* operon, which stands for "photosynthetic Fe (II) oxidation," is assumed to be essential for electron transport by Fe(II) oxidation in this species. This three-gene operon encodes three proteins: PioA, PioB, and PioC (Jiao and Newman 2007), where PioA is a periplasmic decaheme c-type cytochrome, PioB is an outer membrane beta-barrel protein, and PioC is a periplasmic, strong potential iron–sulfur cluster protein. MtrA and MtrB, which are expressed by the Fe (III) reducer *Shewanella oneidensis* MR-1, are the same as PioA and PioB. (Jiao and Newman 2007). Iro, the putative Fe(II) oxidoreductase of *A. ferrooxidans*, is linked to PioC. *Rp. palustris* TIE-1 carries electrons from *PioA* to *PioC*, which gives them to the *bc1* complex. The electrons may be shifted to the phototrophic reaction center in the inner membrane, according to some studies (Bird et al. 2014). The pioABC operon in *Rhodomicrobium vannielii* acts similarly to the operon in *Rp. palustris* TIE-1 (Bryce et al. 2018).

In *Rp. palustris* TIE-1, the deletion of *pioA* consequences in nearly full loss of Fe (II)-oxidizing capacity, although the deletion of *PioB* and *PioC* consequences in only partial loss when correlated to the wild type (Bose and Newman 2011). When Fe(II) is utilized as an electron donor, the pio genes are expressed at their highest levels, but they are transcribed and translated under all anoxic growth conditions. The global regulator *FixK* controls the expression of the pio operon (Bose and Newman 2011). Supplementary clue in what way Fe(II) influences cellular activities in *Rp. palustris* TIE-1 has come from transcriptome and proteome analyses. These findings reveal that high levels of Fe(II) cause stress reactions unexpectedly in anoxic settings, despite the fact that Fe(II) toxicity caused by oxidative stress created by the Fenton's reaction is not be a concern. The induction of many metal efflux pathways characterizes the cellular response, which was observed throughout both short- and long-term periods of time (Bird et al. 2013). The evidence of PioA's location in the cell is currently contradictory. Based on the sequencing results, Jiao and Newman (2007) suggested that PioA appears to be a periplasmic protein.

Nevertheless, Bose et al. (2014) revealed that *Rp. palustris* TIE-1 can oxidize the crossed-valent Fe(II)–Fe(III) mineral magnetite (Fe_3O_4) in the solid phase and utilize electrons straight from positioned electrodes. PioA can oxidize Fe(II) with the association of its electron transport mechanism, which must thus be existing on the cell's outer membrane, according to this discovery. Furthermore, *Rp. palustris* TIE-1 can only approach surface-bound Fe(II) in magnetite, emphasizing the necessity for a straight surface–mineral interaction mechanism (Byrne et al. 2015, 2016). *Rhodobacter ferrooxidans* SW2 is another well-studied "anoxygenic phototrophic Fe(II) oxidation" pathway. This organism's foxEYZ operon permits it to oxidize Fe (II) (Croal et al. 2007).

The genomic sequencing of *Chlorobium phaeoferrooxidans* reveals that these green sulfur bacteria have yet another mechanism. In *Mariprofundus ferrooxidans* PV-1, which is a microaerophilic Fe(II) oxidizer, the outer membrane cytochrome (*Cyc2PV-1*) encoded by this genome is thought to be engaged in Fe(II) oxidation (Crowe et al. 2008). *Cyc2PV-1* is a far relative of *Cyc2*, a lithotrophic Fe(II)-oxidizing bacteria found in a broad range of obligatory lithotrophic bacteria (He et al. 2017). Besides, *Cyc2* is encoded in the genome of *C. ferrooxidans* DSM13031 (He et al. 2017). The electron transport pathways and proteins involved in Fe(II) oxidation are likely varied, and no one mechanism exists across every single one of the physiological groups of Fe(II) oxidizers, neither within a single group of Fe(II) oxidizers, like phototrophs (Bryce et al. 2018).

17.6 Environmental Significance

The NRFeOx mechanism aids biochemically and microbially driven redox shifts of iron and nitrate species (Liu et al. 2019). The potency and remodeling of pollutants like chlorinated organic compounds and heavy metals (arsenic [As], antimony [Sb], and uranium [U]) are created by the "Fe III–Fe II redox wheel."

Nitrate reduction is intimately linked to N pollution in numerous natural and anthropogenic systems of waters, and the generation of N_2O (greenhouse gas) has the ability to affect global climate change.

As a result, an in-depth investigation of the redox reactions that may occur in the middle of reactive Fe and N species will assist in an improved insight into the Fe–N cycle in nature. It has long been understood that immobilizing these pollutants requires the absorption of heavy metals and radioactive nuclides onto Fe and manganese (Mn) oxides (Means et al. 1978a, b). A practical bioremediating technique for heavy metals including iron and radioactive nuclide fixation in reducing settings might be devised depending on the reported anaerobic NRFeOx employing *Dechlorosoma* species. The findings show that the oxidation of Fe(II) by *D. suillum* is a unique strategy for heavy metal and radionuclide stabilization and immobilization in the ecosystem. Senn and Hemond (2002) revealed that nitrate altered the arsenic (As) cycling in anoxic circumstances in an urban Upper Mystic Lake located in Massachusetts, the United States, by oxidizing Fe(II) to generate arsenic-adsorbing particulate hydrous iron oxides and creating the oxidation of As(III) to As(V).

After large-scale Fe(II) oxidation started, arsenate was discarded from the water adjacent to the injection at the U.S. Geological Survey (USGS) test site on Cape Cod, Massachusetts, the United States, by integration into hydrous Fe oxide, which was precipitated in the iron-reduction zone in a sandy aquifer under an anoxic condition (Senn and Hemond 2002; Höhn et al. 2006), revealing the significance of NRFeOx to arsenic immobilization. The inclusion of nitrate in paddy field soils decreased the Fe(II) concentration in the soil solution while increasing NRFeOx bacterial density, resulting in considerably reduced dissolved Fe(II) concentrations in the rhizosphere soil solution (Liu et al. 2019). It was proposed that NRFeOx bacteria activation might result in arsenic coprecipitation with or adsorption to Fe (III) ions in the soil, followed by reduced arsenic absorption utilizing rice plants (Chen et al. 2008). The findings of continuous-flow sand-filled columns revealed that microbial oxidation of arsenate and Fe(II) associated with denitrification boosted aqueous As immobilization in anaerobic conditions by creating hydrous iron oxides–coated sands with adsorbed pentavalent arsenic (Sun et al. 2009). Despite the fact that it does not affect the anaerobic NRFeOx bacteria metabolism, arsenate efficiently immobilized arsenic during Fe(II) oxidation (efficient for more than 96%), lowering the residual dissolved arsenic concentrations to levels approaching or even below the acceptable limit of drinking water of 10 μg/L (Hohmann et al. 2010). The ability of a single anaerobic NRFeOx *Citrobacter freundii* strain PXL1 to reduce and remove As(III) and nitrate from water synchronously was investigated, and it was disclosed that these bacteria are potential microorganisms for in situ remediation of arsenite- and nitrate-contaminated groundwater in China (Li et al. 2015). The concurrent usage of Fe(II) and nitrate successfully reduced the inflation of arsenic (As) in rice paddy plants by intensifying arsenic oxidation or immobilization intervened by biotic or abiotic iron redox transformation and mineralization (Wang et al. 2018), and the conclusions delivered an understanding about the As/Fe/N biogeochemical cycles, which are essential from the perspective of agricultural crop management activity of arsenic toxicity and its mitigation in arsenic-affected area.

Even though nitrate respiration has long been established as a general process in microbes (Ducluzeau et al. 2009), little has been written about the effects of iron oxidation on nitrate reduction and releasing of a greenhouse gas (N_2O) due to a lack of understanding of nitrogen cycle through abiotic and biotic procedures. However, these abiotic N_2O generation mechanisms have been recognized since the nineteenth century; they are typically disregarded in contemporary environmental studies, making it critical to analyze their importance (Zhu-Barker et al. 2015). Following an early idea (the ferrous wheel theory) for abiotic nitrate immobilization in forest soils, reactive Fe(II) species might convert nitrate to nitrite. Nitrite was then combined alongside dissolved organic materials to form dissolved organic nitrogen (Davidson et al. 2003). Despite the fact that the abiotic and biotic interactions were unclear, the data highlighted the realness activity and significance of NRFeOx in the renowned N cycle scenario. The potential of iron-dependent nitrogen cycling in riparian forest sediments also discussed the Fe–N interaction (Clement et al. 2005). Under a variety of environmental circumstances, dual (N and O) isotope

structures were used to investigate the reduction of abiotic nitrite by Fe(II). The findings showed that Fe(II)-mediated nitrite reduction could be a significant origin of abiotic environmental N_2O, particularly in an iron-rich environmental condition with potent redox fluctuations (Buchwald et al. 2016).

17.7   Bioremediation

Various biological approaches, like bioremediation including phytoremediation, have been used to remediate environmental toxins, and they are not only cost-effective but also environmentally beneficial. Bioremediation is a broad word that refers to the transformation of harmful or complicated pollutants into simpler, less toxic forms, or even full degradation, using biological mechanisms including bacteria or microbial products (Datta et al. 2020; Singh et al. 2021). The process of eliminating pollutants from the environment in the absence of the use of chemicals is known as intrinsic bioremediation (Lovley 2003). By altering the environment in which the microorganisms are grown at the polluted location, microbial activity can be increased to achieve higher clean-up rates. The bioremediation technique is regarded as designed in these circumstances (Mishra et al. 2021).

Iron oxidation occurs in most aquatic habitats that include elemental or reduced forms of iron, that is, ferrous iron (Eggerichs et al. 2020). Microorganisms that accelerate iron oxidation gain the energy they need to multiply when they use either nitrate or oxygen as an electron acceptor (Emerson et al. 2010). Iron oxidation of microorganisms can be divided into four categories that have been already mentioned above somewhere in the content. Zagury et al. (1994) demonstrated heavy metal removal by native IOB from polluted soil. Bacteria such as *Acidithiobacillus ferrooxidans* can be used to reduce the soil solution pH lower than 2.5 and to increase the oxidation–reduction potential at room temperature when adjusted to a pH of 4. Iron oxidation through such bacteria was accelerated by the addition of ammonium sulfate $[(NH_4)_2SO_4]$ and potassium phosphate (K_2HPO_4). Zinc and manganese had higher percent removal rates than copper. Metal speciation, together with the soil types studied, affected metal removal by IOB. A potential technique for the efficient removal of arsenic from groundwater was discovered to be the biotic oxidation of iron by the bacteria *Gallionella ferruginea* and *Leptothrix ochracea*, which offered an economical and environmentally beneficial alternative. The microorganisms and iron oxides that were formed in the upflow filtration columns, during this process, provide an ideal environment for the absorption and arsenic removal from the aqueous streams (Katsoyiannis and Zouboulis 2004). Blais et al. (1993) described their research on the function of IOB in the sequestration of toxic metals from sewage sludge. Iron-oxidizing microorganisms lower the pH of sewage sludge and increase its oxidation–reduction potential. These were found to be the metals removed from sludge by *A. ferrooxidans* (previously known as *Thiobacillus ferrooxidans*) in the following ascending order: manganese, zinc, nickel, cadmium, copper, lead, and chromium, with the sludge form used during the experiment having a little effect. Xiang et al. (2000) conducted another batch of investigation

aimed at the heavy metal removal from sewage sludge utilizing indigenous IOB. When iron was supplemented to inoculated sets as the ferrous sulfate form, the sludge pH fell from 2.0 to 2.5. Following 16 days of treatment with iron oxidizers, there was a significant decline in the metal contents (chromium, copper, lead, nickel, and zinc) available in sewage sludge, attaining agriculturally acceptable levels, indicating that biological agents can be used to remediate metal contaminants. Recently, the contribution of microaerophilic IOB in arsenic (As) removal was reported by Tong et al. (2019) through the adsorbed/immobilized of arsenite and arsenate that resulted in ferric oxyhydroxide formation following the prominent activity of iron oxidizers with a significant arsenic adsorption affinity. The As content was reduced from 600 to 4.8 g/L following iron oxidizer treatment. The presence of an arsenite oxidase gene, which is accountable for the formation of arsenite from arsenate in microbes, was also discovered in the study. The generation of biogenic iron oxides as a result of the iron oxidation by the bacteria *Gallionella* and *Leptothrix* has a tremendous potential for phosphate elimination from the solution phase (Buliauskaite et al. 2020). Moreover, *Gallionella* sp. has been shown to have an overall phosphate removal capacity than *Leptothrix* sp. When compared to chemically manufactured iron oxides, biologically derived iron oxides had a greater phosphate sequestration performance, implying that they could be used in phosphate recovery treatment systems. Adsorption and precipitation play a substantial role in phosphate elimination by biogenic iron oxides, according to their findings. Another recent study showed that IOB can fortunately bioremediate groundwater contaminated with prominent levels of iron and manganese (Aziz et al. 2020). Not long ago, the ability of bacteria *A. ferrooxidans* to extract heavy metals (chromium, copper, nickel, and zinc) from electroplating sludge under low-voltage stimulation paves the door for industrial-scale metal contamination treatment (Wu et al. 2020). Under laboratory conditions with a pH of 2.0–3.0 and Fe concentrations near 11 g/L, *A. ferrooxidans* catalyzes the synthesis of crystalline biogenic tooeleite, which is an iron-arsenic-based mineral and is thought to remove roughly 95% of As(III) (Li et al. 2020a, b). The research revealed key principles driving biogenic mineral formation, which could lead to the advancement of a treatment system that uses rapidly proliferating IOB to decontaminate As-damaged environments (Li et al. 2020a, b; Singh et al. 2021).

17.8 Future Direction and Conclusion

In the future, nitrate-reducing bacteria may be a valuable microbe for the Biofloc Technology of fish culture to reduce nitrate, which is a severe concern in the system. However, more research into this topic is required. Besides, the pathogenic nature of these bacteria needs to be thoroughly studied to avoid any disease outbreak in the future. Moreover, bioremediation with iron-degrading bacteria can minimize iron toxicity, which is both economical and ecologically sound. Furthermore, this technology will be a boon. However, it is critical to investigate all of the mechanisms involved in the process. Furthermore, the microorganisms must be completely

defined before they can be deployed in the bioremediation of iron in an environment where in situ bioremediation has limited. In addition, the remediation of environments contaminated by metalloids, metals, and hazardous organics may benefit from the use of IOB that are resilient to greater metal concentrations and can swiftly adapt to changing natural environmental circumstances.

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