Microbial fuel cells: novel microbial physiologies and engineering approaches
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The possibility of generating electricity with microbial fuel cells has been recognized for some time, but practical applications have been slow to develop. The recent development of a microbial fuel cell that can harvest electricity from the organic matter stored in marine sediments has demonstrated the feasibility of producing useful amounts of electricity in remote environments. Further study of these systems has led to the discovery of microorganisms that conserve energy to support their growth by completely oxidizing organic compounds to carbon dioxide with direct electron transfer to electrodes. This suggests that self-sustaining microbial fuel cells that can effectively convert a diverse range of waste organic matter or renewable biomass to electricity are feasible. Significant progress has recently been made to increase the power output of systems designed to convert organic wastes to electricity, but substantial additional optimization will be required for large-scale electricity production.

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Introduction
As supplies of fossil fuels dwindle and concerns about continued contributions of additional carbon dioxide to the atmosphere intensify, there is an increasing need for new sources of energy from renewable carbon-neutral sources with minimal negative environmental impact. Producing electricity from organic matter with microbial fuel cells is a concept that arguably dates back almost 100 years [1]. As recently reviewed [1], the basic principals of microbial fuel cells were established some time ago in pioneering studies by groups led by Bennetto, Kim, Zeikus and others.

In the most general sense, microbial fuel cells function by oxidizing an electron donor with electron transfer to the anode under anoxic conditions (Figure 1). The electron donor can be a reduced product of microbial metabolism or an added artificial mediator that facilitates electron transfer by accepting electrons from the microbes and donating them to the anode. In some instances the microorganisms can produce their own soluble electron transfer mediator. Alternatively, some microorganisms can directly transfer electrons to the anode surface. Electrons donated to the anode pass through a resistor or other type of electrical device to the cathode. The cathode may be exposed to the air or submerged in aerobic water. Protons released from oxidation of the organic matter migrate to the cathode, often through a cation-selective membrane that limits diffusion of oxygen into the anode chamber. Electrons, protons and oxygen combine at the cathode surface to form water.

Although interest in microbial fuel cells was relatively high in the 1960s, the study of microbial fuel cells waned as the cost of other energy sources remained low and the available microbial fuel cells lacked efficiency and long-term stability. However, in the past three to four years there has been a resurgence in microbial fuel cell research. As detailed below, advances have included the development of what could be the first microbial fuel cell that can out compete more conventional power sources for its designated application, significant efforts to better engineer systems for harvesting electricity from organic wastes, and the discovery of microorganisms with enhanced capacities for sustained, efficient electricity production.

BUG Juice
One of the most exciting discoveries in the past few years in microbial fuel cell research was the development by Reimers and Tender of a microbial fuel cell that can harvest electricity from the organic matter in aquatic sediments [2–4]. These systems are now known as Benthic Unattended Generators or BUGs (http://www.nrl.navy.mil/code6900/bug/). BUGs are being designed for powering electronic devices in remote locations, such as the bottom of the ocean, where it would be expensive and technically difficult to routinely exchange traditional batteries [3,5]. BUGs consist of an anode buried in anoxic marine sediments connected to a cathode suspended in the overlying aerobic water (Figure 2). Similar designs could potentially power electronic devices in remote terrestrial locations and could even eventually be modified to harvest electricity from other sources such as compost piles, septic tanks and waste lagoons.
It was initially proposed that the microbes degrading organic matter in sediments produced reduced end products, such as sulfide, Fe (II) and reduced humic substances, which then donated electrons to the electrodes [2]. This hypothesis was consistent with the reactions known to occur in the microbial fuel cells at the time, in which the reduced end products of microbial metabolism or reduced artificial mediators were the direct source of electrons [6]. However, subsequent microbiological analysis has now suggested that microorganisms are more directly involved in electron transfer to the anode of BUGs.

Molecular analysis of the microbial community on anode surfaces revealed that microorganisms in the family Geobacteraceae accounted for about half of the microorganisms, but there was no similar enrichment of Geobacteraceae on graphite buried in the sediment that was not connected to a cathode [3,7,8]. In marine sediments, Desulfuromonas species, which prefer marine salinities, predominated on the anodes, whereas Geobacter species, which prefer freshwater, were most abundant on electrodes buried in freshwater sediments. Geobacter species were also highly enriched on electrodes harvesting electricity from other organic material, such as swine waste (KB Gregory et al. unpublished). Pure culture studies demonstrated that Geobacteraceae are capable of conserving energy to support growth by completely oxidizing acetate and other organic compounds to carbon dioxide with an electrode serving as the sole electron acceptor [7,9,10]. The ability of Geobacteraceae to produce electricity in this manner is probably related to their ability to transfer electrons outside the cell onto Fe(III) and Mn(IV) oxides, which are also insoluble, extracellular electron acceptors [11].

The oxidation of sediment organic matter coupled to the reduction of Fe(III) and Mn(IV) oxides is catalyzed by a consortia of microorganisms. Some microorganisms break down the complex assemblage of organic matter to produce fermentation products, such as acetate, and other potential electron donors for Geobacteraceae, such as aromatic compounds and long-chain fatty acids. The Geobacteraceae can then oxidize these compounds with...
the reduction of Fe(III) or Mn(IV) [11]. It is assumed that a similar microbial food chain, with anodes substituting for the Fe(III) and Mn(IV) that Geobacteraceae would naturally use, provides electrons to BUGs (Figure 2).

However, the microbiology of BUG anodes could be more complex in some environments. In freshwater environments, Geothrix species, although not as abundant as Geobacter species, might contribute to electricity production [8,12]. In some sulfide-rich sediments, microorganisms with 16S rRNA sequences closely related to known Desulfobulbus species predominate on the anodes [8]. The likely reason for this is that sulfide abiotically reacts with the electrode to form $S_8$, the elemental form of sulfur, and Desulfobulbus species then oxidize the $S_8$ to sulfate using the anode as the electron acceptor [13].

A better understanding of how Geobacteraceae and other organisms that colonize the anodes of BUGS transfer electrons to the anode surface could facilitate further optimization of these systems. Electron transfer to electrodes in Geobacteraceae has primarily been studied with Geobacter sulfurreducens, because this organism is closely related to the Geobacteraceae that colonize electrodes in sediments and the complete genome sequence [14], a genetic system [15] and whole-genome DNA microarrays [16] are available for this microorganism. Furthermore, it is possible to track the metabolism of G. sulfurreducens growing on electrodes by monitoring the gene transcript levels. For example, Geobacteraceae possess a unique, eukaryotic-like citrate synthase that catalyzes a key step in acetate oxidation [17]. Levels of transcripts for citrate synthase increased in cells of G. sulfurreducens growing on electrodes as current production from acetate oxidation increased, demonstrating a link between transcript levels and metabolism on electrodes [18]. A combination of gene expression and genetic studies have recently indicated that many of the key components involved in extracellular electron transfer to Fe(III) oxides, such as the outer-membrane $c$-type cytochromes OmcS and OmcE [19], are also involved in electron transfer to electrodes [20]. Surprisingly, under conditions that mimic the BUG system, the electrically conductive pili that are essential for electron transfer to Fe(III) oxides [21] were not required for electron transfer to electrodes [20]. Another route to increasing electricity production could be to alter central metabolism to increase rates of respiration. With the genome-based in silico model of G. sulfurreducens [22] it has been possible to predict strategies for increasing respiration rates and thus to provide increased electricity production.

**Large-scale conversion of organic wastes and renewable biomass to electricity**

One of the most active areas of microbial fuel cell research in the past few years has been in the further development
of fuel cells designed to produce power from organic wastes such as sewage. Like BUGs, the concept is to rely on the microorganisms naturally present in the waste organic matter to transfer electrons to the anode. Unlike BUGs, in which there is generally a predominance of the same types of microorganisms on the anode surface regardless of the site of deployment, the microbiology of prototypes for waste water treatment appears to be highly dependent upon the design and operational parameters of the system. For example, in a system harvesting electricity under highly anoxic conditions, *Geobacter* species accounted for over 70% of the microbes on anode surfaces and were considered to be the predominant organisms involved in electricity production (KB Gregory et al., unpublished). However, in other systems, in which the reactor design permits substantial leakage of oxygen into the anode chamber, organisms more tolerant to oxygen exposure can predominate [23,24,25].

Whether the microbial fuel cells are run in batch or flow-through mode can also impact not only on the type of microorganisms present, but also on the mechanisms by which electrons are transferred to the anode. For example, in a batch system converting glucose to electricity, there appeared to be selection for microorganisms producing compounds that acted as electron shuttles to promote electron transfer to the electrode surface [24]. Although a strain of *Pseudomonas aeruginosa* capable of utilizing glucose and producing an electron shuttle was isolated from this system, the isolated strain was inefficient in converting glucose to electricity owing, at least in part, to the fact that it only incompletely oxidized glucose to fatty acids [26]. Therefore, it is not clear what microorganisms were responsible for the high rates of power production in the mixed community.

The production of electron shuttles is much less likely to be an important strategy for electron transfer to anodes in flow-through systems [27] or other types of open systems in which there is a frequent change of the fluid around the anode. This is because, in an environment in which the shuttle might be rapidly lost to the external environment, the energetic cost of biosynthesizing an electron shuttle puts an electron-shuttle-producing microorganism at a severe disadvantage compared with microorganisms that directly transfer electrons to the anode (Box 1).

Most recent studies on the conversion of organic wastes to electricity have focused on the engineering challenges of developing such systems: the composition, surface area and positioning of the anodes, cathodes and cation-selective membrane [28–31,32,33,34]; the ionic strength of the medium [28,35]; and flow-through characteristics [27,32,36]. These studies included very little microbiology and thus the reader is referred to recent reviews [37–39] for more in-depth coverage of this subject. In some instances, these innovations have substantially increased power output; however, challenges remain. In the flow-through systems that would be required to treat large volumes of liquid waste, the highest power outputs are less than 2 W per square meter of anode surface, even when treating readily degradable pure substrates such as glucose [32]. This power output is unlikely to be sufficient to recover the power expended in pumping the fluid through the system. Scaling of these laboratory systems to the size that would be required to handle large volumes of wastes also remains an issue.

**Sensors**

Systems based on the microorganism *Shewanella* show promise as sensors for quantifying the biological oxygen demand in sewage [40–42]. This concept might readily be expanded to detect other compounds that can act as electron donors for electricity production, such as hydrogen [9] or aromatic contaminants [7].
Microbes on the cathode

Given the ability of *Geobacter* species to make an electrical connection with graphite electrodes, it might not be surprising that, if an electrode is poised at a negative potential, *Geobacter* species can accept electrons from an electrode [43]. When a negatively poised electrode was placed in a sediment inoculum, nitrate was reduced and there was an enrichment of *Geobacter* species on the electrode surface [43]. In another study different, as yet unidentified, organisms were enriched [44]. Pure cultures of *Geobacter* species were able to reduce physiological electron acceptors such as nitrate and fumarate with the electrode serving as the sole electron donor. A poised electrode also promoted the reduction of soluble U(VI) to insoluble U(IV) in uranium-contaminated sub-surface sediments [45]. The U(IV) precipitated on the electrode surface. Thus, reduction of U(VI) with electrodes could be a more preferable strategy for the bio-remediation of uranium-contaminated subsurface environments than the addition of organic electron donors, because electrodes also provide a simple means of removing the uranium from the ground [45]. Electrodes could conceivably be used to provide electrons for the bioremediation of other contaminants, such as chlorinated solvents and perchlorate.

Manganese-oxidizing microorganisms served as the catalysts in a novel cathode system that increased the current by almost two orders of magnitude over plain graphite electrodes in a microbial fuel cell [46**]. Mn(IV) precipitated on the cathode is reduced to Mn(II), which the manganese oxidizers recycle back to Mn(IV).

Conclusions

Microorganisms that can couple the oxidation of organic compounds to electron transfer to electrodes offer the promise of self-sustaining systems that can effectively convert waste organic matter and renewable biomass into electricity. Oxidation of these recently fixed sources of organic carbon does not contribute net carbon dioxide to the atmosphere and, unlike hydrogen fuel cells, there is no need for extensive pre-processing of the fuel or for expensive catalysts. With the appropriate optimization, microbial fuel cells might be able to power a wide range of widely used devices. For example, there is ongoing research on the potential for powering self-feeding robots and even automobiles in this manner [1]. Another possibility is to use systems similar to BUGs for harvesting electricity from domestic and agricultural wastes to provide a decentralized power source in extensive rural areas not served by power grids in developing countries. However, significant optimization of microbial fuel cells will be required for most applications. Further investigations into the physiology and ecology of microbes that transfer electrons to electrodes are essential to carry out these optimizations in a rational manner.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest


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27. Rabaey K, Osseir W, Verhaege M, Verstraete W: Biofuel cells select for microbial consortia that self-mediate electron transfer. Appl Environ Microbiol 2004, 70:5373-5382. This study suggests that under non-flow conditions the production and release of an electron shuttle could be an adaptive strategy for microbes to transfer electrons to an electrode. However, subsequent studies by this group suggest that shuttles are not important in flow-through systems.


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