

1 **Flood regime affects soil stoichiometry and the distribution of the**
2 **invasive plants in subtropical estuarine wetlands in China**

3 Weiqi Wang^{a,b*}, Chun Wang^{a,b}, Jordi Sardans^{c,d*}, Chuan Tong^{a,b}, Ruixia Jia^{a,b}, Congsheng
4 Zeng^{a,b}, Josep Peñuelas^{c,d}

5 ^a *Institute of Geography, Fujian Normal University, Fuzhou 350007, China.*

6 ^b *Key Laboratory of Humid Subtropical Eco-geographical Process, Ministry of Education, Fujian Normal*
7 *University, Fuzhou 350007, China.*

8 ^c *CSIC, Global Ecology CREAM- CSIC-UAB, Cerdanyola del Valles, 08193 Barcelona, Catalonia, Spain.*

9 ^d *CREAF, Cerdanyola del Valles, 08193 Barcelona, Catalonia, Spain.*

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11 *Corresponding author. Fax: +86 591 83465397. *E-mail addresses:* wangweiqi15@163.com (W. Wang);

12 j.sardans@creaf.uab.cat (J. Sardans)

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23 **ABSTRACT**

24 Projections of climate change impacts over the coming decades suggest that rising sea levels
25 will flood coastal wetlands, moving the range of wetlands inland from the current coastline.
26 The intensity of flooding in wetland areas will thus increase, with corresponding impacts on
27 soil properties and coastal ecosystems. We studied the impacts of two levels of water
28 inundation on the concentration and stoichiometry of soil carbon, nitrogen, phosphorus and
29 sulfur in areas dominated by the native C₃ species *Scirpus triqueter* L., the native C₄ species
30 *Cyperus malaccensis* var. *brevifolius* Boeckl. and the invasive Gramineae C₃ species
31 *Phragmites australis* (Cav.) Trin. ex Steud in the Shanyutan wetland areas of the Minjiang
32 River estuary in China. Comparison of the communities dominated by these three species in
33 high- and low- water flood habitats showed that flooding enhanced anaerobiosis and salinity
34 and altered the carbon and nitrogen plant-soil cycles. Higher flooding favored the invasive
35 species more than the two native species. The invasive *P. australis* accumulated more carbon
36 (65% increase in aboveground biomass), and took up more nitrogen under high flooding than
37 did *C. malaccensis* and *S. triqueter*. The more conservative use of soil resources, particularly
38 the limiting nutrient N, appeared to underlie the higher capacity of the invasive species to
39 tolerate higher flooding intensity. Increases in flooding may thus enhance the success and
40 expansion of the invasive *P. australis* to the detriment of the native plant species in these
41 Chinese wetlands.

42 Keywords: China; climate change; ocean level; plant invasion; stoichiometry; wetland

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46 **1. Introduction**

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48 Global change can affect ocean levels (Schewe et al., 2011; Mendelsohn et al., 2012; Piecuch
49 and Ponte, 2014), river flows (Bueh et al., 2003; van Vliet et al., 2013; Grafton et al., 2013)
50 and water stoichiometry (Sardans et al., 2012; Sardans and Peñuelas, 2014) that in turn can
51 affect community structure and function (Peñuelas et al., 2012; 2013). Rising sea levels could
52 be especially critical for wetland ecosystems (Ramsar, 2013). In China, a higher sea level
53 would flood the current coastal wetlands and create new wetlands farther inland. However,
54 most coastal areas in China, included the studied estuary, are protected by seawalls, so
55 wetland areas cannot increase in size, and this is why the areas of these wetlands will only
56 decrease as the sea level rises (Yang et al., 2014). As an example, with a 0.5 m rise in sea
57 level, the Liaohe delta would lose 3530 km² (Xiao et al., 2003) and the Changjiang River
58 estuary would lose 20% of its area (Ji et al., 1994).

59 Flooding can also alter the soil contents and the stoichiometric relationships of carbon
60 (C), nitrogen (N), phosphorus (P) and sulfur (S) by changing the aerobic/anaerobic
61 biogeochemical equilibrium, nutrient inputs and outputs and/or the structure of plant
62 communities (Steinman et al., 2012; Recha et al., 2013). These changes could explain with
63 other impacts of global change such as the success of invasive species (Sardans and Peñuelas,
64 2012). Invasive plant species, such as *Phragmites australis*, are increasing in several Chinese
65 wetland areas (Tong et al., 2011; Wang et al., 2014a). The success of *P. australis* has been
66 associated with changes in its nutrient-use efficiency (Wang et al., 2014a), so we hypothesize
67 that increased flooding could have an impact on its invasive success.

68 Recent stoichiometric ecological studies have shown that S can be more sensitive than N

69 or P to stoichiometric shifts in response to environmental changes (Kirkby et al., 2013). The
70 strong link between C and S justifies the study of S and its stoichiometric relationships with
71 other nutrients (Kirkby et al., 2011), particularly in wetland ecosystems. Water fluxes during
72 tides and the differences of daily flooding time generate nutrient shifts in wetland soils (Tong
73 et al., 2010; Tong et al., 2011; Wang et al., 2012b), but the degree of the impacts on soil
74 stoichiometry and its relationships with other soil properties in wetlands and their possible
75 influence on the success of alien species are poorly known. Because estuarine wetlands are
76 influenced by changes in both river flows and tides, their elemental ratios are likely to be the
77 most variable of the terrestrial ecosystems worldwide. The impact of changes in *water fluxes*
78 during tides and the differences of daily flooding time on the relative balance of soil C:N:P:S
79 stoichiometry in wetlands remains unclear.

80 Coastal wetlands occupy 5.7×10^6 km² globally (Ramsar, 2013; Mitsch and Gosselink,
81 2007) and 1.2×10^4 km² in China (Shen and Zhu, 1999; Huang et al., 2006). They are cradles
82 of biodiversity upon which countless species of plants and animals depend for survival
83 (Ramsar, 2013). Furthermore, wetlands are among the world's most productive environments
84 and provide a wide array of benefits, such as mitigation of pollution (Destandau et al., 2013),
85 provision of bird habitats (Fairbairn and Dinsmore, 2001), and reduction of hurricane storm
86 surges (Barbier et al., 2013). Coastal wetlands are also a sink of C as peat and plant matter
87 (Ramsar, 2013; Mitsch and Gosselink, 2007). Wetlands continue to be among the ecosystems
88 most affected by global change, and yet we lack information on the effect of water fluxes
89 during tides and the differences of daily flooding time on their abiotic and biotic
90 environments (Ramsar, 2013; Mitsch and Gosselink, 2007). A better knowledge of the

91 resulting soil C, N, P and S ecological stoichiometries in wetlands would provide decision
92 makers with the necessary information for developing effective methods to enhance the
93 potential capacity of these ecosystems to fix C and reduce the emission of greenhouse gases
94 (Peñuelas et al., 2013). Moreover, determining the cycles and balances of C, N, P and S and
95 the fertility of the soil could improve our understanding of the impacts on potential wetland
96 uses and regenerative capacities.

97 To further understand the effects of floodwater regime on soil C, N, P and S
98 concentrations and stoichiometries in estuarine wetlands, we: (1) describe the changes in soil
99 C, N, P and S concentrations and stoichiometries, as well as other chemical and physical soil
100 properties associated with floodwater, and the relationships among these parameters at
101 different depths in estuarine tidal wetlands; (2) analyze the relationships among these
102 properties and the capacity of soil to store C; and (3) determine the impact of changes in
103 flooding on the success of invasive plant species.

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105 **2. Material and methods**

106 *2.1. Study area*

107 This study was conducted in the Shanyutan wetlands (26°01'46"N, 119°37'31"E; Fig. 1), the
108 largest tidal wetland area (approximately 3120 ha) in the Minjiang River estuary. The climate
109 in this region is relatively warm and wet with a mean annual temperature of 19.6 °C and a
110 mean annual precipitation of 1346 mm (Zheng et al., 2006). The average salinity of the tidal
111 water from May to December 2007 was 4.2 ± 2.5 ‰. *Scirpus triqueter* L. and *Cyperus*
112 *malaccensis* var. *brevifolius* Boeckl. are the most widespread native plant species (Liu et al.,
113 2006) in the area. *P. australis* has invaded the wetlands over the past 30 years and is now the

114 most prevalent plant species. These three species can grow in both high-flood and low-flood
115 habitats. Currently, *S. triqueter*, *P. australis* and *C. malaccensis* are the three primary plant
116 species in the upper (mid to high) portions of mudflats in the Minjiang River estuary (Liu et
117 al., 2006). *S. triqueter* is a native species, C₃ monocot. *S. triqueter* is short (0.6 m), has a
118 vestigial leaves with marginal importance in photosynthetic function, a stick to aboveground
119 base stem, and a belowground crawl stem. *Phragmites australis* is an invasive species, C₃
120 monocot, a tall plant (2 m during last growth stage) with one leaf on each node of the
121 aboveground stem. *C. malaccensis* is a native species, C₄ monocot, is shorter (1.5 m) than *P.*
122 *australis*, and has a degenerated leaf, a stick to aboveground base stem and a belowground
123 crawl stem. In our study, the high-flood habitats are located on average at 5.2 meters above
124 sea level and flooded by intermediate tides about 240 days per year and are submerged
125 beneath 10-120 cm of water for 0.5-4 h during each tidal inundation. The low-flood habitats
126 are located on average at 5.6 meters above sea level and are flooded only during spring tides,
127 about 80 days per year, submerged beneath 10-50 cm of water for 0.5-2 h during each tidal
128 inundation. At low tide, the soil surfaces of both the low- and high-flood habitats of the entire
129 estuarine wetlands are exposed, but the soil remains flooded in some low areas.

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131 2.2. Collection and analysis of plant and soil samples

132 Samples were collected in October 2007 from *S. triqueter*, *P. australis* and *C. malaccensis*
133 dominated community in the high- and low-flood habitats (Fig. 1). Three replicate plots were
134 randomly established in each community at each flood regime. Plant samples were collected
135 from a consistent height. Each replicate consisted of a large quadrat (10 × 10 m) in each plot

136 and sampled the aboveground and belowground biomass from three randomly selected
137 sub-quadrats (1 × 1 m). All plant material was gently washed with water and then oven-dried
138 to a constant mass (80 °C for 24-36 h) and weighed. The plant biomass of each community
139 was determined by summing the above- and below ground biomasses. The first 0.6 m of the
140 soil profile in a 1x1m area were excavated. This depth was chosen because most root biomass
141 of all studied species (>80%) is located in the first 60 cm of soil depth. Samples were
142 collected with a small sampler (length, 0.3 m; diameter, 0.1 m) from each of six soil layers
143 (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 cm) at the center and both sides of the soil pit.
144 These three samples were combined to form one sample per layer. A total of 108 soil samples
145 (three communities × two flood regime × six soil layers × three replicates) were thus collected.
146 In the laboratory, the soil samples were air-dried, roots and visible plant remains were
147 removed and the soil was finely ground in a ball mill to 0.15 mm.

148 Total soil organic-C content was determined by the $K_2Cr_2O_7-H_2SO_4$ digestion method
149 (Sorrell et al., 1997; Bai et al., 2005), dissolved organic-carbon (DOC) content was
150 determined by extraction with deionized water and measured using a TOC-V CPH total
151 carbon analyzer (Shimadzu Scientific Instruments, Japan) and total soil N concentration was
152 analyzed in a K370 Kjeldahl unit (Buchi Scientific Instruments, Switzerland) by NH_3
153 distillation of soil acid digests (Kjeldahl, 1883; Wang et al., 2014a). NH_4^+ and NO_3^- were
154 extracted with 2 mol L^{-1} KCl. NH_4^+ concentration was determined by the indophenol-blue
155 method using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Japan). NO_3^-
156 concentration was determined by the zinc-cadmium reduction method using a UV-2450
157 spectrophotometer (Shimadzu Scientific Instruments, Japan), although NO_3^- concentration

158 data were low and not accurate for the *S. triquetra* community, so we excluded these data
159 from our analysis to avoid errors. Total soil P concentration was determined by
160 perchloric-acid digestion and measured using a UV-2450 spectrophotometer (Shimadzu
161 Scientific Instruments, Japan), total S concentration was determined by the next steps, first,
162 by magnesium-nitrate digestion and evaporated to dryness at 70 °C on a hot plate, and then
163 the residue was placed in heat oven at 300°C overnight. After this digestion, in a second step,
164 the residue was digested with nitric acid on a water bath, in order to oxidized sulphur to
165 sulphate. Finally, al the resulting sulphate was measured by the barium-sulfate turbidity
166 method and given as total S (g of S kg⁻¹ soil, D.W.). Available-S was determined by
167 phosphate and acetic-acid extraction and measured by the barium-sulfate turbidity method
168 (Lu, 1999).

169 Bulk density was measured from three 5 × 3 cm cores per soil layer, salinity was
170 measured with a DDS-307 conductivity meter (Boqu Scientific Instruments, China), pH was
171 measured with an 868 pH meter (Orion Scientific Instruments, USA), soil particle-size (clay,
172 silt and sand) contents were determined with a SEDIMAT4-12 Particle Size Analyser (UGT
173 Scientific Instruments, Germany) and soil-water content was determined gravimetrically (Lu,
174 1999).

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176 2.3. Determination of soil-C content

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178 The C content for all soil layers was estimated using the equation (Mishra et al., 2010):

$$C_S = \sum_{j=1}^n c_m \times \rho_b \times D$$

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180 where C_S is C content (kg m^{-2}), j is soil-depth interval (1, 2, ... n), C_m is C concentration (g
181 kg^{-1}), ρ_b is soil bulk density (kg m^{-3}), D is the thickness of each soil layer (m) and n is the
182 number of soil layers.

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184 2.4. Statistical analyses

185 The significance of differences in soil parameters and biomass among the communities, soil
186 layers and regimes of flooding were assessed with general linear models (factorial two-way
187 ANOVA) with different plant communities, soil depth and flooding regime as categorical
188 independent variables and Tukey's post-hoc tests. We determined the Pearson correlation
189 coefficients between the soil parameters and total soil C, N, P and S concentrations; DOC,
190 NH_4^+ , NO_3^- and available-S concentrations and total soil C:N, C:P, N:P, C:S, N:S and P:S
191 ratios. Soil C:N, C:P, N:P, C:S, N:S, and P:S ratios were calculated as mass ratios. We also
192 determined the effects of water content and communities dominated by different species on
193 soil-C content and the Pearson correlation coefficients between soil C:N, C:P, N:P, C:S, N:S
194 and P:S ratios and soil-C content. All univariate statistical analyses were performed using
195 SPSS 13.0 software (SPSS Inc., Chicago, Illinois). The effects of community on plant
196 biomass accumulation were determined by a factorial two-way ANOVA with
197 species-community and flooding intensity as independent continuous variables.

198 We also performed multivariate discriminant function analysis (DFA) to determine the
199 importance of total soil C, N, P and S concentrations; DOC, NH_4^+ , NO_3^- and available-S
200 concentrations and total soil C:N, C:P, N:P, C:S, N:S and P:S ratios in the separation of the

201 each replicate sampled at both flood regimes for the three communities. DFA is a supervised
202 statistical algorithm that derives an optimal separation between groups established a priori by
203 maximizing between-group variance while minimizing within-group variance (Raamsdonk et
204 al. 2001). DFA is thus an adequate tool for identifying the variables most responsible for the
205 differences among groups. The DFAs were performed using Statistica 6.0 (StatSoft, Inc. Tulsa,
206 Oklahoma, USA).

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211 **3. Results**

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213 *3.1. Effects of flood regimes*

214 The general linear models indicated that total soil C, N, P and S concentrations (Table 1),
215 salinity, soil available-S and soil NH_4^+ concentrations, N:P and C:P ratios and pH and
216 soil-water, clay and silt contents were significantly higher at the high-flood level of all three
217 communities (Figs. 2-4), whereas soil NO_3^- concentrations sand content and bulk density
218 were lower. The soil C:N ratio were lower in the high-flood than the low-flood habitat for the
219 *S. triqueter* community in the most soil layers (Fig. 3). Sand content (Fig. S1) and C:S, N:S
220 and P:S ratios (Fig. 3) were lower in the high-flood than the low-flood habitat for the *P.*
221 *australis* and *C. malaccensis* communities. Soil DOC concentration and the C:N ratio
222 differed between the flood habitats (Fig.4), but not equally in the three communities. The
223 high-flood habitat had higher soil-C content across all soil depths in the *S. triqueter*
224 community but lower levels in the upper soil layers in the *C. malaccensis* and *P. australis*

225 communities (Fig. 4). The soil C:N ratios were lower in the high-flood than in the low-flood
226 habitat for the *S. triqueter* community in most soil layers (Fig. 3). There was a significant
227 interaction between community x flooding in most studied variables (Table S1). In *S. triqueter*
228 flooding increased soil C, N and P concentrations, silt and clay content and decreases soil
229 C:N ratio in most soil layers, whereas it had no effect in the other two community species
230 (Table S1, Fig 2-4, Fig S1). The DFA analysis indicated that both species community
231 composition and flood regime explained a significant part of the variance of the overall soil
232 elemental and physicochemical traits. The soils properties were more similar in the *P.*
233 *australis* and *C. malaccensis* communities relative to the *S. triqueter* community. The *S.*
234 *triqueter* soils were affected more by flooding (Fig. 5). The squared Mahalanobis distances of
235 community × flood regime for the soil parameters differed significantly (Table 1). Soil-water
236 content, salinity and pH; total-C, DOC, nitrate and sulfate concentrations in the soil solutions
237 and the total soil P:S ratio separated the community × flood regimes (Table 2, Fig. 5).

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239 3.2. Correlation analyses

240 Soil-water content was negatively correlated with soil bulk density ($R=-0.95$, $P<0.001$) and
241 sand content ($R=-0.72$, $P<0.001$) (Table S2). Soil-water content was positively correlated
242 with soil DOC ($R=0.25$, $P=0.010$), clay ($R=0.49$, $P<0.001$) and silt ($R=0.74$, $P<0.001$)
243 contents, salinity ($R=0.51$, $P<0.001$), total C ($R=0.70$, $P<0.001$), total N ($R=0.66$, $P<0.001$),
244 total P ($R=0.32$, $P=0.001$), total S ($R=0.31$, $P=0.001$), NH_4^+ ($R=0.38$, $P<0.001$)
245 concentrations and C:P ($R=0.53$, $P<0.001$) and N:P ($R=0.59$, $P<0.001$) ratios.

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247 3.3. Plant biomass

248 The biomasses were 465 ± 31 and 372 ± 21 g m⁻² ($P>0.05$, Fig. 6), 3825 ± 194 and 2312
249 ± 101 g m⁻² ($P<0.05$, Fig. 6), and 833 ± 50 and 2072 ± 150 g m⁻² ($P<0.05$, Fig. 6), for the
250 high- and low-flood habitats, in *S. triqueter*, *P. australis* and *C. malaccensis* respectively. The
251 biomass of the invasive *P. australis* was higher than those of *S. triqueter* and *C. malaccensis*
252 ($P<0.05$) in the high-flood habitats but was only higher than that of *S. triqueter* ($P<0.05$) in
253 the low flood habitats.

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276 **4. Discussion**

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278 *4.1. General effects of flooding*

279 The observed values of C:N ratio (14.5 on average, 0-10 cm layer) were higher than
280 those of the coastal wetland in the Yellow River delta (9.5, Yu et al., 2010) and the Sanjiang
281 Plain wetland (12.9, Zhang et al., 2012) also in China, which is consistent with the high plant
282 productivity and N-use efficiency in subtropical regions (Singh et al., 2013). N limitation has
283 been found to affect the growth of *Spartina alterniflora* in a similar estuary of the Yangtze
284 River, ~800 km north of the Minjiang estuary (Gan et al., 2011). Plants near our study area
285 resorbed more N than other nutrients in biomass (Wang et al., 2014b). All this suggests N
286 limitation in these wetlands and a high capacity of the natural vegetation to resorb N. The
287 average N:P ratio of soils (2.1, 0-10 cm layer) in our study was lower than the average ratio
288 for China (3.9, Tian et al., 2010) and the average global ratio (5.9, Cleveland and Liptzin,
289 2007), again indicating that N was limited in the soil of this wetland area. The high
290 temperatures and amounts of precipitation in our subtropical study area may contribute to the
291 high rates of N leaching in the highly weathered soil (Laird et al., 2010). Both the
292 concentrations and ratios of soil C, N, P and S varied with soil depth (Fig. 2), consistent with
293 previous studies (Cleveland and Liptzin, 2007; Yang et al., 2011; Li et al., 2012). Only the
294 C:N ratios were stable across the soil profile under different regimes of flood (Fig. 4), in
295 agreement with earlier reports (Schipper and Sparling, 2011; Tian et al., 2010).

296 Most of the available N was in the form of ammonium, with lower amounts as nitrates,
297 especially in the most flooded soils, which is consistent with the shifts in denitrification and
298 anammoxic processes occurring with increasing flooding intensity (Dong et al., 2011;

299 Dodsworth et al., 2011; Jahangir et al., 2012) as a result of the activity of ammonia-oxidizing
300 Archaea (Dodsworth et al., 2011) and denitrifying microbes (Palmer et al., 2011), as observed
301 in several estuarine and coastal sediments (Nicholls and Trimmer, 2009). Some studies also
302 revealed the existence of nitrification in the anaerobic wetland soil (Wang et al., 2012), but
303 the nitrification rates were very small, and in some deep soil samples were nearly zero in this
304 same area of our study (Lin, 2014). Moreover, the more flooded soils had a finer texture,
305 because the water flow was slow and the soils were under water longer, facilitating the
306 sedimentation of fine particles transported by the water. In less flooded habitats where only
307 spring tides can submerge the soil, the water flow was faster, and the matter in the water was
308 coarser.

309 If flooding increases in the future as expected, soil total S, NH_4^+ and available-S
310 concentrations, water content and salinity will also increase. Soil nitrates are expected to
311 decrease, probably linked to higher denitrification under more anaerobic and saline
312 conditions (Elhottova et al., 2006; Brouns et al., 2014). Shifts in community species
313 composition and soil physical properties (more silt and less sand) can also be expected
314 (Chodak and Niklinska, 2010; Dequiedt et al., 2011).

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316 *4.2. Impacts of flooding on soil and C and N plant-soil cycles: differences among* 317 *communities*

318 Under *S. triquiter* community we observed higher C stocks in the high-flood than the
319 low-flood habitat in all soil layers whereas in *C. malaccensis* and *P. australis*, contrary to
320 expected, we observed lower accumulation of C in the high-flood than the low-flood habitat

321 in the upper soil layer which suggested a lower capacity of C mineralization (oxidation) the
322 higher the flooding intensity. The results observed in soils under *S. triquiter* showing that C
323 content increased as the water content increased, were consistent with the findings of a
324 previous study (Nomura et al., 2013) and with the higher anaerobic conditions in saturated
325 soil. Increasing soil anaerobiosis is the most probable cause of C concentration increases
326 (Tiemann and Billings, 2009). Furthermore, the flooding with seawater increased soil salinity
327 more in the high-flood habitat, and salinity can contribute too, as observed in soils under *S.*
328 *triquiter*. The release of soil C has also been negatively correlated with soil salinity (Setia et
329 al., 2010; Setia et al., 2011) because higher salinity inhibits the growth and activity of soil
330 microorganisms due to osmotic stress and inhibits C mineralization (Rietz and Haynes, 2003).
331 This effect of flooding also depends of the species community: soils of the *S. triquiter*
332 community had lower C:N ratios under high flooding regime, whereas the soils of the *C.*
333 *malaccensis* and *P. australis* communities had stable C:N ratios under different regimes of
334 flooding, showing that soil mineralization was less affected by flood regime. Notably the soil
335 under the *S. triquiter* community presents the lowest concentrations of total N and P and also
336 of N:P ratio. This was related with the fact that this species was the species-community with
337 lowest aboveground accumulation both under high and low flooding intensity. The
338 differences in soil N:P ratio among different flooding intensities and communities were due
339 more to N than to P differences, which is consistent with the previously commented N
340 limiting role observed in these wetlands. Low N:P ratios when both N and P concentrations
341 are high had been associated to high mineralization rates in soil (Hartman and Richardson,
342 2013; Li et al., 2014). But the low soil N:P ratios of soils under *S. triquiter* communities were

343 associated to higher C soil accumulation, suggesting a lower soil mineralization than under
344 other communities. In the frame of the growth rate hypothesis, high growth rates and
345 metabolic activity of soil microbes are expected at low N:P ratios but only when N and P
346 contents are high. Our findings appear to be consistent with the model of cellular metabolism
347 described by the biological stoichiometry theory claiming that biomass is limited by N
348 needed to build proteins, in turn limited by the high P demands of ribosomes, and hence at
349 low N and P concentrations, N becomes more critical. In any case, when both concentrations
350 are low, the soil mineralization processes are limited (Hartman and Richardson, 2013). The
351 high N:P ratios thus favor relatively low growth rate when N and P are low, and the low N:P
352 ratios favor high relative growth rates and production activity when N and P are both
353 abundant (Agren 2004). When flooding intensity was higher, some general trends in soil C
354 and nutrient cycles appeared in all communities. For example, the concentration of soil NH_4^+
355 was higher and the concentration of NO_3^- was lower, but also differences in function of the
356 plant species appeared. Under high flooding intensity, the plant:soil C and N ratios were
357 higher in the *P. australis* community, were relatively stable in the *C. malaccensis* community
358 and were lower in the *S. triqueter* community.

359 The total biomass of *S. triqueter* did not differ significantly between the high- and
360 low-flood habitats. The total biomass of *P. australis* was significantly higher in the
361 high-flood than the low-flood habitat. Moreover, biomass was significantly higher for *P.*
362 *australis* than for *S. triqueter* and *C. malaccensis* in the high-flood habitats but only higher
363 than for *S. triqueter* in the low-flood habitats. The higher *P. australis* biomass in the
364 high-flood habitat was accompanied by lower soil-C content in upper soil layer. High

365 flooding in the *C. malaccensis* community was associated with lower biomass and with lower
366 soil-C content in upper soil layer, and high flooding in the *S. triqueter* community had no
367 apparent effect on biomass but was associated with much higher levels of soil-C content. The
368 *P. australis* community under high flooding intensity had more aboveground biomass (by
369 aprox. 55%) than under low flood intensity whereas there was a slight lower soil C contents
370 in the upper soil layers under high flooding intensity than under low flooding intensity
371 showing that flooding tends to high overall C content in this ecosystem. Contrarily, in the *C.*
372 *malaccensis* community, flooding enhancement was related to lower aboveground biomass
373 (aprox 60%) and lower C contents in soil until 20 cm depth, showing a trend towards a lower
374 of C content in this ecosystem related to flooding enhancement. In the *S. triqueter*
375 community, flooding enhancement had no apparent effects on aboveground biomass but was
376 related to higher soil C contents in all studied soil layers, showing a trend to higher C content
377 under high flooding intensity than under low flood intensity in this ecosystem. These results
378 show that flooding enhancement can favor the growth of *P. australis* and decrease that of *C.*
379 *malaccensis*. The results thus suggest that further flooding enhancement will favor *P.*
380 *australis* spread and higher accumulation of biomass and C per surface unit. Soil C input and
381 respiration are frequently positively correlated (Dias et al., 2010; Carbone et al., 2011; De
382 Deyn et al., 2011), indicating that soil respiration can be correlated with plant productivity
383 (Caprez et al., 2012). This correlation can help to interpret our asymmetrical results of
384 flooding enhancement in different species-community. The decrease of soil C content in
385 high-flooding versus low-flooding observed under *C. malaccensis* could be related to the
386 lower aboveground biomass and soil C concentrations observed in this species-community

387 under high-flooding. The lower C concentration in upper soil layers observed in *P. australis*
388 communities under high-flooding regime was more difficult to understand, and contrary to
389 the expected. High N uptake capacity and N-use efficiency of this species has been observed
390 in other study in this same estuary (Wang et al., 2014). Thus according with the previously
391 commented relationships of plant productivity and soil biological activity, the most consistent
392 explanation is that under high soil moisture, a greater N uptake capacity by higher N
393 solubilization could favor aboveground biomass and thereafter plant capacity to improve
394 mineralization processes (by root enzymes, exudates,..), fact that warrants future research.

395 Thus, the results showed a significant relationship between the dominant species of the
396 community and several soil traits despite flooding regime. At this regard, the study did not
397 allow to establish a clear cause-effect, but as discussed above, each species by its specific traits
398 (litter production, biomass production, elemental concentration,...) can change soil properties
399 at some extent without discarding that previous differences in soil traits can be also
400 underlying in these observed differences in soil traits under different species communities.

401

402 **5. Conclusions**

403

404 Higher regimes of flooding increased the anaerobic conditions and salinity of the soil, and its
405 impacts on plant-soil C and N cycles depended on the dominant species of the community.

406

407 Higher regimes of flooding favored the invasive species *P. australis* over the native species *C.*
408 *malaccensis* and *S. triqueter*. *P. australis* was able to accumulate more N and C in its biomass,

409 but the native species were not. This higher capacity of *P. australis* to tolerate increased
410 flooding was associated with its higher capacity to take up N. The success of *P. australis* in
411 other Chinese wetlands has also been associated with a more conservative and efficient use of
412 N in these N-limited ecosystems.

413

414 The results also suggest that the soil stoichiometrical changes in a scenario of flooding
415 enhancement can strongly depend of the species dominating the community. If *P. australis*
416 increases its spread no important changes in soil C:N:P:S stoichiometry could occur, but if *S.*
417 *triquiter* remains or increases its spread, a decrease of soil C:N and an increase of soil N:P
418 and N:S ratios could be expected.

419

420 The existence of a sea wall will prevent the movement of the wetland inland, which could
421 come associated to the increasing dominance of *P. australis* because the results indicated that
422 the overall increase of flooding intensity would give advantage to this species. The sea wall is
423 very important to resist typhoon, storm surge and flood. If the sea wall is removed, the
424 flooded lands will be extended affecting the agricultural and industrial land, which will cause
425 large economic losses. For this reason, the most realistic scenario is a reduction of the
426 wetland extension and a probable drastic change in community species composition, with the
427 spread of *P. australis*.

428

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685 **Table 1**

686 Test statistics for squared Mahalanobis distances among soils under different communities and under
 687 different flooding regimes in the discriminant function analysis with soil-water content, pH, salinity
 688 and bulk density; total C, N, P and S concentrations; C:N, C:P, C:S, N:P, N:S and P:S ratios; DOC,
 689 clay, silt and sand contents and NH_4^+ , NO_3^- and available-S concentrations as variables. A1, *S.*
 690 *triqueter* in high flood; B1, *C. malaccensis* in high flood; C1, *P. australis* in high flood; A2, *S.*
 691 *triqueter* in low flood; B2, *C. malaccensis* in low flood; B3, *P. australis* in low flood.

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	B1	C1	A2	B2	C2
A1	32.9 <i>P</i> <0.0001	39.9 <i>P</i> <0.0001	137 <i>P</i> <0.0001	61.3 <i>P</i> <0.0001	56.5 <i>P</i> <0.0001
B1		11.8 <i>P</i> <0.0001	196 <i>P</i> <0.0001	20.2 <i>P</i> <0.0001	17.7 <i>P</i> <0.0001
C1			204 <i>P</i> <0.0001	22.7 <i>P</i> <0.0001	13.4 <i>P</i> <0.0001
A2				223 <i>P</i> <0.0001	206 <i>P</i> <0.0001
B2					6.75 <i>P</i> <0.0001

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717 **Table 2**

718 Statistics (Wilk's λ and P) of the discriminant function analysis among the soils of the communities with
 719 soil-water content, pH, salinity and bulk density; total C, N, P and S concentrations; C:N, C:P, C:S, N:P,
 720 N:S and P:S ratios; DOC content and NH_4^+ , NO_3^- and available-S concentrations as variables. Bold type
 721 indicates a significant effect of the variable in the model ($P < 0.05$).
 722

Variable	Wilk's	F	P
Water content (%)	0.717	6.79	<0.0001
Bulk density (g cm^{-3})	0.831	3.51	0.0062
pH	0.377	28.6	<0.0001
Salinity (mS cm^{-1})	0.678	8.18	<0.0001
Total C (g kg^{-1})	0.860	2.80	0.022
Total N (g kg^{-1})	0.950	0.915	0.48
Total P (g kg^{-1})	0.893	2.06	0.079
C:N	0.960	0.726	0.62
C:P	0.958	0.755	0.58
N:P	0.959	0.736	0.60
C:S	0.924978	1.35	0.25
N:S	0.975521	0.417	0.83
P:S	0.844620	3.05	0.014
Total S (g kg^{-1})	0.900	1.91	0.10
DOC (mg kg^{-1})	0.657	8.99	<0.0001
NH_4^+ (mg kg^{-1})	0.890	2.13	0.070
NO_3^- (mg kg^{-1})	0.842	3.23	0.010
Available S (mg kg^{-1})	0.306	39.1	<0.0001

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Figure captions

Fig. 1. Location of the six sampling sites for the high- and low-flood habitats.

Fig. 2. Concentrations (mean \pm S.E.) of soil C (A, B, C), N (D, E, F), P (G, H, I), S (J, K, L), DOC (M, N, O), NH_4^+ (P, Q, R), NO_3^- (S, T) and available S (U,V, W) for the *S. triqueter*, *C. malaccensis*, and *P. australis* communities at the various soil depths at the sites of the high- and low-flood habitats. Different letters indicate significant differences between flood effects ($P < 0.05$) from the one-way ANOVA of the flooding effects at each soil depth and plant community.

Fig. 3. Means (\pm S.E.) of soil C:N (A, B, C), C:P (D, E, F), C:S (G, H, I), N:P (J, K, L), N:S (M, N, O) and P:S (P, Q, R) ratios for the *S. triqueter*, *C. malaccensis* and *P. australis* communities at the various soil depths at the sites of the high- and low-flood habitats. Different letters indicate significant differences between flood effects ($P < 0.05$) from the one-way ANOVA of the flooding effects at each soil depth and plant community..

Fig. 4. Means (\pm S.E.) of soil-C content for the *S. triqueter* (A), *C. malaccensis* (B) and *P. australis* (C) communities at the various soil depths at the sites of the high- and low-flood habitats. Different letters indicate significant differences between flood effects ($P < 0.05$) from the one-way ANOVA of the flooding effects at each soil depth and plant community..

Fig. 5. Biplots of the standardized canonical discriminant function coefficients for the first two roots representing the soil parameters as independent variables (A) and the flood levels and communities separated by the first two roots of the discriminant function analysis (B). each represented point with its error bars represents the mean \pm S:E of the canonical scores of the analysed samples of each community plant at each level of flooding.

Fig. 6. Means (\pm S.E.) of total plant biomasses for the *S. triqueter*, *C. malaccensis*, and *P. australis* communities at the sites of the high- and low-flood habitats. Different letters indicate significant differences between flood effects ($P < 0.05$) from the one-way ANOVA of

the community effect on plant biomass.

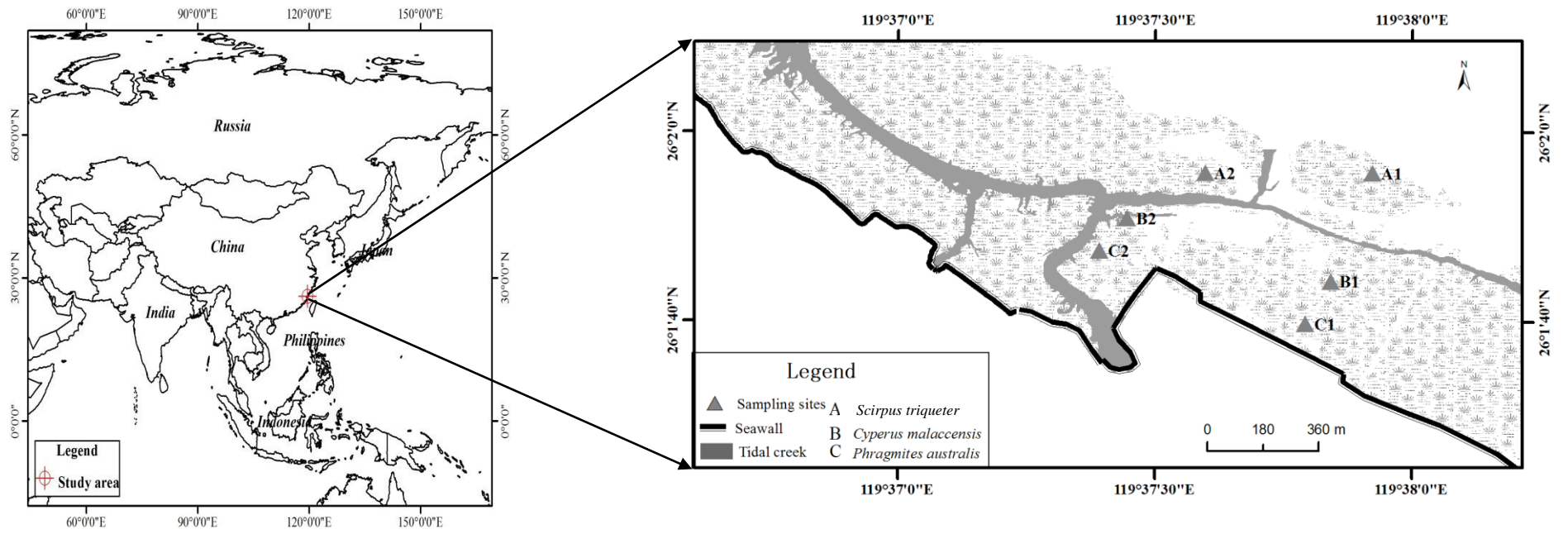
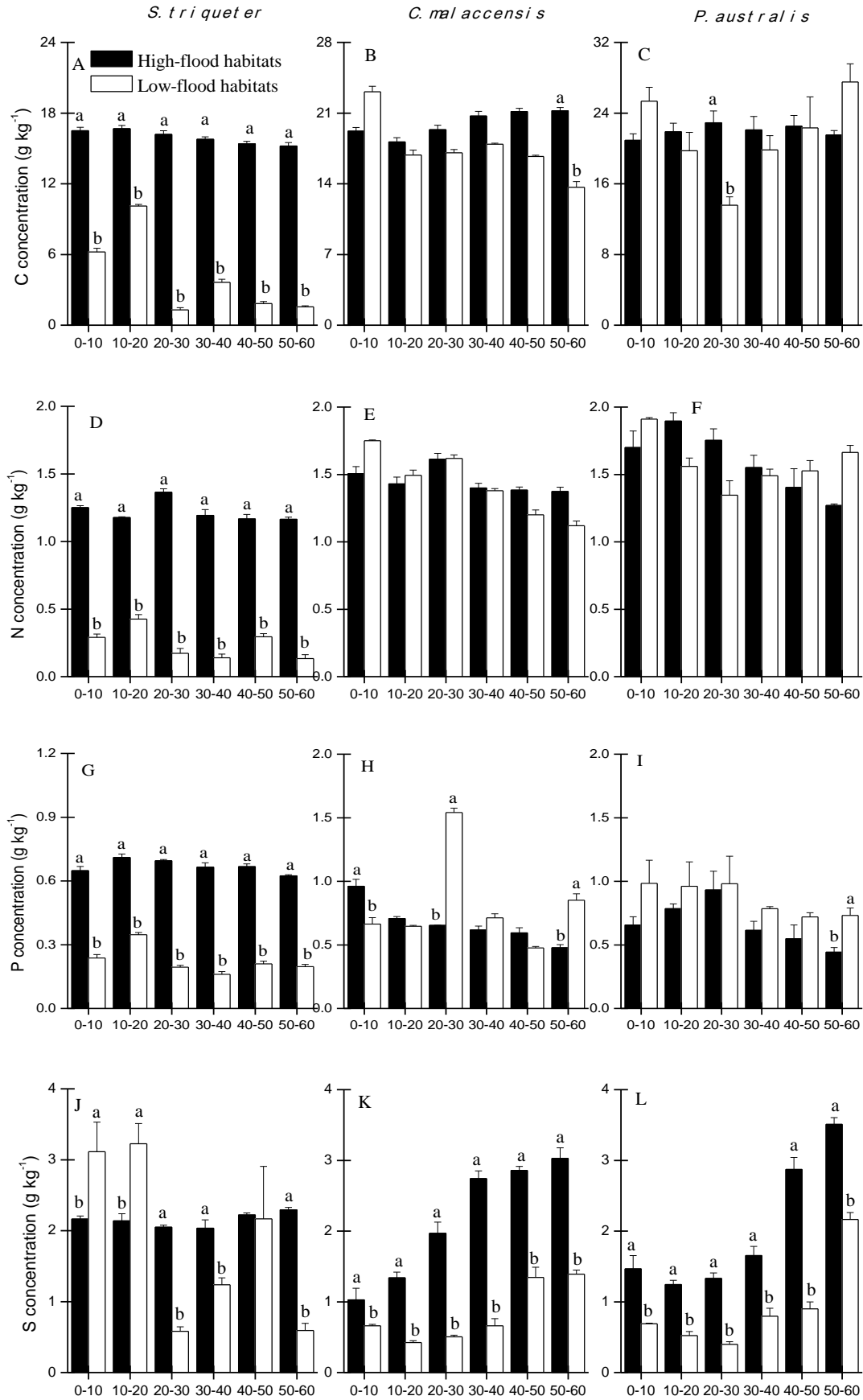


Fig. 1



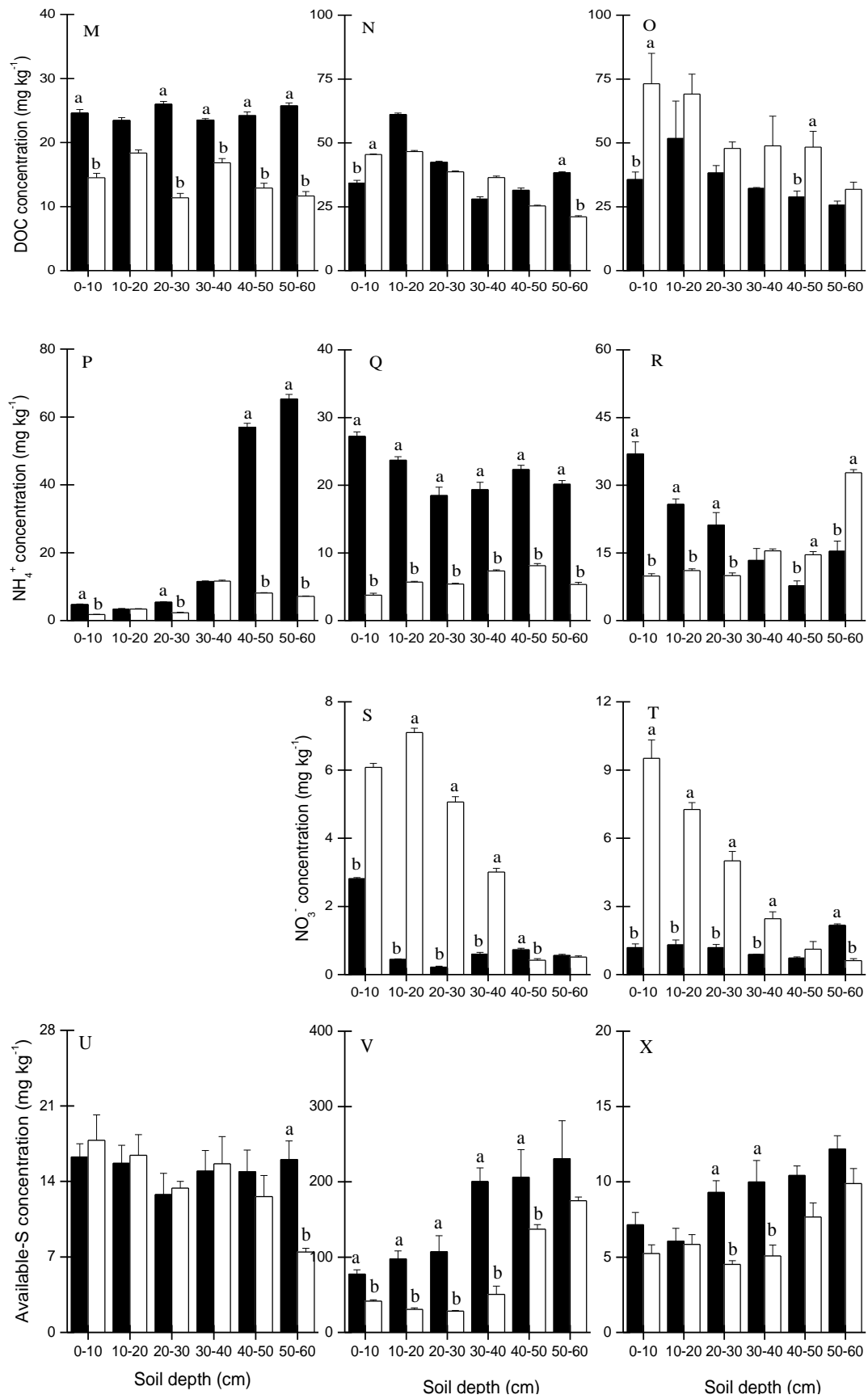
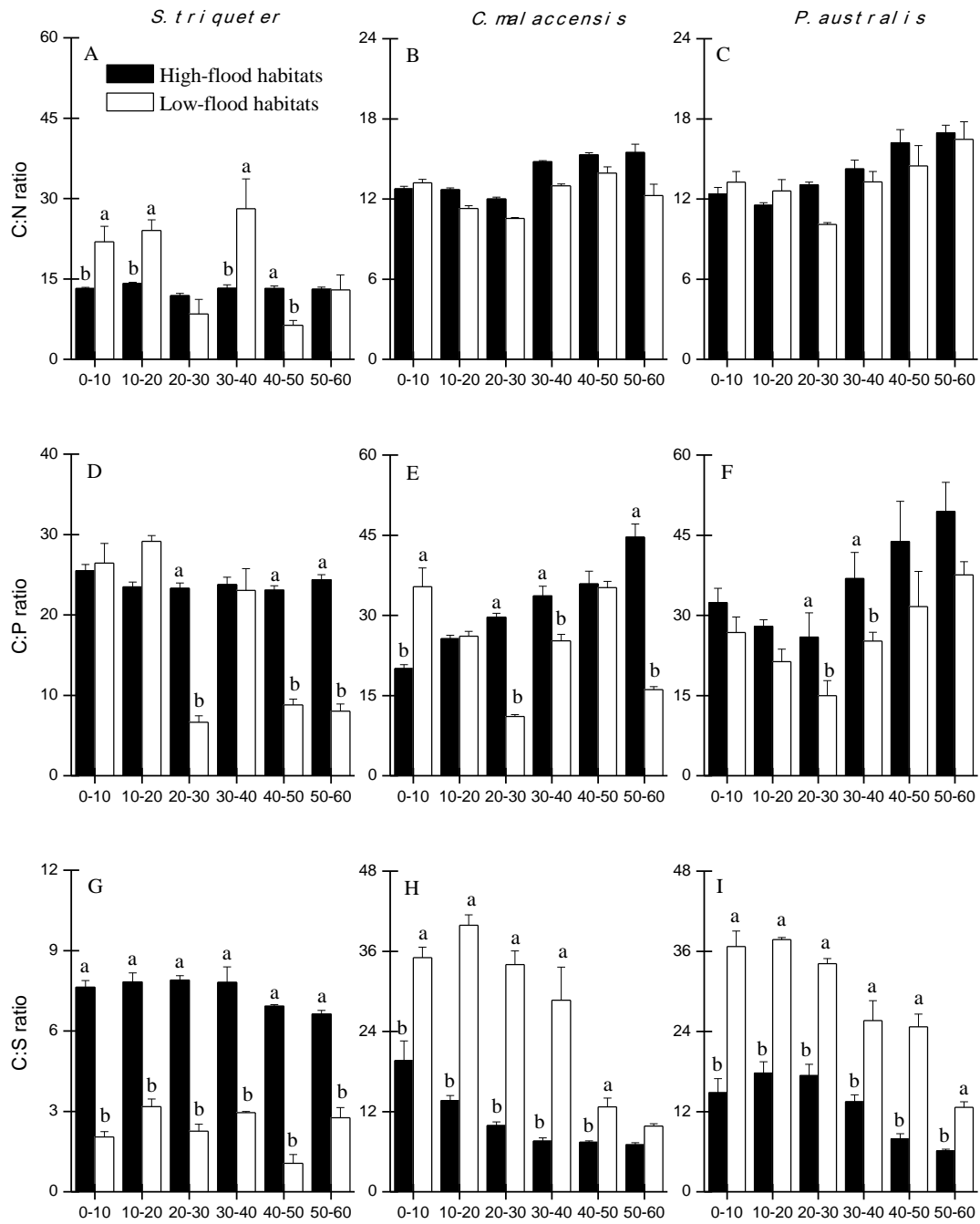


Fig. 2



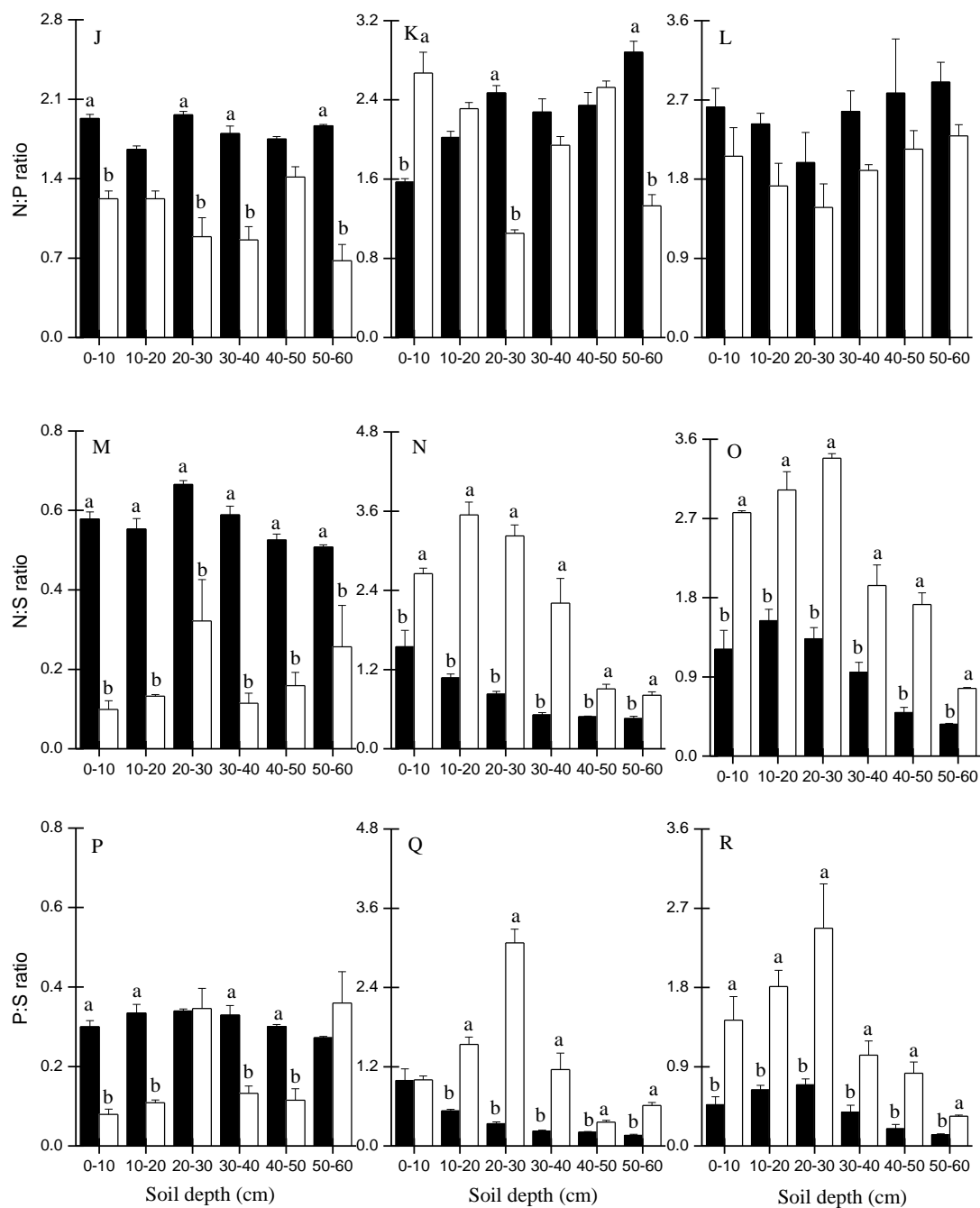


Fig. 3

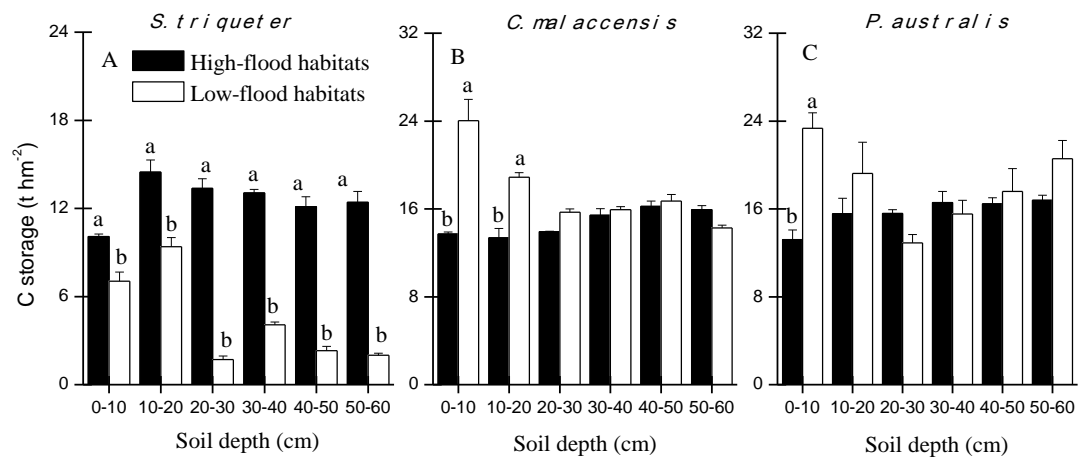


Fig. 4

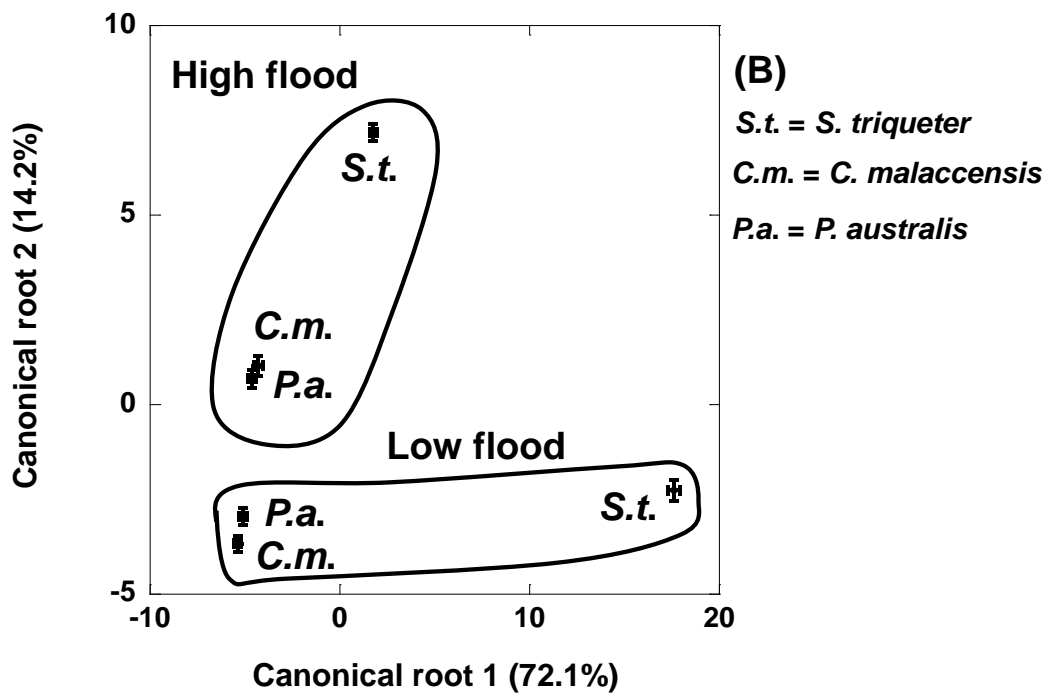
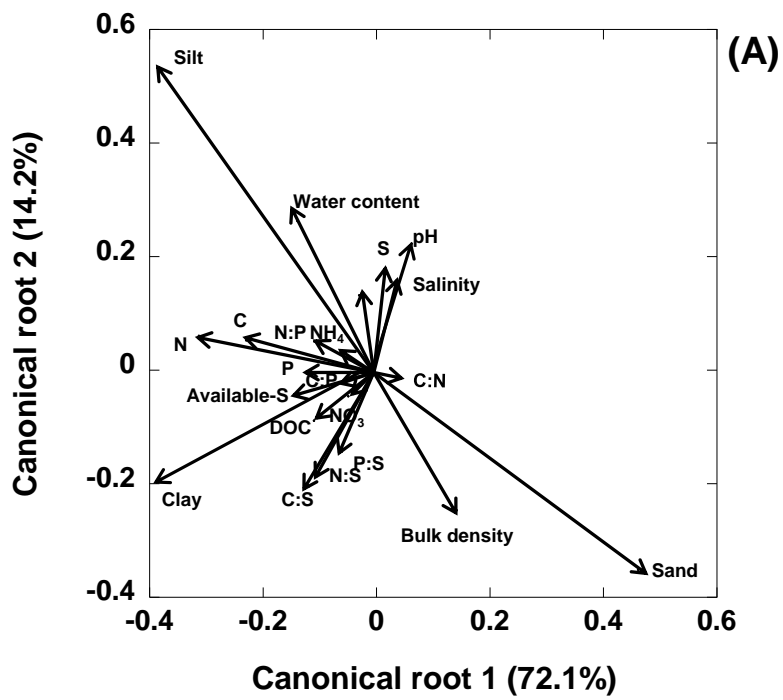


Fig. 5

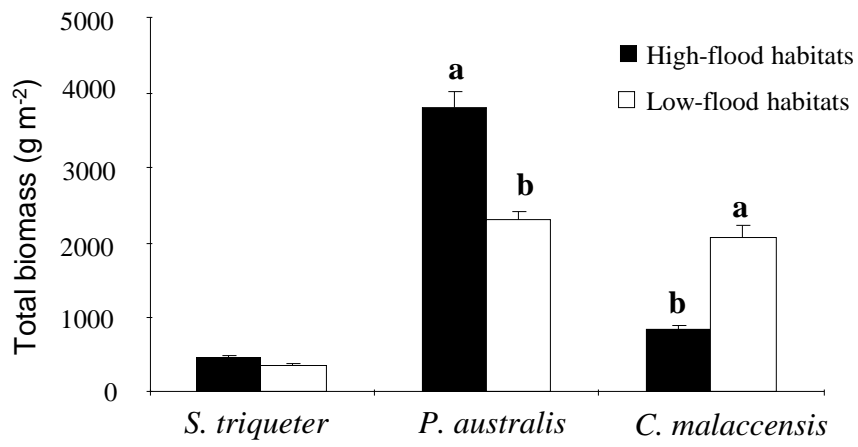


Fig. 6