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Bruce E Logan
Pennsylvania State University
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Exoelectrogenic bacteria that power microbial fuel cells

Bruce E. Logan

Abstract | There has been an increase in recent years in the number of reports of microorganisms that can generate electrical current in microbial fuel cells. Although many new strains have been identified, few strains individually produce power densities as high as strains from mixed communities. Enriched anodic biofilms have generated power densities as high as 6.9 W per m^2 (projected anode area), and therefore are approaching theoretical limits. To understand bacterial versatility in mechanisms used for current generation, this Progress article explores the underlying reasons for exocellular electron transfer, including cellular respiration and possible cell–cell communication.

Fuel cells are used to produce electricity electrochemically from many different chemicals, such as hydrogen gas and methanol, through catalytic oxidation of the fuel at the anode and chemical reduction at the cathode. Microbial fuel cells (MFCs) are unique in that they do not require the use of metal catalysts at the anode. Instead, they use microorganisms that biologically oxidize organic matter and transfer electrons to the anode. These electrons flow through a circuit to the cathode, where they combine with protons and a chemical catholyte (see Glossary), such as oxygen (FIG. 1). The reduction of oxygen is usually catalysed by a precious metal catalyst, such as platinum, although non-precious metals can be used[1–3]. The oxidation of the fuel at the anode in an MFC is not a true catalysis step, as the microorganisms (which contain true catalysts) derive energy from the oxidation of the fuel, creating an overall energy loss. Depending on the energy gain by the bacteria, and energy losses at the cathode, a voltage of 0.3–0.5 V is usually obtained for fuels such as glucose or acetic acid (FIG. 2). Virtually any source of biodegradable organic matter can be used in an MFC for power generation, including simple molecules, such as carbohydrates and proteins, as well as complex mixtures of organic matter present in human, animal and food-processing waste waters. The flexibility of microorganisms to use a range of fuels makes the MFC an ideal technology for renewable bioelectricity generation from biomass.

Early fuel cell studies which used bacteria that achieved appreciable power densities required the addition of electron shuttles, or mediators, to carry electrons from inside the cell to the electrode. The finding that bacteria capable of dissimilatory iron reduction could produce power in an MFC in the absence of exogenous mediators suggested that power production might be a rare trait, limited only to certain microorganisms. Several studies found that MFCs contained diverse microbial communities, which was unexpected given the apparent need for cells to be able to respire using an electrode[4]. Studies that use pure cultures have now confirmed that many different bacteria in anodic biofilms can generate power (TABLE 1). Electrical current generation has been shown for four of the five classes of Proteobacteria, as well as the Firmicutes and Acidobacteria phyla. The yeast *Pichia anomala* has redox enzymes on its outer membrane and can produce current in an MFC[5], and the oxygenic phototrophic cyanobacterium *Synechocystis* sp. PCC 6803 was discovered to produce electrically conductive appendages called nanowires[6]. The microorganisms that are capable of exocellular electron transfer are defined here as exoelectrogens, although they have been described using various other terms, such as electrochemically active bacteria[7], anode respiring bacteria[8] and electricigens[9].

Although many different types of microorganisms produce electrical current in MFCs, many of these strains exhibit low power densities when grown as pure cultures[10,11]. It is therefore unclear whether these bacteria exist as exoelectrogenic oligotrophs among faster-growing competitors, or whether a low level of current generation provides some other benefits through interactions. For example, a Gram-positive bacterium (*Brevibacillus* sp. PTH1) that was abundant in a mixed community in an MFC produced little power as a pure culture unless a *Pseudomonas* sp. was also present or supernatant from an MFC with this bacterium was added[12]. What is the role of other bacteria in relation to exoelectrogenic strains in anodic communities, and how do mixtures of communities affect power production? Answering these questions will provide useful insights into the ecology and complex functions within electrogenic biofilms.

Advantages of exoelectrogenesis

Investigations of how dissimilatory metal-reducing bacteria use iron oxides initially revealed two mechanisms of electron transfer based on either direct contact by outer membrane cytochromes or use of excreted mediators (also known as shuttles)[13,14] (FIG. 1). Subsequent work by two different groups later revealed a third mechanism by providing evidence that bacteria synthesize appendages capable of transferring electrical current called nanowires[6,15]. Evidence to support the possibility of cell respiration using these uninsulated nanowires was initially based on measurements of electrical conductance in the z plane (across the wire diameter). It was recently shown that nanowires produced by *Shewanella oneidensis* MR-1 also exhibit nonlinear electrical transport properties along their length[16].

There are at least three possible reasons why microorganisms can use exocellular electron transfer, which can result in power

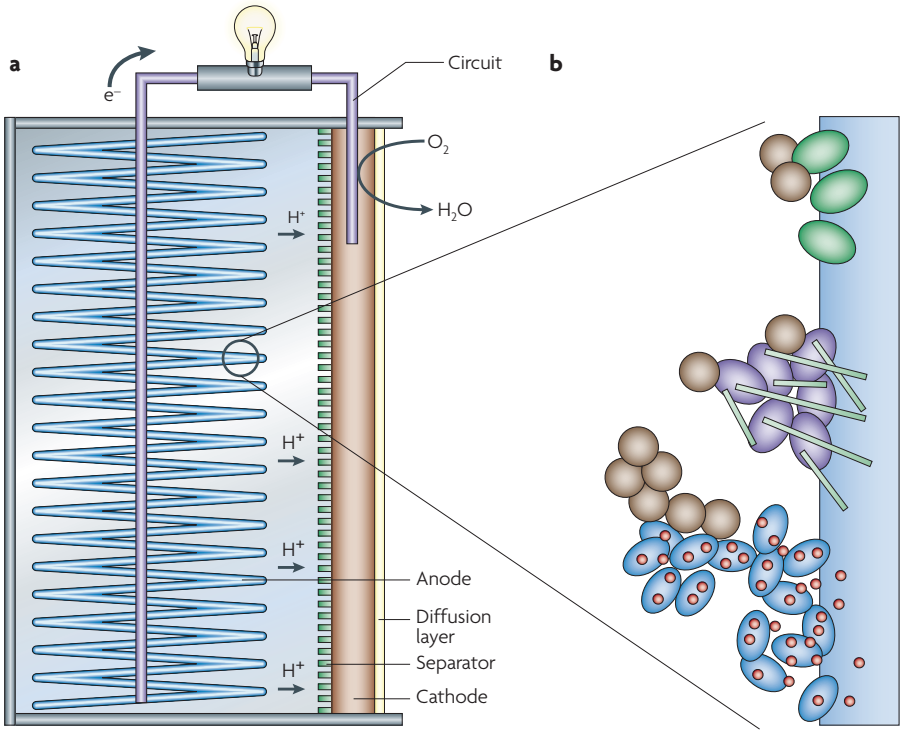

Figure 1 | **Microbial fuel cell architecture. a** | Schematic of a microbial fuel cell (MFC) that contains an electrically conductive graphite fibre brush anode as the surface for bacterial growth and a flat carbon cloth cathode coated with a catalyst on the water-facing side. A diffusion layer, such as PTFE (polytetrafluoroethylene), is placed on the air-facing side to reduce water leakage, and a separator (or ion exchange membrane) is sometimes placed between the electrodes to allow charge transfer. O_2 is reduced to H_2O through a combination of electrons from the circuit and protons in the water. **b** | Shows the different types of microorganisms in an anodic biofilm, including exoelectrogens that transfer electrons by direct contact (green), produce nanowires (purple) and use endogenous (and therefore self-produced) mediators (blue). Other non-exoelectrogenic bacteria (brown) that live off the products produced by other bacteria or possibly use mediators or nanowires produced by other microorganisms can also be present.

generation in an MFC. The first and best-studied reason is cell respiration using solid metal oxides, such as iron. Many strains of bacteria can release electrons from a terminal oxidase in the respiratory chain to Fe III outside the cell, producing soluble Fe II. Second, it is possible that cells can transfer electrons directly to another cell, without the need for intermediates, such as hydrogen. The fermentative bacterium *Pelotomaculum thermopropionicum* was observed to be linked to the methanogen *Methanothermobacter thermautotrophicus* by an electrically conductive appendage, which provided the first direct evidence for interspecies electron transfer[6]. Electron transfer directly into bacteria has been indirectly observed in other situations. Oxygen reduction can be catalysed by bacteria on the cathode (known as a biocathode) of an MFC[17], allowing for bacterial growth using electrons produced at the anode from the oxidation of organic matter. Bacteria can derive energy from this reaction because electrons enter the bacteria on the biocathode at a higher potential than that needed for oxygen reduction. Biocathodes have also been used for nitrate reduction[18] and hydrogen evolution[19]. The evidence that electrons can be both released and accepted by microorganisms suggests that electron exchange between cells is a naturally occurring phenomenon in microbial communities.

A third possible reason for exogenous electron transfer, and one that has not yet been examined experimentally, relates to a possible role of electron transfer for cell–cell communication. The finding that bacteria within a biofilm communicate through quorum sensing chemicals is well established. Many bacteria, such as *Pseudomonas aeruginosa*, generate quorum signals with fatty acyl-homoserine lactones (acyl-HSLs), and recently it was shown that certain *Rhodopseudomonas palustris* strains produce the quorum signal *p*-coumaroyl-HSL[20]. In humans, dozens of transmitters, such as acetylcholine, are produced by neurons for cell–cell communication. This situation is interesting from an evolutionary perspective in the context of the development of cell–cell communication in organisms. The opportunistic pathogen *P. aeruginosa* produces pyocyanin, a chemical that is a signal for the upregulation of quorum sensing-controlled genes[21]. Pyocyanins also function as electron shuttles, allowing electrical current generation in MFCs[14]. The importance of quorum sensing signals in the context of intra-species and inter-species electron transfer, as well as microbial pathogenesis, is not well understood. Pyocyanins produced by one bacterium can be used by other microorganisms to produce current in an MFC, but they also function as antibiotics[14,22]. Another opportunistic pathogen, *Ochrobactrum anthropi*, has been shown to be capable of power generation in an MFC but, unlike most exoelectrogenic bacteria, does not respire using solid metal iron oxides[11]. The yeast *P. anomala* (Fungi kingdom) is also a pathogen that is capable of power generation in an MFC. Through the study of possible reasons for microbial current generation, as well as the mechanisms of electron transfer, we learn more about bacterial respiration, cell–cell communication and the fundamentals of electron transfer through organic molecules. Such information will not only be scientifically interesting, but could be useful in medical applications, as well as in bioelectricity production using MFCs and hydrogen gas production using microbial electrolysis cells[3].

High power-producing bacterial species

The highest power densities in MFCs are almost always produced by inoculating the anode with a rich and diverse source of bacteria, such as a waste water or sludge[23]. The power densities produced by isolates or mixed cultures are often more dependent on the specific architecture, electrode spacing and solution conductivity of the fuel cell rather than the specific bacterium[23]. Thus, power densities produced by a bacterium in one study cannot be directly compared with another bacterium or a mixed culture unless the MFC architecture and chemical solution are the same. In addition, the internal resistance of the device must be low to ensure that differences between different bacterial strains can be detected[23]. Proof that a specific MFC will work in such a comparison can only be determined through extensive testing of different

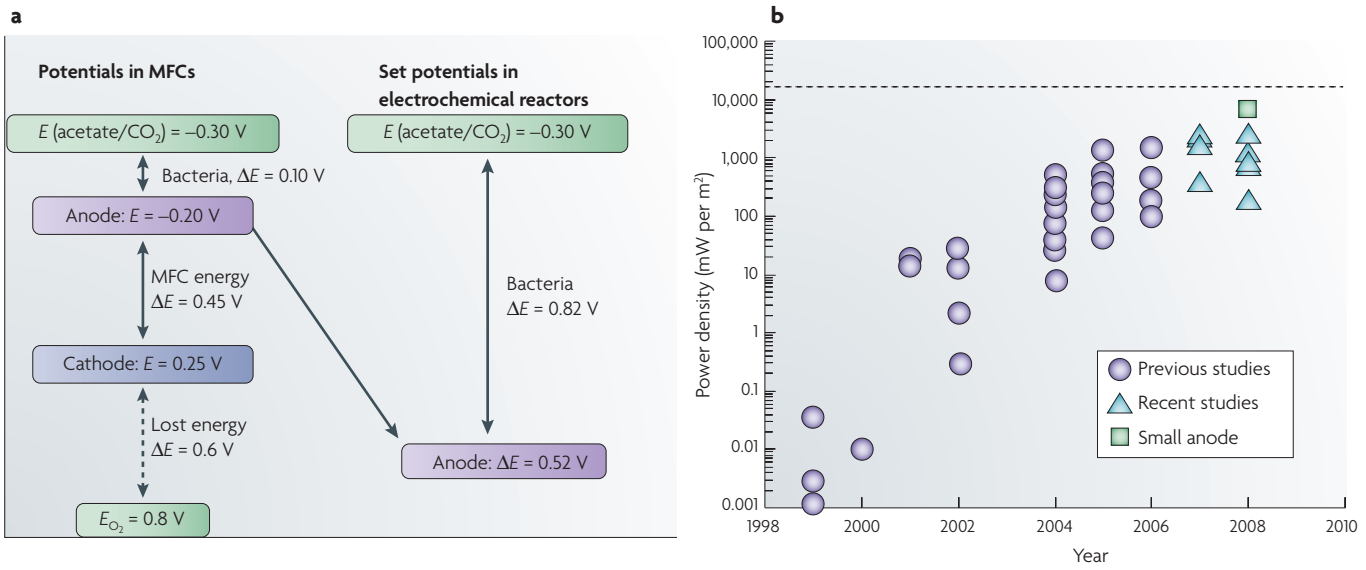

Figure 2 | **Potentials and power densities in microbial fuel cells.** **a** | Potentials in microbial fuel cells (MFCs) compared with reactors with set potentials. The anode potential of an operating MFC is approximately –0.2 V, which is only slightly more positive than the thermodynamic limit for the substrate. This restricts energy gains by the bacteria but allows high energy capture in the MFC. **b** | Power densities reported for MFCs, normalized to electrode-projected surface areas. Data from different researchers who used oxygen at the cathode, as reported by Logan and Regan[4], published during 1999–2006 are represented by circles. Data from selected recent studies that emphasize higher power densities, in which power was usually normalized to the cathode area because power is limited by the cathode, are represented by triangles. A recent test which used an anode with a cathode that was 14 times larger produced a high apparent power density of 6,860 mW per m2 (represented by a rectangle); if the power density was normalized to the cathode area, however, the power density was only 490 mW per m2. The power output of the reactor was therefore not increased, but this does show that the anode can maintain higher power densities if cathode performance is optimized. The line indicates a maximum predicted on the basis of substrate-limited mass transfer to the anode.

strains and inocula in the device. The low power densities obtained using various *Geobacter* strains in MFCs (7–45 mW per m^2) in early two-chamber MFC studies[24,25], for example, are now known to be due to the high internal resistance of these systems.

The development of simple, single-chamber designs with a lower internal resistance have allowed examination of a range of factors that affect power production[26], including the inoculum. With these reactors, a high power-producing bacterium, and the first Alphaproteobacterium to be isolated from an MFC, was shown to produce more power than a mixed culture (TABLE 1). Based on the observation that MFCs inoculated with a waste-water sample often developed a bright red colour over time, which is a characteristic of purple sulphur and non-sulphur bacteria, the members of my laboratory plated and picked colonies that had an obvious red colour. One of these isolates, *R. palustris* DX-1 (FIG. 3), produced a maximum power density (2,720 mW per m^2) that was 56% larger than that produced by the original inoculum (1,740 mW per m^2) and 13% larger than that previously obtained in this device under similar conditions[27].

The maximum power produced in a comparison of pure and mixed cultures is affected by electrode sizes and reactor architecture. Using a single-chamber, air cathode MFC with a low internal resistance, it was shown that an enriched consortium of microorganisms produced 22% more power (576 mW per m^2) than a pure culture of *Geobacter sulfurreducens* (461 mW per m^2; normalized to cathode area; anode to cathode ratio of 1.5) despite the presence of *G. sulfurreducens* in the consortium[28]. With equally sized electrodes in another air cathode MFC, *G. sulfurreducens* produced 240 mW per m^2 (normalized to anode area) but power production was not compared with a mixed culture[29]. When the anode size was reduced (anode to cathode ratio of 1:8), and ferricyanide was used as a catholyte instead of oxygen, *G. sulfurreducens* produced 19% more power (1.9 W per m^2) than a mixed culture (1.6 W per m^2). This different outcome in the complete absence of oxygen suggests that *G. sulfurreducens* is capable of producing high power densities if oxygen intrusion into the MFC (through the cathode) is avoided or perhaps if other microorganisms are present to scavenge the oxygen.

Shewanella putrefaciens was first shown to produce electricity in the absence of exogenous mediators in 1999 (REF. 30). The mechanism used by *Shewanella* spp. to transfer electrons outside the cell continues to be a subject of debate, perhaps owing to the fact that there may be no single answer. *Shewanella* spp. have outer membrane cytochromes for direct electron transfer by contact, but they can also extrude electrically conductive nanowires[6,13]. *S. oneidensis* also produces flavins that can function as electron shuttles[31]. Despite the possibility that this bacterium could use multiple methods for exocellular electron transfer, *S. oneidensis* produced 56% less power than an acclimated waste-water inoculum in an air cathode MFC in fed batch tests[32]. The reasons for these lower power densities could include ineffective interaction of electron-transferring molecules (cytochromes, flavins or those in nanowires) with the carbon electrode compared with a metal oxide. Redox conditions in fed batch MFCs fluctuate over a cycle (the time before current generation substantially decreases after the substrate is depleted), and variations from positive to negative redox potentials over a cycle may interfere with physiological

Table 1 | **Culture studies show exoelectrogenic activity without exogenous mediators***

Year	Microorganism	Comment
1999	*Shewanella putrefaciens* IR-1 (REF. 30)	Direct proof of electrical current generation in an MFC by a dissimilatory metal-reducing bacterium (Gammaproteobacteria)
2001	*Clostridium butyricum* EG3	First Gram-positive bacterium shown to produce electrical current in an MFC (phylum Firmicutes)
2002	*Desulfuromonas acetoxidans*[51]	Identified in a sediment MFC community and shown to produce power (Deltaproteobacteria)
	Geobacter metallireducens[51]	Shown to generate electricity in a poised potential system (Deltaproteobacteria)
2003	*Geobacter sulfurreducens*[40]	Generated current without poised electrode (Deltaproteobacteria)
	Rhodoferax ferrireducens[24]	Used glucose (Betaproteobacteria)
	A3 (*Aeromonas hydrophila*)[52]	Deltaproteobacteria
2004	*Pseudomonas aeruginosa*[10]	Produced low amounts of power through mediators such as pyocyanin (Gammaproteobacteria)
	Desulfobulbus propionicus[53]	Deltaproteobacteria
2005	*Geopsychrobacter electrodiphilus*[38]	Psychrotolerant (Deltaproteobacteria)
	Geothrix fermentans	Produced an unidentified mediator (phylum Acidobacteria)
2006	*Shewanella oneidensis* DSP10 (REF. 33)	Achieved a high power density (2 W per m^2 or 500 W per m^3) by pumping cells grown in a flask into a small (1.2 mL) MFC (Gammaproteobacteria)
	S. oneidensis MR-1 (REF. 54)	Various mutants identified that increase current or lose the ability for current generation (Gammaproteobacteria)
	Escherichia coli[55]	Found to produce current after long acclimation times (Gammaproteobacteria)
2008	*Rhodopseudomonas palustris* DX-1 (REF. 37)	Produced high power densities of 2.72 W per m^2 compared with an acclimated waste-water inoculum (1.74 W per m^2) (Alphaproteobacteria)
	Ochrobactrum anthropi YZ-1 (REF. 11)	An opportunistic pathogen, such as *P. aeruginosa* (Alphaproteobacteria)
	Desulfovibrio desulfuricans[56]	Reduced sulphate when growing on lactate; resazurin in the medium was not thought to be a factor in power production (Deltaproteobacteria)
	Acidiphilium sp. 3.2Sup5 (REF. 57)	Current at low pH and in the presence of oxygen in a poised potential system (Alphaproteobacteria)
	Klebsiella pneumoniae L17‡ (REF. 58)	The first time this species produced current without a mediator (Gammaproteobacteria)
	Thermincola sp. strain JR[59]	Phylum Firmicutes
	Pichia anomala‡ (REF. 5)	Current generation by a yeast (kingdom Fungi).

*Air cathode microbial fuel cells (MFCs), except where noted. ‡Ferricyanide cathode.

optimization of power production. The production of high power densities has been shown to be possible by growing *Shewanella* cells under low oxygen conditions and then pumping the cell suspension through a small (1.2 mL) reactor with an air cathode (2 W per m^2 or 330 W per m^3)[33] or ferricyanide cathode (3 W per m^2 or 500 W per m^3)[34]. *Shewanella* spp. therefore seem to be inherently capable of high power densities under certain reactor conditions.

Setting anode potentials

Setting the anode potential in an electrochemical reactor provides insight into the capabilities of a bacterium for electron transfer by allowing us to measure directly specific electrical potentials that allow electron release from the cell. Without this artificial control of potential, the anode potential in an MFC varies with the load (set using a resistor) owing to the redox potential of the electron carriers. When an MFC circuit is opened, the anode potential becomes more negative and approaches the thermodynamic limit for the oxidation of the substrate under conditions of the medium[23] (FIG. 2). When the circuit is reconnected with a load, the anode potential increases (becomes less negative) because the respiratory enzymes and electron carriers holding electrons are oxidized. The more negative the anode potential at a set resistance, the greater the energy recovery in an MFC (and the greater the power output) and the lower the energy captured by the bacterium. The extent to which the ratio of oxidized to reduced species of electron carriers can vary in a microorganism will affect the potentials at which microorganisms can transfer electrons into or out of the cell. Using a potentiostat to polarize the anode at a specific potential enables us to measure these limits so that we can better understand this process. The ratio of NADH to NAD^+ provides one example of how an electron carrier could affect exocellular electron transfer, as some bacteria appear to have characteristic NADH to NAD^+ ratios that are dependent on redox conditions. For example, this ratio is 0.094:1 for *Escherichia coli* using glucose under aerobic conditions and 0.22:1 for *E. coli* using glucose under anaerobic conditions[3,35]. The accumulation of NADH is known to affect cellular processes. For example, in *Clostridium acetobutylicum*, NADH build-up shuts down the activity of 2-glyceraldehyde-3-phosphate, limiting hydrogen production by glucose fermentation. In terms of exocellular electron transfer, higher accumulations of NADH could allow electron transfer at more-negative anode potentials. Different characteristic ratios of NADH to NAD^+ or other electron carriers among bacteria, or an inability of a bacterium to respire over a wide range of NADH to NAD^+ ratios, could therefore limit potentials that could be achieved by a bacterium. The inability to transfer electrons to a polarized anode, except for at a limited range of potentials, has been observed for *Desulfovibrio desulfuricans* subspecies *desulfuricans* strain ATTC 27774. In this case, the bacterium generated a current at –0.158 V (versus a standard hydrogen electrode (SHE)) but not at –0.358 V or potentials greater than 0.042 V[36]. The optimum potential for electron transfer for a specific bacterium may simply reflect the potential of the respiratory enzyme used as a terminal electron acceptor. For example, respiratory pathways optimized for ferric iron could require different electrode potentials than those optimized for manganese.

It is assumed that setting the anode potential produces conditions in which the biofilm can achieve current densities that are not limited by the system architecture (that is, electrode spacing, materials and electrolyte). However, higher current densities have been obtained in air cathode MFCs (9.9 A per m^2)[37] than those obtained in electrochemical reactors, with poised anodes indicating the importance of the system architecture (0.074 A per m^2)[24]. However, it should be noted that errors in the literature have made it appear that much higher power densities have been achieved using polarized electrodes. For example, a power density of 1.214 A per m^2 reported for an anode polarized to 0.52 V (versus an SHE) was incorrectly reported as 1,214 A per m^2 as a result of unit errors (microamperes versus milliamperes)[38].

The ability of bacterial strains to achieve high current densities at certain anode potentials does not ensure these strains will dominate in an MFC microbial community. Setting the anode potential at 0.52 V (versus an SHE)[23], for example, produces an anode potential that is higher than that typically achieved by the cathode with oxygen (0.25 V) (FIG. 2). The capabilities of a bacterium at this high potential do not give us insight into current in an actual MFC because this potential would not be achieved using oxygen. In a mixed community, the microorganisms that 'win' will probably be those that can respire at the most negative anode potential. When an anode potential originally set positive is disconnected from the potentiostat and allowed to vary using a mixed culture, it will progressively become more negative through competition[39]. Thus, strains unable to adjust to these more negative anode potentials will be out-competed by other strains. This highly negative anode potential is a fortunate situation for capture of energy in an MFC, as it allows for a high voltage. However, the bacteria extract less energy because of the reduced potential (FIG. 2).

Substrate kinetics and microbial growth rates are known to affect competition in a biofilm, but another factor that is important in MFCs is Coulombic efficiency. From the perspective of energy recovery as power in an MFC, high Coulombic efficiencies are desirable. However, bacteria that produce high Coulombic efficiencies will have low biomass yields, as the electrons from the substrate are lost to produce current. Coulombic efficiencies as high as 96.8% have been reported[40], suggesting that only 3.2% or less of the electrons could have gone into biomass production. Substrate not recovered as current in mixed cultures can also be lost to microorganisms that use alternate electrons acceptors, such as oxygen (which leaks through the cathode), nitrate, sulphate or carbon dioxide.

Substrate that does not go into current can also be used to make mediators, which are stored and used later, or can be lost to exocellular products. High power densities have been observed to be maintained after the primary substrate has been reduced to low concentrations in the solution, indicating that substrate storage is important in MFCs[41].

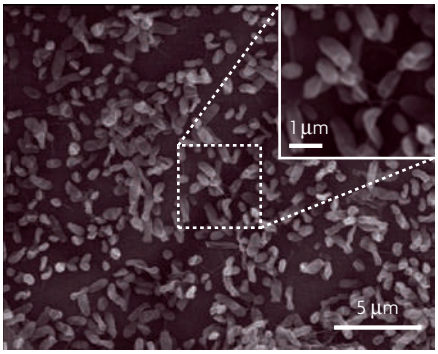

Figure 3 | **Scanning electron micrograph of *Rhodopseudomonas palustris* on a carbon paper anode.** Figure is reproduced, with permission, from REF. 37 © (2008) American Chemical Society.

Limits in power production

We are not yet at the upper limits of maximum power densities for microorganisms in MFCs on either a volumetric or projected-anode area basis. Up to 1.55 kW per m^3 has been achieved in an air cathode MFC[42], yet the limit on volumetric power production is theoretically a function of the growth rate of the microorganism. A single *E. coli* cell that weighs 2×10^{-13} grams, doubles 2 times per hour and has a volume of 0.491 μm^3 could theoretically produce 16,000 kW per m^3 (based on the volume of the cell)[3]. To put this power density in perspective, a person eating 8,400 joules (2,000 Cal or 2 Kcal) every day is consuming the equivalent of 100 W of continuous power or 1 kW per m^3 (assuming a body volume of 0.1 m^3). Harnessing the power of microorganisms in an MFC requires that electrodes be conveyed to a surface, and so the packing of microorganisms on the surface and the amount of surface area in a reactor are important issues for performance.

The projected maximum power densities achieved per electrode surface area in an MFC increased by six orders of magnitude to 1.54 W per m^2 between 1999 and 2006 (FIG. 2). These increases in power resulted from improvements in architecture and our understanding of how to extract power from bacteria more effectively. For example, various *Shewanella* strains and mixed cultures produced less than 1 mW per m^2 before 2000, but we now routinely extract >2 W per m^2 with these inocula owing to improved MFC designs. There have been less dramatic increases in power densities

Glossary

Air cathode
A cathode that is exposed to air on one side and water on the other side.

Anode potential
The potential of the anode relative to a reference electrode (usually a standard hydrogen electrode).

Catholyte
A chemical that accepts electrons at the cathode.

Coulombic efficiency
Amount of Coulombs captured in electrical current generation relative to the maximum possible assuming complete oxidation of the substrate. A Coulomb is the SI unit of electric charge, and is the amount of electric charge transported in 1 second at 1 ampere.

Dissimilatory metal-reducing bacterium
A bacterium that is capable of using metals as a terminal electron acceptor for respiration.

Exocellular
Occurring outside the cell membrane (equivalent to extracellular) in a cell surface or non-cell-associated process.

Exoelectrogenic
Describes the ability of certain microorganisms to generate and transfer electrons exocellularly.

Nanowire
An electrically conductive appendage produced by a bacterium that is proposed to conduct electrons from the cell to surfaces such as metal oxides or electrodes.

Potentiostat
A device that can be used to set a specific potential for an electrode.

Quorum signal
A small molecule that is used as a signal for specialized responses within a bacterial community.

Redox potential
A relative measure of the potential (in volts) for a chemical to gain or lose electrons.

since 2006, but the lack of increased power production is still probably not limited by the bacteria. Higher power densities should be achievable by using thick exoelectrogenic biofilms owing to the large number of bacteria that would contribute to electrical current generation. If power was limited to only a one-cell-thick biofilm, the maximum power for *G. sulfurreducens* (for a doubling time of 2 hours) and a cell voltage of 0.8 V) would be 0.97 W per m^2, assuming steady conditions (that is, substrate utilization for metabolism is proportional to growth)[3]. We have already observed higher power densities based on projected surface areas, supporting evidence that *G. sulfurreducens* maintains electrogenic activity across thick biofilms[29]. Transport of substrate to the biofilm, or metabolism products from the biofilm, will ultimately limit maximum power densities[3]. A power density of 6.9 W per m^2 of the anode area was recently achieved using a cathode that was 14 times larger than the anode[43] (FIG. 2). It is estimated that substrate (for example, acetate) flux to a biofilm would limit power densities to 17 W per m^2 (REF. 3). This value is similar to the 19 W per m^2 that was recently estimated to be possible if internal resistances were eliminated in an MFC[43]. Proton production in the biofilm can lower localized pH, however, which could prohibit us from reaching these upper power densities. In addition, the presence of non-exoelectrogenic bacteria or non-active cells that disrupt the electrical conductivity of the biofilm or occupy surfaces might stop us from achieving these maximum power densities. Models of biofilm activities[44] and a better understanding of the effect of pH and carbon dioxide gradients in the biofilm will help us to better predict the maximum power densities achievable using MFCs.

Future directions

It is possible that MFCs will one day be used as a stand-alone method of power generation, but near-term applications are most likely in the areas of energy recovery during waste-water treatment and remote power generation. In the United States, approximately 1.5% of the electricity produced is used for waste-water treatment, and approximately 4–5% of the electrical energy is used for the whole water infrastructure[3]. Through the recovery of energy from waste waters and waste biomass using energy-producing MFCs, it may be possible to ensure the energy sustainability of the water infrastructure. It is estimated that domestic waste water contains 9.3 times as much energy as that currently used to treat the waste water through energy-intensive aeration-based processes[45]. Using an air cathode MFC can eliminate the need for aeration, and therefore much of the existing energy demands, while producing energy. In addition, the low cell yields of anaerobic processes, such as MFCs, will produce less waste biomass than aerobic-based processes[3]. Sediment MFCs fulfil the different need of providing power in remote locations, such as the ocean floor, where it is difficult to replace batteries regularly. By capturing energy in the sediment[46] or in biodegradable fuels, such as chitin, packed into the sediment MFC[47], it should be possible to power a wide range of monitoring devices in rivers, lakes and oceans.

In the near future, development of MFCs to generate useful power for these applications will be limited by the efficiency and cost of materials, physical architecture and chemical limitations, such as solution conductivity and pH. We need a better understanding of bacterial electron transfer to a surface at a molecular level, so that these surfaces can be optimized for electron transport. For example, pre-treatment of the anode using a high-temperature ammonia gas treatment (ammonia in helium gas at 700 °C) increased power by improving bacterial adhesion to a surface[48]. This treatment also seemed to improve electron transfer by the bacteria to the electrode, as the maximum power was affected, but the mechanism by which this power was increased was not determined. The challenge of optimizing molecule-surface interactions is being addressed for biosensor development and improved performance of enzyme-based fuel cells[49], but needs to be examined in MFCs as well. Further increasing anode surface areas relative to the cathode will have little impact on MFC performance, as anode surface areas in MFCs can already greatly exceed those of the cathode[27]. Cathode performance currently limits current generation in MFCs and will probably continue to do so for some time. This will give microbiologists time to study and perhaps genetically engineer electrogenic bacteria[50], so that higher power densities can one day be achieved when cathodic limitations are overcome in MFCs and bacteria become the limiting factor in power generation.

Bruce E. Logan is at the Hydrogen Energy Center and Department of Civil and Environmental Engineering, 212 Sackett Building, Penn State University, University Park, Pennsylvania 16802, USA.
e-mail: blogan@psu.edu

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DATABASES

Entrez Genome Project: http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=genomeprj
Clostridium acetobutylicum | *Desulphovibrio desulphuricans* subspecies *desulphuricans* strain ATTC 27774 | *Escherichia coli* | *Geobacter sulfurreducens* | *Methanothermobacter thermautotrophicus* | *Ochrobactrum anthropi* | *Pelotomaculum thermopropionicum* | *Pseudomonas aeruginosa* | *Rhodopseudomonas palustris* | *Shewanella oneidensis* MR-1 | *Shewanella putrefaciens* | *Synechocystis* sp. PCC 6803

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Bruce E. Logan's homepage: http://www.engr.psu.edu/ce/enve/logan/

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