REVIEWS

The periodic table of photosynthetic purple non-sulfur bacteria: intact cell-metal ions interactions

Matteo Grattieri[1,2] · Rossella Labarile[1,2] · Gabriella Buscemi[1,2] · Massimo Trotta[2]

Abstract

Photosynthetic purple non-sulfur bacteria (PNB) have been widely utilized as model organisms to study bacterial photosynthesis. More recently, the remarkable resistance of these microorganisms to several metals ions called particular interest. As a result, several research efforts were directed toward clarifying the interactions of metal ions with PNB. The mechanisms of metal ions active uptake and bioabsorption have been studied in detail, unveiling that PNB enable harvesting and removing various toxic ions, thus fostering applications in environmental remediation. Herein, we present the most important achievements in the understanding of intact cell-metal ions interactions and the approaches utilized to study such processes. Following, the application of PNB-metal ions interactions toward metal removal from contaminated environments is presented. Finally, the possible coupling of PNB with abiotic electrodes to obtain biohybrid electrochemical systems is proposed as a sustainable pathway to tune and enhance metal removal and monitoring.

Graphic abstract
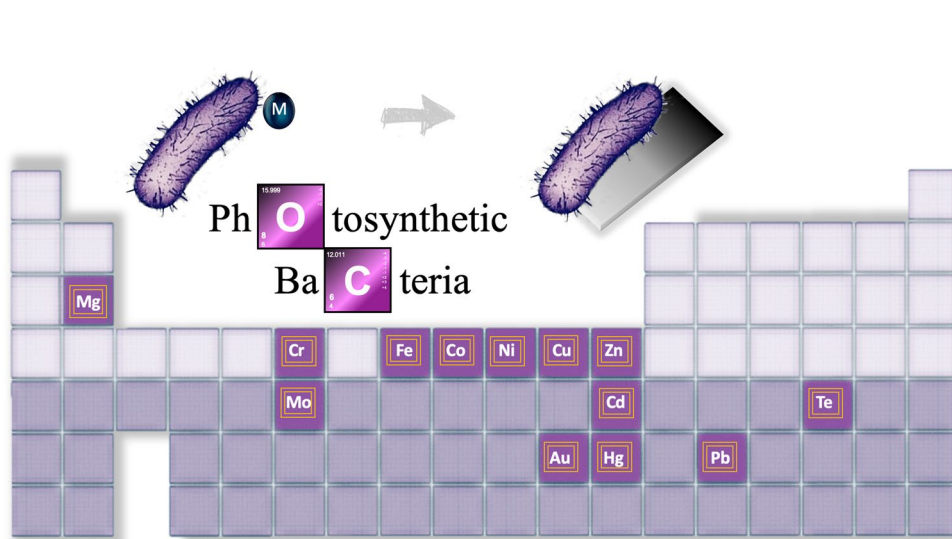
✉ Matteo Grattieri
matteo.grattieri@uniba.it

✉ Massimo Trotta
massimo.trotta@cnr.it

Extended author information available on the last page of the article

1 Introduction

Purple non-sulfur bacteria (PNB) are fascinating anoxygenic photosynthetic microorganisms capable of performing a great variety of light-dependent and light-independent reactions. Their photosynthetic metabolism exploits the enzyme reaction center, where the photochemistry takes place transducing solar energy and driving the metabolism of the organism. PNB, the dominant photoheterotrophs class of bacteria, are very versatile being capable of various metabolism spanning from photoautotrophic and photoheterotrophic to chemotrophic [1–3].

This unique characteristic led to their application as model organisms for the study of the effects of environmental parameters, substrates, and contaminants on the metabolism of photosynthetic bacteria [4]. As discussed in detail below, particular focus has been posed on unveiling the influence and the interaction of various heavy metal ions with PNB, leading to building up their own "periodic table". Traces of metal-ions play essential roles in many proteins and their availability is critical for the functioning of the photosynthetic and respiratory electron transport chain in bacteria [5]. However, high concentrations of metal ions can be harmful to microorganisms, and dedicated regulatory systems have been evolved to avoid/limit their toxic effects. Here we will first introduce and discuss the studies that provided a critical understanding of PNB-metal ions interactions. Toxicity, effects on cell metabolism, mechanisms of metal uptake, and the various approaches utilized to study these aspects are reviewed. Following, the possibility to implement PNB in a contaminated environment with toxic metal ions is investigated. Various approaches for metal removal, monitoring, and metal-nanoparticles synthesis are presented. Finally, the enthralling possibility of establishing an electrochemical communication between intact PNB cells and abiotic electrodes, thus "electrically wiring" a biotic and an abiotic component, is explored. While this latter aspect has been investigated only relatively recently, the detailed understanding of bacteria-metal interactions at the metabolic level poses the bases for the development of biohybrid electrochemical systems for enhanced environmental remediation and monitoring. In conclusion, the future possibilities and major challenges for technologies based on the periodic table of PNB are discussed.

2 PNB-metal ions interaction

In 1992, the resistance or tolerance of PNB to heavy metals was first noticed in a pioneering study performed by Moore and Kaplan focusing on tellurite (TeO_3^{2-}) [6].

Commonly, tellurite is considered an inhibitor for gram-negative bacteria due to its high oxidizing ability, with tellurium compounds long been used as antimicrobial and therapeutic agents [7]. Conversely, *Rhodobacter sphaeroides* (*R. sphaeroides*) cells could be exposed to concentrations up to 1 mg ml^{-1} (4 mM) of tellurite, intracellularly reducing it to Te^0, and leading to the deposition of the metal in the cytoplasmic membrane with two enzymatic steps involved. Such findings shed light on the possible application of PNB for environmental remediation purposes.

Following this pioneering study, reports of PNB-metals interaction remained initially limited. In 1999, it was shown that the mechanism of Ni^{2+} transport and accumulation in *Rhodospirillum rubrum* (*R. rubrum*) is related to the metabolism of CO oxidation [8]. Few years later, the mechanism of selenite reduction in *R. sphaeroides* was reported by Bebien et al. [9]. It was only in 2006 that the presence of a broad variety of metals (Hg^{2+}, Cu^{2+}, Fe^{2+}, Ni^{2+}, Co^{2+}, MoO$_4^{2-}$, and CrO$_4^{2-}$) was utilized to study the possible photosynthetic growth of the PNB *R. sphaeroides* mutant R26 in highly contaminated media [10]. The effects of various concentrations of the heavy metals on photoheterotropic growth rate, maximum cell densities, and lag-time were determined. As reported in Fig. 1, selected metals lead to considerably different effects, with Hg increasing lag-times, but resulting in no substantial changes in maximum cell densities for concentrations as high as 0.03 mM. Conversely, a particularly high resistance was observed for molybdate (no influence for concentrations as high as 60 mM). Co and Ni showed effects also on the photosynthetic apparatus, decreasing the number of pigment molecules obtained. An important aspect is that the ability to cope with the presence of the different heavy metals was not the result of an adaptation process, as bacteria were exposed to the metals without selection procedures.

The same group further investigated the interrelationship in the metabolism of Mg and Co, revealing that high concentration of Mg reduced co-toxicity due to competitive uptake mechanisms [11]. By combining inductively coupled plasma atomic emission spectroscopy and attenuated total reflection Fourier transform infrared spectroscopy (ATR-FTIR), Italiano et al. further clarified the different mechanisms of Co, Ni, and Mg bioadsorption and bioaccumulation [12]. The study unveiled the role of carboxylate groups on the outer membrane of *R. sphaeroides* in binding metal cations, where Co^{2+} is competing with Mg^{2+} for the same binding groups. Furthermore, the coordination of cobalt ions binding to cellular components of *R. sphaeroides* was elucidated by X-ray absorption spectroscopy, differentiating between binding with soluble portions of the cells or the photosynthetic membranes [13]. Specifically, an extensive binding of cobalt ions to sulfolipids on the photosynthetic membrane was determined. Such findings were further supported by a later
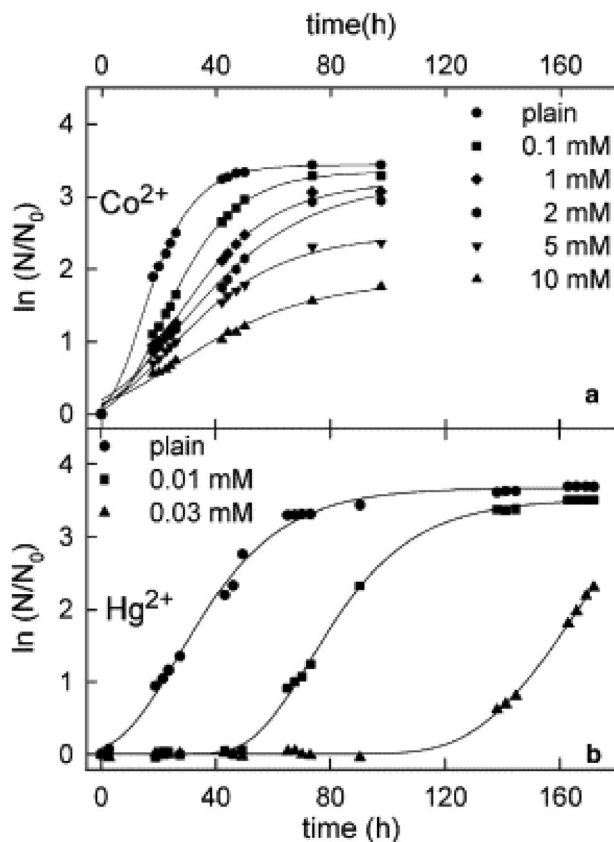
Fig. 1 Growth curves of the carotenoidless strain *R. sphaeroides* R26 obtained utilizing culture media supplemented with different concentrations of Co^{2+} (**a**) and Hg^{2+} (**b**). Reproduced with permission from Giotta et al. [10]. Copyrights 2005 Elsevier Ltd

study where thin-layer chromatography was coupled with matrix-assisted laser desorption ionization mass spectrometry (MALDI-MS), unveiling lipid alterations taking place after Co^{2+} and CrO_4^{2-} exposure in *R. sphaeroides* [14]. Co^{2+} exposure resulted in a significant increase of sulfoquinovosyldiacylglycerols in the membrane lipids, while a decrease in the levels of phosphatidylglycerols was obtained. Interestingly, different analytical approaches were developed to utilize MALDI-MS for the determination of biotransformations in bacteriochlorophylls resulting from metal exposure [15].

Following studies were aimed to further characterize the interaction of cobalt ions with PNB at the gene expression level, unveiling internal reference gene for transcript analysis in presence of heavy metals stress [16], as well as changes in the relative amounts of proteins belonging to the photosynthetic apparatus [17]. Genomic and transcriptomic approaches showed that adaptation to Co presence proceeds through the activation of supplementary energetic metabolism processes [18].

Focusing on chromium contamination, the hexavalent form (Cr VI) is highly toxic and carcinogenic while also

being very soluble in water. These characteristics, together with its extensive use in industries and human activities [19], make it one of the most critical contaminants for water environments. Italiano et al. unveiled the effects of chromate oxyanion on growth and protein expression, as well as cell dimension and morphology [20]. An important insight is that cell cultures were able to completely reduce 0.2 mM chromate to the less toxic Cr III within 80–90 h from light exposure. The largest contribution to chromate reduction was assigned to the soluble intracellular fraction, suggesting that the oxyanions are transported into the cytoplasm for being detoxified. A significant cell elongation was also obtained for the bacteria exposed to chromate as shown in Fig. 2.

The detailed effects of mercury on the photosynthetic apparatus of PNB were investigated by Asztalos et al. showing that Hg^{2+} significantly affected the electron transport sites of the reaction center in *R. sphaeroides* (Q_A and Q_B sites) [21]. Conversely, the light-harvesting system and the bc_1 complex are less affected by the presence of Hg^{2+}. In recent years, Kis et al. studied the stoichiometry and kinetics of Hg uptake by various PNB (*Rubrivivax gelatinous (R. gelatinous)*, *R. rubrum*, and *R. sphaeroides* 2.4.1) [22]. Interestingly, two well-separated kinetic steps were determined for Hg uptake, with a fast initial adsorption to the cell surface and a passive, non-specific diffusion through the cell membrane, followed by a slower and energy-consuming transport mechanism. Ca^{2+} channel could be determined as actively involved in the transport, which was magnified under illumination. pH variations also influenced Hg uptake, as shown in Fig. 3, with decreasing rates for both acidic or alkaline pH values. It should also be noted that the organization of cells from planktonic to biofilm reduced mercury toxicity for the cells.

Finally, Grégoire and Poulain showed that *R. capsulatus*, *R. sphaeroides*, and *Rhodopseudomonas palustris* (*R. palustris*) were capable of utilizing Hg^{2+} as an electron sink to maintain their redox homeostasis, resulting in the production of the less toxic Hg^0 [23]. Specifically, under photoheterotrophic growth conditions (using butyrate or acetate as carbon sources), all the strains where capable of utilizing Hg^{2+} present in the growth medium in sub-lethal concentrations up to 200 nM, indicating that Hg^{2+} reduction plays a physiological role when excess reducing power is available.

As mentioned in the introduction, metal ions are critical non only for PNB, and various studies were performed also to unveil the mechanisms of metal ions transport and regulation in oxygenic photosynthetic microorganisms such as cyanobacteria, for which we refer the reader to other literature [24–27]. Particularly, high concentrations of mercury were shown to have detrimental effects also on the photosynthetic apparatus of cyanobacteria, specifically on photosystem II (PSII) [24]. A cascade inhibition mechanism
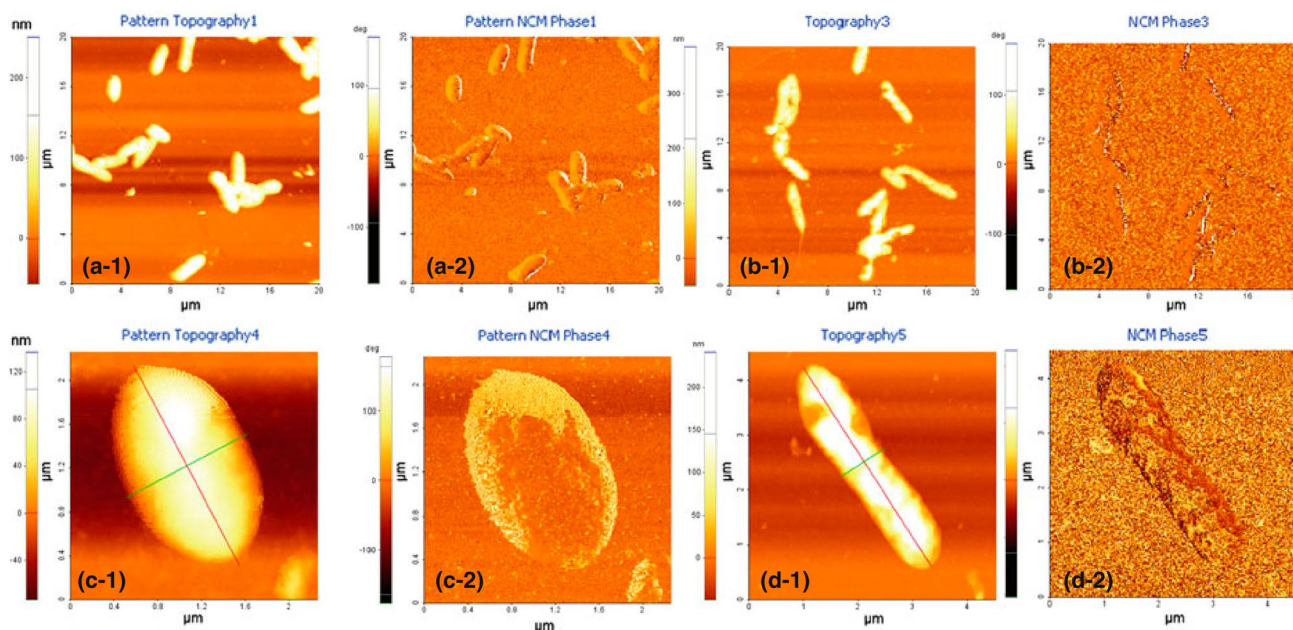
Fig. 2 Atomic force topographic image of *R. sphaeroides* cells (10^8 CFU ml^{-1}) grown in control conditions (**a-1**) and corresponding phase image (**a-2**). Atomic force topographic image of *R. sphaeroides* cells (10^8 CFU ml^{-1}) grown in a medium with 0.2 mM chromate (**b-1**) and corresponding phase image (**b-2**). Atomic force topographic image of a single *R. sphaeroides* cell grown in control conditions (**c-1**) and corresponding phase image (**c-2**). Atomic force topographic image of a single *R. sphaeroides* cell grown in 0.2 mM chromate poisoned medium (**d-1**) and corresponding phase image (**d-2**). Adapted with permission from Italiano et al. [20]. Copyright 2012, Springer Science Business Media, LLC
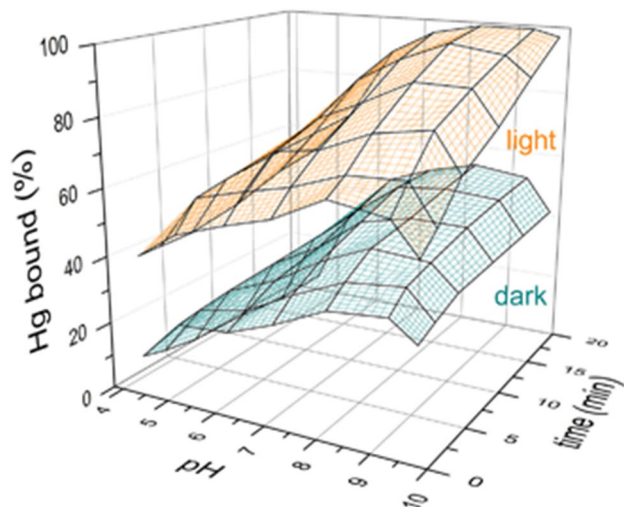

Fig. 3 Quasi-3D representation of the mercury uptake of *R. gelatinosus* cells in the dark (green surface) and under illumination (orange surface) as the functions of mercury treatment duration and pH of the culture. Reproduced with permission from Kis et al. [22]. Copyright 2017, Springer Science + Business Media Dordrecht

was determined for Cd^{2+} on the photosynthetic apparatus of the cyanobacterium, *Synechocystis* PCC 6803, initially inhibiting the dark phase of photosynthesis to following,

in the presence of light, lead to an elevated excitation pressure on PSII impairing its function [26].

3 PNB in environmental monitoring and remediation

3.1 Metal removal

After the capability of PNB to cope with high concentrations of heavy metals was unveiled, the possibility to utilize these organisms to harvest, detoxify, and remove toxic compounds by bioadsorption and bioaccumulation raised interest. Buccoleri et al. reported the relatively high sequestration of Co^{2+} and CrO_4^{2-} in biomass obtained during the photosynthetic growth of *R. sphaeroides* strain R26.1 [28]. A few years later, Vílchez et al., utilized a biofilm-based "biofilter" capable of removing over 99% of Pb(II) even after several months of operation. Interestingly, analysis of the DNA extracted from the biofilm revealed that the majority of the species belonged to the genus *Rhodobacter* [29]. Recently, the excellent capability of *R. sphaeroides* to remove Pb was reported by Su et al., who compared the removal efficiency of Pb, Hg, and Cd from aqueous solutions [30]. *R. sphaeroides* SC01 achieved 98% removal of Pb in solutions containing 160 mg L^{-1} of Pb^{2+}, showing a remarkably higher resistance
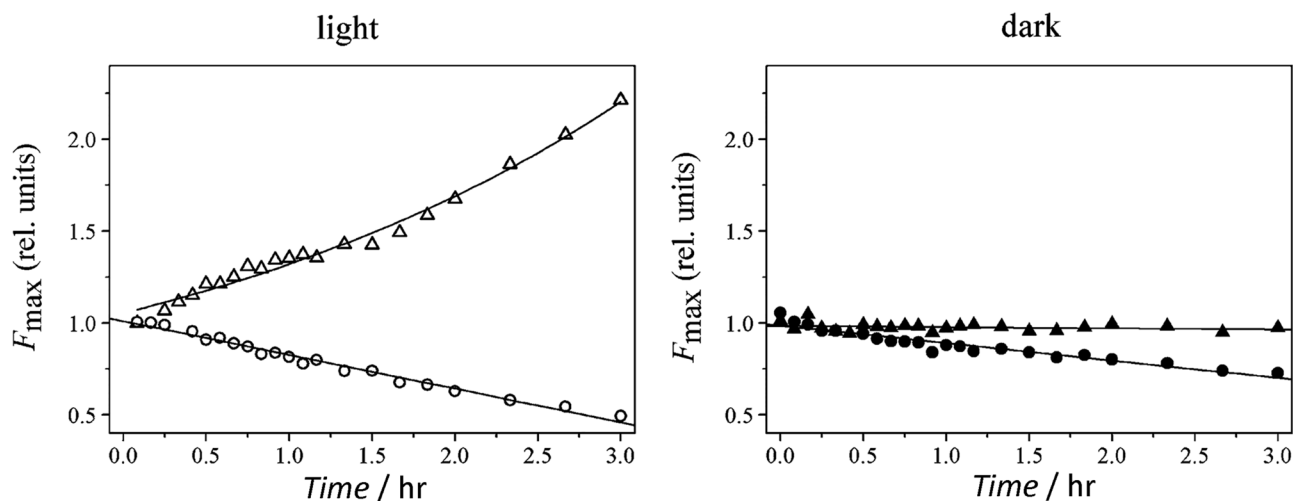
Fig. 4 Variation of Fmax in control cells (not exposed to Hg^{2+}) and after initial exposure to 26 μM Hg^{2+} both in light and dark conditions. Adapted from Asztalos et al. [34] with permission from the European Society for Photobiology, the European Photochemistry Association, and the Royal Society of Chemistry

to Pb compared to Hg and Cd. Under Pb stress, a lower accumulation of reactive oxygen species (O_2^- and H_2O_2) was obtained, together with higher enzymatic antioxidant activity, indicating that the strain has both high resistance and high removal efficiency for Pb through regulating the antioxidant system and the formation of precipitates. Finally, the isolation of three Hg-resistant PNB (*Afifella marina* SSS2-1 and SSW15-1, and *Rhodovulum sulfidophilum* SRW1-5) was utilized to reduce mercury contamination in shrimp ponds by Mukkata et al. [31] The bacterial cells performed Hg volatilization thanks to the activity of the mercuric reductase enzyme.

It should be noted that PNB were investigated also for soil bioremediation, successfully showing that *R. sphaeroides* could be employed in soil contaminated with both Pb and Cd, achieving a reduction of their accumulation in roots and leaf between 25 and 60% [32, 33].

3.2 Metal monitoring

In addition to metal removal, the studies of PNB -metals interactions paved the way also for the development of different approaches for the early monitoring of heavy metals contamination. In this contest, Asztalos et al. showed that, after exposing *R. sphaeroides* R26.1 cells to Hg during their growth (both under photosynthetic conditions and not), fluorescence induction (sudden dark–light transition) allowed fast determination of Hg presence thanks to the decrease of both the maximum and variable fluorescence [34]. It is worth underlining that the variation in both parameters was greater for cells kept in light conditions, as shown in Fig. 4.

Accordingly, the results showed that Hg acts by inhibiting the photosynthetic apparatus of the bacteria.

In a later study, Kis et al. compared three different strains of PNB (*R. gelatinous*, *R. rubrum*, and *R. sphaeroides*) for monitoring Hg, Cr, and Pb stresses through steady-state absorption spectra and fluorescence induction [35]. The various strains showed remarkable differences in the sensitivity to the three metal stresses, with *R. gelatinous* tolerating orders of magnitude higher Hg concentrations (200 μM) while having higher drops in absorbance and maximum fluorescence resulting from exposure to Pb compared to *R. rubrum*. Furthermore, it was shown that Pb^{2+} ions in a broad range of concentrations perform high penetration in the cell wall and caused a significant destruction of the antenna complexes.

3.3 Metals & bio-nanofactories

The capability of PNB to withstand high metal concentrations was utilized also to combine the removal of such metals to the synthesis of nanoparticles, thus obtaining bio-nanofactories. Bai et al. reported that exposing *R. sphaeroides* cells to high concentrations (2.5 mM) of $ZnSO_4$ allowed performing the synthesis of the nanoparticles of the semiconductor ZnS [36]. Specifically, the biosynthesis was performed during the growth of the bacterial cells, under neutral pH and 30 °C, and allowed to almost completely remove soluble zinc in about 30 h. The duration of the incubation influenced the dimension of the nanoparticles, with diameters ranging from 4 to 105 nm for incubation times of 25 and 45 h, respectively. Li et al. [37] expanded the possibilities of utilizing PNB as bio-nanofactories showing that selenite (SeO_3^{-2}) could

Fig. 5 Transmission electron microscopy micrographs of *R. sphaeroides* cells without (**a**) and with exposure to 10 μM Au(III) (**b**) revealing a significant cell elongation after exposure to Au(III). Extracellular aggregates of gold nanoparticles shown at two different magnifications (**c** and **d**). Reproduced from Italiano et al. [38]. Copyright 2018, Elsevier
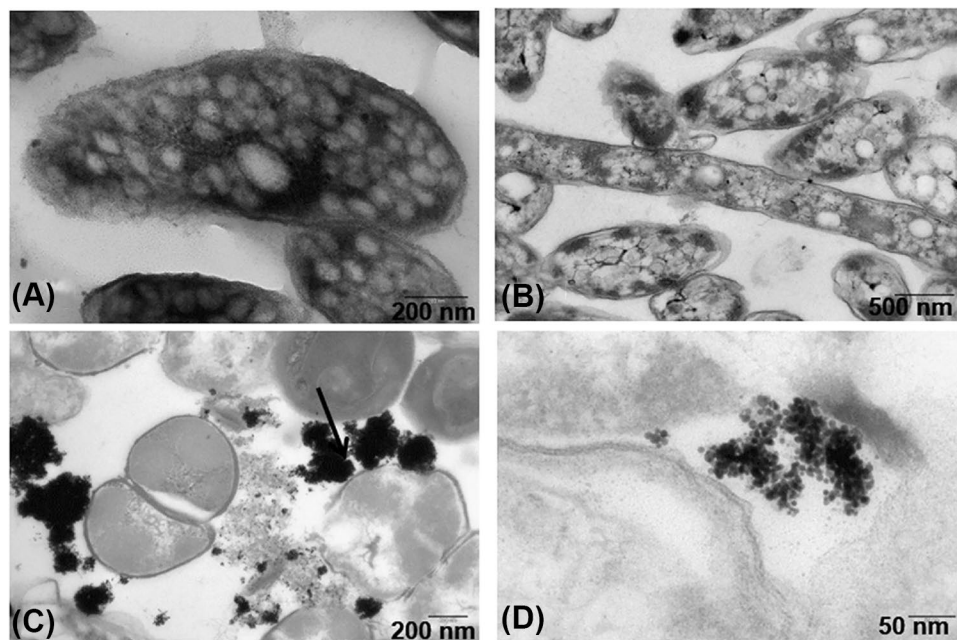
be reduced to red elemental selenium, obtaining nanoparticles with diameters between 80 and 200 nm on the surface of *R. palustris* cells. Later, Italiano et al. [38] reported the extracellular synthesis of gold nanoparticles utilizing *R. sphaeroides* strain R26. When the bacteria were exposed to Au(III) under photosynthetic growth, gold nanoparticles with an average size of 10 nm were obtained, as shown by the transmission electron microscopy micrographs of Fig. 5.

Different mechanisms of nanoparticle synthesis (i.e., intracellular or extracellular production) would strongly affect the following purification and nanoparticle harvesting procedures required. It should be noted that the detailed mechanisms of nanoparticles synthesis have yet to be elucidated for several organisms, and we refer the reader to a recent review on this topic for the most updated literature [39]. Briefly, if nanoparticles were biosynthetized in the intracellular space, cell lysis would be required to harvest them for practical applications; various approaches are available, including the use of ultrasonication, heat treatments, detergents and salts [40, 41]. If nanoparticles assemble on the cell surface, their harvesting might be attained by mild centrifugation, avoiding cell death. Furthermore, it has been recently reported that some organisms act as bio-nanofactories using extracellularly secreted enzymes, thus overruling cell lysis or centrifugation, with the nanoparticles obtained directly in the supernatant and easily recovered by centrifugation [42]. Due to the high relevance of bio-nanofactories, more studies are needed to shed light on these exciting processes.
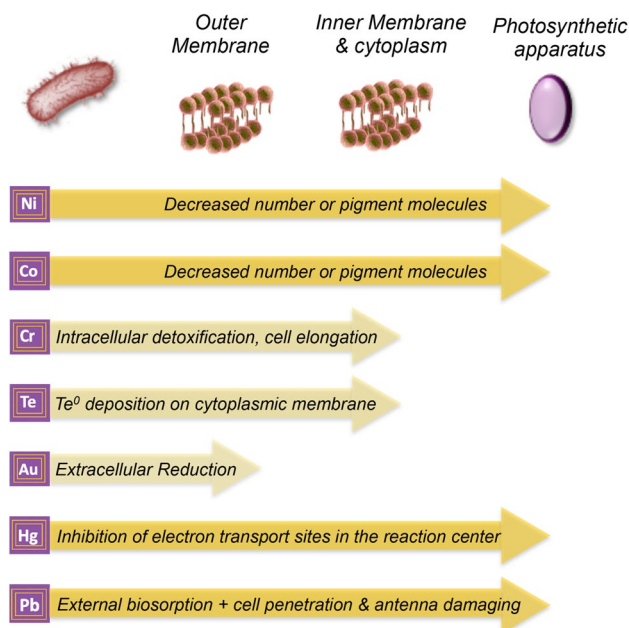
Scheme 1. Effects of the most studied metal ions (ordered by atomic weight) on PNB. The arrow's length refers to the capability of the metal ions to cross or not the outer membrane. The arrows reaching the photosynthetic apparatus indicate the capability of the metal ions to affect the components of the photosynthetic apparatus

The effects of the various metal ions on PNB discussed in the previous sections have been summarized in Scheme 1.

4 From knowledge to future directions: PNB application in biohybrid electrochemical systems

As extensively discussed, the implications of PNB-metals interactions can be critical for environmental remediation and monitoring purposes. In this context, coupling intact PNB cells and electrode surfaces represents an intriguing possibility, which enables the development of biohybrid electrochemical systems (BES). Specifically, the establishment of an electrochemical communication between the biotic and abiotic components would introduce an interface to selectively control, or facilitate, a selected metabolism to enhance the removal of pollutants. Additionally, it has been reported that when bacteria are exposed to solutions containing contaminants, the flow of electrons between the biological catalyst and the abiotic electrode surface might be affected, paving the way to the development of microbial electrochemical biosensors [43]. In such biosensors, the presence of contaminants can be determined "on-line", based on variations in the current response, thus enabling the early and continuous monitoring of toxic compounds. However, while model electroactive bacteria have been extensively studied to clarify the electrochemical processes taking place at the biotic/abiotic interface (with ongoing debates on the electron transfer mechanisms also for these model organisms) [44, 45], the possibility to establish an electrochemical communication between PNB and electrodes has been reported relatively recently [46]. In an early report, Xing et al. [47] showed that the PNB *R. palustris* DX-1 could be isolated from the anode of a microbial fuel cell operating for over 3 months. The isolated strain showed good electron transfer capabilities with the abiotic electrode surface. However, the detailed mechanisms utilized by the bacteria to accomplish extracellular electron transfer was not determined, with biofilm formation that seemed to play a major role. Later, PNB have been "wired" to electrodes surfaces utilizing both osmium-based and quinone-based artificial redox mediators to facilitate the extracellular electron transfer. A scheme of the artificial extracellular mediated electron transfer process is reported in Fig. 6, with examples of various approaches utilized in the literature [48–51]. To date, studies of PNB biohybrid electrochemical systems have been focused on biophotocurrent production, thus on the required "wiring" of the biotic components with the electrode surface, with only a few reports focusing on how the presence of environmental stresses influence the photoexcited electron transfer and biophotoelectrocatalysis [52, 53]. Specifically, it was shown that under prolonged salt stress a decreased expression of genes involved in the photosynthetic electron transfer chain of *R. capsulatus* cells

is obtained, leading to an altered interaction between the exogenous diffusible redox mediator *p*-benzoquinone and the photosynthetic apparatus. Such alteration resulted in decreased biophotocurrent generation and higher loss of biophotoelectrocatalysis over alternated light/dark cycles compared to cells not exposed to salinity [52].

It is clear that the use of such BES for environmental monitoring and remediation remains to be explored, and research efforts should be directed toward this topic. Furthermore, it should be noted that biohybrid electrochemical systems could be used also as a tool to elucidate the mechanisms of metal-bacteria interaction while being utilized in the biohybrid system. In this context, a biohybrid electrochemical system employing exogenous quinone molecules has been recently reported by Borghese et al. [54] to demonstrate how harvesting photoexcited electrons from the photosynthetic apparatus of *Rhodobacter capsulatus* enables reducing the toxic oxyanion tellurite (TeO_3^{2-}) outside the cell membranes of the bacteria.

5 Conclusions and future perspectives

The outstanding tolerance of PNB toward high metal concentrations has attracted the interest of several research groups, and the scientific community achieved a comprehensive understanding of the mechanisms of metal uptake and reduction. These findings resulted in the application of PNB for metal ions removal and monitoring in various environments. As discussed in the review, and further summarized in Table 1, PNB can withstand and remove a broad variety of metal ions from both aqueous and soil environments, while enabling their preliminary monitoring. Biofilters and fluorescence-based biosensors have been shown as a practical application of PNB -metal ions interactions. To fully explore these capabilities, a possible direction to follow is the coupling of these organisms with abiotic electrodes, to obtain biohybrid electrochemical systems. The concept of BES has been shown, and the most recent advancements in PNB photobioelectrochemistry have been presented, with the architectures utilized to actively "wire" intact bacterial cells to the electrode. Rationally controlling the interface between these photosynthetic organisms and the electrode could lead to selectively removing and monitoring metal ions. However, the coupling of intact cells with abiotic electrodes remains challenging due to the location of their photosynthetic apparatus deeply buried in the inner membrane. The recent advancements in the field of artificial electron mediation approaches employed with other photosynthetic organisms and apparatuses (i.e., rational design of conductive/redox polymer and engineering of the biotic/abiotic interface) [55–57], together with synthetic biology solutions to
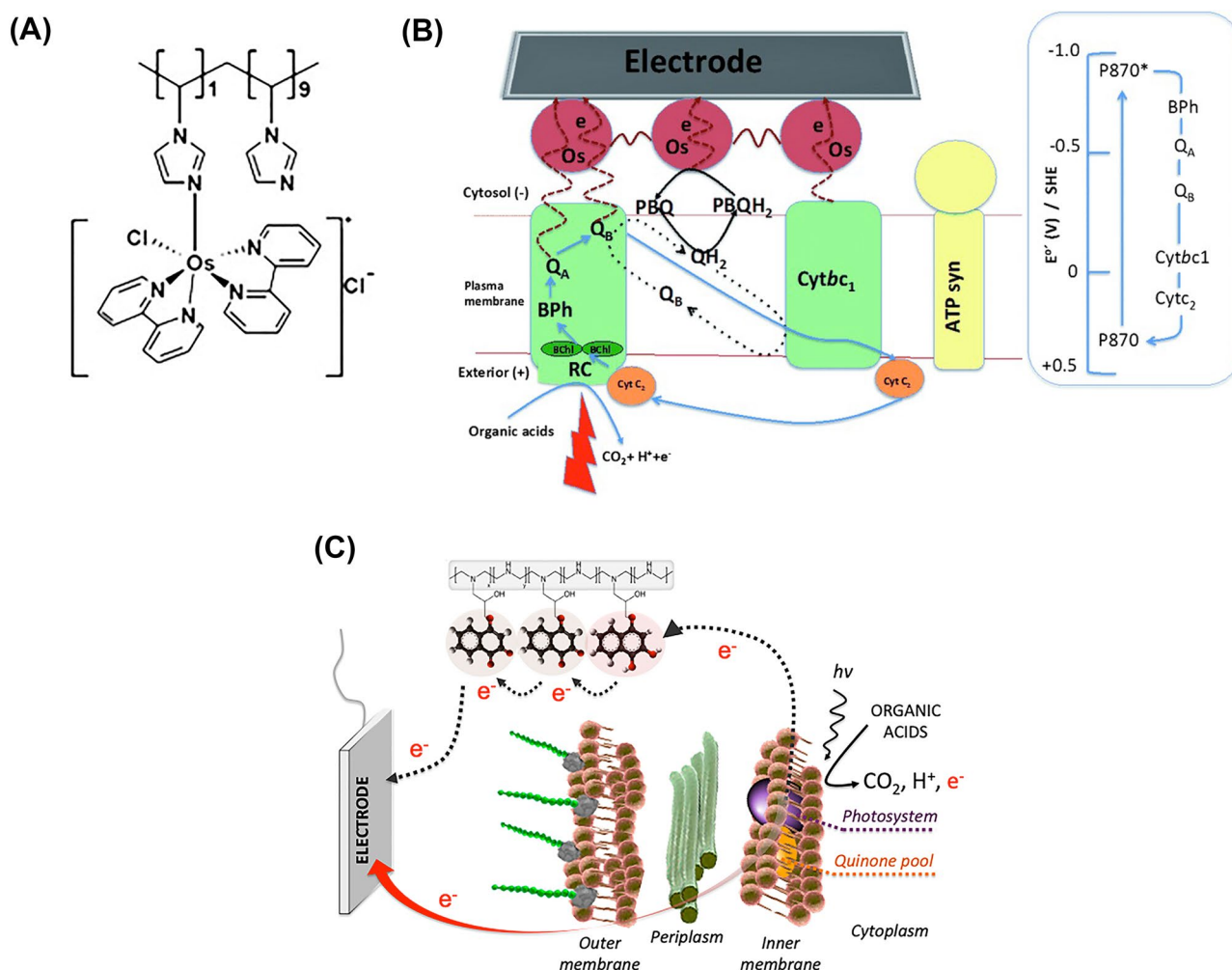
Fig. 6 a Structural representation of the Os-redox polymer utilized by Hasan et al. [48]. Reproduced with permission from Hasan et al. [48]. Copyright 2012, Elsevier B.V. **b** Scheme of the biophotoelectrochemical process taking place in the Os-mediated biohybrid photoanode. The artificial redox mediating system (Os-polymer) might wire the photosynthetic apparatus of *R. capsulatus* through the Q_A or Q_B active sites, the quinone pool (PBQ-$PBQH_2$), or Cyt*bc*$_1$. Reproduced with permission from Hasan et al. [49]. Copyright 2015, Wiley–VCH Verlag GmbH & Co. KGaA, Weinheim. **c** Scheme of the biophoto-electrochemical process taking place in the quinone-mediated biohybrid photoanode. Black dashed arrows indicate the electron transfer process taking place through the quinone redox centers of the polymer, the red arrow represents the direct extracellular electron transfer requiring to cross both the inner and the outer membranes, in addition to the periplasm layer. Reproduced with permission from Grattieri et al. [51]. Copyright 2020, Wiley–VCH Verlag GmbH & Co. KGaA, Weinheim

facilitate the transfer of photoexcited electrons [58], could lead to groundbreaking achievements for PNB biohybrid electrochemical systems. The reader interested in a thorough review on how to upgrade photobioelectrochemical systems is referred to a recent work [59]. Computational approaches are another powerful tool that should be utilized to reach a mechanistic understanding of biohybrid electrochemical systems and rationally designing them for metal ions removal and monitoring [60].

In conclusion, the scientific community is called to address critical research challenges to fully exploit the possibilities enabled by the interaction of photosynthetic PNB and metal ions, but enthralling applications are at the horizon for this technology.

Table 1 Summary of the works dealing with the interactions of metals and PNB discussed in this review

Metals	Organisms	Objective of the study/Main finding	References
Te	*R. sphaeroides*	Intracellular reduction	[6]
Te	*R. capsulatus*	Extracellular reduction with exogenous quinones	[54]
Ni	*R. rubrum*	Mechanism of Ni^{2+} transport & accumulation	[8]
Ni, Hg, Cu, Fe, Co, Mo, Cr	*R. sphaeroides*	Influence of highly contaminated media on photosynthetic growth	[10]
Mg, Co	*R. sphaeroides*	Uptake mechanisms and co-toxicity	[11]
Mg, Co, Ni	*R. sphaeroides*	Bioadsorption and bioaccumulation mechanisms	[12]
Co	*R. sphaeroides*	Binding mechanisms	[13]
Co, Cr	*R. sphaeroides*	Bioalterations due to metal exposure	[14]
Co	*R. sphaeroides*	Determination of reference gene for transcript analysis	[16]
Co	*R. sphaeroides*	Variations in genes expression	[17]
Co	*R. sphaeroides*	Proteomics for adaptation mechanism	[18]
Cr	*R. sphaeroides*	Cell growth and morphology. Changes in protein expression	[20]
Co, Cr	*R. sphaeroides*	Bioadsorption and bioaccumulation	[28]
Hg	*R. sphaeroides*	Metal effects on the photosynthetic apparatus	[21]
Hg	*R. gelatinous*, *R. rubrum*, *R. sphaeroides*	Stoichiometry and kinetic of uptake	[22]
Hg	*R. capsulatus*, *R. sphaeroides*, *R. palustris*	Hg^{2+} as an electron sink for redox homeostasis	[23]
Hg	*R. sphaeroides*	Metal monitoring	[34]
Hg	*A. marina*, *R. sulfidophilum*	Metal removal	[31]
Hg, Pb, Cr	*R. gelatinous*, *R. rubrum*, *R. sphaeroides*	Metal monitoring	[35]
Pb	genus *Rhodobacter*	Biofilm-based "biofilter"	[29]
Pb, Hg, Cd	*R. sphaeroides*	Metal removal	[30]
Cd	*R. sphaeroides*	Soil remediation	[32]
Pb	*R. sphaeroides*	Soil remediation	[33]
Zn	*R. sphaeroides*	Bio-nanofactories	[36]
Se	*R. palustris*	Bionanofactories	[37]
Au	*R. sphaeroides*	Bio-nanofactories	[38]

Declarations

Conflict of Interest The authors declare no conflicting nor competing interests.

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Authors and Affiliations

Matteo Grattieri[1,2] · **Rossella Labarile[1,2]** · **Gabriella Buscemi[1,2]** · **Massimo Trotta[2]**

1   Dipartimento di Chimica, Università degli Studi di Bari "Aldo Moro", via E. Orabona 4, 70125 Bari, Italy

2   Consiglio Nazionale delle Ricerche, IPCF-CNR Istituto per i Processi Chimico Fisici, via E. Orabona 4, 70125 Bari, Italy