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RESEARCH ARTICLE

Microbial photoelectrosynthesis: Feeding purple phototrophic bacteria electricity to produce bacterial biomass

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Abstract
Purple phototrophic bacteria are one of the main actors in chemolithotrophic carbon fixation and, therefore, fundamental in the biogeochemical cycle. These microbes are capable of using insoluble electron donors such as ferrous minerals or even carbon-based electrodes. Carbon fixation through extracellular electron uptake places purple phototrophic bacteria in the field of microbial electrosynthesis as key carbon capturing microorganisms. In this work we demonstrate biomass production dominated by purple phototrophic bacteria with a cathode (−0.6 V vs. Ag/AgCl) as electron donor. In addition, we compared the growth and microbial population structure with ferrous iron as the electron donor. We detect interaction between the cathode and the consortium showing a midpoint potential of 0.05 V (vs. Ag/AgCl). Microbial community analyses revealed different microbial communities depending on the electron donor, indicating different metabolic interactions. Electrochemical measurements together with population analyses point to *Rhodopseudomonas* genus as the key genus in the extracellular electron uptake. Furthermore, the genera *Azospira* and *Azospirillum* could play a role in the photoelectrotrophic consortium.

INTRODUCTION

Microbial anoxygenic photosynthesis is one of the most important processes in the biogeochemical cycle, since it allows light-driven carbon fixation (Bryce et al., 2018; McKinlay & Harwood, 2010; Ozaki et al., 2019). Chemolithotrophic carbon fixation that occurs in subsurface dictates carbon fluxes in environments such as soils and groundwater (Taubert et al., 2021). One of the main actors in this process are purple phototrophic bacteria (PPB), which fix CO_2 using a wide range of electron donors such as H_2, $S_2O_3^{2-}$ or S^{2-}. Surprisingly, some microorganisms of this type are also capable of accepting electrons from solid phases such as ferrous minerals (Widdel et al., 1993) or even graphite electrodes (Xing et al., 2008). In this context, the mechanisms behind extracellular electron uptake to accept electrons from a cathode have been revealed (Bose et al., 2014). Furthermore, carbon fixation (via the Calvin–Benson cycle) has been recently proved to be strongly linked to phototrophic electron uptake using an electrode (cathode) as electron donor (Guzman et al., 2019). Furthermore, other metabolic pathways such as nitrogen fixation or hydrogen production could be also affected (McKinlay & Harwood, 2010) under electrode control. Carbon fixation through extracellular electron uptake places purple phototrophic bacteria in the field of microbial electrosynthesis as key carbon

capturing microorganisms. Microbial electrosynthesis seeks to use the electrons provided by a biocathode to synthesize value-added compounds, generally volatile fatty acids and alcohol like acetate, propanol or butyrate (Ganigué et al., 2015; Izadi et al., 2021; Nevin et al., 2010), but also other compounds such as bioplastics (Chen et al., 2018; Nishio et al., 2013) or microbial biomass as protein source (Xu et al., 2021).

After a decade of effort and scientific advances (Nevin et al., 2010), microbial electrosynthesis is still far from the technical and economic competitiveness of current industrial processes (Prévoteau et al., 2020). Microbial electrosynthesis requires engineering improvements such as electrode material (Jourdin et al., 2014; Nie et al., 2013; Zhang et al., 2012) and reactor design (Jourdin et al., 2018; Kantzow et al., 2015) but also in the selection of the microbial community (Prévoteau et al., 2020). The resilience and versatility of the microbial community will determine the range and rate of products obtained as well as the robustness of the synthesis process. Purple phototrophic bacteria could bridge the gap to these limitations. Despite discoveries based on pure cultures (Bose et al., 2014), the use of consortium dominated by purple phototrophic bacteria under photoelectroautotrophy still in its infancy.

Therefore, understanding the dynamics of a microbial consortium of purple phototrophic bacteria would allow operation under non-sterile conditions. Despite its limitations such as product purification or possible impediments in the food industry, to explore PPB may reduce costs and facilitates the operation (Hülsen et al., 2014), while opening the range of potential products. With the aim of bringing electrode-mediated biomass production closer to reality, in this work we have explored the photoelectroautotrophic cultivation of a mixed culture dominated by purple phototrophic bacteria. In addition, we have compared electrode-dependent biomass production with the most ubiquitous inorganic electron donor, ferrous iron.

EXPERIMENTAL PROCEDURES

Mineral medium and microbial cultivation

In this work, a PPB-dominated microbial consortium was cultured under autotrophic conditions with two electron donors: ferrous iron (Fe^{2+}) and an electrode (cathode). We used a mixed microbial community adapted to electrode interaction (Manchon et al., 2023) as inoculum for all experiments.

Minimal mineral medium was used for all experiments containing $NaHCO_3$ 2.5 gL^{-1}, NH_4Cl 0.5 gL^{-1}, $NaH_2PO_4.2{\cdot}H_2O$ 0.41 gL^{-1}, KCl 0.1 gL^{-1}, a mixed of vitamins 10 ml/L, a mixed of minerals 10 ml/L. Medium was sparged with N_2:CO_2 (80:20) to remove dissolved oxygen. In the Fe^{2+} experiment, Fe^{2+} was added to a final concentration of 20 mM under anoxic conditions. All the reactors (culture bottles and H-Cells) were illuminated with IR-lamps (850 nm) to promote the presence and activity of PPB.

Experimental set-up

Photoferrotrophy

PPB-dominated consortium was cultured in serum bottles (n = 5) under anoxic, autotrophic and IR-illuminated conditions with ferrous iron (Fe^{2+}) as electron donor (Figure 1).

Photoelectrotrophy

To evaluate the photoelectroautotrophic growth (cathode as electron donor) of PPB consortium, we explored biomass production in H-cell reactor and we characterized electroactive behaviour in a single chambered reactor.

We used H-Cell with carbon rod (Mersen, Courbevoie, France) was used as cathode (working electrode), a 3 M KCl Ag/AgCl reference electrode (Hanna Instruments S.L. Gipuzkoa, Spain) and a platinized titanium mesh (Inagasa S.A., Barcelona, Spain) as the counter electrode. Electrochemical measurements were performed with a potentiostat NEV4 v2.0 (Nanoelectra S.L., Alcalá de Henares, Spain; Figure 1).

We used single chambered reactor (100 ml) with a 3 M KCl Ag/AgCl reference electrode (Hanna Instruments S.L.) and a platinized titanium mesh (Inagasa S.A., Barcelona, Spain) as the counter electrode. Carbon felt (Mersen, Courbevoie, France) fragment was connected with a gold filament acting as working electrode (Figure 1).

Experimental design

First, we studied the consortium growth under photoferrotrophy (Fe^{2+} as electron donor), for which we inoculated serum bottles (1/100) and incubated them at 30°C with constant stirring and IR-illumination (IR-lamps, 850 nm). We monitored microbial growth by measuring absorbance (λ = 400–1000 nm) and ferrous iron concentration as described elsewhere (Carpenter & Ward, 2017). The presence of organic compounds in the process was analysed by HPLC. At the end of the experiment, biomass growth was measured as total organic carbon (TOC) and volatile suspended solids (VVS). We also visualized biomass using scanning (SEM) and transmission (TEM) electron microscopy. The microbial population at the end of the experiment was analysed by 16S Illumina.

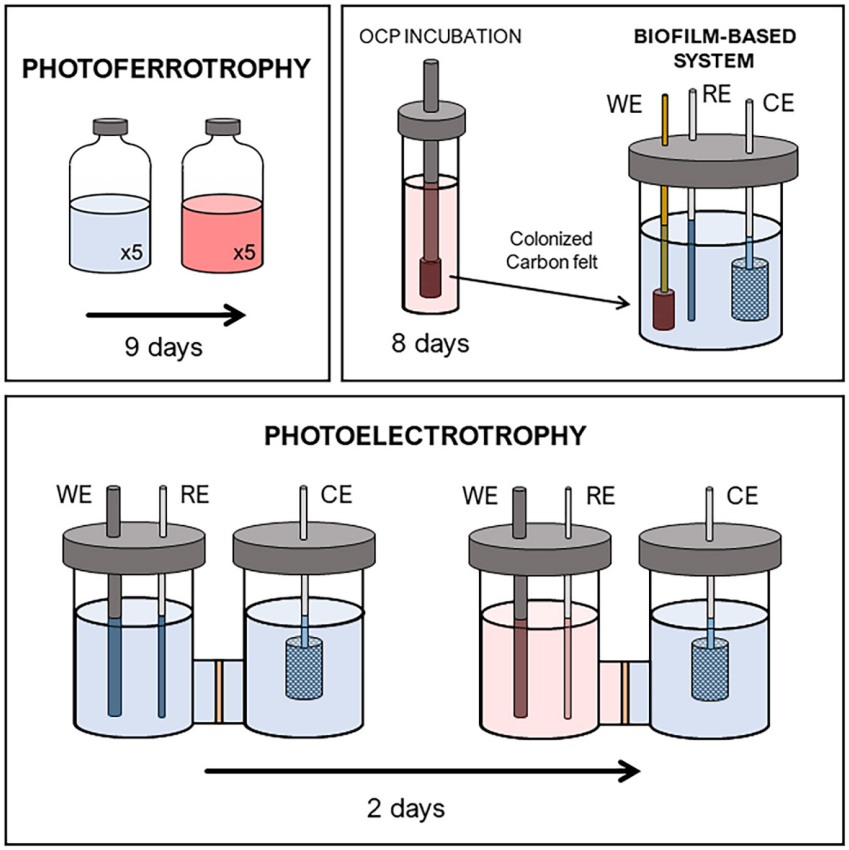

FIGURE 1 Schematic of the experiment set-up. Top left: Photoferrotrophy cultivation experiment. Top right: Biofilm-based experiment to assess electroactivity of the consortium.

Next, we inoculated H-cell reactor (1/100) with the same inoculum and we operated the reactor at −0.6 V (vs. Ag/AgCl). During growth, we measured absorbance (590 nm) by spectrophotometer and organic compounds by HPLC. At the end of the experiment we visualized the biomass produced by transmission electron microscopy and we analysed microbial population (16S Illumina) at the end of the experiment.

Finally, we studied the electroactivity of the consortium in a biofilm-based approach with carbon felt as material. After 200 hours in contact with the consortium under non-polarized autotrophic conditions, a piece of the colonized felt was connected to a gold filament for bioelectrochemical study similar to Rodrigo Quejigo et al. (2019). After 24 h of polarization (−0.6 V vs. Ag/AgCl) as acclimatation, cyclic voltammetries were performed. Another fragment of colonized carbon felt was analysed by transmission electron microscopy (TEM).

Analytical methods

Volatile fatty acids (VFAs) were measured by HPLC 1100 high-pressure liquid chromatograph with a 210 nm UV detector and Supelco C-610H column. H_3PO_4 0.1% (v/v) was used as mobile phase at 0.5 ml/min flow rate. To rule out the presence of organic compounds not measurable by HPLC in the medium, the total organic carbon (TOC) was analysed by TOC-VCSH analyser (Shimadzu).

We used scanning electron microscope (SEM) and transmission electron microscopy (TEM) to explore cell morphology and biofilm formation both in ferrotrophic and electrotrophic experiments. SEM samples were fixed with 5% (v/v) glutaraldehyde in cacodylate buffer (0.2 M, pH 7.2), and gradually dehydrated with ethanol solutions (25%, 50%, 70%, 90% and 100%, 10 min each step). Then, samples were rinsed with acetone for 10 min and immerse in anhydrous acetone at 4°C overnight. Finally, the samples were dried in CO_2 and coated with gold. Micrographs were taken using a scanning electron microscope JSM-IT500 (JEOL).

For the TEM assay, 5 ml planktonic cell suspensions were centrifuged at 10,000 *g* for 5 min. Primary fixation was carried out by resuspending the cells pellets in 2% formaldehyde and 2.5% glutaraldehyde in sodium phosphate buffer (pH 7.2) for ~45 min at room temperature. For second fixation, samples were incubated with osmium tetroxide 1% for 1 h. After second fixation, cells were subjected to dehydration by acetone and resin infiltration. Ultrathin sections (~50–60 nm) were obtained using ultramicrotome. To obtain TEM micrographs were characterized using a JEM 1400 (National Center of electron microscopy, UCM, Madrid, Spain).

The biomass produced in the reactors was quantified by spectrophotometry and analysis of volatile suspended solids (VSS). Spectrophotometric spectrum

(1100 to 400 nm) was measured with a UV-1800 spectrophotometer (Shimadzu). The VSS concentration (gVSS/L) was measured according to standard methods (D. Eaton et al., 2005).

RESULTS AND DISCUSSION

In contrast with previous experiences with pure culture of purple phototrophic bacteria (Guzman et al., 2019), we have explored for the first time the cultivation of a microbial mixed consortium dominated by PPB with a cathode as the sole electron source.

Photoferrotrophic growth: Ferrous iron as electron donor

Our first approach to understand autotrophic growth extracellular electron uptake led us to cultivate a mixed community dominated by purple phototrophic bacteria with ferrous iron (Fe^{2+}). For this purpose, we used an enriched culture dominated by anodic purple phototrophic bacteria to inoculate batch reactors with ferrous iron a sole electron donor.

We observed an increase in optical density (OD_{590}) over time, accompanied by a decrease in Fe^{2+} concentration indicating that the consortium was able to fix inorganic carbon into biomass by using Fe^{2+} as electron donor (Figure 2A). Biomass production was also verified at values concentration of $22.08 \pm 2.71\ g\ L^{-1}$ for total organic carbon (TOC) and $0.1334 \pm 0.0171\ g\ L^{-1}$ VSS at the end of the experiment.

The increase in optical density showed a certain delay with respect to the oxidation of ferrous iron (Figure 2A). This result could indicate that other microorganisms could be playing a role in the process, that is, electroactive acetogens that produce organic compounds that purple phototrophic bacteria can use to grow heterotrophically. We observed two maximum absorption peaks (804 and 870 nm) characteristic peaks of PPB bacteriochlorophylls. In addition to several peaks between the wavelengths 500 and 590 nm, corresponding to carotenoids. These absorption peaks match to those described in purple phototrophic bacteria dominated consortia (Vasiliadou et al., 2018). Therefore, the population of purple phototrophic bacteria remains predominant under photoferrotrophic conditions (Figure 2B).

At the end of the experiment, we studied photoferrotrophically cultured consortium using transmission electron microscopy (TEM) and scanning electron microscopy (SEM; Figure 3). The micrographs showed microbial cells associated with different mineral particles classically observed in processes of biomineralization of iron (Oggerin et al., 2013). The solubility of ferric iron (Fe^{3+}) is considerably less than that of ferrous iron (Fe^{2+}). Therefore, the oxidation of ferrous iron to ferric iron (Fe^{3+}) led to the formation of insoluble ferric iron (Fe^{2+}) minerals (Figure 3B,D,E). Notably, the images revealed lamellar type internal membrane structures arranged parallel to the cytoplasmic membrane, structures typical of purple phototrophic bacteria (Figure 3A,C; LaSarre et al., 2018; Ramana et al., 2010). In addition, despite not having analysed in depth the presence of bioplastics produced, we observed granules in the cytoplasm very similar to the polyhydroxybutyrate (PHB) and polyhydroxyalkanoate (PHA) granules described by other authors (Higuchi-Takeuchi et al., 2016; Figure 3C).

Furthermore, SEM micrographs showed angular crystal structures of iron oxides with bacteria forming rosette-like clusters previously described by other researchers in the model electroactive purple phototrophic bacteria, *Rhodopseudomonas palustris* (Hougardy et al., 2000; Figure 3D,E).

Photoelectrotrophic growth: Cathode as electron donor

After exploring the photoferrotrophic growth of PPB we explored the capacity of such culture to use an electrode (cathode) as the sole electron donor. Our goal was to study both biomass production and bioelectrochemical response. Under these conditions, we carried out two independent assays using: (i) PPB-planktonic cells, and (ii) PPB-biofilm cells.

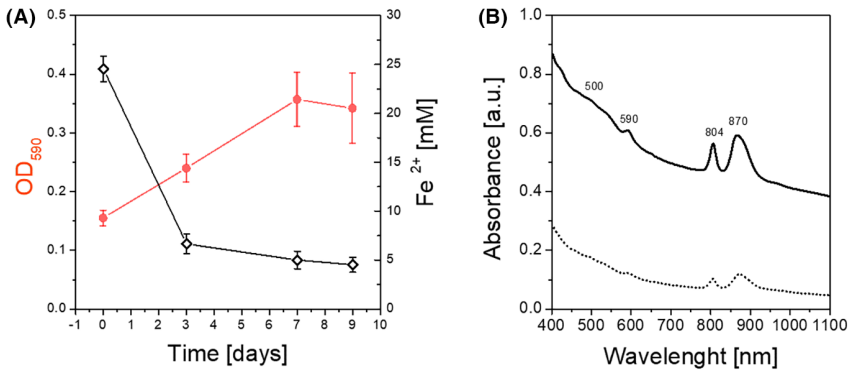

FIGURE 2 Purple phototrophic bacteria dominated consortium under photoferrotrophic conditions. (A) Growth curve. Red circles correspond to optical density (OD_{590}) and white diamonds corresponds to ferrous iron concentration (Fe^{2+}). (B) Absorbance spectrum at time 0 (dashed line) and stationary phase (straight line).

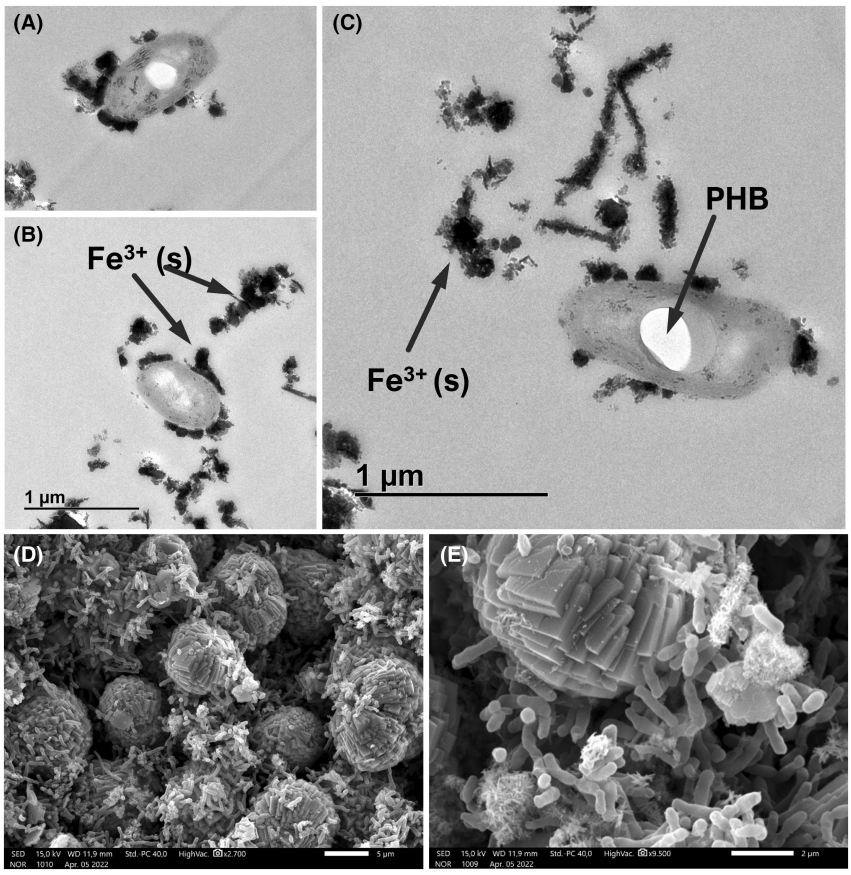

FIGURE 3 Purple phototrophic bacteria dominated consortium under photoferrotrophic conditions. (A) TEM micrograph with type internal membrane structures. (B) TEM micrograph with insoluble iron oxides (Fe^{3+}). (C) TEM micrograph with cell inclusions. (D and E) SEM micrograph with insoluble iron oxides (Fe^{3+}) and bacteria.

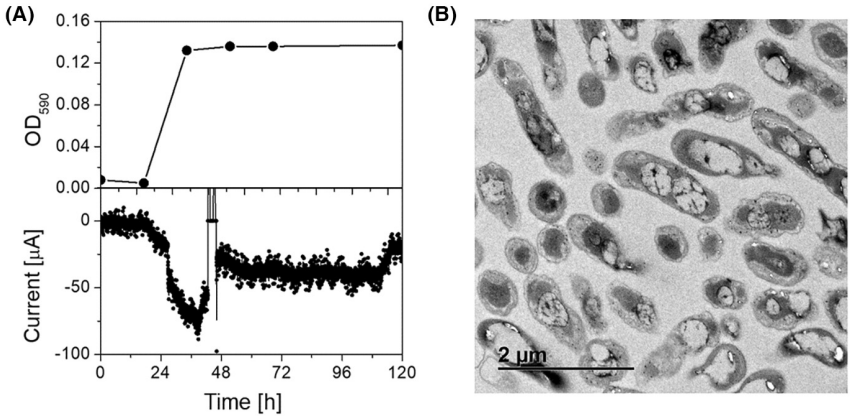

FIGURE 4 Purple phototrophic bacteria dominated consortium under photoelectrotrophic conditions. (A) Growth curve. Up: Optical density (OD_{590}). Down: Current intensity. (B) TEM micrograph with type internal membrane structures.

As previously described, cathodic polarization hinders irreversible cell adhesion, due to the electrostatic repulsion between the electrode and the cell wall charges (Bayer & Sloyer, 1990; Busalmen & de Sánchez, 2001). This phenomenon, despite being a problem to study cathodic biofilms, allowed us to accurately quantify biomass production. To assess biomass production, we inoculated a two-chamber reactor with our bacterial consortium (Figure S1). In this reactor, planktonic growth outcompeted biofilm-based growth by using a carbon rod as working electrode (−0.6 V vs. Ag/AgCl). We monitored electron uptake (current density) and planktonic microbial growth (OD_{590}) (Figure 4A). We observed an increase in biomass growth (OD_{590}) 24 h after inoculation; actually, absorption peaks coincided with those typical of PPB (Figure S2; Vasiliadou et al., 2018). This microbial growth was accompanied by electron uptake, visible by the increase in current intensity from values close to 0 µA to almost reaching −100 µA. Even at the end of the experiment, we did not observe biomass attached to the cathode but planktonic growth (Figure S1). Some species of purple phototrophic bacteria have been previously shown to uptake electrons from cathodes through redox mediators (Borghese et al., 2020; Hasan et al., 2013). In order to clarify the electron transfer mechanism, we

studied the reactor supernatant by cyclic voltammetry and no redox species were detected (Figure S3), which suggests that direct extracellular electron transfer was the main electron uptake mechanism. We hypothesize that extracellular electron transfer could occur through random contacts between bacterial cells and the polarized electrode, in a similar way than previously reported bacteria interact with fluid electrodes (Tejedor-Sanz et al., 2017). Indeed, the electrostatic repulsion caused by cathodic polarization could promote planktonic interaction over biofilm interaction.

At the end of the experiment, we took TEM micrographs of the planktonic biomass to study the cell structure (Figure 4C). The bacteria had markedly different cell structures than those observed in the previous experiment (Figure 3A–C). We identified smaller PHB inclusions (Figure 4C) compared to the iron-oxidizing consortium (Figure 3A–C).

These results unequivocally indicate that the PPB-dominated consortium was able to grow with a cathode as sole electron donor. Unfortunately, planktonic cells did not showed electroactivity after cyclic voltammetry analysis (Figure S4). An alternative strategy, previously explored (Manchon et al., 2023), to acquire electrochemical data from PPB consist of using a biofilm-based approach.

Non-polarized autotrophic conditions allowed biofilm formation on the carbon felt surface. After ca. 200 h of inoculation, a fragment of the inoculated felt was analysed by TEM, revealing the formation of the biofilm on the surface, with clustered cells and exopolysaccharide (Figure 5A,B). Some of these cells formed rosette-like clusters like those described in Figure 3D,E, characteristic of *Rhodopseudomonas palustris*, the model electroactive purple phototrophic bacteria (Hougardy et al., 2000). We observed visible reddish filamentous structures on the surface of the carbon felt (Figure 5C).

Another fragment of the colonized carbon felt was connected through a gold wire in a single-chamber electrochemical cell to assess the electroactivity of the consortium (Figure S5). After 10 h of polarization (−0.6 V vs. Ag/AgCl) cyclic voltammetry analysis revealed a redox couple (E_{mp} = 0.05 V vs. Ag/AgCl) and a reductive process below −0.6 V (vs. Ag/AgCl; Figure 5D). The midpoint redox potential was similar to the redox potential of pure cultures of *Rhodosepudomonas palustris* TIE-1 (Bose et al., 2014). The identified redox pair indicates the presence of redox active components that could participate in the extracellular electron uptake. Electrochemical analyses of the supernatant, both in the planktonic-based approach and in the biofilm-based one, did not reveal the presence of redox mediators. Therefore, the electrochemical characterization of the consortium suggests direct extracellular electron transfer in which the redox site (E_{mp} = 0.05 V) could be involved. In addition, the similarity of our signal/fingerprint to previous signals reported in *Rhodopseudomonas* sp suggest the presence of this bacterial genus in our PPB consortium.

The reduction process observed at redox potential lower than −0.6 V versus Ag/AgCl (Figure 5D, black line) was not observed in the abiotic voltammogram (Figure 5D, grey line), indicating that it was catalysed by the microbial consortium. Based on our knowledge of purple phototrophic bacteria, the reduction process could correspond to hydrogen bioproduction, as we have previously reported (Vasiliadou et al., 2018). These results pointed to the biohydrogen production potential

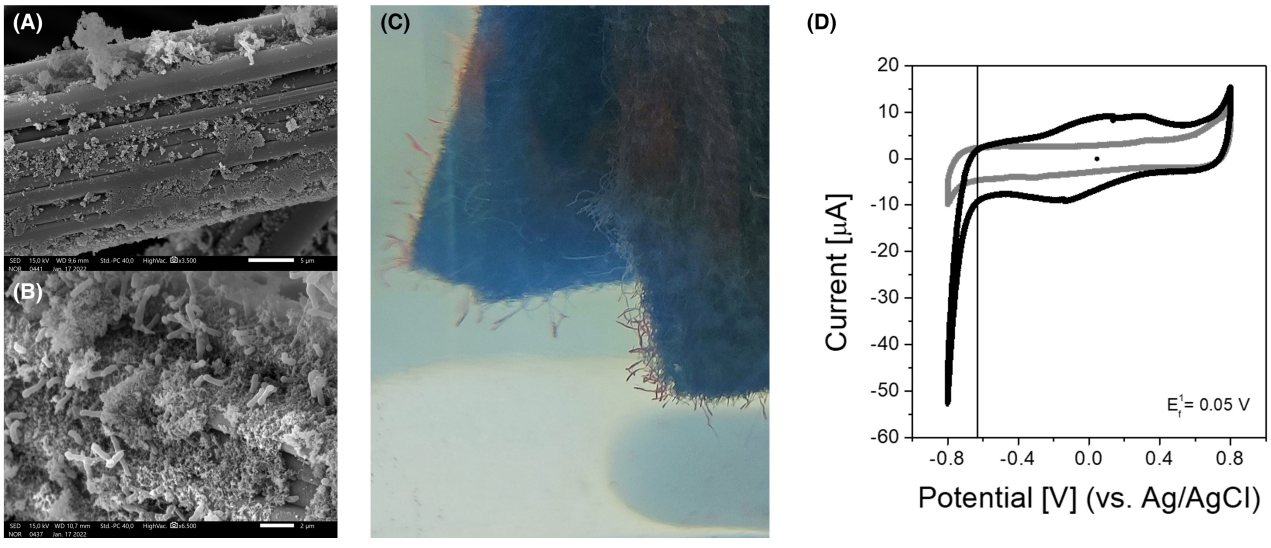

FIGURE 5 Purple phototrophic bacteria dominated consortium biofilm under photoferrotrophic conditions. (A, B) SEM micrograph. (C) Carbon felt photograph after inoculation. (D) Cyclic voltammograms (5 mV s^{-1}). Grey voltammogram corresponds to abiotic conditions carbon felt. Black voltammogram corresponds to inoculated carbon felt. Vertical line corresponds to thermodynamic potential of hydrogen evolution (−0.63 V vs. Ag/AgCl). Mid-point potential (E_{mp}) is indicated by a black point.

by PPB-dominated cathodes. To clarify, during all experiments, at the potential used (−0.6 V vs. Ag/AgCl) hydrogen production is not thermodynamically possible (−0.63 V vs. Ag/AgCl); thus, the H_2-mediated pathway was ruled out.

Iron and cathodes show similar but different pressure on PPB consortium

The microbial community analysis was performed using 16S Illumina in order to understand how different microbial communities were established under autotrophic conditions and to evaluate the impact of the insoluble electron donor (i) ferrous iron; and (ii) carbon electrode.

The predominant genera in common between the two different electron donors are *Rhodopseudomonas*, *Acinetobacter*, *Pseudomonas* and *Acidovorax* which are considered core genera in electroactive communities (Figure 6; Xiao et al., 2015). *Rhodopseudomonas*, the most abundant genus in all the samples, is considered the electroactive PPB model (Bose et al., 2014; Guzman et al., 2019). This genus is capable of fixing carbon dioxide into biomass using an extracellular electron donor, for example, ferrous iron (Widdel et al., 1993) or cathodes (Bose et al., 2014; Guzman et al., 2019). *Acinetobacter*, *Pseudomonas* and *Acidovorax* have been previously found in cathodes (Liu et al., 2014; Rabaey et al., 2008; Rowe et al., 2015) but their electroactivity has not been unequivocally demonstrated. The usual presence of these genera in electroactive consortia indicates a fundamental role. However, the lack of reports demonstrating its electroactivity suggests that *Rhodopseudomonas* is the key genus that performs extracellular electron uptake in our systems, connecting the rest of the community with the extracellular electron donor. Additionally, we observed a strong increase in abundance of *Ralstonia* genus in both ferrotrophy (Fe^{2+}; 2.7-fold) and electrotrophy (cathode; 3.3-fold) compared to the original community used as inoculum. *Ralstonia* was reported in the autotrophic electrode-assisted production of valuable compounds such as PHB (Chen et al., 2018; Nishio et al., 2013) or alcohols (Li et al., 2012). Despite its low abundance in this study, our results indicate that *Ralstonia* could become important in a long-term photoelectrotrophic system.

The structure of the microbial community also revealed differences in terms of the dissimilar abundance and presence of species depending on the extracellular electron donor. First, consortium with Fe^{2+} as electron donor showed lower level diversity (Shannon index: 1.84) respect to the inoculum (Shannon index: 2.266). This result was consistent with the proportion of *Rhodopseudomonas* and *Acinetobacter* genus species that represent more than 75% of the total genera identified in the samples with ferrous iron as electron donor (Figure 6). Both the inoculum and the sample with Fe^{2+} showed a notable presence of the genus *Proteiniphilum*, described as electroactive bacteria (Logan et al., 2019); however, it was not found in cultures with the cathode as electron donor.

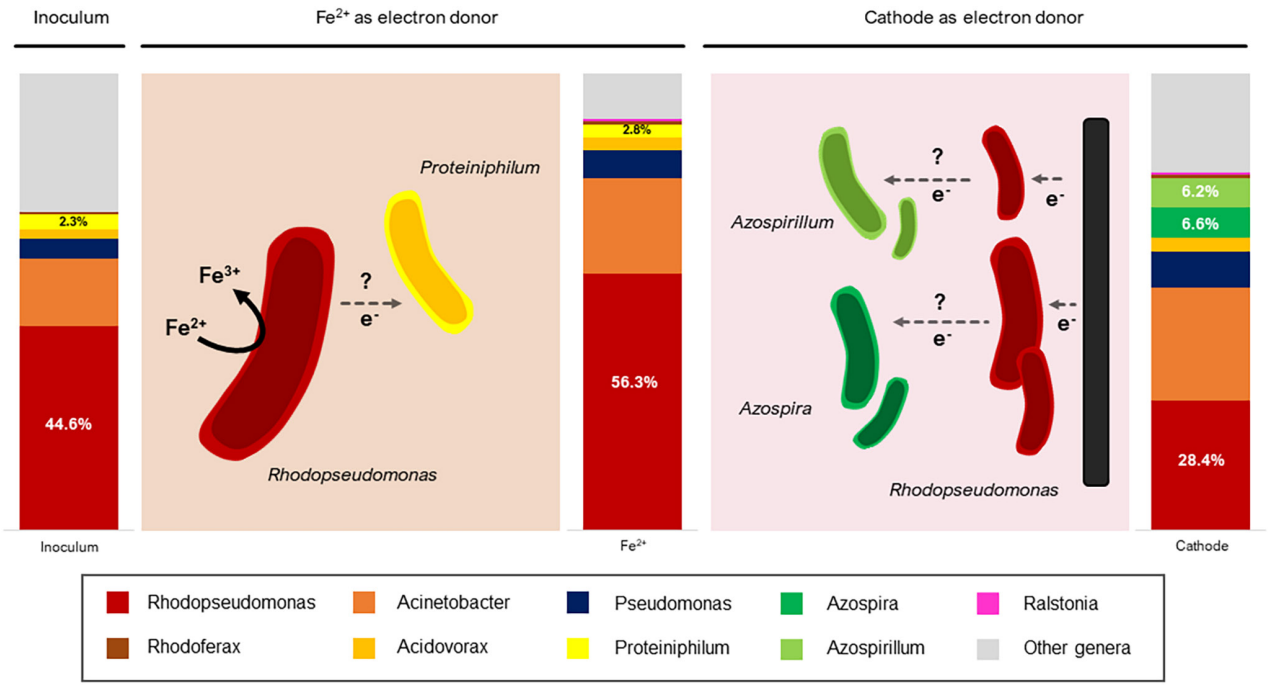

FIGURE 6 Microbial community analysis and schematic of the genus that might coexist depending on the electron donor. Stacked bars correspond to relative abundance at genus level of inoculum, ferrous iron as electron donor (Fe^{2+}) and cathode as electron donor (cathode). Left to the bars (Fe^{2+} and cathode) the main genus and their possible interaction for each electron donor are represented.

In the samples with cathode as electron donor we observed a similar diversity (Shannon index: 2.24) compared with the inoculum. However, the analyses revealed a decrease in the relative abundance of *Rhodopseudomonas* in addition to a drastic decrease in the abundance of *Proteiniphilum* (Figure 6). We discovered that cathode promoted the presence of two bacterial genera: *Azospirillum* and *Azospira*, both considered core genera in electroactive microbial communities (Xiao et al., 2015). *Azospirillum* is a nitrogen-fixing bacterium that has rarely been found in electroactive communities (Pisciotta et al., 2012). *Azospirillum* sp. together with other genera such as *Rhodopseudomonas* and *Ralstonia*, also present in the cathode, have been described as one of the main carbon sequestrants in soils (Yuan et al., 2012). Furthermore, some researchers have reported that *Azospirillum* strains isolated from electrodes are capable of extracellular respiration of anthraquione-2,6-disulfonate (AQDS) (Zhou et al., 2013), a redox mediator classically respirable by electroactive bacteria (Dantas et al., 2018; Lovley et al., 1999). *Azospira*, another genus primarily described as nitrogen-fixing bacteria, has also been detected in electroactive communities (Sun et al., 2011). Furthermore, some authors have described *Azospira sp.* electron uptake from cathodes using AQDS as a redox mediator (Thrash et al., 2007). Therefore, the decrease in the abundance of *Rhodopseudomonas* together with the appearance of *Azospirillum* and *Azospira* points to the possibility of a syntrophy under photoelectroautotrophic conditions.

The PPB-dominated consortium used as inoculum was previously adapted to perform anodic respiration (Manchon et al., 2023), so the electrode was used as an electron acceptor. In contrast, such microbial consortium successfully adapted to conduct the inverse reaction, using the electrode (now as cathode) as extracellular electron donor. So, our PPB-dominated consortium appeared to have bidirectional electron transfer, being able to both accept and donate electrons from an insoluble material. Some authors have already reported that PPB could carry out transfer in both directions (Bose et al., 2014; Xing et al., 2008). Furthermore, we have previously reported the same behaviour using a PPB-dominated consortia growing on fluid-like electrodes under heterotrophic conditions (Manchon et al., 2023).

In summary, our results confirm the *Rhodopseudomonas* genus played the main role in the extracellular electron uptake using Fe^{2+} and with cathode as electron donor. The connection between the cathode and PPB-dominated microbial community still remains unclear. The absence of redox mediators (Figure S3) and organic compounds (Table S1) suggests a direct extracellular electron uptake, as previously reported in pure cultures of purple phototrophic bacteria (Bose et al., 2014). Further studies have shown interspecies electron transfer for methanogenesis (Huang et al., 2022) and carbon fixation (Liu et al., 2021) between purple phototrophic bacteria and other genera. Thus, we hypothesize that *Rhodopseudomonas* strains in our reactors are the link between the electrode and the microbial community.

CONCLUSIONS

This work explored for the first time the cultivation of a PPB-dominated consortium under photoelectrotrophic conditions. Using a cathode as a sole electron donor, we have produced biomass dominated by purple phototrophic bacteria without any prior acclimatization period. Electrochemical measurements together with population analyses point to *Rhodopseudomonas* genus as the key bacterial genus in the extracellular electron uptake. Furthermore, the genera *Azospira* and *Azospirillum* could play a role in the photoelectrotrophic consortium.

The cultivation of a mixed culture allows to operate under non-sterile conditions, drastically improving the applicability as a method of bacterial biomass production. Additionally, the biomass composition dominated by purple phototrophic bacteria gives rise to a new exploratory field in the production of protein-rich biomass and value-added products.

AUTHOR CONTRIBUTIONS

Carlos Manchon: Conceptualization (equal); investigation (equal); methodology (equal); visualization (equal); writing – original draft (lead). **María Llorente:** Conceptualization (equal); investigation (supporting); methodology (supporting); validation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Fernando Muniesa-Merino:** Conceptualization (equal); investigation (equal); methodology (equal); validation (supporting); writing – original draft (supporting). **Abraham Esteve-Núñez:** Conceptualization (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); supervision (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST

There is no conflict to declare.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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