

1 **Factors influencing CO₂ and CH₄ emissions from coastal wetlands in the**
2 **Liaohe Delta, Northeast China**

3 **L. Olsson^{1,2}, S. Ye³, X. Yu³, M. Wei³, K. W. Krauss⁴, H. Brix¹**

4 [1] {Department of Bioscience, Aarhus University, Aarhus, Denmark}

5 [2] {Sino-Danish Centre for Education and Research (SDC), Aarhus, Denmark}

6 [3] {Key Laboratory of Coastal Wetlands, China Geological Survey, Qingdao Institute of Marine Geology,
7 Qingdao, China}

8 [4] {U.S. Geological Survey, National Wetlands Research Center, Lafayette, LA, USA}

9 Correspondence to: H. Brix (hans.brix@bios.au.dk)

10

11

12

13 **Abstract**

14 Many factors are known to influence greenhouse gas emissions from coastal wetlands, but it is still
15 unclear which factors are most important under field conditions when they are all acting
16 simultaneously. The objective of this study was to assess the effects of water table, salinity, soil
17 temperature and vegetation on CH₄ emissions and ecosystem respiration (R_{eco}) from five coastal
18 wetlands in the Liaohe Delta, northeast China: Two *Phragmites australis* (common reed) wetlands,
19 two *Suaeda salsa* (sea blite) marshes and a rice (*Oryza sativa*) paddy. Throughout the growing
20 season, the *Suaeda* wetlands were net CH₄ sinks whereas the *Phragmites* wetlands and the rice
21 paddy were net CH₄ sources emitting 1.2-6.1 g CH₄ m⁻² y⁻¹. The *Phragmites* wetlands emitted the
22 most CH₄ per unit area and the most CH₄ relative to CO₂. The main controlling factors for the CH₄
23 emissions were water table, temperature, soil organic carbon and salinity. The CH₄ emission was
24 accelerated at high and constant (or managed) water tables and decreased at water tables below
25 the soil surface. High temperatures enhanced CH₄ emissions, and emission rates were consistently
26 low (<1 mg CH₄ m⁻² h) at soil temperatures <18°C. At salinity levels >18 ppt, the CH₄ emission rates
27 were always low (<1 mg CH₄ m⁻² h⁻¹) probably because methanogens were outcompeted by
28 sulphate reducing bacteria. Saline *Phragmites* wetlands can, however, emit significant amounts of
29 CH₄ as CH₄ produced in deep soil layers are transported through the air-space tissue of the plants
30 to the atmosphere. The CH₄ emission from coastal wetlands can be reduced by creating
31 fluctuating water tables, including water tables below the soil surface, as well as by occasional
32 flooding by high-salinity water. The effects of water management schemes on the biological
33 communities in the wetlands must, however, be carefully studied prior to the management in
34 order to avoid undesirable effects on the wetland communities.

35 Keywords: Coastal wetlands, common reed, greenhouse gas emissions, *Phragmites australis*, rice
36 paddy, seablite, *Suaeda salsa*

37 **1 Introduction**

38 Wetlands play an important role in the global carbon cycling as they function both as carbon sinks,
39 by storing carbon in soils and vegetation, and as carbon sources, by releasing CO₂ and CH₄ into the
40 atmosphere (Brix et al., 2001; Kayranli et al., 2010; Mitsch et al., 2013; Whiting and Chanton,
41 2001). Carbon dioxide is fixed by plants and autotrophic microorganisms through photosynthesis
42 and thereby transformed to organic compounds locked away from the atmosphere, a process
43 called carbon sequestration (Kayranli et al., 2010). Wetlands can store organic carbon vectored
44 into the soil for a long time due to the generally slow decomposition rates in anaerobic wetland
45 soils (Mitsch et al., 2013). Decomposition of organic matter does however still take place, both
46 through aerobic and anaerobic processes. Aerobic processes are more efficient and mainly form
47 CO₂ as an end-product, whereas anaerobic decomposition is much slower and, along with CO₂,
48 also produces CH₄. Both gases are known as greenhouse gases, which cause global warming due to
49 their ability to absorb solar radiation (IPCC, 2007). The global warming potential (GWP) of CH₄ is 25
50 times greater than that of CO₂ on a 100 year time scale (IPCC, 2007) and high emissions of CH₄ can
51 therefore have disproportionately adverse effects on the climate. According to Whalen (2005),
52 wetlands contribute to about 24% of global CH₄ emissions from all sources, and are the largest
53 natural source of CH₄. Due to the increasing concern of greenhouse gas emissions and global
54 warming, it is important to gain more knowledge about the factors affecting CO₂ and CH₄
55 emissions in different wetland systems, and understand how the balance might be affected by
56 management actions.

57 Previous work has shown that environmental factors like water table (Altor and Mitsch, 2008;
58 Couwenberg et al., 2011; Hargreaves and Fowler, 1998), soil temperature (Bridgham and
59 Richardson, 1992; Inglett et al., 2012), salinity (Bartlett et al., 1987; Weston et al., 2011) and
60 vegetation biomass and type (Inglett et al., 2012; Kandel et al., 2013) may have strong controlling
61 effects on greenhouse gas emissions from wetlands. Decomposition of organic matter in wetland
62 soil is strongly dependent on temperature, and therefore, both CO₂ and CH₄ emissions from
63 decomposition processes tend to increase with increasing soil temperature (Herbst et al., 2011;
64 Inglett et al., 2012). The optimum temperature for methanogenesis is around 20-30 °C, depending
65 on the community of methanogenic archaea (Svensson, 1984). However, methanogens are strictly
66 anaerobic, and for methanogenesis to take place the redox potential must be as low as -200 mV,

67 and other competing terminal electron acceptors must have been reduced (O_2 , NO_3 and SO_4)
68 (Mitsch and Gosselink, 2007). The position of the water table is therefore an important controlling
69 factor on CH_4 emissions, as high water tables lead to oxygen depletion and thus low redox
70 potentials, which favors methanogenesis in the wetland soil (Grunfeld and Brix, 1999).
71 Couwenberg et al. (2011) found that CH_4 emissions in peatlands were practically zero when the
72 water table was below -20 cm, whereas the emissions varied between near zero and 500 kg CH_4
73 $ha^{-1} y^{-1}$ when the water table was above -20 cm. The more oxidized conditions associated with low
74 water tables favor CH_4 oxidation by aerobic methanotrophic bacteria (Whalen, 2005), as well as
75 aerobic decomposition of organic matter, both processes emitting CO_2 . It can therefore be difficult
76 to predict gas emissions under field conditions, as both soil temperatures and water tables may be
77 subject to large seasonal variations.

78 The presence of vegetation affects CO_2 fluxes primarily by photosynthesizing and by increasing the
79 total ecosystem respiration (Han et al., 2013; Kandel et al., 2013). However, the vegetation may
80 also affect CH_4 emissions. Oxygen released from roots create aerobic microsites in the rhizosphere
81 (Brix, 1994), which favors CH_4 oxidation by aerobic methanotrophs (Grunfeld and Brix, 1999). On
82 the other hand, a high primary production also increases the available carbon substrate for
83 methanogens via biomass decomposition and root exudation and can thus lead to higher CH_4
84 emissions (Van der Nat and Middelburg, 2000; Whiting and Chanton, 1993). In addition, wetland
85 plants with internal air spaces (aerenchyma) provide an additional gas transport pathway, apart
86 from diffusion and ebullition from the sediment, that can enhance CH_4 emissions (Brix et al.,
87 1996; Henneberg et al., 2012; Sorrell and Boon, 1994). Methane produced in the soil can be
88 transported through the aerenchyma of the plant tissue and bypass the water column, where it
89 otherwise could have been oxidized by methanotrophs before reaching the atmosphere (Whalen,
90 2005). Thus, wetland vegetation can both decrease and enhance CH_4 emissions depending on the
91 specific site conditions and type of vegetation.

92 Acute saltwater intrusion to freshwater wetlands has been reported to increase soil respiration
93 and lead to elevated CO_2 emissions (Chambers et al., 2011; Weston et al., 2011). However, coastal
94 wetlands with high salinity usually emit less CH_4 than less saline wetlands (Bartlett et al., 1987;
95 Poffenbarger et al., 2011). This has been explained by the high concentration of sulphate ions

96 (SO₄²⁻) in sea water, and the consequent high activity of sulphate reducing bacteria which
97 outcompete methanogens for organic substrate (Bartlett et al., 1987). Poffenbarger et al. (2011)
98 analyzed CH₄ and salinity data from a number of coastal wetlands and found a threshold salinity
99 level of 18 ppt, above which the wetlands emitted significantly less CH₄ than those with a lower
100 salinity.

101 Although many factors are known to influence CO₂ and CH₄ emissions from coastal wetlands, it is
102 still unclear which factors are most important under field conditions when they are all acting
103 simultaneously. Knowledge of the interactive effects of the factors driving greenhouse gas
104 emissions is a prerequisite to be able to manage wetlands in a way that minimizes greenhouse gas
105 emissions, and to predict the effects of future climate change on greenhouse gas emissions from
106 wetlands. The objectives of this study were (i) to quantify the CH₄ emission and ecosystem
107 respiration in the dominant wetland communities in a coastal wetland ecosystem, (ii) to assess the
108 seasonal variation in CH₄ emission and ecosystem respiration in different plant communities, and
109 (iii) to determine the main controlling factors for CH₄ emission and ecosystem respiration under
110 field conditions.

111 **2 Materials and Methods**

112 **2.1 Study sites**

113 The Liaohe Delta is situated in the Liaoning Province in northeast China and comprises a wetland
114 area of around 1,280 km² (Li et al. 2012). About 786 km² of that is marsh vegetated by common
115 reed (*Phragmites australis* (Cav.) Trin. Ex Steud). The reed marshes in the Liaohe Delta represent
116 probably the largest reed fields in the world (Brix et al., 2014). The growing conditions for common
117 reed in the delta marshes have been improved since the 1960s by a freshwater irrigation
118 management practice, that has washed away much of the soil salinity, and as a result, led to an
119 expansion of the reed fields and an increase in productivity (Ji et al., 2009). The reed biomass is
120 extensively used for paper production (Ma et al., 1993), and the hydrology is therefore regulated
121 to maximize the biomass yield (Brix et al., 2014). Apart from reed marshes, the main wetland types
122 in the Liaohe Delta are tidal saltmarshes vegetated by *Suaeda salsa* (L.) Pall., III (seablite), and rice
123 paddies planted with *Oryza sativa* L. (Asian rice). The wetlands of the Liaohe Delta are important

124 breeding areas for many endangered bird species, and are designated as a Shuangtaizihekou
125 (Liaohekou) National Nature Reserve since 1986 and also listed as a Ramsar site since 2004 (Li et
126 al., 2012). However, the wetlands are adversely affected by the polluted water from the Liaohe
127 River (Zhang et al., 2010) and oil extraction activities, as the Liaohe Delta contains the third largest
128 oil field in China (Zhu et al., 2010).

129 Five study sites were selected to embrace the main wetland types of the delta. The five study sites
130 included two *Suaeda* marshes, one created and one natural ('Suaeda1' at 40°52'11.09"N;
131 121°36'21.72"E and 'Suaeda2' at 40°57'38.62"N; 121°48'20.03"E, respectively), two *Phragmites*
132 wetlands for paper production, ('Phrag1' at 40°52'22.34"N; 121°36'08.89"E and 'Phrag2' at
133 41°09'33.75"N; 121°47'42.71"E) and a rice paddy ('Rice' at 41°10'38.69"N; 121°41'17.28"E).

134 **2.2 Gas sampling and analysis**

135 Gas samples for estimation of CO₂ and CH₄ emission were collected monthly from April to
136 November 2012, using the static chamber method (Livingston and Hutchinson, 1995). Six
137 quadratic metal frames (0.6 x 0.6 m) were permanently installed in each study site, and wooden
138 boardwalks were built to facilitate access to the frames without disturbing the soil. Small holes
139 were drilled in the sides of the frames just at the ground surface to facilitate water exchange
140 between the inside of the frames and the surrounding wetland between sampling events. These
141 holes were plugged during sampling. At each sampling event, a white plastic chamber (0.55 x 0.55
142 x 0.30 m) was placed over the metal frame and an airtight seal was created by water (about 1 cm
143 deep) within a trough inside the frame. The chambers were modified from past designs deployed
144 in shaded forested wetlands (Krauss and Whitbeck, 2012; Yu et al., 2008) by using aluminum foil to
145 cover all inside walls to block out light and prevent photosynthesis and to minimize temperature
146 changes. Transparent and opaque chambers have been shown to provide similar CH₄ flux
147 estimates (Minke et al., 2014). If the vegetation was taller than the chamber, the plants were bent
148 to fit inside the chamber. At Phrag2, however, the plants grew so tall that they had to be cut in
149 June; we limited what we had to cut as much as possible. A small fan was used to mix the air inside
150 the chamber during sampling, and a PVC tube with the outer end placed in water was used to
151 equilibrate the air pressure inside the chamber with the outside air pressure. Gas samples were
152 taken from the chamber through a rubber septum using a 15 mL plastic syringe, and immediately

153 transferred into pre-evacuated 10 mL glass vials with a thick rubber cap and an aluminum lid. The
154 first sample was taken immediately after placing the chamber onto the frame, and four additional
155 samples were taken with 20 minute intervals. The temperatures at a soil depth of 10 cm and the
156 air temperature in the chamber were recorded at each sampling time. The gas samples were
157 stored at room temperature for a maximum of one week before analysis. For comparison, the CO₂
158 flux in each chamber was also measured in situ during separate 1 minute incubations on the same
159 day using a portable infrared gas analyzer (LI-COR 8100, Lincoln, NE, USA).

160 The concentrations of CO₂ and CH₄ in the gas samples were analyzed in 0.6 mL injections on a
161 TRACE Ultra GC-TCD (Thermo Fischer Scientific Inc., Waltham, MA, USA) at Qingdao Institute of
162 Marine Geology and an Agilent 7890A at the Ocean University of China, respectively. Signals from
163 the GCs were recorded in GC/MSD ChemStation Software (Agilent Technologies, Inc., Santa Clara,
164 CA, USA) and the peak areas used to calculate the concentrations of CH₄ and CO₂. Gas emissions in
165 mg CH₄ m⁻² h⁻¹ and mg CO₂ m⁻² h⁻¹ (using the weight of the whole molecules of CH₄ and CO₂,
166 respectively) were determined from the increase in concentration in the chambers over time using
167 linear regression analysis. Regression lines with a coefficient of determination (R^2) < 0.6 were not
168 included, except in cases where it was obvious that the low R^2 value was due to extremely low gas
169 fluxes (zero or near-zero fluxes). In a few cases, extremely deviant data were excluded. Because of
170 technical problems, no data on CO₂ emissions are available from Phrag1 in April and from Suaeda1
171 and Suaeda2 in May, and no data on CO₂ and CH₄ emissions in August from Phrag1.

172 Cumulative CO₂ and CH₄ emissions at each site were calculated as the integral of the mean gas
173 emissions (in mg m⁻² d⁻¹) from the monthly sampling campaigns. As the gas sampling chambers
174 were darkened, CO₂ emissions were assumed to be constant on a daily and nightly basis. And
175 although some studies have found diurnal variations in CH₄ emissions (Käki et al., 2001; Neubauer
176 et al., 2000; Tong et al., 2013), no consistent pattern has been found. Hence, we assumed that the
177 CH₄ emissions were also constant on a daily basis.

178 **2.3 Environmental parameters**

179 The water table was measured in a piezometer at each study site, and the soil surface level
180 differences among the six plots at each site were used to calculate individual water tables for each

181 plot. Water samples for salinity and pH analyses were taken from the piezometer, and measured
182 using a Jenco 6010 microcomputer based pH/mV/temperature portable meter (Jenco Electronics,
183 Ltd., Shanghai, China).

184 The aboveground biomass inside the plots was estimated using a non-destructive method. In the
185 *Phragmites* wetlands, the heights of all shoots inside the frames were measured, and 25 shoots
186 encompassing the range of heights in the frames were harvested outside the frames. In the
187 *Suaeda* wetlands, the plant density inside the frames was counted and 20x20 cm plots outside the
188 frame with a similar plant density were harvested. The plants were dried at 60°C and weighed,
189 and the biomass inside the plots was calculated from a regression analysis between plant height
190 and dry mass (*Phragmites*) and between plant density and dry mass (*Suaeda*). In the rice paddy,
191 five rice plants outside the frames were harvested, dried and weighed, and the biomass within the
192 frames was estimated based on the number of plants.

193 Soil core samples were taken to 5 cm depth from the topsoil near each frame using a 5 cm
194 diameter steel cylinder. The samples were dried to constant weight at 60°C for determination of
195 bulk density and water content. Soil redox potentials (Eh) were measured using platinum
196 electrodes installed at a depth of 10 cm at least 24 hours before measuring. Redox electrodes
197 were referenced against a calomel electrode.

198 Two soil core samples were collected to 4 cm depth at each site the following year, mixed and
199 analyzed for selected mineral elements and available nutrients. Total N and TC were analyzed on
200 oven-dried subsamples ground to pass a 2 mm sieve, on a Perkin Elmer 2400 Series II CHNS/O
201 elemental analyzer (Perkin Elmer, Inc., Waltham, MA, USA). For determination of Org-C, another
202 set of subsamples were treated with 4M HCl (Craft, 2007) to remove inorganic carbon before
203 analysis on the same instrument. Available nutrients were extracted by the Mehlich-III method
204 (Mehlich, 1984), using an extraction solution prepared from 22.98 mL concentrated CH₃COOH,
205 40.0 g NH₄NO₃, 1.12 g NH₄F, 1.68 mL concentrated HNO₃, 0.58 g EDTA and 1,600 mL deionized
206 water, diluted to 2 L. Air-dried soil subsamples were ground to pass a 1 mm mesh. 2.5 g of the
207 ground soil were shaken with 25 mL extraction solution on a reciprocating oscillator for 5 minutes
208 and then centrifuged for 20 minutes. The supernatant was diluted ten times and analyzed for Ca,
209 Cu, Fe, K, Mg, Mn, P and Zn by ICP-OES (Optima 2000 DV, Perkin Elmer, USA).

210 2.5 Statistical analysis

211 The in situ measurements of CO₂ emissions with the IRGA were used in the statistical analyses.
212 Methane emissions and ecosystem respiration (R_{eco}) were analyzed by Site and Time with Plot as a
213 random factor nested within Site, in a repeated-measures setup using the General Linear Model
214 (GLM) procedure of Statgraphics Centurion XVI (Statpoint Technologies, Inc., Warrenton, Virginia,
215 USA). The Bonferroni post-hoc test was used to identify significant differences between different
216 sites at the 5 % significance level. Data of CH₄ emissions and R_{eco} were log-transformed to meet
217 the assumption of equal variances, which was checked using Levene's test (p>0.05). Since the
218 dataset included a few negative gas flux values, a constant was added to the fluxes (CH₄ flux+0.6
219 and R_{eco}+25, respectively) before applying the log-transformations. Data from April, May and
220 August were excluded from the analyses due to missing data at some sites.

221 Linear mixed effects models (multiple regressions) using R version 3.0.1 (Team, 2013) were used to
222 assess the relations between the measured environmental factors and CO₂ and CH₄ emissions,
223 respectively. The response variables were CO₂ and CH₄ emissions. The fixed effects were plant
224 species (categorical variable), soil temperature (SoilT), water table (WT), aboveground biomass
225 (Biomass) and Salinity (continuous variables). The random effects were Site and Plot. An
226 interaction effect between plant species and aboveground biomass was also included. The effect
227 of each variable or interaction was evaluated by removing the variable/interaction from the
228 original model and using a likelihood ratio chi-square test to test for significant differences at the
229 5% significance level between the original model and the model excluding the variable/interaction.
230 Data of CO₂ and CH₄ emissions were log-transformed as described before to meet the assumptions
231 of normality and equal variances. The original mixed effects model for CO₂ and CH₄ emissions,
232 respectively, was in the form:

$$233 \text{Log}_{10}(\text{gas flux})_i = \beta_{1i} \cdot \text{Biomass}_i + \beta_2 \cdot \text{SoilT} + \beta_3 \cdot \text{Salinity} + \beta_4 \cdot \text{WT} + b_1(\text{Site}) + b_2(\text{Plot}) + \varepsilon_i \quad (1)$$

234 where β_1 is a coefficient specific for plant species i , β_2 , β_3 and β_4 are coefficients for fixed effects
235 common for all plant species, b_1 and b_2 are coefficients for the random effects and ε_i is the
236 residual error for plant species i .

237 3 Results

238 3.1 Environmental parameters

239 The water tables varied greatly over the season, particularly at Phrag2 where the water table
240 ranged from -35 to +27 cm, and at Suaeda1 where it ranged from -43 to +15 cm (Fig. 1c). At the
241 two *Phragmites* wetlands, the water tables were managed to maximize the yield of *Phragmites*
242 biomass. Hence, the water tables at these sites were above the soil surface during most of the
243 growing season. The water tables at the two *Suaeda* wetlands fluctuated greatly due to tidal
244 variations, but the water tables were at the time of sampling usually below the soil surface. At the
245 rice paddy, the water table was fairly stable around +10 cm from June to September due to
246 regulation according to agricultural practice.

247 Soil temperatures at all sites increased from 18-22°C in May to 23-28°C in August, and then
248 declined to 0-7°C in November (Fig. 1d). We do not have temperature data from the months prior
249 to our sampling, but usually the soils in the delta are frozen until April, whereafter the
250 temperature increases over a few weeks.

251 The amount of aboveground biomass was basically zero during the first sampling campaign in late
252 April. Thereafter, both *Suaeda* and *Phragmites* grew rapidly reaching aboveground biomasses in
253 June of ~800 g dry mass m⁻² for *Suaeda* and ~400 g dry mass m⁻² for *Phragmites* before the cutting
254 in June (Fig. 1e). In the rice paddy, the rice plants were planted in late June. Hence the
255 development of biomass in the rice paddies occurred much later than in the natural *Suaeda* and
256 *Phragmites* wetlands.

257 The salinity at Suaeda1 was 32-39 ppt during most of the sampling period (Fig. 1f). At Sueda2 the
258 salinity was lower: 10-15 ppt from May to July and then decreasing to 5-6 ppt in August to
259 December. In the *Phragmites* wetlands, the salinities varied between 2 and 19 ppt depending on
260 the water management scheme. The highest salinities were found at Phrag1. At the rice paddy the
261 salinity was constantly low at around 2 ppt.

262 Soil bulk density varied between 0.93 g cm⁻³ at Phrag2 to 1.50 g cm⁻³ at Suaeda1, and soil water
263 content between 27% at Suaeda1 and 48% at Phrag2 (Table 1). The mean redox potential was
264 highest at Suaeda1 (+101 mV) and lowest at Phrag1 (-127 mV). The mean soil water pH was in the
265 interval 7.12 – 7.70 at all sites

266 Al topsoils consisted largely of fine silt and clay and had a low content of organic matter (Org-C <
267 2% of the dry matter). However, the contents of organic carbon (12%) and nitrogen (1%) were
268 markedly higher at Phrag2 than at the other sites (Table 1). At Phrag1, the contents of organic
269 carbon (1.8%) and nitrogen (0.17%) were 2-3 times higher than at the Suaeda sites and the rice
270 paddy. Differences in other analyzed mineral elements were less pronounced and probably
271 reflected the predominantly mineral composition of the soils, except for the concentration of P
272 which was higher at Phrag2 and the rice paddy than at the other sites.

273 **3.1 CH₄ emissions**

274 There were large variations in CH₄ emission rates both among sites and over the season (Fig. 1a)
275 and these differences were statistically significant (Table 2). The highest CH₄ emission rates were
276 found at Phrag2 and at the rice paddy. Peak emissions were 2.5 mg m⁻² h⁻¹ at both sites although
277 the peak values were measured in July at Phrag2 and in August at the rice paddy (Fig. 1a). The
278 highest CH₄ emission rates at Phrag1 (around 0.7 mg m⁻² h⁻¹) were only a fourth of those at
279 Phrag2. At the two *Phragmites* wetlands, the CH₄ emission rates were close to zero in April-May,
280 increased rapidly from June to July, and declined again after August. At the rice paddy, the CH₄
281 emission rates were near zero in June, low in July (0.25 mg m⁻² h⁻¹), increased very sharply from
282 July to August and thereafter declined. At the *Suaeda* wetlands, the CH₄ emission rates were close
283 to zero throughout the sampling period. Means and ranges of CH₄ emission rates over the whole
284 sampling period, and significant differences (p<0.05) among sites, are shown in Table 4.

285 The CH₄ emission rates at sites with significant emissions (Phrag1, Phrag2 and Rice) were positively
286 related to both soil temperature and water table (Table 3; Fig. 3). The CH₄ emission rates were less
287 than 1 mg m⁻² h⁻¹ at temperatures below 18°C and at water tables below the soil surface. The
288 highest CH₄ emission rates were measured at Phrag2 when both the temperature and the water
289 table were high (Fig. 3). The CH₄ emissions decreased significantly (Table 3) with increasing
290 salinity, as CH₄ emission rates were less than 1 mg m⁻² h⁻¹ at salinity levels above 18 ppt (Fig. 4). At
291 the highest salinity levels at Suaeda1 (32-38 ppt), CH₄ emission rates were practically zero.

292 Cumulative CH₄ emissions over the entire growing season in 2012 were highest at Phrag2 with 6.1
293 g CH₄ m⁻², corresponding to 154 g CO₂-equivalents m⁻² y⁻¹ (Fig. 2, Table 4). These emissions were
294 about 1.5 times higher than the cumulative CH₄ emissions from the rice paddy, and about five

295 times higher than the CH₄ emissions from Phrag1. CH₄ emissions from the *Suaeda* wetlands were
296 negligible.

297 **3.2 Ecosystem respiration (R_{eco})**

298 The measured flux of CO₂ in the darkened chamber is the sum of the flux of CO₂ from the soil and
299 the respiration of the plant tissue inside the chambers. We here refer to this as the ecosystem
300 respiration (R_{eco}). The ecosystem respiration rates varied significantly both among sites and over
301 time (Fig. 1b, Table 2). The highest ecosystem respiration rates at the rice paddy and at Phrag2
302 (2,400 and 2,300 mg CO₂ m⁻² h⁻¹, respectively) were twice as high as the highest R_{eco} at Phrag1 and
303 three times higher than the R_{eco} at the two *Suaeda* wetlands. At Phrag2, R_{eco} was highest in June
304 and July, whereas at the rice paddy, the R_{eco} was low at this time of the year and highest in August
305 (Fig. 1b). It should, however, be mentioned that the *Phragmites* stems at Phrag2 were cut in June.
306 Hence, the biomass within the chambers from July and onwards was lower than the biomass in
307 the surrounding reed vegetation. Overall, the ecosystem respiration rates were significantly
308 related to plant biomass, soil temperature and salinity (Table 3) whereas water table had no
309 significant effect on R_{eco} (p>0.05).

310 The cumulative CO₂ emissions, without accounting for photosynthetic CO₂ uptake, varied between
311 1.7 kg m⁻² y⁻¹ in the *Suaeda* wetlands to 3.3-4.4 kg m⁻² y⁻¹ in the *Phragmites* (Table 4). The
312 cumulative CO₂ emission in the rice paddy was in-between this range (3.3 kg m⁻² y⁻¹).

313

314

315 **4 Discussion**

316 **4.1 CH₄ emissions**

317 Over one growing season in 2012, the two *Phragmites* wetlands emitted on average 0.15 and 1.01
318 mg CH₄ m⁻² h⁻¹ (Phrag1 and Phrag2, respectively) and the rice paddy 0.75 mg m⁻² h⁻¹, whereas the
319 emissions from the two *Suaeda* wetlands were negligible. The large differences in CH₄ emission
320 rates among the five sites can be explained by the differences in soil organic matter, salinity and
321 water tables, and, to some extent, vegetation type. For methanogenesis to take place there must
322 be a sufficient amount of labile organic substrate available (Mah et al., 1977), such as dead plant
323 material from the previous growing season and root exudates from the standing vegetation (Mann

324 and Wetzel, 1996; Zhai et al., 2013). Previous studies have reported increasing CH₄ emission rates
325 with increasing content of soil organic matter in different types of wetlands (Le Mer and Roger,
326 2001; Picek et al., 2007; Serrano-Silva et al., 2014; Sha et al., 2011; Tanner et al., 1997). At Phrag2,
327 where CH₄ emission rates were significantly higher than at the other sites, there was a many-fold
328 higher content of organic carbon and nitrogen in the soil compared to the soils at the other sites,
329 and the reeds at Phrag2 had a very dense root system in the upper soil layers. Thus, the reason for
330 the high CH₄ emission rates at Phrag2 was most likely the higher content of organic substrate for
331 methanogenesis, originating from dead plant residues and from root exudates. At the rice paddy,
332 where the second highest CH₄ emissions were measured, the organic content of the soil was low,
333 but the soil C:N ratio was lower (8.4) than the ratios at the other sites probably resulting from
334 different plant inputs into the soil. A lower C:N ratio of the organic matter in the soil may increase
335 organic matter lability by decreasing nitrogen limitation for decomposers (Hodgkins et al., 2014).
336 However, the fact that the rice paddy was constantly flooded throughout the growing season
337 probably also stimulated methanogenesis and CH₄ emission.

338 Both *P. australis* and rice have well developed aerenchyma in roots, rhizomes and stems, which
339 provides them with a high ability to transport gases between the soil and the atmosphere through
340 the plant tissue (Brix et al., 1996; Singh and Singh, 1995). When CH₄ is transported from the soil
341 through the air-space tissues of the plants, it bypasses the aerobic zone in the upper part of the
342 soil and the water column, where CH₄ otherwise could have been oxidized by methanotrophic
343 bacteria (Whalen, 2005). Plant-mediated transport has been reported to be the main pathway of
344 CH₄ transport from the soil to the atmosphere and constituting as much as 60-90 % of the CH₄
345 emissions (Butterbach-Bahl et al., 1997; Huang et al., 2005). In the present study, transport of CH₄
346 through the air-space tissue of the plants may explain the relatively high CH₄ emission rates from
347 the *Phragmites* wetlands and the rice paddy, while the lack of well-developed aerenchyma in *S.*
348 *salsa* is consistent with the negligible emission rates from the *Suaeda* wetlands. The aboveground
349 biomass *per se* probably had no effect on the plant-mediated CH₄ emissions, as CH₄ has been
350 shown to be mainly emitted through micropores in the basal parts of rice plants (Nouchi et al.,
351 1990) and through the basal internodes of *P. australis* (Brix, 1989). Also, Henneberg et al. (2012)
352 showed in a manipulation experiment with *Juncus effusus* that aboveground biomass was
353 unimportant for the CH₄ transport through the plants, whereas the removal of fine roots and root

tips of coarse roots led to significant reductions in plant-mediated CH₄ transport. Thus, it is likely that the extensive root system of the reeds at Phrag2 contributed to the high CH₄ emission rates at this site.

At salinity levels above 18 ppt the CH₄ emission rates were always lower than 1 mg m⁻² h⁻¹ across all sites (Fig. 4). This is consistent with Poffenbarger et al. (2011) who found a salinity threshold of 18 ppt, above which CH₄ emission rates were significantly lower than at lower salinity levels. The effect of salinity has been explained by the high concentrations of SO₄²⁻ in seawater, which inhibits CH₄ production due to competition from sulphate reducing bacteria (Bartlett et al., 1987; D'Angelo and Reddy, 1999). Thus, the lack of CH₄ emissions at the *Suaeda* sites is most likely an effect of the high salinity, particularly at the Suaeda1 site where salinities were up to 35 ppt. The salinity was, however, significantly lower at the Suaeda2 site with salinities of 5-15 ppt, and yet there were no CH₄ emissions as SO₄²⁻ concentrations were still high enough to inhibit methanogenesis. At Phrag2, on the other hand, CH₄ emission rates were high although the water salinity was occasionally as high as 15 ppt. These seemingly contradictory results can be explained by the fact that a high salinity in the water mainly affects the upper soil layers, but not necessarily the deeper layers. Therefore, methanogens may be outcompeted by sulphate reducing bacteria in the upper layers of the soil, but CH₄ can still be produced in the deeper soil layers where all SO₄²⁻ have been reduced. The roots of *P. australis* grow to a soil depth of at least 40-60 cm, and CH₄ can therefore be transported from the deeper anoxic zone through the air-space tissue of the plants to the atmosphere. Thus, the relatively high salinity at Phrag2 probably inhibited methanogenesis in the upper soil layers, but the CH₄ produced in the deeper soil layers were still transported to the atmosphere through the plants. At the *Suaeda* wetlands, the generally low and fluctuating water tables indicate that the anaerobic zone where methanogenesis can take place was at a deeper soil depth than at the *Phragmites* wetlands. The roots of *S. salsa* lack aerenchyma and are generally restricted to the upper 20 cm of the soil, and are therefore ineffective conduits for CH₄ from the deeper soil layers to the atmosphere. Thus, although salinity levels at Suaeda2 were not always high, any CH₄ that may have been produced in the soil did not reach the atmosphere because of CH₄ oxidation in the upper soil layer. At the rice paddy, the low salinity of around 2 ppt seemingly had no inhibitory effect on the CH₄ production and emission.

383 The water table is an important parameter affecting the CH₄ emission rate. The highest CH₄
384 emissions occurred at the three sites where the water exchange and water table were managed to
385 maximize the reed biomass (Phrag1, Phrag2) and crop yield (Rice) whereas very low CH₄ emission
386 rates were found at the two *Suaeda* wetlands with a natural tidal hydrology. At the rice paddy, the
387 soil was continuously flooded from June until September, and the two *Phragmites* wetlands were
388 more or less flooded from June until October, resulting in low redox potentials and relatively high
389 CH₄ emission rates. The soils at the tidally influenced *Suaeda* wetlands were periodically drained
390 and hence partly oxidized inhibiting CH₄ production. When water tables at the *Phragmites*
391 wetlands and the rice paddy were below the soil surface, the CH₄ emission rates were always <1
392 mg CH₄ m⁻² h⁻¹ probably because CH₄ produced in deeper soil layers was oxidized in the upper oxic
393 soil layers, reducing the amount of CH₄ reaching the atmosphere. When the water tables
394 approached the soil surface, the CH₄ emission rates increased. This is in agreement with the
395 findings of Zhu et al. (2014), who reported that the seasonal CH₄ emissions from an herbaceous
396 peatland were highly linked to water table fluctuations, and that the water table was the main
397 environmental driver for CH₄ emissions over a single growing season, whereas soil temperature
398 was important on a longer time scale. The important effect of water table on CH₄ emission rates is
399 in agreement with observations in other studies (e.g. Bridgham et al., 2006; Couwenberg et al.,
400 2011; Le Mer and Roger, 2001; Serrano-Silva et al., 2014). However, in the present study both soil
401 water table and temperature were important drivers.

402 The large seasonal variations in CH₄ emission rates at Phrag1, Phrag2 and Rice were primarily
403 related to the variations in soil temperatures. The highest CH₄ emission rates occurred during the
404 summer months July-September, when temperatures were relatively high. We found an
405 exponential relationship between soil temperature and CH₄ emission rates (Fig. 3) similar to those
406 reported elsewhere (Herbst et al., 2011; Inglett et al., 2012) in accordance with the temperature
407 dependency of the methanogenic bacteria. Furthermore, the amount of labile organic carbon
408 substrates from root exudates can be stimulated by high temperatures as Zhai et al. (2013) found
409 significantly higher root exudation rates from *P. australis* roots at 20°C than at 10°C. Also the
410 plant-mediated CH₄ transport may be accelerated at higher temperatures as Hosono & Nouchi
411 (1997) reported that the CH₄ transport through rice plants was twice as high at a rhizosphere
412 temperature of 30°C as compared to the transport at 15°C. Thus, the high CH₄ emission rates at

both Phrag2 and Rice during the warmest months of the year were probably due to the high temperature and its stimulating effect on the activity of the methanogenic bacteria, the root exudation rates and the effectivity of the plant-mediated transport. At soil temperatures below 18°C, which occurred before June and after September, CH₄ emission rates were consistently low (<1 mg CH₄ m⁻² h⁻¹). In the spring, the low rates might be associated with a time-lag in the growth of methanogens as the temperature was increasing over a relatively short period. In the autumn the low rates might be influenced by low availability of organic carbon, as most carbon might have been 'burned off' during the hot summer months.

4.2 Ecosystem respiration (R_{eco})

Ecosystem respiration rates were highest in June-July at the *Phragmites* wetlands, June-August at the *Suaeda* wetlands and August at the rice paddy. The differences among the sites can be explained by the differences in soil organic matter and biomass, whereas the variations over time can be explained mainly by soil temperature and to some extent by differences in biomass. The seasonal pattern of ecosystem respiration was closely related to that of soil temperature at all sites, which suggests that temperature was the main controlling factor for ecosystem respiration. This is in agreement with the findings of other studies (Bridgman and Richardson, 1992; Han et al., 2013; Happell and Chanton, 1993; Kandel et al., 2013; Krauss et al., 2012; Pulliam, 1993). However, biomass respiration also contributed to the ecosystem respiration rates, particularly late in the season when the aboveground biomass was highest. At Phrag1, Suaeda1 and Suaeda2, the seasonal pattern of ecosystem respiration rates correlated to that of the aboveground biomass, indicating that plant respiration may have constituted a large part of the total ecosystem respiration at these sites. This is in agreement with Kandel et al. (2013), who found that plant respiration contributed with about 50% of the total ecosystem respiration in a cultivated peatland during the summer months, and Xu et al. (2014), who found ten times higher CO₂ emissions from marshes with plant communities than from those without. Also, the difference in ecosystem respiration rates between the two *Suaeda* wetlands corresponded to the differences in *Suaeda* biomass. However, at Phrag2 nearly all CO₂ emissions came from the soil and the belowground biomass, since only short stems were left behind after cutting the reeds in June. At the rice paddy, the ecosystem respiration peaked in August when the aboveground biomass was only about 100 g m⁻². The aboveground rice biomass continued to increase after August, but the ecosystem

443 respiration decreased drastically, indicating that soil respiration constituted the main part of
444 ecosystem respiration at the rice paddy.

445 **4.3 Cumulative emissions**

446 The two *Suaeda* wetlands were net CH₄ sinks whereas the two *Phragmites* wetlands and the rice
447 paddy were net CH₄ sources during April to November 2012. Although the peak CH₄ emission rates
448 at the rice paddy were similar to those at Phrag2, the cumulative CH₄ emission rates from Phrag2
449 were 1.5 times higher than those from Rice. The cumulative CO₂ emitted from ecosystem
450 respiration followed a similar pattern, with Phrag2 emitting 1.3 times more CO₂ than the rice
451 paddy. Thus, on a yearly basis Phrag2 emitted the highest amounts of both CH₄ and CO₂ per unit
452 area, and also the most CH₄ relative to CO₂. Since CO₂ emissions from vegetated ecosystems are
453 counteracted by photosynthetic CO₂ uptake and possibly carbon sequestration, the CO₂ emissions
454 measured as ecosystem respiration does not contribute to the greenhouse effect. However, the
455 CH₄ emissions from wetland ecosystems contribute to the radiative forcing, and therefore CH₄
456 emission rates should be minimized. It is, however, the balance between carbon sequestrations on
457 the one hand and CH₄ emission on the other hand that determines if a particular wetland can be
458 considered to be a net source or a net sink for radiative greenhouse gases (Mitsch et al., 2013).
459 Based on the present study, it is unfortunately not possible to estimate the carbon sequestration
460 of the different wetland communities.

461 **4.4 CH₄ emission rates and R_{eco} compared to other studies**

462 The CH₄ emission rates and seasonal pattern at Phrag2 were similar to those measured by Huang
463 et al. (2005) from a reed wetland in the Liaohe delta, where CH₄ emission rates varied from -0.97
464 mg CH₄ m⁻² h⁻¹ in early May to 2.73 mg CH₄ m⁻² h⁻¹ in early September. The average CH₄ emission
465 rate at Phrag2 was within the range of CH₄ emission rates from reed wetlands in other parts of
466 China, varying from 0.75 mg m⁻² h⁻¹ (Xu et al., 2014) to 5.13 mg m⁻² h⁻¹ (Tong et al., 2010). The
467 *Suaeda* wetlands had CH₄ emission rates very similar to those from a *Suaeda salsa* marsh in the
468 Yellow River delta, China, with rates ranging from -0.74 to 0.42 mg m⁻² h⁻¹ (Sun et al., 2013). The
469 CH₄ emission rates from the rice paddy in the present study were lower than those reported from
470 continuously and intermittently flooded rice paddies in Nanjing, China, which emitted 1-3 mg m⁻²
471 h⁻¹ (Zou et al., 2005). This might be due to temperature differences or differences in soil
472 characteristics at the two sites.

473 The yearly cumulative CH₄ emissions from Phrag2 were similar to those reported by Xu et al.
474 (2014) from a coastal saline grass flat dominated by *P. australis* in southeast China (6.28 g m⁻²).
475 However, markedly higher cumulative CH₄ emissions have been measured from other reed
476 wetlands, such as 39.5 g m⁻² from a tidal reed marsh in southeast China (Tong et al., 2010) and
477 65.9 g m⁻² from a restored reed fen in northeastern Germany (Koch et al., 2014). The yearly
478 cumulative CH₄ emissions from the rice paddy in our study were about six times higher than the
479 0.54-0.58 g m⁻² measured from rice paddies in eastern China (Zhang et al., 2014) but much lower
480 than the 57 g m⁻² measured over only two months from a rice paddy in the Philippines (Gaihre et
481 al., 2014). The *Suaeda* wetlands in our study had no net CH₄ emissions over the sampling period, in
482 contrast to a *Suaeda glauca* marsh in southeast China which emitted 0.399 g CH₄ m⁻² y⁻¹ (Xu et al.,
483 2014).

484 The average ecosystem respiration rates in this study were in a comparable range to those
485 recorded from coastal saline wetlands in southeast China by Xu et al. (2014). The average CO₂
486 emission rates at Phrag1 were somewhat lower than the 569.7 mg m⁻² h⁻¹ from the *Phragmites*
487 wetland in their study, whereas the emissions from Phrag2 were higher. Compared to the *Suaeda*
488 *glauca* marsh in Xu et al. (2014), which emitted on average 248.6 mg CO₂ m⁻² h⁻¹, Suaeda1 and 2
489 both had higher average CO₂ emissions.

490 **4.4 Conclusions**

491 We aimed at determining which factors are most important under field conditions for controlling
492 CH₄ and CO₂ emissions from coastal wetlands in order to be able to predict the effects of future
493 climate change on greenhouse gas emissions from wetlands and potentially to be able to manage
494 coastal wetlands in a way that minimizes greenhouse gas emissions. Hence, we quantified the CH₄
495 emissions and ecosystem respiration from April to November 2012 in five coastal wetlands in the
496 Liaohe Delta, northeast China, and determined the main controlling factors for the seasonal
497 variations and the differences among the sites. Over the study period, the two *Suaeda* wetlands
498 were net CH₄ sinks whereas the *Phragmites* wetlands and the rice paddy were net CH₄ sources.
499 The *Phragmites* wetlands had the highest climatic impact as they emitted the most cumulative CH₄
500 per unit area and the most CH₄ relative to CO₂ compared to the other wetland types. The main
501 controlling factors for the CH₄ emissions were water table, soil organic carbon, temperature and

502 salinity. Methane emissions are accelerated at high and constant (or managed) water tables and
503 decrease at water tables below the soil surface, or fluctuating water tables. Methane emissions
504 are also accelerated at high temperatures and depressed at high salinity levels. Saline wetlands
505 can, however, emit significant amounts of CH₄ as aerenchymatous wetland plants with deep root
506 systems can transport CH₄ produced in the deeper soil layers to the atmosphere. The ecosystem
507 respiration of the wetland communities depends largely on temperature and the plant
508 aboveground biomass, but soil organic matter content and belowground biomass are also
509 important. It is, however, necessary to quantify not only the ecosystem respiration, but also the
510 balance between the net CO₂ exchange and the CH₄ emission to determine if a particular wetland
511 can be considered to be a net source or a net sink for radiative greenhouse gases. Our study
512 indicates that the CH₄ emissions from coastal wetlands can be reduced by managing the water in
513 the wetland in a way that creates fluctuating water tables, including water tables below the soil
514 surface, as well as by occasional flooding by high-salinity water. However, the effects of potential
515 water management schemes on the biological communities in the wetlands must be carefully
516 studied prior to the implementation of the management in order to avoid negative and
517 undesirable effects on the wetland communities.

518 **Author contribution**

519 S.Y., K.W.K and H.B. designed the study, L.O. and S.Y. performed the field and laboratory
520 measurements, and L.O. prepared the manuscript with contributions from all co-authors.

521 **Acknowledgements**

522 The authors thank the Sino-Danish Centre for Education and Research (SDC) and the Ministry of
523 Land and Resources program of China: “Special foundation for scientific research on public causes”
524 (Grant No. 201111023), Marine Safeguard Project (Grant No. GZH201200503) and National
525 Natural Science Foundation of China (Grant Nos. 40872167 & 41240022). Many thanks also to
526 Linmiao Wang, Guangming Zhao, Hongming Yuan and Xigui Ding (staff and students at Qingdao
527 Institute of Marine Geology), Anders Henneberg (Aarhus University) and Rebecca F. Moss from
528 Five Rivers, LLC (at USGS National Wetlands Research Center) for assistance during fieldwork. For
529 valuable statistical advice we thank Brian Sorrell, Aarhus University and Christian Ritz, University of

530 Copenhagen. Any use of trade, product, or firm names is for descriptive purposes only and does
531 not imply endorsement by the U.S. Government.

532 **References**

- 533 Altor, A. E. and Mitsch, W. J.: Methane and carbon dioxide dynamics in wetland mesocosms: Effects of
 534 hydrology and soils, *Ecological Applications*, 18, 1307-1320, 2008.
- 535 Bartlett, K. B., Bartlett, D. S., Harriss, R. C., and Sebach, D. I.: Methane Emissions Along a Salt-Marsh
 536 Salinity Gradient, *Biogeochemistry*, 4, 183-202, 1987.
- 537 Bridgham, S. D., Megonigal, J. P., Keller, J. K., Bliss, N. B., and Trettin, C.: The carbon balance of North
 538 American wetlands, *Wetlands*, 26, 889-916, 2006.
- 539 Bridgham, S. D. and Richardson, C. J.: Mechanisms controlling soil respiration (CO₂ and CH₄) in southern
 540 peatlands, *Soil Biology and Biochemistry*, 24, 1089-1099, 1992.
- 541 Brix, H.: Functions of macrophytes in constructed wetlands, *Water Sci Technol*, 29, 71-78, 1994.
- 542 Brix, H.: Gas exchange through dead culms of reed, *Phragmites australis* (Cav.) Trin. ex Steudel, *Aquat. Bot.*,
 543 35, 81-98, 1989.
- 544 Brix, H., Sorrell, B. K., and Lorenzen, B.: Are *Phragmites*-dominated wetlands a net source or net sink of
 545 greenhouse gases?, *Aquat Bot*, 69, 313-324, 2001.
- 546 Brix, H., Sorrell, B. K., and Schierup, H. H.: Gas fluxes achieved by in situ convective flow in *Phragmites*
 547 *australis*, *Aquat Bot*, 54, 151-163, 1996.
- 548 Brix, H., Ye, S. Y., Laws, E. A., Sun, D. C., Li, G. S., Ding, X. G., Yuan, H. M., Zhao, G. M., Wang, J., and Pei, S.
 549 F.: Large-scale management of common reed, *Phragmites australis*, for paper production: A case study from
 550 the Liaohe Delta, China, *Ecological Engineering*, 73, 760-769, 2014.
- 551 Butterbach-Bahl, K., Papen, H., and Rennenberg, H.: Impact of gas transport through rice cultivars on
 552 methane emission from rice paddy fields, *Plant, Cell and Environment*, 20, 1175-1183, 1997.
- 553 Chambers, L. G., Reddy, K. R., and Osborne, T. Z.: Short-term response of carbon cycling to salinity pulses in
 554 a freshwater wetland, *Soil Science Society of America Journal*, 75, 2000-2007, 2011.
- 555 Couwenberg, J., Thiele, A., Tanneberger, F., Augustin, J., Barisch, S., Dubovik, D., Liashchinskaya, N.,
 556 Michaelis, D., Minke, M., Skuratovich, A., and Joosten, H.: Assessing greenhouse gas emissions from
 557 peatlands using vegetation as a proxy, *Hydrobiologia*, 674, 67-89, 2011.
- 558 Craft, C.: Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of
 559 Georgia and U.S. tidal marshes, *Limnol. Oceanogr.*, 52, 1220-1230, 2007.
- 560 D'Angelo, E. M. and Reddy, K. R.: Regulators of heterotrophic microbial potentials in wetland soils, *Soil*
 561 *Biology and Biochemistry*, 31, 815-830, 1999.
- 562 Gaihe, Y. K., Wassmann, R., Tirol-Padre, A., Villegas-Pangga, G., Aquino, E., and Kimball, B. A.: Seasonal
 563 assessment of greenhouse gas emissions from irrigated lowland rice fields under infrared warming,
 564 *Agriculture Ecosystems & Environment*, 184, 88-100, 2014.
- 565 Grunfeld, S. and Brix, H.: Methanogenesis and methane emissions: effects of water table, substrate type
 566 and presence of *Phragmites australis*, *Aquat Bot*, 64, 63-75, 1999.
- 567 Han, G. X., Yang, L. Q., Yu, J. B., Wang, G. M., Mao, P. L., and Gao, Y. J.: Environmental controls on net
 568 ecosystem CO₂ exchange over a reed (*Phragmites australis*) wetland in the Yellow River Delta, China,
 569 *Estuaries and Coasts*, 36, 401-413, 2013.
- 570 Happell, J. D. and Chanton, J. P.: Carbon remineralization in a north Florida swamp forest - effects of water-
 571 level on the pathways and rates of soil organic-matter decomposition, *Global Biogeochemical Cycles*, 7,
 572 475-490, 1993.
- 573 Hargreaves, K. J. and Fowler, D.: Quantifying the effects of water table and soil temperature on the
 574 emission of methane from peat wetland at the field scale, *Atmospheric Environment*, 32, 3275-3282, 1998.
- 575 Henneberg, A., Sorrell, B. K., and Brix, H.: Internal methane transport through *Juncus effusus*: experimental
 576 manipulation of morphological barriers to test above- and below-ground diffusion limitation, *New*
 577 *Phytologist*, 196, 799-806, 2012.
- 578 Herbst, M., Friborg, T., Ringgaard, R., and Soegaard, H.: Interpreting the variations in atmospheric methane
 579 fluxes observed above a restored wetland, *Agricultural and Forest Meteorology*, 151, 841-853, 2011.

580 Hodgkins, S. B., Tfaily, M. M., McCalley, C. K., Logan, T. A., Crill, P. M., Saleska, S. R., Rich, V. I., and Chanton,
 581 J. P.: Changes in peat chemistry associated with permafrost thaw increase greenhouse gas production,
 582 Proceedings of the National Academy of Sciences of the United States of America, 111, 5819-5824, 2014.
 583 Hosono, T. and Nouchi, I.: The dependence of methane transport in rice plants on the root zone
 584 temperature, Plant and Soil, 191, 233-240, 1997.
 585 Huang, G. H., Li, X. Z., Hu, Y. M., Shi, Y., and Xiao, D. N.: Methane (CH₄) emission from a natural wetland of
 586 northern China, Journal of Environmental Science and Health - Part A Toxic/Hazardous Substances and
 587 Environmental Engineering, 40, 1227-1238, 2005.
 588 Inglett, K. S., Inglett, P. W., Reddy, K. R., and Osborne, T. Z.: Temperature sensitivity of greenhouse gas
 589 production in wetland soils of different vegetation, Biogeochemistry, 108, 77-90, 2012.
 590 IPCC: Climate Change 2007. The Physical Science Basis. Contributions of Working Group I to the Fourth
 591 Assessment Report of the IPCC, Cambridge University Press, Intergovernmental Panel on Climate Change,
 592 2007.
 593 Ji, Y. H., Zhou, G. S., Lv, G. H., Zhao, X. L., and Jia, Q. Y.: Expansion of *Phragmites australis* in the Liaohe
 594 Delta, north-east China, Weed Research, 49, 613-620, 2009.
 595 Kandel, T. P., Elsgaard, L., and Laerke, P. E.: Measurement and modelling of CO₂ flux from a drained fen
 596 peatland cultivated with reed canary grass and spring barley, Global Change Biology Bioenergy, 5, 548-561,
 597 2013.
 598 Kayranli, B., Scholz, M., Mustafa, A., and Hedmark, A.: Carbon storage and fluxes within freshwater
 599 wetlands: a critical review, Wetlands, 30, 111-124, 2010.
 600 Koch, S., Jurasinski, G., Koebisch, F., Koch, M., and Glatzel, S.: Spatial variability of annual estimates of
 601 methane emissions in a *Phragmites australis* (Cav.) Trin. ex Steud. dominated restored coastal brackish fen,
 602 Wetlands, 34, 593-602, 2014.
 603 Krauss, K. W. and Whitbeck, J. L.: Soil greenhouse gas fluxes during wetland forest retreat along the lower
 604 Savannah River, Georgia (USA), Wetlands, 32, 73-81, 2012.
 605 Krauss, K. W., Whitbeck, J. L., and Howard, R. J.: On the relative roles of hydrology, salinity, temperature,
 606 and root productivity in controlling soil respiration from coastal swamps (freshwater), Plant and Soil, 358,
 607 265-274, 2012.
 608 Käki, T., Ojala, A., and Kankaala, P.: Diel variation in methane emissions from stands of *Phragmites australis*
 609 (Cav.) Trin. ex Steud. and *Typha latifolia* L. in a boreal lake, Aquat Bot, 71, 259-271, 2001.
 610 Le Mer, J. and Roger, P.: Production, oxidation, emission and consumption of methane by soils: A review,
 611 European Journal of Soil Biology, 37, 25-50, 2001.
 612 Li, X. W., Liang, C., and Shi, J. B.: Developing wetland restoration scenarios and modeling its ecological
 613 consequences in the Liaohe River Delta wetlands, China, Clean-Soil Air Water, 40, 1185-1196, 2012.
 614 Livingston, G. P. and Hutchinson, G. L.: Enclosure-based measurement of trace gas exchange: applications
 615 and sources of error. In: Biogenic Trace Gases: Measuring Emissions from Soil and Water, Matson, P. A. and
 616 Harriss, R. C. (Eds.), Methods in Ecology, Blackwell Science Ltd, Oxford, 1995.
 617 Ma, X., Liu, X., and Wang, R.: China's wetlands and agro-ecological engineering, Ecological Engineering, 2,
 618 291-301, 1993.
 619 Mah, R. A., Ward, D. M., Baresi, L., and Glass, T. L.: Biogenesis of methane, Annual Review of Microbiology,
 620 31, 309-341, 1977.
 621 Mann, C. J. and Wetzel, R. G.: Loading and utilization of dissolved organic carbon from emergent
 622 macrophytes, Aquat Bot, 53, 61-72, 1996.
 623 Mehlich, A.: Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant, Communications in Soil
 624 Science and Plant Analysis, 15, 1409-1416, 1984.
 625 Minke, M., Augustin, J., Hagemann, U., and Joosten, H.: Similar methane fluxes measured by transparent
 626 and opaque chambers point at belowground connectivity of *Phragmites australis* beyond the chamber
 627 footprint, Aquat Bot, 113, 63-71, 2014.
 628 Mitsch, W. J., Bernal, B., Nahlik, A. M., Mander, U., Zhang, L., Anderson, C. J., Jorgensen, S. E., and Brix, H.:
 629 Wetlands, carbon, and climate change, Landscape Ecol, 28, 583-597, 2013.

Mitsch, W. J. and Gosselink, J. G.: Wetlands, John Wiley & Sons, Inc., Hoboken, New Jersey, U.S.A., 2007.
 Neubauer, S. C., Miller, W. D., and Anderson, I. C.: Carbon cycling in a tidal freshwater marsh ecosystem: a
 carbon gas flux study, *Marine Ecology Progress Series*, 199, 13-30, 2000.
 Nouchi, I., Mariko, S., and Aoki, K.: Mechanism of methane transport from the rhizosphere to the
 atmosphere through rice plants, *Plant Physiology*, 94, 59-66, 1990.
 Picek, T., Cizkova, H., and Dusek, J.: Greenhouse gas emissions from a constructed wetland - Plants as
 important sources of carbon, *Ecological Engineering*, 31, 98-106, 2007.
 Poffenbarger, H. J., Needelman, B. A., and Megonigal, J. P.: Salinity influence on methane emissions from
 tidal marshes, *Wetlands*, 31, 831-842, 2011.
 Pulliam, W. M.: Carbon-dioxide and methane exports from a southeastern floodplain swamp, *Ecological
 Monographs*, 63, 29-53, 1993.
 Serrano-Silva, N., Sarria-Guzman, Y., Dendooven, L., and Luna-Guido, M.: Methanogenesis and
 methanotrophy in soil: a review, *Pedosphere*, 24, 291-307, 2014.
 Sha, C., Mitsch, W. J., Mander, U., Lu, J. J., Batson, J., Zhang, L., and He, W. S.: Methane emissions from
 freshwater riverine wetlands, *Ecological Engineering*, 37, 16-24, 2011.
 Singh, S. and Singh, J. S.: Plants as conduit for methane in wetlands, *Proceedings of the National Academy
 of Sciences, India. Section B: Biological sciences*, 65, 147-157, 1995.
 Sorrell, B. K. and Boon, P. I.: Convective gas-flow in *Eleocharis sphacelata* R. Br. - methane transport and
 release from wetlands, *Aquat Bot*, 47, 197-212, 1994.
 Sun, Z., Wang, L., Tian, H., Jiang, H., Mou, X., and Sun, W.: Fluxes of nitrous oxide and methane in different
 coastal Suaeda salsa marshes of the Yellow River estuary, China, *Chemosphere*, 90, 856-865, 2013.
 Svensson, B. H.: Different temperature optima for methane formation when enrichments from acid peat
 are supplemented with acetate or hydrogen, *Applied and Environmental Microbiology*, 48, 389-394, 1984.
 Tanner, C. C., Adams, D. D., and Downes, M. T.: Methane emissions from constructed wetlands treating
 agricultural wastewaters, *Journal of Environmental Quality*, 26, 1056-1062, 1997.
 Team, R. C.: R: A language and environment for statistical computing. R Foundation for Statistical
 Computing, Vienna, Austria, 2013.
 Tong, C., Huang, J. F., Hu, Z. Q., and Jin, Y. F.: Diurnal variations of carbon dioxide, methane, and nitrous
 oxide vertical fluxes in a subtropical estuarine marsh on neap and spring tide days, *Estuaries and Coasts*, 36,
 633-642, 2013.
 Tong, C., Wang, W.-Q., Zeng, C.-S., and Marrs, R.: Methane (CH₄) emission from a tidal marsh in the Min
 River estuary, southeast China, *Journal of Environmental Science and Health - Part A Toxic/Hazardous
 Substances and Environmental Engineering*, 45, 506-516, 2010.
 Van der Nat, F. J. and Middelburg, J. J.: Methane emission from tidal freshwater marshes, *Biogeochemistry*,
 49, 103-121, 2000.
 Weston, N. B., Vile, M. A., Neubauer, S. C., and Velinsky, D. J.: Accelerated microbial organic matter
 mineralization following salt-water intrusion into tidal freshwater marsh soils, *Biogeochemistry*, 102, 135-
 151, 2011.
 Whalen, S. C.: Biogeochemistry of methane exchange between natural wetlands and the atmosphere,
Environmental Engineering Science, 22, 73-94, 2005.
 Whiting, G. J. and Chanton, J. P.: Greenhouse carbon balance of wetlands: Methane emission versus carbon
 sequestration, *Tellus, Series B-Chemical and Physical Meteorology*, 53, 521-528, 2001.
 Whiting, G. J. and Chanton, J. P.: Primary production control of methane emission from wetlands, *Nature*,
 364, 794-795, 1993.
 Xu, X. W., Zou, X. Q., Cao, L. G., Zhamangulova, N., Zhao, Y. F., Tang, D. H., and Liu, D. W.: Seasonal and
 spatial dynamics of greenhouse gas emissions under various vegetation covers in a coastal saline wetland in
 southeast China, *Ecological Engineering*, 73, 469-477, 2014.
 Yu, K. W., Faulkner, S. P., and Baldwin, M. J.: Effect of hydrological conditions on nitrous oxide, methane,
 and carbon dioxide dynamics in a bottomland hardwood forest and its implication for soil carbon
 sequestration, *Glob Change Biol*, 14, 798-812, 2008.

680 Zhai, X., Piwpuan, N., Arias, C. A., Headley, T., and Brix, H.: Can root exudates from emergent wetland
681 plants fuel denitrification in subsurface flow constructed wetland systems?, *Ecological Engineering*, 61, 555-
682 563, 2013.

683 Zhang, H., Zhao, X., Ni, Y., Lu, X., Chen, J., Su, F., Zhao, L., Zhang, N., and Zhang, X.: PCDD/Fs and PCBs in
684 sediments of the Liaohe River, China: levels, distribution, and possible sources, *Chemosphere*, 79, 754-762,
685 2010.

686 Zhang, X., Yin, S., Li, Y., Zhuang, H., and Li, C.: Comparison of greenhouse gas emissions from rice paddy
687 fields under different nitrogen fertilization loads in Chongming Island, Eastern China, *The Science of the*
688 *Total Environment*, 472, 381-388, 2014.

689 Zhu, L., Wu, J., Xu, Y., Hu, R., and Wang, N.: Recent geomorphic changes in the Liaohe Estuary, *Journal of*
690 *Geographical Sciences*, 20, 31-48, 2010.

691 Zou, J. W., Huang, Y., Jiang, J. Y., Zheng, X. H., and Sass, R. L.: A 3-year field measurement of methane and
692 nitrous oxide emissions from rice paddies in China: Effects of water regime, crop residue, and fertilizer
693 application, *Global Biogeochemical Cycles*, 19, n-a-n/a, 2005.

694

695

696 **Table 1.** Physical/chemical topsoil characteristics (0-5 cm depth for bulk density, water content and redox
697 potential; else 0-4 cm depth) at the five wetland sites (two *Suaeda salsa* wetlands, two *Phragmites australis*
698 wetlands and one rice paddy) in the Liaohe Delta, northeast China. Data was collected in 2013 by Siyuan Ye
699 et al. (personal communication).

	Suaeda1	Suaeda2	Phrag1	Phrag2	Rice
Bulk density (g cm ⁻³)	1.50	1.20	1.07	0.93	1.36
Water content (% of FW)	27	37	41	48	30
Redox potential (mV)	101	24	-127	-91	-82
TN (% of DW)	0.08	0.07	0.17	1.02	0.10
TC (% of DW)	0.95	0.83	1.81	12.59	0.88
Org-C (% of DW)	0.53	0.69	1.67	11.81	0.69
C:N ratio	12.4	12.0	9.8	12.3	8.4
Ca (μg g ⁻¹)	6735	4215	3817	2103	2239
Cu (μg g ⁻¹)	9.96	6.78	9.11	7.18	3.44
Fe (μg g ⁻¹)	282	434	396	343	343
K (μg g ⁻¹)	849	576	598	892	109
Mg (μg g ⁻¹)	2043	1120	1395	1687	216
Mn (μg g ⁻¹)	291	368	308	104	78
P (μg g ⁻¹)	19.7	27.8	9.9	46.7	37.0
Zn (μg g ⁻¹)	9.6	11.1	17.8	30.8	8.2

700

701

702

703 **Table 2.** Results from repeated-measures ANOVAs with the response variables CH₄-flux and R_{eco},
704 respectively, the fixed factors Site and Time and their interaction, and the random factor Plot. Gas fluxes
705 were measured during April-November 2012 from six plots at two *Suaeda salsa* wetlands, two *Phragmites*
706 *australis* wetlands and one rice paddy in the Liaohe Delta, northeast China. All measurements from April,
707 May and August were excluded from the analysis due to missing data from some sites.

Response variable	Factor	df	F-ratio	p
CH ₄ -flux	Site	4	19.9	<0.001
	Time	4	7.5	<0.001
	Site × Time	16	5.9	<0.001
	Plot (random factor)	25	2.0	0.007
R _{eco}	Site	4	23.7	<0.001
	Time	4	379.4	<0.001
	Site × Time	16	55.7	<0.001
	Plot (random factor)	25	1.9	0.010

708 df: degrees of freedom

709 **Table 3.** Results from linear mixed effects models, with CH₄ emission rate and ecosystem respiration rate
710 (R_{eco}) as response variables, and the fixed effects Plant species, Biomass, Soil temperature, Water table and
711 Salinity. Shown are the coefficients of the fixed effects to be included in equation 1, standard errors of the
712 means and p-values.

Response variable	Predictor	Coefficient	SE	p
CH ₄ emission rate	Water table	0.0054	0.0014	<0.001
	Soil temperature	0.0017	0.0023	<0.001
	Salinity	-0.0023	0.0030	<0.001
CH ₄ emission rate ^a	Water table	0.0071	0.0019	<0.001
	Soil temperature	0.0074	0.0034	<0.001
R _{eco}	Suaeda*Biomass	-1.93 10 ⁻⁵	3.1 10 ⁻⁴	0.003
	Phrag*Biomass	7.1 10 ⁻⁴	2.5 10 ⁻⁴	0.003
	Rice*Biomass	9.2 10 ⁻⁴	3.0 10 ⁻⁴	0.003
	Soil temperature	0.057	0.0042	<0.001
	Salinity	0.0095	0.0044	0.049

713 ^a Only sites with CH₄ emissions >0 included (Phrag1, Phrag2 and Rice).

714 **Table 4.** Mean CH₄ emission and ecosystem respiration rates (R_{eco}) with ranges in parentheses, and
715 cumulative CO₂ equivalents from CH₄ and CO₂ emissions, respectively, from two *Phragmites australis*
716 wetlands and one rice paddy during April-November 2012 in the Liaohe Delta, northeast China. CH₄ fluxes
717 are converted to CO₂-equivalents using a factor of 25. Superscript letters represent significant differences
718 (p<0.05) among sites.

Site	CH ₄ emission rates (mg m ⁻² h ⁻¹)	R _{eco} (mg CO ₂ m ⁻² h ⁻¹)	Cumulative CO ₂ -equivalents	
			CH ₄ (g CO ₂ -eqv m ⁻² y ⁻¹)	CO ₂ (g CO ₂ -eqv m ⁻² y ⁻¹)
Suaeda1	0.01 (-0.31 - 0.44) ^a	278 (-3.6 - 814) ^{ab}	-0.4	1671
Suaeda2	-0.01 (-0.50 - 0.42) ^a	423 (4.6 - 954) ^b	-1.9	1730
Phrag1*	0.15 (-0.31 - 1.48) ^{ab}	484 (-14.8 - 1300) ^c	31.1	2963
Phrag2	1.01 (-0.28 - 6.38) ^c	811 (27.4 - 3357) ^c	153.7	4443
Rice	0.75 (-0.27 - 4.63) ^b	532 (-0.2 - 3181) ^a	91.6	3337

719 * No data from August

721 **Legends to figures:**

722 **Figure 1.** Seasonal variation in (a) CH₄ emission rates, (b) ecosystem respiration, (c) water table, (d) soil
723 temperature, (e) aboveground dry biomass and (f) salinity in two *Suaeda salsa* wetlands, two *Phragmites*
724 *australis* wetlands and one rice paddy during 2012 in the Liaohe Delta, northeast China. Plotted values are
725 the averages for six plots at each site. Data from Phrag2 is missing in August because it was not possible to
726 sample due to extreme flooding. Aboveground biomass data from Suaeda1 is missing in September due to
727 technical issues.

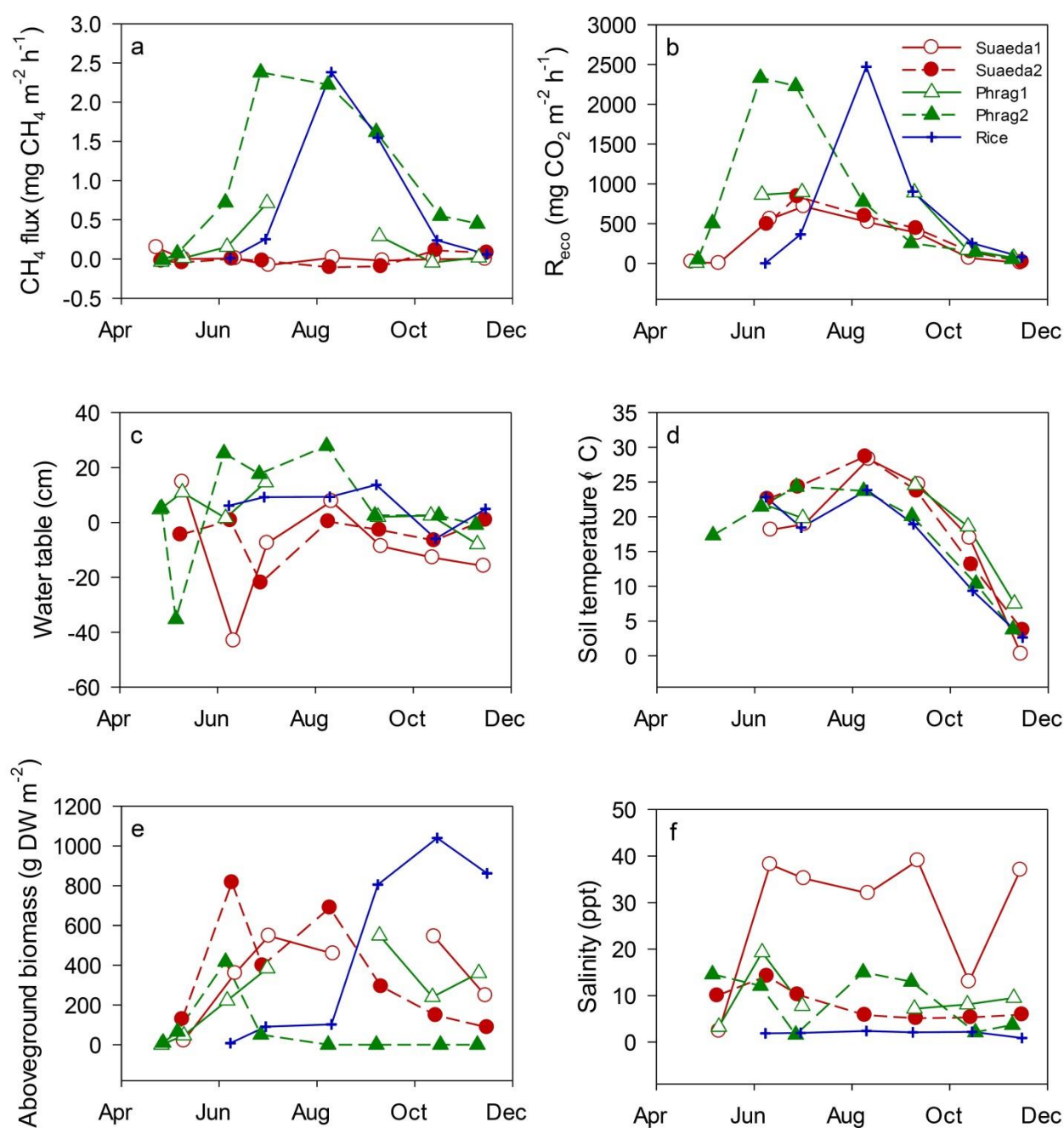
728 **Figure 2.** Cumulative CH₄ emissions during the growing season 2012 from two *Suaeda salsa* wetlands, two
729 *Phragmites australis* wetlands and one rice paddy during 2012 in the Liaohe Delta, northeast China. The
730 points represent integrals of the monthly mean values from six plots at each site. Measurements are
731 missing from Phrag1 in August due to flooding.

732 **Figure 3.** Relationship between CH₄ emission rates and (a) soil temperature, and (b) water table, in two
733 *Phragmites australis* wetlands and a rice paddy in the Liaohe Delta, northeast China. Data points after
734 cutting the vegetation at Phrag2 are represented by downward triangles (Phrag2-cut). Measurements were
735 done from April to November 2012.

736 **Figure 4.** Relationship between salinity and CH₄ emission rates in two *Suaeda salsa* wetlands, two
737 *Phragmites australis* wetlands and one rice paddy during 2012 in the Liaohe Delta, northeast China. Data
738 points after cutting the vegetation at Phrag2 are represented by downward triangles (Phrag2-cut).
739 Measurements were done from April to November 2012.

740

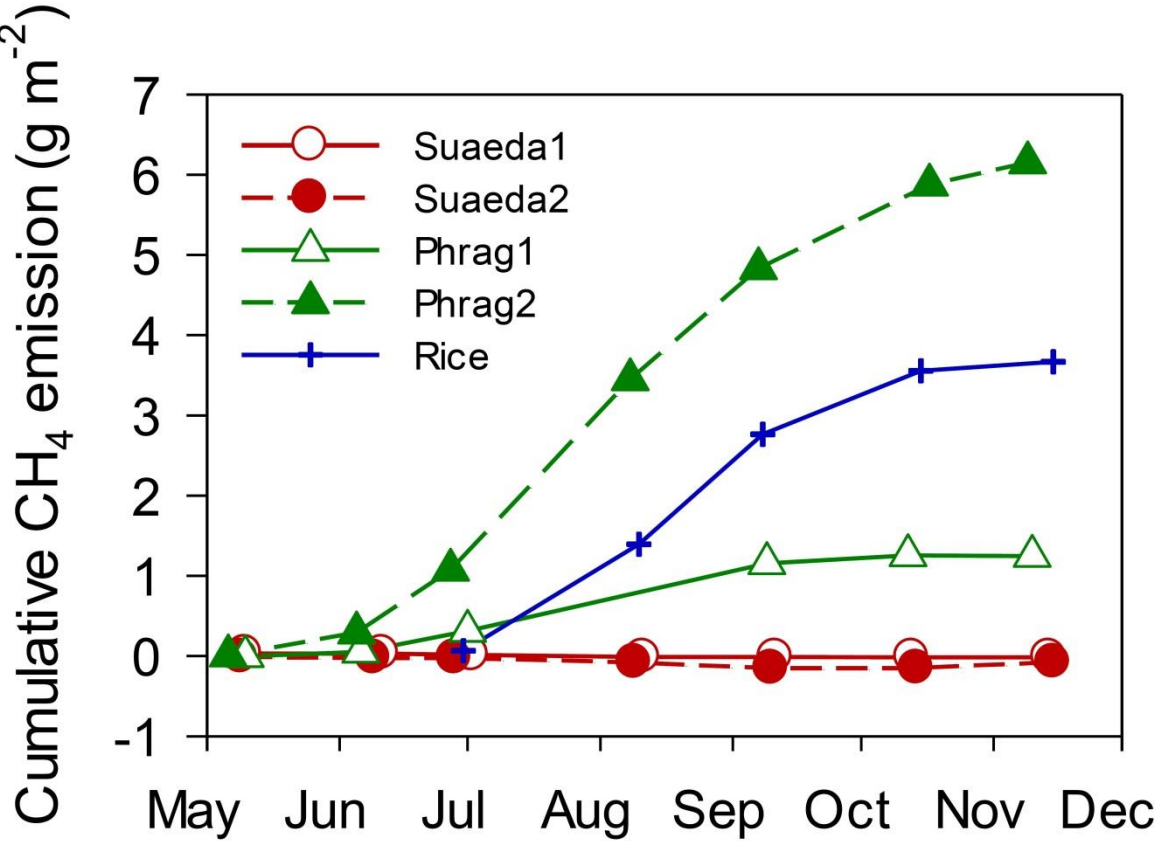
741 Fig. 1



742

743

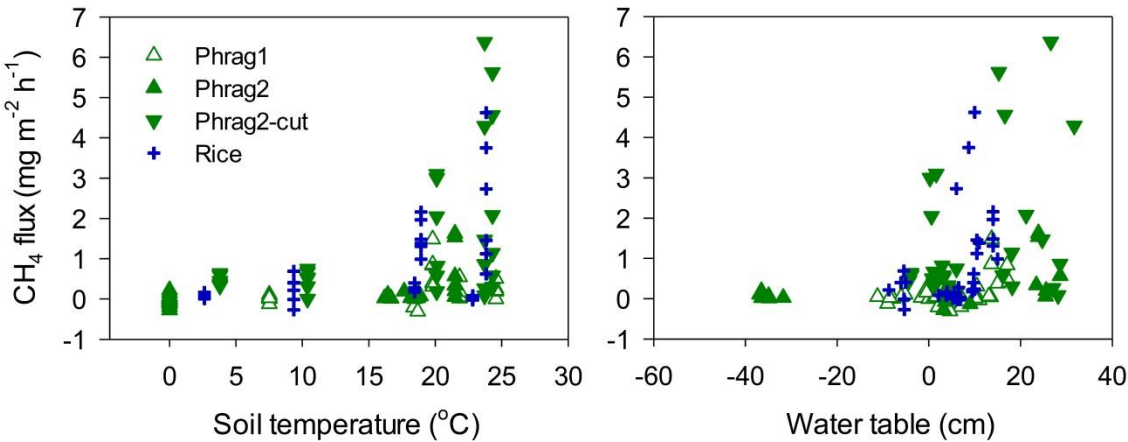
744 Fig. 2



745

746

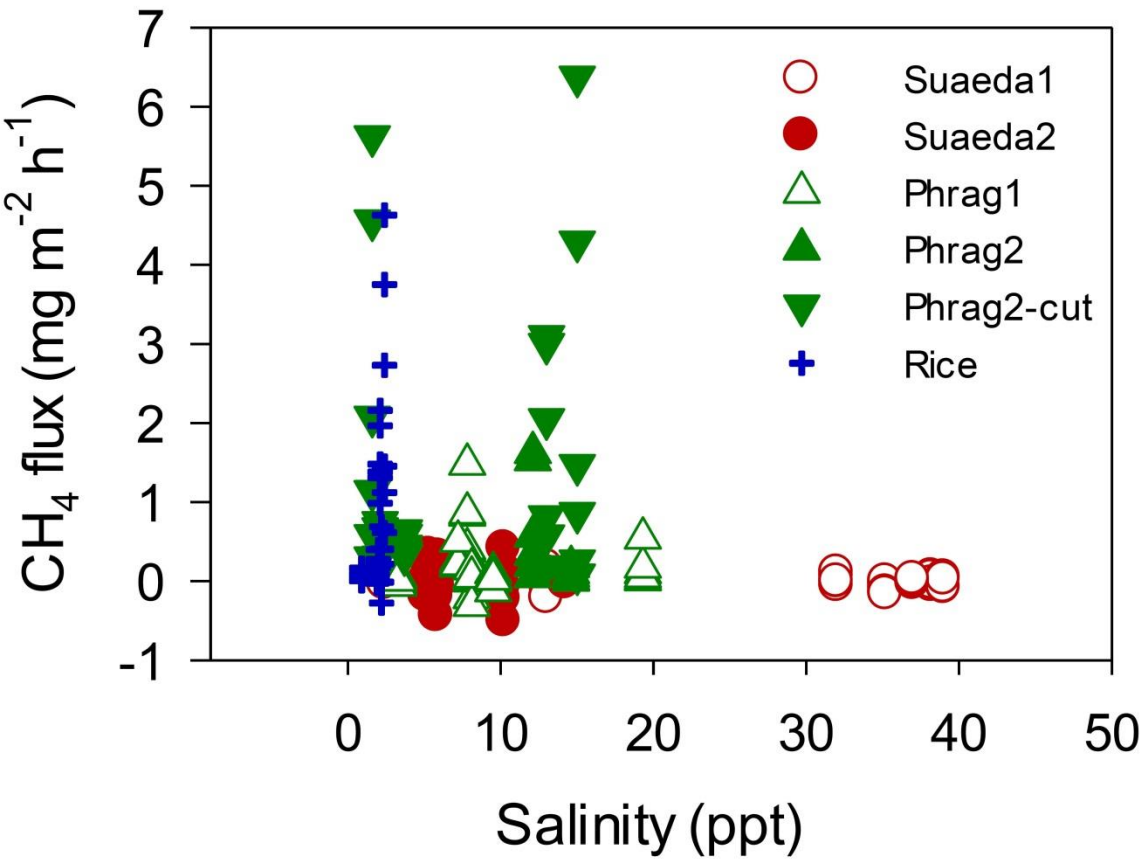
747 Fig. 3.



748

749

750 Fig. 4



751