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All ecosystems potentially host electrogenic bacteria

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ABSTRACT

Instead of requiring metal catalysts, MFCs utilize bacteria that oxidize organic matter and either transfer electrons to the anode or take electrons from the cathode. These devices are thus based on a wide microbial diversity that can convert a large array of organic matter components into sustainable and renewable energy. A wide variety of explored environments were found to host electrogenic bacteria, including extreme environments. In the present review, we describe how different ecosystems host electrogenic bacteria, as well as the physicochemical, electrochemical and biological parameters that control the currents from MFCs. We also report how using new molecular techniques allowed characterization of electrochemical biofilms and identification of potentially new electrogenic species. Finally we discuss these findings in the context of future research directions.

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Contents

1. Introduction

In recent years, industrialization and the global economic system have led to the overexploitation of fossil fuels, especially oil and gas. Indeed, shortage of these latter products has resulted in a global energy crisis warning [1–3]. Alternative green energy has attracted great attention for new means of electricity production, including by

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microorganisms [4,5]. One promising yet challenging emerging technology uses microbial fuel cells (MFCs), in which microorganisms generate electricity by exchanging electrons with electrodes while oxidizing organic or inorganic matter [6,7]. This principle makes use of the fact that bacterial exocellular electron transfer plays an important role in anaerobic microbial communities that degrade organic matter and those that use insoluble electron acceptors (such as iron- and manganese-oxide) for growth [8,9].

The ability of microorganisms to produce electricity was demonstrated at least one hundred years ago by immersing a platinum electrode in a suspension of *Escherichia coli* and *Saccharomyces* [10]. However, a greater interest in this phenomenon only arrived several decades later, when anaerobic bacteria such as *Clostridium butyricum* were used to enhance current density and power output [11]. During this same period, the first fuel cell was conceived with two chambers (one anodic and one cathodic) separated by an ion exchange membrane [12]. Since then, the design of MFCs has evolved, and electrical current output now reaches 2.87 kW m^{-3} [13]. While most prokaryotes can potentially generate electricity [1,14,15], only a few bacteria have been highlighted to form electrochemically active biofilm (EAB) to date. EAB is a generic term used to designate biofilm that are able to transfer electrons towards a final electron acceptor (such as electrodes in a MFC system), thus acting as the catalyst for redox reactions. Different pathways are currently known to be involved in this electron transfer. These species will be detailed later in this review.

Although biofilm construction is rapid and highly durable, EAB diversity can be highly variable depending on culture conditions (which can favor certain bacterial populations), which can therefore modulate electricity production. For example, Logan and Regan [16] reported that power production could vary from <1 $mW \cdot m^{-2}$ to >1500 $mW \cdot m^{-2}$ on the basis of different MFC architectures that use oxygen as the final electron acceptor. This huge variability could be explained by the different existing MFC types that produce more or less current, since the design of the MFC system affects power generation [17].

Different environments have been explored in an attempt to understand the diversity of microorganisms involved in this exocellular electron transfer. Many different types of environments harbor EAB, including anaerobic sludge from treatment plants, anaerobic sediment, and even soil. Although it is supposed that bacteria may belong to the rare biosphere, they may dominate when electrode are in contact with sample [18,19]. Since one of the most promising applications of MFC could be the treatment of wastewater, many efforts have been targeted at wastewater treatment plants, paper mill effluents, etc. [20–24].

The focus of this review is on environments that host EAB, the principle communities of these ecosystems, and their electrogenic potential. Ecosystems that host EAB and the optimal conditions for growth and electron transfer will be described in detail.

2. Electrogenic microorganisms

Many diverse electroactive microorganisms have been studied to date in an effort to improve the energy production of MFCs. An inventory of enrichment cultures as well as pure strains known to be involved in MFCs was made until late 2008 [15,25].

Different EAB communities can interact as consortia and generate energy. This is generally what characterizes natural ecosystems such as wastewater, river, rice field soils or compost [22,26–31]. Identification of single electrochemically active species in these natural environments has been performed with type strains that correspond to predominant species in wild EA biofilms. The few strains of bacteria directly isolated from EAB have displayed a higher electrochemical performance than their type strains [25,27]. For example, *Ochrobactrum anthropi* YZ-1, a strain isolated from EAB originally obtained in a primary clarifier overflow from a wastewater treatment plant, produced 89 $mW \cdot m^{-2}$. This value is two-fold higher than its type strain [32]. The comparison of electroactivity between pure cultures and microbial consortia in wastewater reveals a greater power density with higher columbic efficiency for the consortia [15,33].

3. Do all ecosystems host electrogenic bacteria?

The presence of diverse EAB raises the question of which environments are the most electrogenic. Although most electrical current studies have focused on effluent from diverse wastewater treatment facilities, EAB appear to be widely distributed as suggested by studies of different environmental types (Table. 1) [34]. Many soil and aquatic environments have been tested over the years, complicating the ability to address an exhaustive list. Furthermore, none of these studied environments have been tested under the same MFC conditions. Instead, many studies have focused on optimization and progress towards improving MFCs, even if accurate comparisons of natural inoculums and their electrical performances are lacking. Therefore, even if these advances are highly useful to future MFC commercialization, a basic understanding of MFC biology and electrochemistry is still necessary.

3.1. Natural environments

Various aquatic natural environments have been investigated (Table. 1), and one river with phototrophic biofilm has been reported to have a current of 3.7 $A \cdot m^{-2}$ [35]. River offers further possibilities such as sediment that could perform from about 0.2 to 0.3 $A \cdot m^{-2}$ [36–38]. Environments that assure the transition between continental and marine environments can lead to power production. Mangrove sediment is naturally rich in organic matter due to tides and rich forest litter [39], resulting in a potential for energy output as high as 12 $A \cdot m^{-2}$ [34, 40]. Beach sediments that play the same role as mangroves produce a current density with values ranging from 0.8 to 8.9 $A \cdot m^{-2}$ [26,34]. Even tidal mud has a slight potential to produce current [41]. Sampling direct microbial biofilm from salt marsh [34,42] or marine sediment [26] provides current densities from approximately 4.45 to 85 and 2 $A \cdot m^{-2}$, respectively. Two types of MFC can be employed in marine and salt marsh sediment: a traditional MFC, in which sediment is sampled and serves as the inoculum for a reactor; and a benthic MFC (BMFC), in which two electrodes are placed in situ (the anode is placed under the sediment and the cathode is floating). The BMFC design could be applied to any type of environment, but it is more often used in marine environments, since they could be an energy source for different autonomous oceanographic or environmental sensors [43–45].

Microbial fuel cells have been extensively exploited in aquatic environments such as marine sediments or wastewater [27,31]. Terrestrial environments have been comparatively underexploited despite they hold a high diversity of microorganisms and a wide variety of organic and/or inorganic matters widespread [27,34,46].

Soils that support plant growth (Table. 1) are naturally rich in nutrients (e.g. carbohydrates, amino acids, aliphatic acids, enzymes, vitamins…) and should correspond to an electrogenic environment [46]. Indeed, plants produce organic acids such as acetate that are known to induce a high power density and enrich EAB [47,48]. For example, one previous study demonstrated the potential of rice paddy fields to produce a current density reaching approximately 0.1 $A \cdot m^{-2}$ [49]. Soils with plants are not the only terrestrial ecosystem that can host EAB; rich soils such as compost can also offer a promising host environment for electricity production. Compared to ordinary soil, compost is more enriched in organic matter; this could increase bacterial activity and thus the potential to produce electricity using a MFC system. Composts can display current production up to four times greater than natural soil [29]. This confirms that composition and richness of organic matter greatly affect MFC potential. Garden compost is another good source of organic matter and EAB for MFC, as it displays a current production (1.5 $A \cdot m^{-2}$) on the same order as industrial composts (1.1 $A \cdot m^{-2}$) [29,50]. Anaerobic soils produce a good electrical current density

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