



Geographical pattern of methanogenesis in paddy and wetland soils across eastern China

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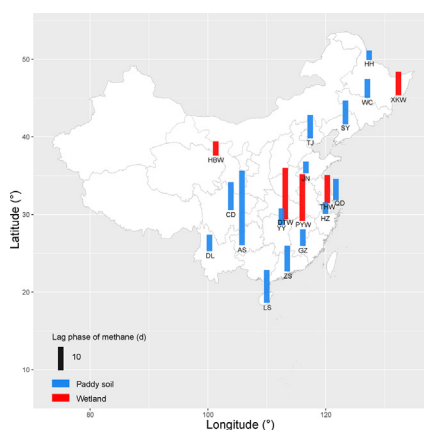
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HIGHLIGHTS

- Lag phase for soil methanogenesis increases from north to south in China.
- Depletion time of Fe(III) and sulfate positively correlated with methanogenesis lag phase.
- Geographical variations in methanogenesis are related to the soil pH variation.
- Greater temperature response for soil methanogenesis from south to north in China

GRAPHICAL ABSTRACT



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ABSTRACT

Large variation of CH₄ emissions from paddy and wetland ecosystems exists across different geographical locations in China. To obtain mechanistic understanding of this variation, we investigated the dynamics of methanogenesis over the course of glucose degradation in fourteen paddy field soils and five wetland soils collected from different regions of China. The results revealed that the maximal rate (2–3 mM per day) and the total amount (25–30 mM) of CH₄ produced were similar across soil samples. The lag phase of methanogenesis, however, differed substantially with the shortest lag phase of 4 days in a paddy soil from north China and the longest of 32 days in a soil from south China, and this difference reflected a general geographical trend among all soils tested. Nitrate was reduced completely within 4 days in all soils. The reduction of Fe(III) and sulfate was completed after 21 days and 29 days, respectively. The depletion time of Fe(III) and sulfate were positively correlated with the lag phase of methanogenesis. Competition for common substrates between methanogens and iron and sulfate reducers, however, does not explain this coincidence because a slow production of CH₄ was detected at the very beginning. It appears that the geographical variations in methanogenesis and the reduction of ferric iron and sulfate are related to the variation in soil pH but not to temperature, soil organic C and nutrient conditions in paddy and wetland soils across eastern China.

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1. Introduction

Methane is the second important greenhouse gas next to CO₂, with its atmospheric concentration approaching 1850 ppb in 2015, almost tripled since the preindustrial times (Saunois et al., 2016; Schaefer et al., 2016). Sources for global CH₄ emissions include natural wetlands, termites and gas hydrates and anthropogenic paddy fields, landfills, livestock, biomass burning and fossil fuel production (Menon et al., 2007). Rice cultivation has been practiced in Asian countries for a long history and presently accounts for over 90% of annual world rice production. As a result, the Asian paddy fields represent the most important contributor to the global methane emissions associated with rice production (Bhatia et al., 2013; Chen et al., 2013; Zhang et al., 2016).

Not only with a long history but rice cultivation is developed in Asia wherever the water availability is proper. Paddy fields are thus widespread geographically from low to high latitudes and from low to high altitudes. Albeit similar cultivation practice across different regions there exist large variations in landscapes, soil properties, climate conditions, farmer's managements, and cultivation histories. Consequently, large geographical variations in processes and functions of paddy ecosystems are expected. Among these processes, methanogenesis is of global change significance, and yet very little has been known. Understanding the geographical variation of CH₄ emissions and deciphering the underlined mechanisms shall help to shape a better knowledge for predicting and mitigating the CH₄ emissions.

Elucidating the biogeographical patterns of microbial communities has been a thematic focus in microbial ecology in recent years (Thompson et al., 2017). It has been recognized that the microbial community assembly is generally controlled by two types of ecological processes, i.e. stochastic and deterministic. How a particular community is formed in a given habitat depends on the balance of these processes. Dissecting the rates of various processes and estimating their contributions, however, remain as a hard task (Tripathi et al., 2018). Furthermore, many of previous studies on geographical distributions have been focused on total microbiomes with little attention paid on functional guilds (Nelson et al., 2016; Thompson et al., 2017). In fact, the elemental biogeochemical cycles are gauged mainly by the functional groups. To this end, though the large geographical difference in CH₄ emissions from paddy fields has been demonstrated (Yan et al., 2003), only a few studies have evaluated the biogeographical distribution of methanogenic archaea in various environments. These studies showed that methanogenic community composition was significantly related to geographic distance, salinity, pH, temperature, and nutrients (Zu et al., 2016; Wen et al., 2017; Zhang et al., 2018). Our preliminary study, however, revealed weak distance-decay relationship of methanogenic archaea in Chinese paddy field and wetland soils (Zhang et al., 2018). Moreover, the translation of methanogenic community into CH₄ production processes has yet to be established. Therefore, it is necessary to determine CH₄ production potentials of soils from different locations in order to predict the geographical variation of CH₄ emissions from paddy fields. In the present experiment, we collected fourteen paddy field soils across eastern China spanning a gradient of latitude from 18.6°N in south to 49.9°N in north. To increase the diversity of soil types for the evaluation of geographical pattern, five natural wetland soils were also collected. The paddy fields have intensively undergone anthropogenic activities, such as ploughing, fertilization and cyclic irrigation and drainage, whereas wetland is natural ecosystem with fewer disturbances of human being. The inclusion of wetland soils shall increase the robustness of geographical pattern if exists.

CH₄ production from anaerobic decomposition of organic matter is driven by a series of complicated microbial activities (Bridgman et al., 2013). Consequently, the pattern of methanogenesis is not only determined by the activity of methanogenic populations but also by the up-stream fermentation (Drake et al., 2009) and the activities of anaerobically respiring microbes using electron acceptors other than CO₂. In the latter case, competition for common substrates H₂ and

acetate has been considered to occur between methanogens and the respiring anaerobes. This concept was first proposed by Winfrey and Zeikus (1977) and later validated in multifarious anaerobic environments (King, 1984; Lovley and Goodwin, 1988). In the light of thermodynamic theory, the electron acceptors are reduced sequentially in the order of nitrate, Mn(IV), Fe(III), sulfate and CO₂ (Zehnder, 1988; Bridgman et al., 2013; Jelen et al., 2016). Consequently, methanogens are considered to be energetically most restricted and get activated only when those electron acceptors have been depleted (Lovley and Phillips, 1987; Thauer et al., 2008). It has been demonstrated that the addition of nitrate, sulfate and Fe(III) to active methane-producing soils suppressed methanogenesis (Acht nich et al., 1995a; Qu et al., 2004; Hori et al., 2009). However, if electron donor substrates are provided sufficiently, the different reduction processes may overlap and take place concomitantly (Acht nich et al., 1995a; Peters and Conrad, 1996; Megonigal et al., 2003).

We hypothesized that large geographical distance may imply large variations of not only methanogenesis but also the processes of fermentation and reductions of oxidants other than CO₂. To obtain a general understanding of methanogenesis, it is important to simultaneously analyze these processes. Therefore, the objectives of the present study were: i) to determine the dynamics of CH₄ production and the reduction of oxidative ions (sulfate, nitrate and ferric iron) in nineteen soils collected across eastern China; and ii) to identify the important factors influencing the variation of methane production across different soils. During the experiment, soil samples were anaerobically incubated under identical laboratory conditions and glucose was added as organic substrate.

2. Materials and methods

2.1. Soil sampling

Fourteen rice paddy soils and five wetlands samples were collected during the time from July to September in 2016 from different regions of China, with sample name abbreviation and geographic information listed in Table 1. At each site, five soil cores (0–20 cm in depth) with a distance of at least 5 m away from each other were collected, mixed thoroughly, and placed in ziplock plastic bags. Soil samples were shipped to lab within 24 h and stored at 4 °C. The chemical properties of the soils, including pH, total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), inorganic nitrogen (NO₃⁻-N and NH₄⁺-N), available phosphorus (AP) and available potassium (AK) were measured using the standard soil testing procedures (Bao, 2000).

2.2. Soil slurries preparation and incubation

For anaerobic incubation, soil samples were taken out from refrigerator and allowed for 24 h recovery under room temperature. The soil samples were then suspended with autoclaved degassed water at a soil-water-ratio of 1:5 (1 g dry weight soil plus 5 ml autoclaved degassed water). Aliquots (20 ml) of homogenized soil slurry were transferred into 60 ml sterile serum bottles. Glucose (10 mM) was added into the bottles to serve as organic substrate. Bottles were evacuated and flushed with N₂ at constant pressure for about 5 min and then capped with black butyl rubber stoppers and aluminum crimps. The bottles were vigorously shaken by hand to homogenize the soil slurry and then incubated under the dark at 30 °C without shaking. The incubation was set up with 40 to 60 replicates. At the predetermined time intervals, four replicates were sacrificed for the destructive sampling of soil slurries for chemical analyses as described below.

2.3. Chemical analyses

Methane was analyzed by Agilent 7890B gas chromatography using a flame ionization detector (Zhang and Lu, 2016). Gas samples (0.1 ml)

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