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REVIEW ARTICLE

Biocatalyst physiology and interplay: a protagonist of MFC operation

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Abstract
Microbial fuel cells (MFC) have been foreseen as a sustainable renewable energy resource to meet future energy demand. In the past, several studies have been executed in both benchtop and pilot scale to produce electrical energy from wastewater. The key role players in this technology that leads to the operation are microbes, mainly bacteria. The dominant among them is termed as "exoelectrogens" that have the capability to produce and transport electron by utilizing waste source. The current review focuses on such electrogenic bacteria's involvement for enhanced power generation of MFC. The pathway of electron transfer in their cell along and its conduction to the extracellular environment of the MFC system are critically discussed. The interaction of the microbes in various MFC operational conditions, including the role of substrate and solid electron acceptors, i.e., anode, external resistance, temperature, and pH, was also discussed in depth along with biotechnological advancement and future research perspective.

Keywords Exoelectrogen · Microbial fuel cell · *Geobacter* · *Shewanella* · *E. coli* · *Pseudomonas*

Introduction

Microbial fuel cell (MFC) is a microbial-assisted process for the direct conversion of stored chemical energy in organics to electrical energy (Kang et al. 2015; Kang et al. 2017; Kim et al. 2017; Mukherjee and Saravanan 2019; Rabaey and Verstraete 2005). The demand for renewable power production pinned the interest in the MFC technology. Since the MFC functions in the presence of microbes (biocatalyst), it accomplishes wastewater treatment and organic waste deterioration too (Mukherjee et al. 2018). This technology is subclassified into two types, namely single- and dual-chambered depending upon the reactor configuration (Mukherjee and Saravanan 2019). In general, an anoxic condition is maintained in the anode section of the dual-chambered, while the same is omnipresent in single-chambered (Logan 2009; Mukherjee and Saravanan 2019). The microbes present in the anode chamber catabolize the complex organic compounds into carbon dioxide and water releasing electrons and protons (Rabaey and Verstraete 2005). Thus, generated electrons are then transferred to the anode, which acts as an electron acceptor for the overall reaction to take place (Kang et al. 2015). The anode must possess the highest potential for the electron transfer to take place (Kang et al. 2015). Though a variety of mechanisms are preferred for this electron transfer, direct electron transfer (DET) and indirect electron transfer (IET) were considered as the two potential pathways (He et al. 2015; Mukherjee and Saravanan 2019). DET mechanism transfers the electrons via physical contact with the bacteria to the anode via pili or c-type cytochromes (Kumar et al. 2016). These types of microbes are also known as anodophiles or anode-respiring bacteria, and examples include *Geobacter sulfurreducens* and *Shewanella oneidensis.* On the other hand, the IET also known as mediated electron transfer (MET) utilizes mediators that act as electron conductor in the transfer process, and example include *S. oneidensis* (Kumar et al. 2016). The system may employ a single or mixed bacterial community. However, a common terminology of "exoelectrogens" is given to such electron-producing bacteria.

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Although these exoelectrogens are a constant in the MFC system, their chemical and biological interactions have not been fully understood. Although the enhancement in power production in MFC was initiated by the crucial advancement in the biological side, most researchers focused their aim on improving the materials, cell architecture, electrolyte, etc. The review focuses on the exoelectrogen species, metabolism, interaction with various MFC components, techniques for isolation, identification and characterization, and finally the recent biotechnological advancements with futuristic

Microbiology of MFC

Varieties of microbes have been found in MFC, of which some are well known while others have recently been acknowledged. Methods like 16sRNA analysis for identifying bacterial pure cultures and denaturing gradient gel electrophoresis (DGGE) for identifying the microbial community composition and dynamics are commonly employed for bacterial identification (Borole et al. 2009). Scanning electron microscopy (SEM), transmission electron microscopy (TEM), and confocal laser scanning microscope (CLSM) are utilized to understand the morphological biofilm development on the electrode. The commonly found bacteria in MFC along with their electron transfer mechanism in the cell are discussed below.

Geobacter

Geobacter sp. is the Gram-negative bacteria belonging to the phylotype Proteobacteria that form thick biofilms in habitable condition (Shi et al. 2019). To a large extent, they are found in anaerobic soils and sediments actively involved in the reduction of insoluble Fe(III) oxides (Sun et al. 2019). The NCBI (National Center for Biotechnology Information) hosts 21 different species of *Geobacter*; however, *G. sulfurreducens* strain was much more emphasized. The reason is being one of the earliest discovered MFC exoelectrogen, having a rapid growth rate and easily cultivable in the laboratory (Coppi et al. 2001). However, the strain lacks in MFC performance as it is not effective in the reduction of Fe(III) oxides and resulting in lower power production as compared to other species of the genus (Rotaru et al. 2015; Sun et al. 2014; Zhou et al. 2014). It was also observed that different species of the genus show different extracellular electron transfer (EET) pathways, but all the genomes have multi-hem c-type chromosome and conductive pili (e-pili) (Butler et al. 2010; Holmes et al. 2016; Lovley 2017). For instance, *G. sulfurreducens* strain use extracellular c-type cytochrome PgcA for Fe(III) oxide reduction, and OmcS facilitates electron transfer to Fe(III) oxide in thin biofilm anodes, while OmcZ is involved for thick anode biofilms (Aklujkar et al. 2013; Holmes et al. 2006; Inoue et al. 2010; Mehta et al. 2005; Nevin et al. 2009; Zacharoff et al. 2017), where else *G. metallireducens* lacks OmcS cytochrome and uses e-pili and another c-type cytochrome (Gmet_2896) for the same (Shrestha et al. 2013; Tremblay et al. 2012). The outer membrane of multi-heme c-type cytochromes OmcP (GSU2913) and OmcO (GSU2912) are inessential for the reduction of Fe(III) oxide in *G. sulfurreducens*, but in the case of *G. metallireducens*, their homologs (Gmet_0557 and Gmet_0558) are mandatory for Fe(III) oxide respiration (Aklujkar et al. 2013; Smith et al. 2013). Some species like *G. bemidjiensis*, although having e-pili and OmcZ cytochrome, are incapable of electron generation (Nevin et al. 2005; Rotaru et al. 2015; Sun et al. 2019).

In a common mechanism for EET expressed by *Geobacter*, the extracellular substrate is used as a terminal electron acceptor. The pathways follow the conduction of electron from the quinone/quinol pool in the inner membrane to the periplasm and finally across the outer membrane to the extracellular environment (Lovley et al. 2011; Shi et al. 2007). Two inner membranes composed of c-type cytochromes and cytochrome c (ImcH) and a cytochrome protein with b- and c-type domains (CbcL) appear to be involved in the early steps of electron transfer to extracellular substrates in *G. sulfurreducens* (Levar et al. 2014; Levar et al. 2017; Zacharoff et al. 2016). A distinctive electron transfer (ET) component of the species is pilin monomers that enable the electrical conductivity in them. The subunits of e-pili were proteins built by aromatic amino acids in specific regions of its surface (Sun et al. 2019). This feature allows thick biofilm growth, and a study has also found that due to such thick attachment, the electricity production by *G. sulfurreducens* was 1047% more than that of *Shewanella* species (Engel et al. 2019). In contrast, the porin-cytochrome (Pcc) protein complex transfers the electron from the outer membrane to the electrolyte in the majority of *Geobacter* species (Liu et al. 2014; Shi et al. 2014). Diagram showing this is presented in Fig. 1a–e.

Shewanella

It is a facultative anaerobe also belonging to the Gammaproteobacteria class found in both aquatic (fresh and marine) and soil environment (Fredrickson et al. 2008). The genus is widely popular owing to its respiratory versatility that enables the utilization of varieties of organic and inorganic substances, including anode (Kouzuma et al. 2015). However, the characteristic of a lack of thick biofilm formation reduces its versatility (Sun et al. 2019). The most widely used among the family is *S. oneidensis* as they can respire using dimethyl sulfoxide (DMSO), fumarate, nitrate, nitrite, N-oxide, and anthraquinone-2,6-disulfonate, oxygen, thiosulfate, trimethylamine sulfur, as well as both solid and soluble metals including chromium, cobalt, iron, manganese,

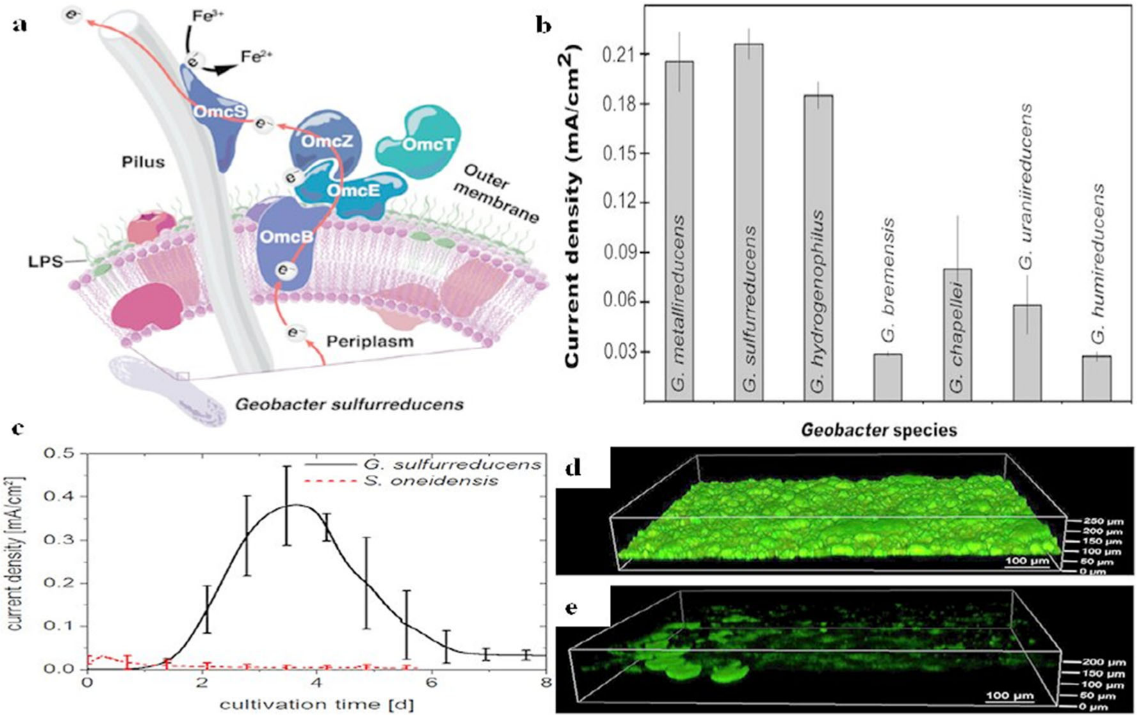

Fig. 1. **a** ET mechanism of *Geobacter sulfurreducens* (Wang et al. 2019). **b** Comparative range of power density produced by various *G. species* showing highest for *G. sulfurreducens* (Rotaru et al. 2015). **c** Comparative study of *Geobacter* and *Shewanella* showing better current generation by *G. species* (Engel et al. 2019). **d** Confocal laser scanning microscope images of *Geobacter* on graphite anode (Engel et al. 2019) showing thick biofilm growth compared to **e.** of *Shewanella* showing thin biofilm growth (Engel et al. 2019).

technetium, uranium, and vanadium as electron acceptors (Fredrickson et al. 2008).

The major pathway followed by them for electron transfer is known as Mtr pathway consisting of mainly 5 protein components (CymA, MtrA, MtrB, MtrC, and OmcA) (Kouzuma et al. 2015). The Mtr protein is capable of ease converting flavin into soluble electron that shuttles for ET from an inner membrane cytochrome (CymA) to the MtrCAB porin-multiheme c-type cytochrome complex (Shi et al. 2016; Shi et al. 2019). The EET is dominated by their outer membrane extensions with multi-heme c-type cytochromes (c-Cyts) via multistep hopping mechanism (El-Naggar et al. 2008; El-Naggar et al. 2010; Gorby et al. 2006; Gorby et al. 2008; Pirbadian and El-Naggar 2012; Pirbadian et al. 2014; Subramanian et al. 2018; Xu et al. 2018). On the bacterial surface, MtrC and probably OmcA transfer electron to the electrode surface either directly or indirectly via electron shuttle flavins (Kouzuma et al. 2015). The ET can also occur from the electrode surface to quinone in the cytoplasmic membrane through the same pathway. Furthermore, the electron transfer reactions to anodes are dominated by MtrC, and solid surface attachment is promoted by OmcA (Coursolle et al. 2010; Mitchell et al. 2012).

Studies have also suggested that both DET and MET are adopted by the species of the family. The DET involves the direct electron transferring from c-Cyts to the solid electron acceptors (anodes) (Kouzuma et al. 2015). In the case of MET, the electrons are transferred via electron-shuttle compounds, such as flavins. It has been reported that purified OmcA and MtrC proteins in MR-1 conduct the electrons to crystalline Fe(III) oxides and graphite anodes in the DET process. In the case of MET, MR-1 can reduce Fe(III) oxides located away from the cells without direct contact. And the species also secrete riboflavin and flavin mononucleotide (FMN), which function as electron shuttles. However, regardless of the pathway followed, soluble flavin secretion is inevitable in the ET by the family (Kouzuma et al. 2015; Roy et al. 2012). The schematics of ET and power performance of *S. oneidensis* strains are shown in Fig. 2.

Escherichia coli

Again it is a facultative anaerobe of class Gamaproteobacteria mainly found in the lower intestine of warm-blooded organisms. The capability of the *E. coli* to utilize a number of organic compounds as a substrate for electron production makes it a viable MFC biocatalyst (Ojima et al. 2020; Qiao et al. 2008; Zhang et al. 2008). However, *E. coli* cannot directly transfer the electron produced in the cell, and electron mediators are necessary for their operation (Qiao et al. 2008). The absence of a direct ET pathway makes it unfamiliar as compared to *Shewanella oneidensis* or *Geobacter sulfurreducens* (Ojima et al. 2020). This has led to gene modification that enables direct ET pathway thereby improving electron transfer

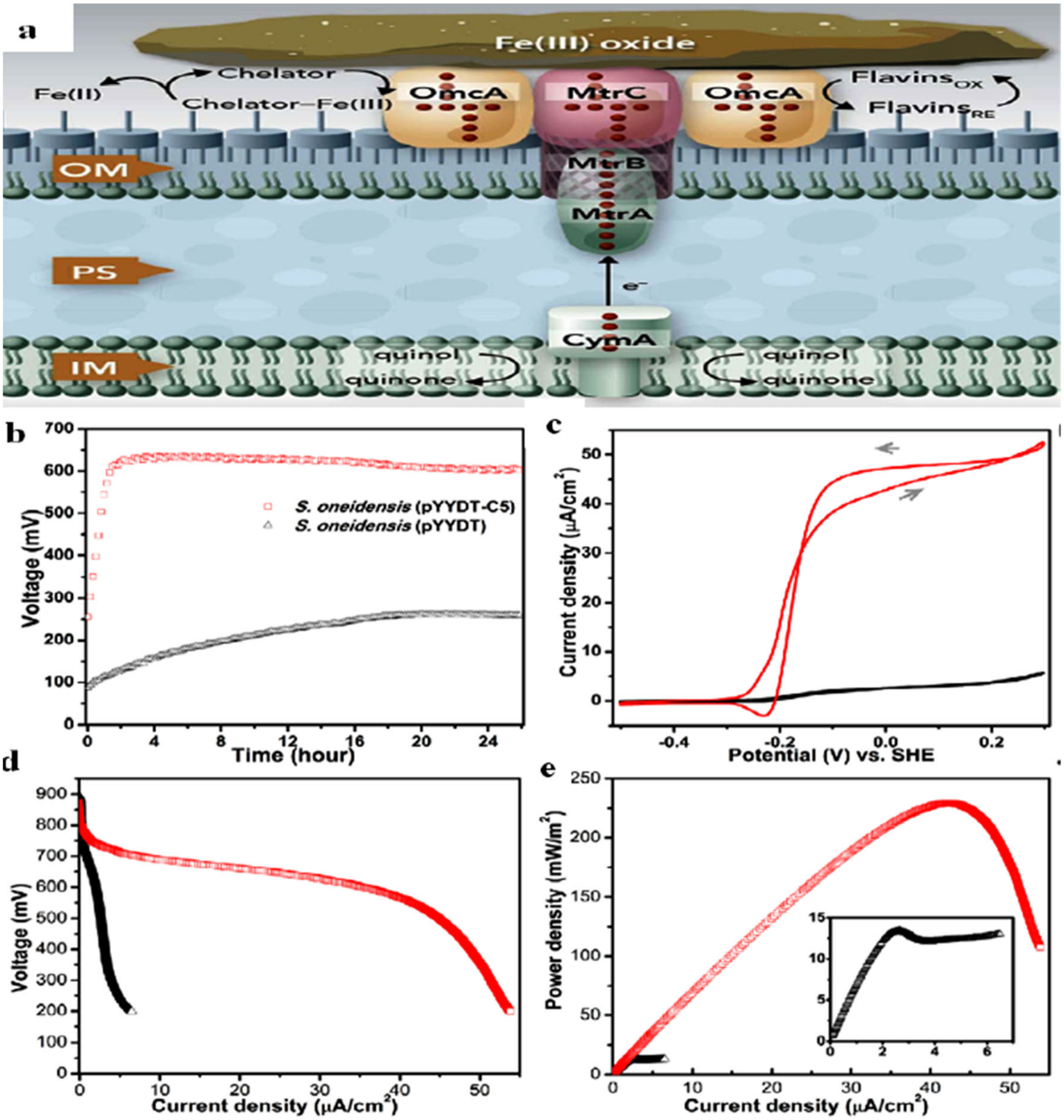

Fig. 2. **a** ET mechanism of *S. oneidensis* (Shi et al. 2012). **b** Voltage output graph of *S. oneidensis* strain wild type in black and flavin modified strain of *S. oneidensis* in red (republished with permission from Yang et al. 2015) **c** CV graph of *S. oneidensis* strains (republished with permission from Yang et al. 2015). **d** Polarization curve *S. oneidensis* strains (republished with permission from Yang et al. 2015). **e** Power density curve of *S. oneidensis* strains (republished with permission from Yang et al. 2015).

rate to the anode (Ojima et al. 2020). MFC involving *E. coli* produced hydroquinone-type endogenous compound. This compound was responsible for the direct electrochemical redox behavior of *E. coli* cells. The study proposed a membrane-related mechanism for the quinone excretion as followed by mature *E. coli* cells (Qiao et al. 2008). The figure showing the mechanism and growth of the *E. coli* cells were reproduced in Fig. 3a–b.

The *E. coli* cells are also commonly found in mixed cultures in wastewater and are often used in co-culture studies aiming at performance enhancement. Figure 3c and d establish that the co-culturing activity of *E. coli* with other exoelectrogens improves the power performance of the MFC.

Pseudomonas

Pseudomonas species are among the well-known exoelectrogenic bacteria that utilizes redox-active metabolites for electron production and transferring (Qiao et al. 2015). *Pseudomonas aeruginosa*, for example, produces pyocyanin (PYO) and 1-hydroxyphenazine (OHPHZ) as secondary metabolites for facilitating ET (Bellin et al. 2014; Chen et al.

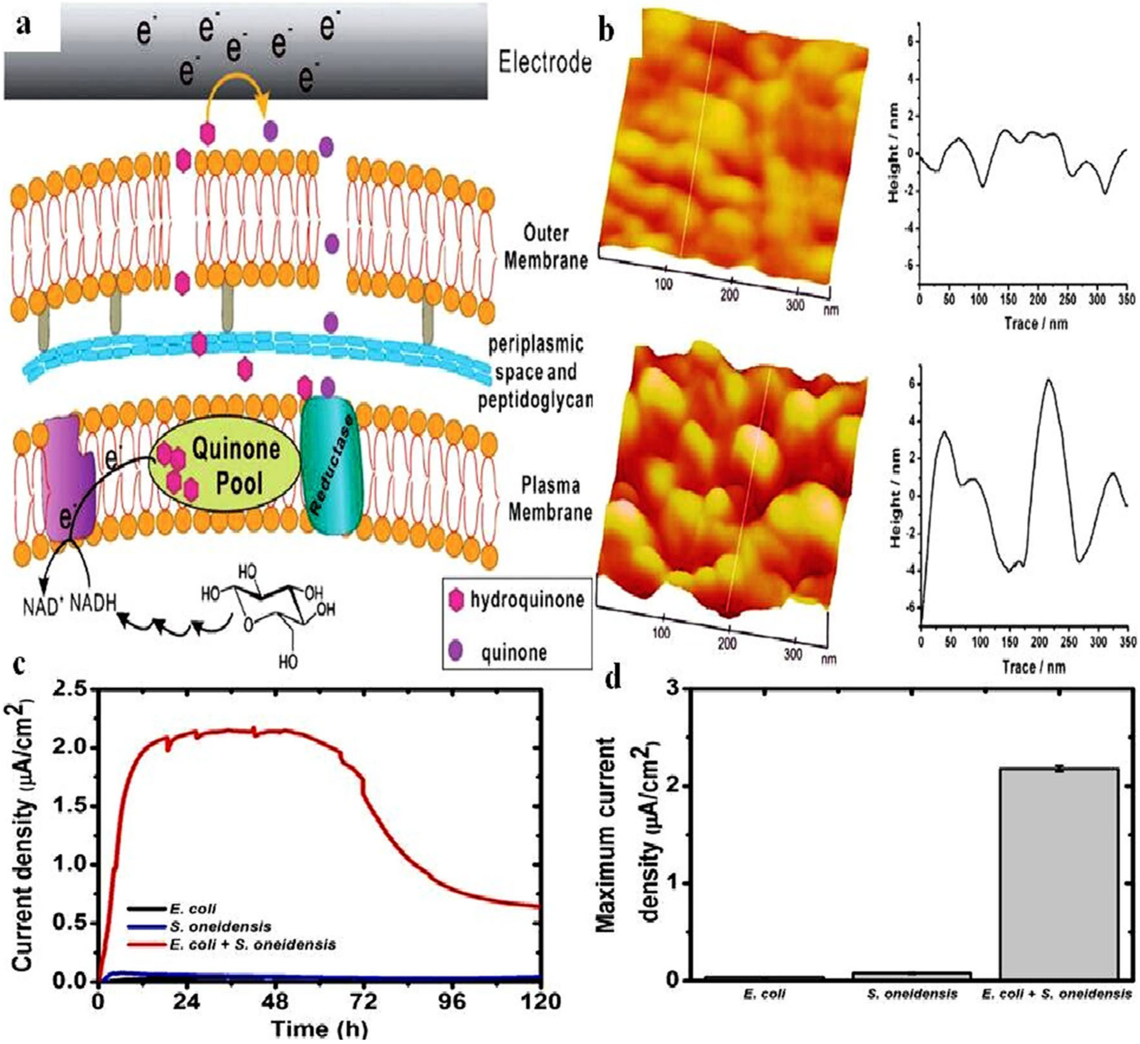

Fig. 3. **a** EET mechanism of *E. coli* (Qiao et al. 2008). **b** AFM topography and section analysis of original and matured *E. coli* cells showing rougher and thicker biofilm growth evolved in *E. coli* cells (Qiao et al. 2008). **c** and **d** The current density performance of pure *E.coli* cells with co-culture growth showing better performance in co-cultures (republished with permission from Wang et al. 2015).

2015). It has also been found in a study by Yong et al. that the overexpression of methyltransferase encoding gene phzM, i.e., one of the dominant genes responsible for PYO biosynthesis, can enhance PYO production. The accelerated PYO production by such genetic mutation significantly improved electrocatalytic activity (Yong et al. 2014a, 2014b). Similarly, Shen et al. (2014) reported that sophorolipid addition promotes bacterial membrane permeability, simultaneously enhancing PYO secretion, thereby improving overall MFC performance (Shen et al. 2014). The increment in phenazines excretion is also studied to produce a positive role in *P. aeruginosa* performance in MFCs. However, the details of these in the cellular mechanism of *P. aeruginosa* are not well defined. The lack of real-time detection of the metabolites during cell operation leads to non-clarity of the mechanism by *Pseudomonas*. Moreover, the *Pseudomonas* species are mainly applied in co-culture either with other exoelectrogens or in mixed cultures. The metabolites supplied by *Pseudomonas* improve the ET in the mixed cultures contributing to MFC performance. The SEM image of *P. aeruginosa* in the initial stage and after acclimatization in the anode is shown in Fig. 4 a and b. The ET mechanism is shown in Fig. 4c, and the power performance and electrochemical activity of *P. aeruginosa* in MFC are represented in Fig. 4d and e, respectively.

Rhodoferax

Rhodoferax is an anoxic genus of Betaproteobacteria belonging to the Comamonadaceae family. It utilizes Fe(III) as an electron acceptor for the oxidation of glucose to CO_2, releasing electrons and falls under metal-reducing bacteria possessing DET (Chaudhuri and Lovley 2003; Schröder 2007). *Rhodoferax* has been reported to produce electricity from different types of sugars like glucose, fructose, xylose,

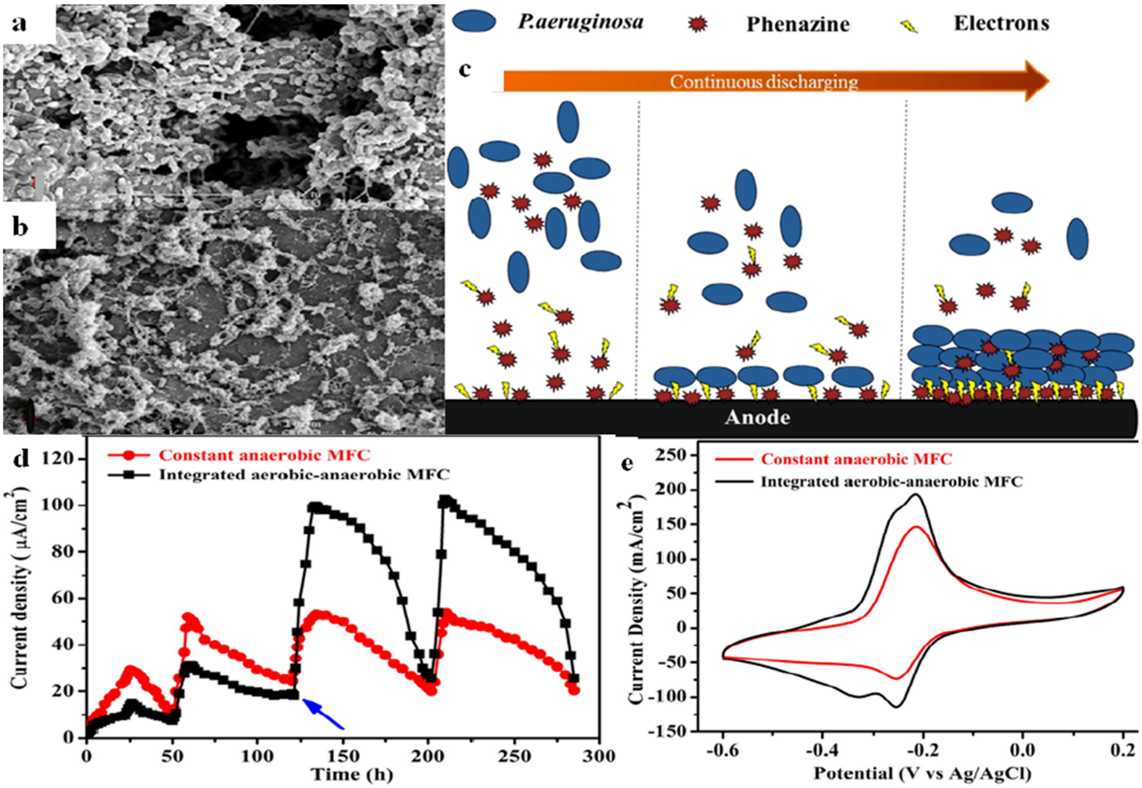

Fig. 4. **a** SEM image of *P. aeruginosa* biofilm at 72 h (Read et al. 2010). **b** SEM image of *P. aeruginosa* biofilm at 144h showing attachment and clustering at the anode (Read et al. 2010). **c** ET mechanism of *P. aeruginosa* (republished with permission from Qiao et al. 2015). **d** Current density performance of *P. aeruginosa* in anaerobic and integrated aerobic-anaerobic MFC (republished with permission from Yong et al. 2017). **e** Cyclic voltammogram of *P. aeruginosa* in anaerobic and integrated aerobic-anaerobic MFC (republished with permission from Yong et al. 2017).

and sucrose. A major advantage of *Rhodoferax* over other bacteria was its conversion of 80% glucose for electricity (Chaudhuri and Lovley 2003). Other microbes, including *Geobacter* and *Shewanella* species, are incapable of utilization of glucose as sole substrate and depend on fermentation by other microbes for the conversion of glucose to low organic acids and alcohols for usage (Chaudhuri and Lovley 2003).

Others

Some other microbes are also highly found in MFC cells that work as exoelectrogens, but the mechanism is not thoroughly studied. Exoelectrogen like *Comamonas* of Comamonadaceae family is one of them having the same family as *Rhodoferax* and similar mechanisms like *Pseudomonas* (Mukherjee and Saravanan 2020). *Desulfovibrio desulfuricans* have also shown an electrogenic response in MFC using microbial nanowires as a DIET mechanism (Kumar et al. 2016). *Klebsiella pneumoniae* is another Gammaproteobacteria found in various MFC cells. *Clostridium* sps. of the phylum Firmicutes are also a common occurrence in many mixed cultures and active in bioelectricity generation (Chandrasekhar et al. 2020). Table 1 lists variously studied exoelectrogens with their advantages and limitations.

Interaction of exoelectrogens with MFC parameters

The activities of the exoelectrogens discussed above however is dominated by the MFC reactor parameters. The MFC system mainly comprises of anode, anolyte, membrane, cathode, and catholyte. The anode and anolyte in combination with microbes make the oxidation half-cell, and the cathode and catholyte makes the reduction half-cell, while both were separated by a membrane. These two half sections were connected by wire and external resistance to ensure the circuit for the flow of electrons from the anode to the cathode section. The exoelectrogens dominate the oxidation half-cell and hence are influenced by the anode and anolyte used in the MFC. The anolyte comprises of substrate used for microbial growth. Apart from the anode and substrate, reactor operating conditions like temperature, pH, external resistance used, or external forces like magnetic field also influences the

Table 1 Variously studied exoelectrogens with their advantages and limitations

Sl. No	Taxon	Species	Advantage	Limitation	Ref
1.	δ-Proteobacteria	*Geobacter sulfurreducens*	Thick biofilm formation	Adequate for acetate oxidation but requires fermentative microbes for complex substrates	(Sun et al. 2019)
		Geobacter metallireducens	Can use complex substrates like butanol, ethanol, toluene, pyruvate, etc. as carbon source	Absence of OmcS homologs	(Aklujkar et al.
	2009;Sun et al. 2019)				
2.	γ-Proteobacteria	*Shewanella oneidensis*	Possess both DIET and MET mechanism	Thin biofilm growth	(Sun et al. 2019)
		Pseudomonas aeruginosa	Produces metabolites for electron transfer	Native pili of *P. aeruginosa* is a poor conductive that cannot be used for DET	(Liu et al. 2019)
		Escherichia coli	Can form co-culture with several species	Prolonged acclimatization time	(Qiao et al. 2008, Wang et al. 2015)
4.	Firmicutes	*Clostridium butyricum*	Can utilize starch, glucose, lactate, and molasses as a substrate	Require mediators, low power production	(Kumar et al. 2016; Niessen et al. 2004)
		Clostridium beijerinckii	Can use acetone, butanol, ethanol as substrate	Mediators required, low power production	(Liu et al. 2015)

exoelectrogenic bacteria growth and activity. The present section deals with the different reactor condition's influence on exoelectrogenic activity.

Influence of substrate

The electrogenesis of complex organic matter in the electrolyte by the microbes is the mechanism that results in electron generation for the overall power production. The exoelectrogens can directly utilize organics like acetate as substrates for electron production whereas complex substrates like glucose and lactate may require fermentation before bacterial utilization. These substrate interactions also lead to substrate-specific anodic communities (Kiely et al. 2011a). A predominance of *Geobacter* is seen in acetate-fed cells, and it is also seen that acetic acid electron donor supports a high range of exoelectrogens. Also, acetate being one of the simplest organics supports a wide range of microbes and hence mostly preferred in MFCs operation (Jung and Regan 2007; Mukherjee and Saravanan 2020; Xing et al. 2009).

Lactate needs to be fermented first by the bacterial group before being utilized as a substrate. The fermentation of lactate produces acetate and propionate in a 1:2 molar ratio (Kiely et al. 2011a). Lactic acid has been used as a substrate for culturing by *S. oneidensis* in MFC operation (Logan et al. 2005). The propionate carbon source supports large communities of Gram-positive microbes, mainly Firmicutes (Chae et al. 2009). Butyrate-supplied MFCs favor *Pseudomonas and Bacillus* sp. (Freguia et al. 2010). Although the power production of butyrate is half of that using acetate, and its low degradability compared to that acetate or propionate makes it is unsuitable as an MFC substrate. The presence of acetate in low concentration in the end product of butyrate-fed MFCs suggests the possibility of fermentation of butyrate to acetate (Kiely et al. 2011a). The bacterial community dominant in the substrate was similar to that of propionate.

Ethanol has also been utilized as a substrate as it can be fermented to generate acetic acid. Syntrophic interaction is used for the conversion of ethanol to electricity. Ethanol-fed MFC study has shown the dominant presence of the *Geobacter* community. The Betaproteobacteria also dominates the ethanol-fed MFCs (Kiely et al. 2011b; Kim et al. 2007). On the other hand, formic acid is less efficient in MFCs performance as compared to acetic acid, ethanol, and lactic acid due to its interaction with microbes (Kiely et al. 2011b). The community profiling data had suggested three possible formic acid conversion for electricity generation by exoelectrogens. The first is the direct oxidation of formic acid by *Desulfitobacterium hafniense* DCB2 in the presence of mediators like humic acids or anthraquinone-2,6-disulfonate (Milliken and May 2007). The second involves syntrophic interactions by microbes mainly homoacetogens for acetate formation from formic acid (Ha et al. 2008). The third archetype requires microbe *Paracoccus denitrificans* that oxidizes formate to hydrogen. This microbe utilizes formate dehydrogenase for the oxidation of formate to produce carbon dioxide and hydrogen. Thus, generated hydrogen molecules are then converted into an electron by Geobacteraceae to deliver electricity (Bond and Lovley 2003).

Simple carbohydrate (glucose)-fed MFCs also rely on the syntrophic process for electricity production employing the fermentation process. The fermentation leads to the production of several by-products like acetate, propionate, and hydrogen (Kiely et al. 2011a). In contrast complex carbohydrates like cellulose requires step like hydrolysis, fermentation, and electrolysis its MFC usage. It has been reported that *Enterobacter cloacae* are able of producing electrons from cellulose substrate (Rezaei et al. 2009). Further, a study has also demonstrated that the co-culturing of fermentative and exoelectrogenic bacteria together for cellulose usage resulted in the generation of high power density. The by-products formed by cellulose fermentation include acetate, ethanol, and hydrogen (Ren et al. 2007).

The substrate concentration also influences ammonia inhibition in the MFC system (Tice and Kim 2014). It is reported that a highly concentrated wastewater used in MFC inoculation contained a high amount of ammonia which negatively affected the exoelectrogens growth. Under low substrate concentration in such ammonia concentrated wastewater, the exoelectrogens activity is limited, leading to deprived power production. On the other hand, under high substrate conditions, the exoelectrogens resist the ammonia influence on their metabolism resulting in improved and stable power production. The higher substrate conditions resulted in the continuous production of H^+ ion by the oxidation of the substrate. The presence of excess H^+ ion drastically declines the pH of the anolyte, and under such lower pH conditions, ammonia (NH_3) exists as ammonium (NH_4^+) ion that is less toxic than NH_3 (Tice and Kim 2014).

The simpler the substrate, the easier is its oxidation by exoelectrogens releasing electron and proton. Utilizing pure cultures reduces the start-up time and aids thick biofilm growth in such case (Ullah and Zeshan 2020). However, in case of complex substrate, much more steps are involved in its oxidation influencing the start-up time and exoelectrogenic metabolism (Zhao et al. 2017). Hence, in such case, a mixed or co-culture species are more beneficial for high power generation (Li et al. 2018). The substrate utilization by exoelectrogens are calculated using Monod's equation shown below.

$$j = j_{max} \frac{S}{K_{s,app} + S} \tag{1}$$

where j is the current density obtained, j_{max} is the maximum current density of the biofilm, S is the concentration of substrate present, and $Ks_{,app}$ is the apparent half-saturation substrate concentration in a biofilm (Torres et al. 2010).

Influence of temperature

The temperature range of 4 °C to 45 °C is reported to be active for the anodic biofilms (Jadhav and Ghangrekar 2009; Patil et al. 2010). Both the biofilm establishment and its performance depend on the initially available temperature of the reactor. Temperature variation study showed that 35 °C was an ideal temperature for MFC operation. In a study on the development of microbial growth on anode surface, it was estimated that biofilm formation time decreased with an increase in temperature, 35 °C for 3.5 days as compared to 15 °C for 40 days (Patil et al. 2010). The spike in temperature from 30 to 45 °C found that the isolates *Proteus* sp. (N6) and *Candida parapsilosis* (S10) demonstrated the highest power densities in the range between 35 and 40°C (Nwagu et al. 2019).

In a psychrophilic MFC system, the electrogenic biofilm grows between −20 and 25°C (Lu et al. 2019). A maximum power density was delivered at 25°C; however, maximized chemical oxygen demand (COD) removal was obtained at 10°C. Moreover, it was also concluded that the pre-treated inoculum at varied temperatures determined the microbial communities on the anode surface. The bacterial population was dominated by *Geobacter* community having a relative abundance of 17–70% varying with the varied pre-acclimated temperature along with the presence of *Arcobacter*, *Dechloromonas*, *Janthinobacterium*, *Limnohabitans*, and *Sejongia*. It has also been found the *Geobacter* species were also majorly present at the lowest temperature (4°C) with a varying population of *Accumulibacter*, *Caldilinea*, *Candidatus Desulfobulbus*, *Methylibium*, and *Nitrospira* (Lu et al. 2019).

In some studies, thermophilic MFC operating at a temperature higher than 40 °C has gained interest. This system operates with microbes like *Calditerrivibrio nitroreducens*, *Thermincola ferriacetica*, and *Thermincola potens* (Fu et al. 2013; Marshall and May 2009; Wrighton et al. 2011). These bacteria utilizes exogenous mediators for the electron transfer for bioelectricity production. A recent study has demonstrated MFC operation as high as 95 °C (Fu et al. 2015).

It has been demonstrated by researchers that for macro and mesoscale MFCs, the *Geobacter* domination exhibits maximum power at a temperature between 25 and 30°C. However, in the case of micro, the optimal temperature range increases and ranged between 49 and 53°C (Ren et al. 2017). This was reasoned due to the limited electron transfer from cytochrome c of the *Geobacter* species when scaled down to micro. It was clarified that with an increase in temperature the cytochrome c contributing to electron transfer also increases leading to high-temperature activation in miniaturized MFCs (Ren et al. 2017).

The temperature variation showed a direct relationship with electrode potential where with a decrease in temperature the cathode potential decreased leading to lower power generation (Gadkari et al. 2020). It also leads to changes in ohmic losses. Thus, the operating temperature thus not only influences the microbial species present in the system but also influences the conductivity of the anolyte, activation energy, and diffusion coefficients further affecting the charge transfer rate (Oliveira et al. 2013; Nouri and Najafpour 2017). Therefore it is concluded that the temperature is a crucial parameter in determining the exoelectrogenic metabolism and start-up time and losses associated with influencing power performance in the MFC system

Influence of pH

pH certainly affects the microbial kinetics and hence is one of the deciding factors for the type of microbes present in the anodic chamber (Nwagu et al. 2019; Cheng et al. 2011). The pH of the system mostly depends upon the substrate used; a highly fermentable substrate leads to the formation of acidic products (Ren et al. 2007). Hence buffer is added to maintain neutral pH in most MFC operation. It has also been found that *Shewanella* can operate at pH as low as 5 (Biffinger et al. 2008). It has also been found in research that the growth and metabolism of *Geobacter sulfurreducens* are negatively affected by a change in pH from neutral to acidic (Franks et al. 2009). A biodegradation experiment employing *Klebsiella* sp. at various pH ranges (5,7, and 10) in MFC found that the neutral pH leads to the highest biodegradation (Holkar et al. 2018), while in the pH variation from 6.0 to 9.5, pH 8.5 produced the highest power generation in the MFC. Bacteria like *Clavispora lusitaniae*, *Candida parapsilosis*, and *Clavispora lusitaniae* dominated the chamber suggesting that alkaline pH is more preferred for MFC operation (Nwagu et al. 2019).

In a recent study, an alkaliphilic electrogenic bacteria (*Bacillus alkalogaya* BW2) was identified and utilized for MFC operation. It is a new culture used in MFC operation at pH as high as 10. The culture was able to utilize both acetate and lactate as substrate and produced higher voltage at pH 10. This extreme pH operation leads to future opportunities for utilizing high pH industrial wastewater as substrate (Dhundale et al. 2020).

In general it can be concluded that an acidic pH negatively impacts the voltage efficiency due to the negative impact on the exoelectrogens metabolism. Studies showed that under low pH conditions, the oxidation of substrate is incomplete releasing lower electron species and leads to concentration over potential (Ou et al. 2017). For instance a lower pH between 5 and 7 can be sustained by exoelectrogens, but power production was drastically affected (Babauta et al. 2011; Ou et al. 2017). Below this pH, concentration losses can occur in the anode chamber. It is also proved that pH influences the proton transport from anode to cathode. A low pH leading to increased acidity also decreases the resistance of the proton exchange membrane. The substrate oxidation is higher in neutral pH conditions indicating neutral pH is the best favored by exoelectrogens (Ou et al. 2017).

Influence of external resistance

It is established that the maximum performance of an MFC can be achieved only when the external resistance equates to its internal resistance. It also affects the anodic biofilm formation. A study on the effect of external resistance on anodic community found that lower external resistance of 100 Ω produced simpler DGGE patterns, whereas the band patterns were considerable in case of higher resistance (Katuri et al. 2012). The biofilm produced by *S. oneidensis* MR-1 was ca. 50 μm thick in case of high resistance (1MΩ) applied anode and was only ca. 5 μm in case of the anode with 100 Ω resistance (Mclean et al. 2010). In another study, external resistance of 20, 200, 470, and 1000 Ω was optimized for 10days, and its influence on exoelectrogens and methanogens distribution was seen (Cai et al. 2018). It was determined that the lower external resistance leads to enhanced dominance of exoelectrogens and limits methanogens growth (Cai et al. 2018).

Zhang et al. showed the influences of the external resistance (10, 50, 250, and 1000 Ω) on the start-up of MFC and biofilm growth. Their reports substantiated that the lower resistance, the start-up time is higher (3days), and under higher external resistance, the start-up time is lower (0.6 days). Their study also confirmed that it would be difficult to start-up an MFC at very low resistance (10Ω) due to unstable anodic potential. Hence, they suggested to start-up the MFC at higher external resistance and then gradually reduce the resistance to obtain higher power performance. It was also revealed that at decreased external resistance, better energy output with thick biofilm formation can be achieved (Zhang et al. 2017).

Study by Cai and co-workers showed that the lower resistance was beneficial for a thick exoelectrogenic biofilm formation (Cai et al. 2018). A number of external resistance were used (20, 200, 470, and 1000 Ω), and its effect on microbial composition and metabolism was studied. It was seen that at higher external resistance, the exoelectrogens bacterial population decreased and the methanogens population increased in the reactor. However, at lower resistance, the exoelectrogens were dominant and leading to more power production (Cai et al. 2018). Their study also discuss on the anode potential where notable such potential was observed at lower external resistances. Such change in anode potential can also change the microbial community present (Cai et al. 2018). Anode potential being an electromotive driving force leads to the electron flow from a bacterial cell to the anode and further to cathode from anode. Lower the external resistance used, the higher is the current generation and substrate oxidation thus enhancing chemical oxygen demand removal rate. (Cai et al. 2018).

Influence of anode material

The pore structure, surface morphology, and properties like roughness and hydrophilicity are the main features affecting microbial acclimatization and stability in the MFC (Mukherjee and Saravanan 2019; Mukherjee and Saravanan 2020). The positively charged anode materials are generally more preferred by exoelectrogens (Kumar et al. 2016). Thus carbon-based anode is highly favorable as an anode in MFC (Mukherjee and Saravanan 2019). In a study, inoculated with *Shewanella putrefaciens*, the performance of an MFC was determined by the anode potential. The microbial growth and power performance increased with an incement in the positive potential of the system (Carmona Martinez et al. 2013), where else the surface functionalization of graphite anode materials with aryl-mannoside layers (provides high hydrophilicity) was also found to result in the accelerated start-up of MFC (Iannaci et al. 2020). Du et al. demonstrated that polydopamine utilization enhanced biofilm growth due to its super hydrophilic nature (Du et al. 2017). Further, their study substantiated that the inclusion of super hydrophilicity enhanced the growth of exoelectrogenic Proteobacteria and Firmicutes phyla leading to the superior performance of MFC (Du et al. 2017). It has also been suggested that the start-up time of MFCs can be minimized by the inclusion of such polymeric substances in the anode. Reports also showed that *Geobacter* colonization was favored by using polyaniline-modified graphene anode (Lin et al. 2019). The polymeric anode improves OmcZ expression level favoring advanced microbial colonization in the anode. The octaheme c-type cytochromes, OmcB, and OmcZ presence in number provided the pathway for electron transfer to the anodes (Lin et al. 2019).

It has also been studied that the exoelectrogens can convert non-conductive graphene to conductive form (Yoshida et al. 2016). The oxidized form of graphene, i.e., graphene oxide (GO), is found to enhance electron transfer to the reaction chamber in MFCs. The non-conductive GO can be made conductive by the microbial reduction of the material. The reduced form is simply stated as reduced GO (rGO), as the chemical identity is not detailed. It was revealed that the GO provided selective growth of the exoelectrogens on its surface. GO-respiring bacteria (GORBs) were hence obtained from the environment for the purpose. A composite with rGO and GORBs formed a conductive hydrogel showing preferable Geobacteraceae growth having 51–68% relative abundance. Secondly, *Azospira*, well-known acetate oxidizers, comprised 28–42% of the anodic species. *Shewanella* and *E. coli* along with mixed cultures were also capable of GO reduction (Akhavan and Ghaderi 2012; Salas et al. 2010). The redox protein and biomolecules like vitamin C of the ET were critically involved in the reduction (Fernandez-Merino et al. 2010). This insight shows that GO may probably serve as an electron acceptor from the microbial cell by the exoelectrogens favoring their acclimatization. It has also been identified that GO has antibacterial or bactericidal properties limiting their role in MFCs anode. Thus, further information on GO electrode is required for the possible mechanism followed by microbes. However, GO being more economic and hydrophilic provides better properties as MFC anode compared to graphene providing better bacterial attachment on its surface. The self-aggregation of GO to hydrogel on reduction in solution favors its stability and reusability as a terminal electron acceptor for exoelectrogens (Yoshida et al. 2016).

Recent trends focused on utilizing 3D anode material with high surface area and high surface to volume ratio for enhanced exoelectrogenic colonization and ease anolyte transfer in the anode for bacterial substrate (Mukherjee and Saravanan 2020). These 3D anodes are favored by anodophilic bacteria for colonization increasing exoelectrogens concentration in anode.

Influence of magnetic field

In general, magnets are a good conductor and are applied for various fields marking its entry into MFC operation as well (Li et al. 2018a; Zhou et al. 2019). The researches in MFCs have established that magnetic fields utilized in the system can promote power generation owing to oxidative stress and magneto-hydrodynamic effects produced by it (Tong et al. 2015). It has also been found that the magnetic fields affect biofilm growth and biodegradability (Łebkowska et al. 2011;

Wang et al. 2012). A weaker magnetic field is capable of increasing microbial growth by more than 40% (Yavuz and Çelebi 2000). In some instances, it was shown that bacterial diversity has declined under magnetic exposed conditions (Liu et al. 2008). It has been evident through researches that the cytochrome c-mediated bioelectrochemical transformations are also facilitated by its application (Katz et al. 2004; Katz et al. 2005). This in turn facilitates enhanced performance of the biofuel cells. A pulse electromagnetic field enhanced ET and favored *Geobacter* establishment on the anode surface resulting in higher efficiency (Zhou et al. 2017). The intensity of the magnetic field decides the stimulation and inhibition of biofilm growth (Zhou et al. 2019). However, an appropriate or optimum range of intensity for the enrichment of exoelectrogens has not yet been clarified, providing a new research stream for its application in MFCs. The direction of the magnetic field and its respective intensity are constantly changing in the case of a pulsed system, which leads to changes in aggregation and stability of the microbes (Zhou et al. 2019). However, in the case of a static, the direction and intensity remain the same leading to stable biofilm growth in MFCs. Several studies have been focused on a low stable magnetic field intensity on the anode side of MFCs showing positive results on power performance (Li et al. 2018a; Zhou et al. 2019). The enhancement is known to be due to stimulating enzyme activity of the exoelectrogenic community on the anode surface. In a recent study exploring magnetic fields effects on MFC performance and exoelectrogenic growth, magnets were used as anodes. Stable magnetic field intensities were achieved by utilizing different thermal-demagnetizing temperatures. The result obtained showed that both voltage and power production increased in the case of the magnetic anode and the diffusion resistance of the system is decreased due to the presence of a magnetic field (Zhou et al. 2019). The study also demonstrated a higher abundance of *Geobacter* growth in the magnetic MFC compared to the non-magnetic one (Zhou et al. 2019). The effect of low intensity stable magnetic field on mixed culture on anode showed that a magnetic field of (105 and 150 mT) on anodic biofilms significantly decreased the start-up time and hence enhanced the power generation of the single-chambered MFC (Li et al. 2018a). It also concluded that the application of the magnetic field enhanced the microbial conductivity likely due to the increment of the Geobacteraceae population (Li et al. 2018a). Table 2 presents the interaction of exoelectrogens for improved MFC performance.

Co-culturing and genetic modifications and new developments in exoelectrogens

The exoelectrogens can also form co-culture with other non-exoelectrogenic bacteria for better efficiency. For instance, *G. sulfurreducens* have been studied to form co-cultures with a number of other microbes for improving electron transport to the anode in the cell. Co-culture of *G. sulfurreducens-E. coli* showed improved power production compared to the pure culture of *G. sulfurreducens* (Qu et al. 2012). The improved performance of the co-culture is attributed to O_2 reduction by *E. coli* in the cell and DET by the *G. sulfurreducens* to anodes (Qu et al. 2012). Similarly, co-culturing demonstrated a higher conversion of methane to electricity. A genetically modified methanogen *Methanosarcina acetivorans* was used for the conversion of methane to acetate. This acetate was then further oxidized to produce electron by *G. sulfurreducens* for anode electron transfer. The transport of electron is also facilitated by *Paracoccus denitrificans* that produces redox molecules along with other microbes in the reactor (McAnulty et al. 2017).

In a co-culture study for ET mechanism by *Geobacter sulfurreducens* and *Pseudomonas aeruginosa*, it was revealed that the co-culture evolved to utilize the pathway between DIET and hydrogen IET (HIT) (Semenec et al. 2018). The co-culture was also capable of growing using formate and fumarate as substrate. It was also revealed by sequential window acquisition of all theoretical spectra (SWATH) and mass spectrometry studies that upregulation in HybA was seen in the co-cultures. This gene is critical for HIT pathway by *Geobacter* species. The study had also seen an increment in OmcS, PgcA, OmcC, and MacA genes required for *Geobacter* electron transfer metabolism (Semenec et al. 2018). The schematics showing the mechanism of conversion is shown in Fig. 5.

In another co-culture study, *S. oneidensis* MR-1 along with *Klebsiella pneumoniae* was utilized for glycerol oxidization as substrate. A pure culture of *S. oneidensis* MR-1 is incapable for glycerol metabolization; however, the syntropic culture was capable of electron generation. The *K. pneumoniae* oxidized the glycerol to lactate that was then oxidized by *S. oneidensis* MR-1 for electron generation (Li et al. 2018b).

C. ljungdahlii was genetically modified by heterogeneous expression of the formate dehydrogenase gene. This gene modification in the microbe results in the regeneration of nicotinamide adenine dinucleotide (NADH). This higher NADH pool the facilitated ease electron transfer leading to higher power production of the system (Han et al. 2016).

Feng and coworkers genetically modified *S. oneidensis* species for utilizing xylose as a carbon source (Li et al. 2017). The utilization of this wood sugar as a substrate in MFC for electricity generation benefited sustainability as it is one of the primary ingredients of lignocellulosic hydrolysis. It is also the second most carbohydrate biomolecule present after glucose. However, as discussed above, xylose is not effectively utilized by many microbes and is limited by a slow consumption rate due to inefficient metabolism. The genetic modification within the study was enforced by collecting one

Table 2 Exoelectrogens interaction in MFC for power production.

Sl. no	Exoelectrogen	Substrate	Anode	Max. current density	Max. power density	Ref
1.	*Geobacter* sp.	Acetate	Graphene/polyaniline modified carbon cloth	~1100mA/m^2	~300mW/m^2	(Lin et al. 2019)
2.	*Geobacter* sp.	Acetate	Cylindrical neodymium iron boron (NdFeB) magnets	~0.6A/m^2	0.57 W/m^2	(Zhou et al. 2019)
3.	*S. oneidensis GS*	Xylose	Carbon cloth	~50mA/m^2	~2.1 ± 0.1 mW/m^2	(Li et al. 2017)
4.	*Clostridium ljungdahlii*	Sodium formate	Carbon felt	400mA/m^2	35 mW/m^2	(Han et al. 2016)
5.	*Klebsiella* sp.	Glucose	Graphite anode	533 mA/m^2	84 mW/m^2	(Holkar et al. 2018)
6.	*Escherichia coli*	Glucose	Carbon fiber bundles	NA	0.27 mW/cm^3	(Ojima et al. 2020)
7.	*Pseudomonas aeruginosa*	Glucose	Carbon brush	0.06μA	NA	(Qiao et al. 2015)
8.	*Rhodoferax ferrireducens*	Glucose	Graphite foam	74 mA/m^2	NA	(Chaudhuri and Lovley 2003)
9.	*Klebsiella pneumoniae-Shewanella oneidensis*	Glycerol	Carbon cloth	~70mA/m^2	19.9 mW/m^2	(Li et al. 2018b)
10.	*Escherichia coli-Geobacter sulfurreducens*	Acetate	Graphite fiber brush	~5.5mA/m^2	918±27 mW/m^2	(Qu et al. 2012)

in every of the wood sugar transporters from fungus intermedia (*Candida intermedia*)and true bacteria (*Clostridium acetobutylicum*) with one wood sugar metabolic pathways from the enzyme pathway from *E. coli* and also the enzyme pathway from *Scheffersomyces stipites*. It was found that the strain generated by modifying *C. intermedia* and *S. stipites* as xylose facilitator and xylose oxidoreductase respectively showed the highest result (Han et al. 2016).

A new species of *Geobacter* (*Geobacter anodireducens*) has been isolated for producing high power performance in

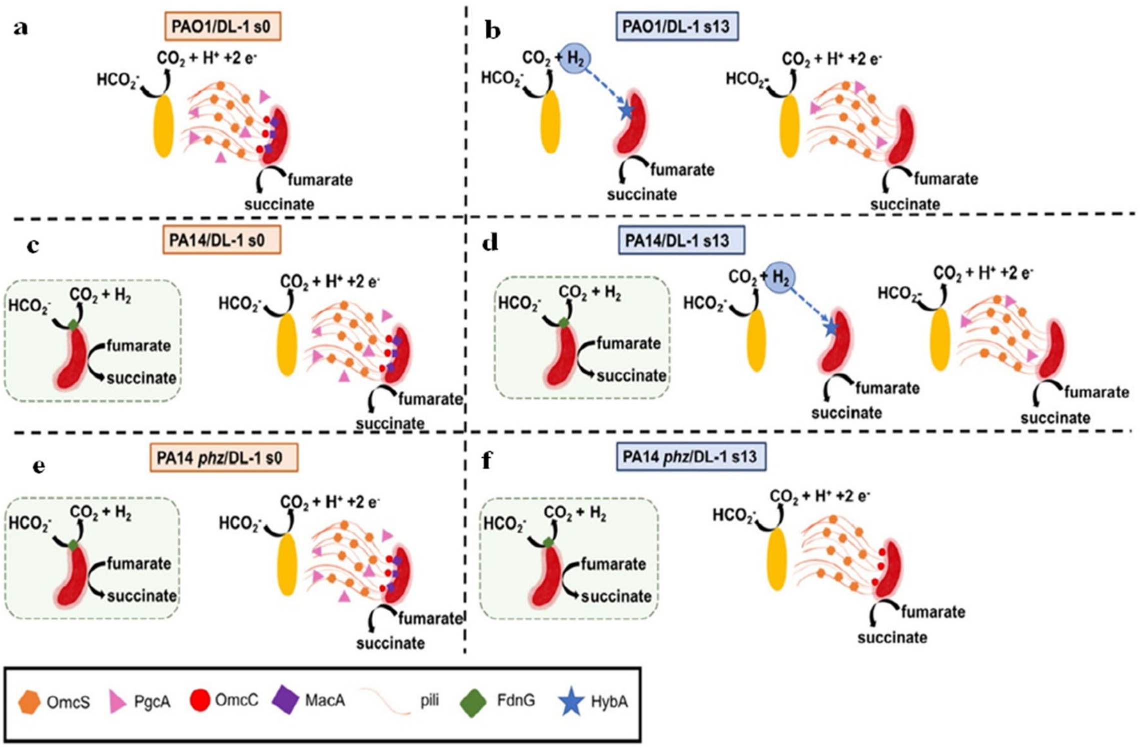

Fig. 5 Proposed ET mechanism in the co-culture of *G. sulfurreducens* DL-1 strain (red cells) and *P. aeruginosa* PAO1, PA14, and PA14 phz strains (yellow cells) throughout evolution for electron production (republished with permission from Semenec et al. 2018).

excessive salt conditions (Sun et al. 2019). The *G. anodireducens* species has about 81 of the 87 c-type cytochromes homologous as compared to *G. soli* and *G. sulfurreducens* species. The species showed the presence of OmcS, OmcZ, and PgcA cytochromes responsible for ET. The presence of several membrane complexes and channels are responsible for proton and sodium ion transfer in their cell and thus protect them from osmotic shock. The presence of relatively additional polymer repair genes than most *Geobacter* species provides them protection in high salt and low pH scale conditions (Sun et al. 2019). Thus, power production was higher in high salt condition by *G. anodireducens* compared to *metallireducens*, *sulfurreducens*, and *soli* species of *Geobacter*.

Another novel exoelectrogen, namely *Kluyvera georgiana* MCC 3673, has been isolated from MFC culture grown in oilseed cake substrate. Genetic analysis by 16S rDNA sequencing disclosed that this organism is closely associated with *Kluyvera georgiana*. *K. georgiana* MCC 3673 is a facultative being, Gram-negative, non-spore-forming, non-motile, rod-shaped, measurement 0.3–0.6 μm × 1–2 μm being. Growth is fast in Luria-Bertani (LB) broth during a temperature variation between 25 and 37°C. Tiny yellowish smooth circular colonies with a diameter of 0.2–0.3mm were fashioned on agar within 12h of incubation. The power density produced by the culture was 379±8 mW/m^2 (Thapa and Chandra 2019).

Future perspective and conclusion

This review dealt with the key role players, i.e., bacterial metabolism for electron transfer for the commonly occurring exoelectrogens of MFC. The factors affecting the exoelectrogenic electron production and transfer abilities are also discussed. The low power production and instability in the MFC system, in the long run, is a hindrance in its commercialization. The exoelectrogens are the crucial members for its interaction with various MFC parameters that influences the power production behavior. Hence the understanding of the EET by exoelectrogens in power production is of paramount importance. The knowledge of the proteins involved in EET electron production and transfer can lead to the development of new strategies for improving EET pathways of exoelectrogens. This provides scope in genetic engineering for manipulating existent exoelectrogens and discovery of new exoelectrogens having similar protein pathway for electron transfer. However, the MFC systems are still limited by the EET pathways of well-known exoelectrogens like *G. sulfurreducens*, *S. oneidensis*, *E. coli* only. A number of new exoelectrogens have been discovered along with genetic mutation of the widely known exoelectrogens in the recent studies. However real-time analysis of the changes in the cell activity during MFC operation is not yet thoroughly focused. The mechanism of electron transfer from the mentioned exoelectrogens in various growth media to obtain the stage-wise breakdown of substrate and number of electrons generated needs to be focused. The competition in case of mixed culture growth also presents future research opportunities. The isolation and transfer of EET genes present in *Geobacter* or *Shewanella* species to other non-exoelectrogens also presents biotechnological growth in future times. The MFC operation factors influencing exoelectrogenic growth and metabolism are also not studied completely, mostly only one factor influencing on the exoelectrogenic growth is discussed. However, the various factors like, temperature, pH, and substrate as a whole can affect other parameters providing future opportunities for establishing the interdependency of the factors on each other.

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Declarations

Ethics approval and consent to participate Not applicable

Consent of publication Figs 1a–e and 2a are open access articles with copyright by citation and are cited in the manuscript as per instruction. Citation is provided for Figs 3a and b and 4a and b. Copyright has been taken for reuse of Figs 2b, c, d, and e; 3 c and d; 4 c, d, and e; and 5.

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