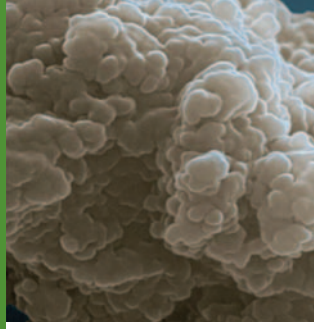

IRON IN MICROBIAL METABOLISMS

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Microbes are intimately involved in the iron cycle. First, acquisition of iron by microorganisms for biochemical requirements is a key process in the iron cycle in oxygenated, circumneutral pH environments, where the solubility of Fe(III) (oxyhydr)oxides is extremely low. Second, a number of aerobic (using O_2) and anaerobic (living in the absence of O_2) autotrophic bacteria gain energy for growth from the oxidation of dissolved and solid-phase Fe(II) compounds to Fe(III) (oxyhydr)oxides. Third, heterotrophic Fe(III)-reducing bacteria close the chemical loop by reducing solid-phase Fe(III) minerals back to dissolved and solid-phase Fe(II). Together these metabolic processes control the partitioning of the Earth's fourth most abundant crustal element, and they are additionally tied to the cycling of several major nutrients (e.g. carbon, oxygen, nitrogen, sulfur) and trace elements (e.g. phosphorus, nickel) in modern and ancient environments.

KEYWORDS: iron, bacteria, metabolism, oxidation, reduction, autotrophic bacteria, heterotrophic bacteria

INTRODUCTION

Iron is essential to nearly all known organisms. In animals, iron forms an organic complex known as heme that serves as the structural backbone to proteins such as hemoglobin. These proteins are found in red blood cells and are responsible for carrying oxygen from the lungs to the rest of the body. Heme is also found in the center of a number of metalloenzymes (proteins that contain a metal ion) that play a role in cellular metabolism. One of the most important metalloenzymes is cytochrome. It facilitates the transfer of electrons sourced from reduced molecules, such as organic carbon, to oxygen, and in the process the animal harnesses energy for cellular functions and growth. Ferritin is a protein used by almost all livings organisms to store and release iron, and in humans, it acts as a buffer against iron deficiency or iron toxicity.

In microorganisms, cytochromes are involved in a larger range of metabolisms because different species can use different electron donors (i.e. H_2, Fe^{2+}, HS^-) and different electron acceptors (i.e. NO_3^-, Fe^{3+}, SO_4^{2-}). Other key microbial metalloenzymes include nitrogenase, which is used by the so-called nitrogen-fixing organisms to obtain useable nitrogen from atmospheric N_2; hydrogenase, which is used to produce H_2 from water; and methane monooxygenase, which is used by a group of bacteria known as methanotrophs to oxidize methane to methanol.

Why Fe became important for so many enzymes is almost certainly related to the origin and early evolution of life. According to the "Wächtershäuser theory," primitive forms of metalloenzymes may have played a key role in catalyzing reactions relevant to the synthesis of prebiotic organic macromolecules (Wächtershäuser 1990). Wächtershäuser suggested that metal ions such as iron, cobalt, and nickel functioned as catalysts for the synthesis of organic compounds by fixing carbon, thus promoting growth of larger organic molecules and setting the scene for the origin of life.

IRON ACQUISITION

The poor solubility of ferric iron minerals at circumneutral pH values and their correspondingly low dissolved Fe(III) concentrations (~10^{-10} mol per liter) mean that iron is often a limiting nutrient for growth under oxygenated conditions. Many bacteria and fungi get around this impasse by excreting low molecular weight organic compounds known as siderophores that specifically complex dissolved Fe(III). Indeed, siderophores or their breakdown products can be so abundant that they dominate ferric iron speciation in surface ocean water and soils (e.g. Wilhelm and Trick 1994).

Siderophores have two properties that make them ideal Fe(III) scavengers: they are soluble, and they provide reactive sites (known as ligands) that can bind to the central Fe(III) cation. Significantly, they form especially strong surface complexes, and their binding capacity for Fe(III) can be several times higher than that of common soil organic acids (e.g. oxalic acid). This is an important property because it maintains ferric iron in a dissolved form, which minimizes its loss from the aqueous environment by the precipitation of solid-phase ferric (oxyhydr)oxides (Hider 1984).

The biosynthesis of siderophores is tightly controlled by iron levels. When dissolved Fe(III) concentrations are low, siderophore production becomes activated by the presence of minerals containing ferric iron: the more insoluble the iron source the more siderophores are produced (e.g. Hersman et al. 2000). In fact, many microorganisms produce siderophores in great excess of their requirements because a large proportion of the siderophores are lost via diffusion and advection. Other studies have documented

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that some species generate different types and amounts of siderophores depending on the type of iron mineral present (Page and Huyer 1984). Importantly, different siderophores are required to sequester Fe(III) from different iron minerals, and changing the iron mineralogy can elicit a specific response from the same microorganism. In any event, siderophores represent an extremely successful solution to the problem of obtaining dissolved ferric iron under oxygenated conditions.

AEROBIC Fe(II) OXIDATION

The occurrence of autotrophic bacteria that can synthesize their own organic compounds and gain energy from the oxidation of Fe(II) to Fe(III) is generally limited by the availability of dissolved Fe(II). This is a significant problem because at neutral pH and under fully aerated conditions, ferrous iron rapidly oxidizes inorganically to ferric iron, which then hydrolyzes to ferric (oxyhydr)oxides. The most efficient way for a bacterium to overcome the stability limitations is to grow either under acidic conditions (such organisms are known as acidophiles) or under low oxygen concentrations at circumneutral pH (these are known as microaerophiles). In both cases the chemical reaction kinetics are sufficiently diminished that the bacteria can harness Fe(II) oxidation for growth.

Acidophilic Fe(II)-oxidizing bacteria typically use O_2 as an oxidant—in biology this is referred to as the terminal electron acceptor:

$$2Fe^{2+} + 0.5O_2 + 2H^+ \rightarrow 2Fe^{3+} + H_2O\ .$$

The best-characterized acidophiles are *Acidothiobacillus ferrooxidans* and *Leptospirillum ferrooxidans*. They grow well at mine-waste disposal sites where reduced sources of iron are continuously generated during acid mine drainage (see Templeton 2011 this issue). Since it takes on average 50 mol of Fe(II) to assimilate 1 mol of carbon (Silverman and Lundgren 1959), the acidophiles must oxidize a large amount of ferrous iron in order to grow. Consequently, even a small number of bacteria can be responsible for generating significant concentrations of dissolved Fe(III).

Under neutral pH, but with O_2 levels below 1.0 mg per liter and redox conditions about 200–300 mV lower than those of typical surface waters (characteristic of some iron springs, stratified bodies of water, and hydrothermal vent systems), microaerophilic bacteria such as *Gallionella ferruginea* play an important role in Fe(II) oxidation and lead to the formation of ferrihydrite, $Fe^{3+}{}_{4-5}(OH,O)_{12}$ (Fig. 1).

Figure 1 Iron mineral precipitation as a coating on boulders from iron- and carbonate-rich mineral water near Scuol-Tarasp, Engadin, Switzerland. Bacteria exist within the coatings. Photo by Andreas Kappler, University of Tübingen

Gallionella ferruginea has bean-shaped cells that grow at the terminus of a helical structure called a stalk, which is made up of polysaccharides. Fe(II) oxidation can generate significant energy at circumneutral pH to support cellular growth. Interestingly, *G. ferruginea* does not form a stalk at pH <6, or under very microaerobic conditions where O_2 is present but the redox potential is –40 mV. This suggests that the stalk represents an organic surface upon which ferrihydrite can precipitate and, in doing so, protect the cell itself from becoming mineralized (Hallbeck and Pederson 1990). In a similar manner, Nealson (1982) suggested that another bacterium, *Leptothrix ochracea*, induces ferrihydrite precipitation on its sheath as a means to remove any free oxygen and thus detoxify its environment. These examples show how such bacteria have adapted different strategies for coping with their unique chemical environment.

ANAEROBIC Fe(II) OXIDATION

Ferrous iron is relatively stable under anoxic conditions, but the biological oxidation of Fe(II) may still occur with nitrate as the electron acceptor via the following reaction (Straub et al. 1996):

$$10Fe^{2+} + 2NO_3^- + 24H_2O \rightarrow 10Fe(OH)_3 + N_2 + 18H^+\ .$$

The tolerance of both autotrophic nitrate-reducing and photosynthetic Fe(II)-oxidizers (see below) to low levels of oxygen allows them to harvest substrate and energy along, and partly across, the oxic–anoxic interface where competition with aerobic Fe(II) oxidation could occur. Although nitrate-dependent Fe(II) oxidation has been shown to be widespread in sediments (Straub and Buchholz-Cleven 1998), most bacteria that use this metabolism depend on an organic cosubstrate (e.g. acetate), and truly autotrophic nitrate-reducing strains have not been isolated in pure culture. Furthermore, culture studies have demonstrated that, in fact, a consortium of bacteria is involved in Fe(II) oxidation coupled with a nitrate-reduction reaction (Blöthe and Roden 2009). This drives home the point that, in nature, bacteria typically work in close association with their neighbors, and a full understanding of biogeochemical cycling of elements requires knowing not only who is there, but how they interact with one another.

One interesting aspect of nitrate-dependent Fe(II) oxidation is that a variety of different Fe(III) minerals (including magnetite, ferrihydrite, goethite, lepidocrocite, and green rusts; for mineral definitions, see Taylor and Konhauser 2011 this issue) are formed depending on the geochemical conditions (e.g. Kappler et al. 2005a) (Fig. 2). Moreover, Hohmann et al. (2010) recently showed that during iron biomineralization some toxic metals, such as arsenic, can be efficiently precipitated. This observation has obvious environmental significance, suggesting that Fe(II)-oxidizing and Fe(III)-mineral-precipitating bacteria have the potential to influence the fate and mobility of toxic metal ions in the environment.

PHOTOSYNTHETIC Fe(II) OXIDATION

The existence of anoxygenic photosynthetic Fe(II) oxidation (a form of photosynthesis that does not produce oxygen, in this case called photoferrotrophy) was suggested nearly 10 years before the discovery of the first microorganisms that actually catalyze this reaction. Hartman (1984) first proposed photoferrotrophy as a depositional mechanism for a class of ancient iron mineral deposits, the so-called banded iron formations (BIFs), under O_2-free conditions during the Precambrian (see Poulton and Canfield 2011 this issue). A decade later, this hypothesis was validated by the discovery of the first photoferrotrophic microorganisms (Widdel et al. 1993). Since then, diverse strains of anoxygenic Fe(II)-oxidizing phototrophs,

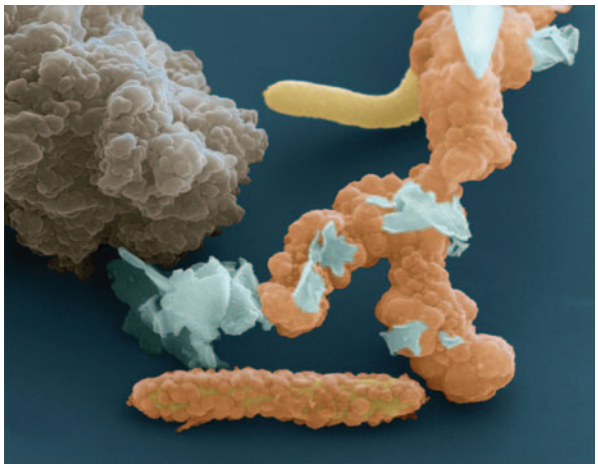

Figure 2 Formation of different biogenic Fe(III) minerals during Fe(II) oxidation by the nitrate-reducing *Acidovorax* strain BoFeN1 isolated from Lake Constance sediments (Kappler et al. 2005a). Cells are partially or fully encrusted by Fe(III) minerals: the orange globular structures at cell surfaces, blue tabular crystals, and brown-colored minerals precipitated at a distance from the cells are all ferric (oxyhydr)oxides of different crystallinity. The cell in the front is about 1.5–2 µm in length. Scanning electron microscope image provided by Oliver Meckes and Nicole Ottawa, Eye of Science (www.eyeofscience.com)

including purple sulfur, purple nonsulfur, and green sulfur bacteria, have been identified. They catalyze this process according to the following reaction:

$$4Fe^{2+} + HCO_3^- + 10H_2O + \text{light} \rightarrow 4Fe(OH)_3 + (CH_2O) + 7H^+ .$$

Photosynthetic Fe(II)-oxidizing bacteria require very restricted and specialized habitats as they need to be close to the surface to get light, but they also require a reduced environment devoid of oxygen because in the presence of O_2 dissolved Fe(II) is rapidly oxidized inorganically. Accordingly, these microorganisms can circumvent this problem in two ways. They can tolerate low concentrations of oxygen, which allows them to live closer to the surface but requires that the cells oxidize the Fe(II) faster than the molecular oxygen. Alternatively, they can lower their requirement for light and thus be able to live deeper in soils, sediments, and the water column, where the concentration of Fe(II), replenished from below, is higher. In modern microbial iron-rich mats, light wavelengths that are useable by the phototrophic Fe(II) oxidizers penetrate on average about 2–3 mm; therefore, the bacteria must live in the upper anoxic millimeter of such an environment. However, Kappler et al. (2005b) demonstrated that, in the water column, these bacteria are capable of oxidizing Fe(II) even at very low light intensities (<1% of surface light) and can grow at a depth below one hundred meters.

Both the aerobic and anaerobic Fe(II)-oxidizing bacteria face the same problem of limited availability of dissolved Fe(II) and the possible inhibitory effect of the very poor solubility of the ferric (oxyhydr)oxide end product of their metabolism. For the stalk- or sheath-forming aerobic Fe(II)-oxidizing bacterial genera, *Gallionella* and *Leptothrix,* it is likely that the microbially produced and excreted organic matrices are used for extracellular capture of Fe(III) minerals produced. In terms of the photoferrotrophs, it has recently been proposed that Fe(II) oxidation happens in the periplasm (the space between the inner and outer membranes) of the cells (Jiao et al. 2005). However, since cell encrustation is not observed, this raises the question of how Fe(III) is transported out of the cytoplasm (the cell interior) to the cell exterior and then away from the cell without adsorbing to the outer surface. The presence of a low-pH microenvironment immediately around the cell, the use of organic ligands to keep the Fe(III) in solution in close cell proximity, or the shedding of organic-mineral aggregates from the cell surface have all been suggested as plausible strategies used by the bacteria (Schaedler et al. 2009).

ANAEROBIC Fe(III) REDUCTION

A number of bacterial species heterotrophically break down existing organic carbon to either carbon dioxide or methane gas. The type of heterotrophic metabolism that occurs in nature depends on what oxidants are available and, in the situation where multiple electron acceptors are present (as in the uppermost sediment layers), on the energy yield of the specific reaction. Thus, the decomposition of freshly deposited organic material in sediments proceeds in a continuous sequence of redox reactions, with the most electropositive oxidants, such as O_2 and NO_3, being consumed at or near the surface and progressively poorer oxidants, like Mn(IV), Fe(III), SO_4, and CO_2, being consumed at depth. Decomposition continues until the labile organic fraction is exhausted and the deeper sediments are left with a composition very different from that of the sediments originally deposited (see Konhauser 2007).

Fe(III) reduction occurs below the zone of manganese reduction and at the depth of complete nitrate removal from porewaters (see Taylor and Macquaker 2011 this issue). The reduction of Fe(III) is coupled to the oxidation of H_2 and/or simple fermentation products, including short- and long-chain fatty acids, alcohols, and various monoaromatic compounds. The amorphous to poorly ordered iron (oxyhydr)oxides, such as ferrihydrite, are the preferred sources of solid-phase ferric iron for Fe(III)-reducing bacteria (Lovley and Phillips 1987):

$$CH_3COO^- + 8Fe(OH)_3 \rightarrow 8Fe^{2+} + 2HCO_3^- + 15OH^- + 5H_2O .$$

More-crystalline Fe(III) oxides (e.g. hematite and magnetite) and Fe(III)-rich clay minerals are also microbially reducible (Fig. 3), and some experimental observations suggest that these minerals may provide energy for cellular growth comparable to that derived from the poorly crystalline phases (e.g. Roden and Zachara 1996). The variations in reductive rates are related to a number of factors, including the amount of surface area exposure, crystal morphology, particle aggregation, the composition of the aqueous solution in which the microorganisms grow, and the amount of Fe^{2+} sorbed to the oxide surface. Importantly, with such wide variations in reactivity towards microbial reduction, it is not surprising that ferric iron can represent a long-term electron acceptor for organic matter oxidation, even at depths where other anaerobic respiratory processes are thermodynamically predicted to dominate (e.g. Roden 2003).

Until recently, it was believed that the reduction of ferric iron–containing minerals necessitates direct contact of the bacterium with the mineral surface. Furthermore, once in contact with the surface, the Fe(III)-reducers are still faced with the problem of how to effectively access an electron acceptor that cannot diffuse into the cell. Some species, such as *Geobacter metallireducens*, are able to sense the proximity of oxidized metal, and thereby they move towards the solid phases. Once in their proximity, the bacteria specifically express cellular appendages, such as flagella and pili, to help them adhere to the Fe(III) (oxyhydr)oxides. Once a bacterium is attached to a mineral surface, it begins shuttling electrons from a reduced source within its cytoplasm, across the plasma membrane and periplasmic space, to the outer membrane (e.g. Lower et al. 2001). Reguera et al. (2005) also suggested that electron transfer via direct contact between cells and the mineral surface is mediated via conductive pili known as nanowires.

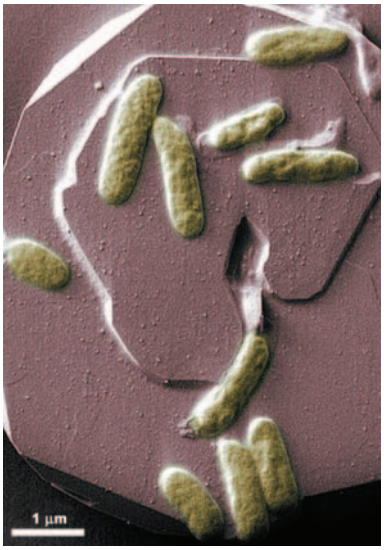

Figure 3 SEM image of an Fe(III)-reducing bacterium, *Shewanella putrefaciens* CN32, growing on a crystal of hematite. Image courtesy of Yuri Gorby and Alice Dohnalkova, Pacific Northwest National Laboratory

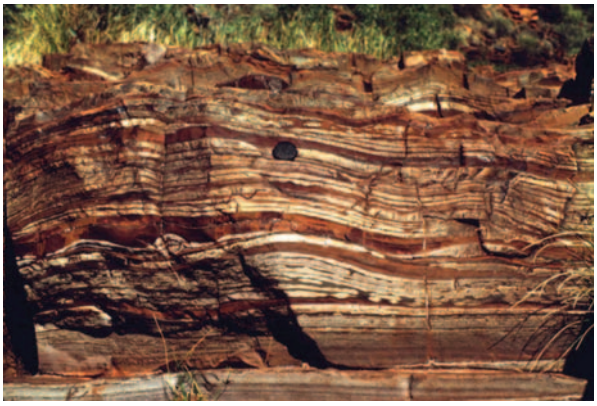

Figure 4 Banded iron formation from the Dales Gorge Member, Western Australia. The characteristic banding comprises brown layers of iron oxides (hematite and magnetite) and pale layers of chert. The black lens cap gives scale. Photo courtesy of Roger Buick, University of Washington

Other Fe(III)-reducing bacteria overcome the insolubility problem by utilizing organic compounds, such as dissolved humic substances, to shuttle electrons between the cell surface and the ferric (oxyhydr)oxides, which may be located at some distance away from the cell (e.g. Roden et al. 2010). The reduced humic substances subsequently transfer electrons abiotically to Fe(III), producing Fe(II); in this process, the oxidized form of the humic compound is regenerated for another cycle. Significantly, Fe(III) reduction rates are faster in the presence of organic electron shuttles than in their absence because the organic shuttles are likely to be more accessible for microbial reduction than poorly soluble Fe(III) oxyhydroxides (Nevin and Lovley 2000).

ANCIENT MICROBIAL Fe METABOLISMS

Obvious geological features intimately tied to ancient microbial metabolism are banded iron formations, which were deposited throughout much of the Precambrian. They are composed of iron-rich (~20–40% Fe) and siliceous (~40–50% SiO_2) sedimentary precipitates (Fig. 4). They have alternating Fe-rich and Si-rich layers that occur on a wide range of scales. The mineralogy of the least metamorphosed BIF consists predominantly of microcrystalline quartz, magnetite, hematite, siderite, and iron silicates. However, it is generally agreed that these minerals reflect both diagenetic and metamorphic overprinting: the primary minerals were most likely a combination of ferrihydrite, amorphous silica, and iron-rich clays (Klein 2005).

It is now generally accepted that the presence of ferric iron minerals in BIF is due to the metabolic activity of planktonic bacteria in the oceans' photic zone. Chemical oxidation of Fe(II) by photosynthetically produced O_2 is one possibility, which would allow for the indirect biogenic precipitation of ferrihydrite. During the Archean (more than 2.5 billion years ago), this O_2 could have been confined to localized "oxygen oases" associated with cyanobacterial blooms in coastal settings (Cloud 1965). At some later stage in the Paleoproterozoic (between 2.5 and 1.6 billion years ago), some Fe(II)-oxidizing bacteria, such as *Gallionella*, may even have evolved the means to gain energy from Fe(II) oxidation (Holm 1989). By 1.89 billion years ago, iron-rich stromatolites around Lake Superior had iron isotope values that certainly seem to indicate the existence of Fe(II)-oxidizing bacteria at that time (Planavsky et al. 2009). It is also plausible that light, not O_2, may have coupled the carbon and iron cycles, via photoferrotrophy as described above (Hartman 1984). Experimentally determined photosynthetic Fe(II) oxidation rates even suggest that such microorganisms could have accounted for all of the Fe(III) initially deposited in primary BIF sediment (Kappler et al. 2005b).

If a biological mechanism was important in the initial process of Fe(II) oxidation in the ancient ocean water column, it is expected that biomass would have settled to the seafloor along with the Fe(III) minerals. This organic carbon would subsequently have served as an oxidizable substrate during diagenesis and metamorphism, but the relevant question is: what terminal electron acceptors were present at the seafloor? The paucity of O_2 would have meant minimal nitrate and sulfate availability. By contrast, there was abundant ferric (oxyhydr)oxides deposited as BIF, and given the presence of partially reduced iron phases such as magnetite, and to a lesser extent siderite, a microbial process coupling the oxidation of organic carbon to the reduction of ferric iron seems very likely (Konhauser et al. 2005). Supporting evidence for an ancient Fe(III) reduction pathway comes from highly negative δ^{56}Fe stable isotope values in early Archean BIF that are comparable with the negative fractionations observed from cultures of Fe(III)-reducing bacteria (e.g. Johnson et al. 2003).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

As modern studies demonstrate, bacteria play a key role in a number of iron transformations in nature (Fig. 5). Yet, despite our increasing understanding of how microbial metabolisms affect our surface environment, much remains to be learned. For instance, how is the modern iron cycle (i.e. the different Fe-transformation reactions) spatially

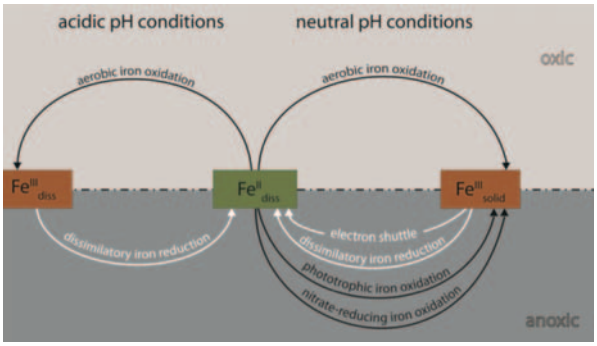

Figure 5 Microbial Fe(III)-reduction (white arrows) and Fe(II)-oxidation (black arrows) processes in acidic and circumneutral pH environments under oxic and anoxic conditions. Figure courtesy of Caroline Schmidt, University of Tübingen

structured in various environments, particularly at the aerobic–anaerobic interface in natural waters, sediment, or soils, where Fe(II)-oxidizing and Fe(III)-reducing bacteria may live within millimeter- to centimeter-scale redox gradients? Significant interest is also being directed at understanding how crucial bacteria were in the ancient iron cycle. In terms of BIF, were bacteria the dominant oxidizers of dissolved Fe(II)? Similarly, did the evolution of microbial iron metabolisms leave a signature in the ancient rock record? The search for answers to these questions will be facilitated only by applying an increasingly broad spectrum of geochemical, microbiological, and molecular genetic/genomic tools to the study of the internal complexity of modern Fe-rich environments. Therefore, our ability to relate modern porewater, solid-phase, and organic matter signatures to specific microbial assemblages will offer us the opportunity to assess, through isotopes, biomarkers, and trace element compositions, the ancient community structure and paleodepositional environment of sediments prior to their lithification.

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Functionality of Iron Minerals (FIMIN) established

The European Science Foundation (ESF) Research Network Programme Functionality of Iron Minerals (FIMIN) was established in 2009.

FIMIN relies and builds on existing national and international projects and initiatives dedicated to the understanding of the chemical and biological fundamentals of surface processes and iron mineral transformation reactions. FIMIN operates along the following research themes:

- The role of iron oxide surfaces in biogeochemistry
- Iron as a key redox species in microbiological processes
- Environmental biogeochemistry of iron
- Techniques to identify processes related to the biogeochemistry of iron

The ultimate goal of FIMIN is to elucidate the functionality of iron minerals. Cycling of electrons and matter through iron minerals is relevant to contrasting disciplines in the environmental sciences, including geochemistry, biogeochemistry, microbiology, soil and hydrological sciences, and biotechnology. FIMIN therefore aims to:

- Improve our understanding of the surface reactivity of iron minerals from a mechanistic point of view
- Understand the mechanisms and strategies microorganisms adopt to cope with surface chemical constraints
- Integrate this knowledge into the modelling and quantification of electron fluxes in natural systems
- Develop sound strategies to make use of the functionality of iron minerals in (bio)technological applications

PROGRAMME

FIMIN strives to integrate scientists working on scales ranging from molecular geochemistry, through reactor dimension and catchment size, to the global scale, using diverse methods (e.g. spectroscopy, geochemical techniques, stable isotope techniques, molecular biology, microbiology, field techniques and modelling) and investigating various environmental systems (e.g. soils, sediments, waters and remediation systems). Primarily, FIMIN will promote and facilitate exchange of knowledge and materials, as well as access to and support of analytical equipment and potential study sites.

The following initiatives will serve to stimulate mutual learning within the Programme:

- Provide a platform for European researchers of different disciplines to promote and integrate various concepts and techniques related to the understanding of the functionality of iron in natural and anthropogenic processes
- Facilitate exchange of know-how and materials (microbes, cultivation techniques, reference minerals, preparation procedure)
- Initiate new research activities that utilise state-of-the-art techniques and technologies for studying the role of iron in environmental (bio)geochemistry
- Provide means, including exchange visits, conferences, workshops, summer schools, common databases and an interactive web page
- Enable access to analytical equipment and interesting field sites
- Provide opportunities for training young investigators in the latest advances in relevant techniques

Several tools exist to support these initiatives:

Long- and **short-term exchange grants** for researchers are provided to enable visits to institutions in other participating countries. Calls for grants are made, with application deadlines on 15 October, 15 February and 15 June of each year.

Scientific workshops will be organised or supported and will focus on specific topics:

- 25 May–9 June 2010, in Lund, Sweden, and Lyngby and Copenhagen, Danemark: Magnetic Methods in Biogeochemistry – From Field to Microscopy and Mössbauer Spectroscopy (Christian Bender Koch and Mihály Pósfai)
- 7–11 August 2011, in Tübingen, Germany: Tools in Environmental Biogeochemistry – Opportunities and Limitations (Andreas Kappler and Ruben Kretzschmar)
- Late 2011, early 2012, in the United Kingdom: Environmental Iron Microbiology (Jon Lloyd and Barrie Johnson)
- 2012, in Vienna, Austria: The Use of Stable Isotopes of Fe in Environmental Geochemistry and Biogeochemistry (Stephan Kraemer and Yigal Erel)

A **spring school** entitled Iron in the Environment: From Nature to the Laboratory was set up for junior researchers interested in the nature and dynamics of iron and iron minerals in natural environments (7–11 March 2011, in Cordoba, Spain; Jose Torrent, Eric Smolders, Thilo Behrends, Stefan Peiffer). It dealt with iron in soils, sediments, surface water and groundwater, and geological systems. Reviews on iron minerals and their environmental significance, as well as on the principles and state of the art of analytical techniques were presented.

All scientists active in any of the FIMIN research themes are encouraged to apply for our programmes. Applications will be selected based on scientific excellence and in accordance with ESF priority rules (www.esf.org/RNP-guidelines).

For more and up-to-date information, please visit the FIMIN websites: **www.fimin.eu** and **www.esf.org/fimin**.

STEERING COMMITTEE

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