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MINI REVIEW

The dual role of microbes in corrosion

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Corrosion is the result of a series of chemical, physical and (micro) biological processes leading to the deterioration of materials such as steel and stone. It is a world-wide problem with great societal and economic consequences. Current corrosion control strategies based on chemically produced products are under increasing pressure of stringent environmental regulations. Furthermore, they are rather inefficient. Therefore, there is an urgent need for environmentally friendly and sustainable corrosion control strategies. The mechanisms of microbially influenced corrosion and microbially influenced corrosion inhibition are not completely understood, because they cannot be linked to a single biochemical reaction or specific microbial species or groups. Corrosion is influenced by the complex processes of different microorganisms performing different electrochemical reactions and secreting proteins and metabolites that can have secondary effects. Information on the identity and role of microbial communities that are related to corrosion and corrosion inhibition in different materials and in different environments is scarce. As some microorganisms are able to both cause and inhibit corrosion, we pay particular interest to their potential role as corrosion-controlling agents. We show interesting interfaces in which scientists from different disciplines such as microbiology, engineering and art conservation can collaborate to find solutions to the problems caused by corrosion.

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Introduction

Corrosion is a global problem that affects a large variety of industries and municipal services, such as shipping, oil refinery, construction, sewage and drinking water systems, and upkeep of historical buildings and statues (Sánchez del Junco *et al.*, 1992; Warscheid and Braams, 2000; Videla and Herrera, 2005).

Corrosion refers to the deterioration of materials, such as iron, steel, concrete and stone (see for other reviews Warscheid and Braams, 2000; Videla and Herrera, 2005, 2009). Biocorrosion is the result of electrochemical reactions that are influenced or driven by microorganisms, which are often present as biofilms. In recent years it has become clear that microbes do not only cause corrosion, but they can also inhibit or protect against corrosion, which is summarized in the terms microbiologically influenced corrosion (MIC) and MIC inhibition (MICI) (Zuo, 2007). This review aims to show the recent progress on MIC and MICI mechanisms and tries to integrate the data from studies on different materials and from different scientific fields to update on the present state of knowledge and on the identification of promising approaches for corrosion prevention and protection.

Metal corrosion

Metal corrosion results from (bio) chemical reactions that release either electrons or ions from the metal. Corrosive chemicals, like acids, stimulate anodic reactions. By consuming hydrogen, microbes stimulate cathodic reactions (Videla and Herrera, 2005) and they may also stimulate corrosion through the secretion of enzymes and acidic metabolites (Table 1).

The main types of bacteria associated with the corrosion of iron and steel are sulfate-reducing bacteria (SRB), sulfur-oxidizing bacteria, iron oxidizers, iron reducers, manganese oxidizers and microbes that secrete organic acids and produce extracellular polymeric substances (EPS) (Hamilton, 2003; Zuo, 2007; Table 2). The microbiology and corrosion effect of SRB and iron oxidizers have recently been reviewed (Herrera and Videla, 2009; Emerson *et al.*, 2010; Enning and Garrelfs, 2013). Genomic analysis might provide interesting information on the genetics and regulation of the metabolic processes leading to corrosion, but there are only few genomes available of pure cultures of microbes published related to corrosion and a few molecular studies on corroded materials, which will be discussed in the 'Perspectives' section.

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Most damaging corrosion takes place in the presence of a multispecies biofilm. In such biofilms the interactions between different species may induce a cascade of biochemical reactions in the oxic and anoxic parts of the biofilm and exacerbate corrosion (Zuo, 2007; Videla and Herrera, 2009). Multiple corrosion-causing organisms in a biofilm can act synergistic and contribute to more severe corrosion than when only one single species is present (Zuo, 2007; Lee *et al.*, 2013).

Recently, two different mechanisms of iron corrosion were described, that is, chemical MIC (CMIC) and electrical MIC (EMIC) (Enning *et al.*, 2012; Enning and Garrelfs, 2013; Venzlaff *et al.*, 2013). These two mechanisms differ in the source of electrons used by the SRB, which was shown to be species specific. The electrons originate from a hydrogen film on the metal surface (CMIC) or they can be directly extracted from Fe^{o} (EMIC). In EMIC the produced sulfuric corrosion crust enables the transfer of electrons to the microbes even if they are not in direct contact with the iron. This explains why microorganisms and the crust can continue to grow, which is not the case in CMIC, where corrosion and crust formation stop upon loss of direct metal contact (see Figure 1). Direct electron uptake is also shown for methanogens, but the produced corrosion crust is not conductive and so corrosion will probably stop once direct metal contact is lost, that is, the methanogenic Archaea are no longer in direct contact with the metal surface (Enning *et al.*, 2012).

Table 1 Examples of corrosion reactions influenced by microbes

Anodic reaction	$Me \rightarrow Me^{2+} + 2e^{-}$
	$H_2O \rightarrow H^{+} + OH^{-}$
Anodic depolarization by sulfide	$Fe^{2+} + S^{2-} \rightarrow FeS$
Cathodic reaction	$2H^{+} + 2e^{-} \rightarrow H_2$
	$½\ O_2 + H_2O + 2e^{-} \rightarrow 2OH^{-}$
Cathodic depolarization by SRB	$SO_4^{2-} + H_2 \rightarrow S^{2-} + 4\ H_2O$

Abbreviation: SRB, sulfate-reducing bacteria.

Stone and concrete corrosion

Biofilms on concrete, stone and marble are visible as a colored slimy layer or a dry crust (Warscheid and Braams, 2000). These microbial assemblages can directly cause physical and chemical deterioration of historical buildings and works of art (Gaylarde *et al.*, 2011). Moreover, the slimy (EPS) biofilms retain moisture, which may induce mechanical stress on the structure upon freeze–thaw cycles.

Different groups of microorganisms are involved in stone corrosion. At the stone–air interface, the available light may result in growth of phototrophs such as algae and cyanobacteria (Lamenti *et al.*, 2000). Fungi can bore into the stone and produce extracellular enzymes and metabolites that cause chemical and physical damage (Warscheid and Braams, 2000). Bacteria-producing acids, for example, nitrifying bacteria dissolve calcareous stone, whereas other bacteria and fungi feed on paint or other coatings applied to protect the material (Vollertsen *et al.*, 2008; Mapelli *et al.*, 2012).

Corrosion may also occur at the stone–soil interface, including the foundations of buildings and sewer systems. Sewer systems made of concrete can be severely damaged by microorganisms such as *Acidothiobacilli* spp., which produce sulfuric acids that react with the calcitic binding material of the concrete (Crispim and Gaylarde, 2005).

Table 2 Examples of microorganisms found related to microbiologically influenced corrosion of metal (reviewed as well in Beech and Gaylarde, 1999)

Type		*Trait*	*Effect*	*References*
Sulfide reducers *Desulvovibrio* sp. *Desulfomonas* sp.	Anaerobic	Use H_2 to reduce SO_4^{2-} to S^{2-}: precipitation of H_2S and FeS	Cathodic depolarization by hydrogen uptake, anodic depolarization by corrosive iron sulfides	Enning *et al.*, 2012; Rao *et al.*, 2000; Venzlaff *et al.*, 2013; Wikieł *et al.*, 2014
Iron oxidizers/manganese oxidizers *Gallionella* sp. *Leptothrix* sp. *Mariprofundus* sp.	Aerobic	Fe^{2+} to Fe^{3+} and Mn^{2+} to Mn^{3+}: Iron oxide and manganese dioxide formation	Deposition of cathodically reactive ferric and manganic oxides	Lee *et al.*, 2013; McBeth *et al.*, 2011; Rao *et al.*, 2000; Linhardt, 2010
Iron reducers *Pseudomonas* sp. *Shewanella* sp. *Geothermobacter* sp.	Aerobic	Reduce Fe^{3+} to Fe^{2+}, manganese or iron oxide reduction	Reduction of iron and manganese oxides	Lee *et al.*, 2013; Rao *et al.*, 2000
Sulfide oxidizers *Thiobacillus* sp.	Aerobic	Oxidizes S^{2-} and SO_3^{2-} to H_2SO_4	Acids corrode metal	Li *et al.*, 2008
Acid producing bacteria and fungi *Clostridium* sp. *Fusarium* sp. *Penicillium* sp. *Hormoconis* sp.	Aerobic and anaerobic	Production acids, e.g., nitric acid, sulfuric acid, and organic acids	Dissolve iron, chelate copper, zinc and iron	Juzeliūnas *et al.*, 2007; Little *et al.*, 2001; Usher *et al.*, 2014
Slime forming bacteria *Clostridium* sp. *Bacillus* sp. *Desulfovibrio* sp. *Pseudomonas* sp.	Aerobic and anaerobic	Production of extracellular polymeric substances (biofilm)	Exopolymers capable of binding metal ions	San *et al.*, 2011; Stadler *et al.*, 2008; Stadler *et al.*, 2010

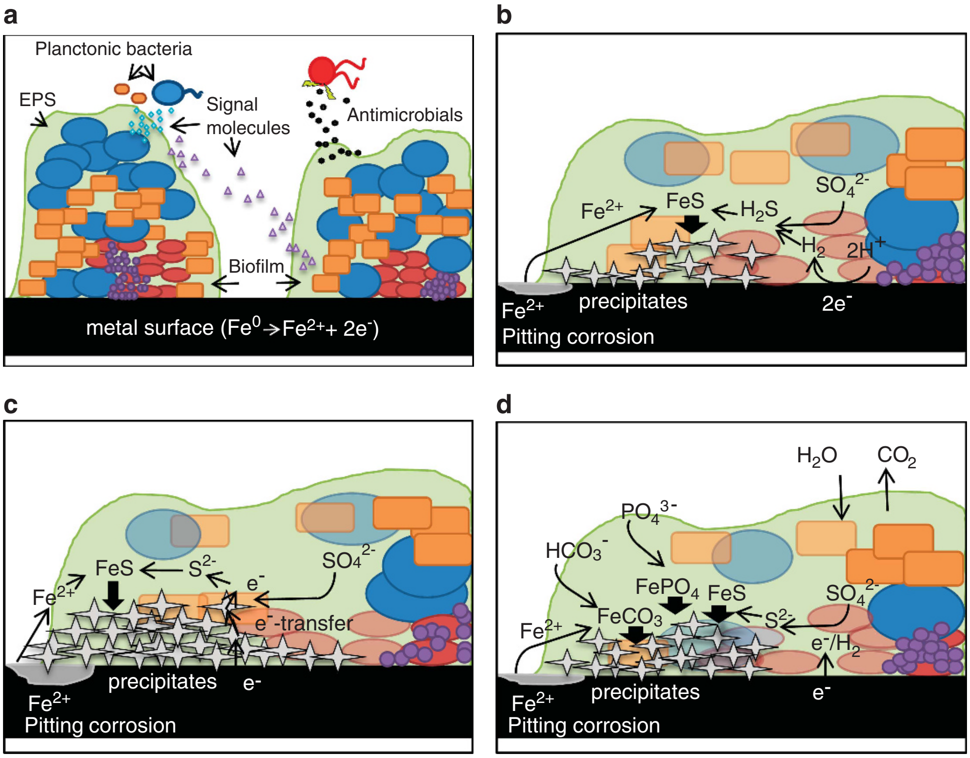

Figure 1 Schematic overview of a multispecies biofilm on a metal surface showing the possible reactions between the biofilm, the metal surface and the anaerobic environment. (**a**) A biofilm on a metal surface producing signal molecules and antimicrobials. (**b**) CMIC, chemical microbially induced corrosion by marine sulfate reducers. (**c**) EMIC, electrical microbially induced corrosion by marine sulfate reducers. (**d**) A multispecies biofilm showing the precipitation of several different precipitates.

Conventional corrosion inhibition and prevention methods

Current (bio) corrosion prevention methods, such as cleaning, coatings and electrochemical interference, are based on the inhibition of microbial growth and metabolism. Owing to the resistant nature of biofilms the treatment of established biofilms is often not effective for corrosion control (Simões *et al.*, 2010). Regular cleaning and disinfection is used to reduce microbial attachment, but this is not always an option, for example, on pipelines buried in soil or in oceans (Parkar *et al.*, 2004; Simões *et al.*, 2010).

Another biocorrosion prevention method is to inhibit certain electrochemical reactions (Zuo, 2007; Neoh and Kang, 2011). This can be achieved by the application of protective coatings or either anodic or cathodic protection. However, many coatings have been shown to be subject to microbial degradation (Kopteva *et al.*, 2004). Coatings with added antimicrobials were shown to inhibit microbial degradation (Gottenbos *et al.*, 2002; Park *et al.*, 2004), for example, silver-based coatings were effective in the inhibition of biofilm formation (Liedberg and Lundeberg, 1989). Unfortunately, the fact that antimicrobials can dissolve from the coating into the environment raises serious concerns. The cathodic protection method uses a sacrificial anode, which is an easily corroded metal that is attached to the protected metal. However, this method is expensive and only works in certain environments.

To protect stone and concrete, coatings are also applied, for example, consolidants, like epoxy resins, which bind the stone particles together (Karatasios *et al.*, 2009). These resins polymerize inside the pores of the stone. However, this treatment clogs the pores and is subject to deterioration and in time can peel off, which aggravates the situation rather than improving it (Le Métayer-Levrel *et al.*, 1999).

Metal corrosion inhibition using microbially based techniques

The use of microbes to protect metals against corrosion has been shown to have great potential (Potekhina *et al.*, 1999; Videla and Herrera, 2005). Zuo (2007) described three possible mechanisms of the inhibition of biofilm-induced metal corrosion: (1) removal of corrosive substances through microbial activity; for example, microbes consuming reactive oxygen through aerobic respiration, (2) growth inhibition of corrosion-causing microbes, for example, from antimicrobial production by non-corrosive microorganisms and (3) the formation of a protective layer, which could be established by overproduction of EPS by non-damaging microbes (Zuo, 2007; Videla and Herrera, 2009).

In multispecies biofilms a combination of the different mechanisms may occur. In 1991, Pedersen and Hermansson already showed the inhibition of steel corrosion by two marine isolates, *Pseudomonas* sp.S9 and *Serratia marcescens* EF190. Corrosion inhibition was also detected when the metal and cell suspensions were separated, which led to the conclusion that corrosion protection was the result of metabolic activity, including oxygen consumption. Since then MICI has been studied by testing different materials and different bacterial species in different environments (see Table 3). The corrosion-inhibition effect was tested by using aerobic biofilms grown on different types of metals. The single-species biofilms tested included *Bacillus* spp, *Pseudomonas* spp., *Shewanella* spp. and *Spirulina platensis* (nowadays *Arthrospira*) (Jayaraman *et al.*, 1999a, b; Nagiub and Mansfeld, 2002; Chongdar *et al.*, 2005; Mert *et al.*, 2011). Both aerobic *P. fragi* biofilms and anaerobically grown *Escherichia coli* biofilms were shown to inhibit corrosion, but the aerobic biofilms decreased corrosion to a greater extent, which indicates that oxygen removal has a significant role in MICI (Jayaraman *et al.*, 1997a, c). When *Shewanella oneidensis* mutants in which biofilm formation and/or iron respiration had been knocked down were grown on metal, an increase in corrosion rates was found when compared with the wild type, which indicates that the microbial respiration of the wild type and biofilm formation inhibit the corrosion processes (Dubiel *et al.*, 2002).

The second MICI mechanism is the growth inhibition of corrosion-causing microorganisms. This has been investigated using biofilms that naturally produce antimicrobials, or using genetically engineered organisms, which produce antimicrobials that inhibit the growth of SRB (Jayaraman *et al.*, 1997a, b, c; Jayaraman *et al.*, 1999b; Zuo and Wood, 2004). The best results were obtained when antimicrobial-producing biofilms were applied, instead of only adding the antimicrobials. *Bacillus brevis* naturally produces gramicidin S, which inhibits corrosion by SRB on mild steel and stainless steel (Jayaraman *et al.*, 1999a). Genetically

Table 3 Overview of MICI studies using different types of organism and materials

Organism type	*Organism(s)*	*Material(s)*	*Mode of action*	*Reference(s)*
Bacteria	*Pseudomonas spp.* and *Escherichia coli*	Carbon steel (SAE 1018)	Protective biofilm, (oxygen removal?)	Jayaraman *et al.*, 1997a, b, c
	Pseudomonas Sp9 and *Serratia marcescens EF190*	Steel	Metabolic activity (oxygen removal?)	Pedersen and Hermansson, 1991
	Bacillus Brevis	Carbon steel (SAE 1018)	SRB inhibition by production of antimicrobials	Jayaraman *et al.*, 1999a
	Pseudomonas fragi K and *Bacillus brevis 18*	Unalloyed copper and aluminum alloy 2024	Protective biofilm (oxygen removal?)	Jayaraman *et al.*, 1999c
	Pseudomonas cichorii	Mild steel	Protective biofilm, phosphate precipitation layer	Chongdar *et al.*, 2005
	Shewanella algae and *S. ana*	Aluminum, mild steel & brass	Protective biofilm	Nagiub and Mansfeld, 2002
	Shewanella oneidensis strain MR-1	Mild steel 1018	Protective precipitation layer	Dubiel *et al.*, 2002
	Pseudomonas flava	Mild steel	Protective biofilm, phosphate precipitation layer	Gunasekaran *et al.*, 2004
	Bacillus licheniformis and *B. subtilis*	Aluminum 2024-T3 and C26000 brass	Production of anionic corrosion inhibitors	Mansfeld *et al.*, 2002; Örnek *et al.*, 2002a, b
	Spirulina platensis (Arthrospira):	Carbon steel	Protective biofilm	Mert *et al.*, 2011
	Bacillus pasteurii	Cement-based building material	Calcium carbonate precipitation	Chunxiang *et al.*, 2009
	Myxococcus xanthus and other carbonatogenic bacteria	porous limestone (calcarenite)	MICP	Jroundi *et al.*, 2010; Jroundi *et al.*, 2012; Piñar *et al.*, 2010
	Brevundimonas diminuta	Calcitic and silicate substrates	MICP	Rodriguez-Navarro *et al.*, 2012
	Bacillus sphaericus	Concrete and mortar	MICP	De Muynck *et al.*, 2008
	Bacillus lentus and *Bacillus sphaericus*	Limestone	MICP	Dick *et al.*, 2006
	Bacillus pseudofirmus DSM 8715 and *B. cohnii* DSM 6307	Concrete	MICP	Jonkers *et al.*, 2010
	not determined	Limestone	MICP	Zamarreño *et al.*, 2009
Unidentified bacteria	Not determined	Aluminum 2024, mild steel and brass	Protective biofilm	Nagiub and Mansfeld, 2001b; 2002
	Bacillus subtilis BE1500 and *B. subtilis* WB600	Carbon steel (SAE 1018)	SRB inhibition by production of antimicrobials	Jayaraman *et al.*, 1999b
Genetically engineered microorganisms	*Bacillus subtilis, Bacillus licheniformis* and *E. coli*	Aluminum 2024 and C26000 brass	Secretion of anionic corrosion inhibitors	Mansfeld *et al.*, 2002; Örnek *et al.*, 2002a, b
	Beauveria bassiana	Ancient copper coins	Protective copper oxalate layer	Joseph *et al.*, 2012
Fungi	*Aspergillus niger, Aspergillus alliaceae,* *Penicillium* sp.*, Beauveria bassiana* and *Fusarium* sp.	Bronze and copper	Protective oxalate layer	Joseph *et al.*, 2011

Abbreviations: MICP, microbial-induced carbonate precipitation; SRB, sulfate-reducing bacteria engineered *B. subtillus* biofilms secreting the antimicrobials indolicidin and bactenecin also reduced SRB-induced corrosion significantly (Jayaraman *et al.*, 1999b). An additional advantage of the antimicrobial-producing biofilm is that relatively high local antimicrobial concentrations in the biofilm can be maintained without excessive diffusion into bulk fluids. Although there are different microbes involved in MIC, growth-inhibition studies have only been targeting the growth inhibition of SRB.

Other compounds have been shown to protect metals against corrosion, such as the negatively charged corrosion inhibitors, polyaspartate and γ-polyglutamate, secreted by bacterial biofilms (Mansfeld *et al.*, 2002; Örnek *et al.*, 2002a). As with coatings, the possible dissolution of antimicrobials into the environment remains a point of discussion.

Another corrosion control approach is biocompetitive exclusion (BE) (Videla and Herrera, 2005), which is applied in oil industries to exclude SRB from the local microbial community by promoting the growth of competing bacteria such as nitrate-reducing bacteria (Gieg *et al.*, 2011).

Finally, recent studies showed that using the EPS, separated from the microbes, could reduce corrosion by SRB (Stadler *et al.*, 2008, 2010; Finkenstadt *et al.*, 2011). This corrosion protection by EPS appeared to be species dependent. The EPS of *Desulfovibrio alaskensis* inhibited corrosion, whereas the EPS of *D vulgaris* and *D indonesiensis* induced corrosion.

In all cases the mechanisms of the corrosion inhibition are not fully understood and different studies sometimes result in opposite conclusions, for example, in the case of iron-reducing bacteria that can cause or inhibit corrosion (Lee and Newman, 2003; Herrera and Videla, 2009). The above-mentioned studies are performed under controlled laboratory conditions with mostly single-species biofilms, which makes it difficult to extrapolate the results to realistic field conditions. In order to develop an application, there is a strong need for multispecies analyses under *in situ* conditions and samples from the field.

Stone corrosion inhibition using microbially based techniques

Corrosion of stone and concrete is fundamentally different from metal corrosion, and so corrosion protection needs a different approach. Alternative approaches, including the use of microbes in stone and concrete protection, have been under research for several decades and are already being used in recent years on historical buildings (Le Métayer-Levrel *et al.*, 1999; De Muynck *et al.*, 2010).This environmentally friendly approach to stone and concrete protection is called microbial-induced carbonate precipitation (MICP; De Muynck *et al.*, 2010; Phillips *et al.*, 2013). This includes the precipitation of carbonate by so-called carbonatogenic bacteria (Le Métayer-Levrel *et al.*, 1999) as well as algae and diatoms (Zavarzin, 2002). The microbially produced carbonate precipitates resemble the concrete and mortar material, attach to it and so reinforce the material and they can even small cracks are filled and repaired (Jonkers *et al.*, 2010). Therefore, this is sometimes called self-healing concrete. The precipitation is called biologically induced or biologically controlled, depending on the influence of microbes and the environment. Biologically controlled precipitation is independent of environmental conditions and specific types of minerals are formed depending on the microorganisms (De Muynck *et al.*, 2008). In the case of biologically induced precipitation, the environmental conditions have a large influence, for example, in the case of calcium carbonate production by bacteria, which is determined by calcium concentration, dissolved inorganic carbon concentration, pH and the availability of nucleation sites (De Muynck *et al.*, 2010; Rodriguez-Navarro *et al.*, 2012). Calcium carbonate precipitation by *Sporosarcina pasteurii* decreased water uptake, permeability and chloride penetration, enhancing the durability of concrete structures (Bang *et al.*, 2010; Achal *et al.*, 2011). In view of the conservation of archeological and historical sites and structures, carbonatogenic bacteria have successfully been used to protect limestone and concrete against corrosion as well (Le Métayer-Levrel *et al.*, 1999; Ettenauer *et al.*, 2011). Different types of bacteria have been tested for the consolidation of stone statues and buildings, including *Bacillus* spp. and *Myxococcus* sp. (Table 3; Rodriguez-Navarro *et al.*, 2003; Jimenez-Lopez *et al.*, 2008; Ettenauer *et al.*, 2011). *Myxococcus xanthus* is able to induce the precipitation of a range of carbonates, phosphates and sulfates, which is important because the biomineralized cement must be compatible with the substrate. Another advantage is the motility of *M. xanthus*, which increases the potential protected surface because they are able to migrate inside the porous material, thereby increasing the consolidation efficiency (Jimenez-Lopez *et al.*, 2008). Addition of *M. xanthus* to stone also was shown to induce the growth of other carbonatogenic microorganisms present in and on the stone, such as *Pseudomonas* sp., *Bacillus* sp. and *Brevibacillus* sp. (Piñar *et al.*, 2010).

Two types of stone consolidation treatments based on biomineralization are used: (1) the inoculation of a carbonatogenic bacterial culture and (2) the application of culture media that will activate the *in situ* carbonatogenic bacterial community (Jroundi *et al.*, 2012). As the mineral precipitates should be compatible with the material, the use of the *in situ* bacterial community enlarges the chances of successful bioconsolidation (Zamarreño *et al.*, 2009; Jroundi *et al.*, 2012).

Perspectives

Microbial investigations on MIC and MICI, especially on metal, have been focused on laboratory experiments with single-species biofilms, even though the synergistic effect of multispecies biofilms is already known. Also, there is an increase in contradictory reports on both accelerating and inhibiting actions on the corrosion process of the same functional group of microorganisms, such as sulfate reducers (Enning *et al.*, 2012; Venzlaff *et al.*, 2013), iron reducers (AlAbbas *et al.*, 2013) and methanogens (Uchiyama *et al.*, 2010). These studies show a strong species specificity for either MIC or MICI, which indicates that there is an urgent need to focus on the mechanisms rather than on the presence of certain functional groups, which is common practice at the moment. The use of molecular techniques for community analysis is still rare in corrosion studies. Denaturing gradient gel electrophoresis (DGGE) on corroded iron and oil pipelines (Bermont-Bouis *et al.*, 2007; Duncan *et al.*, 2009; Oliveira *et al.*, 2011; Cote *et al.*, 2014; Marty *et al.*, 2014) showed that the microbial communities involved in corrosion are much more complex than was found so far with culturing methods. Standard metal biocorrosion-monitoring procedures focus mainly on SRB detection, and although SRB are also found in many molecular studies they are not always the most abundant or most relevant microorganisms. Some of the above-mentioned studies do not make use of the full potential of the current molecular tools. Modern metagenomics approaches have only scarcely been applied in corrosion studies. Gomez-Alvarez *et al.* (2012) analyzed the microbial community in corroded wastewater pipes and they were able to relate the corrosion to sulfur and nitrogen pathways. Sampling is an important issue, because in oil industry most samples are water samples and they do not represent the microbial community attached to the pipeline walls (Skovhus *et al.*, 2011).

Full understanding of the MICI and MIC processes requires the combination of expertise of scientists from different disciplines; as this is often not the case, great opportunities to improve the fundamental knowledge of the processes involved have been missed. For example, material scientists discovered that a bacterial contamination inhibited corrosion after insufficient sterilization of their electrodes (Nagiub and Mansfeld, 2001). However, this bacterial contamination was not further examined. Also, applying recent advances in molecular microbiological detection techniques to archeological excavation sites where natural protective layers are found may provide vital information on long-term processes, and, together with geochemical and mineralogical data, it might be a step closer to understanding the different mechanisms.

Recent discoveries have shown the importance of the ability to use Fe^0 as an electron donor, rather than hydrogen, as was shown in the CMIC *vs* EMIC mechanisms in marine SRB. Electrochemically active biofilms have been investigated in microbial fuel cell research and researchers have tried to understand the mechanisms of electron transfer between microorganisms and metals (Babauta *et al.*, 2012). Several molecular studies revealed the role of pili and of multiheme outer-membrane c-type cytochromes in electron transfer (Butler *et al.*, 2010, Lovley, 2012). A comparative metatranscriptomic analysis revealed eight genes with no annotated protein function to be related to electrochemical activity (Ishii *et al.*, 2013). Both the fields of corrosion and microbial fuel cell research can benefit from these in-depth studies.

When analyzing the existing literature, several approaches emerge as potentially successful MICI mechanisms. The first is a protective biofilm that works primarily as a coating and delivers protection when the metabolic activity reduces corrosion-causing reactions or growth of corrosion-causing organisms. There are only few examples of lab experiments in which single-organism biofilms were tested.

The second MICI mechanism is microbially induced precipitation of compounds to protect the material against corrosion. In stone protection, microbially induced precipitation is already applied in certain industries. However, for metal corrosion microbially induced protection requires better understanding of the processes involved before it can be applied in full practice. One application is known to be successful: *Beauveria bassiana* produces copper–oxalate complexes, thereby forming a protective coating on copper objects (Joseph *et al.*, 2012). There are few examples, such as the biofilms of *Pseudomonas* spp. grown on steel electrodes, that showed the production of a protective layer of iron oxides and iron phosphates (Chongdar *et al.*, 2005). Also, *Pseudomonas* and *Rhodococcus* sp. biofilms were shown to produce corrosion-inhibiting layers of phosphate minerals on metal surfaces (Volkland *et al.*, 2000, 2001). The EPS layer of biofilms has an important role in the mineral precipitation process, for example, the organo-metal (iron-EPS) complex in which the EPS interacts with the dissolved metal to form a complex (Chongdar *et al.*, 2005; Decho, 2010). For EPS also species specificity has a role, for example, EPS of *P. cichorii* comprising neutral carbonyl groups forms a protective complex, but the EPS of *P. alcaligenes* was acidic and even aggravated the corrosion of mild steel (Chongdar *et al.*, 2005).

Corrosion-inhibiting mineral layers deposited by microbes on iron have great biotechnological potential. This natural coating may even thrive in the natural environment because in marine and soil environments the precipitation of phosphate and that of carbonate are common processes (Castanier *et al.*, 1999; Krumbein, 1974). There are some examples of naturally formed mineral precipitation layers, for example, on metallic radioactive waste containers stored in deep geological environments, in which a protective magnetite layer (Fe_3O_4) was observed (Esnault *et al.*, 2011). Other examples are found in archeological excavation sites, where iron objects thousand years old can still be found relatively unaffected by corrosion (Booth *et al.*, 1962a, b). These objects contained a protective layer of mixed ferrous and ferric phosphates, even in highly aggressive soils. It is still not understood how these protective layers are formed and what the influence of microbes is on these systems. The input of microbial and molecular analysis of these unique field samples might enable a better understanding of the processes that take place at the metal surface in natural environments. New corrosion-mitigation strategies can be developed, for example, using microbial communities that are naturally present in the soil to produce a protective mineral layer on metal, similar to the approach in stone consolidation processes.

Finally, corrosion science lags behind in using the molecular toolkit to its full extent, but based on recent developments with respect to species specificities and EMIC *vs* CMIC, these approaches may be prerequisite *sine qua non* to get to a better understanding of MIC and MICI. Also interdisciplinary collaborations are needed to obtain a better understanding of electrochemically active biofilms.

Conflict of Interest

The authors declare no conflict of interest.

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