SPECIAL TOPIC: Elemental cycling by microorganisms in the hydrosphere •EDITORIAL•

October 2019 Vol.62 No.10: 1271–1274 https://doi.org/10.1007/s11427-019-1554-y

Microbes: the hidden giant behind the biogeochemical cycling of elements in the hydrosphere

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Received September 25, 2019; published online September 27, 2019

Citation: Huang, L., Xiao, X., and Zhao, G. (2019). Microbes: the hidden giant behind the biogeochemical cycling of elements in the hydrosphere. Sci China Life Sci 62, 1271–1274. https://doi.org/10.1007/s11427-019-1554-y

Microbes are the oldest inhabitants of Earth. Through billions of years of coevolution with Earth, these creatures, usually invisible to the naked eye, have contributed to shaping the Earth surface, creating an ecosystem habitable for higher organisms including humans. By some estimates, microbes account for up to half of the biomass on the planet today (Whitman et al., 1998). They thrive in every corner of Earth, including harsh habitats such as hot springs, hydrothermal vents, salt and soda lakes, acid mine drainage, deep subsurface, and thus define the boundaries of the biosphere. Microbes also exhibit immense genetic and metabolic diversity. Therefore, it is not surprising that these organisms play a pivotal role in driving elemental cycling on Earth, a process essential for maintaining the habitability of the planet Earth.

About 3/4 of the Earth surface is covered with water, and the hydrosphere comprising oceans, lakes, rivers, glaciers, wetlands, groundwater, etc. is home to over half of the microbes on Earth. It is increasingly being recognized that microbial activity in the hydrosphere has a great impact on the Earth ecosystem. For example, one half of the O_2 that we breathe comes from the oceans, and about half of the CO_2

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generated by human activities is absorbed by the oceans. Over half of the CH₄, a greenhouse gas, is produced in wetlands, marshes and paddy fields. N2 fixed in the oceans accounts for 2/3 of the naturally fixed N₂. 30% of atmospheric N₂O, another greenhouse gas, is released from the oceans. Microbes are clearly a hidden giant driving these diverse and fundamental biogeochemical processes in the hydrosphere. Thanks to the rapid progress in sequencingbased technologies and significant improvement in sampling, cultivation and analytical capabilities, our knowledge of the roles of microbes in elemental cycling in the hydrosphere has been expanded dramatically in the past two decades. The new field of geomicrobiology has attracted fast growing research interests. Some long-held concepts have been shattered by the discoveries of novel microbes and novel metabolic pathways. For example, novel anaerobic methanotrophic archaea (ANME) were found to oxidize methane in cooperation with sulfate reducing bacteria (Hinrichs et al., 1999). This reaction is believed to help prevent the release of vast amounts of CH₄ stored beneath the seafloor into the atmosphere. A group of bacteria of the phylum Planctomycetes were shown to be capable of anaerobic ammonium oxidation, a novel pathway in nitrogen cycle (Strous et al., 1999). Previous to this finding, ammonium oxidation was thought to occur only under aerobic



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conditions. Anaerobic ammonium oxidation is responsible for the loss of ~50% of the nitrogen compounds from the oceans in the form of N₂. Despite the remarkable progress, a huge knowledge gap remains in our understanding of the roles of microbes in driving elemental cycling in the hydrosphere. The vast majority of the microbes in the environment still evade cultivation, not to mention further functional studies. Therefore, it is anticipated that this flourishing field will continue to produce fascinating new discoveries in years to come.

China has been an active player in geomicrobiological research and has made important contributions to the understanding of the biogeochemical roles of microbes in various aquatic habitats. In 2016, the National Natural Science Foundation of China launched a major research program titled "Mechanisms underlining elemental cycling on Earth by microorganisms in the hydrosphere" (or "Hydrosphere Microbes") (Huang et al., 2017). This Program aims to learn how microbes carry out carbon, nitrogen and sulfur cycling at the cellular, community and ecological levels in representative aquatic habitats, including oceans, estuaries, lakes, wetlands, and extreme aquatic environments, through joint efforts by scientists in life sciences, earth sciences, chemical sciences, information sciences, etc. Knowledge gained through the implementation of the Program will enhance our ability to predict and respond to the impact of environmental changes on the Earth ecosystem. In this issue, we compiled one research paper and three review articles authored by well-known experts in the field. These articles are intended to offer a taste of excitement that might come out of the research entailed in the Program.

Much of the emphasis of the Program is placed on oceans, where microbial activities are known to exert a huge impact on the Earth ecosystem. For example, anaerobic oxidation of methane (AOM), which occurs predominantly in oceans, plays a key role in controlling global methane emission. Coupling of AOM with sulfate reduction has been extensively characterized. Over the years, AOM has also been shown to be coupled with the reduction of other external electron acceptors such as manganese and iron (Beal et al., 2009; Scheller et al., 2016). However, metabolic mechanisms involved in these processes remain largely unknown. In this issue, Liang et al. reviewed geochemical evidence for metal-dependent AOM in various marine environments and discussed the possible biochemical mechanisms in the processes (Liang et al., 2019). The biogenic trace gas dimethyl sulfide (DMS) is the dominant natural source of volatile organic sulfur compounds emitted into the atmosphere from the marine environment. DMS is mainly produced by the enzymatic cleavage of dimethylsulfoniopropionate (DMSP) (Curson et al., 2011). Both DMS and DMSP play important roles in driving the global sulfur cycle and thus may affect climate. It was long believed that only marine eukaryotes

such as phytoplankton could produce DMSP. However, the authors of a review article (Zhang et al., 2019) in this issue recently discovered that marine heterotrophic bacteria also produced DMSP (Curson et al., 2017). In the review, they describe the global distribution pattern of DMSP and DMS, the relative contributions of marine phytoplankton and bacteria to the production of DMSP and its degradation to DMS, and the physiological and ecological functions of these important organosulfur molecules to permit a better understanding of the mechanisms of DMSP and DMS production and their roles in the environment (Zhang et al., 2019).

Microbes in aquatic environments other than oceans also serve unique biogeochemical roles. Microbial community structures and activities in lakes have attracted substantial research interests in recent years. However, a biogeographic distribution pattern in global lakes and its controlling factors have not been fully disclosed. In their research article, Yang et al. compiled and analyzed a large number of environmental 16S rRNA sequences from 431 lakes across a wide range of geographical distance and environmental conditions. Their work allows a better understanding of the impact of geographic distance, environmental conditions, and stochastic processes on microbial distribution in global lakes (Yang et al., 2019).

Microbes are able to exchange electrons between cells (Shi et al., 2016; Summers et al., 2010). Electron exchanges between the quinol/quinone pools in microbial cytoplasmic membrane and extracellular substrates are known as microbial extracellular electron transfer (EET). Microbes with EET capabilities are widespread in the hydrosphere, such as sediments of rivers, lakes and oceans, where they play crucial roles in biogeochemical cycling of key elements, including carbon, nitrogen, sulfur, iron and manganese (Kappler and Bryce, 2017; Myers and Nealson, 1988; Nielsen et al., 2010). In this issue, Jiang et al. review the molecular mechanisms underlying the microbial ability for extracellular redox transformation of iron, direct interspecies electron transfer as well as long distance electron transfer mediated by the cable bacteria in the hydrosphere (Jiang et al., 2019).

Obviously, areas of research covered in this collection of articles represent only a very small fraction of those in the Program-sponsored projects. The ultimate goal of the Program is to improve the picture of the biogeochemical roles of microbes in the hydrosphere.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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Biographical Sketch



Dr. Li Huang received his Ph.D. from the University of Guelph, Canada, in 1988. From 1988 to 1993, he was a postdoctoral fellow at the Johns Hopkins University, USA. From 1993 to 1996, he was assistant professor at Pomona College, USA. Since 1996, he has been on faculty at the Institute of Microbiology, Chinese Academy of Sciences. He was promoted to the rank of full professorship in 1998. From 1996 to 2008, he was initially deputy director and then director of the State Key Laboratory of Microbial Resources. From 2008 to 2013, he served first as executive deputy director-general and later as director-general of the Institute of Microbiology. He was awarded the China National Fund for Distinguished Young Scientists in 1999, and was leading a research group supported by the Funds for Creative Research Groups of China from 2007 to 2012. He is currently vice president of the Chinese Society for Microbiology. He also serves as managing editor of *Extremophiles*, associated editor of *Acta Microbiologica Sinica*, and editorial board member of *SCIENCE CHINA Life Sciences*. His areas of research include genetic mechanisms in Archaea, archaeal viruses and marine viruses. Dr. Li Huang is vice chair of the steering committee of the Hydrosphere Microbes Program.



Dr. Xiang Xiao is distinguished professor of Shanghai Jiao Tong University (Since 2009). He obtained his Ph.D. in molecular biology at Huazhong Agricultural University, China in 1998 and was a postdoctoral fellow in Biology/Chemistry Department, Osnabrueck University, Germany from 1999 to 2001. He was awarded the China National Fund for Distinguished Young Scientists in 2006. He has been supported by grants from several major research programs including the Deep Sea Biological and Genetic Resources Program from the China Ocean Mineral Resources R&D Association (COMRA), the Deep-Sea Cold Seep Research and the Deep-Sea Hydrothermal Vent Research Programs from National Natural Science Foundation of China. He was chief scientist on the COMRA Deep-Sea Hydrothermal Vent Biodiversity Research Cruise in 2008 and the Chinese Manned Deep-Sea Submersible Cruise in 2014–2015. Dr. Xiao's research is focused on deep-sea high-pressure ecosystems and extremophiles in hydrothermal vents, cold seeps and sediments. He has successfully isolated and genetically manipulated several groups of extremophiles such as piezophiles, thermophiles and psychrophiles. Dr. Xiang Xiao currently serves on the steering committee of the Hydrosphere Microbes Program.



Dr. Guoping Zhao is molecular microbiologist and has been working on microbial physiology and metabolic regulation since he received his B.S. degree in biology from Fudan University in 1982. He obtained his Ph.D. degree in biochemistry from Purdue University, Indiana, USA in 1990. He returned to China in 1992 as the founding production manager of Shanghai Promega Biological Products, Ltd, a subsidiary joint venture of Shanghai Research Center of Biotechnology (SRCB), CAS, and an adjunct associate professor of Shanghai Institute of Plant Physiology (SIPP, currently SIPPE), CAS. Currently, he is professor and chairman of the Advisory Committee of CAS Key Laboratory of SIPPE, after serving as its founding director for the term of 2008–2016. He has been the chief scientist of the Big Data Center for BioMedicine at the Shanghai Institutes for Biological Sciences (SIBS), CAS since 2016, and the professor and director of Department of Microbiology and Microbial Engineering at the School of Life Sciences, Fudan University since 2004. He also has been appointed as the adjunct chair professor of Microbiology by the Faculty of Medicine of the Chinese University of Hong Kong since 2008. He was elected the member of CAS in 2005 and the president of the Chinese Society for Microbiology for the term of 2006-2011. Along with his scientific duties in program/project organization and institutional administration, he focused his research activities on genomics and systems biology, largely for microorganisms, of which, he devoted and contributed to a few important projects including the molecular evolution study of SARS-CoV during the 2003 and 2005 SARS epidemic. Dr. Guoping Zhao currently serves as chair of the steering committee of the Hydrosphere Microbes Program.