Bug juice: harvesting electricity with microorganisms

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Abstract | It is well established that some reduced fermentation products or microbially reduced artificial mediators can abiotically react with electrodes to yield a small electrical current. This type of metabolism does not typically result in an efficient conversion of organic compounds to electricity because only some metabolic end products will react with electrodes, and the microorganisms only incompletely oxidize their organic fuels. A new form of microbial respiration has recently been discovered in which microorganisms conserve energy to support growth by oxidizing organic compounds to carbon dioxide with direct quantitative electron transfer to electrodes. These organisms, termed electricigens, offer the possibility of efficiently converting organic compounds into electricity in self-sustaining systems with long-term stability.

"The disintegration of organic compounds by microorganisms is accompanied by the liberation of electrical energy." M.C. Potter, 1911.

It is well known that microorganisms can produce fuels, such as ethanol, methane and hydrogen, from organic matter. It is less well known that microorganisms can also convert organic matter into electricity in devices known as microbial fuel cells. However, interest in microbial fuel cells is increasing. Microbial fuel cells offer the possibility of harvesting electricity from organic waste and renewable biomass. These are attractive sources of energy because they are 'carbon-neutral'; the oxidation of the organic matter only releases recently fixed carbon back into the atmosphere.

Furthermore, microbial fuel cells could fill a niche that is significantly different from that of the better-known abiotic hydrogen- and methanol-driven fuel cells. For example, abiotic fuel cells require expensive catalysts to promote oxidation of the electron donors[1], whereas naturally occurring microorganisms catalyse the oxidation of the fuels in microbial fuel cells. Abiotic fuel cells often operate at high temperatures[1], but microbial fuel cells can be operated at room temperature and could potentially be designed to function at any temperature at which microbial life is possible. The fuels for abiotic fuel cells are highly explosive or toxic and have to be highly purified to avoid poisoning the catalysts. By contrast, the microorganisms that power microbial fuel cells can oxidize a diverse range of 'dirty' fuels that are often of little perceived value, such as organic waste and the

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organic matter in soils and sediments. The ubiquitous and innocuous properties of fuels for microbial fuel cells alleviates the need for the complex and highly regulated distribution systems that are required for hydrogen and methanol. Therefore, microbial fuel cells might be particularly attractive power sources in remote locations and regions of developing countries that are not served by well-developed, centralized power grids.

Microbial fuel cells are also distinct from the better-developed enzymatic fuel cells in which electricity is generated through enzymes or cell extracts rather than whole cells[2]. Enzymatic fuel cells can produce high levels of power for their size and are well suited to applications such as sensors. However, enzymatic fuel cells typically only harvest a small percentage of the electrons available in organic fuels, because incorporating the full complement of enzymes necessary to completely oxidize organic fuels to carbon dioxide is not yet technically feasible. By contrast, as detailed below, microbial fuel cells offer the possibility of extracting over 90% of the electrons from organic compounds, and can be self-sustaining and renewing when populated with microorganisms that conserve energy from electron transfer to electrodes.

One reason that microbial fuel cells are not commonly considered a part of the energy portfolio for the future, is that microbial fuel technology is not yet sufficiently well developed to produce substantial quantities of power in a cost-effective manner. Over the past 40 years it has been suggested that microbial fuel cells might be developed for a wide range of applications, including serving as household electrical generators[3] and powering items

such as small portable electronic devices[3,4], boats[4], automobiles[3,5], electronics in space[6] and self-feeding robots[7]. There is also interest in developing large-scale microbial fuel cells for the conversion of sewage and other organic waste to electricity[8–10], and the bioremediation of contaminated environments (BOX 1). However, none of these applications is yet practical. The only microbial fuel-cell application with short term potential is to power monitoring devices in remote locations[11].

At present, microbial fuel cells can produce enough current to power small electronic devices for short periods or to trickle-charge capacitors for applications with higher power demands. However, the size of these microbial fuel cells precludes their incorporation into the electronic devices they can power. At the time that this review was completed, the highest power densities reported for the type of microbial fuel cell most likely to be sustainable for long periods of time were approximately 50 Watts per cubic metre of fuel cell volume[12]. Therefore, further optimization is required for most envisioned applications.

Most of the research into optimizing power output from microbial fuel cells has focused on altering their designs in order to overcome electrochemical barriers to electron and proton flow, and to enhance the surface area and reactivity of the anode and cathode (for excellent reviews see REFS 8–10). The literature in this area is extensive, but, for the most part, the actual microbiological processes taking place in the microbial fuel cells were not well defined, and such studies will not be reviewed in detail

here. In addition to further electrochemical engineering, a better understanding of the physiology and ecology of microbial electricity production might be helpful in further optimizing microbial fuel cells. Furthermore, better understanding of the interaction of microorganisms with electrically conductive surfaces will also aid in the development of as-yet-unimagined technologies where small amounts of power or specialized conductive materials are required for micro- or nano-electronic applications.

The purpose of this review is to summarize our present knowledge of the microbiology of electricity production. As detailed below, many microorganisms can contribute to electricity production. However, it is the recent discovery of a new metabolic class of electricity-producing microorganisms that has, for the first time, indicated that a wide diversity of organic compounds can be effectively converted to electricity in self-sustaining microbial fuel cells. These organisms, known as electricigens, can completely oxidize organic compounds to carbon dioxide, with an electrode serving as the sole electron acceptor, and conserve energy to support growth from this electron transfer. The known physiology and ecology of electricigens, their potential mechanisms for electron transfer to electrodes and present concepts for optimizing their performance are reviewed.

What is a microbial fuel cell?

A fuel cell converts chemical energy into electrical energy, without the inefficiencies that arise from combusting fuel

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Box 1 | Microbial fuel cells and bioremediation

One of the main difficulties in the bioremediation of subsurface environments contaminated with organic compounds or metals is the optimum delivery of an electron acceptor or donor to best promote the desired biodegradation. For example, bioremediation of petroleum-contaminated groundwater is often impeded because the introduction of oxygen into the subsurface is technically challenging and expensive. Alternative electron acceptors, such as Fe^{3+} and sulphate, that support anaerobic respiration can also be exploited[78,79], but electrodes represent another, possibly more convenient, electron acceptor. For example, in one study *Geobacter metallireducens* oxidized the prevalent aromatic hydrocarbon contaminant toluene with an electrode serving as the sole electron acceptor[58], and preliminary studies have indicated that electrodes placed in petroleum-contaminated subsurface sediments can accelerate the degradation of aromatic hydrocarbons (R.T. Anderson, personal communication).

Microbial reduction of the oxidised form of uranium, U^{6+}, with an electrode serving as the electron donor represents a potential strategy for improving the bioremediation of groundwater contaminated with uranium. A simple strategy for preventing the further spread of uranium contamination in groundwater is to add an organic electron donor, such as acetate, to the groundwater[80]. This stimulates the growth of *Geobacter* species, which obtain most of their energy from the oxidation of the acetate with the reduction of the Fe^{3+} oxides that are abundant in most subsurface environments. As U^{6+}-containing groundwater enters the zone of acetate addition, the *Geobacter* species also transfer electrons to the soluble U^{6+} reducing it to U^{4+}, which is highly insoluble. This effectively prevents further migration of the uranium, which is beneficial, but has the drawback that the uranium remains in the subsurface. However, when an electrode serves as an electron donor, the U^{4+} that is produced precipitates on the electrode surface[72]. Therefore, it is possible to envision that by placing electrodes in wells drilled into uranium-contaminated subsurface environments, it will be possible to not only prevent the further mobility of uranium by reducing U^{6+} to U^{4+}, but also to extract the uranium when the electrodes are withdrawn from the wells. The precipitated uranium can easily be extracted from the electrodes with bicarbonate and the electrodes can then be redeployed[72]. Field trials of this concept are underway.

Electrodes could potentially serve as electron donors for the biological removal of other contaminants from contaminated groundwater or waste streams. For example, a diversity of microorganisms, including some Geobacteraceae species[81,82], can remove chlorinated solvents from contaminated groundwater through reductive dechlorination, and a typical strategy to promote dechlorination is to add organic electron donors. However, the electron donors must be added at the right level; adding too little electron donor doesn't adequately promote the process, whereas adding too much stimulates unwanted competitive processes, such as methane production. It might be possible with electrodes to 'dial in' just the right amount of electron donor amendment. Nitrate is a common contaminant with substantial impacts on water quality. Although *Geobacter* species colonizing a nitrate-reducing electrode system in a sediment slurry only reduce nitrate to nitrite[73], other organisms can further reduce nitrite to nitrogen gas[76].

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to produce electricity[13]. In microbial fuel cells the fuel source is generally microbially degradable organic matter. These organic fuel sources cannot be used in currently conceived abiotic fuel cells because, unlike hydrogen, these fuels are not electrochemically active. However, microorganisms can catalyse the release of electrons from organic matter and transfer them to various electron carriers that are electrochemically active.

It is generally regarded that electricity production in microbial cultures was first observed over 90 years ago by Potter[14,15]. Potter's studies embodied most of the principles of modern-day microbial fuel cells. The microbial fuel cell consists of an anode, which accepts electrons from the microbial culture, and a cathode, which transfers electrons to an electron acceptor, typically oxygen for most perceived practical applications. The anode compartment is typically maintained under anoxic conditions, whereas the cathode can be suspended in aerobic solutions or exposed to air. Electrons flow from the anode to the cathode through an external electrical connection that typically includes a resistor, a battery to be charged or some other electrical device. The anode and cathode are often separated by a semi-permeable membrane that restricts oxygen diffusion from the cathode chamber to the anode chamber, while allowing protons that are released from organic matter metabolism, or oxidation of reduced metabolic products, to move from the anode to the cathode. At the cathode, electrons, protons and oxygen combine to form water.

Separating the microorganisms from the source of oxygen in a microbial fuel cell intercepts the flow of electrons to oxygen that microorganisms would catalyse if oxygen were available. Although, as detailed below, some microorganisms can conserve energy from electron transfer to anodes, the electrical connection between the anode and the cathode abiotically completes the final electron transfer steps to oxygen, harvesting some of the energy that the microorganisms would otherwise convert to ATP by oxidative phosphorylation.

Liberating electrons from organic matter

With current microbial fuel-cell technologies, anaerobic metabolism must be promoted at the anode in order to convert organic matter to electricity in an effective manner. Fermentation is a well-known mechanism for anaerobic metabolism of organic matter and, until recently, many microbial fuel-cell studies relied solely on fermentative microorganisms[2,5]. However, fermentation alone cannot be a strategy for efficiently converting organic matter to electricity, because most of the electrons available in the organic fuel remain in fermentation products that do not readily react with electrodes.

Effective anaerobic oxidation of complex assemblages of organic matter, such as those found in most wastes and biomass, requires the fermentation products from the metabolism of sugars, amino acids and related compounds, in addition to other constituents, such as aromatic compounds and long-chain fatty acids, to be oxidized with electron transfer to an electron acceptor. The closest analogues to electrodes for microbial metabolism in natural environments are probably Fe^{3+}
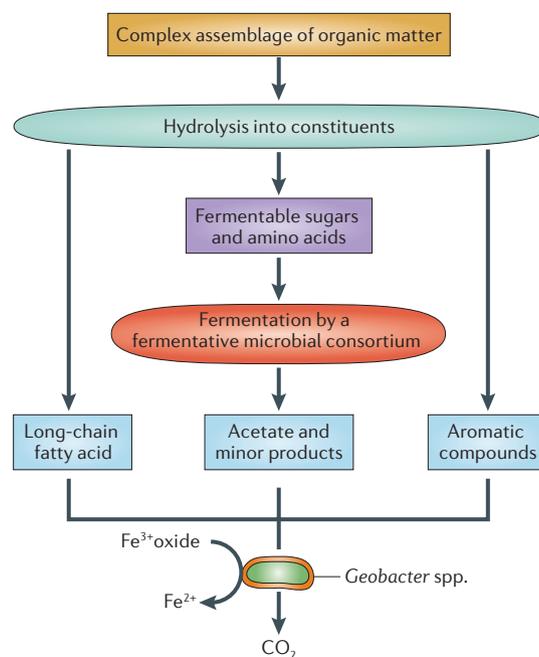
Figure 1 | **Generalized pathway for the anaerobic oxidation of organic matter to carbon dioxide with Fe^{3+} oxide serving as an electron acceptor in temperate, freshwater and sedimentary environments.** The process is mediated by a consortium of fermentative microorganisms and *Geobacter* species.

oxides, because both electrodes and Fe^{3+} oxides are insoluble, extracellular electron acceptors. The oxidation of organic matter, coupled to the reduction of Fe^{3+} oxides in sedimentary environments, requires the cooperation of a consortium of fermentative microorganisms and Fe^{3+}-reducing microorganisms (FIG. 1). Fe^{3+}-reducing microorganisms (most often *Geobacter* species in temperate environments[16] and Fe^{3+}-reducing archaea in hot environments[17]) metabolize the fermentation products and the organic compounds that fermentative microorganisms do not readily metabolize, oxidizing them to carbon dioxide, with Fe^{3+} oxides serving as the electron acceptor. Although there are Fe^{3+} reducers that can completely oxidize fermentable compounds, such as sugars[18] or amino acids[19], to carbon dioxide with the reduction of Fe^{3+}, food chains composed of fermentative microorganisms and Fe^{3+} reducers that oxidize fermentation products are more commonly found, which can be attributed to thermodynamic considerations[20]. It seems likely that, in order to effectively convert organic matter to electricity, similar cooperative consortia and pathways are required, with the exception that an anode serves as the final electron acceptor.

Mechanisms for electron transfer to electrodes

The key difference in microbial electricity production versus natural biogeochemical processes, such as Fe^{3+} reduction, is that the electrons are transferred to an electrode rather than a natural electron acceptor. Four primary mechanisms for microorganisms to transfer electrons to electrodes have emerged to date.