Final Report

Genome-Based Models to Optimize In Situ Bioremediation of Uranium and Harvesting Electrical Energy from Waste Organic Matter

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The goal of this research was to provide computational tools to predictively model the behavior of two microbial communities of direct relevance to Department of Energy interests: 1) the microbial community responsible for *in situ* bioremediation of uranium in contaminated subsurface environments; and 2) the microbial community capable of harvesting electricity from waste organic matter and renewable biomass. During this project the concept of microbial electrosynthesis, a novel form of artificial photosynthesis for the direct production of fuels and other organic commodities from carbon dioxide and water was also developed and research was expanded into this area as well.

The major research goal was met with the clear demonstration that natural microbial communities could be evaluated and predictively modeled with a systems biology approach. For example, the growth of subsurface microorganisms was predictively modeled *in silico* with genome-scale metabolic models of key components of the microbial community coupled to hydrological and geochemical models to predict the outcome of subsurface uranium bioremediation. This approach was developed to such a degree that other DOE researchers were able to adopt our models and approaches for their own independent research. Furthermore, as highlighted below, this project established several new paradigms extracellular electron transfer and interspecies interactions.

At the end of our project the major findings of the project were summarized in several extensive peer-reviewed review articles including:

Lovley, D. R., T. Ueki, T. Zhang, N. S. Malvankar, P. M. Shrestha, K. Flanagan, M. Aklujkar, J. E. Butler, L. Giloteaux, A.-E. Rotaru, D. E. Holmes, A. E. Franks, R. Orellana, C. Risso, and K. P. Nevin. 2011. Geobacter: the microbe electric's physiology, ecology, and practical applications. Adv. Microb. Physiol. 59:1-100.

Mahadevan, R., B. O. Palsson, and D. R. Lovley. 2011. *In situ* to *in silico* and back: elucidating Geobacter physiology and ecology with genome-scale modeling. Nature Rev. Microbiol. 9:39-50.

Lovley, D. R. 2011. Live wires: direct extracellular electron exchange for bioenergy and the bioremediation of energy-related contamination. Energy & Environmental Science 4:4896-4906.

Malvankar, N. S., and D. R. Lovley. 2012. Microbial nanowires: a new paradigm for biological electron transfer and bioelectronics. ChemSusChem 5:1039– 1046.
Lovley, D. R. 2012. Electromicrobiology. Ann. Rev. Microbol. 66:391-409.

Detailed accounts of research progress can also be found in the annual progress reports. Research highlights are listed below.

Environmental Genome-Scale Metabolic Modeling

We developed an a novel approach for predicting the activity of environmentally relevant microorganisms under a diversity of environmental conditions which we have designated bottom-up genome-scale modeling, abbreviated BUGS modeling. In this approach appropriate conditons are designed for the isolation of the most important microorganisms in the environment of interest. Genome-scale metabolic models of these organisms are developed and then the models are coupled to the appropriate hydrological and geochemical models. The utility of BUGS modeling was demonstrated for predicting the outcome of stimulating subsurface microbial metabolism with the addition of acetate to promote *in situ* uranium bioremediation and for predicting the distribution of different species of iron reducers and sulfate reducers in the subsurface. The BUGS modeling approach is scalable to complex microbial communities and is the only modeling process demonstrated to be capable of predicting microbial activities in natural environments based on first principles of genome-encoded metabolic properties and without empirically derived performance parameters. At the end of this project we used the BUGS modelling approach to design optimized *in situ* uranium bioremediation strategies predicted to lead to long-term solutions to groundwater uranium contamination.

Extracellular Electron Transfer

When the project was initiated it was understood that *Geobacter* species needed to be in contact with iron oxides in order to reduce them, but the mechanisms for this extracellular electron transfer were not known. A completely unexpected mechanism for extracellular electron transfer was elucidated. We discovered that the pili of *Geobacter sulfurreducens* are electrically conductive along their length. The pili have metallic-like conductivity. This is surprising because it had been concluded that metallic-like conductivity would not be feasible in biological protiens. Reduction of iron oxides requires not only the conductive pili, but also the multi-heme *c*-type cytochrome, OmcS. The model for long-range electron transport to iron oxides is that electrons are transported along the pili and that OmcS facilitates electron transfer from the pili to the iron oxides. This model is based on multiple lines of evidence including mutational studies, adaptive evolution studies, and novel biophysical approaches.

Microbe-Electrode Interactions

A systems biology approach to the study of biofilms transferring electrons to graphite electrodes elucidated the biological properties that contribute to the production of high current densities in microbial fuel cells. Whole-genome analysis of gene expression patterns identified genes specifically expressed at high levels when the biofilm was producing current and gene deletion studies identified which of these genes were essential for current production. Purification, characterization and localization of key proteins required for current production, coupled with biophysical studies, suggested a model in which conductive pili are responsible for long-range electron transport through the biofims, which have conducitivies rivaling those of synthetic conducting polymers. The multi-heme *c*-type cytochrome, OmcZ, is required for high current denstities and specifically accumulates at the biofilm-electrode interface. The proposed role of OmcZ is to facilitate electron transfer from the biofilm to the electrode. Gene reporter systems that could be monitored in real-time during biofilm growth on electrodes further confirmed this model for electrode biofilm function.

Direct Interspecies Electron Transfer

A study on the adaptive evolution of interspecies electron transfer in *Geobacter* species lead to the surprising discovery that different *Geobacter* species could directly exchange electrons to support syntrophic growth under conditions in which neither of the two strains could grow indpendently. Genome resequencing and gene deletion studies demonstrated a role for conductive pili and OmcS in the electron transfer. This discovery led to a new Genomic Sciences project which has determined that direct interspecies electron transfer is an important phenomenon in some methanogenic communities, including those converting organic wastes to methane.

Detailed Understanding of Geobacter Physiology and Physiological Status in the Subsurface

When this project began almost nothing was known about the physiology of *Geobacter* species. Genome-sequencing of mutliple *Geobacter* species followed by detailed manual genome annotation, functional genomics, and protein isolation and characterization, coupled with genome-scale metabolic modeling provided an in-depth understanding of organisms in this genus, as well as closely related *Pelobacter* species. Analysis of the regulatory networks of *Geobacter sulfurreducens* gave additional insight into how *Geobacter* species respond to enviornmental changes. Enviromental transcriptomic and proteomic studies made it possible to diaganose the *in situ* physiological status of *Geobacter* species in the subsurface and determine what factors were limiting the activity during in situ uranium bioremediation.

Microbial Electrosynthesis

A question about the inefficiency of photosynthesis by our Genomic Sciences program manager led us to consider and develop an artificial form of photosynthesis, known as microbial electrosynthesis. In this novel bioenergy strategy solar energy is captured with photovoltaic technology and the electrical energy obtained is used to extract electrons from water. The electrons are fed to microbial biofilms growing on electrodes that can accept electrons from the electrode for the direct reduction of carbon dioxide to multi-carbon organic molecules that are excreted from the cell. Microbial electrosynthesis is orders of magnitude more efficient in converting solar energy and carbon dioxide to biocommodities that processes depending on natural photosynthesis. Furthermore, microbial electrosynthesis avoids the significant environmental degradation associated with biomass-based bioenergy strategies. Microbial electrosynthesis is now being further developed in the Electrofuels Program of the Department of Energy's ARPA-E.

In summary, this project demonstrated that a systems approach to the study of natural microbial communities could provide the ability to predictively model the response of those communities to environmental perturbations. The computational approach that was developed for genome-scale modeling of microbial activity and the interaction of microbial communities with their environment will be useful not only for bioremediation applications, but also for predicting the activity of microbial communities in a wide range of other environments. The environmental transcriptomic approach developed for diagnosing the *in situ* physiological status of subsurface microorganisms is expected to become standard practice for in the study of bioremediation. The discovery of metallic-like conductivity in *Geobacter* pili is a paradigm shift in biological electron transport with broad implications not only in microbiology but also for the production of new materials in the emerging field of bioelectronics. The discovery of direct interspecies electron transfer revolutionizes our understanding of the functioning of methanogenic environments and it has already been demonstrated how this new understanding can lead to reactor design modifications that can greatly accelerate conversion of wastes to methane, making this a much more attractive bioenergy strategy. Another unforeseen discovery that emerged from this research was the development of microbial electrosynthesis, a novel bioenergy strategy with substantial potential for efficient, sustainable production of transportation fuels and other organic commodities.

Comprehensive List of Publications

2003 Publications

1. Bond, D.R., and D.R. Lovley. 2003. Electricity production by Geobacter sulfurreducens attached to electrodes. Appl. Environ. Microbiol. 69:1548-1555.

2. Lovley, D.R. 2003. Cleaning up with genomics: applying molecular biology to bioremediation. Nature Rev. Microbiol. 1:35-44.

3. Jara, M., C. Nunez, S. Campoy, A. R. Fernandez de Henestrosa, D.R. Lovley, and J. Barbe. 2003. Geobacter sulfurreducens has two autoregulated lexA genes whose products do not bind the recA promoter: differing responses of lexA and recA to DNA damage. J. Bacteriol. 185:2493-502.

2004 Publications

1. Butler, J.E., F. Kaufmann, M.V. Coppi, C. Nunez, and D.R. Lovley. 2004. MacA, a di-heme c-type cytochrome involved in Fe(III) reduction by Geobacter sulfurreducens. J Bacteriol 186:4042-4045.

2. Chin, K.-J., A. Esteve-Núñez, C. Leang, and D.R. Lovley. 2004. Direct correlation between rates of anaerobic respiration and levels of mRNA for key respiratory genes in Geobacter sulfurreducens. Appl. Environ. Microbiol. 70:5183-5189.

3. Coppi, M.V., R.O. O'Neil, and D.R. Lovley. 2004. Identification of an uptake hydrogenase required for hydrogen-dependent reduction of Fe(III) and other electron acceptors by Geobacter sulfurreducens. J. Bacteriol. 186:3022-3028.

4. Esteve-Núñez, A., C. Núñez, and D.R. Lovley. 2004. Preferential Reduction of Fe(III) over Fumarate by Geobacter sulfurreducens. J. Bacteriol. 186:2897-2899.

5. Holmes, D.E., D.R. Bond, R.A. O'Neil, C.E. Reimers, L.R. Tender, and D.R. Lovley. 2004. Microbial communities associated with electrodes harvesting electricity from a variety of aquatic sediments. Microbial Ecol. 48:178-190.

6. Holmes, D.E., K.P. Nevin, and D.R. Lovley. 2004. Comparison of 16S rRNA, nifD, recA, rpoB, and fusA genes within the family Geobacteraceae. Int. J. Sys. Evol. Microbiol. 54:1591-1599.

7. Holmes, D.E., K.P. Nevin, and D.R. Lovley. 2004. In situ expression of Geobacteraceae nifD in subsurface sediments. Appl. Environ. Microbiol. 70:7251-9.

8. Holmes, D.E., J.S. Nicoll, D.R. Bond, and D.R. Lovley. 2004. Potential role of a novel psychrotolerant Geobacteraceae, Geopsychrobacter electrodiphilus gen. nov., sp. nov., in electricity production by the marine sediment fuel cell. Appl. Environ. Microbiol. 70:6023-6030.
9. Lin, W.C., M.V. Coppi, and D.R. Lovley. 2004. Geobacter sulfurreducens can grow with oxygen as a terminal electron acceptor. Appl Environ Microbiol 70:2525-8.
10. Núñez, C., L. Adams, S. Childers, and D.R. Lovley. 2004. The RpoS sigma factor in the dissimilatory Fe(III)-reducing bacterium Geobacter sulfurreducens. J. Bacteriol. 186:5543-5546.
11. Yan, B., B.A. Methé, D.R. Lovley, and J. Krushkal. 2004. Computational prediction of conserved operons and phylogenetic footprinting of transcription regulatory elements in the metal-reducing bacterial family Geobacteraceae. J Theor Biol. 230:133-44.

2005 Publications

1. Afkar, E. A., G. Reguera, M. Schiffer, and D.R. Lovley. 2005. A novel *Geobacteraceae*-specific outer membrane protein, OmpJ, is essential for electron transport to Fe (III) and Mn (IV) oxides in *Geobacter sulfurreducens*. BMC Microbiol 5:41.
2. Bond, D.R., and D.R. Lovley. 2005. Evidence for involvement of an electron shuttle in electricity generation by *Geothrix fermentans*. Appl Environ Microbiol 71:2186-9.
3. Bond, D.R., T. Mester, C. Nesbø, A.V. Izquierdo-Lopez, F.L. Collart, and D.R. Lovley. 2005. Characterization of citrate synthase from *Geobacter sulfurreducens* and evidence for a family of citrate synthases similar to those of eukaryotes throughout the *Geobacteraceae*. Appl Environ Microbiol 71:3858-3865.
4. Coppi, M.V. 2005. The hydrogenases of *Geobacter sulfurreducens*: a comparative genomic perspective. Microbiology:1239-1254.
5. Esteve-Núñez, A., M.M. Rothermich, M. Sharma, and D.R. Lovley. 2005. Growth of *Geobacter sulfurreducens* under nutrient-limiting conditions in continuous culture. Environ. Microbiol. 7:641-648.
6. Holmes, D.E., K.P. Nevin, R.A. O'Neil, J.E. Ward, L. Adams, T.L. Woodard, H.A. Vrionis, and D.R. Lovley. 2005. Potential for quantifying expression of the *Geobacteraceae* citrate synthase gene to assess the activity of *Geobacteraceae* in the subsurface and on current-harvesting electrodes. Appl. Environ. Microbiol. 71:6870-6877.

7. Kim, B.-C., C. Leang, Y.R. Ding, R.H. Glaven, M.V. Coppi, and D.R. Lovley. 2005. OmcF, a putative *c*-Type monoheme outer membrane cytochrome required for the expression of other outer membrane cytochrome in *Geobacter sulfurreducens*. J. Bacteriol. 187:4505-13.

8. Leang, C., L.A. Adams, K.-J. Chin, K.P. Nevin, B.A. Methé, J. Webster, M.L. Sharma, and D.R. Lovley. 2005. Adaption to disruption of the electron transfer pathway for Fe(III) Reduction in *Geobacter sulfurreducens*. J. Bacteriol. 187:5918-5926.

9. Leang, C., and D.R. Lovley. 2005. Regulation of two highly similar genes, omcB and omcC, in a 10 kb chromosomal duplication in *Geobacter sulfurreducens*. Microbiol. 151:1761-1767.

10. Mehta, T., M.V. Coppi, S.E. Childers, and D.R. Lovley. 2005. Outer membrane c-type cytochromes required for Fe(III) and Mn(IV) oxide reduction in *Geobacter sulfurreducen*s. Appl. Environ. Microbiol. 71:8634-8641.

11. Methé, B.A., J. Webster, K.P. Nevin, J. Butler, and D.R. Lovley. 2005. DNA Microarray Analysis of Nitrogen Fixation and Fe(III) Reduction in *Geobacter sulfurreducens*. Appl. Environ. Microbiol. 71:2530-2538.

12. Nevin, K.P., D.E. Holmes, T.L. Woodard, E.S. Hinlein, D. W. Ostendorf, and D.R. Lovley. 2005. *Geobacter bemidjiensis* sp. nov. and *Geobacter psychrophilus* sp. nov., two novel Fe(III)-reducing subsurface isolates. Int. J. Sys. Evol. Microbiol. 55:1667-1674.

13. Reguera, G., K.D. McCarthy, T. Mehta, J.S. Nicoll, M.T. Tuominen, and D.R. Lovley. 2005. Extracellular electron transfer via microbial nanowires. Nature 435:1098-1101.

2006 Publications

1. Butler, J.E., R.H. Glaven, A. Esteve-Nunez, C. Nunez, E.S. Shelobolina, D.R. Bond, and D.R. Lovley. 2006. Genetic characterization of a single bifunctional enzyme for fumarate reduction and succinate oxidation in *Geobacter sulfurreducens* and engineering of fumarate reduction in *Geobacter metallireducens*. J. Bacteriol. 188:450-455.

2. Ding, Y.H.R., K.K. Hixson, C.S. Giometti, A. Stanley, A. Esteve-Nunez, T. Khare, S.L. Tollaksen, W.H. Zhu, J.N. Adkins, M.S. Lipton, R.D. Smith, T. Mester, and D.R. Lovley. 2006. The proteome of dissimilatory metal-reducing microorganism *Geobacter sulfurreducens* under various growth conditions. Biochim. Biophys. Acta 1764:1198-1206.

3. Haveman, S.A., D.E. Holmes, Y.H. Ding, J.E. Ward, R.J. DiDonato Jr, and D.R. Lovley. 2006. *c*-type cytochromes in *Pelobacter carbinolicus*. Appl. Environ. Microbiol. 72:6980-6985.

4. Holmes, D.E., S.K. Chaudhuri, K.P. Nevin, T. Mehta, B.A. Methe, A. Liu, J.E. Ward, T.L. Woodard, J. Webster, and D.R. Lovley. 2006. Microarray and genetic analysis of electron transfer to electrodes in *Geobacter sulfurreducens*. Env. Microbiol. 8:1805-1815.

5. Khare, T., A. Esteve-Nunez, K.P. Nevin, W.H. Zhu, J.R. Yates, D.R. Lovley, and C.S. Giometti. 2006. Differential protein expression in the metal-reducing bacterium *Geobacter sulfurreducens* strain PCA grown with fumarate or ferric citrate. Proteomics 6:632-640.

6. Kim, B.C., X.L. Qian, C. Leang, M.V. Coppi, and D.R. Lovley. 2006. Two putative c-type multiheme cytochromes required for the expression of OmcB, an outer membrane protein essential for optimal Fe(III) reduction in *Geobacter sulfurreducens*. J. Bacteriol. 188:3138-3142.

7. Londer, Y.Y., I.S. Dementieva, C.A. D'Ausilio, P.R. Pokkuluri, and M. Schiffer. 2006. Characterization of a *c*-type heme containing PAS sensor domain from *Geobacter sulfurreducens* representing a novel family of periplasmic sensors in *Geobacteraceae* and other bacteria. FEMS Microbiol. Lett. 258:173-181

10. Lovley, D.R. 2006. Bug juice: harvesting electricity with microorganisms. Nature Rev. Microbiol. 4:497-508.

11. Mahadevan, R., D.R. Bond, J.E. Butler, A. Esteve-Nunez, M.V. Coppi, B.O. Palsson, C. H. Schilling, and D.R. Lovley. 2006. Characterization of metabolism in the Fe(III)-reducing organism *Geobacter sulfurreducens* by constraint-based modeling. Appl. Environ. Microbiol. 72:1558-1568.

12. Mehta, T., S.E. Childers, R. Glaven, D.R. Lovley, and T. Mester. 2006. A putative multicopper protein secreted by an atypical type II secretion system involved in the reduction of insoluble electron acceptors in *Geobacter sulfurreducens*. Microbiol. 152:2257-64.

13. Nunez, C., A. Esteve-Nunez, C. Giometti, S.L. Tollaksen, T. Khare, W. Lin, D.R. Lovley, and B.A. Methe. 2006. DNA microarray and proteomic analyses of the RpoS regulon in *Geobacter sulfurreducens*. J. Bacteriol. 188:2792-2800.

14. Reguera, G., K.P. Nevin, J.S. Nicoll, S.F. Covalla, T.L. Woodard, and D.R. Lovley. 2006. Biofilm and nanowire production leads to increased current in *Geobacter sulfurreducens* fuel cells. Appl. Environ. Microbiol. 72:7345-7348.

15. Yan, B., C. Núñez, T. Ueki, A. Esteve-Núñez, M. Puljic, R.M. Adkins, B.A. Methé, D.R. Lovley, and J. Krushkal. 2006. Computational prediction of RpoS and RpoD regulatory sites in *Geobacter sulfurreducens* using sequence and gene expression information. Gene 384:73-95.

2007 Publications

1. Butler, J.E., Q. He, K.P. Nevin, Z. He, J. Zhou, and D.R. Lovley. 2007. Genomic and microarray analysis of aromatics degradation in *Geobacter metallireducens* and comparison to a *Geobacter* isolate from a contaminated field site. BMC Genomics 8:180.

2. Coppi, M.V., R.A. O'Neil, C. Leang, F. Kaufmann, B.A. Methé, K.P. Nevin, T.L. Woodard, A. Liu, and D.R. Lovley. 2007. Involvement of *Geobacter sulfurreducens* SfrAB in acetate metabolism rather than intracellular Fe(III) reduction. . Microbiology 153:3572-3585.

3. Holmes, D.E., R.A. O'Neil, H.A. Vrionis, L.A. N'Guessan, I. Ortiz-Bernad, M.J. Larrahondo, L.A. Adams, J.E. Ward, J.S. Nicoll, K.P. Nevin, M.A. Chavan, J.P. Johnson, P.E. Long, and D.R. Lovley. 2007. Subsurface clade of Geobacteraceae that predominates in a diversity of Fe(III)-reducing subsurface environments. The ISME Journal 8:663-677.

4. Krushkal, J., B. Yan, L.N. DiDonato, M. Puljic, K.P. Nevin, T.L. Woodard, R.M. Adkins, B.A. Methe, and D.R. Lovley. 2007. Genome-wide expression profiling in *Geobacter sulfurreducens*: identification of Fur and RpoS transcription regulatory sites in a rel$_{\mathrm{Gsu}}$ mutant. Funct Integr Genomics 7:229-255.

5. Nevin, K.P., D.E. Holmes, T.L. Woodard, S.F. Covalla, and D.R. Lovley. 2007. Reclassification of *Trichlorobacter thiogenes* as *Geobacter thiogenes* comp. nov. . Int J Syst Bacteriol 57:463-6.

6. Qian, X., G. Reguera, T. Mester, and D.R. Lovley. 2007. Evidence that OmcB and OmpB of *Geobacter sufurreducens* are outer membrane surface proteins. FEMS Microb Lett 277:21-27.

7. Reguera, G., R.B. Pollina, J.S. Nicoll, and D.R. Lovley. 2007. Possible non-conductive role of *Geobacter sulfurreducens* pilus nanowires in biofilm formation. J. Bacteriol. 189:2125-7.

8. Richter, H., M. Lanthier, K.P. Nevin, and D.R. Lovley. 2007. Lack of electricity production by *Pelobacter carbinolicus* indicates that the capacity of Fe(III) oxide reduction does not necessarily confer electron transfer ability to fuel cell anodes. Appl Environ Microbiol 73:5347-5353.

9. Ueki, T., and D.R. Lovley. 2007. Heat-Shock Sigma Factor RpoH from *Geobacter sulfurreducens*. Microbiol. 153:838-846.

10. Yan, B., D.R. Lovley, and J. Krushkal. 2007. Genome-wide similarity search for transcription factors and their binding sites in a metal-reducing prokaryote *Geobacter sulfurreducens*. Biosystems 90:421-441.

2008 Publications

1. Ding, Y.-H. R., K.K. Hixson, M.A. Aklujkar, M.S. Lipton, R.D. Smith, D.R. Lovley, and T. Mester. 2008. Proteome of *Geobacter sulfurreducens* grown with Fe(III) oxide or Fe(III) citrate as the electron acceptor. Biochim. Biophys. Acta 1784:1935-1941.

2. Esteve-Nunez, A., J. Sosnik, P. Visconti, and D.R. Lovley. 2008. Fluorescent properties of c-type cytochromes reveal their potential role as an extracytoplasmic electron sink in Geobacter sulfurreducens. Environ. Microbiol. 10:497-505.

3. Haveman, S.A., R.J. DiDonato, L. Villanueva, E.S. Shelobolina, B.L. Postier, B. Xu, A. Liu, and D.R. Lovley. 2008. Genome-wide gene expression patterns and growth requirements suggest that *Pelobacter carbinolicus* reduces Fe(III) indirectly via sulfide production. Appl. Environ. Microbiol. 74:4277-4284.

4. Holmes, D.E., T. Mester, R.A. O'Neil, M.J. Larrahondo, L.A. Adams, R. Glaven, M.L. Sharma, J.E. Ward, K.P. Nevin, and D.R. Lovley. 2008. Genes for two multicopper proteins required for Fe(III) oxide reduction in *Geobacter sulfurreducens* have different expression patterns both in the subsurface and on energy-harvesting electrodes. Microbiol 145:1422-1435.

5. Izallalen, M., R. Mahadevan, A. Burgard, B. Postier, R. DiDonato, J. Sun, C.H. Schilling, and D.R. Lovley. 2008. *Geobacter sulfurreducens* strain engineered for increased rates of respiration. Metabolic Engineering 10:267-275.

6. Kim, B.-C., and D.R. Lovley. 2008. Investigation of direct vs. indirect involvement of the c-type cytochrome MacA in Fe(III) reduction by *Geobacter sulfurreducens*. FEMS Microb Lett 286:39-44.

7. Kim, B.-C., B.L. Postier, R.J. DiDonato, S.K. Chaudhuri, K.P. Nevin, and D.R. Lovley. 2008. Insights into genes involved in electricity generation in *Geobacter sulfurreducens* via whole genome microarray analysis of the OmcF-deficient mutant. Bioelectrochemistry 73:70-75.

8. Krushkal, J., G. Reguera, M. Puljic, C. Leang, L.N. DiDonato, B. Yan, C. Nuneez, J.F. Barbe, R. Mahadevan, B.A. Methe, R.M. Adkins, B. Postier, R.A. O'Neil, and D.R. Lovley. 2008. Genome regions involved in multiple regulatory pathways identifed using GSEL, a genome-wide database of regulatory sequence elements of *Geobacter sulfurreducens*. International Conference on BioMedical Engineering and Informatics 424-431.

9. Lanthier, M., K.B. Gregory, and D.R. Lovley. 2008. Growth with high planktonic biomass in *Shewanella oneidensis* fuel cells. FEMS Microbiol Lett 278:29-35.

10. Lovley, D.R., R. Mahadevan, and K.P. Nevin. 2008. Systems biology approach to bioremediation with extracellular electron transfer, p. 71-96. *In* E. Díaz (ed.), Microbial Biodegradation: Genomics and Molecular Biology. Caister Academic Press, Norfolk, UK.

11. Lovley, D.R., and K.P. Nevin. 2008. Electricity production with electricigens, p. 295-306. *In* J. D. Wall, C.S. Harwood, and D. A.L. (ed.), Bioenergy. ASM Press, Washington, DC.

12. Mahadevan, R., and D.R. Lovley. 2008. The degree of redundancy in metabolic genes is linked to mode of metabolism. Biophysical J. 94:1216-1220.

13. O'Neil, R.A., D.E. Holmes, M.V. Coppi, L.A. Adams, M.J. Larrahando, J.E. Ward, K.P. Nevin, T.L. Woodard, H.A. Vrionis, A.L. N'Guessan, and D.R. Lovley. 2008. Gene transcript analysis of assimilatory iron limitation in *Geobacteraceae* during groundwater bioremediation. Environ. Microbiol. 10:1218-1230.

14. Postier, B.L., R.J. DiDonato Jr., K.P. Nevin, A. Liu, B. Frank, D.R. Lovley, and B.A. Methe´. 2008. Benefits of electrochemically synthesized microarrays for analysis of gene expression in understudied microorganisms. J Microbiol Methods 74:26-32.

15. Richter, H., K. McCarthy, K.P. Nevin, J.P. Johnson, V.M. Rotello, and D.R. Lovley. 2008. Electricity generation by *Geobacter sulfurreducens* attached to gold electrodes. Langmuir 24:4376-4379.

16. Risso, C., B.A. Methe, H. Elifantz, D.E. Holmes, and D.R. Lovley. 2008. Highly conserved genes in *Geobacter* species with expression patterns indicative of acetate limitation. Microbiology 154:2589-2599.

17. Segura, D., R. Mahadevan, K. Juarez, and D.R. Lovley. 2008. Computational and experimental analysis of redundancy in the central metabolism of *Geobacter sulfurreducens*. PLoS Comput Biol 4:e36.

18. Shelobolina, E.S., H.A. Vrionis, R.H. Findlay, and D.R. Lovley. 2008. Geobacter uraniireducens sp. nov., isolated from subsurface sediment undergoing uranium bioremediation. Intern. J. Syst. Evol. Microbiol. 58:1075-1078.

19. Tran, H.T., J. Krushkal, F. Antommattei, D.R. Lovley, and R.M. Weis. 2008. Comparative genomics of *Geobacter* chemotaxis genes reveals diverse signaling function. BMC Genomics 9:471.

20. Villanueva, L., S.A. Haveman, Z.M. Summers, and D.R. Lovley. 2008. Quantification of *Desulfovibrio vulgaris* dissimilatory sulfite reductase gene expression during electron donor and acceptor-limited growth. Appl. Environ. Microbiol. 74:5850-5853.

2009 Publications

1. Franks, A. E., K.P. Nevin, H. Jia, M. Izallalen, T.L. Woodard, and D.R. Lovley. 2009. Novel strategy for three-dimensional real-time imaging of microbial fuel cell communities: monitoring the inhibitory effects of proton accumulation within the anode biofilm. Energy & Environ. Sci. 2:113-119.

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