



Review

Molecular ecological perspective of methanogenic archaeal community in rice agroecosystem

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HIGHLIGHTS

- Methane leads to global warming.
- Rice fields represent the major source of methane emission.
- Biogenic methane is produced by anaerobic methanogenic archaea.
- We summarize the current knowledge on the diversity and activity of methanogens.
- Review will contribute to formulating strategies for CH₄ mitigation.

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ABSTRACT

Methane leads to global warming owing to its warming potential higher than carbon dioxide (CO₂). Rice fields represent the major source of methane (CH₄) emission as the recent estimates range from 34 to 112 Tg CH₄ per year. Biogenic methane is produced by anaerobic methanogenic archaea. Advances in high-throughput sequencing technologies and isolation methodologies enabled investigators to decipher methanogens to be unexpectedly diverse in phylogeny and ecology. Exploring the link between biogeochemical methane cycling and methanogen community dynamics can, therefore, provide a more effective mechanistic understanding of CH₄ emission from rice fields. In this review, we summarize the current knowledge on the diversity and activity of methanogens, factors controlling their ecology, possible interactions between rice plants and methanogens, and their potential involvement in the source relationship of greenhouse gas emissions from rice fields.

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1. Introduction

Since the beginning of the industrial era, anthropogenic activities are identified as the major factor for the increased emission of the three major greenhouse gases (GHGs) viz., carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O). Increased emissions of GHGs are anticipated to raise the mean ambient global temperature by 2 °C by 2050, thus causing a change in the global climatic patterns, and thereby, affecting the life systems on the planet (IPCC, 2013). Alternately, increased temperature and elevated CO₂ would result in an increased emission of GHGs, especially CH₄. CH₄ has about 23 times potential to absorb infrared radiation than CO₂, thus responsible for its higher global warming potential (Forster et al., 2007). It is second only to carbon dioxide (CO₂) in terms of contribution to the current enhanced global warming, adding about one-third to the radiative force as exerted by CO₂ (Denman et al., 2007). About 74% of emitted CH₄ is derived from biological methanogenesis (Whitman et al., 2006). Among all the anthropogenic sources, rice ecosystem is one of the most important sources of CH₄ production and emission approximating 10% of total through anthropogenic CH₄ emissions or about 1.5% of gross GHG emissions globally (Nazaries et al., 2013; FAOSTAT, 2014). Thus, intensive rice cultivation is likely to be one of the probable reasons for the gradual rise in the atmospheric CH₄ concentrations. It is reported that out of the total CH₄ emission (28.2 Tg year⁻¹), the Asian rice fields contribute 25.1 Tg (Yan et al., 2005) or roughly about 90% of the global CH₄ emission from such ecology.

Methanogenic microbes widely occur in the anaerobic environments because of their unique ability to harvest energy using CO₂ (electron acceptor) and/or methylated compounds as the energy source (Lever, 2012). The capacity of methanogens to metabolize methylated compounds favours their growth and multiplication in suitable ecological niche with sulphate and metal reduction as the dominant respiratory pathways (Deppenmeier and Müller, 2007). Despite the widespread methanogens, global CH₄ production mainly from subsurface sediments contains the minor fraction of methanogenic population corresponding to <1% of the total microbiome, and also the small fraction of archaea (Lever, 2013). Dynamics of methanogenesis and methanogen community structure in flooded rice fields depends on various parameters such as the soil attributes (Yao et al., 1999), the rice cultivars (Conrad et al., 2008), fertilizer applications (Hou et al., 2000; Linquist et al., 2012), rice plant growth stages, seasonal variability (Kruger et al., 2002), crop rotation (Liu et al., 2015), climate change, and pollution (Hashimoto-Yasuda et al., 2005; Zheng et al., 2011).

The structure of methanogenic archaeal community, responsible for methanogenesis in soils, has been little explored by the enrichment-based methods due to its biasness, time consumption and technical complexity (Luton et al., 2002). Molecular methods, such as gene hybridization microarrays, RFLP (Restriction Fragment Length Polymorphism), T-RFLP (Terminal Restriction Fragment Length Polymorphism), DGGE (Denaturing Gradient Gel Electrophoresis), or PCR-cloning-DNA sequencing, pyrosequencing, DNA stable isotope probing (DNA-SIP) technique have emerged successful in the identification and characterization of methanogens in many rice field ecosystems even when the number of microbial population was small (Ramakrishnan et al., 2001; Krüger et al., 2005; Watanabe et al., 2006; Watanabe et al., 2010; Singh and Dubey, 2012; Singh et al., 2012; Dubey et al., 2013; Lee et al., 2014). For estimating the methanogen population in the rice fields, recent technique of real-time PCR has been used variously (Watanabe et al., 2007; Yuan and Lu, 2009). There are several reports on methanogen dynamicity in the rice fields (Dubey, 2005; Conrad, 2007; Fazli et al., 2013). Therefore, analyzing methanogenic community structure and its function in the rice fields will be helpful in better understanding the ecology of methanogens and CH₄ production potential of soils that is essential for formulation of strategy to mitigate CH₄ emission from the rice fields. In this brief review, we collated recent findings on methanogens governing CH₄ production in rice fields. We also

discussed the factors affecting methanogenic community dynamics in rice fields including rice plant-methanogen association as well as the ecological role(s) and succession of methanogenic community in CH₄ production in such ecosystems. In addition, we highlighted the impact of climate change feedback on methanogen diversity and functionality. This may add clarity to our understanding of the role of methanogenic community and their functional activity in the rice agro-ecosystem with focus on CH₄ dynamics.

2. Classification of methanogens

Archaea consist of phyla Euryarchaeota, Crenarchaeota, Thaumarchaeota, Korarchaeota, Nanoarchaeota, Aigarchaeota, Parvarchaeota, and Bathychaeota (Huber et al., 2002; Brochier-Armanet et al., 2008). Methanogens are the distinct group of microorganisms which are classified under the phylum Euryarchaeota of the domain Archaea (Woese et al., 1990). Euryarchaeota includes seven orders that is exclusively comprised of methanogens (Borrel et al., 2013) viz. Methanosarcinales, Methanocellales, Methanomicrobiales, Methanobacteriales, Methanococcales, Methanopyrales, Methanomassiliococcales (Table 1) and additional several orders (e.g., Archaeoglobales, Halobacteriales). Using DNA sequences targeting *mcrA* gene (phylogenetic marker for methanogens) it was proposed that the number of CH₄-cycling archaeal orders in the Euryarchaeota, rise to twelve (Lever and Teske, 2015).

Methanogens so far identified are separated into three categories i) hydrogenotrophic ii) acetoclastic, and iii) methylotrophic. The two major physiological groups of methanogens found in rice fields are acetoclastic and hydrogenotrophic. Acetoclastic methanogens convert acetic acid to CH₄ and CO₂, and comprise two families, Methanosarcinaceae and Methanosaetaceae. The hydrogenotrophic methanogens reduce CO₂ to CH₄. The acetoclastic genera dominate the rice soils of several countries viz. Italy, Philippines, China, Japan and Thailand (Ramakrishnan et al., 2001; Krüger et al., 2005; Watanabe et al., 2006; Conrad et al., 2012). In addition, such fields also recorded the presence of hydrogenotrophic group. The rice roots are dominated by hydrogenotrophic methanogens belonging to Methanomicrobiales, Methanobacteriales and Methanocellales (Grosskopf et al., 1998; Chin et al., 2004; Hashimoto-Yasuda et al., 2005). However, Methanosarcinaceae showed hydrogenotrophic and acetotrophic nutritional mode (Jetten et al., 1992). Methylated compounds are utilized by methylotrophic methanogens restricted to the order Methanosarcinales. Methanomassiliococcales (*Methanomassiliococcus*) also utilize methylated compounds for growth substrate. Exceptionally, however, members of Methanobacteriales and *Methanospaera* also depend on methylated substrate (Liu and Whitman, 2008).

3. Isolates of methanogens and molecular approaches for identification

Characterization and identification of isolates from paddy soils helps in understanding the ecology of methanogenic archaea in the rice agrosystems. Asakawa et al. (1993, 1995) were the first to characterize *Methanobrevibacter arboriphilus* strain SA and *Methanosarcina mazei* strain TMA isolated from rice fields. Using DNA analysis technique, Kudo et al. (1997) reported presence of *Methanosarcina*, *Methanogenium*, *Methanosaeta* and *Methanobacterium* in cultures isolated from Japanese rice fields. Großkopf et al. (1998) reported prevalence of *Methanosarcina*, *Methanosaeta* and *Methanobacterium* species in Italian rice field soils. Joulain et al. (1998) investigated microbial cultures from 13 rice field soils using 16S rDNA based technique and reported presence of *Methanobacterium bryantii*, *Methanobacterium formicicum*, *Methanosarcina barkeri*, *Methanosarcina mazei* and *Methanoculleus marisnigri*. Joulain et al. (2000) reported *Methanobacterium oryzae*, the novel species of methanogens from rice fields. Using DNA-DNA hybridization approach, *Methanoculleus chikugonsis* sp. nov. has been reported

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