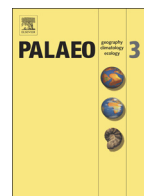




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Change of methane production pathway with sediment depth in a lake on the Tibetan plateau

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ABSTRACT

Methane production is the terminal step in the degradation of organic matter in most anoxic lake sediments. It has been suggested that CH₄ production in lake sediments is dominated by hydrogenotrophic methanogenesis, especially in deeper layers. We investigated the vertical sediment profile from the surface to 50 cm depth in the sediment of Bangong Co, an oligotrophic high altitude lake on the Tibetan plateau. We measured CH₄ production, stable carbon isotope fractionation and the archaeal community structure. We found that the methane production rates, the acetate concentrations and the numbers of bacteria and archaea strongly decreased with sediment depth. The enrichment factor (ϵ) for hydrogenotrophic methanogenesis also decreased with depth, while $\delta^{13}\text{C}$ of acetate stayed fairly constant. The contribution of hydrogenotrophic methanogenesis to total CH₄ production increased with depth from ~36% to 100%. Analysis of terminal restriction fragment polymorphism (T-RFLP) of archaeal 16S rRNA genes showed that the relative abundance of aceticlastic (*Methanosaetaceae*) methanogens also decreased with depth disappearing completely at 50 cm depth. Our study firstly showed that the methanogenic pathway and the methanogenic archaeal community systematically changed with sediment depth in a high altitude lake, probably controlled by the availability of easily degradable organic matter.

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1. Introduction

Methane emission from lakes contributes 6–16% to the atmospheric CH₄ budget (Bastviken et al., 2004, 2011). Hence, methanogenesis in profundal lake sediments is important for the global carbon cycle. However, the mechanisms involved in the microbial production of CH₄ in lake sediments are still not completely understood. Methane is a terminal product in the anaerobic degradation of organic matter. The anaerobic microbial community degrades organic matter originating from plant and algal material (e.g., carbohydrates) by hydrolysis to monomers and eventual fermentation to acetate, hydrogen and CO₂. These simple compounds then serve as main substrates for methanogenic archaea, which produce CH₄. Thus, CH₄ mainly originates from the dismutation of acetate (aceticlastic methanogenesis) and the reduction of CO₂ (hydrogenotrophic methanogenesis) (Liu and Whitman, 2008; Rudd and Taylor, 1980). The relative contribution of these two pathways to CH₄ production can be determined by isotope labeling, inhibitor studies and/or analysis of $\delta^{13}\text{C}$ (Conrad, 2005; Conrad and Schütz, 1988). Data show that contribution of hydrogenotrophic (f_{H_2}) or aceticlastic (f_{ac}) methanogenesis can vary between 0 and 100%

(Conrad, 1999). However, we do not yet fully understand how f is controlled by the environmental conditions.

Complete degradation of organic matter under methanogenic conditions theoretically results in the fermentative production of acetate, CO₂ and H₂, at such a stoichiometry that CH₄ should be produced by aceticlastic and hydrogenotrophic methanogenesis at a ratio of 2:1, i.e. $f_{\text{ac}} = 67\%$ and $f_{\text{H}_2} = 33\%$ (Conrad, 1999). The percentage contribution of aceticlastic methanogenesis can be greater (up to 100%), if acetate is produced by homoacetate fermentation (Conrad, 1999). Since homoacetogenesis is enhanced at low temperatures (Conrad et al., 1989; Nozhevnikova et al., 1994), it is not surprising that CH₄ production has been found to be dominated by aceticlastic methanogenesis in profundal lake sediments, since these sediments usually exhibit low temperatures (4–10 °C) (Glissmann et al., 2004; Phelps and Zeikus, 1985; Schulz and Conrad, 1996; Zepp-Falz et al., 1999). High temperatures (>40 °C), by contrast, were found to enhance syntrophic acetate oxidation, which is the reverse of homoacetate fermentation (Zinder, 1994) thus resulting in the conversion of acetate to H₂ plus CO₂ and the stimulation of f_{H_2} , which can reach 100% (Nozhevnikova et al., 2007; Conrad, 2002). Intermediate temperatures (20–35 °C) then often result in values of $f_{\text{H}_2} = 33\%$ as theoretically expected from the stoichiometric fermentation of polysaccharides (Fu et al., 2015; Glissmann et al., 2004; Schulz and Conrad, 1996).

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However, high temperatures ($>40\text{ }^{\circ}\text{C}$) are only realized under experimental conditions and do normally not occur in lake sediments, which are either cold or temperate. Nevertheless, recent studies in tropical but also temperate freshwater sediments often demonstrated a dominance of hydrogenotrophic methanogenesis (Conrad et al., 2010; Conrad et al., 2011; Conrad et al., 2014b; Nüsslein and Conrad, 2000). In fact, dominance of hydrogenotrophic methanogenesis has also been observed in cold lake sediments (Wand et al., 2006). Such dominance of hydrogenotrophic methanogenesis cannot be explained by regulation through temperature. Instead, the relatively high values of f_{H_2} may be caused by incomplete degradation of organic carbon in the sediments. Such incomplete degradation would circumvent the constraints imposed by stoichiometry and possibly result in production of relatively less acetate versus H_2 as methane precursor, thus increasing the proportion of hydrogenotrophic methanogenesis (Conrad et al., 2010). We further proposed a hypothesis that the proportion of hydrogenotrophic methanogenesis increases with sediment depth as age of organic matter increases. However, this hypothesis has yet only been confirmed for the sediment of a temperate lake (Chan et al., 2005).

Our recent study revealed that hydrogenotrophic methanogenesis was dominant in surface sediments of cold lakes from the Tibetan plateau (Liu et al., 2013). However, the surface sediment of one of the lakes, i.e. Bangong Co, was found to follow the theoretically expected pathway of CH_4 production with $f_{\text{H}_2} = 33\%$ (Liu et al., 2013). These results were obtained by measuring the $\delta^{13}\text{C}$ of CH_4 , CO_2 and acetate in the lake sediments and determining the pathway of CH_4 production from the relatively larger kinetic isotope effect of hydrogenotrophic versus aceticlastic methanogenesis (Conrad, 2005; Whiticar, 1999). Here we focused on the methanogenic pathway in Bangong Co as function of sediment depth. We determined the relative contribution of the methanogenic pathways to potential CH_4 production and analyzed the abundance and composition of the methanogenic archaeal communities in order to test our hypothesis.

2. Material and methods

2.1. Sampling sites and procedure

Bangong Co (Co is the Tibetan word for lake) ($33^{\circ}26' - 33^{\circ}58'\text{N}$, $78^{\circ}25' - 79^{\circ}56'\text{E}$) is an oligotrophic lake on the western Tibetan Plateau (Fig. 1). The western Tibetan Plateau is a cold desert, which lies

in the rain shadow of the Kunlun and Karakorum mountain ranges. The mean annual precipitation is 62 mm; the mean annual air temperature ranges from -4 to $-2\text{ }^{\circ}\text{C}$ (Wang and Dou, 1998). Bangong Co is in a long submerged valley and has a surface area of 604 km^2 . Its maximal depth (41.3 m) is near the eastern shore. There is a marked gradient in salinity from east to west across Bangong Co. The eastern part of the lake is fresh to oligosaline with a total dissolved salt content of 0.7 g L^{-1} (Wang and Dou, 1998). Salinity is 2.8 g L^{-1} in the middle part of the lake, and reaches 19.6 g L^{-1} in the west (Wang and Dou, 1998). Bangong Co is characterized by low primary production and little human influence. The average value of Chl *a* in the lake water is $2.6 \pm 5.7\text{ }\mu\text{g L}^{-1}$ ($n = 50$). There is no permanent human habitation, only pasturing during summer. The lake is covered with ice from the end of October to May.

In July 2010, three sediment cores (5 cm in diameter; 50 cm in length) were sampled using a gravity corer in the eastern basin at Site 1 (Fig. 1) at a water depth of 28 m. The cores were sliced into five subcores (S11, 0–9 cm; S12, 10–19 cm; S13, 20–29 cm; S14, 30–39 cm; S15, 40–50 cm) under a flow of N_2 . The slices of three cores were pooled together. The age of the sediment in 9, 19, 29, 39, 50 cm depth was 86, 244, 403, 561, and 738 years, respectively (Hou J. Z., 2016, personal communication). Sediment age for the uppermost 15 cm was constrained by ^{210}Pb and ^{137}Cs measurement. The lower parts were determined by measurement of the ^{14}C content of bulk organic carbon using accelerator mass spectrometry. In January 2011, three short sediment cores (5 cm in diameter; ~15 cm in length) from Site 2 (Fig. 1) were sampled immediately after ice break (~40 cm in thickness). The top 9 cm of the cores were pooled together. All samples were stored at $4\text{ }^{\circ}\text{C}$ until use in the Institute of Tibetan Plateau Research, Chinese Academy of Science, Beijing, China and in the Max Planck Institute for Terrestrial Microbiology, Marburg, Germany. All samples were analyzed within 2 weeks after sampling.

2.2. Incubation experiments

The potential for CH_4 production was measured by incubation experiments as described in Conrad et al. (2007). Briefly, about 10-mL aliquots (~3 g dry wt) of the sediment were transferred in triplicate to 27-mL sterile serum tubes. The exact amount of sediment was determined gravimetrically. The tubes were flushed with N_2 , closed with butyl rubber stoppers, and incubated at $10\text{ }^{\circ}\text{C}$ (in situ temperature is typically

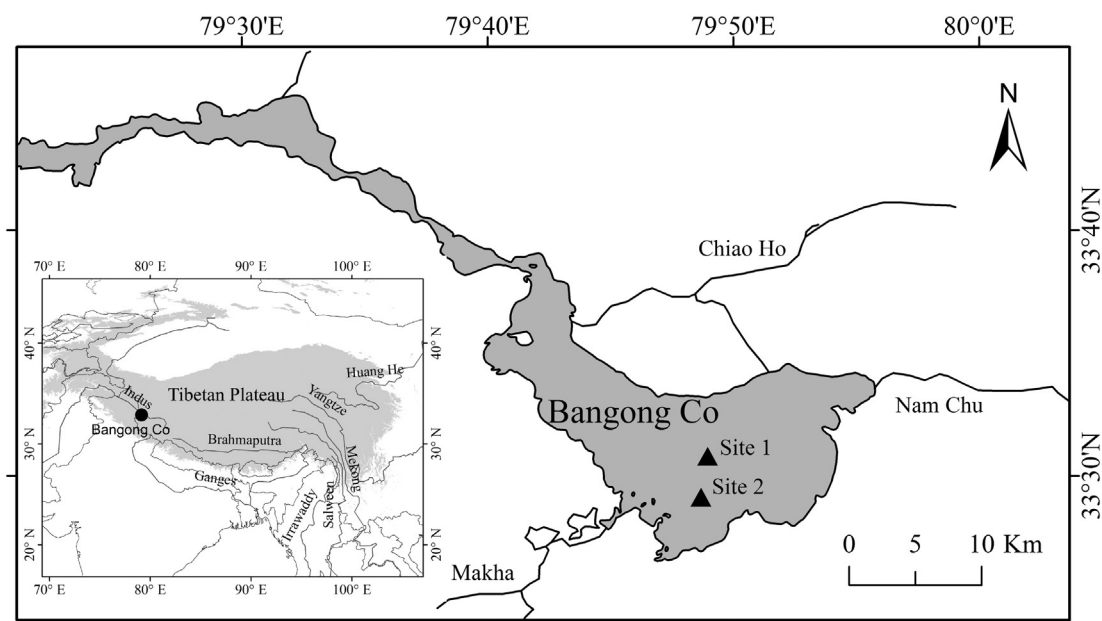


Fig. 1. Location of Bangong Co on the Tibetan Plateau and the sample sites in Bangong Co.

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