Mineral – microbe interactions: biotechnological potential of bioweathering

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Abstract

Mineral-microbe interaction has been a key factor shaping the lithosphere of our planet since the Precambrian. Detailed investigation has been mainly focused on the role of bioweathering in biomining processes, leading to the selection of highly efficient microbial inoculants for the recovery of metals. Here we expand this scenario, presenting additional applications of bacteria and fungi in mineral dissolution, a process with novel biotechnological potential that has been poorly investigated. The ability of microorganisms to trigger soil formation and to sustain plant establishment and growth are suggested as invaluable tools to counteract the expansion of arid lands and to increase crop productivity. Furthermore, interesting exploitations of mineral weathering microbes are represented by biorestoration and bioremediation technologies, innovative and competitive solutions characterized by economical and environmental advantages. Overall, in the future the study and application of the metabolic properties of microbial communities capable of weathering can represent a driving force in the expanding sector of environmental biotechnology.

Keyword: mineral weathering, biomining, soil genesis, plant growth promotion, biorestoration, bioremediation

1. Introduction

Bioweathering has been definied as the dissolution of rocks and mineral substrates carried out by microorganisms and plants through mechanical and chemical processes (Gadd, 2007). Microbial mineral weathering has been extensively studied on the role played by bacteria in biomining, a biotechnological method for the extraction and recovery of metals from ores (Rawlings and Johnson, 2007). Bioweathering is not only a key process that impacted the evolution of the Earth's surface over geological time but it also affects human life through its influence on water quality, soil development and agriculture, as well as monuments and statues preservation. Microbes interact with minerals as a strategy to colonize and exploit habitats where the environmental parameters disadvantage other microorganisms (Ehrlich, 1996) and they show the ability to scavenge essential elements that have poor bioavailability, such as iron and phosphorus.

The need to increase soil fertility and crop productivity, especially in arid lands, to remediate contaminated soils, to clean stone artworks and buildings exist. A deeper insight into the ecology of mineral weathering processes mediated by the microbiome may represent a real opportunity for researchers to design innovative solutions to emerging problems in agriculture, the environment and the industry. By developing the so called "Microbial Resource Management" strategy (Vestraete, 2007) mainly based on the enhancement of the natural functional ability of the residing microbial communities, scientists will promote an environmental-friendly use of biotechnology.

In this review we discuss the importance of bioweathering in different artificial and natural ecosystems, evaluating its potential in soil fertility, plant growth promotion, biorestoration and bioremediation of inorganic pollutants.

2. The ecology of microbial consortia involved in biomining processes

In the past the mobilization of metals from minerals in nature was thought to be an abiotic process and only in the 1950's the first acidophilic iron and sulfur-oxidizing bacteria were isolated from acid mine drainage (Colmer et al., 1950). Starting from the second half of the last century the capability of microorganisms to promote the solubilization of various metals from minerals has been studied in detail, and research has been economically sustained also in the light of the commercial interests behind the mineral bioprocessing operations (Fig. 1a). Most of our knowledge about ecological interactions and biodiversity of microbes involved in mineral weathering derives thus from the study of biomining plants and acid mine effluents.

Compared to traditional methods, biomining allows to process deposits characterized by low metal concentration and to decrease energy consumption and the amount of chemical waste (Johnson, 2008), which dramatic consequences on the environment are well known worldwide (Haferburg and Kothe, 2010 and references therein). The low pH of bioleachate fluids, their elevated concentration of metals and the high temperature achieved during mineral oxidation reactions (Okibe and Johnson, 2004) make biomining reactors a highly selective habitat where only thermophilic and thermotolerant acidophilic prokaryotes thrive. The biodiversity of microbial communities involved in bioprocessing is strongly correlated with the selected industrial option. During biooxidation processes conducted in stirred tanks, temperature, pH, oxygen concentration and other parameters can be efficiently directed. The uniform conditions established in biooxidation tanks determine a low degree of species richness. The continuous flow nature of the process indicated that cell division time is a crucial factor for prokaryotes to dominate the microbial community (Rawlings and Johnson, 2007). The most common microorganisms involved in the biomining processes are bacterial species of the genera *Acidithiobacillus* and *Leptospirillum*, representatives of the Archaea genus *Ferroplasma* and few bacterial species belonging to the order *Sulfolobales* (Johnson, 2008). Combining culture dependent and independent analyses, Okibe and Johnson (2004) identified the most efficient microbial consortium for pyrite oxidation in a mixed culture of moderately thermophilic acidophiles. A consortium comprising *Acidithiobacillus ferrooxidans*, *Acidithiobacillus caldus* and *Leptospirillum ferriphilum* enhanced pyrite dissolution compared to pure bacterial cultures or mixed cultures comprising two of the three strains. Denaturing Gradient Gel Electrophoresis (DGGE), a useful tool for the investigation of the microbiome composition and its evolution over time and space, was applied to monitor changes of the bacterial community structure during bioleaching operations (He et al., 2010). It is interesting to note that these data confirmed *Acidithiobacillus* and *Leptospirillum* spp. as the prevailing microbes retrieved during the final stages of pyrite bioleaching processes. Moreover, the study of ecological interactions within acidophilic mineral-oxidizing consortia showed that iron- and sulfur-oxidizing bacteria belonging to the genus *Sulfobacillus* likely play a secondary role in mineral oxidation but are extremely important in the regulation of organic carbon compounds levels (Nanchucheo and Johnson 2009). Chemoautotrophic acidophiles such as *Leptospirillum* spp. are very sensitive to low-molecular weight molecules, abundant products in the culture of actively growing acidophilic chemolithotrophic bacteria (Borichewsky, 1967; Schnaitman and Lundgren, 1965). The ability of *Sulfobacillus* spp. to scavenge glycolic acid through their metabolism emphasized the relevance of ecological relationships established during bioleaching (Nanchucheo and Johnson 2009). The genetic approach as well was fundamental in the explanation of microbial adaptation to adverse conditions occourring during the biooxidation of arsenic-containing ores. Genes encoding for enzymes involved in arsenic resistance have been recently identified in the genome of *Sulfobacillus thermosulfidooxidans* (van der Merwe et al., 2010). Furthermore a microbial consortium formed by *Acidithiobacillus caldus* and *Leptospirillum ferriphilum* showed the presence of rare transposons containing genes for resistance to high arsenic level that were absent in less resistant strains of the same species (Tuffin et al., 2005; Tuffin et al., 2006). Biooxidation can be accomplished also in heap leaching, and it is widely applied to low value minerals. In this kind of facilities only a partial control on the operational parameters can be reached, determining changes of the irrigation efficiency, nutrients and oxygen availability, pH, redox potential and temperature (Johnson, 2008; Rawlings and Johnson, 2007). The high number of microhabitats in heap leaching results in a greater biodiversity compared to the biooxidation ones and the microbiome composition can vary according to the fluctuations of the physico-chemical parameters. Moreover, the fitness of prokaryotes in heap leaching depends on their ability to adhere on the surface of the minerals and form biofilms (Sand and Gehrke, 2006). The presence of quorum sensing-signaling molecules involved in biofilm formation has been indeed reported in *Acidithiobacillus* and *Leptospirillum* spp. (Rivas et al., 2007; Ruiz et al., 2008) whereas they could not be detected in the biofilm forming acidophile archaeon *Ferroplasma acidarmus* (Baker-Austin et al., 2010). Many efforts have been focused on the identification of the ideal microbial consortium in order to obtain the best bioleaching performances. Some commercial artificial inocula are formulated by mesophilic, moderately thermophilic and extremely thermophilic prokaryotes. A second opportunity consists in the natural selection of the consortium inside the industrial plant and the use of the drainage fluids as an inoculum for a new reactor (Rawlings and Johnson, 2007).

Due to its importance and ubiquity in biomining processes *Acidithiobacillus ferrooxidans* was the first extreme acidophile which genome has been fully sequenced (Selkov et al., 2000) and available genomic information about this species is constantly increasing. In the future bioinformatic tools could unravel the unknown properties of acidophilic proteins codified by the key actors of biomining processes, possibly resulting in their enhanced effectiveness and in the exploitation of this huge biotechnological reservoir (Cardenas et al., 2010).

Besides biomining processes, bioweathering is nevertheless occurring in many natural environments less extensively studied. The microbial communities implicated in such processes have wider diversity, due to the heterogeneous physico-chemical conditions, and are still poorly described (Balloi et al., 2010; Borin et al., 2009; Cappitelli et al., 2010).

3. Importance of microorganisms in mediating mineral weathering

The importance of bioweathering during vital ecological processes such as soil formation and plant growth promotion has been recognised in different climates and geographical areas (Egamberdieva et al., 2008; Gulati et al., 2008; Khan et al., 2009 and references therein; Mapelli et al., 2011; Siddikee et al., 2010). Since the ongoing climate changes are leading to an increase of arid lands on Earth, in the present review a special attention will be devoted to these type of ecosystems. Especially, in cold deserts and lands subjected to desertification the processes of soil formation and regression are primarily affected by mineral bioweathering, due to the lower extent of the organic fraction in maintaining soil properties.

3.1 The role of bioweathering in soil development

Rocks are normally made by a combination of one or more minerals in different proportions. Weathering is dependent on climate and may be increase due to acid rains and air pollution (Goudie and Parker, 1999). Mineral particles also can be exploited by microbial metabolism as a source of energy, e.g. as terminal electron acceptor or for microorganisms' nutrient requirements (Ehrlich, 1996). Soil is a biologically active mixture of weathered rock fragments and organic compounds (Gadd, 2007). The stability and genesis of soil aggregates is directly linked to the clay mineralogy and dissolution processes (Denef et al., 2005) and the presence of binding factors such as plant root exudates, fungal hyphae (Rillig and Mummey, 2006) and extracellular polysaccharides produced by the photosynthetic activity of cyanobacteria (Mager and Thomas, 2010). Fungi, which importance has been demonstrated applying fungicide molecules, weather rocks both mechanically and through the production of exopolysaccharides (Tang et al., 2011) and their contribution to sand particles aggregation has been experimentally tested (Degens et al., 1995). Moreover glomalin and glomalin-related proteins produced by fungal hyphae have been positively correlated with soil structure (Rillig and Mummey, 2006). The factors influencing soil development and starting pedogenesis, especially in arid regions, are still poorly understood. Cold and hot deserts indeed are key biomes for the elucidation of soil genesis processes, comprising those sites where both the positive aspects of pedogenesis and the negative effects of soil regression into desert landscapes take place. Mineral dissolution occurs in hot and cold arid lands, where it enhances water and nutrients availability in soils resulting in increased fertility (Fig. 1b) (Borin et al., 2009; Puente et al., 2004b). Lichens are important players implicated in rock weathering and their occurrence has been extensively reported in biological soil crusts present in hot and cold desert regions (Belnap and Lange, 2003; Jie and Blume, 2002). As stated for fungi, lichen mediated mineral dissolution is performed through both physical and chemical actions (Jie and Blume, 2002). Moreover, humic substances are among the main constituents of soil organic matter, which decomposition is a prerequisite for pedogenesis, and are divided in fulvic and humic acids and humin according to their level of recalcitrance (Konhauser, 2007). The structure of humic substance aggregates in soil can influence their accessibility to microbes, affecting in turn the level of organic matter degradation in different type of soils (Myneni et al., 1999). The roles of plant roots (Angers and Caron, 1998; Bashan et al., 2002; Bashan et al., 2006) and their associated microflora (Puente et al., 2004a; Uroz et al., 2007) in soil genesis and the improvement of soil structure are well known. The ability to grow on rocky soilless substrates and the occurrence of plant-microbe symbiosis have been described for several cacti and desert plants. The first report about rock colonising trees regards the species *Pachycormus discolor*, observed in the desertic area of Baja California, in Mexico (Bashan et al., 2006). The roots of this pioneering plant, able to grow in an ecosystem characterized by poor water availability and high temperature, penetrate into the volcanic rocks and are responsible for their weathering (Bashan et al., 2006). The tight interplay between rhizospheric and endophytic bacteria and cacti has been studied in detail in *Pachycereus pringlei* and *Mammillaria fraileana*, two endemic species of the Baja California region (Puente et al., 2009a; Puente et al., 2009b; Lopez et al, 2011). The ability of endophytic bacteria to colonize different portions of *Mammillaria fraileana* once re-inoculated in the cactus was demonstrated (Lopez et al, 2011). Overall, the association occurring between microbes and first colonizer plants plays a critical function in the recovery of essential elements from barren rocks, triggering the natural succession process and counteracting land erosion.

Only few studies focused nevertheless on the microbially mediated mineral weathering before plant establishment. Investigation of weathering process rates is important in measuring the release of nutrients during primary succession (Mavris et al., 2010). The analysis of chronosequences on the forefront of receding glaciers was proposed as a useful tool to calculate short- and long-term weathering rates and to describe soil formation after glacier retreat (Egli et al., 2003). Glacier moraines are ideal environments to assess the factors driving the first stages of soil genesis from mineral proto-soil released by the ice, and different studies have been reported in alpine (Frey et al., 2010) and arctic regions (Borin et al., 2009; Mapelli et al., 2010). Moreover, due to global warming, additional areas will become uncovered by ice and subjected to weathering and soil formation. Borin and co-workers (2009) recently described a new time-independent model for soil development and plant biocoenosis establishment driven by iron weathering in the forefield of the Midtre Lovénbreen glacier (Svalbard islands 78°53’N). In the site ML-RS1, estimated to be released by ice about 27 years ago (Hodkinson et al., 2003), several spots densely colonized by typical moraine mosses and vascular plants were detected at the border of a red weathering area departing from a conglomerate rock rich in pyrite (Borin et al., 2009). The constant pyrite input downstream the rock, led by its progressive disgregation due to the winter freezing, permitted to a chemolithoautotrophic bacterial community to flourish. The oxidation of ferrous iron released from pyrite decreased soil pH and produced jarosite and ferric oxy-hydroxides which were responsible for the higher soil crust specific area, water holding capacity and cation exchange capacity in surrounding vegetated area, fundamental to support improved conditions for plant growth in the desert ecosystem of Svalbard islands (Borin et al., 2009). The low pH occurring in the weathered area represented a strong selective force that allowed only specific adapted populations to survive in this ecological niche, as previously reported in artificial ecosystems like biomining plants. The weathered area showed indeed the lowest bacterial diversity value in terms of operational taxonomic unit (OTU, defined at the genus level), Shannon index and Evenness (Mapelli et al., 2010). The metabolisms of *Acidithiobacillus ferrooxidans*, recently renamed *A. ferrivorans* according to the classification proposed by Hallber et al. (2010), was suggested as the main responsible for the high iron oxidation activity in the weathered area, since it was isolated from both stone and weathered soil (Borin et al., 2009). In spite of the same range of biodiversity degree, the phylogenetic composition of the microbiome clearly distinguished the vegetated area and the barren moraine (Mapelli et al., 2010). The former showed lower pH (the pH of the barren moraine is above 8) and hosted taxa normally found in mature soils and typical of the rhizosphere.

A different process of soil development was described for the Clarens formation in South Africa, affected by a strong desquamation of the upper stone parts, where the endolithic cyanobacterial communities contributed to the silica dissolution through substratum alkalinization (Büdel et al., 2004). Silicate minerals are major components of natural rocks, such as sandstone and granite, and their chemical weathering has been suggested to be significantly enhanced under biotic conditions (Schwartzman and Volk, 1989). In the Clarence sandstone formation, the increase of pH up to 11 in the endolithic growth zone massively colonized by cyanobacteria, not only enhanced silica weathering but also helped to reduce carbonate precipitation. As a result of this phototroph-mediated bioweathering the upper portion of the stone was eroded away from wind and water flow (Büdel et al., 2004). The world-wide diffusion of cyanobacterial soil crusts in hot and cold deserts indicates the bioalkalinization activity as an important factor affecting the soil formation in these biomes. Together with nitrogen fixation activity and production of exopolysaccharides, cyanobacteria bioalkalinization contributes to maintain soil stability (Bashan et al.,2010).

Established and putative bacterial mineral dissolution mechanisms comprise nevertheless other processes like oxidoreduction reactions, organic acid and chelating molecules production (Uroz et al., 2009). *In vitro* functional experiments on the weathering potential of bacterial strains isolated from previously glaciated areas were performed by Frey et al. (2010) to clarify the mechanisms adopted during mineral dissolution. The weathering ability was tested on bacteria isolated from granitic rocks collected in the forefront of the Damma glacier, in the Swiss Alps. The four most efficient isolates in terms of granite dissolution were able to adhere to the surface of the mineral particles, to produce both oxalic acid and cyanide, the latter a commonly used compound during biooxidation, and to decrease the pH of the culture media during the first days of growth (Frey et al., 2010). The isolates, identified as *Arthrobacter* sp., *Polaromonas* sp., *Leifsonia* sp. and *Janthinobacterium* sp., belong to the Actinobacteria and Betaproteobacteria classes, previously reported to enhance mineral dissolution (Abdulla et al., 2009; Uroz et al., 2009), and displayed an accelerated mobilization from granite of key elements for soil fertility such as iron, magnesium and potassium.

Mineral weathering abilities of bacteria that firstly colonize barren mineral substrates play a fundamental role in soil genesis. Further ecological and quantitative studies will allow estimating the impact of bioweathering on soil genesis and establishment of plant biocoenosis in extremely arid ecosystems.

3.2 Effects of mineral dissolution on plant growth

Minerals are the primary source of inorganic nutrients in soils, where the weathering activity of both plant roots and microorganisms is crucial for plant establishment and growth, especially in nutrient poor ecosystems (Fig. 1c). Fungi are involved in the degradation of organic matter and the subsequent production of newly formed compounds released as dissolved organic carbon in soil matrices, where the fungal activity enhance metal release from the immobilized forms (Wengel et al., 2006). Mineral weathering is accelerated in the rhizosphere rather than in bulk soil far from plant influence (Uroz et al., 2010). However, it is not easy to distinguish the relative contribution of roots from their rhizosphere associated weathering microbes in the improvement of plant nutrition. Pioneering plants can enhance soil structure by means of growing roots penetration and exudate release (Bashan et al., 2002; Bashan et al., 2006). A further contribute is given by highly abundant and diverse microbial communities inhabiting the rhizosphere of different plants that were demonstrated to display the ability to increase nutrients availability by means of their bioweathering activity (Calvaruso et al., 2006; Carrillo-Garcia et al., 1999; Puente et al., 2004a). Microorganisms impact mineral dissolution through acidification and complexation processes, sometimes exploiting both the strategies simultaneously. Microbes can alter the rhizosphere pH secreting low-molecular weight organic compounds and can also produce chelating molecules, such as siderophores with a very high affinity for iron. Both gram-positive and gram-negative bacteria, mycorrhizal and non-mycorrhizal fungi are able to weather poorly soluble phosphorous compounds and to increase the dissolution of silicates (Uroz et al., 2007). Phosphorous is an abundant element in many soil types, nevertheless it often limits plant growth because it is generally present in organic and inorganic insoluble forms that require bacterial and fungal solubilizing activity to become available for plant nutrition (Altomare et al., 1999; Raddadi et al., 2007). The inoculation of chickpea plants with phosphate-solubilizing fungi belonging to *Aspergillus awamori* and *Penicillium citrinum* species showed positive effect on plant development and yield (Mittal et al., 2008). Phosphate solubilization ability is a widespread plant growth promotion trait detected in bacterial isolates from different plants such as maize and sunflower grown in arid land in India (Sandhya et al., 2010). Several bacteria were isolated by Puente et al. (2004b) from the rhizoplane of the giant cactus *Pachycereus pringlei* and the ability to solubilize powdered igneous rocks *in vitro* was investigated. Four rhizobacteria, belonging to the genera *Bacillus* and *Citrobacter*, showed the ability to weather igneous rocks supplying inorganic nutrients for cacti. This ability could be exploited to promote plant growth in environments characterized by harsh conditions similar to those of Baja California Sur, in Mexico (Bashan et al., 2002; Lopez et al., 2009). Recently, the presence of nitrogen fixing endophytic bacteria able to solubilize phosphates and weather several nutrients from rocks has been reported in roots of cacti growing without connection to soil in the same area of Mexico (Puente et al., 2009b). The bacteria were also detected in cactus seeds where they positively influenced the seedling in dry hot soils. It seems thus that bacteria capable of mineral weathering play a fundamental role during the whole cacti life cycle, sustaining nutrition requirements of these primary colonizer plants (Puente et al., 2004a; Puente et al., 2009b) and improving soil structure that can also benefit other plant species.

In arid ecosystems many desert plants are known to be mycorrhizal (Carrillo-Garcia et al., 1999). Mycorrhizae stimulate plant growth providing their hosts an increased uptake of water and essential elements, and improve soil fertility through the penetration action of their hyphae. Moreover mycorrhizal fungi are known to live associated to bacterial communities, exerting a selective pressure on their associated microbiome with the described bioweathering potential (Calvaruso et al., 2010). The importance of bioweathering in plant nutrition is not limited to arid lands and has a great significance also in forest ecosystems, quite often located in acidic and nutrient poor soils. To assess the relative contribution to mineral dissolution of plant roots and of bacteria associated to the mycorrhizosphere of the fungus *Scleroderma citrinum*, Calvaruso and co-workers (2006) set up an experiment using a growth chamber, associating pine seedling with different *Burkholderia glathei* strains. They determined a strong increase of biotite weathering in presence of pine roots in comparison to the abiotic control. Biotite is a widespread mineral in soils and its mobilization rate changed using different strains, even if they showed the same degree of activity during *in vitro* tests, highlighting the importance of multitrophic interactions between the key actors of plant nutrition: plant roots, mycorrhizae and bacteria (Calvaruso et al., 2006). In addition, weathering mechanisms in natural ecosystems are affected by the reactivity of the mineral surface area, that in turn depends on microstructural parameters such as mineral grain sizes (Pollok et al., 2008). In a similar study Uroz et al. (2007) measured the release of iron from biotite and showed that the most efficient bacteria in terms of weathering activity belonged to the genera *Collimonas* and *Burkholderia* and were more abundant in the oak and beech-associated mycorrhizospheres than in the bulk soil (Calvaruso et al., 2010; Uroz et al., 2007). *Collimonas* spp. are widespread in oligotrophic habitats and have been recently shown to mobilize iron from biotite both through acidification and the production of hydroxamate- and catechol-type siderophores. The mineral weathering potential has hence been proposed as a functional feature of this genus (Uroz et al., 2009), nonetheless the ability of different bacterial genera to affect biotite dissolution has been determined experimentally (Hopf et al., 2009). Siderophores are specifically produced in response of iron deficiency but can complex a number of trivalent and divalent cations, fundamental for the dissolution of several soil minerals such as goetite, hematite and hornblende (Konhauser, 2007). Iron bioavailability limits the primary productivity in different ecosystems and it has been shown that natural iron fertilization positively influences the carbon uptake of phototrophic microorganisms, sustaining the flourishing of phytoplancton in the iron depleted waters of the Southern Ocean (Blain et al., 2007). Although soil represents a totally different ecosystem, the role of bacteria in iron acquisition by plants is well known (Borin et al., 2009; Raddadi et al., 2007). Iron assimilated by plants is often delivered to the root as a chelating complex formed by ferrous iron and siderophores produced by bacteria. Dimkpa and coauthors studied in detail the role of siderophores in plant growth promotion of different plant species growing in soils characterized by high concentration of toxic metals. Their results showed that siderophores containing crude culture filtrates supported cowpea growth in contaminated soil by a simultaneous enhancement of iron solubilization and attenuation of nickel uptake (Dimkpa et al, 2008a). Siderophores also play a crucial role in the regulation of auxin level in plant growing in metal polluted soils: here, microbially produced siderophores were demonstrated to bind the toxic metals, decreasing free metals concentration and thus attenuating their inhibition of auxin synthethis (Dimkpa et al, 2008 a; Dimkpa et al, 2008 b). Efficient mineral weathering microorganisms, such as those able to solubilize phosphorous and iron from their immobilized mineral reservoir, have been utilized as inoculants during the restoration of arid lands (Bashan et al., 2009; Puente et al., 2004a; Puente et al., 2009b) and mine tailings (de-Bashan et al., 2010) on different type of cacti and desert shrub. In both cases weathering bacteria demonstrated to promote plant growth and showed rhizosphere fitness, an essential trait for the positive result of the inoculation treatment (de-Bashan et al., 2010).

Despite the great potential of transgenic plants, in many countries the public opinion is asking the research community to develop sustainable practices in agriculture, setting up problem solving strategies without the spread of genetically modified organisms (GMO) in the environment. In this frame, the exploitation of mineral weathering microorganisms able to promote seedling establishment and plant growth is a promising tool that in the future may lower the environmental pollution reducing the intensive use of chemical pesticides in fields and water waste in agriculture, thus contributing to maintain biodiversity and natural resources essential to food production (www.fao.org).

3.3 Impacts of weathering on cultural heritage conservation

Weathering includes key processes for stone artworks conservation. Deterioration of cultural heritage, especially outdoor, is the result of the combined actions of different abiotic and biotic factors, such as the exposure to weather conditions and polluted environments as well as the degrading activity of microorganisms. Microbial deterioration, defined as any undesirable change in the properties of a material caused by the activities of microorganisms, plays a significant role in the decay of a wide range of cultural heritage items: historic monuments, sculptures, photographs, frescoes, paintings, paper and contemporary artworks (Cappitelli et al., 2006; Cappitelli et al., 2007; Cappitelli et al., 2009; Cappitelli et al., 2010; Ioanid et al., 2010; Milanesi et al., 2009; Polo et al., 2010). Stone is a widely employed material for monuments and sculptures. Stone decay, which comprises both *in situ* degradation and the removal of weathering products, begins from the moment in which the stone is incorporated into works of art, in the same way as, in nature, rocks are weathered during soil formation process. Bacteria, fungi, algae and lichens contribute to stonework damage through weathering processes, physical disruption through penetration into the material, and aesthetic damage (Fernandes, 2006). Stone dissolution can be due to the nitric and nitrous acids produced by *Nitromonas* and *Nitrobacter* spp. as well as to the sulfuric acid secreted by

Acidithiobacillus spp. Besides chemolithoautotrophs, other microorganisms are able to remove cations like iron and manganese from the stone (Fernandes, 2006). Cyanobacteria can release chelating organic molecules, favor calcite dissolution of calcareous stone, live and actively create cavities inside the stone, and stain the substratum through the production of pigments (Crispim and Gaylarde, 2005). Nowadays prevention is preferred to intervention actions and research has been devoted to predict the microbial risk to stone cultural heritage. In this respect a new index of Lichen Potential Biodeteriogenic Activity has been proposed to evaluate lichen overall impact on stone cultural heritage (Gazzano et al., 2009). One of the most important drivers of biodeterioration is the capacity of bacteria to grow as biofilm. The different biofilm pigmentation observed on the surface of monuments around the world is partially due to the diverse climates and the time of exposure to such climatic conditions. Indeed, even though at variable extents, these factors affect the composition of the dominant microbial population (Gorbushina et al., 2009). Strategies to prevent alteration may avoid microbial adhesion to the surface and repress intercellular communication involved in biofilm formation (Cappitelli et al., 2006). In addition, it is important to avoid certain synthetic materials applied on stone sculptures and monuments as preserving substances from physico-chemical damage, since they might support microbial growth and consequently promote further deterioration of the material (Cappitelli et al., 2007).

Although microorganisms are generally associated with detrimental effects on stone, it has been recently seen that their weathering activity can be used for the removal of harmful compounds on cultural heritage objects (Fig. 1d). An effective biocleaning treatment exploits the ability of sulfate-reducing bacteria to reduce sulfate to gaseous hydrogen sulfide removing black crusts. These pigmented crusts are a deteriorated surface layer of stone material spontaneously formed from the interaction between a calcareous substratum and the polluted atmosphere in a humid environment, resulting in the chemical transformation of the substrate (calcite) into gypsum. The activity of bacteria such as *Desulfovibrio vulgaris* was recently tested on the Demetra and Cronos sculptures of the Buonconsiglio castle in Trento resulting in the homogeneous dissolution and removal of black crusts (Polo et al., 2010). With the same mechanism, denitrifying bacteria could be applied for the removal of nitrate alterations (Alfano et al., 2011). The patent based on the use of microorganisms for the biocleaning of cultural heritage has been acquired and commercially exploited by the Italian spin-off company Micro4yoU. Microorganisms actively assist the formation of a variety of minerals, including calcium carbonate (Verrechia et al., 2003). Many researchers have proposed carbonate mineralization by calcifying bacteria as a method to protect monuments and sculptures made of carbonate stone. The first was the team of Gauri and Atlas who, using *Desulfovibrio desulfuricans* to remove black crusts from stone, also evidenced the effects of biocalcification (Atlas et al., 1988; Gauri and Chowdhury, 1988). The same process, based on the use of *Bacillus cereus*, led to the creation of the French enterprise Calcite (Le Metayer-Levrel et al., 1999).

Thanks to its powerful and non-invasive nature, biorestoration of weathered historic stoneworks is of great interest in the ambit of cultural heritage conservation and a tight collaboration between microbiologists and conservators is desirable. Along with this, efforts are being made to develop and implement methodologies aimed at preventing bioweathering phenomena caused by biodeteriogen agents.

3.4 Application of bioweathering in bioremedation procedures

The ability of microorganisms to grow using various molecules naturally occurring as pollutants is the driving force of bioremediation. In different natural habitats, such as serpentine soils, microbes are in contact with remarkable high concentration of metals, and they evolved resistance strategies that permit them to flourish under harsh conditions (Haferburg and Kothe, 2007 and references therein). In the phytoremediation of metal contaminated soils, it is possible to take advantage of the positive interactions of plants and their associated rhizospheric microorganisms (Fig. 1e), the so-called "rhizoremediation" (Gerhardt et al., 2009). Mycorrhizae, in particular those isolated from metalliferous sites, boost phytoextraction directly or indirectly by increasing plant development

(Azcón et al., 2010), reducing metal induced toxicity (Meier et al., 2011) and enhancing plant bioaccumulation of metals (Ma et al., 2009). The efficiency of pollutant uptake in plants is affected by bioavailability, a parameter that can be greatly enhanced by the metabolic activity of bacteria and fungi inhabiting the rhizosphere. Root associated microbiome adopts several mechanisms to trigger metal mobilization and immobilization, respectively, in phytoextraction and phytostabilization technologies (Ma et al., 2011 and references therein). The importance of microbes in phytoremediation and restoration strategies has been widely investigated. The inoculation of Glomeromycota fungi isolated from metal polluted soils mitigated oxidative stress commonly occurring in plants during metal reclamation treatments (Meier et al., 2011). During greenhouse experiments, the inoculation of *Trifolium repens* growing in a metal polluted soil with pure or mixed microbial cultures of *Bacillus cereus*, *Candida parapsilosis* and mycorrhizal fungi resulted in the increase of plant biomass and established symbiotic association (Azcón et al., 2010). The tested bacterium and yeast, previously isolated in the same soil utilized in the above-mentioned study, showed the best weathering activity for different heavy metals (Azcón et al., 2010). Bacterially produced siderophores have been recently proposed as valuable substitute of not easily degradable chelating molecules commonly used to improve phytoremediation of soil polluted by toxic metals. Due to the dual role of siderophores, the increase of plant growth and biomass and the enhanced solubilization of metals, siderophores treated sunflower plants showed the best cadmium extraction levels compared to EDTA-treated plant (Dimkpa et al., 2009). Furthermore, a nitrogen fixing rhizobacterium capable of rock weathering and isolated from cactus, promoted plant growth of desert shrub in acidic soil with high metal concentration (de-Bashan et al., 2010).

Continuous industrial progresses have been often accomplished in the past without a careful risk assessment for ecosystem and human health, and for this reason the relevance of microorganisms mediated mineral weathering is not limited to soil matrices. Asbestos fibers were intensively used during last century to renforce cement and applied as a roofing material because of their chemical and physical resistance (Favero-Longo et al., 2009). *In vitro* bioweathering experiments showed that *Verticillium leptobactrum* isolated from the asbestos-rich soils of two abandoned chrysotile mines in the Italian Western Alps efficiently removed iron from asbestos fibres (Daghino et al., 2009). Iron is involved in the chrysotile toxicity and the ability to weather it determined a reduced reactivity of asbestos fibres, making *V. Leptobactrum* a suitable candidate for asbestos bioremediation (Daghino et al., 2009). The lichen effects on the durability of asbestos-cement materials are currently under debate. Some studies indicated that lichens increase the dangerousness of this material promoting the exposure of the fibres and the air dispersal of asbestos. However, the combined application of chemical and image analyses recently demonstrated that lichen biocovering of roofs can result in the limitation of the detachment of asbestos fibres, which composition was chemically altered by the physical interaction with lichens (Favero-Longo et al., 2009).

Though additional investigations are required, overall data indicate that mineral weathering microorganisms are a valuable tool to maximize the efficacy of bioremediation methods. In particular the application of rhizospheric microbes able to dissolve essential nutrients for plant development and to influence metal speciation and mobilization represents a promising biotechnological approach for in field phytoremediation.

4. Conclusions and future perspectives

The discovery of the interactions of microorganisms with minerals sustained the importance of microbes in making the Earth a suitable environment for all forms of life. The value of bioweathering mediated by microorganisms is known since tens of years and is widely exploited in industrial processes aimed at the recovery of metals from ores. The study of mineral-microbe interactions is nevertheless a crucial step for the development of promising strategies in other biotechnological sectors, especially concerning environmental biotechnology:

(i) deeper insights on bioweathering involvement during soil formation could permit to set up microbial consortia to promote these mechanisms, especially in arid regions which extension on Earth is constantly rising; (ii) increased knowledge of beneficial association established by weathering rhizospheric microbes and plants will contribute to develop specific microbial inoculants to promote plant growth, boost crop yield and food production respecting global biodiversity and ecosystem safety and reducing the constant need to expand agriculture dedicated lands; (iii) the elucidation of the mechanisms adopted by microorganisms during metal speciation, mobilization and uptake will lead to the implementation of bioremediation technologies; (iv) on one hand, innovative biorestoration treatments will apply microbial resources to reduce chemical weathering of stone and, on the other hand, further research will be devoted to counteract bioweathering microflora and prevent microbial deterioration of stone objects and buildings of historical value.

The literature data reported in the present review clearly indicate that some applications of the bioweathering potential of microorganisms have been exploited since a long time but others are emerging in different areas like for instance that of stone artworks and monument protection and restoration. To obtain the best performance from the existing and the novel microbial weathering-based technologies it is essential to consider the whole bioweathering network involved in applied processes, that includes both bacteria and fungi, and to develop strategies for a sustainable management of the involved microbial resource.

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Figure caption

Figure 1. Microorganisms with weathering activities (represented by rod-shaped cells in the different figure panels) can be exploited in industrial and environmental biotechnology. (a) The ability of different prokaryotic acidophiles to dissolve minerals from ores is well known in the biomining industry and it is exploited in the recovery of several elements such as copper and gold; (b) weathering of rock minerals, utilized by microorganisms as energy, electron acceptors and nutrients, is one of the driving forces of soil formation in different arid ecosystems; (c) mineral weathering microbes sustain plant nutrition mobilizing essential nutrients, such as phosphate and iron, from insoluble forms in soils, thus increasing bioavailability; (d) the idea behind biocleaning treatment is the ability of microorganisms to dissolve elements present in stone alterations. With this purpose specific microbial consortia can be successfully applied on monuments and statues to remove detrimental compounds; (e) plant- microbes interaction play a crucial role in phytoremediation. Weathering bacteria and fungi can promote plant growth, reduce stress levels in presence of different kind of pollutants, and influence pollutants mobilization for example favouring the plant uptake of pollutants during clean-up procedures.

Figure(s)
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