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Variability of soil microbial respiration under different vegetation succession stages in Jiuduansha wetland

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ABSTRACT

The soil microbial respiration (SMR) and physicochemical characteristics of Jiuduansha wetland at the Yangtze Estuary were analyzed in order to clarify the variability of SMR under different vegetation succession stages and its influencing factors. The results indicated that SMR of different vegetation succession stages are significantly various ($P < 0.05$). The SMR of the *Spartina alterniflora* (*S. alterniflora*) zone (0.43 $mgCO_2 \cdot g^{-1}.24\ h^{-1}$) was the highest. These findings implied that *S. alterniflora* could enhance the SMR. Based on both the SMR and input of organic matter from plant decay, the *Phragmites australis* (*P. australis*) community likely possesses a higher organic carbon accumulation capability. Considering both SMR and input of organic matter from decayed plant biomass of wetland with different vegetation type, the *P. australis* community, in theory, has higher organic carbon accumulation capability. Path analysis shows that the main bio-factors influencing on SMR include bacterial diversity and soil microbial biomass (SMB). Soil moisture, inorganic N (IN), salinity and available P (AP) in soil also have significant effects on the mentioned biological factors.

Keywords: Path analysis; Carbon sink; Vegetation type; Salt marsh wetland

1. Introduction

Soil microbial respiration (SMR) is an important part of the soil respiration, through which carbon is released from the soil [1]. Wetland regions contain large amounts of stored organic carbon (about 10% of the carbon pool of the global terrestrial ecosystem); therefore, their potential for the exchange of greenhouse gases (CO_2 and CH_4) with the atmosphere is great [2]. Soil microenvironments and plant communities are the most important factors when determining the carbon sinks capability of wetlands because they influence the quality of mixed litter in the soil and its decomposability, as well as the microbial activities of wetland soil to a certain extent. Therefore, there may be different SMR among vegetation succession stages because of the interaction between vegetation type and soil microenvironment.

But previous investigations into SMR have largely focused on the effects of heavy metals and pesticides on SMR [3], the change in SMR under different fertilizer regimes and the special function and contribution of SMR on soil quality assessment [4]. Although many studies have been conducted to evaluate the relationship between plant and soil respiration [5–7], few have attempted to

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describe the variability in the SMR of tidal wetlands under different vegetation succession stages.

Jiuduansha wetlands are the sole original landform wetland in the Yangtze Estuary and an important part of the natural and ecological conservation network in China, providing carbon sink capability and important ecological services to nearby cities. However, few studies of the SMR associated with different vegetation succession stages in Jiuduansha wetlands have been reported to date. In this study, the objective of the current study was to employ a suite of molecular microbial ecology technique polymerase chain reaction-denaturing gradient gel electrophoresis (PCR–DGGE) to describe the variability of SMR among different vegetation succession stages in Jiuduansha wetland and its mechanism. To accomplish this, five zones which represent a range of succession stages and vegetation types were sampled periodically to obtain information regarding: (1) the difference in the SMR among the five zones, (2) the physicochemical and microbial mechanism of the variation in the SMR.

2. Materials and methods

2.1. Site description and experimental design

The Jiuduansha Wetland is located between the southern and northern watercourse of the Yangtze Estuary (31°03′–31°17′N, 121°46′–122°15′E), 12 km east of the Pudong International Airport (Fig. 1). The wetland covers 423.2 km2 and consists of four shoals named Jiangyanansha, Shangsha, Zhongsha and Xiasha. The Jiuduansha Wetland was designated as a wetland nature reserve of the Shanghai Municipality in 2003 and as the Jiuduansha National Wetland Nature Reserve in 2005. The Jiuduansha Wetland is subject to the East Asia subtropical monsoon climate, with an average annual temperature of 17.3°C. The vegetation in the wetland is in the primary stage of system succession and mainly consists of the tidal flat pioneer plants, *Scripus triqueter* (*S. triqueter*), *Scirpus mariqueter* (*S. mariqueter*), *Spartina alterniflora* (*S. alterniflora*) and *Phragmites australis* (*P. australis*). Adopting the concept of "substituting space for time" [8], the plants distributed belts along elevation in estuary wetland are considered as vegetation succession.

2.2. Soil sampling and pretreatment

Five sampling zones denoted S1, S2, S3, S4 and S5, were set in Xiasha of the Jiuduansha Wetland with an interval of 500 to 600 m along areas of different vegetation succession stages. Three parallel points denoted P1, P2 and P3, were set in each main sampling zone with an interval of 30 m. The details describing each sampling point are shown in Fig. 1 and Table 1. A total of 15 soil samples were collected during each month in April, July, September and December of 2008. All soil samples were taken from the sub-surface layer (–5 to –20 cm). Specifically, random cores were collected from each point with a 5 cm diameter tube auger and bulked [9]. At the same time, aboveground plant biomass was sampled by clipping the entire contents of five 0.1 m^2 plots equally spaced along each zone at the soil surface. The belowground plant biomass was estimated by collecting three soil cores 4.8 cm in diameter and 30 cm in depth from within each 0.1 m^2 plot.

All of the samples, which were free of major debris, were packed in individual sterile plastic bags and immediately stored at 4°C. Part of the fresh soil was handled

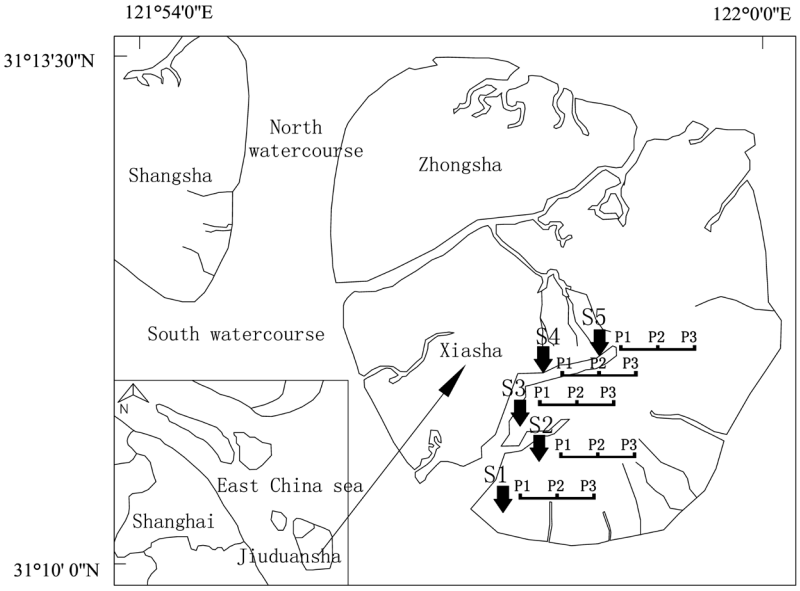

Fig. 1. Map of the study areas in Xiasha of the Jiuduansha wetland (The short black arrows stand for five sample points).

Table 1
The sampling stations

Sample station	Vegetation	Location (°'N,°'E)	Height (m)	Average waterlogging time (h. d^{-1})
S1	Mudflats	31 10.22–31 10.23, 121 57.61–121 57.63	0.8–2.0	15.1
S2	*S. mariqueter*	31 10.24–31 10.26, 121 57.77–121 57.78	3.0–3.3	14.0
S3	*S. alterniflora*	31 10.56–31 10.57, 121 57.83–121 57.85	3.9–4.0	11.2
S4	*S. alterniflora* / *P. australis*	31 11.13–31 11 18, 12158.25–12158.31	3.9–4.0	7.6
S5	*P. australis*	31 11.18–31 11.19, 121 58.43–121 58.47	4.3–4.4	5.4

Note: Height was provided by the State Key Laboratory of Estuarine and Coastal Research, East China Normal University. Waterlogging time was calculated using tide tables.

immediately for SMR, soil microbial biomass (SMB) and soil enzyme activity (sieved < 2 mm) analysis, and the rest was air-dried and stored at room temperature until assay of the other soil characteristics. All results reported are the means of triplicate analyses and expressed on an oven-dry basis. The remainder of the soil was stored at –70°C for subsequent DNA extraction.

2.3. Analysis methods

2.3.1. SMR

CO_2 decomposed and released by microorganisms from 40 g original fresh soil samples incubated in 250 mL serum bottles within 24 h at 28°C was measured by gas chromatography using a gas chromatograph (GC-14B, Shimadzu) with a stainless steel column (10 m × 2 mm) and a TCD detector [10,11]. The column temperature, inlet temperature and detector temperature were 40ºC, 40ºC and 90°C, respectively. Nitrogen gas was applied as the carrier at a flow rate of 30 mL min^{-1}. The CO_2 injection volume was 0.2 mL. 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.

2.3.2. Denaturing gradient gel electrophoresis and gel pattern analysis

A molecular approach was used to analyzing the genetic diversity of complex microbial populations. This technique is based on the separation of polymerase chain reaction-amplified fragments of genes coding for 16S rRNA by denaturing gradient gel electrophoresis (DGGE) [12].

Total DNA extraction was conducted using a FastDNA® spin kit for soil (Qbiogene, Inc., Irvine, CA, USA) according to the manufacturer's instructions. DNA was stored at –20°C for PCR–DGGE analyses. Nested PCR was conducted using the 8f and 1492r primer set for the 1st PCR amplification. The 2nd PCR amplification for DGGE was conducted using the generally conserved 16S rRNA gene primers 341f-GC and 534r [12]. In addition, a GC clamp (CGCCCGCCGCGCGCGGCGGGC-GGGGC-GGGGGCACGGGGGG) was attached to the 5'-end of the forward primer. For DGGE analysis, 400 ng of PCR product generated from each sample was separated on a 10% acrylamide gel with a linear denaturant gradient range of 35% to 65% and run at 80 V for 12 h (Bio-Rad, USA). Gels were stained with ethidium bromide solution for 30 min, and the images were captured using Smart View (Furi, Shanghai, China).

2.3.3. Routine analysis

The SMB was estimated based on the ATP levels, which were measured using an improved bioluminescent method as previously described [13]. Soil invertase activities were tested according to the 3, 5-dinitrosalicylic acid colorimetry method (sucrose as substrate, 508 nm) [14]. The soil dehydrogenase and β-glucosidase activities were determined based on the standard method described by the Soil Science Society of America [15].

Plant roots were separated from the soil by hand, and both above- and below-ground plant tissues were oven dried at 80°C to a constant weight. The plant biomass reported is the sum of the above- and belowground tissue per unit area ($kg.m^{-2}$).

Other soil variables including the pH, soil moisture, salinity, IN and AP were assayed by routine methods [16].

2.4. Statistical analysis

Statistical analysis was conducted using One-way ANOVA and Duncan's multiple-comparison tests with the SPSS software (version 16.0, SPSS Inc.). Path analysis was performed using DPS v9.50. The structural diversity

of the microbial community was examined by the Shannon index (H), which is given by:

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

H was used to evaluate the diversity index of bacterial community diversity and calculated on the basis of the bands on the gel tracks that were applied for the generation of the dendrograms by using the intensities of the bands as judged by peak height in the densitometric curves. S is the number of bands in the DGGE gel. P_i was calculated as follows: $P_i = n_i/n'$, where ni is the height of a peak and n' is the sum of all peak heights in the densitometric curve.

3. Results and discussion

3.1. Variability of SMR and plant biomass under different vegetation succession stages

The results showed that the soil microbial respiration varied greatly among succession stages of vegetation ($P < 0.05$) (Fig. 2). When compared with reclaimed farm land in Dongtan of Chongming (0.41 mg CO_2.g^{-1}.24 h^{-1}), the SMR in the Jiuduansha Wetland was lower (0.28 mg CO_2.g^{-1}.24 h^{-1}). In addition, the SMR in the *P. australis* zone was lower than that in the *S. mariqueter* zone, and the SMR of the bare flat zone (0.17 mg CO_2.g^{-1}.24 h^{-1}) was the lowest among the five vegetation types. In contrast, the highest SMR was observed in the *S. alterniflora* zone (0.43 mg CO_2.g^{-1}.24 h^{-1}). The results suggest that *S. alterniflora* may enhance SMR. In addition, as shown in Fig. 2, the vegetation biomass increased along the tidal elevation variation, with that of the *P. australis* zone (3.11 kg.m^{-2}) being the highest among the five vegetation types. The ratio of microbial respiration to plant biomass in S5 was lower than in the other samples. When both the SMR and input of organic matter from plant decay of different vegetation types were considered, the zone composed of a *P. australis* community, in theory, had the highest capability to accumulate organic carbon.

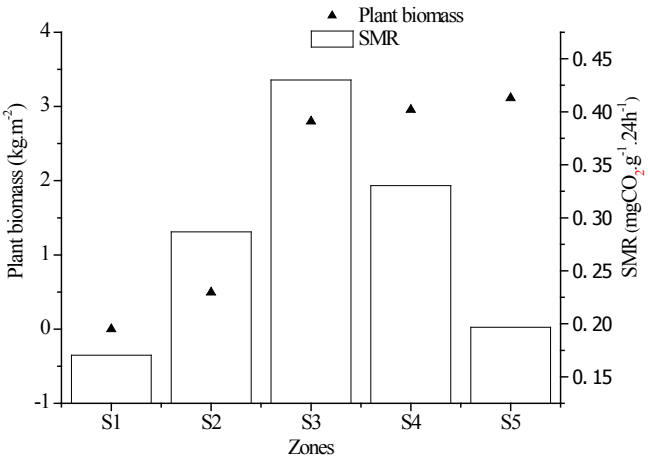

Fig. 2. The characteristics of SMR and vegetation biomass in Jiuduansha Wetland (The ratios of respiration to plant biomass are: S1, salt marsh plants biomass is negligible; S2 = 0.58; S3 = 0.15; S4 = 0.11; S5 = 0.063).

3.2. Variability of soil microbial characteristics under different vegetation succession stages and its impact on SMR

To date, most studies conducted to evaluate soil respiration have been conducted on a plot or ecosystem scale and have focused on its effects on carbon cycling on regional and global scales. However, respiration is basically a series of biochemical processes that occur in the cells of all organisms in an ecosystem, including plants, animals and microorganisms [17]. Soil microbial characteristics such as microbial enzyme activity, microbial biomass and the microbial community are closely related to soil enzyme activity and SMR [18]. Therefore, it is important to identify the main factors influencing the SMR from a microbial standpoint; it is worthwhile to elucidate the microbial mechanisms that lead to differences in SMR to more deeply probe into the effects of vegetation succession stages on the SMR of tidal wetlands.

Soil enzyme activities can indicate microbial activities and have a close relationship with SMR. The activity of soil enzymes associated with the metabolism of carbon such as invertase, β-glucosidase and dehydrogenase were assayed along the vegetation succession stage. Generally, the tendency of soil enzyme activities to vary is similar to the soil microbial respiration as shown in Fig. 3. Generally, the soil enzyme activities increased from S1 to S4, being lowest in the mudflats and highest in the S. alterniflora/P. australis zone. The soil enzyme activities in S5 were modestly lower, but still higher than those of S1 and S2.

SMB and soil microbial community structures are two key factors that influence the soil enzyme activity, and hence soil respiration. The results of the present study showed that SMB was the lowest in the mudflats zone and the highest in the *S. alterniflora* zone, but that there was no significant difference between S3 and S4 (S1: 5.88×10^{-11}, S2: 1.28×10^{-10}, S3: 2.18×10^{-10}, S4: 2.23×10^{-10}, S5: 1.32×10^{-10}, mol ATP.g^{-1}). Comparison of the fingerprints obtained by the DGGE analysis was used to describe the structure of the microbial communities at each zone (Fig. 4). The Shannon index showed that the diversity in S1 and S2 was obviously lower than in other zones (S1: 3.09, S2: 4.42, S3: 5.39, S4: 6.03, S5: 5.29). These findings suggest that each site supports unique molecular species and different numbers of bacterial species.

To analyze the key microbial activity index affected SMR, path analysis was performed to study the relationship between microbial activity factors and SMR. Path analysis not only can determine the relationship among variables, but also can give the emphasis of reason on

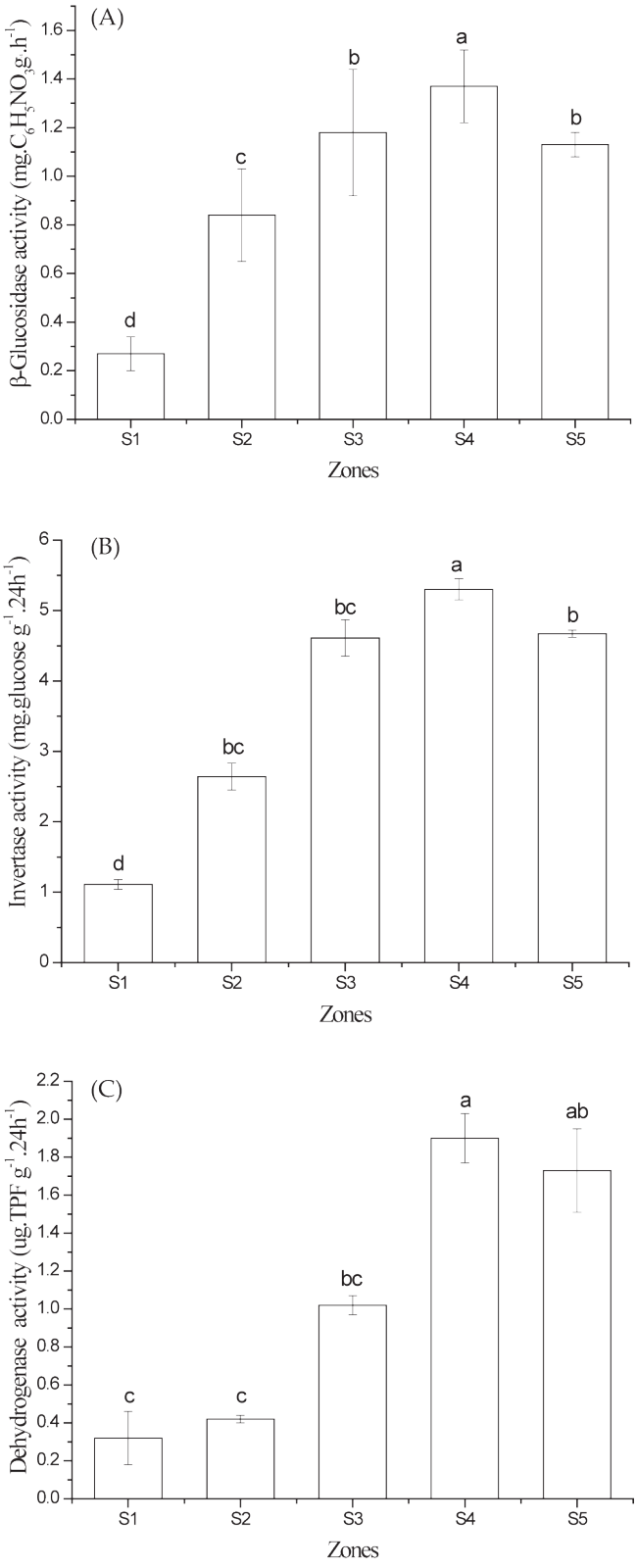

Fig. 3. Soil enzymatic activities of sampling zones (The data from the five zones were calculated according to four seasons and three parallel samples. A: β-glucosidase activity; B: Invertase activity; C: Dehydrogenase activity. Different lowercase letters indicate a significant difference at $P < 0.05$).

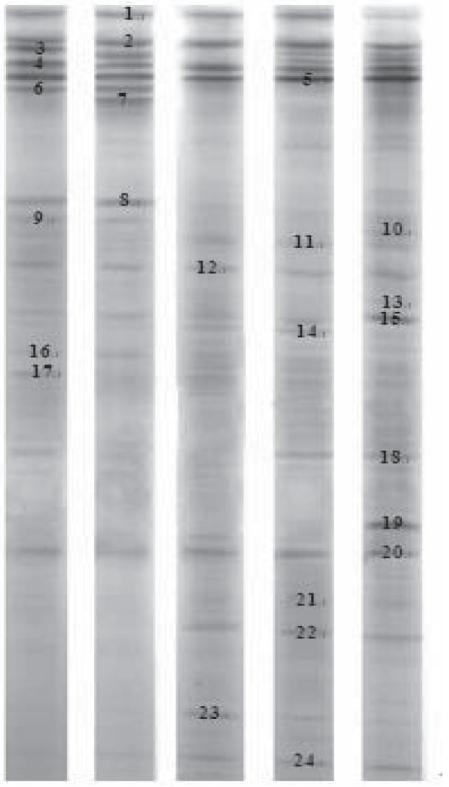

Fig. 4. DGGE profiles of microbial communities inhabiting each sampling site (Numbers indicate bands that were cut and sequenced for the phylogenetic analysis).

result. In addition, the correlation coefficient can be divided into direct and indirect affection and suggest the relative importance of factors on result [19]. Path analysis indicated that the effect of the sequence of microbial factors on SMR was Shannon index > SMB (Table 2). The underlined numbers stand for the direct path coefficient. Furthermore, the results indicated that the Shannon index had a greater positive direct correlation with SMR than SMB and was therefore the main determinant of SMR. The difference in the diversity of prokaryotic organisms indicates a change in the microbial community structure. As a result, the difference in the soil prokaryotic microorganism community structure may be the primary cause of the difference in the SMR of different vegetation succession stages.

Table 2
The path analysis of SMR

Dependent variable	Independent variable	Shannon index	SMB	Total
SMR	Shannon index	0.7839	0.0015	0.7854
	SMB	0.1311	0.0325	0.1636

Many reports indicated the change in the soil microbial community structure will obviously influence SMR. Teng et al. [20] found that the change in soil microbial community structure was associated with the change in soil respiration in eroded soils. Additionally, a study conducted to evaluate the distribution of microbial communities in a forest soil profile based on the microbial biomass, soil respiration and DGGE of total and extracellular DNA also indicated that there was a close relationship between soil microbial structures and soil respiration [21]. There was abundant microbial diversity and many heterotrophs could grow and reproduce in the *S. alterniflora* zone of the Jiuduansha Wetland, which led to a higher soil microbial respiration.

3.3. Relationship between soil environmental conditions and soil microbial community structure

The soil microbial structure and diversity had a direct effect on the SMR, and the structure and diversity of the soil microorganisms were affected by a series of non-living factors such as soil moisture, salinity and soil nutrients. So that the physical-chemical properties of wetland soil with different vegetation succession stages were analyzed. The variability of soil physical-chemical parameters of different zones is shown in Table 3. Obviously the soil physical-chemical properties were different in different zones. Path analysis indicated that the effects of soil physicochemical factors on the Shannon index occurred in the following order: soil moisture > IN > salinity > AP (Table 4), and that soil moisture and IN are the primary factors that positively influence the soil bacterial diversity, and thus have a positive effect on SMR. The variability of these soil physicochemical characteristics among zones resulted from different vegetation types, while the waterlogging time likely led to different soil characteristics, and thus different prokaryotic microbial community structures and SMR.

In general, shifts in the structure of bacterial communities can be associated with changes in a number of soil properties. Soil moisture is considered to be a fundamental indicator of such changes because of a number of biochemical processes of soil that are closely connected with moisture. Zahran [22] indicated that the negative effects of salinity and water content on soil bacteria can lead to the degradation of bacterial ecosystem functions, thus influencing the soil organic carbon decomposition processes. However, our results showed that high water contents in the *S. alterniflora* zone led to a high soil enzyme activity and SMR. This likely occurred because *S. alterniflora* may hold more water and thus dissolve more available organic matter and phosphorus for microbial growth. In addition, many studies have found that the soil prokaryotic microbial community structure could be easily changed by the addition of IN [23], that is similar to the case in the activated sludge system for treating wastewater [24,25].

Many studies have indicated that vegetation type can change factors in the soil microenvironment, such as soil moisture, N and P [26–28]. Wang [29] found that *S. alterniflora* had strong absorption ability to nitrogen. Moreover, different elevations of tidal wetlands have also been found to lead to variations in the soil physical and chemical properties, such as soil moisture and salinity, due to different periods of water submersion. Therefore, differences among the vegetation type and elevation of

Table 3
Basic properties of sampling zones

Sample station	Soil pH	Soil moisture (%)	Salinity ($g.kg^{-1}$)	IN ($mg.kg^{-1}$)	AP ($mg.kg^{-1}$)
S1	8.75	42.07	1.95	8.08	1.85
S2	8.51	45.43	2.31	6.08	2.37
S3	8.42	52.66	2.38	7.20	2.60
S4	8.76	47.22	2.01	6.07	2.36
S5	8.51	36.45	1.60	4.59	1.78

Table 4
Path analysis of soil biological factors

Dependent variable	Independent variable	Soil moisture	IN	Salinity	AP	Total
Shannon index	Soil moisture	0.7128	–0.0482	0.0083	0.1793	0.8552
	IN	0.0052	–0.6821	0.0133	0.0192	–0.6444
	Salinity	0.0668	–0.1694	0.5136	0.0163	0.4273
	AP	0.1342	0.0098	–0.0475	0.2965	0.3930

different vegetation succession stages could lead to differences in the soil physical and chemical characteristics, such as soil moisture and IN. In the present study, *S. alterniflora* was found to have a large root system that held more nitrogen and water; therefore, the IN and soil moisture of the *S. alterniflora* zone were both higher than that of the *S. mariqueter* zone.

Overall, the different soil environmental conditions resulted from different vegetation types and elevation, including soil moisture, IN, AP and salinity lead to different soil microbial compositions in different vegetation succession stage. Subsequently, the special soil microbial compositions occurred in the *S. alterniflora* zone may be the important reasons of its stronger SMR.

4. Conclusions

Based on the results of this study, the following conclusions were drawn: (1) the SMR of different succession stages of vegetation varied significantly and were highest in the *S. alterniflora* zone; (2) when both plant biomass and soil microbial respiration were considered, the *P. australis* community zone likely possessed the highest organic carbon accumulation capability; (3) different soil microbial characteristics, especially the soil prokaryotic microbial community structure and diversity in different wetland soils, are the main cause of the different SMR; (4) the soil moisture and IN content of the soil changed with elevation and vegetation type, thereby altering the soil prokaryotic communities.

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