

MICROBIAL Challenges *and*

**Harnessing
the metabolic
activity of bacteria
can provide energy for a
variety of applications,
once technical and
cost obstacles are
overcome.**

**BRUCE E. LOGAN
JOHN M. REGAN**
PENNSYLVANIA STATE UNIVERSITY

The late Nobel laureate Richard Smalley often said that “energy is the single greatest challenge facing humanity.” Energy needs in the U.S. and the world continue to increase, driving demand at an unsustainable pace. Possible options are carbon-based alternatives to oil, such as methane hydrates and the conversion of coal into methane gas, and the use of less readily available oil reservoirs and oil shale. But do we really want to use these fuels? Climate change is being driven by the atmospheric release of greenhouse gases like CO₂ (1), and an impending global energy crisis is coming at a time when we can least afford to release additional stored carbon. Nuclear power offers a carbon-free approach to energy generation, but no good solutions for nuclear waste exist. Perhaps Smalley should have said that energy is the single greatest *environmental* challenge facing humanity.

BRUCE LOGAN

Oil will not suddenly run out, but it is a finite resource. We must develop energy-saving technologies that can stretch oil reserves while we modify our energy-use patterns and infrastructure to become more sustainable over the next few decades—and perhaps even centuries. A sustainable energy portfolio should include a variety of carbon-neutral and renewable energy technologies. Existing technologies based on solar, wind, and biomass energy will all be needed to meet our future energy demands.

Microbial fuel cells (MFCs), which convert biochemical to electrical energy, may be part of the picture. MFCs could be used in biomass-based energy production, but many technical challenges must be overcome before they will be practical for renewable energy production.

The most immediate need for an MFC-based technology is a scalable or modular technology that can provide, in a cost-effective manner, the large surface areas needed for the anodes and cathodes. We must address these materials issues related to MFC development, and we must also advance our understanding of the biological basis for the process. We have only begun to understand how electrons can travel from inside the cell to a carbon electrode, or why so many different bacterial species seem able to participate in extracellular electron transfer.

on the basis of the potential difference between the electron carrier (NADH) and oxygen under standard conditions. Bacteria can produce as much as 38 molecules of ATP per molecule of glucose by aerobic respiration (this includes ATP production by substrate-level and oxidative phosphorylation). Some bacteria can use insoluble metal oxides, such as Fe(III) and Mn(IV), as electron acceptors. If electrons exit the respiratory chain at some reduction potential less than that of oxygen, then the bacteria obtain less ATP. A potential relative to oxygen (or an alternative oxidant) remains; this can be used for electricity generation in an MFC.

The essential physical components of the MFC are the anode, cathode, and electrolyte (Figure 2). In an MFC, bacteria catalyze the oxidation of reduced substrates, releasing some of the electrons produced from cell respiration to the anode, where they flow through an external circuit to the counterelectrode (cathode) and create current. For each electron that is produced, a proton must be conducted to the cathode through the electrolyte (the aqueous solution) to sustain the current. Typically, the electrons and protons react with oxygen at the cathode, aided by a catalyst such as platinum, to form water (2–4). Chemicals other than oxygen can be used, such as ferricyanide, resulting in greater overall potentials

FUEL CELLS

Applications

The emergence of a new technology will be aided by finding the most immediate and useful niche applications. For MFCs, these are probably in wastewater treatment and as power sources for environmental sensors, but opportunities for other applications exist, as described below.

How do MFCs work?

To understand how an MFC produces electricity, we must understand how bacteria capture and process energy. Bacteria grow by catalyzing chemical reactions and harnessing and storing energy in the form of adenosine triphosphate (ATP). In some bacteria, reduced substrates are oxidized and electrons are transferred to respiratory enzymes by NADH, the reduced form of nicotinamide adenine dinucleotide (NAD). These electrons flow down a respiratory chain—a series of enzymes that function to move protons across an internal membrane—creating a proton gradient (Figure 1). The protons flow back into the cell through the enzyme ATPase, creating 1 ATP molecule from 1 adenosine diphosphate for every 3–4 protons. The electrons are finally released to a soluble terminal electron acceptor, such as nitrate, sulfate, or oxygen.

The maximum potential of the process is ~1.2 V,

(5). A cation-exchange membrane can also be used to separate the catholyte and the liquid in contact with the anode into different chambers, or just to act as a barrier that keeps chemicals and materials other than protons from reaching the cathode.

Technical challenges

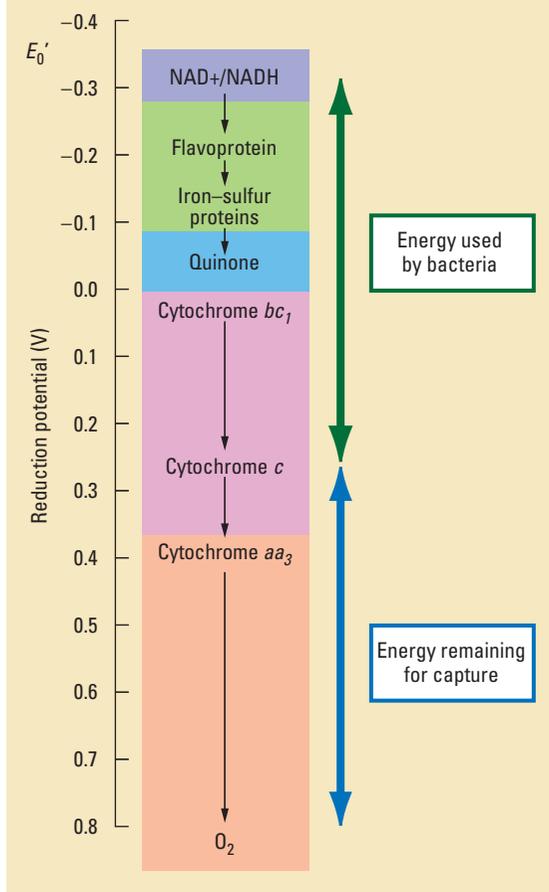
System architecture. The idea of using bacteria to capture electricity has been around for some time, but in early systems, power production was very low and required the addition of exogenous mediators to shuttle electrons from inside to outside the cell (6). In new systems, exogenous mediators are not needed, and power production from MFCs has increased dramatically in just the past few years, in part because of designs that lower the reactor's internal resistance.

MFCs are tested in the laboratory under a load, which is usually provided by a fixed external resistor, R_{ext} (Figure 2). The system components act as a second (internal) resistor, R_{int} , which can be considered to be in series with the external resistor. The maximum system power generation, P , often normalized by the surface area of the anode, varies inversely with the total resistance of the system

FIGURE 1

Respiratory chain shows how the voltage that could be recovered in a microbial fuel cell (MFC) is dependent on where electrons exit the chain of respiratory enzymes

In the case shown here, bacteria could derive energy from the potential between NADH (the reduced form of nicotinamide adenine dinucleotide) and cytochrome *c* (green arrow), whereas the MFC could be used to recover energy from the potential between cytochrome *c* and oxygen (blue arrow). Actual potentials depend on concentrations and potentials of specific enzymes and electron acceptors. (Respiratory-chain and standard potentials shown here are adapted with permission from a figure in Ref. 51 for *Paracoccus denitrificans*.)



squared, $(R_{\text{int}} + R_{\text{ext}})^2$. Whereas R_{ext} can be varied, R_{int} is fixed. Therefore, P is limited by R_{int} . For example, in a simple 2-bottle MFC built in a traditional H-design (Figure 2), $P = 2 \text{ mW/m}^2$ for a system with a salt bridge that had a high internal resistance ($R_{\text{int}} = 19,900 \Omega$) (7). Replacing the salt bridge with a proton-exchange membrane decreased R_{int} to 1290Ω , and P increased to 40 mW/m^2 (7). In these systems, air was bubbled into the water to provide oxygen at the cathode (aqueous cathode), but the solubility of oxygen in water is low, limiting the performance of the cathode. Substantially higher power densities

can be achieved in systems with lower internal resistance and more efficient cathodes.

P increases in proportion to the square of the open-circuit voltage, OCV, which is a function of the individual electrode potentials when the circuit is open. The anode potential, E_{an} , is set by the respiratory enzymes of the bacteria, typically at $E_{\text{an}} = -300 \text{ mV}$ (defined with respect to a normal hydrogen electrode [NHE]); 3) and does not appear to vary substantially in different systems or with different substrates (fuels). On the other hand, the cathode potential, E_{cat} , varies depending on the catholyte and oxidant, with $E_{\text{cat}} = 500 \text{ mV}$ usually obtained for oxygen, producing a typical $\text{OCV} = E_{\text{cat}} - E_{\text{an}} = 800 \text{ mV}$. This E_{cat} is lower than that expected on the basis of equilibrium calculations of 805 mV for water as an end product, but higher than that for H_2O_2 as an end product (328 mV , $\text{pH} = 7$, $\text{H}_2\text{O}_2 = 0.005 \text{ M}$, $= 0.2 \text{ atm}$) (4). With current flow through the system, E_{cat} (working potential) is much lower ($200\text{--}300 \text{ mV}$), reducing the cell voltage to $500\text{--}600 \text{ mV}$ (8). With ferricyanide (361 mV) or MnO_2 (470 mV) as the final electron acceptor instead of oxygen, higher cell voltages can be achieved because E_{cat} for these two chemicals is higher than that obtained with oxygen. However, power generation with ferricyanide or MnO_2 is not sustainable. Ferricyanide must be externally regenerated, and soluble manganese can be lost over time.

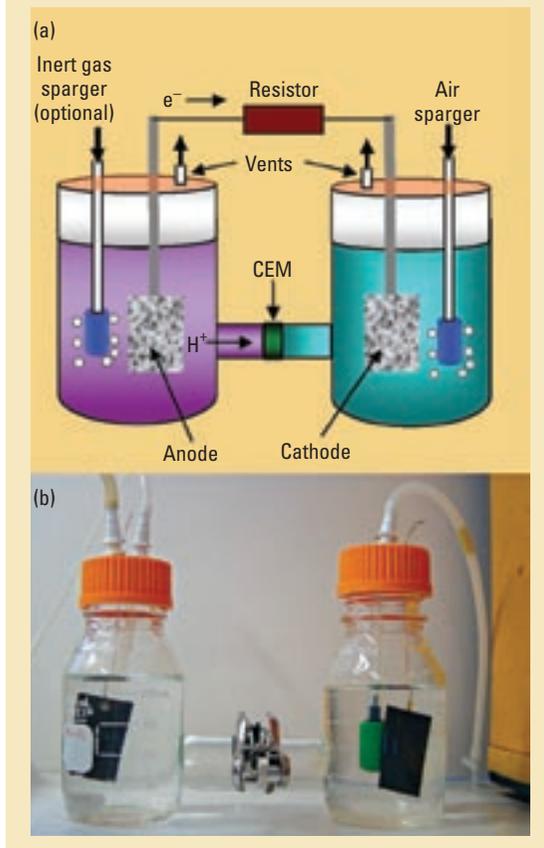
With oxygen as the electron acceptor at the cathode, the main technical challenge in improving power generation is to create a system architecture that minimizes R_{int} but, at the same time, allows for continuous flow through the system. Exposing the cathode directly to air (an air cathode), instead of dissolved oxygen in water, can substantially increase system performance. Power densities of air-cathode systems have increased to 1540 mW/m^2 through the use of an air cathode combined with other modifications of system architecture that have maximized E_{cat} and decreased R_{int} (9, 10). Removing the proton-exchange membrane in systems with two carbon cloth or paper electrodes raised the OCV from 226 to 425 mV (vs NHE), increasing P values with glucose from 262 to 494 mW/m^2 (10). Decreasing the electrode spacing from 4 to 2 cm increased P in a similar system from 720 to 1210 mW/m^2 because of a reduction in R_{int} from 161 to 77Ω (11). However, when the electrode spacing was further reduced, to 1 cm , P decreased despite a lower R_{int} of 16Ω . When the flow was directed through a porous carbon-cloth anode toward the cathode, P increased to 1540 mW/m^2 , consistent with that expected for the reduction in R_{int} (9).

The highest P values have been reported in ferricyanide systems with low R_{int} . Rabaey et al. (5) attained an impressive 4310 mW/m^2 anode projected surface (a total of 268 W/m^3) by using closely spaced graphite blocks with a large ion-exchange membrane surface and a ferricyanide catholyte, achieving a low R_{int} (3Ω). The system was run only in batch mode, which allowed electron mediators produced by the bacteria to accumulate in solution. In a continuous-flow, biofilm-based system,

FIGURE 2

Example of an H-type microbial fuel cell

(a) Schematic showing the anode where bacteria form a biofilm on the surface (with a gas sparger to remove air in the bottle) and a cathode, which is exposed to dissolved oxygen. The two chambers are separated by a cation-exchange membrane (CEM), which ideally allows the exchange of protons through the electrolyte (water) and not through oxygen or the substrate. (b) An example of a simple two-chamber system with the CEM clamped between the ends of two tubes, each joined to a bottle.



the same research group produced a total of 38 W/m³ (total anode chamber volume; $R_{int} = 4\text{--}8\ \Omega$; 14–47 mW/m² anode surface area) with glucose and 48 W/m³ (18–59 mW/m²) with acetate, by flowing the substrate solution through a packed bed of conductive graphite granules (1.5–5-mm diam) (Figure 3b). In this packed-bed system, a ferricyanide solution flowed over a cathode wrapped around the outside of the packed bed, with the electrodes separated by an ion-exchange membrane (12). Using a different approach, He et al. (13) modified an upflow reactor so that fluid was directed through a bed of reticulated vitreous carbon (RVC) toward an ion-exchange membrane that separated the anode chamber from a cathode chamber containing ferricyanide. They produced a maximum of 170 mW/m² (3.1 W/m³) with a sucrose and yeast-extract solution (Figure 3c). They noted that the main limitation to power generation

was the internal resistance ($R_{int} = 84\ \Omega$).

It is clear from these studies that maximizing power generation in MFCs requires innovative flow patterns and electrode orientations that minimize R_{int} . Finding methods to increase the cathode potential, with oxygen as the electron acceptor, can have a substantial impact on power generation, because the current cathode potentials (~300 mV) are relatively low compared with those theoretically possible (~800 mV).

Materials. The cost of materials used to construct MFCs will be a key factor for the successful application of the technology at large scales. Very large surface areas are needed for supporting the biofilm, and the structure must be able to bear the weight of the water and biofilm. Electrode materials range from carbon cloth and carbon paper, to graphite rods, plates, granules, and RVC. Cathodes are made from the same materials, but they also contain precious metals, such as platinum, when oxygen is used as the electron acceptor. Catalysts are not needed for ferricyanide or MnO₂ cathodes.

Some materials are not expected to be suitable for scale-up because of their inherent lack of durability or structural strength (e.g., carbon paper), or cost (e.g., graphite rods). Future designers will need to consider conductive coatings on structurally strong supporting materials. Cathode materials may also be extended to carbon fibers linked with noncorrosive metals, such as nickel and titanium, for seawater fuel-cell applications (14, 15).

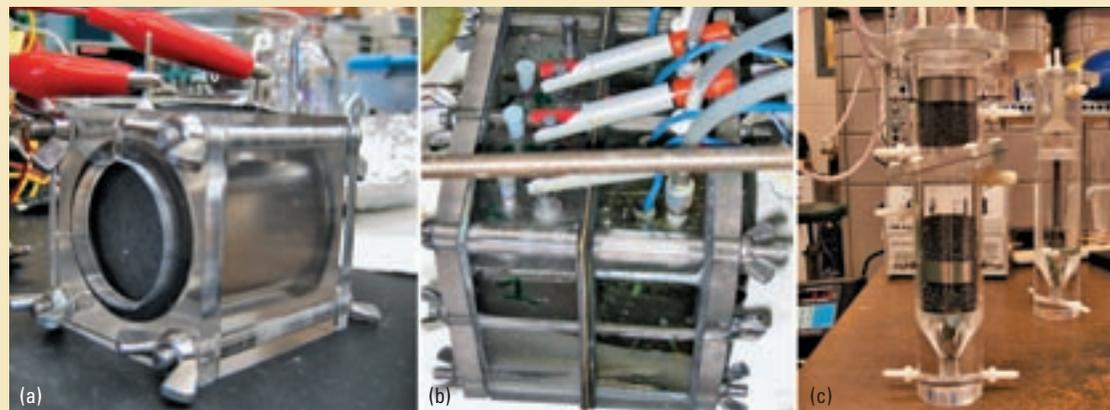
Platinum is usually used as a catalyst with oxygen and is generally held on the support with a binder such as Nafion (perfluorosulfonic acid) or polytetrafluoroethylene (PTFE). Research has shown that the density of platinum loading can be greatly reduced compared with those required for hydrogen fuel cells, but less expensive metals are still needed (16). Platinum can be replaced by cobalt- and iron-organic-mixture catalysts, although the longevity of such materials is not well studied (16, 17). System scale-up will also require that the design and application of these materials be adaptable to mass-manufacturing approaches.

Microbiology. Our understanding of electrochemically active microbes is still in its infancy, but clearly a whole new field of microbial ecology is emerging that is based on anodophilic bacteria and possible interspecies electron transfer. These bacteria may be referred to as exoelectrogens, based on their ability to exocellularly release electrons. Initial understanding of electron transfer by bacteria to electrodes came from studies of dissimilatory metal-reducing bacteria such as *Geobacter* and *Shewanella* species, which can produce electricity in MFCs (18, 19). Biochemical and genetic characterizations indicated that outer-membrane cytochromes can be involved in exogenous electron transfer (20, 21). Also, some bacteria produce and use soluble electron shuttles that eliminate the need for direct contact between the cell and electron acceptor (22). For example, phenazine production by a strain of *Pseudomonas aeruginosa* stimulated electron transfer for several bacterial strains (23).

FIGURE 3

Photographs of microbial fuel cells (MFCs)

(a) Single-chamber MFC, showing the cathode exposed to air (adapted with permission from Ref. 7); (b) packed-bed reactor that uses ferricyanide as a catholyte (adapted from Ref. 10); and (c) upflow packed-bed MFC (adapted from Ref. 13).



The recent discovery of nanowires (Figure 4) introduces a whole new dimension to the study of extracellular electron transfer. These conductive, pilus-like structures, identified so far in *Geobacter sulfurreducens* PCA (24), *Shewanella oneidensis* MR-1 (25), a phototrophic cyanobacterium *Synechocystis* PCC6803 (25), and the thermophilic fermenter *Pelotomaculum thermopropionicum* (25), appear to be directly involved in extracellular electron transfer. Disruption of a pili gene in *G. sulfurreducens* eliminated the bacterium's ability to reduce insoluble electron acceptors (24). Deletion of the genes associated with two *c*-type cytochromes (MtrC and OmcA) in *S. oneidensis* resulted in poorly conductive nanowires, loss of electrochemical activity, and loss of the ability to reduce insoluble electron acceptors (25). These nanowire structures allow the direct reduction of a distant electron acceptor. This removes the need for soluble mediators that would be lost in a continuous-flow MFC and may allow for direct interspecies electron transfers.

Bacteria that thrive in MFC biofilms, either through electron transfer to the anode or through non-electrochemical metabolisms, such as fermentation or symbiotic relationships with other bacteria, are distributed across many phylogenetic subclasses. Molecular characterizations of MFC anode communities demonstrate that they are phylogenetically diverse, with systems dominated by α - (26), β - (26, 27), δ - (28, 29), and γ -subclass (30) *Proteobacteria*. The functional significance of these dominant community members remains unknown. Isolates obtained in one study were electrochemically active, yet their power densities when they were grown in pure culture were 2–3 orders of magnitude less than those of the consortium from which they were derived (31). These diverse anode communities probably possess a wealth of undiscovered electrochemical capabilities that can be exploited in different MFC applications.

Bioprospecting to enrich consortia that increase

power can improve MFC performance by a variety of mechanisms, including an increase in the OCV, greater rates of electron transfer with specific substrates, and electron transfer to the anode by bacteria distant from it in the biofilm. The cell potentials measured in MFCs are significantly lower than the OCV. This is due in part to overpotential at the cathode, which is not a microbially influenced constraint. However, if electrons can be transferred earlier in the respiratory chain (see Figure 1), then power could be increased.

Substrate-affected differences in microbial activity is one area in which the microbiology does constrain performance. Variations in *P* can be associated with different electron donor substrates. In similar MFC systems, 494 mW/m² was produced with glucose (10) and 506 mW/m² with acetate (8), but only 305 mW/m² was achieved with butyrate (8), 261 mW/m² with swine wastewater (32), and 146 mW/m² with domestic wastewater (10). The associated polarization curves for glucose, acetate, and butyrate showed very similar anode OCVs and E_{cat} values at low current density (i.e., high resistance). The butyrate-fed system was unable to sustain a high current density, resulting in a high anode overpotential and therefore a decrease in *P*. The technical challenge is to identify and select microbial communities that can overcome this reduced power production from certain substrates, whether that involves increased substrate degradation rates, more efficient electron-transfer mechanisms, or microbial structures that increase the electrical conductance of the biofilm matrix to sustain a high current density.

Substrate versatility provides another opportunity for bioprospecting. MFCs have been operated successfully on a variety of substrates, from pure chemicals to complex wastes (2, 32). However, a need exists for electrochemically active community enrichment and optimization for a variety of reduced substrates. For example, if cellulose hydrolysis can be integrated with microbially mediated anode re-

duction, this will expand biomass-derived electricity production. Other potential applications include the use of inorganic substrates, such as ammonia in wastewaters, ferrous iron in acid mine drainage, and bioremediation applications.

Wastewater and niche applications

When a new technology is introduced into the market, the greatest likelihood for success occurs when the most immediately profitable application is targeted first. As the technology develops, becomes better understood, and improves, more difficult applications can be chosen. The most immediate and useful applications of MFCs appear to be for wastewater treatment and niche applications. Renewable energy production is a longer-term prospect that requires substantial technical and manufacturing advances from more near-term applications.

Wastewater treatment. Worldwide, >2 billion people do not have adequate sanitation, in large part because of a lack of start-up capital as well as operating costs. In the U.S., ~\$25 billion is spent annually for water and wastewater treatment. Over the next 20 years, water and wastewater infrastructure demands will require >\$2 trillion for building, maintaining, and operating these systems (33). In the U.S., ~4% of the electricity produced is used for the operation of the whole water and wastewater infrastructure (34). A treatment system based on an MFC provides a great opportunity to develop the technology, because the substrate is “free” and wastewater must be treated. At a modern treatment plant, the wastewater may contain 9.3× as much energy as is used to treat it (35).

Energy recovery at a wastewater treatment plant could lead not only to a sustainable system based on energy requirements but also to production of a net excess of energy. An MFC would be used in a treatment system as a replacement for the existing energy-demanding bioreactor (such as an activated sludge system), resulting in a net energy-producing system. However, we do not yet know how to economically scale up an MFC or what the costs would be to replace a conventional system with an MFC-based design. Scale-up and materials issues are the greatest challenges in the application of MFCs for wastewater treatment.

The MFC process is biofilm-based. Therefore, surface areas typical of trickling filters can be used as a basis for anticipated MFC applications. Surface areas of plastic-media trickling filters range from 89 m²/m³ for structured media to several hundred square meters per cubic meter for random media. Removal rates of organic matter in trickling filters are based on removal of soluble biochemical oxygen demand (sBOD); the sBOD removal rate is equivalent to 1 W/m² for a typical application rate of domestic wastewater (0.68 L/m²·s, based on cross-sectional or top-surface area) (36). Thus, we might expect a typical 6-m-tall system with 100–500 m²/m³ of biofilm surface area to generate 600–3000 W/m² of projected surface area. This assumes complete energy recovery, however, which is not achievable because of bacterial consumption of energy and energy losses as heat.

An MFC system could even be useful for individual homes or other small applications, although power production would probably be too low to warrant recovery of electricity. Septic tanks are typically used for single- to multiple-house applications, but they are inefficient systems for removing BOD or nutrients. An MFC-based system, however, might provide the opportunity for better removal of BOD and even nutrients (32). MFC applications may be particularly useful in areas where septic tanks cannot be used because of the need for high BOD removal. Such applications are currently carried out by small aerobic systems that consume energy, often in remote areas with little power available to run them.

Environmental sensors. Data on the natural environment can be helpful in understanding and modeling ecosystem responses, but sensors distributed in the natural environment require power for operation. MFCs can possibly be used to power such devices, particularly in river and deep-water environments where it is difficult to routinely access the system to replace batteries. Sediment fuel cells are being developed to monitor environmental systems such as creeks, rivers, and the ocean (37, 38) (Fig-

FIGURE 4

Images of nanowires

(a) Transmission electron microscopy image of the wild-type strain of *Geobacter sulfurreducens* (adapted with permission from Ref. 24); (b) scanning electron micrograph of wild-type *Shewanella oneidensis* MR-1, taken for cells under electron-acceptor-limited conditions (adapted with permission from Ref. 25).

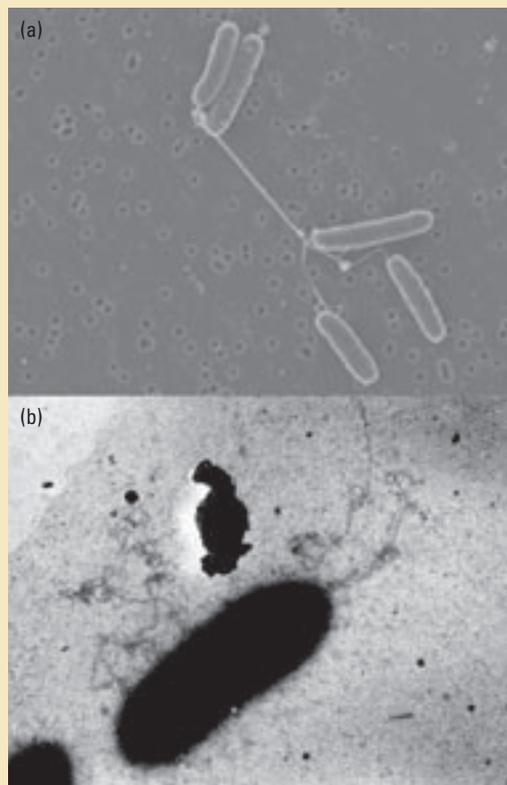


FIGURE 5

Sediment microbial fuel cell

The Benthic Unattended Generator (BUG) powered a data buoy that monitored air temperature, pressure, and humidity as well as water temperature. The system transmitted data every 5 min to a shore-based receiver via an rf transmitter.



L. M. TENDER, U.S. NAVAL RESEARCH LABORATORY

ure 5). Power for these devices can be provided by organic matter in the sediments. Power densities are low in sediment fuel cells because of both the low organic matter concentrations and their high intrinsic internal resistance. Systems developed to date are limited to producing $<30 \text{ mW/m}^2$ (38). However, the low power density can be offset by energy storage systems that release data in bursts to central sensors (39).

Bioremediation. An MFC can be modified in interesting and useful ways, and this can lead to new types of fuel-cell-based technologies. With such modifications, however, these systems may no longer be true fuel cells because they do not produce electricity. One such application is the modification of the basic two-electrode system for bioremediation. The MFC is not used to produce electricity; instead, power can be put into the system to drive desired reactions to remove or degrade chemicals, such as converting soluble U(VI) to insoluble U(IV) (40). Bacteria are not only able to donate electrons to an electrode but can also accept electrons from the cathode. By poisoning the electrodes at -500 mV , Gregory et al. (40) were able to precipitate uranium directly onto a cathode because of bacterial reduction. Nitrate can also be converted to nitrite when electrodes are used as electron donors (41). Electrolytic cultivation has been used to extend the growth rates of suspensions of iron-oxidizing bacteria in the laboratory (42).

Hydrogen production. MFCs can also be modified to produce hydrogen gas (H_2) by removing oxygen at the cathode and adding in a small voltage via the bioelectrochemically assisted microbial reactor (BEAMR) process or the biocatalyzed electrolysis process (43–46). Bacteria produce an anode working potential of $\sim -0.3 \text{ V}$. The protons and electrons that are produced at the anode can combine at the

cathode to produce H_2 with only an additional total cell potential of 0.11 V (44). In practice, however, 0.25 V or more must be put into the circuit to make H_2 , because of overpotential at the cathode (44–47). As much as $8\text{--}9 \text{ mol-H}_2$ could be produced in a process that uses glucose, in which a first-stage fermentation system achieves $2\text{--}3 \text{ mol-acetate/mol-glucose}$ and a second-stage BEAMR process recovers $2.9 \text{ mol-H}_2/\text{mol-acetate}$ produced. The power needed for the second stage is estimated to be equivalent to $0.5 \text{ mol-H}_2/\text{mol-acetate}$ (44). This may be an economically viable process for producing H_2 , because a recent U.S. Department of Energy report estimates that $10\text{--}12 \text{ mol-H}_2$ would need to be made per mole of glucose to make this route of H_2 production viable (48).

Biohydrogen production via the BEAMR process is not limited to glucose. Any biodegradable substrate that produces electricity in an MFC should work in a BEAMR system. Recent research has shown that the process works with domestic wastewater, but H_2 recoveries in current reactor designs are still too low to make H_2 production with BEAMR likely to be as viable as electricity production with MFCs (43). For the BEAMR process, high-strength wastewaters appear to have the most immediate promise for H_2 recovery.

Renewable electricity production from biomass. Because of uncertainty about the materials needed and their costs, combined with relatively low costs for oil, the application of MFCs for renewable energy production from crops such as corn is not likely in the next 5 years or so. In the near term, MFCs will have to compete with more mature renewable-energy technologies, such as wind and solar power. The operating costs needed for electricity production with MFCs will probably be too great if the substrate for the MFC is grown as a crop in a manner similar to that for ethanol production from corn.

Renewable energy production from waste biomass is likely to be a more viable route for near-term energy recovery. Great interest exists in using wood-based materials for renewable energy production. Steam explosion is currently the most cost-effective treatment process for the production of soluble sugars from solid lignocellulosic materials, such as agricultural residues and hardwoods (49). The use of a neutral hydrolysate, produced by steam explosion of corn stover in an MFC, was recently shown to be feasible, producing as much as 933 mW/m^2 in MFC tests (50). Thus, MFC technologies appear to be technically feasible for energy recovery from this and other waste biomass materials.

Education

Probably the most immediate and useful applications of MFCs are in the classroom: Students find electricity generation by bacteria both fascinating and fun! We have found MFCs to be an effective educational tool to capture student interest. These small and portable systems serve as a wonderful platform for motivating students to study and understand complex concepts of cell respiration, microbi-

al ecology, electrochemistry, and materials science. And a process that can couple sustainable energy production with waste treatment has innate appeal to environmentally minded students. The MFC is a model system for science instruction that dissolves disciplinary boundaries and shows how technology can help solve significant social and environmental issues. We have seen direct evidence for the appeal of this technology through recent science-fair projects on MFCs by students in middle and high schools around the world. At our own university, the MFC has been used in our undergraduate and graduate laboratory course in environmental microbiology to teach students methods of microbial-community analysis. With one experimental system, we can expand the discussion of molecular characterization techniques to include methods of detecting function and activity (as opposed to strictly phylogeny), and the importance of biofilm structure such as stratification of functional groups. The potential links between these microbial-ecology issues and MFC system performance are readily apparent to students.

Outlook

MFCs represent a promising technology for renewable energy production; their most likely near-term applications are as a method of simultaneous wastewater treatment and electricity production. They will be useful in other specialized applications as well—for example, as power sources for environmental sensors and environmental bioremediation. With modifications, MFC technologies could find applications ranging from H₂ production to renewable energy production from agricultural biomass. The ability of a diverse range of bacteria to function and persist in an MFC is a truly fascinating occurrence, and understanding why high bacterial diversity appears to exist in such communities will enhance our knowledge of the microbial ecology of biofilms and bacteria. MFCs are rapidly evolving technologies that will fascinate scientists and engineers who are challenged with waste technologies and energy production in the coming decades.

Bruce E. Logan is the Stan and Flora Kappe Professor of Environmental Engineering at Pennsylvania State University and director of Penn State's Hydrogen Energy (H₂E) Center and the Engineering Environmental Institute. John M. Regan is an assistant professor of civil and environmental engineering at Penn State. Address correspondence about this article to Logan at blogan@psu.edu.

References

- U.S. Department of Energy. *Basic Research Needs for the Hydrogen Economy*, Report on the Basic Energy Sciences Workshop on Hydrogen Production, Storage, and Use, May 13–15, 2003; www.sc.doe.gov/bes/hydrogen.pdf.
- Liu, H.; Ramnarayanan, R.; Logan, B. E. Production of Electricity During Wastewater Treatment Using a Single Chamber Microbial Fuel Cell. *Environ. Sci. Technol.* **2004**, *38*, 2281–2285.
- Logan, B. E. Extracting Hydrogen and Electricity from Renewable Resources. *Environ. Sci. Technol.* **2004**, *38*, 160A–167A.
- Logan, B. E.; et al. Microbial Fuel Cells: Methodology and Technology. *Environ. Sci. Technol.* **2006**, *40*, 5181–5192.
- Rabaey, K.; et al. A Microbial Fuel Cell Capable of Converting Glucose to Electricity at High Rate and Efficiency. *Biotechnol. Lett.* **2003**, *25*, 1531–1535.
- Davis, J. B.; Yarbrough, H. F. Preliminary Experiments on a Microbial Fuel Cell. *Science* **1962**, *137*, 615–616.
- Min, B.; Cheng, S.; Logan, B. E. Electricity Generation Using Membrane and Salt Bridge Microbial Fuel Cells. *Water Res.* **2005**, *39*, 1675–1686.
- Liu, H.; Cheng, S.; Logan, B. E. Production of Electricity from Acetate or Butyrate in a Single Chamber Microbial Fuel Cell. *Environ. Sci. Technol.* **2005**, *39*, 658–662.
- Cheng, S.; Liu, H.; Logan, B. E. Increased Power Generation in a Continuous Flow MFC with Advective Flow Through the Porous Anode and Reduced Electrode Spacing. *Environ. Sci. Technol.* **2006**, *40*, 2426–2432.
- Liu, H.; Logan, B. E. Electricity Generation Using an Air-Cathode Single Chamber Microbial Fuel Cell in the Presence and Absence of a Proton Exchange Membrane. *Environ. Sci. Technol.* **2004**, *38*, 4040–4046.
- Liu, H.; Cheng, S.; Logan, B. E. Power Generation in Fed-Batch Microbial Fuel Cells as a Function of Ionic Strength, Temperature, and Reactor Configuration. *Environ. Sci. Technol.* **2005**, *39*, 5488–5493.
- Rabaey, K.; et al. Tubular Microbial Fuel Cells for Efficient Electricity Generation. *Environ. Sci. Technol.* **2005**, *39*, 8077–8082.
- He, Z.; Minteer, S. D.; Angenent, L. T. Electricity Generation from Artificial Wastewater Using an Upflow Microbial Fuel Cell. *Environ. Sci. Technol.* **2005**, *39*, 5262–5267.
- Hasvold, Ø.; et al. Sea-Water Battery for Subsea Control Systems. *J. Power Sources* **1997**, *65*, 253–261.
- Hasvold, Ø.; et al. The Alkaline Aluminum/Hydrogen Peroxide Power Source in the Hugin II Unmanned Underwater Vehicle. *J. Power Sources* **1999**, *80*, 254–260.
- Cheng, S.; Liu, H.; Logan, B. E. Power Densities Using Different Cathode Catalysts (Pt and CoTMPP) and Polymer Binders (Nafion and PTFE) in Single Chamber Microbial Fuel Cells. *Environ. Sci. Technol.* **2006**, *40*, 364–369.
- Zhao, F.; et al. Application of Pyrolysed Iron(II) Phthalocyanine and CoTMPP Based Oxygen Reduction Catalysts as Cathode Materials in Microbial Fuel Cells. *Electrochem. Commun.* **2005**, *7*, 1405–1410.
- Bond, D. R.; Lovley, D. R. Electricity Production by *Geobacter sulfurreducens* Attached to Electrodes. *Appl. Environ. Microbiol.* **2003**, *69*, 1548–1555.
- Kim, H.-J.; et al. A Mediator-Less Microbial Fuel Cell Using a Metal Reducing Bacterium, *Shewanella putrefaciens*. *Enzyme Microb. Technol.* **2002**, *30*, 145–152.
- Magnuson, T. S.; et al. Isolation, Characterization and Gene Sequence Analysis of a Membrane-Associated 89 kDa Fe(III) Reducing Cytochrome *c* from *Geobacter sulfurreducens*. *Biochem. J.* **2001**, *359*, 147–152.
- Myers, J. M.; Myers, C. R. Role for Outer Membrane Cytochromes OmcA and OmcB of *Shewanella putrefaciens* MR-1 in Reduction of Manganese Dioxide. *Appl. Environ. Microbiol.* **2001**, *67*, 260–269.
- Turick, C. E.; Tisa, L. S.; Caccavo, F., Jr. Melanin Production and Use as a Soluble Electron Shuttle for Fe(III) Oxide Reduction and as a Terminal Electron Acceptor by *Shewanella algae* BrY. *Appl. Environ. Microbiol.* **2002**, *68*, 2436–2444.
- Rabaey, K.; et al. Microbial Phenazine Production Enhances Electron Transfer in Biofuel Cells. *Environ. Sci. Technol.* **2005**, *39*, 3401–3408.
- Reguera, G.; et al. Extracellular Electron Transfer via Microbial Nanowires. *Nature* **2005**, *435*, 1098–1101.
- Gorby, Y. A.; et al. Electrically Conductive Bacterial Nanowires Produced by *Shewanella oneidensis* Strain MR-1 and Other Microorganisms. *Proc. Natl. Acad. Sci. U.S.A.* **2006**, *103*, 11358–11363.
- Phung, N. T.; et al. Analysis of Microbial Diversity in Oligotrophic Microbial Fuel Cells Using 16S rDNA Sequences. *FEMS Microbiol. Lett.* **2004**, *233*, 77–82.
- Kim, B. H.; et al. Enrichment of Microbial Community Generating Electricity Using a Fuel-Cell-Type Electrochemical Cell. *Appl. Microbiol. Biotechnol.* **2004**, *63*, 672–681.

- (28) Bond, D. R.; et al. Electrode-Reducing Microorganisms That Harvest Energy from Marine Sediments. *Science* **2002**, *295*, 483–485.
- (29) Holmes, et al. Microbial Communities Associated with Electrodes Harvesting Electricity from a Variety of Aquatic Sediments. *Microb. Ecol.* **2004**, *48*, 178–190.
- (30) Logan, B. E.; et al. Electricity Generation from Cysteine in a Microbial Fuel Cell. *Water Res.* **2005**, *39*, 942–952.
- (31) Rabaey, K.; et al. Biofuel Cells Select for Microbial Consortia that Self-Mediate Electron Transfer. *Appl. Environ. Microbiol.* **2004**, *70*, 5373–5382.
- (32) Min, B.; et al. Electricity Generation from Swine Wastewater Using Microbial Fuel Cells. *Water Res.* **2005**, *39*, 4961–4968.
- (33) Water Infrastructure Network. *Water Infrastructure Now: Recommendations for Clean and Safe Water in the 21st Century*; 2001; www.win-water.org/win_reports/pub2/winow.pdf.
- (34) Electric Power Research Institute. *U.S. Water Consumption for Power Production—The Next Half Century*; Water and Sustainability, Vol. 3; 2002; www.epri.com.
- (35) Shizas, I.; Bagley, D. M. Experimental Determination of Energy Content of Unknown Organics in Municipal Wastewater Streams. *J. Energ. Eng.* **2004**, *130*, 45–53.
- (36) Logan, B. E. Simultaneous Wastewater Treatment and Biological Electricity Generation. *Water Sci. Technol.* **2005**, *52*, 31–37.
- (37) Reimers, C. E.; et al. Harvesting Energy from the Marine Sediment–Water Interface. *Environ. Sci. Technol.* **2001**, *35*, 192–195.
- (38) Tender, L. M.; et al. Harnessing Microbially Generated Power on the Seafloor. *Nat. Biotechnol.* **2002**, *20*, 821–825.
- (39) Shantaram, A.; et al. Wireless Sensors Powered by Microbial Fuel Cells. *Environ. Sci. Technol.* **2005**, *39*, 5037–5042.
- (40) Gregory, K. B.; Lovley, D. R. Remediation and Recovery of Uranium from Contaminated Subsurface Environments with Electrodes. *Environ. Sci. Technol.* **2005**, *39*, 8943–8947.
- (41) Gregory, K. B.; Bond, D. R.; Lovley, D. R. Graphite Electrodes as Electron Donors for Anaerobic Respiration. *Environ. Microbiol.* **2004**, *6*, 596–604.
- (42) Matsumoto, N.; et al. Extension of Logarithmic Growth of *Thiobacillus ferrooxidans* by Potential Controlled Electrochemical Reduction of Fe(III). *Biotechnol. Bioeng.* **1999**, *64*, 716–721.
- (43) Heilmann, J. Microbial Fuel Cells: Proteinaceous Substrates and Hydrogen Production Using Domestic Wastewater. Department of Civil and Environmental Engineering, Pennsylvania State University, University Park, PA, 2005.
- (44) Liu, H.; Grot, S.; Logan, B. E. Electrochemically Assisted Microbial Production of Hydrogen from Acetate. *Environ. Sci. Technol.* **2005**, *39*, 4317–4320.
- (45) Logan, B. E.; Grot, S. A Bioelectrochemically Assisted Microbial Reactor (BEAMR) that Generates Hydrogen Gas. U.S. Patent Application 60/588,022, 2005.
- (46) Rozendal, R. A.; Buisman, C. J. N. Bio-Electrochemical Process for Producing Hydrogen. International Patent WO-2005-005981, 2005.
- (47) Rozendal, R. A.; et al. Principle and Perspectives of Hydrogen Production through Biocatalyzed Electrolysis. *Int. J. Hydrogen Energy* **2006**, in press, doi 10.1016/j.ijhydene.2005.12.006.
- (48) U.S. Department of Energy. *National Hydrogen Energy Roadmap*; Based on the results of the National Hydrogen Energy Roadmap Workshop, Washington, DC, 2002; www1.eere.energy.gov/hydrogenandfuelcells/pdfs/national_h2_roadmap.pdf.
- (49) Sun, Y.; Cheng, J. Hydrolysis of Lignocellulosic Materials for Ethanol Production: A Review. *Bioresour. Technol.* **2002**, *83*, 1–11.
- (50) Zuo, Y.; Maness, P.-C.; Logan, B. E. Electricity Production from Steam Exploded Corn Stover Biomass. *Energy Fuels* **2006**, *20*, 1716–1721.
- (51) Madigan, M. T.; Martinko, J. M. *Brock Biology of Microorganisms*, 11th ed.; Pearson Prentice Hall: Upper Saddle River, NJ, 2006.