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Variability of soil organic carbon reservation capability between coastal salt marsh and riverside freshwater wetland in Chongming Dongtan and its microbial mechanism

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Abstract

Two representative zones in Chongming Dongtan which faced the Yangtze River and East China Sea respectively were selected to study the variability of soil organic carbon (SOC) reservation capability between coastal wetland and riverside wetland in the Chongming Dongtan wetland as well as its mechanism by analyzing soil characteristics and plant biomass. The results showed the SOC content of riverside wetland was only 48.61% ($P = 0.000 < 0.05$) that of coastal wetland. As the organic matter inputs from plant litter of the coastal wetland and riverside wetland were approximately the same, the higher soil microbial respiration (SMR) of riverside wetland led to its lower SOC reservation capability. In the riverside wetland, the high soil microbial biomass, higher proportion of β-Proteobacteria, which have strong carbon metabolism activity and the existence of some specific aerobic heterotrophic bacteria such as *Bacilli* and uncultured *Lactococcus*, were the important reasons for the higher SMR compared to the coastal wetland. There were additional differences in soil physical and chemical characteristics between the coastal wetland and riverside wetlands. Path analysis of predominant bacteria and microbial biomass showed that soil salinity influenced β-Proteobacteria and microbial biomass most negatively among these physical and chemical factors. Therefore the low salinity of the riverside area was suitable for the growth of microorganisms, especially β-Proteobacteria and some specific bacteria, which led to the high SMR and low SOC reservation capability when compared to the coastal area.

Key words: soil organic carbon; carbon reservation capability; community diversity; coastal wetland; riverside wetland; Chongming Dongtan

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Introduction

Soil is an important carbon pool which plays a significant role in the global carbon cycle. The global soil carbon pool of 2500 gigatons (Gtons) includes about 1550 Gtons of soil organic carbon (SOC) and 950 Gtons of soil inorganic carbon (SIC), and the soil carbon pool is 3.3 times the size of the atmosphere pool (760 Gtons) and 4.5 times the size of the biotic pool (560 Gtons) (Lal, 2004). The soil carbon pool has a dynamic balance with the atmosphere pool as well, such that a 1% decrease in the soil organic matter of the land will lead to an increase of atmospheric carbon dioxide by 5 mg/kg (Mullen et al., 1999).

Wetlands, which are known for their high productivity, low decomposition rate and soil respiration resulting from their long flooded time (Gorham, 1991; Whitting and Chanton, 2001), only cover 2%–6% of the earth's surface (Aselmann and Crutzen, 1989; Matthews and Fung, 1987; Mitsch and Gosselink, 1993), but contain a large amount of the stored organic carbon. The SOC pool in wetlands is about one-third of the total SOC pool (Bernal and Mitsch, 2008). Therefore, wetland ecosystems have important ecological and environmental functions such as atmospheric regulation (Mitsch and Gosselink, 2000) and play an important role as natural carbon sinks (Bernal and Mitsch, 2008; Whitting and Chanton, 2001) in global warming caused by greenhouse gas emission. However, many previous studies about the carbon storage of wetlands have focused on inland and freshwater wetlands, especially inland alpine wetlands. These wetlands usually experience high SOC accumulation caused by a low rate of succession and thus long growth history (Peña et al., 2009; Turunen et al., 2002; Euliss et al., 2006). Few studies on carbon reservation in coastal salt marsh wetland soils have been reported before. This may be due to coastal wetlands' quick succession and thus short growth history which results in low SOC content (Chmura et al., 2003).

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Generally, coastal wetlands are characterized by high biodiversity and rates of primary productivity (Perry and Atkinson, 2009; D'Alpaos, 2011), so their accumulation rate of organic carbon should be high as well. With the heightening global warming, many scholars have begun to focus on the soil carbon pool or SOC sequestration of salt marsh wetlands (Elsey-Quirk et al., 2011; Li et al., 2010). However, compared to the freshwater wetlands in the same latitude, the question of whether the carbon accumulation rate and reservation capability of salt marsh wetlands are higher has not been examined in detail.

Chongming Dongtan is an internationally important young tidal wetland located at the Yangtze River Estuary, with the Yangtze River to the southeast and East China Sea to the northeast. Therefore the salinity of the tide in the two different zones is quite different. Many previous studies on Chongming Dongtan focused on the effect of *Spartina alterniflora* invasion on bacterial communities (Nie et al., 2009), as well as biodiversity conservation (Chen et al., 2005) and the efficiencies of control technology for *S. alterniflora* (Li and Zhang, 2008). There were also many studies concerning soil carbon content and the capability for soil carbon sequestration (Li et al., 2010; Zhang et al., 2011; Guo et al., 2009a). But as a wetland with a coastal area and riverside area, whether there is variability in the capability of soil carbon reservation between these two areas has not been reported in detail.

Therefore, the objective of the current study was to illustrate the variability of soil carbon reservation capability between a coastal wetland and riverside wetland in the Chongming Dongtan wetland and its microbial mechanism. Two representative zones which faced the Yangtze River and East China Sea respectively were sampled periodically to obtain information regarding: (1) variability of SOC reservation capability between coastal/riverside wetlands; (2) the physicochemical and microbial mechanism of the variation in the SOC reservation capability. Consequently, the results will provide theoretical directions toward the dynamic protection and reasonable development of Chongming Dongtan wetlands in view of the carbon sink capability of the wetlands.

1 Materials and methods

1.1 Study areas

Chongming Dongtan wetland, the largest and youngest tidal flat, is located in the east of Chongming Island (121°050′E–122°005′E, 31°025′N–31°038′N) (Fig. 1), China, and it has a northern subtropical ocean climate with an average annual temperature of 15°C and precipitation of 1117.1 mm. The vegetation area of the tidal flat covers 27.51 km^2, and the vegetation previously included mainly *Phragmites communis* and *Scirpus mariqueter*. However, with its recent rapid spread and growth, the invasive *S. alterniflora* has occupied 33.1% of the vegetation area, mainly distributed in the northeast part of Chongming Dongtan (Li et al., 2006).

1.2 Study zones and soil sampling

Two zones of typical natural wetlands (Areas A and B) were selected as the study areas due to the different water properties after an in-depth field survey. Area A, located at Tuanjiesha of Chongming Dongtan (31°27′1.88″N–121°53′40.03″E), was selected as the riverside wetland because this area is beside the Yangtze River (Fig. 1), and the water salinity is low. The soil of Area A was characterized by sandy soil (Zhou et al., 2007; Yang, 1990) and contains only *P. communis*. Area B, located at Dongwangsha of Chongming Dongtan (31°34′46.00″N–121°54′28.16″E), was selected as the coastal wetland because this area is at the side of East China Sea (Fig. 1), and the water salinity is higher compared with Area A. The soil of Area B was characterized by saline-alkaline clay soil (Zhou et al., 2007; Yang, 1990) and contains *P. communis*, *S. alterniflora* and *S. mariqueter*.

Three parallel transects were set up at Area A and Area B (Fig. 1) with an interval of approximately 100 m. Three sampling sites, from A1 to A3, B1 to B3 (Fig. 1), with a distance of about 100–200 m between each two adjoining sampling points, were set up along each transect from the levee to the sea. Approximately 1 kg soil was collected following standard sampling methods (Pennock et al., 2007) in April (spring), July (summer), September

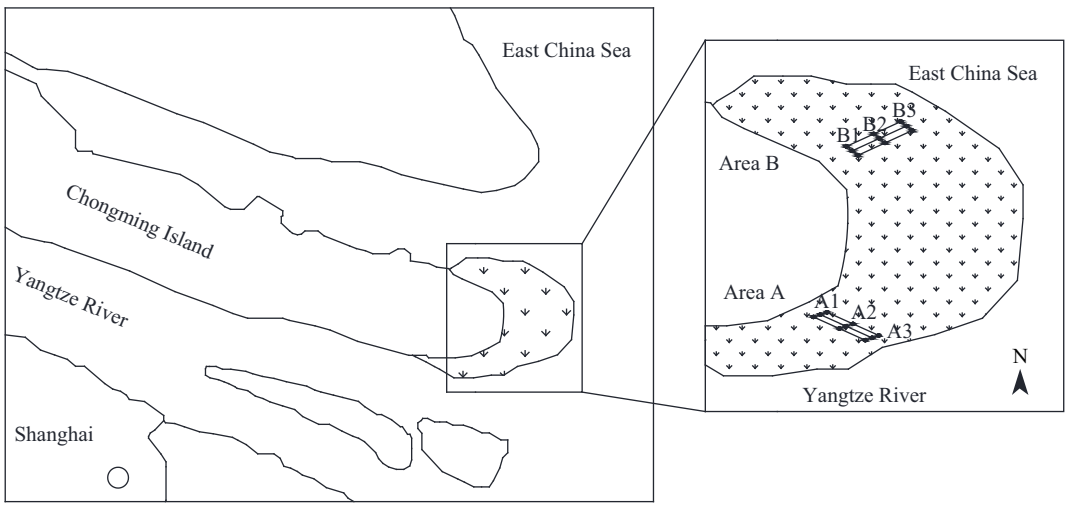

Fig. 1 Map of study areas at Dongtan of Chongming Island.

(autumn), and December (winter) of 2008, and all soil samples were taken from the subsurface layer (–5~–20 cm). After sampling, all the samples were transported to the laboratory immediately. Part of the soil was air-dried and ground, then was sieved < 0.25 mm for the assay of the organic carbon content, and invertase activity (EC 3.2.1.26), part of the soil was stored at –70°C for subsequent DNA extraction and molecular analysis, and the remainder was stored at 4°C until subsequent assays. Some soil physicochemical properties were analyzed in a previous study (Li et al., 2010) and the general description is shown in Table 1.

1.3 Analysis methods

1.3.1 Routine analysis

The SOC was measured with a total organic carbon analyzer (TOC-VCPN, Shimadzu, Japan) while maintaining accuracy within 5%. The soil microbial biomass (SMB) was estimated based on ATP levels, which were measured using an improved bioluminescent method as previously described (Nakatsu et al., 2006). Soil catalase activity (EC1.11.1.6) was determined by measuring the oxygen absorbed by potassium permanganate after the addition of hydrogen peroxide to the samples (Rodríguez-Kábana and Truelove, 1982). Soil invertase activity (EC 3.2.1.26) was monitored using sodium thiosulfate (Zhou, 1987).

1.3.2 Soil microbial respiration (SMR)

After adjusting to 60% water holding capacity (Howard and Howard, 1993), CO_2 decomposed and released by microorganisms from 25 g original fresh soil samples incubated in 250 mL serum bottles during 24 hr at 28°C was measured by gas chromatography (GC-14B, Shimadzu, Japan) with a stainless steel column (10 m × 2 mm) and a TCD detector (Orchard and Cook, 1983; Yao and Huang, 2006). The column temperature, inlet temperature and detector temperature were 40, 40 and 90°C, respectively. Nitrogen gas was used as the carrier at a flow rate of 30 mL/min. The CO_2 injection volume was 0.2 mL and the CO_2 released per unit of time from microorganisms that were in the period between the adaptation phase and the logarithmic growth phase was assayed and reported as the SMR.

1.3.3 DGGE and gel pattern analysis

The microbial diversity in the soil was measured by 16S rDNA fingerprinting. Total DNA was extracted using an E.Z.N.A.® Soil DNA kit (50) according to the manufacturer's instructions (Omega Bio-Tec, Inc., USA). DNA extraction was visualized on 1% agarose gels, and then stored at –20°C for PCR-DGGE analyses. The 16S rDNA V3 region was then amplified by PCR using the total soil DNA extraction as the template and the universal primers 341f-GC and 534r (Table 2). The primers were produced by Shanghai Sangon Biological Engineering Technology and Services Company, China. The reaction was conducted by subjecting the samples to 94°C for 3 min followed by 30 cycles of 94°C for 30 sec, 56°C for 30 sec, 72°C for 30 sec and a 72°C extension for 10 min, followed by cooling to 4°C. PCR products were analyzed by 0.8% agarose gel electrophoresis followed by staining with ethidium bromide to confirm their sizes.

Denaturing gradient gel electrophoresis (DGGE) profile analysis can be used to reveal differences in the composition of microbial communities, although the bands in that profile represent only the dominant microbial populations (Muyzer et al., 1993). DGGE was conducted using the D-Code system (Bio-Rad, USA) with 10% polyacrylamide gel and a 40%–65% denaturing gradient (100% denaturing was equivalent to 7 mol/L urea and 40% deionized formamide). There was 800 ng of PCR product in each lane and the electrophoresis conditions were as follows: 60°C, 80 V, 1× TAE buffer, 16 hr. The results were photographed after ethidium bromide staining for 10 min upon completion of the electrophoresis.

Table 1 Soil physicochemical properties of the two areas

Wetland	Salinity (g/kg)[a]	Moisture (%)[a]	TN (mg/kg)	AP (mg/kg)
Area A	0.47 ± 0.05	23 ± 2	135.11 ± 42.06	4.39 ± 0.47
Area B	5.06 ± 0.52	33 ± 6	306.00 ± 56.24	6.64 ± 0.33
A/B	0.09	0.70	0.44	0.66

TN: total nitrogen; AP: available phosphorus.
Available phosphorous was determined based on the Olsen method (Olsen et al., 1954). Total nitrogen was assayed with the routine method (Du and Gao, 2006).
All data are expressed as mean ± SD. [a]Data from Li et al. (2010).

Table 2 Primer sequences used for PCR-amplification of 16S rDNA fragments

Primer	Sequence 5′–3′ (target 16S rDNA)	Reference
F203[ac]	CCGCATACGCCCTACGGGGGAAAGATTTAT	Gomes et al., 2001
R534[ac]	ATTACCGCGGCTGCTGG	Muyzer et al., 1993
F341[abc]	CCTACGGGAGGCAGCAG	Muyzer et al., 1993
F948[ac]	CGCACAAGCGGTGGATGA	Gomes et al., 2001
R685[ac]	TCTACGCATTTCACC/TGCTAC	Lane, 1991
R1401[ac]	CGGTGTGTACAAGACCC	Erardi et al., 1987

[a] F and R designations indicate forward and reverse primers respectively; [b] typically used with a GC clamp for DGGE analysis in combination with F341; GC clamp CGCCCGCCGCGCGCGGCGGGCGGGGCGGGGGCACGGGGG; [c] the special primers 203f/534r, 948f/1401r, 341f/685r for α-, β-, γ-Proteobacteria, respectively.

1.3.4 Sequencing of excised bands and phylogenetic analysis

An individual band excised with a razor blade was eluted in 40 μL distilled-deionized water (4°C overnight). Each supernatant (1 μL) was used as the PCR template with the 341f and 534r primers (without GC clamp) (Table 2). Prior to cloning into the pMD18-T Easy Vector System (Takara Biotechnology, Japan), the PCR products were purified with a purification kit (Biodev-Tech Co., Ltd., Beijing, China) according to the manufacturer's instructions. Four clones from each DGGE band were selected at random for sequencing (Invitrogen, Shanghai, China). The resulting sequences were then submitted to the GenBank database using BLAST (Basic Local Alignment Search Tool) to search for homologues.

1.3.5 Real-time quantitative PCR assay

The abundances of α-Proteobacteria, β-Proteobacteria and γ-Proteobacteria were determined by quantifying the copy number of α-Proteobacteria, β-Proteobacteria and γ-Proteobacteria 16S rDNA using real-time quantitative PCR, which was conducted on a Rotor Gene 3000 thermal cycler (Corbett Research, Australia). All primers shown in Table 2 were produced by the Shanghai Sangon Biological Engineering Co., China. Real-time quantitative PCR was conducted in a 25 μL reaction mixture that contained 12.5 μL of SYBR Premix Ex Tag™ (Perfect real time) (Takara Biotechnology, Japan), 0.5 μL of each primer (10 μmol/L) and 1.5 μL of 50-fold diluted extracted DNA (1–5 ng) as the template. Real-time quantitative PCR was conducted by subjecting the reaction mixture to the following conditions: 1 min at 95°C for initial denaturation, followed by 40 cycles of 15 sec at 95°C and 30 sec at 55°C. SYBR Green I (Takara, Japan) assays were conducted using melting curve analysis to ensure the specificity of the products. A standard curve for each primer was created using 10-fold dilution series of triplicate linearized plasmids containing the α-Proteobacteria, β-Proteobacteria and γ-Proteobacteria from environmental samples with a known number of target gene copies. Triplicate analyses of each sample were performed on a single plate and the standard error was calculated.

1.4 Statistical analysis

Statistical analyses were conducted using one way ANOVA and LSD's multiple-comparison tests with the SPSS software (version 11.5, SPSS Inc.). Errors were indicated as the standard deviation (SD) of the mean of triplicate parallel sampling of every site. The DGGE fingerprints were analyzed with Smartview software and soil microbial diversity was expressed by the Shannon Index (H, Shannon and Weaver, 1963), which is as follows:

$$H = -\sum_{i=1}^{S} P_i \ln P_i \quad (1)$$

where, S is the numbers of bands in the gel, and P_i is the relative abundance of the ith phenotype fraction. The DGGE profiles were analyzed with the UPGMA method (unweighted pair-group method with arithmetic mean) using Quantity One software to determine the clustering similarity of soil microorganisms in different samples. The phylogenetic tree of 16S rDNA sequences was performed using MEGA 4 software (MEGA, molecular evolutionary genetics analysis). The Path Analysis was performed with DPS 9.50. The amplification efficiency of realtime quantitative PCR was calculated based on the slope of the standard curve. Copy numbers were log-transformed to normalize the values prior to statistical analysis and ANOVA analysis was used. In addition, Statistica 8.0 software was employed to conduct principal component analysis of the different microbial parameters in response to variations in soil respiration.

2 Results and discussion

2.1 Variability of SOC reservation capability between coastal wetland and riverside wetland

SOC consists of all vegetation and animal residues and various organic substances decomposed by microorganisms in the soil, and it reflects the balance of the organic matter inputs (from the death of plants and animals) and organic matter outputs (dominated by soil respiration) (Davidson and Janssens, 2006). The results showed that the mean SOC content at Area A was 4.00 g/kg, while it was 8.23 g/kg at Area B. In another words, the organic carbon content at Area A throughout the year was only 48.61% ($P = 0.000 < 0.05$) of that at Area B (Fig. 2).

According to the earlier research, the average annual dry weight of the aboveground biomass from *P. communis* and *S. alterniflora* in Chongming Dongtan wetlands was 1.74 and 2.08 kg/m^2 respectively (Chen, 2006; Li et al., 2010). If the proportion of *P. communis* and *S. alterniflora* were 1:1 in Area B, the average theoretical organic matter inputs of Area A and Area B were 1.74 and 1.91 kg/m^2 respectively. Consequently the theoretical organic matter inputs from vegetation residues can be considered approximately

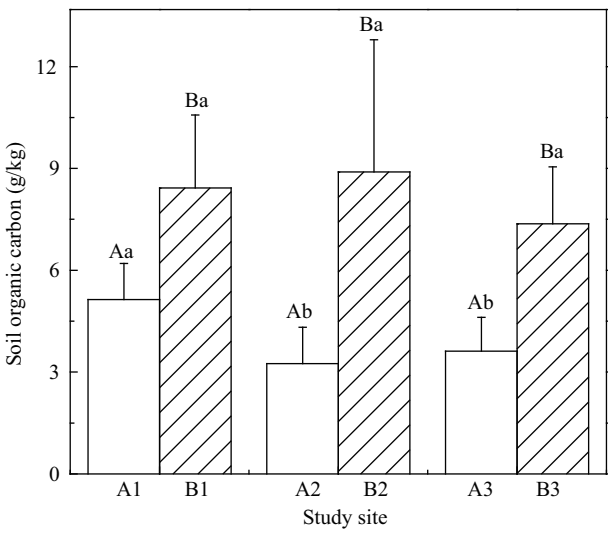

Fig. 2 Soil organic carbon of the study areas (mean ± SD). Different capital letters above the error bar represent significant difference between two areas at the 0.05 level (the same below); different lower-case letters above the error bar represent significant difference among three sampling sites on each area at the 0.05 level (the same below).

the same between Area A and Area B. This indicated that the organic carbon output of Area A should have been high. Outputs are dominated by soil respiration (Davidson and Janssens, 2006) and SMR is an important part of soil respiration (Fang and Wang, 2007). Accordingly the SMR of both areas was assayed. As shown in Fig. 3, the mean SMR of Area A was 10.62% (P = 0.599 > 0.05) higher than that of Area B. Therefore, with the similar inputs, the higher SMR (outputs) in Area A mainly led to the lower SOC reservation capability of riverside wetland. In other words, the SMR is the most important cause of the variability of SOC reservation capability between Area A and Area B.

Soil enzyme activities can also reflect soil microbial activities and interrelate with SMR (Guo et al., 2009b; Blagodatskaya and Kuzyakov, 2008). The activity of catalase and invertase which are associated with the carbon metabolism (Lagomarsino et al., 2009) were assayed in Area A and Area B. Throughout the year, the mean catalase activity of Area A was 49.04% (P = 0.033 < 0.05) higher than that of Area B, and the invertase activity was 32.33% (P = 0.047 < 0.05) higher (Fig. 4). The results of catalase and invertase activity between Area A and Area B were similar to the SMR as shown in Fig. 3. Therefore, compared to Area B, Area A had higher soil enzyme activities, hence higher microbial respiration.

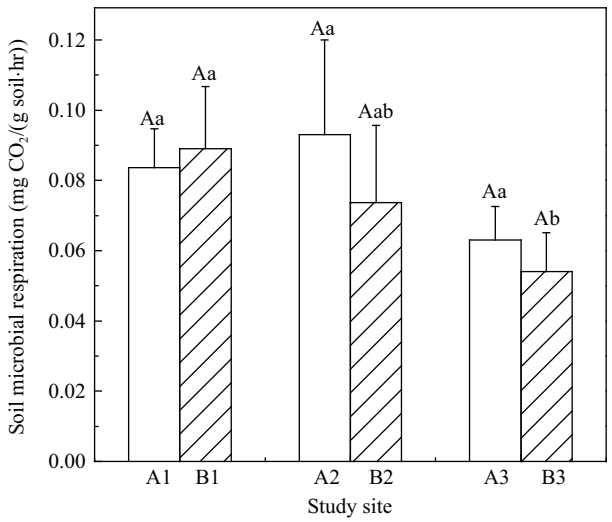

Fig. 3 Soil microbial respiration of the study areas (mean ± SD).

2.2 Variability of SMB and community structure between coastal/riverside wetland and its influence to the SMR

Soil microorganisms are the major producer of soil active enzymes and contribute substantially to the soil respiration (Sall et al., 2006). The SMB and soil microflora structure in both areas were studied to clarify the microbial mechanism of the variability of soil enzyme activities and SMR. Figure 5 shows the SMB comparison of Area A and Area B. The results revealed that the SMB of Area A is 2.46 (P = 0.054 > 0.05) times higher than that of Area B. Generally, the SOC content is higher where the SMB is higher (Hao et al., 2008). However our result is the opposite. The probable reason may be that in the study by Hao et al. (2008), the organic matter inputs in different sites had significant differences. The larger the inputs are, the higher the SOC content will be, leading to the higher SMB. But in our study, the organic matter inputs between Area A and Area B were almost the same. The higher SMB in Area A revealed that the soil properties of Area A were more suitable for the growth of microorganisms than Area B. Consequently it was more conducive for the transformation of soil organic matter into carbon dioxide (outputs) and microbial cells, which led to the decrease of SOC content and increase of microbial biomass.

Besides SMB, the soil microbial community structure is also a key factor that affects soil enzyme activities, as well as the SMR (Gao et al., 2010; Bending et al., 2002). DGGE analysis indicated that the microbial community structure differed between Area A and Area B (Fig. 6). UPGMA analysis of DGGE profiles (Fig. 7) revealed that the microflora of both areas clearly belonged to two different groups with the exception of A2. The Shannon index based on the results in Fig. 6 for each sampling point is shown in Table 3. The results indicate that in general the diversity in Area A was lower than that in Area B. The possible reason may be that there were some abundant species of bacteria with powerful carbon metabolism

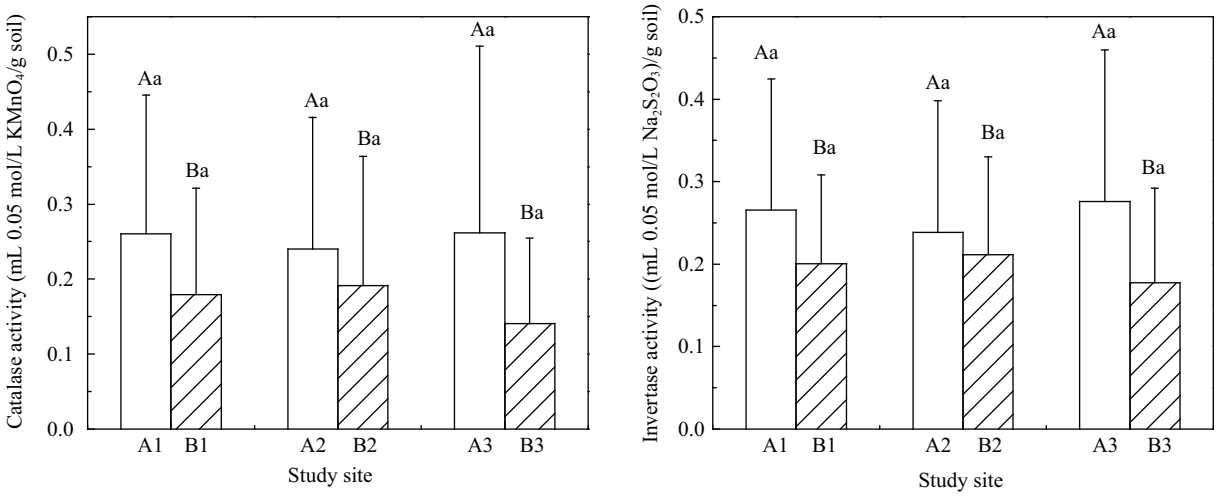

Fig. 4 Enzyme activities of the study areas (mean ± SD).

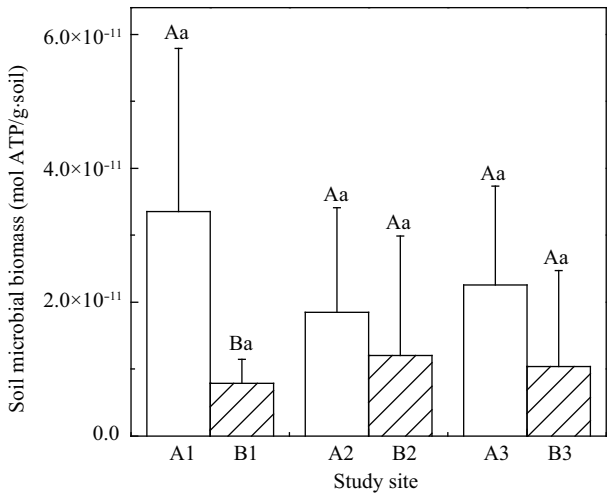

Fig. 5 Soil microbial biomass of the study areas (mean ± SD).

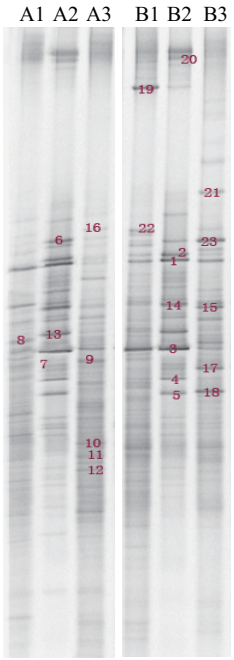

Fig. 6 DGGE Profiles of microbial communities inhabiting each sampling site. Numbers indicate bands that were cut and sequenced for the phylogenetic analysis.

activity growing in Area A, and they restrained the growth of other kinds of bacteria competitively, leading to lower bacterial diversity. Moreover, the vegetation diversity has a positive correlation with the microbial community diversity (Zhang et al., 2010). The vegetation of Area A is single-species *P. communis*, while the vegetation of Area B is *P. communis* and *S. alterniflora* combined, which led to higher microbial diversity.

To further examine the variability of the microbial community in both areas, 23 prominent bands from the DGGE profile (Fig. 6) were selected for sequencing. Comparison of the obtained sequences with the database using BLAST revealed that all of the sequencing exhibited similarities ranging from 96% to 100% (Fig. 8).

According to the result of sequencing (Fig. 8), the dominant microorganisms were clearly different in the two areas. Microorganisms specific to Area A were uncultured

Table 3 Analysis of DGGE fingerprinting

Study site	Bands number of DGGE	Shannon index
A1	31	2.425
A2	30	2.911
A3	42	4.159
Mean	34	3.165
B1	51	4.174
B2	32	2.880
B3	43	3.538
Mean	42	3.530

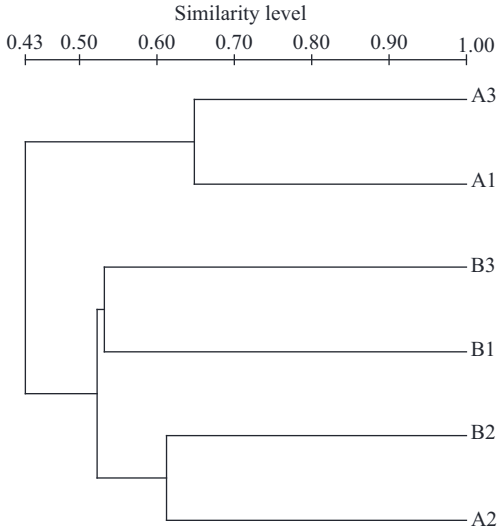

Fig. 7 UPGMA analysis of DGGE banding profiles at six different sites.

Azovibrio sp., uncultured *δ*-Proteobacterium, uncultured *Bacilli* bacterium, uncultured *Lactococcus* sp., uncultured *Niastella* sp. and *Flavobacterium* sp. Microorganisms specific to Area B were: uncultured ε-Proteobacterium, uncultured Campylobacteraceae bacterium and uncultured Bacteroidetes bacterium. Microorganisms common to both areas were uncultured β-Proteobacterium, uncultured γ-Proteobacterium, *Rhodopseudomonas* sp., uncultured α-Proteobacterium, uncultured Acidobacteria bacterium and uncultured *Streptococcus* sp.

In 23 sequenced bands, twelve bands were genetically similar with or belonged to Proteobacterium (Fig. 8). Consequently, Proteobacterium was the dominant phylum of bacteria in both areas. Janssen (2006) reported that Proteobacteria, which were the most abundant bacteria in soils, accounted for more than 40% of all validly published prokaryotic genera, contained the most gram-negative bacteria and had extreme metabolic diversity. Additionally, α-Proteobacterium, β-Proteobacterium and γ-Proteobacterium appeared both in Area A and Area B and they might play an important role in the microbial communities of the two areas. To determine the abundance of α-, β-, and γ-Proteobacteria and their function in SMR, real-time quantitative PCR was assayed to identify their copy numbers of 16S rDNA. The results (Table 4) indicated that the quantity of α-Proteobacteria in Area A, which was 13% ($P = 0.023 < 0.05$) of that in Area B, was obviously lower than that in Area B. On the other hand, the quantity of β-Proteobacteria in Area A was 3.34 ($P = 0.028 < 0.05$) times higher than that in Area B. However,

Table 4 Abundance of α-, β-, γ-Proteobacteria in the different soil samples

Study site	α-Proteobacteria (copy numbers/g soil)	β-Proteobacteria (copy numbers/g soil)	γ-Proteobacteria (copy numbers/g soil)
A1	1.65E6 ± 5.59E5 b	5.59E6 ± 9.82E5 a	1.01E8 ± 3.46E6 a
A2	2.10E7 ± 9.48E6 b	1.01E7 ± 3.43E6 a	2.90E8 ± 9.55E7 a
A3	1.82E7 ± 5.09E6 b	3.12E7 ± 6.45E6 a	2.44E8 ± 9.19E6 a
B1	2.40E8 ± 2.12E6 a	4.08E6 ± 6.73E5 b	3.93E8 ± 2.19E7 a
B2	3.72E7 ± 1.05E7 a	2.24E6 ± 3.82E5 b	2.18E8 ± 2.26E7 a
B3	4.64E7 ± 1.29E7 a	7.47E6 ± 1.13E6 b	3.97E8 ± 3.54E6 a

Different letters following the error value show significant difference between the two study areas at the 0.05 level.

the abundance of γ-Proteobacteria in both areas showed no significant difference.

To identify the influences of various microbial-factors on the SMR, principal component analysis was conducted. As shown in Fig. 9, it could be found that the SMR had the most positive correlation with β-Proteobacterium (0.7362), meanwhile it also had positive correlation with specific microorganisms (uncultured *Bacilli* bacterium and uncultured *Lactococcus* sp.). Microbial biomass had less effect on SMR with little contribution to both factor 1 and factor 2. The results implied that the SMR increased as the abundance of β-Proteobacteria increased and with the existence of specific microorganisms such as uncultured *Bacilli* bacterium and uncultured *Lactococcus* sp.

Moreover, SMR had a significant negative correlation with the Shannon index (–0.8112) and α-Proteobacterium (–0.8339), which meant that increase of the Shannon index and α-Proteobacterium would lead to a decrease of SMR. Although γ-Proteobacterium had a negative contribution to factor 2 as well, the abundance of γ-Proteobacterium had no significant difference between the two areas (Table 4), so that generally the variability of SMR between Area A and Area B was not associated with γ-Proteobacterium.

β-Proteobacteria included several aerobic and facultative bacterium with multifunctional degradation. Sato et al. (2009) and Yang et al. (2005) reported some bacteria with the ability for cellulose degradation which belong to β-Proteobacterium, moreover *Silvimonas terrae* gen. nov, sp. nov. which belongs to β-Proteobacterium, could make use of many sorts of carbon sources. Thus β-Proteobacteria might have strong respiratory activity. Specific microorganism *Lactococcus* sp. in Area A is a kind of typically aerobic bacteria. Generally, the microbial activity of aerobic bacteria is higher than that of anaerobic bacteria. Thus *Lactococcus* sp. may have higher respiration. *Bacilli* bacterium in Area A was found to have the ability to degrade

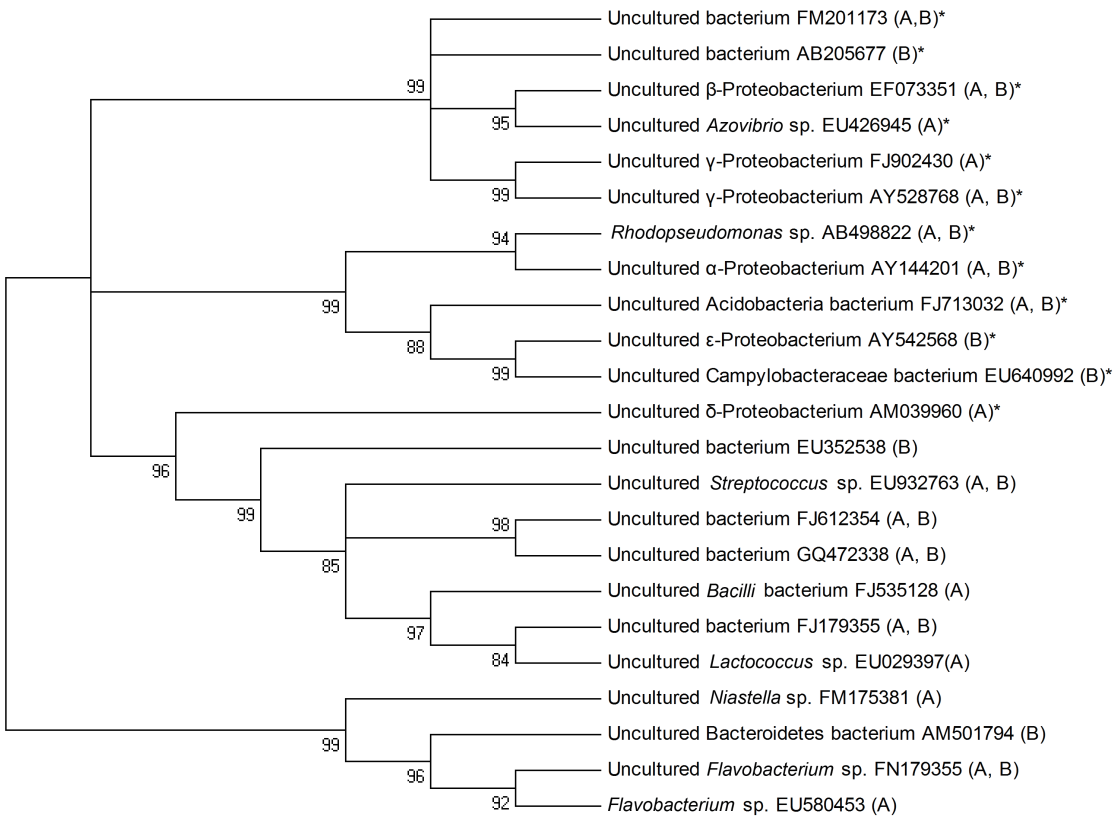

Fig. 8 Phylogenetic tree of 16S rDNA sequences of DGGE bands in six soil sites. The tree was constructed using a neighbor-joining algorithm; the capital letters A and B in the round brackets denote Area A and Area B where bacteria were observed. The code behind the bacteria name denotes the origin from BLAST analysis. * Means the identified bacteria is genetically similar with or belongs to Proteobacterium.

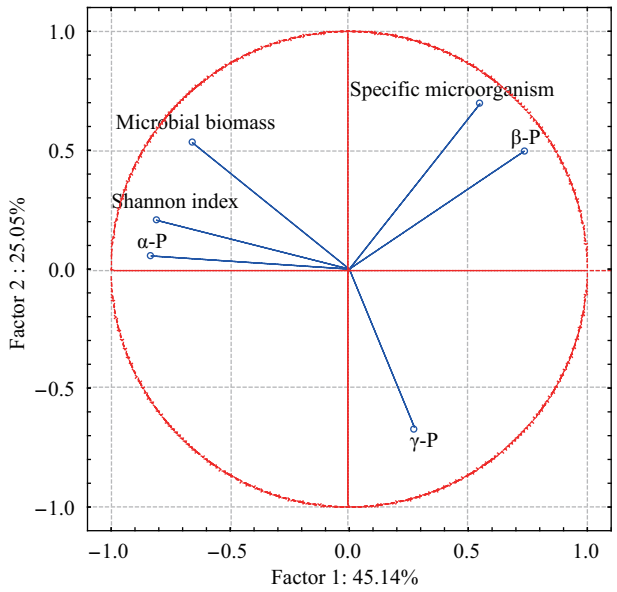

Fig. 9 Principal component analysis biplot on the impact of different bacterial communities on the soil respiration in six difference sites from both areas. The arrows indicate the direction of maximum correlation, and the length of the arrow reflects the strength of the correlation. Special microorganisms: uncultured *Bacilli* bacterium and uncultured *Lactococcus* sp.; α-P, β-P, γ-P: abundance of α-, β-, γ-Proteobacterium.

cellulose (Rastogi et al., 2009), and *Bacilli* sp. had a strong ability to decompose proteins and polysaccharides (Huang, 2000). Consequently, it may lead to the increase of the SMR in Area A. On the other hand, few previous studies have reported that α-Proteobacteria had high degradation ability.

In Area A, the soil microbial diversity (Shannon index) and the amount of α-Proteobacterium were both lower than those in Area B. However there were more β-Proteobacteria and several special microorganisms, so this may lead to its higher SMR. To sum up, more β-Proteobacteria and less α-Proteobacteria, as well as the existence of several special microorganisms such as uncultured *Bacilli* bacterium and uncultured *Lactococcus* sp. in Area A may be the main reason for its higher SMR.

2.3 Important environmental factors influencing the reproduction of soil predominant bacteria of coastal/riverside wetlands

Soil physicochemical properties, such as soil salinity, soil moisture, as well as the degradability of plant litter can affect the growth and metabolism of microorganisms in soils, thus influencing the SMR (Tripathi et al., 2006; Tang et al., 2011). Due to the different water qualities and vegetation types of the two mudflats, the soil physicochemical properties and the degradability of plant litter in the two areas were different as well. As shown in Table 1, the soil salinity of Area A was significantly lower than that of Area B ($P = 0.000 < 0.05$). Other physicochemical properties in both areas had differences, but were not as significant as soil salinity.

However, it is difficult to find the most significant factor influencing the soil microbial activity in complex soil environments. To determine the relationship between soil condition and soil microbial factors, path analysis has the advantage of being more precise and practical when compared to correlation analysis and regression analysis (Jia et al., 2010). To clarify the important environmental factors which led to the microbial variability, and then the variability of SMR in both areas, path analysis was used to research the direct and indirect influences of four important soil environmental factors on the microbial biomass and predominant bacteria's growth and reproduction.

The results in Table 5 show that soil salinity had positive direct and indirect effects on α-Proteobacteria and γ-Proteobacteria. To the contrary, soil salinity had negative direct effects on β-Proteobacteria; though the indirect coefficient was positive, the total influencing coefficient was still negative. This implied that α-Proteobacteria and γ-Proteobacteria could grow in high salinity conditions, while β-Proteobacteria was restrained by the salinity most notably. Moreover soil salinity had negative direct effects on microbial biomass while other environmental factors all had positive total influencing coefficients with the three predominant bacteria and microbial biomass.

Many studies have illustrated the variation trend of α-Proteobacteria and β-Proteobacteria with salinity;

Table 5 Path analysis of predominant bacteria and microbial biomass in study areas

Soil predominant bacterium and microbial biomass	Environmental factors	Direct path coefficient	Indirect path coefficient	Total influencing coefficient
α-Proteobacteria	Salinity	0.175	0.442	0.617
	Moisture	0.030	0.520	0.550
	TN	0.227	0.472	0.699
	AP	0.487	0.181	0.668
β-Proteobacteria	Salinity	–0.612	0.316	–0.382
	Moisture	–0.004	0.765	0.761
	TN	–0.466	1.010	0.544
	AP	1.107	–0.979	0.128
γ-Proteobacteria	Salinity	0.242	0.900	1.142
	Moisture	0.029	0.792	0.820
	TN	–0.324	0.981	0.657
	AP	1.010	–0.056	0.954
Microbial biomass	Salinity	–1.020	1.082	0.062
	Moisture	–0.620	0.730	0.110
	TN	0.596	–0.451	0.145
	AP	1.034	–0.840	0.194

β-Proteobacteria were always found to be dominant in estuarine fresh water zones, while α-Proteobacteria were dominant in areas with higher salinity (Cottrell and Kirchman, 2004; Garneau et al., 2006). γ-Proteobacteria were restrained by the local environment (Bouvier and del Giorgio, 2002). Our results are similar to these reports. In addition, Zwart et al. (2002) and Mueller-Spitz et al. (2009) reported that β-Proteobacteria was found to be a kind of predominant bacterium living in many of the world's fresh water zones. Though there were more nutrients in Area B (Table 1), β-Proteobacteria grew very slowly in Area B because of the high salinity. This indicated that soil salinity had a more significant influence on β-Proteobacteria than soil nutrients. Relatively, α-Proteobacteria and γ-Proteobacteria were more suitable for growing in the high salinity areas and increased as the soil nutrients increased. Thus with similar temperature, nutrients and vegetation biomass, coastal wetland (Area B) had lower SMR compared to riverside wetland (Area A) caused by less β-Proteobacteria and more α-Proteobacteria in Area B, which benefited the SOC reservation.

Soil salinity has significant influences on the growth and reproduction of common bacteria in soil. Most bacteria which live in high salinity conditions have osmoregulation functions (Zahran, 1997), and they can produce some special compatible osmotic pressure regulators, such as glutamate, proline and glycine. Subsequently, this affects the bacteria community structures. The SMB of Area A was 2.46 times higher than that of Area B (Fig. 5). The possible reason was the higher salinity (Table 1) in Area B, which restrained the growth of the bulk of microorganisms in the soil. Generally, the growth and metabolism of microorganisms were restrained by the soil salinity, and the increase of soil salinity would lead to the decrease of SMB and soil enzyme activities (Omar et al., 1994), as well as SMR (Tripathi et al., 2006).

In addition, according to the study by Tang et al. (2011), the area where *S. alterniflora* grew had a higher SMR than the area where *P. communis* grew in the Yangtze River Estuaries' wetland. As the vegetation of Area A is single-species *P. communis* and the vegetation of Area B is *P. communis* and *S. alterniflora* combined, the theoretical SMR of Area B should be higher than that of Area A if the water quality was the same. Furthermore, it was reported that watershed-derived sediments were also important inputs of organic carbon to the wetland soil (Morris et al., 2002; Reed, 1995). So, as a result of the salting out (Poulson et al., 1999; Gross, 1933), there should be more organic carbon inputs from watershed-derived sediments in Area B where the salinity was much higher. Consequently, it should also enhance the SMR of Area B. However, the result was that SMR of Area B was still clearly lower than that of Area A, and this further confirmed that the soil salinity restrained the SMR of Area B significantly as well.

3 Conclusions

Based on the results of this study, the following conclusions were drawn: (1) The SOC content of the riverside area was lower than that of coastal area. Under conditions of the same inputs of organic matter (plant biomass), the higher SMR was the most important reason. (2) In the riverside area, the high SMB, more β-Proteobacterium which has strong carbon metabolism activity and the existence of some specific aerobic heterotrophic bacterium were the major reasons for its higher SMR when compared to the coastal area. (3) The low salinity condition of the riverside area was suitable for the growth of microorganisms, especially β-Proteobacteria and some specific bacteria, which led to a high SMR and low SOC reservation capability when compared to the coastal area.

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