

Review

Significance of Archaea in terrestrial biogeochemical cycles and global climate change

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Received 26 July, 2014; Accepted 19 January, 2015

Our understanding of the role of archaea, and their significance, in the biosphere has changed substantially with recent advances in molecular techniques. Large numbers of environmental rRNA gene sequences currently flooding into GenBank illustrates that, archaea are ubiquitous and sometimes quantitatively abundant in the environment. Their importance in carbon (C) and nitrogen (N) turnover in marine ecosystems and their dominant role in ammonium oxidation in terrestrial environments has been acknowledged. Knowledge of archaea and the factors determining their metabolism has potential implications for our understanding of plant productivity, carbon sequestration, nitrogen leakage and greenhouse gas (GHG) production. To mitigate global change and rise in GHGs like methane (CH₄), nitrous oxide (N₂O) and carbon dioxide (CO₂), a multidimensional approach is needed to understand the complex processes. Particularly, we need to understand how different microbial groups participate in the GHG cycling processes. The relationship between high diversity of archaea and functionality in the terrestrial ecosystem is far less understood. This review defined two fundamental aspects of the ecological significance of the archaea. First, it highlighted the role of archaea in biogeochemical cycles of major elements, such as carbon, nitrogen and sulfur. Second, it identified their significance in the GHG cycling processes and global climate change.

Key words: Archaea, ecology, biogeochemical cycles, greenhouse gas, climate change.

INTRODUCTION

The microbial world is much more complex and diverse than previously predicted. Between the two prokaryotic phylogenetic domains, bacteria and archaea, members of the former group have been shown to be ubiquitous in nature, with ample evidence of vast assemblages of uncultured organisms. Recently, environmental genomic sequences have contributed dramatically to our understanding of archaeal diversity, which continues to

expand. Uncultured archaea have been documented in highly diverse locales, extending their habitat from the upper part of the oceans to the meso- and bathypelagic zones (Blank, 2009). They also have been detected in environments varying from lakes to soils and sediments; and they show up in close association with animals and bacteria (Madsen, 2011). Their diversity in all types of ecosystems indicates that they can be major players in

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various biogeochemical cycles (Offre et al., 2013). Constant recycling of elements in various forms derives from a variety of geophysical processes as well as biological metabolic processes that take place in various life forms (Odum, 1985). Hydrogen, carbon, nitrogen, sulfur, oxygen and phosphorus are six major elements, that form the skeleton of these biogeochemical cycles (Falkowski et al., 2008).

Biogeochemicals cycle in soil is an important phenomenon for the cycling of elements including C, N, P and metals. Role of bacteria during this process has been studied extensively (Mohanty et al., 2014; Zhao et al., 2014). However, the participatory role of Archaea in biogeochemical cycles had been less studied and is mostly based on *in vitro* experiments. Laboratory investigations of this kind are not capable of illustrating the exact growing condition of these life forms in their natural habitats. Lack of knowledge regarding adequate culturing techniques has also been a major hurdle in these experiments. Microbial ecologists have adopted various new strategies to study the interaction and impact of Archaea on element cycling and nutrient fluxes in microbial communities. These new techniques include molecular techniques and physiological-based approaches. The latter include use of relatively low amounts of nutrients (Connon et al., 2005), inoculum dilution to extinction (Brauer et al., 2006; Davis et al., 2004) and addition of selective inhibitors against bacteria and archaea (Brauer et al., 2006). In this review, we highlighted the phylogeny and prevalence of Archaea in various ecosystems and their significance in biogeochemical cycles of major elements and global climate change.

PHYLOGENY AND ECOLOGY OF ARCHAEA

Two major cultivated archaeal phyla were first defined by Carl Woese as *Euryarchaeota* and *Crenarchaeota*. *Euryarchaeota* includes methanogens, methane-oxidizing archaea, denitrifiers, sulfate reducers, iron oxidizers and organotrophs (Kletzin, 2007). The hyperthermophilic, parasitic *Nanoarchaeum equitans* was initially suggested to represent a new candidate phylum (Huber et al., 2002) that replicates only when attached to the surface of another hyperthermophilic archaeon in the genus *Ignicoccus*, originally isolated from marine hydrothermal vents. It is currently recognized as an important member of the *Euryarchaeota* lineage (Brochier et al., 2005).

The *Crenarchaeota* contain only one taxonomic class *Thermoprotei* and five taxonomic orders *Acidilobales*, *Desulfurococcales*, *Fervidicoccales*, *Sulfolobales* and *Thermoproteales*. *Acidilobales* and *Fervidicoccales* were discovered only recently (Perevalova et al., 2010; Prokofeva et al., 2009). Ammonia oxidizing archaea have been isolated recently. This includes *Nitrosopumilus maritimus*, a small marine organism closely related to an

abundant population of planktonic marine archaea (Falkowski et al., 2008; Fuhrman, 1992). Organisms of the crenarchaeota are globally distributed and are found in high numbers in marine and freshwater environments, soils and sediments. They also occur in extreme environments including hot springs. On the basis of genomic data, additional archaeal phyla have recently been proposed. They include Korarchaeota (Miyashita et al., 2009), Aigarchaeota (Nunoura et al., 2011) and Geoarchaeota (Kozubal et al., 2012). Major archaeal groups and their ecological significance are presented in Table 1.

Archaea in global carbon cycle

The global carbon cycle is modulated by complex microbial communities. The Archaea have established their significance in the carbon cycle by mediating certain key processes (Table 2). Archaea dominate in the anoxic methanogenic environment. These microbial groups are closely associated with the carbon cycle and also anaerobic CH₄ oxidation (Hinrichs et al., 1999). Compound-specific isotope studies have been done to track the flow of organic and inorganic carbon into the lipids of naturally occurring archaea in deep ocean waters (De La Torre et al., 2008). Apart from photo- or chemoautotrophic bacteria, archaea also contribute to the global CO₂ budget. Results extend and confirm the notion that one group of marine archaea, the Crenarchaea, are autotrophic in nature and derive their carbon from CO₂. Thus, it was convincingly demonstrated that CO₂ is a main carbon source for deep-sea Crenarchaea, indicating one major biogeochemical role for archaea in the sea. Various members from archaeal phyla, including *Crenarchaeota*, *Thaumarchaeota* and *Euryarchaeota*, undergo autotrophic growth by carbon assimilation, thereby reducing oxidized inorganic compounds such as carbon dioxide (CO₂) or bicarbonate (HCO₃⁻), and form simple organic molecules (Berg et al., 2010). The genomic DNA sequences of *Crenarchaeum symiosum*, revealed its potential to mediate carbon (CO₂) assimilation in marine ecosystem (Hallam et al., 2006).

The pathway involving the 3-hydroxypropionate cycle components mediating carbon assimilation was recently studied in several thermophilic crenarchaeotes within the Sulfolobales (Barns and Nierzwicki-Bauer, 1997; Brochier-Armanet et al., 2008; Brochier et al., 2005). Species, including *C. symbiosum* genomic sequences, possessed evidence of two metabolic pathways, including the reductive tricarboxylic acid pathway (Evans et al., 1997) and 3-hydroxypropionate cycle (Herter et al., 2001) mediating carbon assimilation. Some members of *Euryarchaeota* and *Crenarchaeota* include various autotrophic organisms but are also obligate heterotrophs and mixotrophic in nature (Kletzin, 2007). The genome sequence of uncultivated extremophilic archaeal

Table 1. Ecology of archaea in terrestrial ecosystems. Phyla and major species of archaea found in different habitats are mentioned.

Phyla	Species	Habitat	References
<i>Crenarchaeota</i>	<i>Thermoproteales, Sulfolobales, Desulfurococcales, Acidilobales, Fervidicoccales</i>	Hot, acidic environments, hot springs and submarine hydrothermal vents	(Perevalova et al., 2010; Prokofeva et al., 2009; Woese, 1987)
<i>Geoarchaeota</i>	<i>Geoarchaeota</i>	Thermophilic iron-oxide mats.	(Kozubal et al., 2012)
<i>Thaumarchaeota</i>	Crenarchaeotic Group III, ALOHA group (Group 1.1c/psL12 group), Marine Benthic Group A Group 1.1a, Group 1.1b	Marine and freshwater environments, soils, sediments and hot springs.	(Brochier-Armanet et al., 2008; Stahl, 2004)
<i>Aigarchaeota and Candidate lineages</i>	<i>Aigarchaeota; Crenarchaeotic Group I, Deep Sea Archaeal Group, Marine Benthic Group, Marine Hydrothermal Vent Group 2B</i>	Marine, Terrestrial and marine geothermal systems	(Berg et al., 2006)
<i>Korarchaeota</i>	<i>Candidatus Korarchaeum</i>	Hydrothermal environments	(Barns and Nierzwicki-Bauer, 1997; Teske et al., 1998)
<i>Euryarchaeota</i>	<i>Methanosarcinales; Methanocellales; Methanomicrobiales, ANME 1–3, Halobacteriales, Archaeoglobales, Thermoplasmatales, Aciduliprofundum sp., Methanoplasmatales, Nanosalinarum sp., Methanobacteriales, Methanococcales, Methanopyrales Thermococcales, Micrarchaeum sp. Parvarcheum sp./ Deep Sea Hydrothermal Vent Group 6</i>	Marine ecosystem, soils, and sediments extreme environments	(De Vries and Schröder, 2002; Teske et al., 1998; Tomlinson et al., 1986; Woese, 1987)
<i>Nanoarchaeota</i>	<i>Nanoarchaeum</i>	Hyperthermophilic environment	(Angel and Conrad, 2009; Boetius et al., 2000; Shima et al., 1995)

representatives of the *Korarchaeota*, *Geoarchaeota*, *Aigarchaeota*, has provided evidence that they can grow organotrophically (Baker et al., 1986; Barns and Nierzwicki-Bauer, 1997; Ghai et al., 2011; Nunoura et al., 2011). This indicates that these groups can perform catabolic degradation of organic substrates and produce CO₂ as a main product.

Archaea and global methane cycle

Methane is an important GHG because the global warming potential is ~25 times higher than CO₂. Most of it on Earth is produced by methanogenesis, usually the final step in the fermentation of organic matter, which takes place in rice fields, the guts of animals, soils, wetlands and landfills, and in freshwater and marine sediments. Methanogens comprise an important group of archaea that in the absence of oxygen produces CH₄ as the major product of their energy conserving metabolism. All methanogenic archaea characterized so far belong to the *Euryarchaeota*, and are distributed among five taxonomic classes: *Methanopyri*, *Methanococci*, *Methanobacteria*, *Methanomicrobia*, and *Thermoplasmata*

(Dridi et al., 2012; Ferry, 2011; Paul et al., 1989).

On the basis of substrate utilization, methanogens are categorized as hydrogenotrophic methanogens, which rely on CO₂ reduction using H₂. Moreover, formatotrophic methanogens use formate, acetotrophic methanogens ferment acetate and methylotrophic methanogens use methanol, methylamines, dimethylsulfide (DMS) or methanethiol; thereby causing their dismutation in the process of using them as their substrate (Ferry, 2011). Methanogens reside in various anoxic environments (Chaban et al., 2006) and are usually abundant where electron acceptors such as NO₃⁻, Fe³⁺ and SO₄²⁻ are scarce.

In oxic conditions, they have been prominently identified in various aerated soils (Angel and Conrad, 2009) and the oxygenated water column of oligotrophic lakes (Burns et al., 1996). In flooded rice field ecosystem, methanogens play crucial role in the CH₄ emission. These archaeal groups are influenced by agricultural practices and agrochemicals applications (Bharati et al., 1999; Mohanty, 2009; Mohanty et al., 2004). Methanogens in aerated soils become active under wet anoxic conditions, and those in oxygenated lake waters were attached to photoautotrophs, which might enable

Table 2. Role of archaea in carbon metabolism and the greenhouse gas (CO₂, CH₄) cycling in the terrestrial ecosystem.

Archaea	Carbon cycle	References
<i>Sulfolobales, Candidatus Crenarchaeum symbiosum, Candidatus Nitrosopumilus maritimus, Candidatus Caldiarchaeum subterraneum</i>	Carbon (CO ₂) assimilation	(Berg et al., 2006; Ishii et al., 2009; Menendez et al., 2006; Walker et al., 2011)
<i>Few members of Euryarchaeota and Crenarchaeota, Korarchaeota, Geoarchaeota, Aiarchaeota, Euryarchaeota: Nanohaloarchaeal</i>	Organic carbon mineralization	(Baker and Vervier, 2004; Kletzin, 2007)
<i>Euryarchaeota Methanopyri, Methanococci, Methanobacteria, Methanobacteria, Methanomicrobia, & Thermoplasmata</i>	Methanogenesis or CH ₄ production	(Dridi et al., 2012; Sowers and Ferry, 1983)
<i>Euryarchaeota (ANME 2, ANME 2 & ANME 3)</i>	Anaerobic CH ₄ Oxidation	(Hallam et al., 2003; Kruger et al., 2005a; Shima et al., 1995; Weidler et al., 2007)

anaerobic growth and supply of methanogenic substrates (Grossart et al., 2011). Several other processes, such as the microbial decomposition of methylphosphonate (Day et al., 1995; Karl, 2002), could be responsible for CH₄ production in oxygenated waters and soils (Keppler et al., 2000).

Global methane mitigation by archaea

Recently, CH₄ production is suspected to rise considerably in arctic soils because of climate warming and is thus a major focus of current arctic research (Keppler et al., 2002). It is assumed that about 10-20% of reactive organic material buried in soils and sediments can be converted to CH₄. In oceans, the annual rate of CH₄ production has been estimated to be 85-300 Tg CH₄ year⁻¹. Of the net CH₄ produced, more than 90% is compensated for anaerobic oxidation of methane (AOM) (Reeburg, 1993).

AOM takes place by the syntrophic cooperation between a methanogenic archaea and sulfate-reducing bacteria (SRB). The 16S rRNA gene sequences of the euryarchaeal anaerobic methanotrophs (ANMEs) determine three sequence clusters, namely ANME-1, ANME-2 and ANME-3. The ANME represent special lines of descent within the Euryarchaeota and appears to gain energy exclusively from the AOM, with sulfate as the final electron acceptor. The existence of ANME was found in sulfate-methane transition zones (SMTZ) (Reeburg, 1993), which forms in all anoxic aquatic systems. Transport of CH₄ from below and sulfate from above provides a niche defined by a minimum yield of energy to the anaerobic methanotrophs. Anaerobic CH₄ oxidation results in a significant increase in inorganic carbon and alkalinity. Thus, ANME habitats are characterized by a massive deposition of carbonate plates and chimney-like structures in CH₄ seeps (Reitner et al., 2005). Prevalence of ANME has also been reported in terrestrial environments, including terrestrial mud volcanoes located

in the Carpathian Mountains (Romania) (Alain et al., 2006), landfills (Grossman et al., 2010) and from the anoxic strata of an eutrophic freshwater Lake (northern Germany) (Eller et al., 2005); wherein low *in situ* numbers (<1%) of single ANME-1 and ANME-2 archaea were detected. ANME sequences have also been repeatedly reported from diverse soils, aquifers and oil-field production waters.

On the basis of various studies (Angel and Conrad, 2009; Hoehler et al., 1994), it has been hypothesized that the initial step in CH₄ oxidation is essentially a reversal of the terminal reaction in methanogenesis, that is, the reduction of methyl-coenzyme M (CoMS-CH₃) with coenzyme B (H-S-CoB), yielding CH₄ and the heterodisulfide (CoM-SS-CoB) (Simankova et al., 2003). Methyl-coenzyme M reductase (MCR), which catalyses this reaction in methanogens, has two tightly but noncovalently bound molecules of a nickel porphyrinoid, cofactor F430, with a molecular mass of 905 Da. The first evidence of the existence of MCR in sediments from AOM zones or enrichment cultures was given by the identification of novel *mcrA* genes that could be assigned to ANME-1 and ANME-2 archaea (Hallam et al., 2006). Biochemical proof for the existence of MCR in ANME has been confirmed by extracting the nickel compound from AOM microbes inhabiting microbial mats, and confirming that it displays the same absorption spectrum as the authentic cofactor F430 of the MCR (Kruger et al., 2005a). The nickel compound is part of an abundant protein (Ni-protein I) that is present in concentrations of up to 7% of the total extracted mat proteins and has not been found in any methanogenic archaea investigated so far (Shima et al., 2000). The structure of this cofactor F430 is reported as 172-methylthio-F430 (Mayr et al., 2008). In addition, a minor fraction of extracted proteins contained Ni-protein II with an unmodified cofactor (Kruger et al., 2005a). Ni-protein I could be assigned to ANME-1 archaea, while ANME-2 archaea are the source of Ni-protein II, which appears to contain the same variant of F430 that is in methanogens. This suggests

Table 3. Archaeal role in nitrogen transformation and the greenhouse gas (nitrous oxide N_2O) cycle. Archaea involved in N_2 fixation, nitrification and denitrification are indicated. Greenhouse gas N_2O is produced by the nitrifying and denitrifying archaea.

Archaea associated	Biological processes in N transformation and N_2O cycle	References
Methanogenic archaea (<i>Methanobacteria</i> , <i>Methanococci</i> , and <i>Methanomicrobia</i>), anaerobic methane-oxidizing euryarchaea (ANME-2)	Nitrogen fixation	(Leigh et al., 2007; Roger et al., 1993)
Ammonia-oxidizing archaea (AOA) (<i>Thaumarchaeota</i>)	Nitrification (N_2O production)	(Treusch AH, 2005)
<i>Haloarcula marismortui</i> and <i>Ferroglobus placidus</i> , <i>Pyrobaculum aerophilum</i> , <i>Haloferax denitrificans</i> and <i>Pyrobaculum aerophilum</i>	Denitrification (N_2O to N_2)	(Tomlinson et al., 1986; Vaupel et al., 1998; Werber and Mevarech, 1978)

that Ni-protein I and Ni-protein II may catalyze the first step of AOM (Mayr et al., 2008).

Archaea and global nitrogen cycle

Archaea exhibit a multifaceted role in all the reductive pathways of the N-cycle, either dissimilatory reactions, such as nitrate respiration and denitrification, or assimilatory pathways like N_2 fixation and nitrate assimilation. Because archaea are the predominant microbial populations in extreme or harsh environments, such as highly saline water and hot springs, they sustain the N-cycle in these special and severe ecosystems (Hatzenpichler, 2012; Monteiro et al., 2014). Important N-cycle processes carried out by archaea are cited in Table 3. Autotrophic nitrification is a two-step process consisting of the oxidative conversion of ammonia to nitrite via hydroxylamine, carried out by ammonia-oxidizing bacteria, and the further oxidation of nitrite to nitrate, performed by nitrite oxidizing chemolithoautotrophic bacteria. Denitrification is a respiratory process where nitrate is successively reduced to nitrite, NO, N_2O and N_2 , which takes place predominantly under anoxic environmental conditions by many facultative bacteria (Berks et al., 1995; Richardson and Marshall, 1986). Some heterotrophic bacteria are able to combine nitrification and aerobic denitrification by oxidizing ammonia to nitrite, which is later reduced to N_2 (de Boer et al., 2010). Dinitrogen, an important constituent of our atmosphere, is produced mainly via two processes; namely, denitrification (Cabello et al., 2004) and the anaerobic oxidation of NH_4^+ with NO_2^- (anammox) (Kartal et al., 2012).

Role of archaea in global nitrous oxide cycle

Denitrification is a form of anaerobic respiration that uses NO_3^- or NO_2^- as an electron acceptor, and results in the sequential formation of gaseous compounds like NO,

N_2O and N_2 . Denitrifiers are the group of microbes that constitute both archaea as well as eukarya (Cabello et al., 2004; Zumft, 1992). In the case of anammox, it is solely performed by bacteria. All denitrifying archaea characterized thus far are either organotrophic halophiles or lithoautotrophic (facultative or obligate) hyperthermophiles using NO_3^- as an electron acceptor (Mancinelli et al., 1981), with the exception of *Pyrobaculum aerophilum*, which accepts both NO_3^- and NO_2^- (Volk et al., 1997). Furthermore, a metagenomic study suggested that the uncultivated archaeon *C. subterraneum* might also be able to use NO_3^- as an electron acceptor (Nunoura et al., 2011). Archaeal denitrifiers produce various mixtures of NO_2^- , NO, N_2O and N_2 , and hence play a key role in the rise of atmospheric GHG concentrations in atmosphere. In some archaea, such as *Haloarcula marismortui* and *Ferroglobus placidus*, the predominant gas species produced by denitrification is N_2O (Werber and Mevarech, 1978), although other archaea such as *Haloferax denitrificans* and *Pyrobaculum aerophilum* are able to reduce N_2O to N_2 , having a complete denitrification pathway (De Vries and Schröder, 2002; Tomlinson et al., 1986). The ammonia-oxidizing thaumarchaeon *Candidatus Nitrosopumilus maritimus* and thaumarchaeal, grown in enrichment cultures using isolates obtained from pelagic waters, were shown to produce N_2O (Santoro et al., 2011), and the comparison of the isotopic signature of the N_2O emitted by cultures and ocean waters indicated that archaea could account for most of the oceanic production of this greenhouse gas (Santoro et al., 2011), which represents up to 30% of the worldwide emissions of N_2O to the atmosphere.

Archaea in the sulfur cycle and climate change

Archaea play a significant role in a variety of processes involved in the sulfur cycle. Elemental sulfur may be either respired with H_2 or organic compounds as electron donors. This metabolism is performed by various members

of *Crenarchaeota* and *Thermoplasmata*. The sulfur cycle has no role in GHG emission but it indirectly regulates global warming or global change. This is carried out by release of a gaseous compounds to the atmosphere. This S-based compound is known as dimethyl sulphide (DMS). In the atmosphere, this compound acts as nuclei for cloud formation. Clouds reflect back the sun's infrared radiation, thus reducing global warming. Chemically, DMS a volatile organic sulfide (thioether), is an important intermediate in the sulfur cycle that is produced and oxidized biologically by aquatic archaea. Processes controlling the production of DMS in marine surface waters have received special attention owing to the potential effect of DMS on cloud formation and global climate (Charlson et al., 1987; Lee et al., 2004). Archaea involved in DMS production belong to *Euryarchaeota*, including representatives of *Halobacteria* (Miller et al., 2010) and possibly members of the uncultivated euryarchaeal phototrophic organotrophs (Marine group II) (Martin-Cuadrado et al., 2008). *Halobacteria* produce DMS through the dissimilatory reduction of dimethylsulfoxide (DMSO) as a form of anaerobic respiration (Miller et al., 2010). Archaeal representatives of Marine group II, widespread in ocean waters, have a similar ability (Martin-Cuadrado et al., 2008). DMSO is abundant in aquatic environments and could act as an important precursor to the production of DMS (Lee et al., 2004).

CONCLUDING REMARKS AND FUTURE PERSPECTIVE

This review concluded that as with bacteria, archaea play crucial roles in biogeochemical cycles, particularly in the carbon, nitrogen and sulfur cycle. Archaea are involved in CH₄ production as well as oxidation. We defined that methanogenesis and anaerobic CH₄ oxidation are two processes of global importance that are performed exclusively by archaea. Anaerobic oxidation of CH₄ can efficiently control the atmospheric CH₄ efflux from the ocean. Moreover, this review highlighted the role of archaea in N₂O production from aerobic agricultural soils and anoxic environments. The involvement of recently identified *Crenarchaeota* in N₂O production from agricultural soils was also addressed in relation to their role in the nitrous oxide cycle. We outlined the role of archaea in the sulfur cycle and indicated that these groups may regulate global warming through production and oxidation of various cloud forming compounds like DMS. However, the quantification of archaeal abundance and their involvement in biogeochemical processes are not clearly understood. There is need for further research to understand the role of archaea in complex biogeochemical processes using advance molecular tools. Specifically, archaeal global diversity, and the interaction between bacteria and other microbes involved

in GHG cycling should be explored.

Conflict of interests

The authors did not declare any conflict of interest.

ACKNOWLEDGEMENTS

This manuscript is part of the project "metagenomic characterization of nutrient cycling microbes associated with the bioenergy cop *J. curcas*" funded by the Department of Biotechnology, Government of India to SRM. We thank the two anonymous reviewers for their comments toward improving the manuscript.

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