

1 **Soil methane production, anaerobic and aerobic oxidation in**  
2 **porewater of wetland soils of the Minjiang River estuarine,**  
3 **China**

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Post-print of: Wang, W. et al. "Soil methane production, anaerobic and aerobic oxidation in porewater of wetland soils of the Minjiang River Estuarine, China" in Wetlands (Springer), vol. 38 issue 3 (2018) p. 627-640. The final version is available at DOI 10.1007/s13157-018-1006-9

18 **Abstract**

19 Wetlands are important sources of methane emission. Methane anaerobic oxidation,  
20 aerobic oxidation and production, and dissolved methane are important process of  
21 methane metabolism. We studied methane metabolism and the soil influencing factors.  
22 Potential soil methane production, anaerobic oxidation and aerobic oxidation rates,  
23 and dissolved methane in soil porewater changed seasonally and the annual average  
24 was  $21.1 \pm 5.1 \mu\text{g g}^{-1}\text{d}^{-1}$ ,  $11.0 \pm 3.9 \mu\text{g g}^{-1}\text{d}^{-1}$ ,  $20.9 \pm 5.8 \mu\text{g g}^{-1}\text{d}^{-1}$ , and  $62.9 \pm 20.6 \mu\text{mol l}^{-1}$ ,  
25 respectively. Potential soil methane production and anaerobic and aerobic oxidation  
26 were positively correlated among them and with soil pH and negatively correlated  
27 with soil redox potential (Eh). Potential soil methane production and aerobic and  
28 anaerobic oxidation rates were negatively related to pore soil methane concentration.  
29 Thus, the more water saturated the soil (the lower Eh), the higher its capacity to  
30 methane production was, but even higher was soil potential capacity to methane  
31 oxidation both in the same anaerobic circumstances and when the soil was suddenly  
32 submitted to aerobic conditions. All these results suggested a buffer effect in the  
33 methane balance in wetland areas, the environmental circumstances favoring methane  
34 production are also favorable to methane anaerobic oxidation.

35 **Keywords** Methane production · methane anaerobic oxidation · methane aerobic  
36 oxidation · dissolved methane · Minjiang River estuarine wetland

37

38 **Introduction**

39 Although, the total area occupied by wetlands currently accounts for only 4.6% of the  
40 total land area (Costanza et al. 1997), their ecosystem services value accounts for 32%  
41 of the total value of the world, especially coastal wetlands whose ecosystem service  
42 value accounts for 17% of the global total value (Costanza et al. 1997). Wetland is  
43 sensitive to the external stress and becomes the ideal area for global change research  
44 (Simas et al. 2001). Methane is one of the important greenhouse gases affecting  
45 global climate change. Although, wetlands only represent a small fraction of the  
46 Earth's land surface, they are the main sources of methane to the atmosphere,  
47 representing between 20%-39% of global methane emissions (Laanbroek 2010). The  
48 relative increase of methane at the scale of 100-year is about 25 times than that of  
49 carbon dioxide (IPCC, 2007). Thus, improving the knowledge of methane metabolism  
50 in wetland soils warrants intense research.

51 Methane metabolism is in several phases: production, oxidation, dissolved  
52 methane, transport and emission (Buckley et al. 2008). Methane production, oxidation  
53 and dissolved methane in water have great impacts on the ultimate reduction of  
54 methane emissions in wetlands (Singh 2011). In the 21st century, methane anaerobic  
55 oxidation has become the core and hot issues (Raghoebarsing et al. 2006; Kniermeyer  
56 et al. 2007). However, the reports about methane anaerobic oxidation in coastal  
57 estuarine wetlands are few. Furthermore, the relationships between potential soil  
58 methane anaerobic oxidation capacity with potential soil methane production and with  
59 potential soil methane aerobic oxidation capacity are uncertain in wetland areas.

60 Whether relationships exist between the soil capacity to produce methane and the soil  
61 capacity to oxidize methane when the soil is in anaerobic conditions and whether  
62 between production and oxidation in wet conditions in dry-aerobic periods are two  
63 important questions that warrant research.

64 Methane metabolism in wetlands is strongly influenced by environmental factors  
65 that vary both spatially and temporally (Datta et al. 2013). The availability of electron  
66 acceptors and donors in soils plays a key role in regulating CH<sub>4</sub> production and  
67 consumption (Moran et al. 2008; Ettwig et al. 2010; Ro et al. 2011) and thereby  
68 controlling dissolved methane and the emission. Electron acceptors (e.g. Fe<sup>3+</sup>, NO<sub>3</sub><sup>-</sup>,  
69 and sulfate) are reduced during wet periods, but regenerated (oxidized) during dry  
70 periods (Neubauer et al. 2007). Soils can also provide carbon substrates to microbes  
71 for mediating CH<sub>4</sub> production and enhancing plant growth that in turn governs more  
72 than 90% of CH<sub>4</sub> transport (Le Mer and Roger 2001). Other environmental variables,  
73 include soil temperature, pH, redox potential (Eh) and salinity also influences CH<sub>4</sub>  
74 metabolism (Song et al. 2008; Wang et al. 2017). Better knowledge and  
75 characterization of CH<sub>4</sub> metabolism and transport of CH<sub>4</sub>, are essential for better  
76 understanding and characterizing of GHG emissions from wetlands advancing in the  
77 knowledge of soil and soil pore water circumstances can favor the production and  
78 oxidation processes in soil media and thus, the final methane contents in  
79 soil-atmosphere interface and emission can give clues to choose between soil and  
80 plant community management strategies to diminish as much as possible the methane  
81 emissions. This information can also provide clues to improve the models and

82 projections of methane production and emissions on regional and global scale.

83 China has a coastline of 18,000 km in length, with numerous estuaries and bays  
84 and a diversity of coastal wetlands which are important component of China's  
85 wetlands, as well as the world's wetlands. Minjiang River estuarine wetland is the  
86 main natural wetland of southeast coast of China. The wetland of Minjiang River  
87 estuary is rich in biological species and abundant in waterbird resources (Liu et al.,  
88 2006). Moreover, the Minjiang River estuary is an important tidal wetland ecosystem  
89 due to its unique location at the transition between central and southern subtropical  
90 climatic zones (Zheng et al. 2006). The tidal wetlands are rich in animal and plant  
91 biodiversity (Zhou et al. 2006) being an excellent site representing the wide coastal  
92 wetland areas of this part of China coast-

93 We studied the: (1) the seasonal variation potential of soil methane production,  
94 soil methane anaerobic oxidation, soil methane aerobic oxidation, dissolved methane,  
95 emission and the relationships among these variables and (2) the soil variables that  
96 have significant relationships with methane-related variables in Minjiang River  
97 estuarine wetland along the year. The results obtained in this study were also aimed to  
98 provide a scientific basis for a suitable management of wetland avoiding as much as  
99 possible CH<sub>4</sub> emissions.

100

## 101 **Materials and Methods**

### 102 **Study area**

103 This study was conducted in the Shanyutan wetland (26°01'46"N; 119°37'31"E,

104 Fig. 1), the largest tidal estuarine wetland (approximately 3120 ha) in the estuary of  
105 the Minjiang River.

106 The climate in this region is relatively warm and wet with a mean annual temperature  
107 of 19.6 °C and a mean annual precipitation of 1346 mm (Zheng et al. 2006). The soil  
108 surface is submerged across the study site beneath 10-120 cm of water for 3-3.5 h  
109 during each tidal inundation. Soil surfaces of the entire wetland are exposed at low  
110 tide during 24 h and the weight percentage of water in the soil and soil redox potential  
111 are 116.39% and 12.57 mV respectively and soil remains flooded at some depths. The  
112 average salinity of the tidal water between May and December 2007 was  $4.2 \pm 2.5\%$ .

113 *C. malaccensis* is one of the two dominant species of plants in this estuarine wetland.

114 *C. malaccensis* is a native plant typically found in the upper (mid to high) portions of  
115 mudflats that grow between April and October, the highest population height is about  
116 1.5 m and the density is about 1000 m<sup>-2</sup>. Below-ground rhizomes are creeping growth  
117 in the topsoil layers.

118

### 119 **Experimental design**

120 Seasonal variation samples were collected from April in 2012 to March in 2013 from  
121 Shanyutan wetland in Minjiang River estuary. We established a plot of 900 m<sup>2</sup> in  
122 Shanyutan wetland and then collected the *C. malaccensis* wetland soil randomly after  
123 selecting three quadrats (100 m<sup>2</sup>) within the big plot. Soil samples of 0-20 cm were  
124 collected with a small core sampler (length and diameter of 0.3 and 0.1 m). The  
125 sampling was conducted every month during one-year. Thus, a total of 36 soil

126 samples (one wetland type × one soil layer × twelve months' × three replicate plots)  
127 were thus collected.

128

### 129 **Measurements of potential methane production**

130 In each sampled soil, potential soil methane production rate was determined by  
131 placing 30 g of the fresh soil sample in a 120 ml incubation bottle and injecting 30 ml  
132 of distilled water (water: soil ratio was thus 1:1) (Wang et al. 2010; Bergman et al.  
133 2000). The incubation bottles were filled with oxygen-free nitrogen through a small  
134 hole in the bottle stopper to eliminate the possibility of methane consumption caused  
135 by carrying oxygen during the sampling process and slowly equilibrated with the  
136 atmospheric pressure for 24 h to consume the residual oxygen in incubation bottles,  
137 which ensures the soil sample is in a strictly anaerobic environment (Smemo and  
138 Yavitt 2007; Wrede et al. 2012). Three replicates were set and placed in an anaerobic  
139 incubator (YQX-II, Shanghai Yuejin Medical Equipment Factory) in the dark place  
140 using the average soil temperature in situ. Then the gas samples were taken at 0, 24,  
141 48, 72, and 96 h, and the sample incubation bottles were gently swirled for 1-2 min  
142 before gas sampling. Each extraction was 2 ml and supplemented with the  
143 corresponding volume of oxygen-free nitrogen. Methane concentration was  
144 determined by a GC-2010 gas chromatograph (Shimadzu Scientific Instruments,  
145 Kyoto, Japan). The potential methane production rate was calculated by the methane  
146 concentration increment during the incubation time in the incubation bottles.

147

### 148 **Measurements of potential methane anaerobic oxidation**

149 In each collected soil sample, potential soil methane anaerobic oxidation rate was

150 determined by placing 30 g of fresh soil sample in a 120 ml incubation bottles and  
151 injecting 30 ml of 40 mmol l<sup>-1</sup> of methane production inhibitor (BES,  
152 bromoethanesulfonate) solution (Müller et al. 1993; Hoehler et al. 1994) at a water:  
153 soil ratio of 1:1 (Bergman et al. 2000). The incubation bottles were filled with  
154 oxygen-free nitrogen through a small hole in the bottle stopper to eliminate the  
155 possibility of methane consumption caused by carrying oxygen during the sampling  
156 process and slowly equilibrated with the atmospheric pressure for 24 h to consume the  
157 residual oxygen in the incubation bottles, ensuring the soil sample is in a strictly  
158 anaerobic environment (Smemo and Yavitt 2007; Wrede et al. 2012). Then, pure  
159 Methane standard gas was injected into each incubation bottles so that the  
160 concentration of methane in the incubation bottle was 10000 µmol mol<sup>-1</sup>, and 3  
161 replicates were set and placed in an anaerobic incubator (YQX-II, Shanghai Yuejin  
162 Medical Equipment Factory) in the dark place using the average soil temperature *in*  
163 *situ*. Then the gas samples were taken at 0, 24, 48, 72, and 96 h, and the sampled  
164 incubation bottles were gently swirled for 1-2 min before gas sampling. Each  
165 extraction was 2 ml and supplemented with the corresponding volume of oxygen-free  
166 nitrogen. Methane concentration was determined by a GC-2010 gas chromatograph  
167 (Shimadzu Scientific Instruments, Kyoto, Japan). Potential methane anaerobic  
168 oxidation rate was calculated by the methane concentration decrement as the  
169 incubation time in the incubation bottles.

#### 170 **Measurements of potential methane aerobic oxidation**

171 In each soil sampled potential soil methane aerobic oxidation rate was determined by  
172 Krüger et al. (2002) and Supparattanapan et al. (2009), by placing 30 g of fresh soil  
173 sample in a 120 ml incubation bottle and injecting 30 ml of distilled water into it, the  
174 water: soil ratio was 1:1 (Wang et al. 2010; Bergman et al. 2000). Then, pure methane



175 standard gas was injected into each incubation bottles so that the concentration of  
176 methane in the incubation bottles was  $10000 \mu\text{mol mol}^{-1}$ , and three replicates were set  
177 and incubation in the dark place using the average soil temperature in situ. Then the  
178 gas samples were taken at 0, 24, 48, 72, and 96 h, and the sampled incubation bottles  
179 were gently swirled for 1-2 min before gas sampling. Each extraction was 2 ml and  
180 supplemented with the corresponding volume of oxygen-nitrogen. Methane  
181 concentration was determined by a GC-2010 gas chromatograph (Shimadzu Scientific  
182 Instruments, Kyoto, Japan). Potential soil methane anaerobic oxidation rate was  
183 calculated by the methane concentration decrement as the incubation time in the  
184 incubation bottles.

185

#### 186 **Measurement (in situ) of porewater dissolved CH<sub>4</sub> concentration**

187 Porewater was sampled *in situ* once each month. Three specially designed stainless  
188 steel tubes (2.0 cm inner diameter) were installed to a depth of 30 cm in each plot.  
189 Porewater samples were collected immediately after the measurements of CH<sub>4</sub>  
190 emission using 50-ml syringes to inject it into pre-evacuated vials (20 ml) and stored  
191 in a cooling box in the field. After transporting to the laboratory, the samples in the  
192 vials were stored at  $-20 \text{ }^{\circ}\text{C}$  until the analysis of CH<sub>4</sub> concentration. Before analysis,  
193 the vials were first thawed at room temperature and were then vigorously shaken for 5  
194 min to equilibrate the CH<sub>4</sub> concentrations between the porewater and the headspace.  
195 The gas samples were taken from the headspace of the vials and analyzed for CH<sub>4</sub>  
196 concentration with the above gas chromatograph (Ding et al. 2003).

197

198 **Determination of methane concentrations**

199 Methane concentrations in the headspace air samples were determined by gas  
200 chromatography (Shimadzu GC-2010, Kyoto, Japan) using a stainless steel Porapak Q  
201 column (2 m long, 4 mm outer diameter, 80/100 mesh). A flame ionization detector  
202 (FID) was used for the determination of the methane concentrations. The operating  
203 temperatures of the column, injector and detector for the determination of methane  
204 concentrations were adjusted to 70, 200 and 200 °C. The gas chromatograph was  
205 calibrated before and after each set of measurements using 1.01, 7.99 and 50.5 µL  
206 methane L<sup>-1</sup> in He (CRM/RM Information Center of China) as primary standards.

207

208 **Calculation of potential methane production, anaerobic oxidation, aerobic**  
209 **oxidation, and porewater dissolved CH<sub>4</sub> concentration**

210 Potential methane production, anaerobic oxidation, and aerobic oxidation rates were  
211 estimated by (Wassmann *et al.*, 1998):

212 
$$P = \frac{dc}{dt} \cdot \frac{V_H}{W_s} \cdot \frac{MW}{MV} \cdot \frac{T_{st}}{T_{st} + T}$$

213

214 where  $P$  is the potential rate of methane anaerobic oxidation, aerobic oxidation and  
215 production ( $\mu\text{g}^{-1} \text{g}^{-1} \text{d}^{-1}$ ),  $dc/dt$  is the recorded change in the mixing ratio of C  
216 (methane) in the headspace over time ( $\text{mmol mol}^{-1} \text{d}^{-1}$ ),  $V_H$  is the volume of the  
217 headspace (L),  $W_s$  is the dry weight of the soil (g),  $MW$  is the molecular weight of  
218 methane (g),  $MV$  is the molecular volume (L),  $T$  is the temperature (K) and  $T_{st}$  is the  
219 standard temperature (°K).

220 The concentration of CH<sub>4</sub> dissolved in the porewater was calculated following  
221 (Ding et al. 2003):

$$222 \quad C = \frac{Ch \cdot Vh}{22.4 \cdot Vp}$$

223

224 where *Ch* is the CH<sub>4</sub> concentration (μl l<sup>-1</sup>) in the air sample from the vials, *Vh* is the  
225 volume of air in the bottle (ml), and *Vp* is the volume of the porewater in the bottle  
226 (ml).

227

### 228 **Measurements of soil properties**

229 Total soil porewater (collected by centrifugation at 5000 r min<sup>-1</sup>) dissolved organic-C  
230 (DOC) concentration was measured using a TOC-V CPH total carbon analyzer  
231 (Shimadzu Scientific Instruments, Kyoto, Japan). Porewater (collected by  
232 centrifugation at 5000 r min<sup>-1</sup>) NO<sub>3</sub><sup>-</sup>, SO<sub>4</sub><sup>2-</sup> and Cl<sup>-</sup> concentrations were determined by  
233 ICS2100 ion chromatography (American Dionex Production, Sunnyvale, USA). Soil  
234 temperature, Eh and pH were measured with an Eh/pH/temperature meter (IQ Scientific  
235 Instruments, Carlsbad, USA) and salinity was measured using a 2265FS EC Meter  
236 (Spectrum Technologies Inc., Paxinos, USA). Total Fe content was determined by  
237 digesting fresh soil samples with 1 mol HCl L<sup>-1</sup>. Ferrous ions were extracted using  
238 1,10-phenanthroline and measured spectrometrically (Wang et al. 2012). Ferric  
239 concentration was calculated by subtracting the ferrous concentration from the total  
240 Fe concentration.

241

### 242 **Statistical analyses**

243 The significance of the differences in potential methane production, anaerobic  
244 oxidation, aerobic oxidation and dissolved methane, soil variables and other  
245 properties among the seasonal variation were assessed by One-Way ANOVA. We  
246 analyzed the relationships of the potentials of soil methane production, soil methane  
247 anaerobic oxidation, soil methane aerobic oxidation and dissolved methane among  
248 them and with soil DOC, soil temperature, Eh, pH, salinity, soil  $\text{NO}_3^-$ ,  $\text{SO}_4^{2-}$  and  $\text{Cl}^-$   
249 concentrations and plant biomass. Plot and time of sampling (month) were introduced  
250 into the models as random factors. If a variable was non-normally distributed we  
251 transform it to normalize its distribution. In concrete soil nitrate and soil ferric  
252 concentrations were log-transformed to reach their normal distribution. We used the  
253 “nlme” (Pinheiro et al. 2016) and “lme4” (Bates et al. 2015) R packages with the  
254 “lme” and “lmer” functions to conduct the mixed linear models. We chose the best  
255 model for each dependent variable using Akaike information criteria. We used the  
256 MuMIn (Barton 2012) R package in the mixed models to estimate the percentage of  
257 variance explained by the model. We presented in significant relationships the total  
258 variance explained by the model including the fixed and random factors ( $R^2c$ ) and  
259 also the variability explained by only the fixed factor ( $R^2m$ ).

260 We used Principal component analyses (PCA) to assess the multiple  
261 correlations among total potential methane production, anaerobic oxidation, aerobic  
262 oxidation and dissolved methane and environmental factor and the analyzed soil  
263 variables and their relative importance in the separation of soil samples from different  
264 seasons. The PCA were performed using Statistica 6.0 (StatSoft, Inc. Tule, Oklahoma,

265 USA).

266

## 267 **Results**

268

### 269 **Potential soil methane production, methane anaerobic oxidation, methane** 270 **aerobic oxidation, and dissolved methane along the year**

271 Potential soil methane production rates changed seasonally in the Shanyutan wetland  
272 of Minjiang River estuary (Figs. 2, 3), with a maximum value of  $57.4 \pm 7.7 \mu\text{g g}^{-1} \text{d}^{-1}$  in  
273 January 2013 and a minimum value of  $4.85 \pm 1.1 \mu\text{g g}^{-1} \text{d}^{-1}$  in August 2012. The annual  
274 average value was  $21.1 \pm 5.1 \mu\text{g g}^{-1} \text{d}^{-1}$ . In general, potential soil methane production  
275 rate was significantly higher in winter than that of the summer (Fig. 3,  $P < 0.05$ ).  
276 However, there were not significantly different among other seasons (Fig. 3,  $P > 0.05$ ).

277 Potential soil methane anaerobic oxidation rates changed seasonally in the  
278 Shanyutan wetland of Minjiang River estuary (Figs. 2, 3), with a maximum value of  
279  $41.8 \pm 13.4 \mu\text{g g}^{-1} \text{d}^{-1}$  in January 2013 and a minimum value of  $3.46 \pm 0.97 \mu\text{g g}^{-1} \text{d}^{-1}$  in  
280 August 2012. The annual average value was  $11.0 \pm 3.9 \mu\text{g g}^{-1} \text{d}^{-1}$ . In general, potential  
281 soil methane anaerobic oxidation production rate was significantly higher in winter  
282 than those of spring and autumn (Fig. 3,  $P < 0.05$ ). However, there were not  
283 significantly different among other seasons (Fig. 3,  $P > 0.05$ ).

284 Potential soil methane aerobic oxidation rates changed seasonally in the  
285 Shanyutan wetland of Minjiang River estuary (Figs. 2, 3), with a maximum value of  
286  $70.2 \pm 24.5 \mu\text{g g}^{-1} \text{d}^{-1}$  in January 2013 and a minimum value of  $6.55 \pm 1.42 \mu\text{g g}^{-1} \text{d}^{-1}$  in

287 May 2012. The annual average value was  $20.9 \pm 5.8 \mu\text{g g}^{-1} \text{d}^{-1}$ . In general, potential soil  
288 methane aerobic oxidation production rate was not significantly different among  
289 seasons (Fig. 3,  $P > 0.05$ ).

290 Dissolved methane in soil porewater changed seasonally in the Shanyutan  
291 wetland of Minjiang River estuary (Figs. 2, 3), with a maximum value of  $261 \pm 39$   
292  $\mu\text{mol l}^{-1}$  in August 2012 and a minimum value of  $7.52 \pm 0.37 \mu\text{mol l}^{-1}$  in January 2012.  
293 The annual average was  $62.9 \pm 20.6 \mu\text{mol l}^{-1}$ . In general, dissolved methane in soil  
294 porewater was significantly higher in summer than other seasons (Fig. 3,  $P < 0.05$ ).  
295 However, there were not significantly different among other seasons (Fig. 3,  $P > 0.05$ ).

296

### 297 **Relationship among potential soil methane production, methane anaerobic** 298 **oxidation, methane aerobic oxidation and dissolved methane along the year**

299

300 The linear mixed models showed that soil potential soil methane anaerobic oxidation,  
301 potential soil methane production and potential soil methane aerobic oxidation rates  
302 were positively related to each other (Table 1). The statistical models of the  
303 corresponding three relationships (including plots and time as random factors) had  
304 very high total significance ( $R^2\text{c}=0.99$ ,  $P < 0.0001$ ) (Table 1). Methane concentrations  
305 in soil porewater were negatively correlated with potential soil anaerobic oxidation  
306 rates ( $R^2\text{m}=0.15$ ,  $R^2\text{c}=0.91$ ), potential soil methane production rates ( $R^2\text{m}=0.24$ ,  
307  $R^2\text{c}=0.99$ ) and potential soil aerobic methane oxidation ( $R^2\text{m}=0.13$ ,  $R^2\text{c}=0.94$ ) (Table  
308 1).

309

310 **Seasonality in environment variables**

311 Soil temperature changed seasonally in the Shanyutan wetland of Minjiang River  
312 estuary (Fig. 4), with a maximum value of  $31.5\pm 0.1$  °C in September 2012 And a  
313 minimum value of  $12.4\pm 0.6$  °C in February 2013. The annual average was  
314  $21.4\pm 2.0$  °C.

315 Soil ferric concentration changed seasonally in the Shanyutan wetland of  
316 Minjiang River estuary (Fig. 4), with a maximum value of  $87.0\pm 9.9$  mg g<sup>-1</sup> in June  
317 2012. In September 2012 which is the lowest value was  $12.2\pm 2.3$  mg g<sup>-1</sup>, and annual  
318 average was  $37.8\pm 6.9$  mg g<sup>-1</sup>.

319 Soil pH changed seasonally in the Shanyutan wetland of Minjiang River estuary  
320 (Fig. 4), with a maximum value of  $7.62\pm 0.01$  in January 2013 and a minimum value  
321 of  $6.30\pm 0.02$  in November 2012. The annual average was  $6.72\pm 0.11$ .

322 Soil Eh changed seasonally in the Shanyutan wetland of Minjiang River estuary  
323 (Fig. 4), with a maximum value of  $41.1\pm 0.7$ mV in November 2012. In January 2013  
324 that had the lowest value, was  $-36.5\pm 0.7$  mV and annual average was  $16.3\pm 6.5$ mV.

325 Soil salinity changed seasonally in the Shanyutan wetland of Minjiang River estuary  
326 (Fig. 4), with a maximum value of  $4.21\pm 0.71$  mS cm<sup>-1</sup> in April 2012. In February  
327 2012 the lowest value was  $1.91\pm 0.33$  mS cm<sup>-1</sup> and annual average was  $3.08\pm 0.21$  mS  
328 cm<sup>-1</sup>.

329 Dissolved sulfate in soil porewater concentration changed seasonally in the  
330 Shanyutan wetland of Minjiang River estuary (Fig. 4), with a maximum value of  
331  $362\pm 36$  mg l<sup>-1</sup> in December 2012. In February 2013 the lowest value was  $128\pm 12$  mg

332 l<sup>-1</sup> and annual average was 227±25 mg l<sup>-1</sup>.

333 Dissolved nitrate in soil porewater concentration changed seasonally in the  
334 Shanyutan wetland of Minjiang River estuary (Fig. 4), with a maximum value of  
335 2.46±0.44 mg l<sup>-1</sup> in December 2012. In October 2012 the lowest value were  
336 0.106±0.039 mg l<sup>-1</sup> and annual average was 0.828±0.212 mg l<sup>-1</sup>.

337 Dissolved chloridion in soil porewater concentration changed seasonally in the  
338 Shanyutan wetland of Minjiang River estuary (Fig. 4), with a maximum value of  
339 4595±279 mg l<sup>-1</sup> in November 2012. In August 2012 the lowest value were 1412±92  
340 mg l<sup>-1</sup>, and annual average was 2821±283 mg l<sup>-1</sup>.

341 Plant biomass changed seasonally in the Shanyutan wetland of Minjiang River  
342 estuary (Fig. 4), with a maximum value of 2313±657 g m<sup>-2</sup> in December 2012. April  
343 2012 had the lowest value were 759±320 g m<sup>-2</sup>, and annual average was 1462±198 g  
344 m<sup>-2</sup>.

345 Air temperature changed seasonally in the Shanyutan wetland of Minjiang River  
346 estuary (Fig. 4), with a maximum value of 35.5±0.0 °C in July 2012. February 2013  
347 had the lowest value was 10.2±0.1 °C, and annual average was 23.0±2.4 °C.

348

349 **Potential soil methane production, methane anaerobic oxidation, aerobic**  
350 **oxidation rates, dissolved methane, and their relationships with soil properties**

351

352 The linear mixed models showed that potential soil methane production rates were  
353 positively related to soil pH ( $R^2_m=0.15$ ,  $R^2_c=0.90$ ) and negatively related to soil Eh  
354 ( $R^2_m=0.15$ ,  $R^2_c=0.90$ ) and with soil temperature ( $R^2_m=0.13$ ,  $R^2_c=0.90$ ) (Table 1).



355 Potential soil methane anaerobic oxidation rates were positively related to soil pH  
356 ( $R^2_m=0.14$ ,  $R^2_c=0.99$ ) and negatively with soil Eh ( $R^2_m=0.15$ ,  $R^2_c=0.99$ ) (Table 1).  
357 Finally, methane concentration in soil pore water was positively related to soil  
358 temperature ( $R^2_m=0.32$ ,  $R^2_c=0.99$ ) (Table 1).

359 The PCA analysis was completely consistent with the previous commented  
360 univariant analyses. Soil samples collected in summer were located across the PC1  
361 axis coinciding with higher porewater methane concentrations, higher soil and air  
362 temperature and soil Eh and lower soil pH and potential soil methane production and  
363 oxidation rates, both anaerobic and aerobic (Fig. 5). Just the contrary patterns were  
364 related to soil samples collected in winter that were placed in the other side of the PC1  
365 axis (Fig. 5).

366

## 367 **Discussion**

### 368 **Seasonal variation of potential methane production, anaerobic oxidation, aerobic** 369 **oxidation and dissolved methane**

370 Potential soil methane production rate was higher in winter than in summer. In winter  
371 there are lots of the plant litter input and thereby the soil carbon concentration which  
372 is the most important substrate for methane production, increases (Yagi and Minami  
373 1990), thereby promoting the soil methane production (Van der Gon and Neue 1995).  
374 Moreover, the optimum temperature of methane production is about 20 C (Wagner  
375 and Pfeiffer 1997) and in our study, the average temperature was 14.4 and 29.2 C in  
376 winter and summer, respectively, thus more closely to the optimum for soil methane  
377 production in winter than in summer. Moreover, in summer, the plant growth was

378 higher than in other seasons, and more O<sub>2</sub> was released into the soil, generating soil  
379 redox conditions which were not proper for methane production. Furthermore, in  
380 Fujian province the acid rain was high and the summer was main rainy season, so the  
381 soil pH decreased in summer and thereby inhibiting methane production. In contrast,  
382 winter was the dry season and had relatively higher pH, favoring methane production.  
383 In our study, the linear mixed models showed that potential soil methane production  
384 rates were positively related to soil pH and negatively related to soil Eh and  
385 temperature.

386 Potential soil methane anaerobic oxidation rates were also higher in winter than  
387 those of spring and autumn, and also than those of summer, although, not significantly  
388 different. As commented in Fujian province acid rain is high and the summer was the  
389 main rainy season, so in summer the soil pH decrease and thereby inhibited the  
390 methane anaerobic oxidation microbial activity. In contrast, winter was the dry season  
391 with relatively higher pH which was favorable to the growth of microbes involved in  
392 methane anaerobic oxidation. In our study, supporting these comments, the linear  
393 mixed models showed that potential soil methane anaerobic oxidation rates were  
394 positively related to soil pH. Moreover, Nauhaus et al. (2002) showed that the  
395 optimum temperature value was between 4-16 ° C for methane anaerobic oxidation.  
396 In our study, the average seasonal temperatures were 18.7, 29.2, 23.3 and 14.4 ° C for  
397 spring, summer, autumn and winter respectively, so obviously, the winter was the  
398 most suitable season for methane anaerobic oxidation.

399 Potential soil methane aerobic oxidation rate was not significantly different

400 among seasons. However, there was still a trend to higher values in winter than in the  
401 other seasons. The reason would be the same than for methane anaerobic oxidation,  
402 that winter was the dry season, with relative higher soil pH. In our study, the linear  
403 mixed models showed that potential soil methane aerobic oxidation rates were also  
404 positively related to soil pH. Moreover, Dasselaar et al. (1998) found that temperature  
405 promotion of the methane aerobic oxidation was higher when the temperature was  
406 4~12°C than when it was 12~18 °C. In our study, the temperatures closer to 12°C were  
407 those of winter.

408 Dissolved methane in soil porewater was instead higher in summer than in the  
409 other seasons, which had no significant differences among them. The dissolved  
410 methane in soil porewater resulted from many factors, such as methane production,  
411 oxidation and transportation, etc. The lower summer methane anaerobic and aerobic  
412 oxidation were likely the most determinant factors of these higher values of dissolved  
413 methane in summer.

414 The soils with highest soil pH and lowest Eh were those that showed the highest  
415 potentials of methane production and anaerobic oxidation. But the most interesting  
416 result was that soil samples with the highest soil pH and lowest Eh were also those  
417 that showed the highest potentials of aerobic methane oxidation. Consistently, with  
418 these results, Kettunen et al (1999) also observed that the maximum potential capacity  
419 to methane aerobic oxidation was higher in soils below than above table level. Similar  
420 results have also been observed in boreal pine fen areas (Saarino et al. 1998).

421 These results thus suggested a buffer effect in the methane balance in wetland

422 areas. Environmental and soil conditions favoring methane production are also more  
423 favorable for methane anaerobic oxidation during the same circumstances and also in  
424 drier periods, for aerobic methane oxidation. In fact alternation between wet-dry  
425 periods related to wetland source-sink of methane have been observed everywhere  
426 (Juutinen et al. 2003; Knorr et al. 2008; Brown et al. 2014; Goodrich et al. 2015). But  
427 the fact that as more favorable the conditions of soil are to produce methane higher is  
428 also its capacity to oxidize methane was observed in both flooded (anaerobic) and dry  
429 (aerobic) periods. This observation warrants future research to corroborate this  
430 possible general pattern.

431

### 432 **Relationship among potential methane production, anaerobic oxidation, aerobic** 433 **oxidation and dissolved methane**

434

435 Potential methane anaerobic oxidation and potential methane production showed a  
436 very significant positive correlation. This pattern has been previously observed in  
437 tropical and boreal wet soils and peatlands where these two variables have also shown  
438 to be significantly correlated, in agreement with our results (Smemo and Yavitt 2011;  
439 Blazewicz et al. 2012). The relationship between methane anaerobic oxidation and  
440 methane production was mainly related to the functional microbial association, where  
441 anaerobic methanotroph (ANME) *archaea* was the main microorganism involved in  
442 methane production and can also participate in the methane anaerobic oxidation  
443 (Alperin and Hoehler 2009; Lloyd et al. 2011). Methane production *archaea* can

444 oxidize methane as observed in pure culture experiments (Moran et al. 2005; Joye and  
445 Samarkin 2009; Roberts and Aharon 1994). In addition, there was a significant  
446 positive correlation between methane anaerobic oxidation and methane aerobic  
447 oxidation in this study. Recent studies have demonstrated that aerobic and anaerobic  
448 methane oxidation bacteria can coexist in the same places, suggesting that the  
449 proportion of different species can depend on the oxygen and methane availability and  
450 also that diverse microbial activity was important to sustain methanotrophic activity  
451 (Siniscalchi et al., 2017). Eller et al. (2005) observed the co-occurrence of methane  
452 aerobic and anaerobic process in the same soil samples and water columns. Moreover,  
453 potential methane aerobic oxidation and potential methane production processes  
454 showed a very significant positive correlation as expected from methane being the  
455 substrate of methane oxidation (Nesbit and Breitenbeck 1992). However, negative  
456 relationships between methane concentrations in soil porewater and the studied  
457 potential methane production rates and also potential soil methane oxidation, both in  
458 anaerobic and aerobic conditions were then observed. These results suggest that  
459 methane production was not the most determinant factor controlling the dissolved  
460 methane in soil porewater. However, porewater dissolved methane was directly  
461 limited by methane anaerobic oxidation and aerobic oxidation in Minjiang estuarine  
462 wetland. These results were not in agreement with the fact that methane storage was  
463 the key factor in the oxidation of methane in coastal sulphate-rich marine sediments  
464 (Nauhaus et al. 2002; Treude et al. 2005; Orcutt et al. 2005). This possible  
465 explanation was consistent with the linear mixed models showing the inverse

466 relationships between methane present in porewater and the soil potential capacity of  
467 methane production and also of methane oxidation.

468

## 469 **Conclusions**

470 1. Potential methane production, anaerobic oxidation and aerobic oxidation were all  
471 shown to be higher in winter than other seasons, however, the dissolved methane in  
472 soil porewater was higher in summer than other seasons.

473 2. The concentration of soil pH and Eh are the studied factors that had the stronger  
474 relationships with potential soil methane production and anaerobic and aerobic  
475 oxidation rates. This showed thus, strong relationships among the different soil  
476 metabolic methane processes and the basic potential chemical activities of soils.

477 3. The positive correlation between methane production, methane anaerobic oxidation  
478 and methane aerobic oxidation suggested that at least some of the soil conditions and  
479 of the overall set of microorganisms communities that favor methane production also  
480 favor its oxidation.

481 4. The negative relationships between methane concentrations in soil porewater with  
482 the potential soil of methane production and oxidation in anaerobic and aerobic  
483 conditions suggest that the higher the soil potential to produce methane, the higher the  
484 potential soil capacity to oxidize methane in aerobic and anaerobic conditions.

485

## 486 **Acknowledgments**

487 The authors would like to thank Hongchang Ren, Xuming Wang and Dongping Zeng

488 for their assistance in field sampling and laboratory analysis. Funding was provided  
489 by the National Science Foundation of China (41571287, 31000209), Natural Science  
490 Foundation Key Programs of Fujian Province (2018R1101006-1), Fujian Provincial  
491 Outstanding Young Scientists Program (2017), the European Research Council  
492 Synergy grant ERC-SyG-2013-610028 IMBALANCE-P, the Spanish Government  
493 grant CGL2016-79835-P and the Catalan Government grant SGR 2014-274.

494

#### 495 **Conflicts of Interest**

496 The authors declare no conflicts of interest.

497

#### 498 **References:**

- 499 Alperin MJ, Hoehler TM (2009) Anaerobic methane oxidation by  
500 archaea/sulfate-reducing bacteria aggregates: 1. Thermodynamic and physical  
501 constraints. *American Journal of Science* 309:869-957
- 502 Barnes RO, Goldberg ED (1976) Methane production and consumption in anaerobic  
503 marine sediment. *Geology* 4:297-300
- 504 Barton K (2012) MuM. In: Multi-model inference. R package version 1.7.2.  
505 <http://CRAN.R-project.org/package=MuMIn>. at [http://cran.r-project.org/](http://cran.r-project.org/package=MuMIn)  
506 [package=MuMIn](http://cran.r-project.org/package=MuMIn)>
- 507 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects  
508 Models Using lme4. *Journal of Statistical Software* 67:1-48
- 509 Bergman I, Klarqvist M, Nilsson M (2000) Seasonal variation in rates of methane  
510 production from peat of various botanical origins: effects of temperature and  
511 substrate quality. *FEMS Microbiology Ecology* 33:181-189
- 512 Blazewicz S, Petersen DG, Waldrop MP, Firestone MK (2012) Anaerobic oxidation of  
513 methane in tropical and boreal soils: ecological significance in terrestrial

514 methane cycling. *Journal of Geophysical Research* 117:G02033.

515 Brown, BG, Humpherys ER, Moore TR, Roulet NT, Lefleur PM (2014) Evidence for  
516 a nonmonotonic relationships between ecosystem-scale peatland methane  
517 emissions and water table depth. *Journal of Geophysical*  
518 *Research-Biogeosciences* 119:826-835

519 Buckley DH, Baumgartner LK, Visscher PT (2008) Vertical distribution of methane  
520 metabolism in microbial mats of the Great Sippewissett salt marsh.  
521 *Environmental Microbiology* 10:967-977

522 Costanza R, d'Arge R, de Groot RD, Farber S, Grasso M, Hannon B, Limburg K,  
523 Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The  
524 value of the world's ecosystem services and natural capital. *Nature* 387:253-260

525 Cassman, K. G. et al. (1998) Opportunities for increased nitrogen-use efficiency from  
526 improved resource management in irrigated rice systems. *Field Crops Research*  
527 56:7-39.

528 Crutzen P., The role of methane in atmospheric chemistry and climate, in: Von  
529 Engelhardt W., Leonhard-Marek S., Breves G., Giesecke D. (Eds.), *Ruminant*  
530 *Physiology: Digestion, Metabolism, Growth and Reproduction*, Ferdinand Enke  
531 Verlag, Stuttgart, 1995, pp. 291-316

532 Dasselaar AP, Beusichen ML, Oenema O (1998) Effects of soil moisture content and  
533 temperature on methane uptake by grasslands on sandy soils [J]. *Plant Soil*  
534 204:213-222

535 Datta A, Yeluripati JB, Nayak DR, Mahata KR, Santra SC, Adhya TK (2013)  
536 Seasonal variation of methane flux from coastal saline rice field with the  
537 application of different organic manures. *Atmospheric Environment* 66:114–122

538 Deutzmann JS, Schink B (2011) Anaerobic oxidation of methane in sediments of lake  
539 Constance, an oligotrophic freshwater lake. *Applied and Environmental*  
540 *Microbiology* 77:4429-4436

541 Ding WX, Cai ZC, Tsuruta H, Li XP (2003) Key factors affecting spatial variation of  
542 methane emissions from freshwater marshes. *Chemosphere* 51:167–173



543 Eller G, Kanel L, Kruger M (2005) Cooccurrence of aerobic and anaerobic methane  
544 oxidation in the water column of Lake Plubsee. *Applied Environment*  
545 *Microbiology* 71:8925–8928

546 Ettwig KF, Bulter MK, Paslier DL, et al. (2010) Nitrite-driven anaerobic methane  
547 oxidation by oxygenic bacteria. *Nature* 464:543-548

548 Gauthier M, Bradley RL, Simek M (2013) Anaerobic methane oxidation may be more  
549 prevalent in surface soils than was originally thought//EGU General Assembly  
550 Conference Abstracts 15:14169

551 Goodrich JP, Campbell DI, Roulet NT, Clearwater MJ (2015) Overriding control of  
552 methane flux temporal variability by water table dynamics in a southern  
553 hemisphere, raised bog. *Journal of Geophysical Research* 120:819-831

554 Hartzell J L, Jordan R E. (2012) Shifts in the relative availability of phosphorus and  
555 nitrogen along estuarine salinity gradients. *Biogeochemistry* 107:489-500

556 Hoehler TM, Alperin MJ, Albert DB, et al. (1994) Field and laboratory studies of  
557 methane oxidation in an anoxic marine sediment-evidence for a  
558 methanogen-sulfate reducer consortium. *Global Biogeochemical Cycles*  
559 8:451-463

560 IPCC (2014). Intergovernmental Panel on Climate Change, IPCC, 2014. *Climate*  
561 *Change 2014: Mitigation of Climate Change. Contribution of Working Group III*  
562 *to the Fifth Assessment Report of the Intergovernmental Panel on Climate*  
563 *Change* [Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Farahani, E., Kadner, S.,  
564 Seyboth, K., Adler, A., Baum, I., Brunner, S., Eickemeier, P., Kriemann, B.,  
565 Savolainen, J., Schlömer, S., von Stechow, C., Zwickel T. & Minx, J. C. (eds.)].  
566 Cambridge University Press, Cambridge, United Kingdom & New York, NY,  
567 USA. 1435 p.

568 Iversen N, Blackburn TH (1981) Seasonal rates of methane oxidation in anaerobic  
569 marine sediments. *Applied and Environmental Microbiology* 41:1295-1300

570 Joye SB, Samarkin VA (2009) Metabolic variability in seafloor brines revealed by  
571 carbon and sulphur dynamics. *Nature Geoscience* 2:349-354

572 Juutinen S, Alm J, Larmola T, Huttunen JT, Moreno M, Saarnio S, Martikainen PJ,

573 Silvola J (2003) Methane (CH<sub>4</sub>) release from litoral wetlands of Boreal lakes  
574 during an extended flooding period. *Global Change Biology* 9:413-424

575 Kettunen A, Kaitala V, Lehtinen A, Lohila A, Alm J, Silvola J, Martikainen PJ (1999)  
576 Methane production and oxidation potentials in relation to water table  
577 fluctuations in two boreal mires. *Soil Biology and Biochemistry* 31:1741-1749

578 Knorr KH, Oosterwoud MR, Blodau C (2008) Experimental drought alters rates of  
579 soil respiration and methanogenesis but not carbon exchange in soil of a  
580 temperate fen. *Soil Biology and Biochemistry* 40:1781-1791

581 Kniemeyer O, Musat F, Sievert SM, et al. (2007) Anaerobic oxidation of short-chain  
582 hydrocarbons by marine sulphate-reducing bacteria. *Nature* 449:898-901

583 Krüger M, Eller G, Conrad R, et al. (2002) Seasonal variations in CH<sub>4</sub> oxidation and  
584 pathways of CH<sub>4</sub> production in rice fields determined by stable carbon isotopes  
585 and specific inhibitors. *Global Change Biology* 8:265-280

586 Krüger M, Treude T, Wolters H, et al. (2005) Microbial methane turnover in different  
587 marine habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology* 227:6-17

588 Laanbroek HJ (2010) Methane emission from nature wetland: interplay between  
589 emergent macrophytes and soil microbial process. *Annals of Botany* 105:141-153

590 Le Mer J., Roger P. (2001) Production, oxidation, emission and consumption of  
591 methane by soils: a review. *European Journal of Soil Biology* 37:25–50

592 Liu JQ, Zeng CS, Chen N (2006) Research of Minjiang River estuary wetland.  
593 Beijing: Science Press

594 Lloyd KG, Alperin MJ, Teske A (2011) Environmental evidence for net methane  
595 production and oxidation in putative anaerobic methanotrophic (ANME) archaea.  
596 *Environmental Microbiology* 13:2548-2564

597 Moran JJ, Beal EJ, Vrentas JM, et al. (2008) Methyl sulfides as intermediates in the  
598 anaerobic oxidation of methane. *Environmental Microbiology* 10:162-173

599 Moran JJ, House CH, Freeman KH, et al. (2005) Trace methane oxidation studied in  
600 several Euryarchaeota under diverse conditions. *Archaea* 1:303-309

601 Moran JJ, Beal EJ, Vrentas JM, Orphan VJ, Freeman KH, House CH (2008) Methyl  
602 sulfides as intermediates in the anaerobic oxidation of methane. *Environmental*

603 Microbiology 10:162-173

604 Müller V, Blaut M, Gottschalk G. (1993) Bioenergetics of methanogenesis. In Ferry J  
605 G, editor. Methanogenesis: ecology, physiology, biochemistry, and genetics. New  
606 York: Chapman and Hall, pp. 360-406

607 Nauhaus K, Boetius A, Krüger M, Widdel F (2002) In vitro demonstration of  
608 anaerobic oxidation of methane coupled to sulphate reduction in sediment from a  
609 marine gas hydrate area. Environmental Microbiology 4:296-305

610 Nesbit SP, Breitenbeck GA (1992) A laboratory study of factors influencing methane  
611 uptake by soils [J]. Agriculture Ecosystems and Environment 41:39-54

612 Neubauer SC, Toledo-Duran GE, Emerson D (2007) Returning to their roots:  
613 iron-oxidizing bacteria enhance short-term plaque formation in the wetland-plant  
614 rhizosphere. Geomicrobiology Journal 24:65–73

615 Neue, H. U. (1997) Fluxes of methane from rice fields and potential for mitigation.  
616 Soil Use Management 13: 258-267.

617 Orcutt B, Boetius A, Elvert M, Samarkin V, Joye SB (2005) Molecular  
618 biogeochemistry of sulfate reduction, methanogenesis and the anaerobic  
619 oxidation of methane at Gulf of Mexico cold seeps. Geochimica et  
620 Cosmochimica Acta 69:4267-4281

621 Pinheiro J, Bates D, DebRoy S, Sarkar D, Core TR (2016) *nlme*: Linear and Nonlinear  
622 Mixed Effects Models. R *package* version 3.1-126, <http://CRAN>

623 Raghoebarsing AA, Pol A, van des Pas-Schoonen KT, Smolders AJP, Ettwig KF,  
624 Rijpstra, WIC, Schouten, S, Damsté JSS, den Camp HJMO, Jetten MSM, Strous  
625 M (2006) A microbial consortium couples anaerobic methane oxidation to  
626 denitrification. Nature 440:918-921

627 Ro S, Seanjan P, Tulaphitak T (2011) Sulfate content influencing methane production  
628 and emission from incubated soil and rice-planted soil in Northeast Thailand. Soil  
629 Science and Plant Nutrition 57:833–842

630 Roberts HH, Aharon P (1994) Hydrocarbon-derived carbonate buildups of the  
631 northern Gulf of Mexico continental slope: a review of submersible investigations.  
632 Geo-Marine Letters 14:135-148

633 Saarnio S, Alm, Silvola J, Lohila A, Nykanen H, Martikainen PJ (1997) Seasonal  
634 variation in CH<sub>4</sub> emissions and production and oxidation potentials at microsites  
635 on an oligotrophic pine fen. *Oecologia* 110:414-422

636 Shima S, Thauer RK (2005) Methyl-coenzyme M reductase and the anaerobic  
637 oxidation of methane in methanotrophic Archaea. *Current Opinion in*  
638 *Microbiology* 8:643-648

639 Simas T, Nunes JP, Ferreria JG (2001) Effects of global climate change on coastal salt  
640 marshes. *Ecological Modelling* 139:1-15

641 Singh JS (2011) Methanotrophs: the potential biological sink to mitigate the global  
642 methane load. *Current Science* 100:29-30

643 Siniscalchi, L.A.B., Babelo Leite, L., Oliveira, G, Chernicharo, C.A.L., Calabria de  
644 Araújo, J. (2017). Illumina sequencing-based analysis of a microbial community  
645 enriched under anaerobic methane oxidation condition coupled to denitrification  
646 revealed coexistence of aerobic and anaerobic methanotrophs. *Environmental*  
647 *Science Pollution Research* 24:16751-16764.

648 Smemo KA, Yavitt JB (2011) Anaerobic oxidation of methane: an underappreciated  
649 aspect of methane cycling in peatland ecosystems? *Biogeosciences* 8:779-793

650 Smemo KA, Yavitt JB (2007) Evidence for anaerobic CH<sub>4</sub> oxidation in freshwater  
651 peatlands. *Geomicrobiology Journal* 24:583-597

652 Song CC, Zhang JB, Wang YY, Wang YS, Zhao ZC (2008) Emission of CO<sub>2</sub>, CH<sub>4</sub> and  
653 N<sub>2</sub>O from freshwater marsh in north of China. *Journal of Environmental*  
654 *Management* 88:428–436

655 Supparattanapan S, Saenjan P, Quantin C, et al. (2009) Salinity and organic  
656 amendment effects on methane emission from a rain-fed saline paddy field. *Soil*  
657 *Science and Plant Nutrition* 55:142-149

658 Tong C, Wang WQ, Huang JF, Gauci V, Zhang L.H, Sheng ZC (2012) Invasive alien  
659 plants increase CH<sub>4</sub> emissions from a subtropical tidal estuarine wetland.  
660 *Biogeochemistry* 111:677-693

661 Treude T, Krüger M, Boetius A, Jorgensen AB (2005). Environmental control on  
662 anaerobic oxidation of methane in the gassy sediments of Eckernförde Bay

663 (German Baltic). *Limnology and Oceanography* 50:1771-1786

664 Van der Gon DHAC, Neue HU (1995) Influence of organic matter incorporation on  
665 methane emission from wetland rice field [J]. *Global Biogeochemical Cycles*  
666 9:11-22

667 Wagner D, Pfeiffer EM (1997) Two temperature optima of methane production in a  
668 typical soil of the Elbe river marshland [J]. *FEMS Microbiology Ecology*  
669 22:145-153

670 Wang WQ, Li PF, Zeng, CS, Tong C (2012) Evaluation of silicate iron slag as a  
671 potential methane mitigating method. – *Advances in Materials Research*  
672 468:1626–1630

673 Wang C, Lai DYF, Sardans J, Wang W, Zeng C, Peñuelas J (2017) Factors Related  
674 with CH<sub>4</sub> and N<sub>2</sub>O Emissions from a Paddy Field: Clues for Management  
675 implications. *PLOS ONE* 12:e0169254

676 Wang WQ, Tong C, Zeng, CS (2010) Stoichiometry characteristics of carbon,  
677 nitrogen, phosphorus and anaerobic carbon decomposition of wetland soil of  
678 different texture. – *China Environment Sciences* 30:1369–1374

679 Wassmann R, Neue HU, Bueno C, Lantin RS, Alberto MCR, Buendia LV, Bronson K,  
680 Papen H, Rennenberg H (1998) Methane production capacities of different rice  
681 soil derived from inherent and exogenous substrates. – *Plant Soil* 203:227–237

682 Wrede C, Brady S, Rockstroh S, et al. (2012) Aerobic and anaerobic methane  
683 oxidation in terrestrial mud volcanoes in the Northern Apennines. *Sedimentary*  
684 *Geology* 263:210-219

685 Yagi K, Minami K (1990) Effect of organic matter applications on methane emission  
686 from some Japanese paddy fields [J]. *Soil Science and Plant Nutrition* 36:599-610

687 Zheng CH, Zeng CS, Chen ZQ, Lin MC (2006) A study on the changes of landscape  
688 pattern of estuary wetlands of the Minjiang River. *Wetland Science* 4:29–34.

689 Zhou LJ, Tu YY, Song YC (2006) The biodiversity of wetland and its prevention  
690 measures in Min River Estuary. *Ecological Science* 25:330–334.

691

692 Table 1. Significant observed relationships of the potentials of soil methane  
 693 production, soil methane anaerobic oxidation and soil methane aerobic oxidation  
 694 among them and with soil properties. Plot and time of sampling (month) were  
 695 introduced in the models as random factors.

model <- lme(Variable~fixed factor, data=dades, random=~1 plot/time,method="REML")			
Variable	Fixed factor	Fixed factor statistics	Model statistics ( $R^2_m$ =fixed factor, $R^2_c$ =fixed + random factor)
Potential soil anaerobic CH <sub>4</sub> oxidation	Potential soil CH <sub>4</sub> production	Estimates=0.578 F=43.7 P<0001	$R^2_m$ =0.56 $R^2_c$ =0.99
Potential soil aerobic CH <sub>4</sub> oxidation	Potential soil CH <sub>4</sub> production	Estimates=0.707 F=21.2 P<0001	$R^2_m$ =0.38 $R^2_c$ =0.99
Potential soil aerobic CH <sub>4</sub> oxidation	Potential soil anaerobic CH <sub>4</sub> oxidation	Estimates=1.14 F=49.0 P<0001	$R^2_m$ =0.58 $R^2_c$ =0.99
CH <sub>4</sub> pore-water soil concentration	Potential soil CH <sub>4</sub> production	Estimates=-0.029 F=11.8 P=0.0016	$R^2_m$ =0.24 $R^2_c$ =0.91
CH <sub>4</sub> pore-water soil concentration	Potential soil anaerobic CH <sub>4</sub> oxidation	Estimates=-0.42 F=6.31 P=0.017	$R^2_m$ =0.15 $R^2_c$ =0.91
CH <sub>4</sub> pore-water soil concentration	Potential soil aerobic CH <sub>4</sub> oxidation	Estimates=-0.46 F=5.09 P=0.031	$R^2_m$ =0.13 $R^2_c$ =0.94
Potential soil anaerobic CH <sub>4</sub> oxidation	Soil pH	Estimates=6.17 F=5.47 P=0.026	$R^2_m$ =0.14 $R^2_c$ =0.99
Potential soil anaerobic CH <sub>4</sub> oxidation	Soil Eh	Estimates=-0.016 F=5.89 P=0.021	$R^2_m$ =0.15 $R^2_c$ =0.99
Potential soil CH <sub>4</sub> production	Soil pH	Estimates=5.80 F=6.55 P=0.015	$R^2_m$ =0.15 $R^2_c$ =0.90
Potential soil CH <sub>4</sub> production	Soil Temperature	Estimates=-0.045 F=5.87 P=0.021	$R^2_m$ =0.13 $R^2_c$ =0.90
Potential soil CH <sub>4</sub> production	Soil Eh	Estimates=-0.015 F=6.76 P=0.014	$R^2_m$ =0.15 $R^2_c$ =0.90
CH <sub>4</sub> pore-water soil concentration	Soil Temperature	Estimates=0.082 F=16.4 P<0001	$R^2_m$ =0.32 $R^2_c$ =0.99

696 **Figure legends**

697 **Fig. 1.** Study area and sampling site (▲) in southeastern China.

698 **Fig. 2.** Monthly variation of potential soil methane production rate, potential soil  
699 methane anaerobic oxidation, potential soil methane aerobic rate, and dissolved  
700 methane concentration in soil porewater.

701 **Fig. 3.** Seasonal values of potential soil methane production rate (A), potential soil  
702 methane anaerobic oxidation rate (A), potential soil methane aerobic oxidation rate  
703 (A), and dissolved methane concentration in soil porewater (B). Different letters  
704 indicate significantly different among seasons.

705 **Fig. 4.** Monthly variation of soil properties (A), porewater properties (B), plant  
706 biomass (C), and air temperature (D).

707 **Fig. 5.** Principal component analyses (PCA) to observe the multiple correlations  
708 among potential soil methane anaerobic oxidation, potential soil methane production,  
709 potential soil methane aerobic methane oxidation and the environmental factors and  
710 the analyzed soil variables. We represented the position of different cases (soil  
711 samples) (a) and the loads of the commented variables (b) in the layout generated by  
712 the two first PCA axes (explaining together a 52.0% of the total variance). Ait T<sup>a</sup> =  
713 Air temperature, Cl =concentration of Cl<sup>-</sup> in soil, Eh = soil potential redox, Fe<sup>3+</sup> =  
714 Soil Fe<sup>3+</sup> concentration, Maerox=Potential soil methane aerobic oxidation,  
715 Manaox=Potential soil methane anaerobic oxidation, Mprod=Potential soil methane  
716 production, Msoil=concentration of methane in soil porewater, pH = soilpH,  
717 salinity=soil salinity, Soil T<sup>a</sup> =soil temperature, sulfate=soil sulfate concentration, aut

718 = autumn, su = summer, sp = spring, wi = winter.



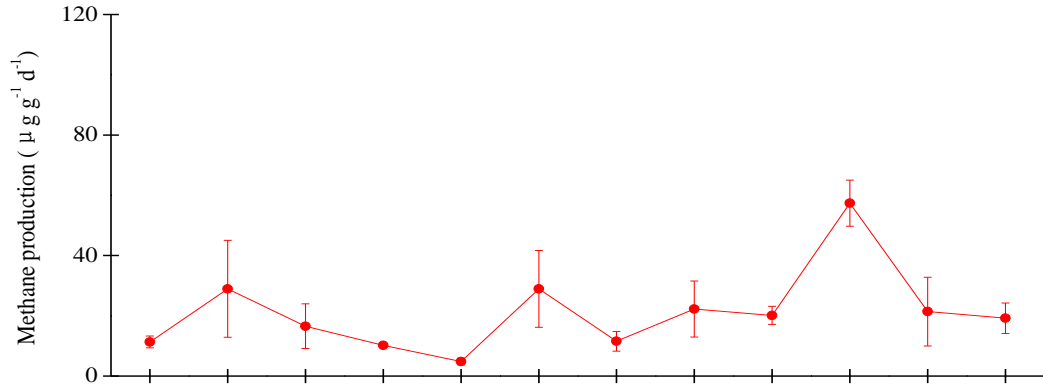
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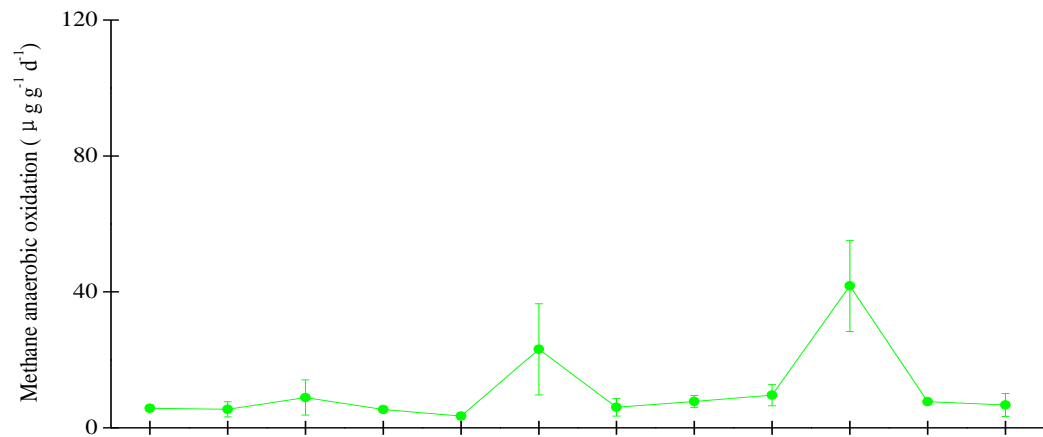
746 **Fig. 1.**

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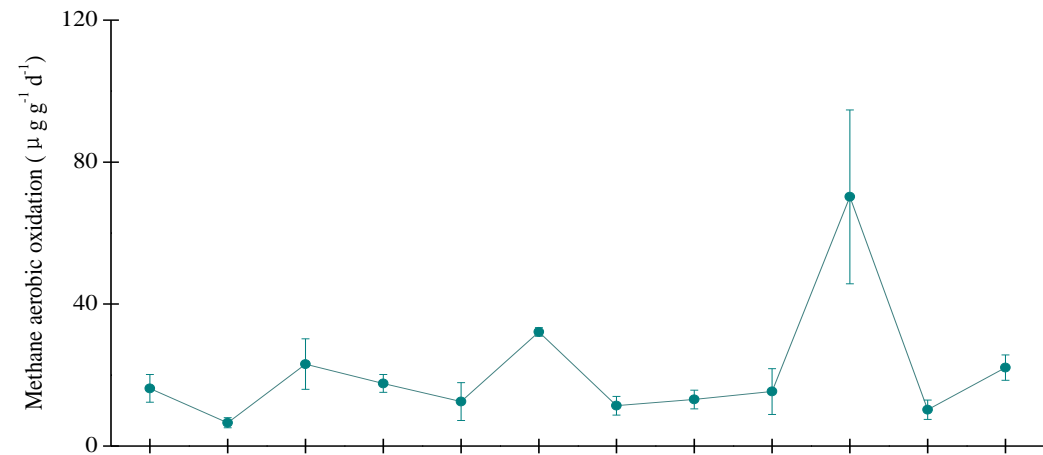
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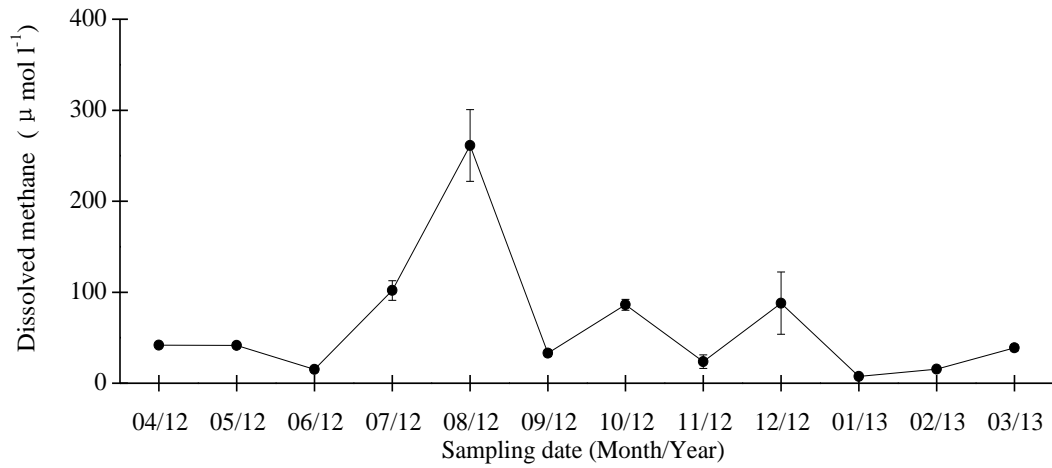
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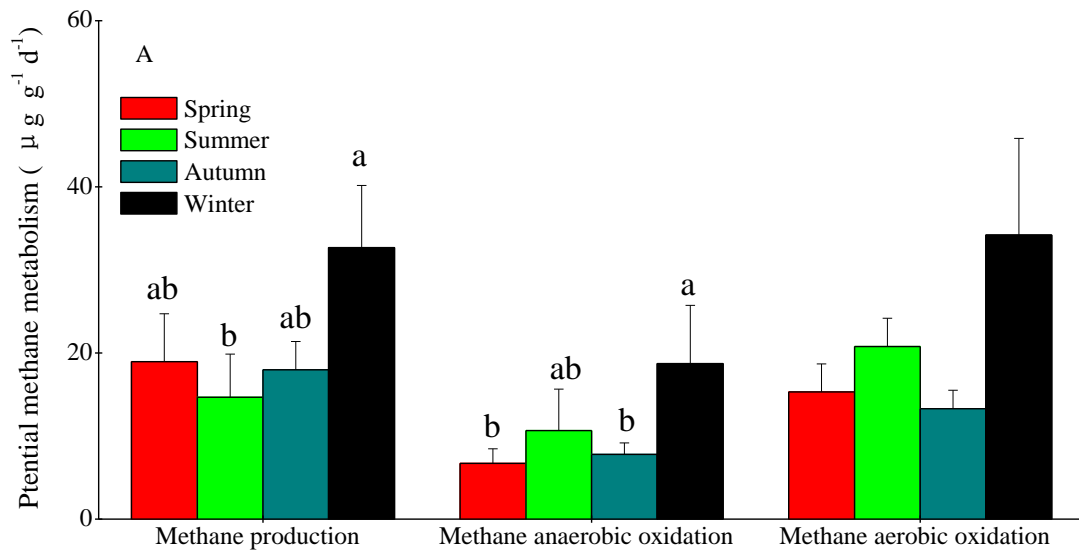
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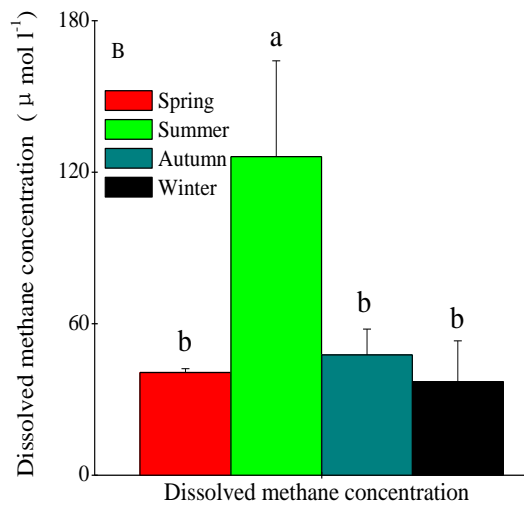
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753 **Fig. 2.**

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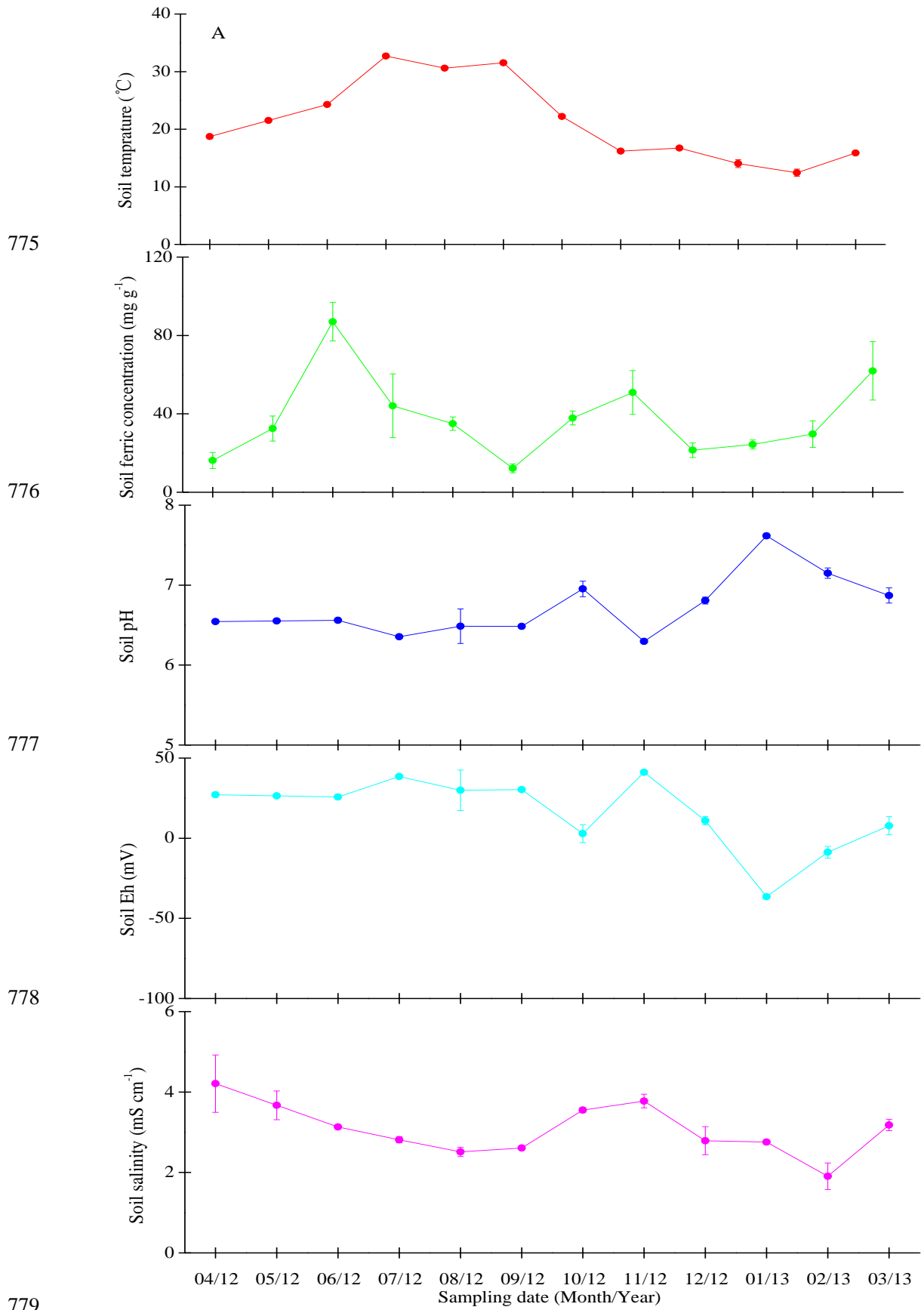


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**Fig. 3.**



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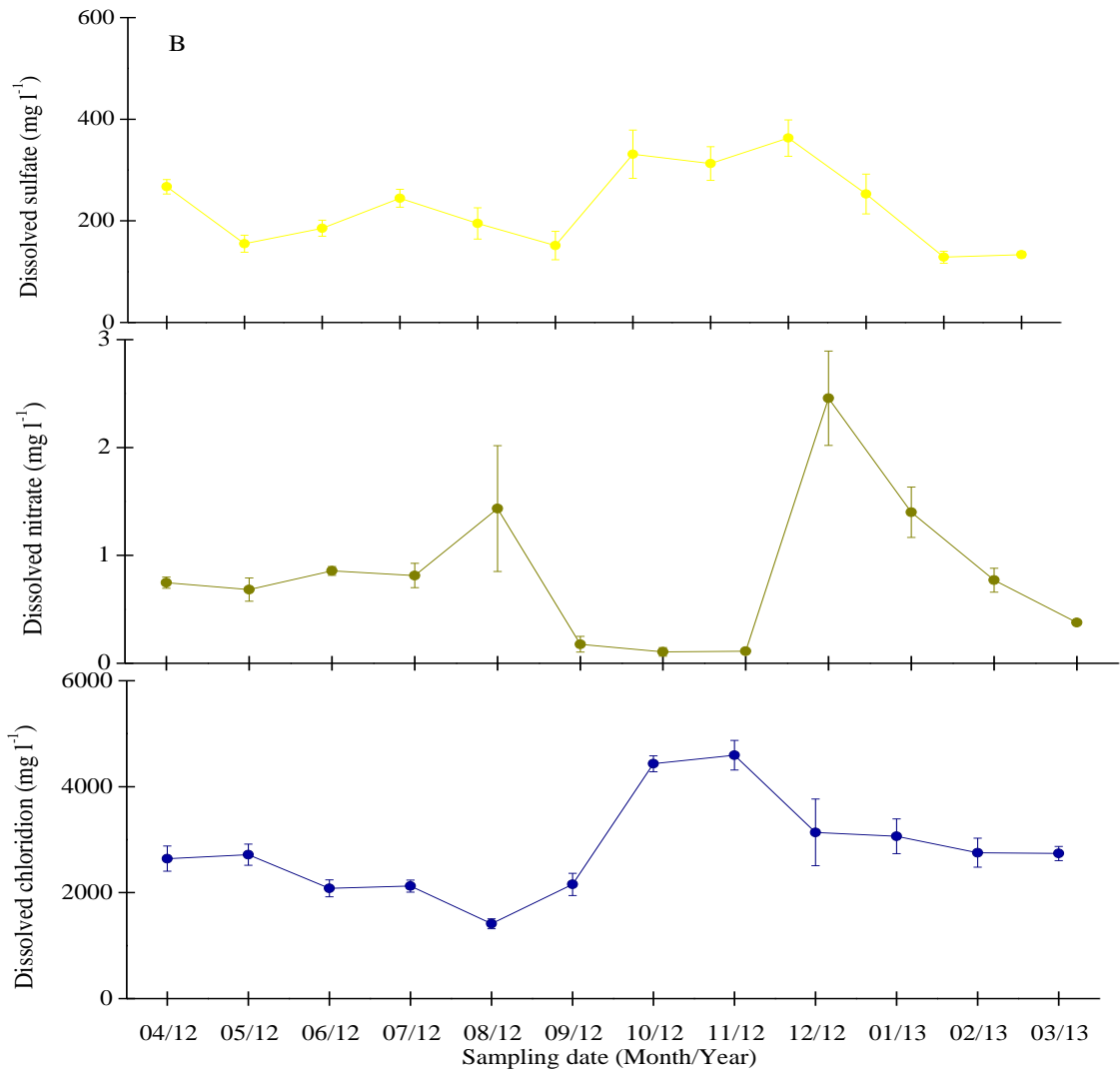
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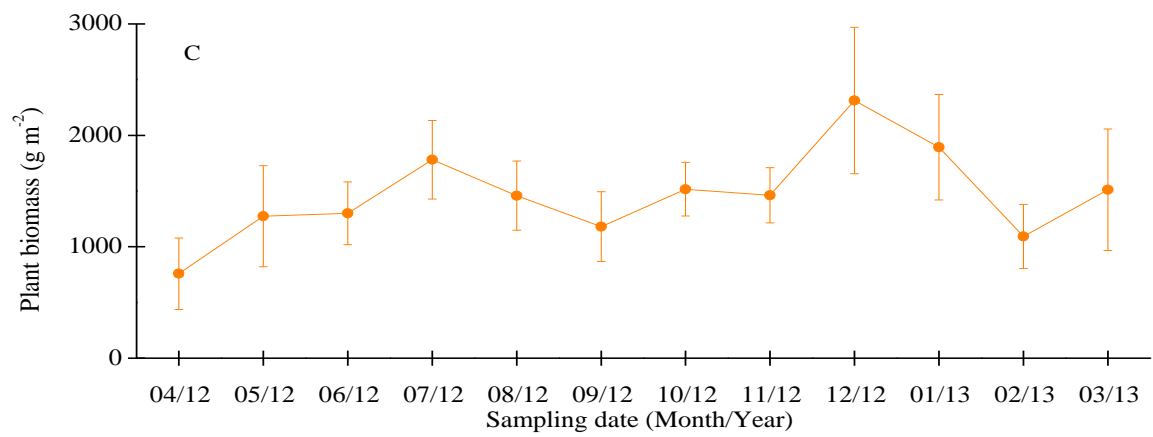
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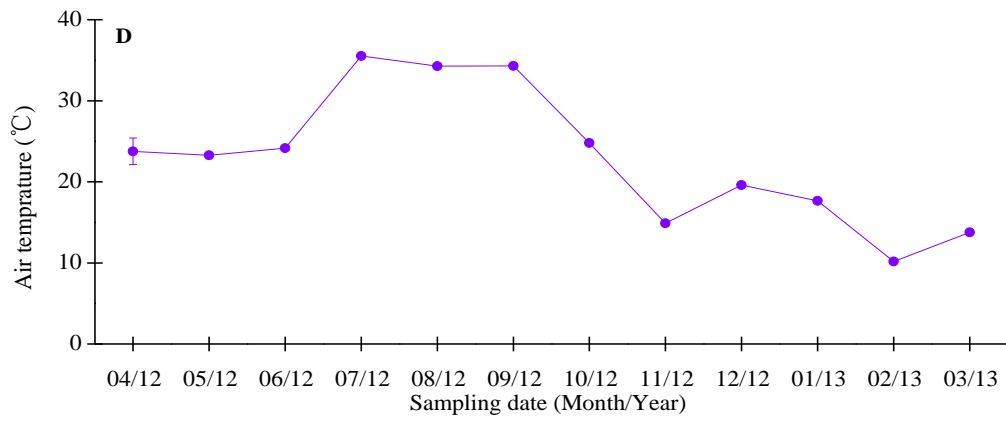
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796 **Fig. 4.**

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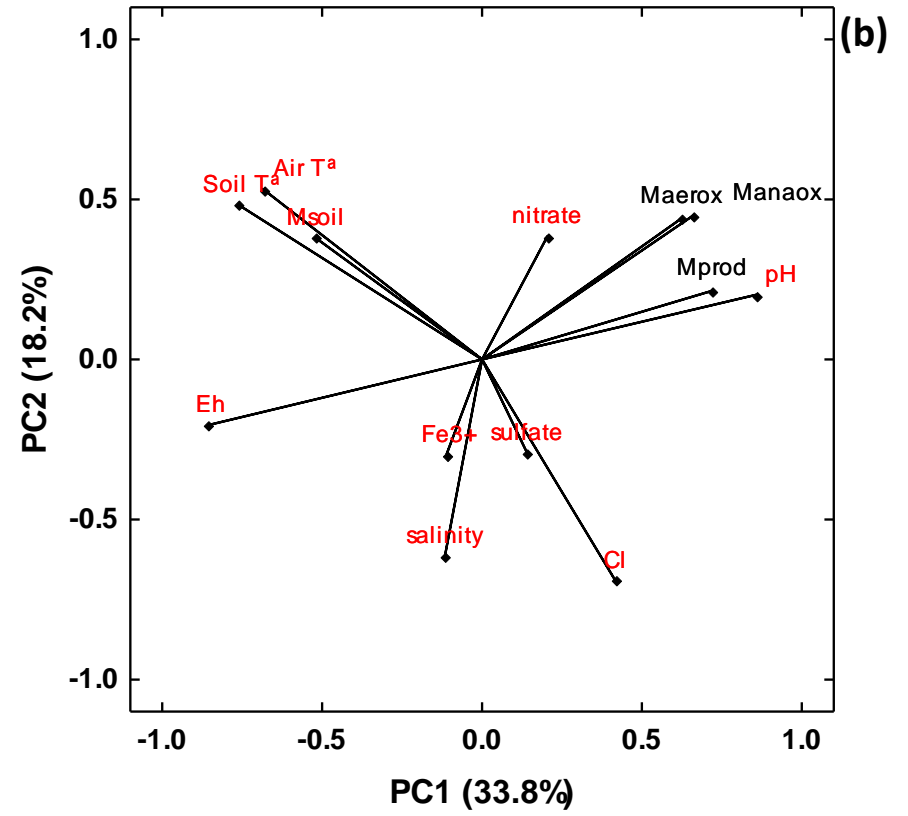
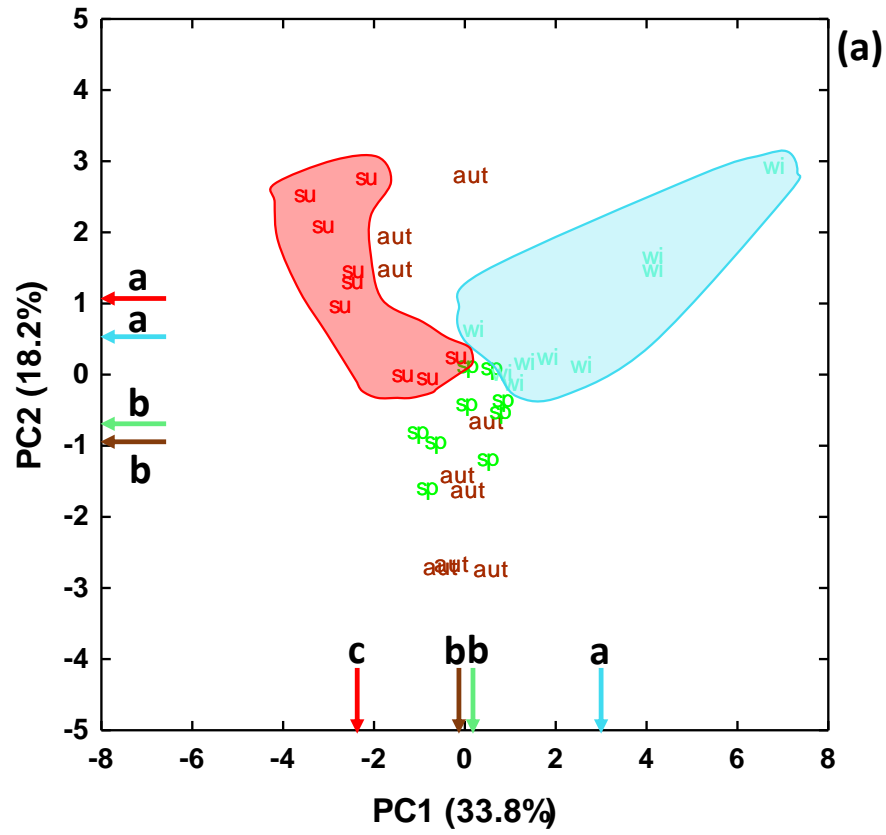
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815 Fig. 5.





