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Factors regulating community composition of methanogens and sulfate-reducing bacteria in brackish marsh sediments in the Min River estuary, southeastern China

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ABSTRACT

Assessing the diverse communities of methanogenic *Archaea* and sulfate-reducing bacteria (SRB) is important to understand methane (CH_4) production in wetland ecosystems. However, the vertical distribution of composition and diversity, and the effects of environmental factors on the methanogen and SRB communities in the sediments of subtropical estuarine brackish marshes have been poorly characterized. To assess the effects of variable environmental conditions on methanogenic and SRB communities in marshes, we studied three brackish marsh zones dominated by *Phragmites australis*, *Cyperus malaccensis* and *Spartina alterniflora*, respectively, in the Min River estuary, southeastern China. Methanogens of the Methanomicrobiales order was the dominant group at sediment depths of 0–30 cm, which indicated that the main pathway of methane production was H_2/CO_2 in this zone. In general, methanogens of the genus *Methanoregula* were dominant in the three marsh zones. For SRB, Desulfobacterales was the dominant group, and *Desulfobacterium* and *Desulfosarcina* were the predominant genera at the depth of 0–30 cm. The community composition of methanogens and SRB changed with vegetation type and soil depth. Compared with SRB, vegetation type demonstrated a stronger influence on the community composition of methanogens. Canonical correspondence analysis (CCA) analysis further revealed that the main factors affecting the methanogens community composition were EC (electric conductivity) and pH, and the main factors affecting SRB community composition were pH, SOC and TN, suggesting that pH is a common factor influencing the community compositions of both methanogen and SRB in the sediments of brackish marshes.

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1. Introduction

Methanogenesis represents a key process in the terminal phases of anaerobic organic matter mineralization in wetlands. In anoxic estuarine marsh sediments, methanogens, in cooperation with other microbes, produce methane as the end-product of their metabolism (Garcia et al., 2000; Liu and William, 2008). In addition to methanogenesis, sulfate reduction also plays a key role in the terminal phases of anaerobic organic matter mineralization in estuarine marshes (Jorgensen, 1982; Fukui et al., 1997). Sulfate-reducing bacteria (SRB) coexist with methanogens and compete with methanogens for such substrates as acetate and hydrogen (Nedwell et al., 2004; Winfrey and Ward, 1983; Oremland et al., 1982; Holmer and Kristensen, 1994). Sulfate reduction has also been identified as the key factor related to the methanogens distribution (Munson et al., 1997; Purdy et al., 2002, 2003). Numerous studies determining methanogen and SRB community composition have been performed across different wetland types including peatlands, or high altitude wetlands, rice soils, marine sediments, and salt marshes (Galand et al., 2005a,b; Cadillo-Quiroz et al., 2008; Ramakrishnan et al., 2001; Liu et al., 2009; Zhang et al., 2008;

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Blazejak and Schippers, 2011; Yuan et al., 2014; Klepac-Ceraj et al., 2004), but relatively few studies have reported on tidal estuarine wetlands (Zeleke et al., 2013; Torres-Alvarado Mdel et al., 2013), especially in subtropical brackish tide marshes.

The Shanyutan is the largest tidal wetland located in the mouth of the Min River estuary in southeastern China. In its west section, three macrophyte marsh zones are dominated respectively by native species *Phragmites australis*, *Cyperus malaccensis* Lam. var. *brevifolius* Bocklr. and the invasive plant *Spartina alterniflora* from the dam to the sea. Several studies concerning nutrient stocks and litter decomposition (Tong et al., 2011a,b) and methane fluxes (Tong et al., 2010) were conducted in the Shanyutan wetland. However, methanogen and SRB composition and diversity in this estuarine wetland have not been studied, and which environmental factors control the community compositions also remains unclear. Previous studies have demonstrated a link between biotic and abiotic environmental factors (such as vegetation type or soil pH) and methanogens (or SRB) in peatlands and salt marshes (Tian et al., 2012; Galand et al., 2003; Juottonen et al., 2005; Cadillo-Quiroz et al., 2006; Kotiaho et al., 2010; Nie et al., 2009; Moreau et al., 2010), but little is known regarding how methanogen and SRB communities are linked with environmental factors in tidal estuarine marshes (Nie et al., 2009; Zeleke et al., 2013). It is urgent to characterize methanogen and SRB communities in tidal estuarine marshes to understand how their communities respond to environmental and biogeochemical factors in this area.

The first objective of the current study was to reveal the vertical pattern of composition and diversity of methanogens and SRB communities in three different marsh vegetation zones dominated respectively by *P. australis*, *C. malaccensis* and *S. alterniflora* within the Min River estuary. The compositions of methanogen and SRB communities were evaluated by restriction fragment length polymorphism (RFLP) analysis of functional genes, including *mcrA* (Methyl coenzyme M reductase) and *dsrAB* (dissimilatory sulfite reductase). The second objective was to determine which environmental factors are more likely to regulate the community compositions of methanogen and SRB at a subtropical brackish marsh landscape in the Min River estuary.

2. Materials and methods

2.1. Study site and sample collection

This work was conducted in the Shanyutan, the largest tidal wetland (ca. 3120 ha) in the Min River estuary in southeastern China. The climate is relatively warm and wet, with a mean annual temperature of 19.6 °C and a mean annual precipitation of ca. 1350 mm (Tong et al., 2010). Tides are semi-diurnal. The study site was located in the west section of the Shanyutan, consisted of three macrophytes marsh zones dominated by native species *P. australis*, *C. malaccensis* and the invasive plant *S. alterniflora* from the dam to the sea (Fig. 1), with mean relative elevations of 1.5, 0.5 and 1.0 m above sea level, respectively. The maximum height of *C. malaccensis* was 1.5 m tall, and the heights of *P. australis* and *S. alterniflora* were approximately 2 m tall. Soil texture was characterized by silt soil in the three vegetation zones; the percentages of silt soil in the depth of 30 cm were 63.3, 60.6 and 59.2% in the *P. australis*, *S. alterniflora* and *C. malaccensis* marsh zone, respectively, and the total soil organic carbon contents of the soil (0–30 cm) were 22.3, 15.5 and 15.6 g kg^{-1} and the soil total nitrogen contents (0–30 cm) were 0.83, 0.59 and 0.58 g kg^{-1} in the three marsh zones (Tong et al., 2015).

A sampling line transect crossing the three marsh zones was made. In the middle of the transect within each marsh zone (*P. australis*: 26°01′55″N, 119°36′59″W; *C. malaccensis*: 26°01′58″N, 119°37′02″W and *S. alterniflora*: 26°02′01″N, 119°37′04″W) (Fig. 1), we established three quadrats (1 m × 1 m) at intervals of 5 m on a line parallel to the dam. Soil samples were collected on a neap tide day in May 2011. Within the center of each quadrat two sediment cores were collected using steel soil samplers (d = 5 cm), first core was split into three depths of 0–10, 10–20 and 20–30 cm, second core was split into six depths of 0–5, 5–10, 10–15, 15–20, 20–25 and 25–30 cm. The first core were immediately stored in sterile bags and kept on ice in coolers and transported to the laboratory within 6 h. Upon arriving at the laboratory, soil samples were immediately processed for DNA extraction. The second cores, for measuring sediment physical and chemical properties, were sealed in plastics bags and also were transported to the laboratory within 6 h.

2.2. DNA extraction and PCR amplification

10 cm soil column of the sample was fully mixed to form a composite representation of the sampled soil column and 0.25 g of the soil sample were picked randomly three times, respectively, for DNA extraction. Finally, the three extractions of DNA were pooled in a single tube for subsequent analysis. DNA was extracted using Power Soil DNA Extraction Kits (MoBio Laboratory, USA) according to the manufacturer's instructions. Briefly, 0.25 g fresh marsh soil was added to the PowerBead Tubes provided. Subsequently, the cells were lysed by a combination of detergents and mechanical disruption. The released DNA was bound to a silica spin filter. The filter was washed and the DNA was recovered in Solution C6. The extracted DNA was evaluated on a 1% agarose gel in 1 × TAE buffer after staining with ethidium bromide. The concentration and purity of the extracted DNA were estimated by spectrophotometry (NanoDrop, USA).

The *mcrA* genes were PCR-amplified with ME1 (5′-GCMATGCARATHGGWATGTC-3′) and ME2 (5′-TCATKGCRTAGTTDGGRTAGT-3′) primer sets as previously described (Hales et al., 1996), producing a 760 bp fragment. Amplification was performed in a 50 μl final volume with 5 μl 10 × PCR buffer, 4 μl 2.5 mM dNTPs, 0.5 μl Taq polymerase (5 U μl^{-1}) (Takara, Japan), 1.5 μl of each primer (final concentration of 0.3 μM), and 20 ng of extracted DNA. The amplification reaction was conducted as follows: 5 min at 94 °C, 33 cycles at 94 °C for 45 s, 50 °C for 45 s and 72 °C for 1.5 min, and a final extension at 72 °C for 7 min. The PCR products were confirmed by a 1% agarose gel electrophoresis and purified with the Wizard SV Gel and PCR Clean-Up System (Promega, USA).

The *dsrAB* genes were PCR-amplified with DSR1F (5′-AC[C/G]CACTGGAAGCACG-3′) and DSR4R (5′-GTGTAGCAGTTACCGCA-3′) primer sets as previously described (Wagner et al., 1998), producing a 1900 bp fragment. Amplification was performed in a 50 μl final volume with 5 μl 10 × PCR buffer, 4 μl 2.5 mM dNTPs, 0.5 μl Taq polymerase (5 U μl^{-1}) (Takara, Japan), 1.5 μl of each primer (final concentration of 0.3 μM), and 20 ng of extracted DNA. The amplification reaction was conducted as follows: 5 min at 94 °C, 33 cycles at 94 °C for 45 s, 58 °C for 45 s and 72 °C for 2.5 min, and a final extension at 72 °C for 7 min. The PCR was performed using a Gene Amp PCR System 2700 (Applied Biosystems, USA). The PCR products were also confirmed by a 1% agarose gel electrophoresis and purified with the Wizard SV Gel and PCR Clean-Up System (Promega, USA).

2.3. Construction of mcrA and dsrAB gene clone libraries and RFLP analysis

The *mcrA* and *dsrAB* clone libraries of the purified PCR products of all samples were constructed using the pMD-18T Vector Systems (Takara, Japan), and *E. coli* DH5α was transformed as competent

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