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Molecular genetics of electricity production in bacteria: A review

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ABSTRACT

As the population of the world increases, the search for new energy sources has become a necessity. Much research has been conducted on renewable energy sources that may substitute traditional energy sources; these include solar energy, wind energy, and wave power. Microbes play an important role in producing energy by generating electrical conductivity through the transport of electrons generated from their metabolism. Such bacteria are known as electro-active bacteria and are used in microbial fuel cells, where microbes are used to generate electric energy from the degradation of organic compounds. The role of microbial fuel cells are not only important in generating electricity, but also in reducing organic contaminants in the environment. Microbial fuel cells are also important in producing electricity in locations where it is costly to maintain batteries periodically, such as the bottom of the oceans. One of the best-known electro-active bacteria is Geobacter, which has the ability to transfer electrons outside its membrane. Researchers have developed a genetic system that functions in Geobacter in order to construct mutants and study gene knockout strains, and they found that this bacterium uses multiple c-type cytochromes to iron oxides by direct contact. In the past few decades, Shewanella has gained the attention of scientists due to its respiratory adaptability. This bacterium can respire different inorganic compounds as electron acceptors, including, thiosulfate, nitrate, arsenate, elemental sulfur, and fumarate. This ability came from its unique electron-transport pathways, which helped to adapt changes in electron acceptor availability which fluctuate according to environmental conditions.

Introduction

As the population of the world increases, the search for new energy sources has become a necessity. At one point, natural resources such as coal and petroleum will not be able to provide energy for the increased population due to the fact that the rate of their formation is much lower than the rate of their combustion [1]. Therefore, research on renewable energy sources such as solar energy, wind energy, and wave power is being conducted worldwide, and such technologies have already been applied [2,3]. Microbes play a part in this field because of their ability to produce electrons that are generated from the utilization of organic compounds [4].

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However, only those that are able to deliver electrons outside their membrane, are useful in electricity production and are called electro-active bacteria (EAB) [5].

Electroactive bacteria use different methods to transfer electrons outside their cell membrane such as using electrically conductive nanowires and flagella or by using c-type cytochromes located on their outer membrane [6].

The ability of bacteria to produce electricity was reported more than a hundred years ago, however, such projects has only started to receive attention in the past few years [7]. Electro-active bacteria were first applied in microbial fuel cells at where microbes were used to generate electric energy from the degradation of organic compounds.

Basically, bacteria applied in microbial fuel cells deliver electrons gained from the anaerobic oxidation of chemical compounds at the anode compartment through

a proton exchange membrane to the cathode compartment that is usually supplied with oxygen that acts as an electron acceptor [8]. The production of electricity in microbial fuel cells can be used for many purposes including the decomposition of organic waste in wastewater treatment plants which eliminates toxic substance besides generating electric power [9]. This technique not only reduces toxic organic compounds from wastewater that is used as electron donors, but also may reduce detrimental inorganic compounds such as nitrate, copper, iron, and mercury by using them as electron acceptors in the cathode compartment [10]. Moreover, this technique can be used to produce electricity in remote locations, such as unattended terrestrial areas or the bottom of the oceans were it would be relatively costly to maintain batteries periodically [11].

Microbes that were found to possess such capabilities are mostly limited to the genus Geobacter and Shewanella, however, some Pseudomonas species and other photosynthetic bacteria have been applied in microbial fuel cells such as Anabaena and Nostoc due to their ability to obtain energy autotrophically and use that energy to fix CO2 thus reducing this concentrations in the atmosphere besides generating electricity [12]. Electricity production by this method have faced many obstacles, one of the major obstacles was that most electro-active bacteria do not completely oxidize their substrate leading to waste in electron donors used. Other bacteria were incapable of transferring electrons directly to the cathode unless a mediator (thionine, azure A, potassium ferricyanide, etc.) was added to their growing cultures. Most of these mediators are toxic, thus could not be used in open environments which increased the limitations of this process [13,14,15]. However, subsequent studies isolated a strain of *Geobacter sulfurreducens* that had a high ability to completely metabolize acetate as an electron donor and transfer the electrons obtained directly to the cathode as an electron acceptor without the need of mediators [14].

The production of electricity from microbes is a challenging area that requires deep knowledge into the molecular biology of the process in order to better understand it and to manipulate more efficient strains. For this reason, this review was conducted to shed light on the recent biochemical and genetic advances in this field and to introduce possible future uses of this methodology.

Genetics of electricity production in Geobacter

Species belonging to the genus Geobacter are environmentally important obligate anaerobes that possess the ability to fully oxidizes several organic compounds, including acetate and different mono-aromatic hydrocarbons using a wide variety of metals as electron acceptors [16]. The ability of this bacterium to transfer electrons outside its membrane has made it one of the best candidates for bacterial electricity production [5]. The importance of this genus has made the study of its genetics a necessity. Researchers have developed a genetic system that functions in *Geobacter* in order to construct mutants and study gene knockout strains [17]. *G. sulfurreducens* utilizes multiple c-type cytochromes to reduce iron oxides by direct contact; however, genetic studies have shown that not all these cytochromes are capable of transferring electrons to electrodes [18]. Analysis of whole genome expression data in *G. sulfurreducens* revealed 474 genes highly expressed when grown with an electrode compared with a soluble Fe(III) electron acceptor. Two major outer membrane proteins that were expressed during growth on Fe(III) oxides are OmcS and OmcE [19]. These proteins are c-type cytochromes that were found to be directly involved in electron transfer to Fe(III) oxides. Knockout mutants of either OmcS or OmcE were incapable of reducing Fe(III) oxides unless the electron shuttle anthraquinone 2,6-disulfonate was added. However, these mutants were capable of reducing soluble Fe(III) citrate. This indicates that both of these proteins are responsible for the direct contact with Fe(III) oxides for appropriate electron transfer and thus Fe(III) reduction while mutants do not require these proteins to deal with soluble Fe(III) compounds that are available near to bacterial cell surface [20].

In a study by Kim et al., they found that deleting OmcF (outer membrane cytochrome F) inhibited electricity production, however, microarray analysis results showed that OmcF deficient mutants had low expression of genes previously found to be up-regulated during electricity production. In addition mutants for OmcF lacked the outer membrane proteins, OmcS and OmcE, this suggests that OmcF is indirectly responsible

for transcription of genes involved in electricity generation such as those responsible for the export of membrane proteins [21]. Surprisingly, major genes that were previously known to be involved in electricity production such as those responsible for producing the electrically conductive nanowires and the outer membrane c-type cytochrome, OmcB, were not adversely expressed when grown with electrodes as an electron acceptor neither was electricity production inhibited when these genes were deleted [19].

Genetics of electricity production in Shewanella

The *Shewanella* genus was first isolated from tainted Canadian butter in 1931 [22]. The genus *Shewanella* belongs to the class Gammaproteobacteria, which comprises over 70 species that are widely spread in different environments, including soil, marine, freshwater sediment, and deep-sea sediment [23]. Members of *Shewanella* are Gram negative, facultative aerobic bacteria that use organic compounds as sources of carbon and energy [24]. Recently, these species have attracted considerable attention, especially *Shewanella oneidensis* MR-1, due to their respiratory adaptability. Where they can respire different inorganic compounds as electron acceptors, including, thiosulfate, nitrate, arsenate, elemental sulfur, and fumarate, in addition to soluble and solid metals, such as Fe(III), Mn (III,IV), uranium, and cobalt. This ability came from the unique electron-transport pathways of the MR-1 which help this strain to adapt based on the electron acceptors availability which change frequently due to fluctuations in the environmental conditions [25]. In addition, *Shewanella* have evolved special electron transport pathways in order to deliver electrons from NADH and quinones (electron carriers) to a solid and insoluble electron acceptors, termed 'extracellular electron-transport (EET) pathways. These pathways were also found to have significant role in exchanging electrons with electrodes in bioelectrochemical systems (BESs), hence, *Shewanella* was also called 'electrochemically active bacteria (EAB)' [26].

There are two important applications of BESs, (i) microbial fuel cells (MFCs), which involved in power generation from biomass wastes; (ii) microbial electrolysis cells (MECs), which are designed to generate CO2-free energy. The mechanism of the electricity generation in the MFCs is based on oxidative catabolism of the organic wastes, such as sugar, cellulose, and organic acids, in the bacterial cell where the electrons are transferred to extracellular electrodes via various electron carriers. For that reason, many studies were focused on the physiology and genetics of EAB as it plays an important role in MFCs [26,27,28].

EET pathway in *Shewanella*

Based on genetic, physiological, and biochemical studies, five essential proteins, MtrA, MtrB, MtrC, CymA, and OmcA, were identified in the EET pathway of *Shewanella* (Fig. 1). These proteins are responsible for transferring electrons across the inner membrane and outer membrane to the extracellular solid electron acceptor [29]. Where Mtr serves as an electron channel that connects the inner membrane quinone pool with the outer membrane. Furthermore, some studies have demonstrated that there are two proteins, small tetraheme cytochromes (STC) and flavocytochrome c (FccA), that are also involved in the EET pathway [30, 31].

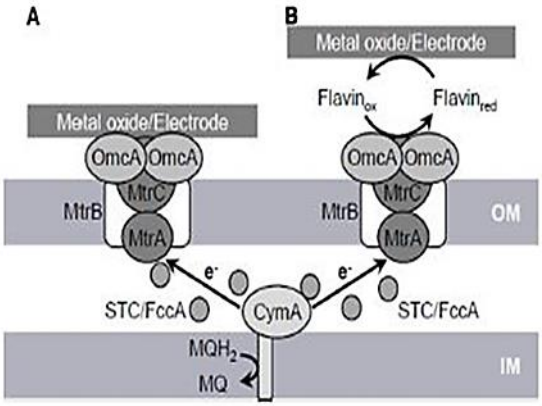

Figure 1. A proposed pathway for the extracellular electron transfer in S. oneidensis MR-1. (A) indirect EET (B) mediated EET [27].

The mechanism of electron transfer starts at the CymA protein, which receives the electrons from the IM quinone pool. The CymA protein has two regions: (i) the N-terminal region (short), which is anchored in the IM, and (ii) the C- terminal region (long) which extends to the periplasm [32]. MtrC and OmcA, OMc-type cytochromes, receive the electrons from MtrA which is localized in the OM by the supports of the β-barrel protein MtrB. Also, many evidences were proposed that

MtrB is responsible for appropriate localization of MtrC and OmcA into OM. Where MtrB facilitates electron exchange between MtrA and MtrC by forming a stable complex that serves as an OM-spanning sheath. Interestingly, studies on mtrB-deletion stain have shown that MtrA was detected in the periplasmic space, which emphasizes the hypothesis that MtrB supports the localization of MtrA to the OM [33,34]. In the Mtr pathway, both OmcA and MtrC, which form complex with stoichiometry of 2:1, act as the ultimate reductases for the final electon acceptors.

Several genetic studies were conducted on *Shewanella* MR-1 in order to figure out the effect of the OMc-type cytochromes (MtrC and OmcA) on current generation in the MFCs. where the results showed that the current generation was decreased in the mutant strain with single knockout of mtrC and omcA. Also, similar results were observed in the double-knockout mutants of both mtrC/omcA with severe current impair [35,36]. Furthermore, other studies have demonstrated that the current generation can be induced up to 35% by using mtrC over expressed strain in the MFC instead of the wild type MR-1. These findings have showed the importance of OmcA and MtrC in the extracellular electron-transport reactions at the OM surface [37,38]. The function of these two OM-cyts can be interfered, as the over expression of mtrC can overcome the effects of MnO2 reduction by omcA-deletion mutants. However, there are many evidences of functional differences between MtrC and OmcA such as the higher affinity of OmcA toward hematite in comparison to MtrC. Also, OmcA play an important role in cells attachment while MtrC is responsible for delivering the electrons to electrodes [39,40].

Even though several studies have clarified the importance of MtrCAB and OmcA in EET pathways, it is still not clear how electrons transfer from IM-CymA to OM-MtrA across the periplasmic space. Where Fonseca and his co-workers reported soluble electron carrier, STC and FccA,which diffuse through the periplasm and facilitate electron transfer from CymA to MtrA [30]. Also, genetic study by Sturm and his co-workers have demonstrated that fccA/stc double-deletion mutant showed significant growth scarcity when tested on different soluble electron acceptors. these two studies have showed the importance of the STC and FccA in Mtr pathway as they mediating electron transfer from CymA to MtrCAB complex [31].

There are two pathways of electron transfer from OM-cyts to electrodes; (i) direct electron transfer (DET), where electrons are transferred directly to solid electron acceptors, (ii) mediated (indirect) electron transfer (MET), where electrons are transferred to remote solid electron acceptors via electron-shuttle compounds [41]. Several studies have supported these two pathway where Lower and his co-workers have supported the DET according to the fact that OmcA and MtrC transfer electrons to graphite electrodes [39] while Lies and his co-workers have supported the MET after the observe that MR-1 can reduce distinct Fe (III) without direct contact [42]. Also, many studies have indicated that Shewanella spp. excrete flavins which function as electron shuttles between OmcA/MtrC and distinct electrodes in the MET [43,44]. Where Marsili and his co-workers found that electron transfer has increased by over threefold in MR-1 biofilms with high concentration of flavins. Cooperatively, these researches indicate that flavins play a crucial role in EET via the Mtr pathway [45].

EET Genes Regulation in Shewanella oneidensis MR-1

There are four genes, omcA, mtrC, mtrA, and mtrB, that code for the proteins which involved in the Mtr pathway. These genes are arranged in a cluster and aligned in the same direction. However, Kasai and his co-workers suggested that *mtrC* and *omcA* are autonomously regulated as they have different promoters in the upstream regions of these two genes [46]. Several studies have illustrated that the activation of the *mtr* genes is controlled by cyclic AMP, adenylate cyclase (CyaC) and receptor protein (CRP) [47]. CRP molecule is a universal regulator which normally forms a complex with cAMP and bind to promoters in order to activate the transcription process of the downstream genes. However, studies on *Shewanella* spp. have demonstrated that CRP is mostly involved in the regulation of anaerobic respiration such as arsenate reduction in Shewanella ANA-3 [48,49]. In addition, researches have suggested that there are other types of transcriptional regulators which may control the mtr gene. Where they found that considerable increase in *omcA* promoter activity was noticed even with the

deletion of the CRP-binding site under aerobic conditions. This observation has led the researchers to think about other unidentified regulators that bind to the deleted region and regulate transcription of omcA [46].

There are three different transcriptional regulators, ArcA, Fur, and Fnr, that are believed to be participating in regulating mtr genes in *Shewanella*. First, aerobic respiration control (Arc) is a bacterial regulatory system which is well characterized in *E. coli* and consists of ArcA and ArcB. This system works as a redox sensor of the menaquinone and ubiquinone [50]. On the other hand researchers have discovered a unique type of Arc system in *S. oneidensis* MR-1 which consist of three components, ArcS, HptA, and ArcA instead of two as in *E. coli*. Also, MR-1 Arc system was found to target genes which are completely different from those found in *E. coli* [51]. Gao and his co-workers conducted a study that prove the importance of ArcA in regulating the mtr gene where they noticed that the expression of these gene is considerably decreased in MR-1 mutant with arcA-deletion. Also, it has been found that ArcA indirectly regulate the mtr genes as there is no specific binding site of this regulator in the upstream region of omcA and mtrC [52].

The second type of mtr gene regulators is the ferric uptake regulator (Fur) which is found in Shewanella as well as other Gram-negative bacteria and acts as an intracellular iron sensor [53]. Since OM-cyts contains large amounts of iron, these proteins are affected by the concentration of the intracellular iron which controls the expression of the mtr genes by forming complexes with Fur. Results of Yang and his co-workers showed that the expression of mtr genes is commensurable to the iron concentration and its expression was induced as the iron concentration increased. Other studies have demonstrated that mtr-gene expression is significantly lower in the fur-deletion mutant of MR-1[54]. In addition, a presumed Fur-binding site has been indicated in the upstream of omcA [53].

The third transcriptional regulator of mtr genes is the fumarate nitrate-reduction (Fnr) which also functions as oxygen sensor in *E. coli* [55]. Where Cruz-García and his co-workers demonstrated that fnr-deletion mutant of MR-1 have showed remarkable decreases in the expression level of cyma, omcA, and mtr CAB. Nevertheless, their study reported that reduction rates of Fe(III) and Mn (IV) oxides by fnr-deletion mutant was not significantly affected which indicating that Fnr has least role than CRP in Mtr pathway regulation. Eventually, the above studies indicated that the main regulator of the mtr genes is the cAMP/CRP system as well as other regulatory systems[56]. However, it is still unclear how these regulatory systems cooperate in Mtr pathway regulation [27].

Conclusion

Generation of electricity from renewable sources is the objective of many research articles worldwide. This is due to the increase of pollution rates as a result of generating electricity by traditional methods. Interestingly, microbes have played their own role in this technology benefiting from their ability to transfer electrons outside of their plasma membrane to designed electrodes that act as electron acceptors. *Geobacter* and *Shewanella* are the best two microbes studied so far that showed their ability to produce electricity in Microbial fuel cells. Applications of microbial fuel cells have not been restricted to electricity production but went further on to reduce toxic pollutants from the environment thereby providing healthier environments for the generations.

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Conflict of Interest

None

Abbreviations

Extracellular electron-transport (EET), Bio-electrochemical systems (BESs), Electro-active bacteria (EAB),

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الوراثة الجزيئية لعملية إنتاج الكهرباء من قبل البكتريا: مقالة

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الخلاصة:

مع ازدياد اعداد السكان عالميا اصبح الحاجة الى البحث عن مصادر جديدة للطاقة. نفذت العديد من الدراسات حول امكانية استبدال مصادر الطاقة التقليدية بمصادر الطاقات البديلة والتي شملت الطاقة الشمسية وطاقة الرياح وطاقة الامواج. لعبت الاحياء المجهرية دورا هاما في انتاج الطاقة من خلال توليدها للتيار الكهربائي الناتج من نقل الالكترونات الناتجة من فعالياتها الايضية، تعرف هذه الجراثيم بالجراثيم النشطة كهربائيا والتي تستعمل في البطاريات الجرثومية Microbial fuel cells والتي فيها يتم استعمال الجراثيم في انتاج الطاقة من تحلل المركبات العضوية. إن اهمية البطاريات الجرثومية لا يقتصر فقط على انتاج الطاقة الكهربائية وانما تقليل الملوثات العضوية في البيئة، البطاريات الجرثومية لها اهمية ايضا في توليد الكهرباء في المواقع التي يكون فيها المحافظة على ديمومة البطاريات التقليدية مكلفة مثلا في اعماق البحار. أحد أشهر الجراثيم النشطة كهربائيا هي *Geobacter*، والتي لها القابلية على نقل الالكترونات خارج غشائها الخلوي، تمكن الباحثين من تطوير نظام وراثي فعال في *Geobacter* من اجل توليد طافرات ودراسة السلالات الفاقدة لبعض الجينات حيث اتضح ان هذه الجرثومة تستخدم السايتوكرومات نوع C في اختزال اوكسيد الحديد الثلاثي من خلال الاتصال المباشر به. في العقود القليلة الماضية جذبت جرثومة *Shewanella* انتباه ملحوظ نتيجة لتكيفها التنفسي، حيث تتمكن هذه الجرثومة من تنفس انواع مختلفة من المركبات اللاعضوية كمستقبلات للالكترونات والتي تشمل الثايوسلفات والنترات والارسينيت والكبريت المعدني والفيوميريت. هذه القابليات أتت من امتلاكها لمسار نقل الكترونات فريد يساعد في التكيف حسب توفر مستقبلات الالكترونات والتي غالبا ما تتغير حسب الظروف البيئة.

الكلمات المفتاحية: انتاج الكهرباء، *Shewanella*، *Geobacter* .