

1 **Ecological stoichiometry of C, N and P of invasive *Phragmites australis* and**
2 **native *Cyperus malaccensis* species in the Minjiang River tidal estuarine**
3 **wetlands of China**

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14 **Abstract** Tidal estuarine wetlands of China are rich in plant diversity, but several global
15 change drivers, such as species invasion, are currently affecting the biogeochemical cycles of
16 these ecosystems. We seasonally analyzed the carbon (C), nitrogen (N) and phosphorus (P)
17 concentrations in litters and soils and in leaves, stems and roots of the C₃ invasive species
18 *Phragmites australis* (Cav.) Trin. ex Steud. and of the C₄ native species *Cyperus malaccensis*
19 var. *brevifolius* Boeckeler to investigate the effect of C₃ plant invasion on C, N and P
20 stoichiometry in the C₄ plant-dominated tidal wetlands of the Minjiang River. When averaged
21 across seasons, the invasive species *P. australis* had higher N concentrations and lower P
22 concentrations in leaves than the native species *C. malaccensis*. N and P concentrations were
23 lower in litter (stem and leaf) whereas C concentrations in leaf litter were higher in *P.*
24 *australis* than in *C. malaccensis*. The C, N and P concentrations of the soil also did not differ,
25 but plants had a lower C:N and much higher N:P ratios than soils. Root C:P and N:P ratios
26 were lower in the growing season, both in the invasive and the native species. The leaf C:N,
27 C:P and N:P ratios peaked in summer. The invasive species had lower C:N ratio in leaves and
28 roots, and higher N:P ratios in all biomass organs and litter than the native species, an effect
29 related with the higher N-resorption capacity of the invasive species. Interspecific differences
30 in C:N, C:P and N:P ratios may likely reflect the differences in plant morphology,
31 nutrient-use efficiency and photosynthetic capacity between the C₃ (*P. australis*) and C₄ (*C.*
32 *malaccensis*) plants. Our results generally suggested that the success of *P. australis* in these
33 wetlands was related to its slow-growth and higher resorption capacity of N and P. This
34 implies a more conservative use of limited nutrients, particularly N, by *P. australis*, and to
35 higher N concentration in its biomass thus potentially contributing to its invasiveness in these

36 estuarine wetlands.

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38 **Key words:** Carbon; *Cyperus malaccensis*; Ecological stoichiometry; Invasive species;

39 Minjiang River estuary; Nitrogen; N:P ratio; N resorption; Phosphorus; *Phragmites australis*;

40 Plant; Soil; Wetlands.

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58 **Introduction**

59 Tidal estuarine wetlands cover an estimated 12 000 km² of China's 18 000-km coastline (Shen
60 and Zhu 1999; Huang et al. 2006). These tidal wetlands are generally rich in animal and plant
61 biodiversity (Zhou et al. 2006) and are reported to have important biogeochemical roles
62 within the entire estuarine ecosystem (Zeng et al. 2009a,b; Wang et al. 2010a,b; Tong, Wang
63 and Zeng 2010). The Minjiang River estuary in southeastern China is an important tidal
64 wetland ecosystem due to its unique location at the transition between central and southern
65 subtropical climatic zones (Zheng et al. 2006).

66 *Phragmites australis* (Cav.) Trin. ex Steud. and *Cyperus malaccensis* var. *brevifolius*
67 Boeckeler (syn. *Cyperus malaccensis* subsp. *monophyllus* (Vahl) T. Koyama) comprise much
68 of the emergent macrophytic biomass in the Minjiang River estuary (Liu et al. 2006). Some
69 stands of *C. malaccensis* have been invaded over the past 30 years by *P. australis*, which is
70 now the single most prevalent plant species in the wetland. This change in dominance may be
71 affecting the biogeochemical cycles of the estuarine wetland, because the soil properties and
72 rates of litter decomposition in the stands of *P. australis* and *C. malaccensis* are known to
73 differ (Zhang et al. 2008; Jia et al. 2008; Zeng et al. 2009; Tong and Liu 2009). Here we
74 examine the nutrient stoichiometry of *P. australis* and *C. malaccensis* as a potential source of
75 the differences between the litters and soils associated with these species and with the success
76 invasive plants.

77 The elemental composition of plant tissues is tightly associated with the nutrient
78 concentration of litter, which in turn can feed back into the soils (McClaugherty et al. 1985;
79 Bridgham et al. 1995; Ehrenfeld et al. 2005; Townsend et al. 2007). Higher ratios of carbon

80 (C) to other nutrients in litter can increase C storage and reduce the mobilities and rates of
81 mineralization of key nutrients (Wang et al. 2010b; Wang and Yu 2008). Such effects appear
82 to be caused by the increasing nutrient limitation of soil microbial communities when
83 provided with nutrient-poor organic material. Plant-litter-soil interactions have been
84 extensively modeled (Vitousek and Peter 1984; Northup et al. 1998; Meier and Bowman
85 2008), observed in numerous ecosystems (Cebrian 1999; Cebrian and Lartigue 2004;
86 Güsewell and Verhoeven 2006; Wurzburger and Hendrick 2009) and experimentally
87 examined (Jobbágy and Jackson 2001; Hawlena and Schmitz 2010) in terrestrial ecosystems,
88 but little is known about the effect of the relative flux of nutrients through estuarine plants
89 into the litter on the soils of tidal estuarine ecosystems.

90 Variable leaf ratios of C to nitrogen (N) (C:N) and to phosphorus (P) (C:P) are assumed
91 to be caused by the physiological adjustment of plant species to the local supplies of nutrients
92 (Broadley et al. 2004; Kerkhoff et al. 2006; Demars and Edwards 2007; Townsend et al. 2007;
93 Elser et al. 2010; Peñuelas et al. 2010; Sardans and Peñuelas 2014). Evidence, however, is
94 accumulating that intraspecific differences in terrestrial plants can match or exceed
95 interspecific variability (Wright et al. 2004; Elser et al. 2010; Peñuelas et al. 2010; Sardans
96 and Peñuelas 2013). These species-specific patterns of elemental composition likely reflect
97 important differences in plant functional traits that have unique biochemical, and hence
98 elemental, requirements. The elemental composition of *C. malaccensis* may thus differ from
99 that of *P. australis*, even for individuals growing under very similar environmental conditions,
100 and thereby may affect the dynamics of soil nutrients by affecting the elemental composition
101 of litter and/or the capacity to take up nutrients. Shifts in nutrient stoichiometry have

102 frequently been associated with the success of invasive plants (Sardans and Peñuelas 2012).
103 Successful invasive species in nutrient-rich environments usually have low C:nutrient ratios
104 (Peñuelas et al. 2010) and high N:P ratios (Neves et al. 2010) in their tissues, but the effect of
105 N:P ratios on the success of invasive plants is still unclear. Moreover, positive relationship
106 between N:P ratio and invasive success has not often been reported for nutrient-poor
107 environments.

108 In drier environments, plants with C₄ metabolism traits, such as *C. malaccensis*,
109 frequently have an advantage over C₃ metabolism plants, such as *P. australis* (Wilson et al.
110 2007; Zand et al. 2006; Kocacinar and Sage 2003). However, less is known with respect the
111 competitive advantage between these two strategies in wetland areas with other limiting
112 resources than water. In wetland environments where water is not the limiting factor,
113 nutrient-use strategy can be crucial in the competitive relationships among plant species and
114 also in invasive success. To test this hypothesis, we have examined the link between the
115 invasion of a C₃ monocot with the seasonal variation of the C, N and P stoichiometry of a C₄
116 monocot that dominates the subtropical tidal wetlands of the Minjiang River in China. Our
117 aims were (1) to study the C:N, C:P and N:P ratios of the leaves, stems and roots and their
118 relationships in the invasive C₃ plant, *P. australis*, and of the native C₄ plant, *C. malaccensis*,
119 over the year and specially during the growing season, and (2) to examine the relationships
120 between the success of plant invasion and the nutrient concentrations and stoichiometries of
121 the plants, litters and soils.

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124 **Materials and methods**

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126 Study area

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128 This study was conducted in the Shanyutan wetland (26°01'46"N; 119°37'31"E, Fig. 1), the

129 largest tidal estuarine wetland (approximately 3120 ha) in the estuary of the Minjiang River.

130 The climate in this region is relatively warm and wet, with a mean annual temperature of 19.6

131 °C and a mean annual precipitation of 1346 mm (Zheng et al. 2006). The soil surface is

132 submerged across the study site beneath 10-120 cm of water for 3-3.5 h during each tidal

133 inundation. Soil surfaces of the entire wetland are exposed at low tide, and the average annual

134 weight percentage of water in soil and soil redox potential are 116.39% and 12.57 mV,

135 respectively, and soil remains flooded at some depths. The average salinity of the tidal water

136 between May and December 2007 was $4.2 \pm 2.5\text{‰}$.

137 *P. australis* and *C. malaccensis* are the two dominant species of plants in this estuarine

138 wetland. They are typically found in the upper (mid to high) portions of mudflats. *P. australis*

139 is an invasive plant that has invaded this area over the past 30 years, to now become the

140 single most prevalent plant species in the wetland. It mainly invaded the native *C.*

141 *malaccensis* wetland, typically found in the upper (mid to high) portions of mudflats. *P.*

142 *australis* grows between April and October, the highest population height is about 2 m, and

143 the density is about 250 m⁻². *C. malaccensis* is a native plant, typically found in the upper

144 (mid to high) portions of mudflats that grows between April and October, the highest

145 population height is about 1.5 m, and the density is about 1000 m⁻². Below-ground rhizomes

146 are mainly distributed in the top soil layers. The primary mode of reproduction is vegetative
147 growth via belowground rhizomes which spread via creeping growth in the topsoil layers.
148 The decomposition rates of the litter of *P. australis* are slower than those of *C. malaccensis*
149 (Tong et al. 2009). Both species are located in sites with similar flooding intensity, but despite
150 this, wetland soils in areas dominated by *P. australis* generally have a lower pH and bulk
151 density and a higher salinity than do areas dominated by *C. malaccensis* (Jia et al. 2008).

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153 Sample collection and measurements

154

155 Plant, litter and soil samples were collected in May, July, September and December 2007 to
156 capture potential seasonal differences in chemical composition. Most plant growth occurs
157 between April and October, and litter is produced largely toward the end of the growing
158 season into early winter. Plant samples always were collected at the same height above the
159 ground. We selected stands of the two plant communities for the collection of aboveground
160 biomass, randomly established one large quadrat (10 × 10 m) in each stand and sampled the
161 aboveground biomass from three randomly selected sub-quadrats (1 × 1 m). The harvested
162 aboveground biomass was sorted into living and dead (litter) material. The plant organs and
163 litter fraction were then sorted into stems and leaf tissues. Litter was sampled each week
164 during the studied seasons and only fresh litter was used to conduct the analyses. Root
165 biomass was also harvested from these sample sub-quadrats. All plant material was gently
166 washed with water and then oven dried to a constant mass (80 °C for 24-36 h) and weighed.
167 Soil samples from the top layer (0-30 cm) were concurrently collected from the three

168 replicate sub-quadrats and air dried, and any other roots or visible plant remains were
169 removed. These dried and cleaned soil samples were then finely ground in a ball mill. The
170 total numbers of analyzed samples of plants, litters and soils were 30, 24 and 12, respectively,
171 for the *P. australis* wetland and 33, 15 and 12, respectively, for the *C. malaccensis* wetland.
172 We also determined biomasses by ha to calculate mineralomasses in above- and
173 below-ground biomass, especially in summer after at the end growing season, and those
174 mineralomasses produced by litter during entire year.

175 Concentrations of C and N in plants and litters were determined using a Vario EL III
176 Elemental Analyzer (Elementar Scientific Instruments, Germany). Total soil organic C was
177 determined by the $K_2Cr_2O_7$ - H_2SO_4 digestion method (Sorrell et al. 1997; Bai et al. 2005).
178 Total soil N was analyzed with the Kjeldahl method (K-370, Buchi Scientific Instruments,
179 Switzerland). P concentration of plants, litters and soils were measured using molybdate-blue
180 reaction (Lu 1999) with a UV-2450 spectrophotometer (Shimadzu Scientific Instruments,
181 Japan).

182

183 Data analysis

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185 We used analysis of variance (ANOVA) to compare C, N and P concentrations and C:N, C:P
186 and N:P ratios of the plants, litters and soils of the two plant communities using species and
187 seasonality as independent categorical factors. We also used ANOVA to analyze the
188 community species differences of mineralomasses (C, N and P) in above- and below-ground
189 biomasses in summer, after the growing season. We calculated average C, N and P

190 concentrations and mineral masses, and mass ratios (C:N, C:P and N:P ratios) of different
191 plant organs (leaves, stems and roots), litters and soils and performed all these statistical
192 analyses using SPSS 13.0 (SPSS Inc., Chicago, USA). Pearson correlation analyses identified
193 the relationships among the C:N, C:P and N:P ratios of the plants, litters and soils of the
194 estuarine system. We used major axis (MA) and standardized major axis (SMA) (SMATR
195 package; <http://www.bio.mq.edu.au/ecology/SMATR>) regression to compare the slopes of
196 the regressions of the relationships among the C:N, C:P and N:P ratios of the plants, litters
197 and soils. Due to the large number of repeated statistical analyses performed to test the same
198 model hypotheses on “n” dependent variables we have applied Bonferroni correction to test
199 each individual hypothesis at a significance level of α/n (0.05/n).

200 The rate of nutrient resorption (NRE) was estimated as the percentage of nutrient
201 withdrawn from green leaves before leaf abscission:

$$202 \text{ NRE} = 100\% \times [(N_{\text{biomass}} - N_{\text{litter}}) / N_{\text{biomass}}]$$

203 where N_{biomass} and N_{litter} are the concentrations of nutrient in the biomass and litter in winter
204 because it is in this season that there is the largest litter production (Huang et al. 2008).

205

206 **Results**

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208 Seasonal variation of C, N and P concentrations and ratios in plant organs, litters and soils

209 C, N and P concentrations varied seasonally in *P. australis* and *C. malaccensis* and in the

210 litters and soils of the stands dominated by these species (Tables 1 and 2). In general, in

211 aboveground plant organs (leaf and stems) N and P concentrations were higher in spring and

212 C:N, C:P and N:P ratios in summer, whereas C concentrations were higher in summer (leaves)
213 and in autumn (stems) (Table 1). In the most cases stem litter, leaf litter, roots and soils, the C,
214 N and P concentrations and C:N, C:P and N:P ratios frequently changed among seasons, but
215 without any clear patterns (Table 1). *P. australis* had higher N concentrations in leaves than *C.*
216 *malaccensis* (Tables 1 and 2). *P. australis* had lower P concentrations and higher C:P ratio in
217 stems and stems litter and greater N:P ratio in leaves and stem litter than *C. malaccensis*
218 (Tables 1 and 2).

219 There was a significant interaction effect of species x season on the N concentration
220 in leaf and soil, C:N ratios in stem litter and soil, C:P in stem and N:P ratios in stem and roots,
221 and P concentration in stems ($P < 0.05$, Tab. 1, Fig. S1-S6).

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223 Relationships among C:N, C:P and N:P ratios

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225 The correlations of C:N, C:P and N:P ratios among plant organs (leaf, stems and roots), litters
226 and soils are shown in Figs. 8-10. Litter C:N ratios were positively correlated with plant
227 organs C:N ratios for *C. malaccensis* ($P < 0.01$), and litter C:P ratios were positively
228 correlated with plant organs C:P ratios for both *P. australis* and *C. malaccensis* ($P < 0.01$).
229 Litter N:P ratios were positively correlated with those of plant organs for *P. australis* ($P <$
230 0.05), however, these relationships were not observed in *C. malaccensis*. Plant organs N:P
231 ratios were negatively correlated with those of the soil for both *P. australis* and *C.*
232 *malaccensis* ($P < 0.05$). Soil C:N, C:P and N:P ratios were not significantly correlated with
233 those of litter for either species ($P > 0.05$). Furthermore, none of the slopes of the regression

234 lines of the C:N, C:P and N:P ratios differed significantly between *P. australis* and *C.*
235 *malaccensis* ($P > 0.05$, SMA test of common slopes, Figs. 2-4).

236

237 N and P resorption

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239 The average seasonal rates of N resorption for *P. australis* and *C. malaccensis* were $35.4 \pm$
240 9.0% and $9.0 \pm 6.6\%$, respectively, and the rates of P resorption for *P. australis* and *C.*
241 *malaccensis* were $41.2 \pm 10.9\%$ and $26.5 \pm 8.1\%$, respectively. The rates of both N and P
242 resorption for *P. australis* were significantly higher than those for *C. malaccensis*,
243 particularly for N ($P < 0.05$, Fig. 5).

244

245 Mineralomasses production

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247 At the end of the growing season, total C content in aboveground biomass was higher in *P.*
248 *australis* than in *C. malaccensis* and the C content in belowground biomass was higher in *C.*
249 *malaccensis* than in *P. australis*. The total C content in total biomass was not different
250 between the two species (Fig. 6). The total N content in aboveground and total biomass was
251 higher in *P. australis* than in *C. malaccensis*, whereas total P contents were not statistically
252 different between the two species biomasses (Fig. 6).

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256 **Discussion**

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258 Seasonal variation in C:N, C:P and N:P ratios

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260 C:N, C:P and N:P ratios of the plant matter from *P. australis* and *C. malaccensis* changed
261 considerably over the seasons. Leaf C:N, C:P and N:P ratios peaked in summer coinciding
262 with the main growth phase for *P. australis* and *C. malaccensis*. The invasive species
263 generally had lower C:N ratios and higher C:P and N:P ratios than did the native species, an
264 effect associated with the higher capacity of the invasive species to resorb N and P. This also
265 reflects the generally higher concentrations of N and lower of P in different tissues of the
266 invasive *P. australis* than in the native *C. malaccensis*. Interspecific differences in C:N, C:P
267 and N:P ratios may likely reflect differences in plant morphology, nutrient-use efficiency and
268 photosynthetic capacity between the C3 (*P. australis*) and C4 (*C. malaccensis*) monocots.

269 C:N, C:P and N:P ratios also changed seasonally in the soils. Both C:N and C:P ratios
270 peaked in the autumn, but N:P ratios were lowest in autumn for both the *P. australis* and *C.*
271 *malaccensis* wetlands. Soil properties such as pH, salinity and water content can influence the
272 seasonal variation in C, N, P concentrations and therefore in C:N, C:P and N:P ratios, as
273 reported by Wang et al. (2010). Seasonal variation in the total soil C:N, C:P and N:P ratios in
274 both wetlands may also have been affected by the absorption of nutrients by the plants and
275 the release of nutrients from the litter.

276

277 Relationships of changes in C:N, C:P and N:P ratios with ecosystem functioning

278

279 C:N ratios of litter are generally strongly correlated with the rates of litter decomposition in
280 wetlands, with lower C:N ratios usually associated with higher rates of decomposition
281 (Windham 2001). Litter accumulates in the winter, which is consistent with the low rates of
282 litter decomposition in the Minjiang River estuary (Tong and Liu 2009) and with the negative
283 correlation between rate of decomposition of soil C and litter C:N ratio in this estuary (Wang
284 et al. 2010b). Our results also support the C:N ratio as an indicator of litter and
285 organic-matter decomposition (Elser et al. 2003; Mulder et al., 2013) and further suggest that
286 rates of litter decomposition can be lower in invaded than in native stands since litter C:N
287 ratios of *P. australis* were higher than those of *C. malaccensis*.

288 C:P and N:P ratios were lower in the native plants than in the invasive plants during the
289 growing season, consistently with a higher growth rate for *C. malaccensis* than for the
290 invasive *P. australis*. The average rates of growth of *C. malaccensis* and *P. australis* were
291 2.1% and 1.4% weekly, respectively (Zhang et al. 2008; Zeng et al. 2009a,b). Furthermore,
292 net primary productivity of the roots was higher for *C. malaccensis* ($724.25 \text{ gC m}^{-2} \text{ y}^{-1}$) than
293 for *P. australis* ($443.04 \text{ gC m}^{-2} \text{ y}^{-1}$, Zhang et al. 2008; Zeng et al. 2009a; Zeng et al. 2009b),
294 which is thus associated with the lower C:P and N:P ratios in *C. malaccensis*. Lower C:P and
295 N:P ratios are usually associated with higher growth rates (Elser et al. 2003; Peñuelas et al.
296 2013).

297 The invasive plant species in our study is a slower growing species than the native
298 species (Zhang et al. 2008; Zeng et al. 2009a; Zeng et al. 2009b), suggesting that invasive
299 success in the Minjiang River estuarine tidal wetland depends on a lower growth rate and a

300 more conservative use of nutrients. Most studies in environments with no limitation of any
301 resource such as water, light or nutrients generally find that plant invasion is frequently
302 dependent on higher rates of nutrient uptake and cycling (Funk and Vitousek, 2007; González
303 et al., 2010; Matzek, 2011; Sardans and Peñuelas 2012), whereas invasive success in
304 environments with a serious limitation of resources is instead frequently dependent on a more
305 conservative use of the limiting resource, despite the low number of studies and the
306 frequently contradictory results (González et al., 2010; Neves et al., 2010; Sardans and
307 Peñuelas 2012). In this study, *P. australis*, had a high capacity to allocate N to photosynthesis.
308 Interestingly, this ability enhances invasive success in both nutrient-rich and nutrient-poor
309 sites (Feng, 2008; Matzek, 2011).

310 Subtropical zones have high precipitation and temperatures that favor the erosion and
311 loss of N and P, so nutrients are limited (Olde Venterink et al. 2003; Tian et al. 2010).
312 Nutrient limitation is especially significant in tidal wetlands, likely because of the periodic
313 inundation of the soil that limits the access of the plants to the soil nutrients by the anoxic
314 effects on root growth (Amlin and Rood 2001; Kirwan and Guntenspergen 2012), by slowing
315 mineralization (Adame et al. 2010) and by high levels of leaching of P and particularly of N
316 (Noe and Hupp 2007; Kobayashi et al. 2009). The higher N:P and lower C:N ratios together
317 with the higher capacity of *P. australis* to resorb N and P indicate a more conservative use of
318 nutrients in this invasive species than in the native species.

319 The average N:P ratios (on a mass basis) were 14.0 ± 2.6 and 8.1 ± 1.0 for *P. australis* and
320 *C. malaccensis*, respectively, which are from similar to lower than the average N:P ratios
321 (14-16) of terrestrial plants and aquatic macrophytes and algae in their natural environments

322 (Elser et al. 2000; Güsewell and Koerselman 2002; Geider and La Roche 2002; Knecht and
323 Göransson 2004; Sardans et al., 2012). Leaf N:P ratio is often used to represent nutrient
324 limitation during plant growth (Tessier and Raynal 2003; Wang and Yu 2008). Thus, the foliar
325 N:P ratios of this study suggest that N can be limiting. The wetland soils of our study had
326 particularly low N:P ratios, 2.5-2.7 on a mass basis, compared to the soils from other
327 ecosystems, on average 5.9 on a mass basis, at global scale (Cleveland and Liptzin 2007; Tian
328 et al. 2010), indicating that N probably should be more limiting in the soil of this wetland
329 area. The higher N:P ratios in plants than in soils and the negative relationships between plant
330 N:P ratio and soil N:P ratio (Fig. 3) suggested again N limitation since plants made a greater
331 effort to conserve N than P, especially when soil N:P ratios were lower, whereas the opposite
332 occurred with P. Both plant species had much higher N:P ratio than soil, and the negative
333 relationship between plant N:P ratio and soil N:P ratio further suggest that when N is more
334 limiting, plants tend to accumulate even more N. Moreover, the slopes between plant C:N
335 ratio and soil C:N ratio are below 1 whereas the corresponding slopes of C:P ratio are above 1
336 suggesting again that plants retain more strongly N than P. Despite this general trend toward a
337 high retention capacity of N in biomass observed in these wetlands, this capacity to retain and
338 efficiently use N was greater in the invasive *P. australis* than in the native *C. malaccensis*. *P.*
339 *australis* had higher resorption capacity for P, and specially for N, higher foliar N
340 concentration and C:N ratio in stem litter, and lower C:N ratio in leaves and roots than *C.*
341 *malaccensis*. All this was also related with the observed higher N content in total biomass in
342 *P. australis* than in *C. malaccensis* despite the total biomass was lower (but not significantly)
343 in the invasive species. Altogether, these findings suggest greater N use efficiency in the

344 community dominated by the invasive plant.

345 To summarize, we found low N and P soil availabilities and low soil N:P ratios in the
346 Minjiang River tidal estuarine wetlands. We observed lower C:N ratios and much higher N:P
347 ratios in the plants than in the soils indicating that plants retain nutrients, especially N. *P.*
348 *australis* was more efficient than the native *C. malaccensis* in the use of N to fix C. This
349 likely contributes to *P. australis*' invasive success in these estuarine wetlands. As frequently
350 observed in previous studies a more conservative use of resources, when limiting, is related
351 with the invasive capacity (Funk and Vitousek, 2007; Matzek, 2011; Sardans and Peñuelas
352 2012). These results were consistent with previous studies indicating that the success of
353 invasive plants in nutrient-poor soils depended on conservative strategies, such as a higher
354 nutrient-use efficiency (Funk and Vitousek 2007; González et al. 2010; Matzek 2011),
355 especially on short time scales (Funk and Vitousek 2007) and long nutrient residence times
356 (Laungani and Knops 2009). The results of our study thus suggest that a conservative use of
357 nutrients (in particular N, that the results suggested as limiting) could contribute to the
358 invasive success of *P. australis* in the Minjiang River tidal estuarine wetlands in China and
359 determines the N-cycle in this wetland area.

360 As a group, C4 plants are generally considered more conservative in their use of limited
361 resources and consequently more stress tolerant than C3 plants. Plants with C4 metabolism,
362 such as *C. malaccensis*, have frequently been shown to have a competitive advantage over
363 plants with C3 metabolism plants, such as *P. australis*, in drier environments (Zand et al.
364 2006; Kocacinar and Sage 2003). In general, reductions in water availability have greater
365 negative effects on C3 than C4 plants (Wilson et al. 2007; Luo et al., 2013), and during dry

366 periods in wetlands C4 plants tend to displace C3 plants (Malone et al. 2013). However, less
367 is known with respect the competitive advantage between these two strategies in wetland
368 areas where resources other than water are limiting plant growth and survival Our results
369 show that the invasive C3 species has more conservative traits such as slow growth rates,
370 higher foliar N:P ratios and higher N nutrient resorption efficiency. We assessed the two
371 dominant plant species in these estuarine wetlands and found that our data are contrary to the
372 typical expectations of competitive outcomes between C3 and C4 plants in resource limiting
373 conditions. For the plant traits examined in our study, the invasive C3 plant showed values
374 consistent with conservative resource use strategy compared to the native C4 plant. *P.*
375 *australis* has invaded these wetlands during the past 30 years and is now the single most
376 prevalent plant species, thus suggesting that other traits, such as the use of nutrients and the
377 growth strategy can be underlying its invasive success.

378

379 **Conclusions**

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381 The nutrient composition and stoichiometry in plants, litters and soils showing low
382 concentration of soil N and very low soil N:P ratio strongly suggested that N would be a
383 limiting factor in these tidal estuarine wetlands. Plant strategies under these environmental
384 conditions are based on slow plant growth and a high capacity to retain nutrients in the
385 biomass associated with a high capacity to resorb nutrients. Our results also suggested that
386 the success of plant invasion was related to a more conservative use of nutrients, in this case
387 P and mainly N, in the invasive relative to the native species.

388

389 **Acknowledgements**

390 This work was supported by grants from the National Science Foundation of China
391 (41371127), the Fujian Provincial Department of Education Foundation (JA13081), the
392 Program for Innovative Research Team at Fujian Normal University (IRTL1205), the Key
393 Sciences and Technology Project of Fujian Province (2014R1034-1) and by the European
394 Research Council Synergy grant ERC-2013-SyG-610028 IMBALANCE-P, the Spanish
395 Government grant CGL2013-48074-P and the Catalan Government grant SGR 2014-274.

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576 **Table 1.** C, N and P concentrations and ratios (Average \pm SD) in plants, stem litters and soils.
 577 We have applied Bonferroni correction to test each individual hypothesis at a significance
 578 level of α/n (0.05/n).

Variable	<i>Leaf</i>	<i>Stem</i>	<i>Root</i>	<i>Stem litter</i>	<i>Soil</i>
C					
Spring (both species)	410 \pm 20b	400 \pm 16	326 \pm 45b	386 \pm 17c	19.0 \pm 2.1a
Summer (both species)	430 \pm 4a	406 \pm 19	370 \pm 24a	411 \pm 24ab	18.7 \pm 1.4ab
Autumn (both species)	404 \pm 8b	410 \pm 12	382 \pm 32a	404 \pm 27b	20.0 \pm 1.7a
Winter (both species)	—	409 \pm 9	367 \pm 35a	417 \pm 23a	17.5 \pm 1.0b
Season	<i>F</i> = 22.2 <i>P</i> < 0.001	<i>F</i> = 5.0 <i>P</i> = 0.039	<i>F</i> = 8.46 <i>P</i> = 0.003	<i>F</i> = 10.2 <i>P</i> < 0.001	<i>F</i> = 10.4 <i>P</i> < 0.001
<i>P. australis</i> wetland	420 \pm 18	419 \pm 6a	360 \pm 21	424 \pm 23a	19.4 \pm 2.4
<i>C. malaccensis</i> wetland	410 \pm 28	396 \pm 16b	363 \pm 57	385 \pm 20b	18.2 \pm 2.1
Species	<i>F</i> = 4.22 <i>P</i> = 0.109	<i>F</i> = 131 <i>P</i> < 0.001	<i>F</i> = 0.016 <i>P</i> = 0.907	<i>F</i> = 104 <i>P</i> < 0.001	<i>F</i> = 3.23 <i>P</i> = 0.147
Season \times species	<i>F</i> = 11.4 <i>P</i> = 0.005	<i>F</i> = 2.39 <i>P</i> = 0.154	<i>F</i> = 3.39 <i>P</i> = 0.054	<i>F</i> = 0.878 <i>P</i> = 0.480	<i>F</i> = 11.59 <i>P</i> < 0.001
N					
Spring (both species)	31.5 \pm 7.7a	13.8 \pm 2.8a	8.2 \pm 0.9	11.2 \pm 1.3a	2.4 \pm 0.3a
Summer (both species)	22.4 \pm 4.4b	8.4 \pm 1.2b	8.1 \pm 1.1	8.0 \pm 1.8b	2.4 \pm 0.2a
Autumn (both species)	21.7 \pm 5.0b	11.3 \pm 1.6ab	9.1 \pm 1.3	8.8 \pm 1.9b	1.6 \pm 0.3b
Winter (both species)	—	13.1 \pm 0.6a	8.3 \pm 1.9	10.1 \pm 1.5ab	2.2 \pm 0.3a
Season	<i>F</i> = 39.8 <i>P</i> < 0.001	<i>F</i> = 25.8 <i>P</i> < 0.001	<i>F</i> = 2.71 <i>P</i> = 0.092	<i>F</i> = 11.6 <i>P</i> < 0.001	<i>F</i> = 10.4 <i>P</i> < 0.001
<i>P. australis</i> wetland	30.0 \pm 12.6a	10.6 \pm 3.5	9.1 \pm 1.0	8.5 \pm 3.6	2.2 \pm 0.5
<i>C. malaccensis</i> wetland	20.4 \pm 6.2b	12.1 \pm 5.4	7.8 \pm 0.7	10.6 \pm 1.6	2.0 \pm 0.7
Species	<i>F</i> = 69.6 <i>P</i> < 0.001	<i>F</i> = 1.38 <i>P</i> = 0.306	<i>F</i> = 2.01 <i>P</i> = 0.229	<i>F</i> = 185 <i>P</i> = 0.013	<i>F</i> = 3.23 <i>P</i> = 0.147
Season \times species	<i>F</i> = 4.61 <i>P</i> = 0.047	<i>F</i> = 5.48 <i>P</i> = 0.032	<i>F</i> = 1.00 <i>P</i> = 0.425	<i>F</i> = 2.93 <i>P</i> = 0.077	<i>F</i> = 11.5 <i>P</i> < 0.001
P					
Spring (both species)	2.6 \pm 0.3a	1.8 \pm 0.7a	1.0 \pm 0.2b	1.1 \pm 0.2a	0.8 \pm 0.1
Summer (both species)	1.5 \pm 0.3b	1.0 \pm 0.6c	1.3 \pm 0.4a	0.7 \pm 0.4b	0.8 \pm 0.1
Autumn (both species)	1.6 \pm 0.2b	1.3 \pm 0.4b	0.6 \pm 0.2d	0.7 \pm 0.3b	0.8 \pm 0.2
Winter (both species)	—	1.9 \pm 0.3	0.8 \pm 0.4c	0.5 \pm 0.2c	0.8 \pm 0.2
Season	<i>F</i> = 407 <i>P</i> < 0.001	<i>F</i> = 128 <i>P</i> < 0.001	<i>F</i> = 21.3 <i>P</i> < 0.001	<i>F</i> = 30.2 <i>P</i> < 0.001	<i>F</i> = 1.54 <i>P</i> = 0.256
<i>P. australis</i> wetland	1.7 \pm 0.5	0.9 \pm 0.7b	0.8 \pm 0.5	0.5 \pm 0.2b	0.8 \pm 0.2
<i>C. malaccensis</i> wetland	2.1 \pm 0.5	1.9 \pm 0.5a	1.1 \pm 0.5	1.0 \pm 0.2a	0.8 \pm 0.3
Species	<i>F</i> = 19.4 <i>P</i> = 0.012	<i>F</i> = 543 <i>P</i> < 0.001	<i>F</i> = 1.55 <i>P</i> = 0.281	<i>F</i> = 52.2 <i>P</i> = 0.002	<i>F</i> = 0.039 <i>P</i> = 0.854
Season \times species	<i>F</i> = 1.80 <i>P</i> = 0.226	<i>F</i> = 25.1 <i>P</i> < 0.001	<i>F</i> = 1.91 <i>P</i> = 0.182	<i>F</i> = 6.90 <i>P</i> = 0.006	<i>F</i> = 0.679 <i>P</i> = 0.114
C:N ratio					
	<i>Leaf</i>	<i>Stem</i>	<i>Root</i>	<i>Stem litter</i>	<i>Soil</i>

Spring (both species)	13.6±2.7b	30.2±7.3bc	39.9±2.0	35.0±4.9c	8.1±0.5c
Summer (both species)	18.3±5.5a	43.2±16.5a	41.0±15.8	47.8±22.1a	8.1±0.9c
Autumn (both species)	17.9±5.1a	33.0±11.9b	37.8±13.3	42.5±18.9b	11.9±1.6a
Winter (both species)	—	27.1±8.8c	41.1±14.6	37.9±12.1bc	9.0±2.4b
Season	F = 49.2 P < 0.001	F = 25.6 P < 0.001	F = 2.54 P = 0.106	F = 23.4 P < 0.001	F = 164 P < 0.001
<i>P. australis</i> wetland	14.6±3.0b	41.7±10.2	40.0±4.4	52.5±12.8a	8.9±1.8
<i>C. malaccensis</i> wetland	20.6±3.4a	34.6±8.7	47.2±6.6	37.1±5.5b	9.4±2.4
Species	F = 93.2 P < 0.001	F = 2.34 P = 0.201	F = 11.2 P = 0.029	F = 73.7 P < 0.001	F = 0.711 P = 0.447
Season × species	F = 1.33 P = 0.317	F = 2.06 P = 0.190	F = 2.97 P = 0.074	F = 11.6 P < 0.001	F = 8.52 P = 0.003
C:P ratio	<i>Leaf</i>	<i>Stem</i>	<i>Root</i>	<i>Stem litter</i>	<i>Soil</i>
Spring (both species)	161±23c	255±112c	324±52c	363±82c	23.8±2.9a
Summer(both species)	294±53a	640±432a	312±71c	792±531a	22.3±2.9b
Autumn(both species)	218±90b	300±157b	556±291a	611±427b	26.0±4.8a
Winter (both species)	—	172±99d	462±226b	799±498a	23.0±5.3ab
Season	F = 196 P < 0.001	F = 120 P < 0.001	F = 17.8 P < 0.001	F = 8.64 P < 0.003	F = 8.20 P < 0.003
<i>P. australis</i> wetland	264±71	609±323a	517±206	981±408a	23.8±3.8
<i>C. malaccensis</i> wetland	206±50	218±46b	390±142	414±142b	23.2±4.2
Species	F = 24.3 P = 0.008	F = 1273 P < 0.001	F = 5.08 P = 0.087	F = 140 P < 0.001	F = 0.045 P = 0.843
Season × species	F = 7.33 P = 0.016	F = 86.7 P < 0.001	F = 0.945 P = 0.450	F = 4.00 P = 0.035	F = 1.55 P = 0.252
N:P ratio	<i>Leaf</i>	<i>Stem</i>	<i>Root</i>	<i>Stem litter</i>	<i>Soil</i>
Spring (both species)	12.5±4.2	8.2±2.4b	8.1±1.2c	10.3±1.3c	2.9±0.3a
Summer (both species)	13.9±7.2	11.4±8.6a	6.3±2.2d	11.8±6.7c	2.8±0.1a
Autumn (both species)	12.0±5.4	8.5±3.7b	13.7±7.0a	12.3±5.6b	2.2±0.4b
Winter (both species)	—	5.8±2.4c	10.8±5.5b	19.0±9.9a	2.6±0.2ab
Season	F = 5.15 P = 0.037	F = 16.2 P = 0.002	F = 20.5 P < 0.001	F = 18.8 P < 0.001	F = 19.8 P < 0.001
<i>P. australis</i> wetland	18.0±2.8a	14.1±5.2	13.1±5.5	18.5±6.9a	2.7±0.4
<i>C. malaccensis</i> wetland	9.9±0.9b	6.4±0.9	8.3±2.7	11.1±3.1b	2.5±0.4
Species	F = 829 P < 0.001	F = 35.7 P = 0.004	F = 17.9 P = 0.013	F = 65.8 P < 0.001	F = 1.64 P = 0.270
Season × species	F = 1.58 P = 0.265	F = 24.7 P < 0.001	F = 3.83 P = 0.039	F = 3.97 P = 0.035	F = 2.10 P = 0.154

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580 Different letters within season indicate statistical differences ($P < 0.003$).

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583 **Table 2.** C, N and P concentrations and ratios (Average \pm SD) in leaf litter. We have applied
 584 Bonferroni correction to test each individual hypothesis at a significance level of α/n (0.05/n).

Variable	<i>C</i>	<i>N</i>	<i>P</i>	<i>C:N</i>	<i>C:P</i>	<i>N:P</i>
Season						
Spring (<i>P. australis</i>)	363 \pm 15	17.2 \pm 5.4	1.3 \pm 0.2a	22.2 \pm 5.4c	298 \pm 60d	13.7 \pm 2.8c
Summer (<i>P. australis</i>)	408 \pm 2	14.4 \pm 2.1	1.1 \pm 0.2a	28.7 \pm 4.3b	388 \pm 63c	13.5 \pm 0.7c
Autumn (<i>P. australis</i>)	386 \pm 18	11.5 \pm 0.6	0.7 \pm 0.1b	33.5 \pm 0.8a	584 \pm 16b	17.4 \pm 0.4b
Winter (<i>P. australis</i>)	390 \pm 10	15.0 \pm 2.9	0.6 \pm 0.1b	26.7 \pm 6.0b	693 \pm 144a	26.0 \pm 1.1a
	<i>F</i> =6.07	<i>F</i> =0.546	<i>F</i> =14.0	<i>F</i> =3.11	<i>F</i> =13.7	<i>F</i> = 41.8
Species	<i>P</i> =0.019	<i>P</i> =0.276	<i>P</i> =0.002	<i>P</i> =0.089	<i>P</i> =0.002	<i>P</i> < 0.001
<i>P. australis</i> (Spring)	363 \pm 15	17.2 \pm 5.4	1.3 \pm 0.2	22.2 \pm 5.4	298 \pm 60	13.7 \pm 2.8
<i>C. malaccensis</i> (Spring)	368 \pm 2	17.9 \pm 1.5	1.8 \pm 0.2	20.7 \pm 1.7	205 \pm 23	9.9 \pm 0.6
	<i>F</i> =0.272	<i>F</i> =0.040	<i>F</i> =9.46	<i>F</i> =0.221	<i>F</i> =8.18	<i>F</i> =7.69
	<i>P</i> =0.629	<i>P</i> =0.851	<i>P</i> =0.037	<i>P</i> =0.663	<i>P</i> =0.042	<i>P</i> =0.049

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586 Different letters within season and species indicate statistical differences ($P < 0.008$)

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589 **Figure captions**

590 **Figure 1:** Study area and sampling site (▲) in southeastern China.

591 **Figure 2:** Relationships of litter C:N(a), C:P(b) and N:P(c) ratios with the corresponding
592 ratios in the plants.

593 **Figure 3:** Relationships of plant C:N(a), C:P(b) and N:P(c) ratios with the corresponding
594 ratios in the soils.

595 **Figure 4:** Relationships of soil C:N (a), C:P (b) and N:P (c) ratios with the corresponding
596 ratios in the litters.

597 **Figure 5:** Nutrient-resorption rates of *P. australis* and *C. malaccensis*. Different letters
598 indicate significant differences between species ($P < 0.05$).

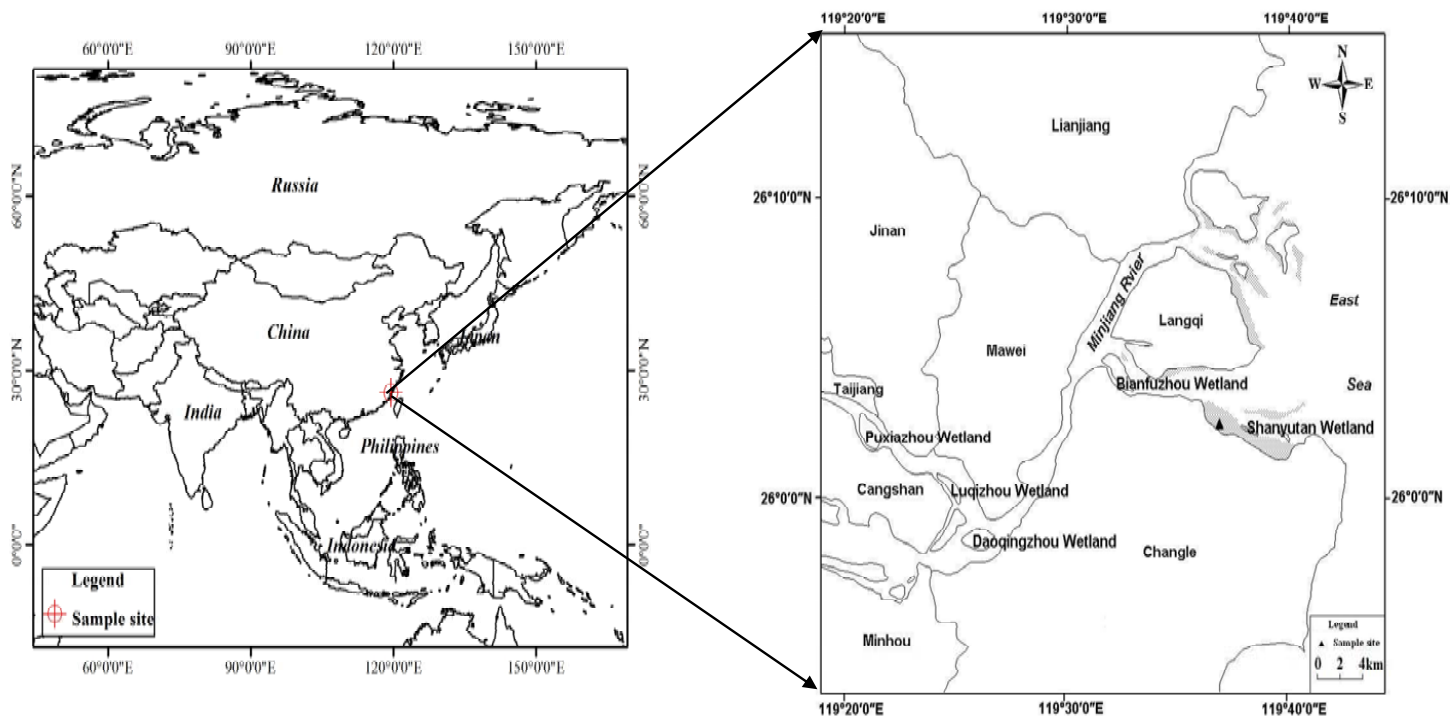
599 **Figure 6:** C (a), N (b) and P (c) contents (mean \pm S.E., kg ha⁻¹) in *P. australis* and *C.*
600 *malaccensis* in above-, below- and total biomass at the end of growing season. Different
601 letters indicate significant differences between species ($P < 0.05$).

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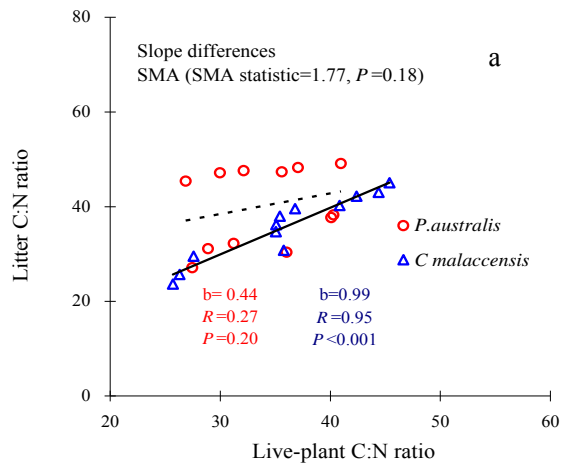
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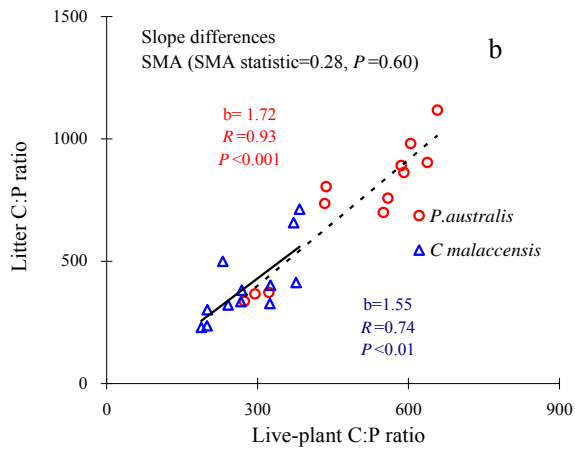
608 **Fig. 1**

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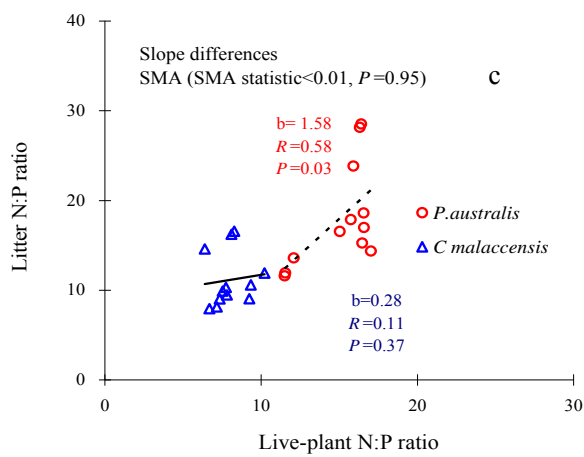
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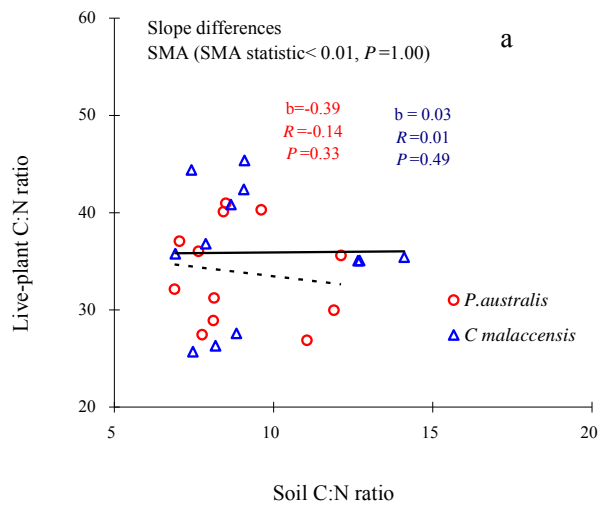
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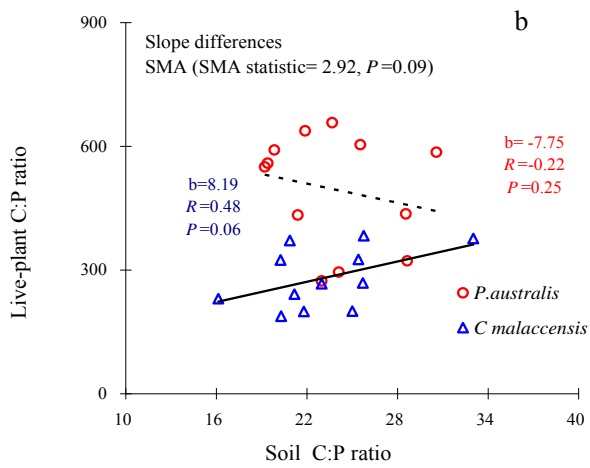
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614 **Fig. 2**

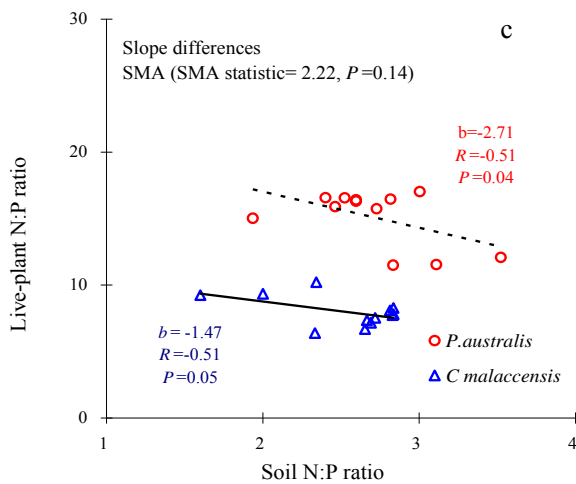
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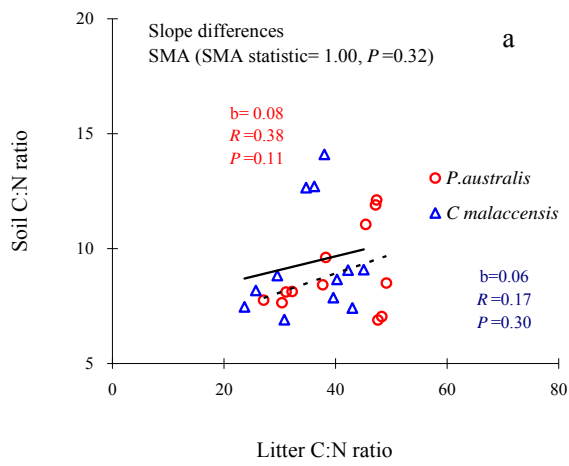


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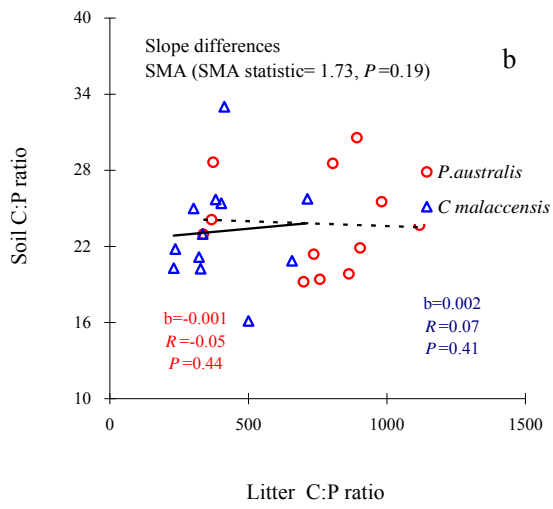


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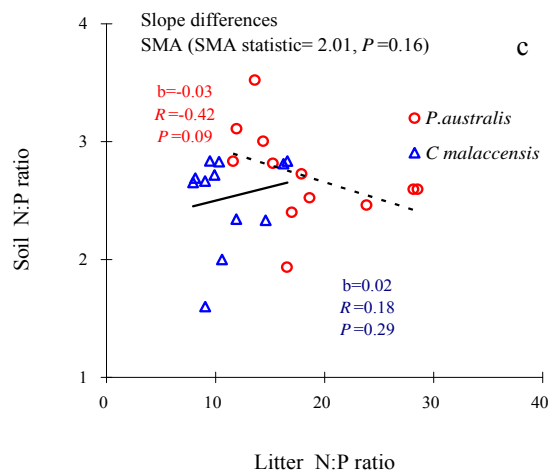
619 **Fig. 3**



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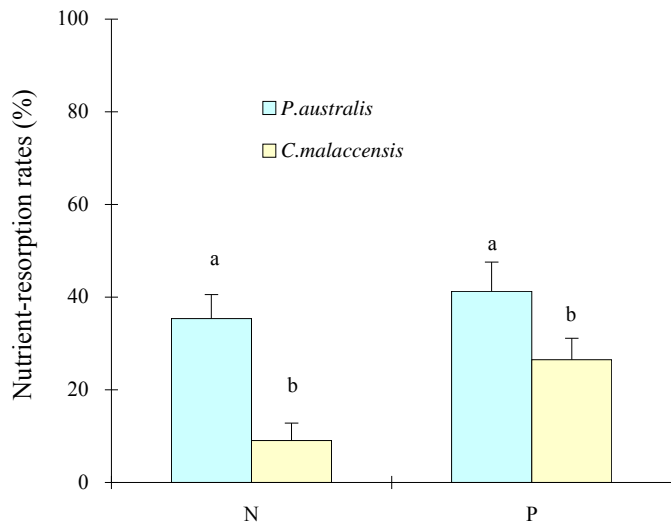
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623 **Fig. 4**

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626 **Fig. 5**

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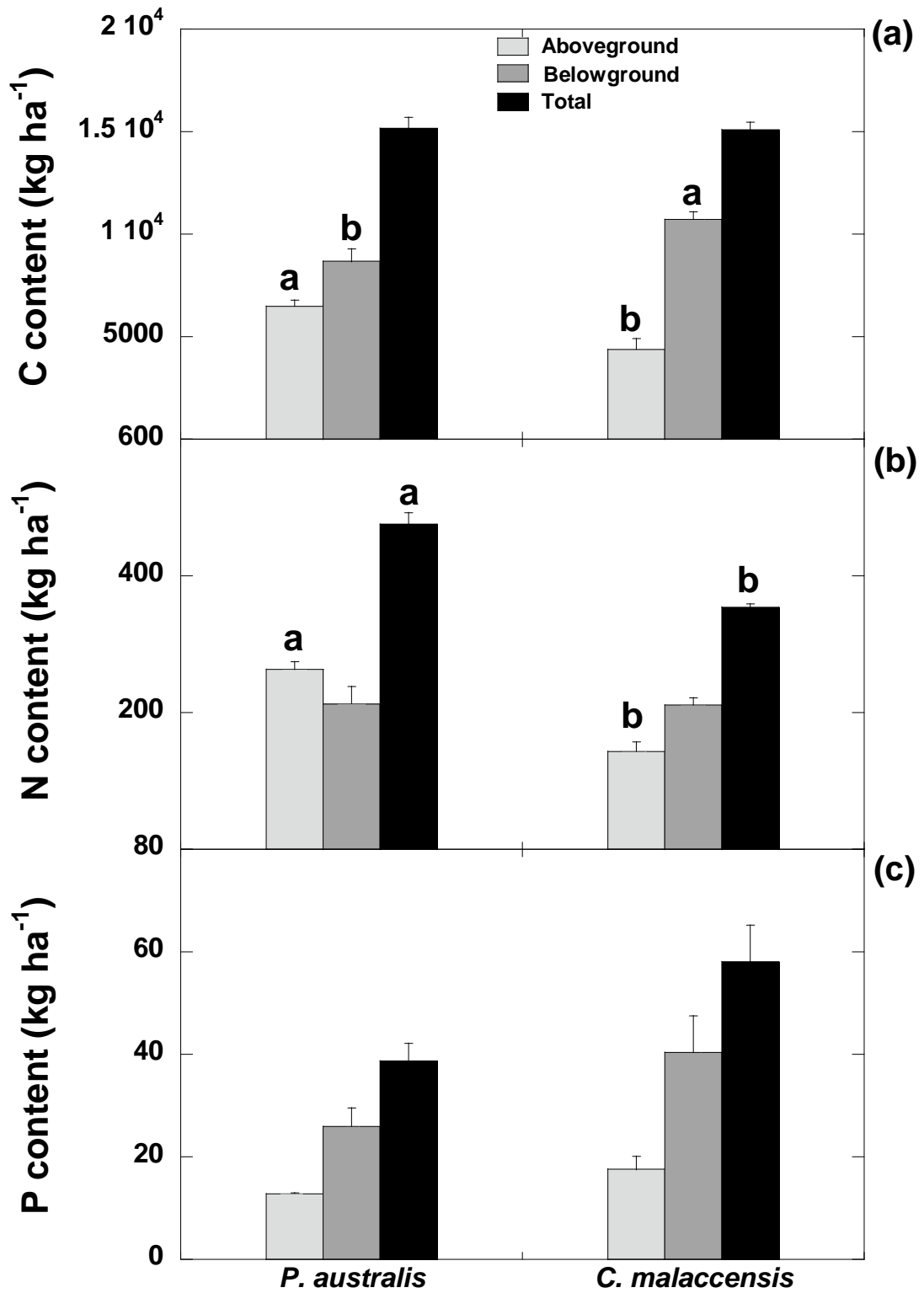
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Figure 6

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1 **Supplementary information**

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4 **Table S1** Summary of two-way ANOVAs for nutrient concentrations with land use and soil depth

	df	<i>F</i>	<i>P</i>
C concentration			
Soil depth	4,60	8.083	<0.001
Land-use type	5,60	58.660	<0.001
Soil depth × Land-use type	20,60	3.142	<0.001
N concentration			
Soil depth	4,60	11.364	<0.001
Land-use type	5,60	26.992	<0.001
Soil depth × Land-use type	20,60	2.797	0.001
P concentration			
Soil depth	4,60	3.698	0.001
Land-use type	5,60	14.135	<0.001
Soil depth × Land-use type	20,60	2.894	0.001
K concentration			
Soil depth	4,60	0.505	0.73
Land-use type	5,60	140.688	<0.001
Soil depth × Land-use type	20,60	1.434	0.14

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21 **Table S2** Soil C, N, P and K (mean \pm S.E., n=15) in the five types of land use

Nutrient	Natural wetland	Flat breeding	Vegetable cultivation	Flower cultivation	Fruit cultivation	Rice cultivation
C (mg g ⁻¹)	22.1 \pm 0.3 a	15.8 \pm 0.5b	10.4 \pm 1.4c	11.7 \pm 0.5cd	15.6 \pm 2.1b	12.7 \pm 0.4d
N (mg g ⁻¹)	1.66 \pm 0.08 a	1.36 \pm 0.04b	1.07 \pm 0.14c	1.07 \pm 0.04c	1.26 \pm 0.12b	1.27 \pm 0.04b
P (mg g ⁻¹)	0.71 \pm 0.07 ab	0.65 \pm 0.02b	0.80 \pm 0.12a	0.46 \pm 0.02c	0.82 \pm 0.03a	0.58 \pm 0.05b
K (mg g ⁻¹)	16.2 \pm 0.4 a	14.8 \pm 0.2b	14.4 \pm 0.3b	13.3 \pm 0.2c	8.84 \pm 0.11	12.7 \pm 0.1c

22 Different letters within a row indicate significant differences ($P < 0.05$).

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44 **Table S3** Summary of two-way ANOVAs for nutrient ratios with land use and soil depth

	df	<i>F</i>	<i>P</i>
C:N ratio			
Soil depth	4,60	0.572	0.68
Land-use type	5,60	41.258	<0.001
Soil depth × Land-use type	20,60	4.898	<0.001
C:P ratio			
Soil depth	4,60	0.684	0.61
Land-use type	5,60	13.278	<0.001
Soil depth × Land-use type	20,60	1.268	0.24
C:K ratio			
Soil depth	4,60	4.898	0.002
Land-use type	5,60	34.136	<0.001
Soil depth × Land-use type	20,60	3.040	<0.001
N:P ratio			
Soil depth	4,60	0.459	0.77
Land-use type	5,60	10.004	<0.001
Soil depth × Land-use type	20,60	0.794	0.710
N:K ratio			
Soil depth	4,60	6.147	<0.001
Land-use type	5,60	30.893	<0.001
Soil depth × Land-use type	20,60	2.544	0.003
P:K ratio			
Soil depth	4,60	2.257	0.073
Land-use type	5,60	46.360	<0.001
Soil depth × Land-use type	20,60	2.382	0.005

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56 **Table S4** Soil C, N, P and K ratios (mean \pm S.E., n=15) in the five types of land use

Nutrient ratio	Natural wetland	Flat breeding	Vegetable cultivation	Flower cultivation	Fruit cultivation	Rice cultivation
C:N	15.7 \pm 1.0a	13.6 \pm 0.2b	11.4 \pm 0.1c	12.8 \pm 0.1d	14.3 \pm 0.8b	11.6 \pm 0.2c
C:P	86.3 \pm 8.3a	63.1 \pm 2.4bd	34.7 \pm 1.1c	65.4 \pm 0.7d	50.0 \pm 5.7b	68.5 \pm 7.3d
C:K	4.45 \pm 0.17b	3.46 \pm 0.12c	2.38 \pm 0.32d	2.86 \pm 0.10bd	5.80 \pm 0.86a	3.24 \pm 0.11c
N:P	5.48 \pm 0.30ab	4.65 \pm 0.14b	3.05 \pm 0.11c	5.13 \pm 0.08ab	3.45 \pm 0.25c	5.86 \pm 0.61a
N:K	0.28 \pm 0.02b	0.25 \pm 0.01bc	0.20 \pm 0.06cd	0.22 \pm 0.01c	0.39 \pm 0.07a	0.27 \pm 0.02b
P:K	0.12 \pm 0.02b	0.12 \pm 0.01b	0.15 \pm 0.05c	0.10 \pm 0.01d	0.25 \pm 0.02a	0.11 \pm 0.02b

57 Different letters within a row indicate significant differences ($P < 0.05$).

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69 **Table S5** Summary of two-way ANOVAs for soil C storage and release with land use and soil depth

	df	<i>F</i>	<i>P</i>
Soil C storage			
Soil depth	4,60	3.509	0.012
Land-use type	5,60	6.343	<0.001
Soil depth × Land-use type	20,60	2.083	0.015
Soil C release			
Soil depth	4,60	9.807	<0.001
Land-use type	5,60	25.360	<0.001
Soil depth × Land-use type	20,60	4.846	<0.001

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93 **Table S6** Soil C storage and release (mean \pm S.E., n=15) in the five types of land use

	Natural wetland	Flat breeding	Vegetable cultivation	Flower cultivation	Fruit cultivation	Rice cultivation
C storage (t hm^{-2})	$15.5 \pm 1.4\text{a}$	$15.8 \pm 1.3\text{a}$	$11.5 \pm 2.7\text{c}$	$13.6 \pm 1.1\text{b}$	$15.3 \pm 3.7\text{abc}$	$14.7 \pm 1.6\text{abc}$
C release ($\text{mg g}^{-1} \text{d}^{-1}$)	$50.9 \pm 4.9\text{c}$	$166 \pm 15\text{b}$	$526 \pm 401\text{a}$	$211 \pm 47\text{b}$	$435 \pm 268\text{a}$	$116 \pm 44\text{bc}$

94 Different letters within a row indicate significant differences ($P < 0.05$).

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113 **Table S7** Summary of two-way ANOVAs for soil parameters with land use and soil depth

	df	<i>F</i>	<i>P</i>
pH			
Soil depth	4,60	1.072	0.38
Land-use type	5,60	342.724	<0.001
Soil depth × Land-use type	20,60	3.737	<0.001
Water content			
Soil depth	4,60	1.997	0.11
Land-use type	5,60	199.878	<0.001
Soil depth × Land-use type	20,60	3.051	<0.001
Bulk density			
Soil depth	4,60	4.044	0.006
Land-use type	5,60	25.510	<0.001
Soil depth × Land-use type	20,60	2.138	0.012
Salinity			
Soil depth	4,60	2.356	0.064
Land-use type	5,60	910.337	<0.001
Soil depth × Land-use type	20,60	1.865	0.033
Clay			
Soil depth	4,60	0.510	0.73
Land-use type	5,60	166.152	<0.001
Soil depth × Land-use type	20,60	1.034	0.44
Silt			
Soil depth	4,60	0.374	0.83
Land-use type	5,60	26.279	<0.001
Soil depth × Land-use type	20,60	1.121	0.354
Sand			
Soil depth	4,60	0.257	0.90
Land-use type	5,60	52.096	<0.001
Soil depth × Land-use type	20,60	0.993	0.48

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118 **Table S8** Soil parameters (mean \pm S.E., n=15) in the five types of land use. Different letters within a row indicate significant differences ($P < 0.05$)

Soil parameters	Natural wetland	Flat breeding	Vegetable cultivation	Flower cultivation	Fruit cultivation	Rice cultivation
pH	5.48 \pm 0.09a	4.55 \pm 0.24b	5.10 \pm 0.18c	4.38 \pm 0.33d	6.99 \pm 0.14e	5.73 \pm 0.18f
Water content (%)	110 \pm 5a	80.8 \pm 15.2b	34.7 \pm 3.2cd	33.7 \pm 5.4c	21.2 \pm 4.7e	41.1 \pm 13.6d
Bulk density (g cm ⁻³)	0.70 \pm 0.05c	1.01 \pm 0.10b	1.14 \pm 0.19a	1.17 \pm 0.06a	1.01 \pm 0.19b	1.16 \pm 0.06a
Salinity (mS cm ⁻¹)	1.23 \pm 0.09a	0.27 \pm 0.02b	0.20 \pm 0.02c	0.15 \pm 0.01d	1.18 \pm 0.04ab	0.23 \pm 0.03bc
Clay percentage (%)	26.4 \pm 1.3a	19.1 \pm 0.7b	18.3 \pm 1.5b	16.1 \pm 0.9c	11.5 \pm 0.5d	11.3 \pm 0.2d
Silt percentage (%)	66.8 \pm 1.3a	63.9 \pm 3.6a	64.7 \pm 2.5a	59.0 \pm 3.2b	49.4 \pm 4.6c	51.9 \pm 2.6c
Sand percentage (%)	6.82 \pm 0.50d	17.0 \pm 4.2c	17.0 \pm 3.6c	24.9 \pm 3.9b	39.1 \pm 5.1a	36.8 \pm 2.6a

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140 **Fig. S1** Concentrations of C (A), N (B), P (C) and K (D) at the various soil depths for the five
141 types of land use. Error bars indicate standard errors (n=3). Different letters within each
142 layer indicate significant differences between land uses ($P<0.05$)

143 **Fig. S2** C:N (A), C:P (B), C:K (C), N:P (D), N:K (E) and P:K (F) ratios at the various soil
144 depths for the five types of land use. Error bars indicate standard errors (n=3). Different letters
145 indicate significant differences between land uses ($P<0.05$)

146 **Fig. S3** C release (A) and C storage (B) at the various soil depths for the five types of land
147 use. Error bars indicate standard errors (n=3). Different letters indicate significant differences
148 between land uses ($P<0.05$)

149 **Fig. S4** Soil properties at the various soil depths for the five types of land use. Error bars
150 indicate standard errors (n=3). Different letters indicate significant differences between land
151 uses ($P<0.05$). pH (A), water content (B), bulk density (C), salinity (D), clay percentage (E),
152 silt percentage (F) and sand percentage (G)

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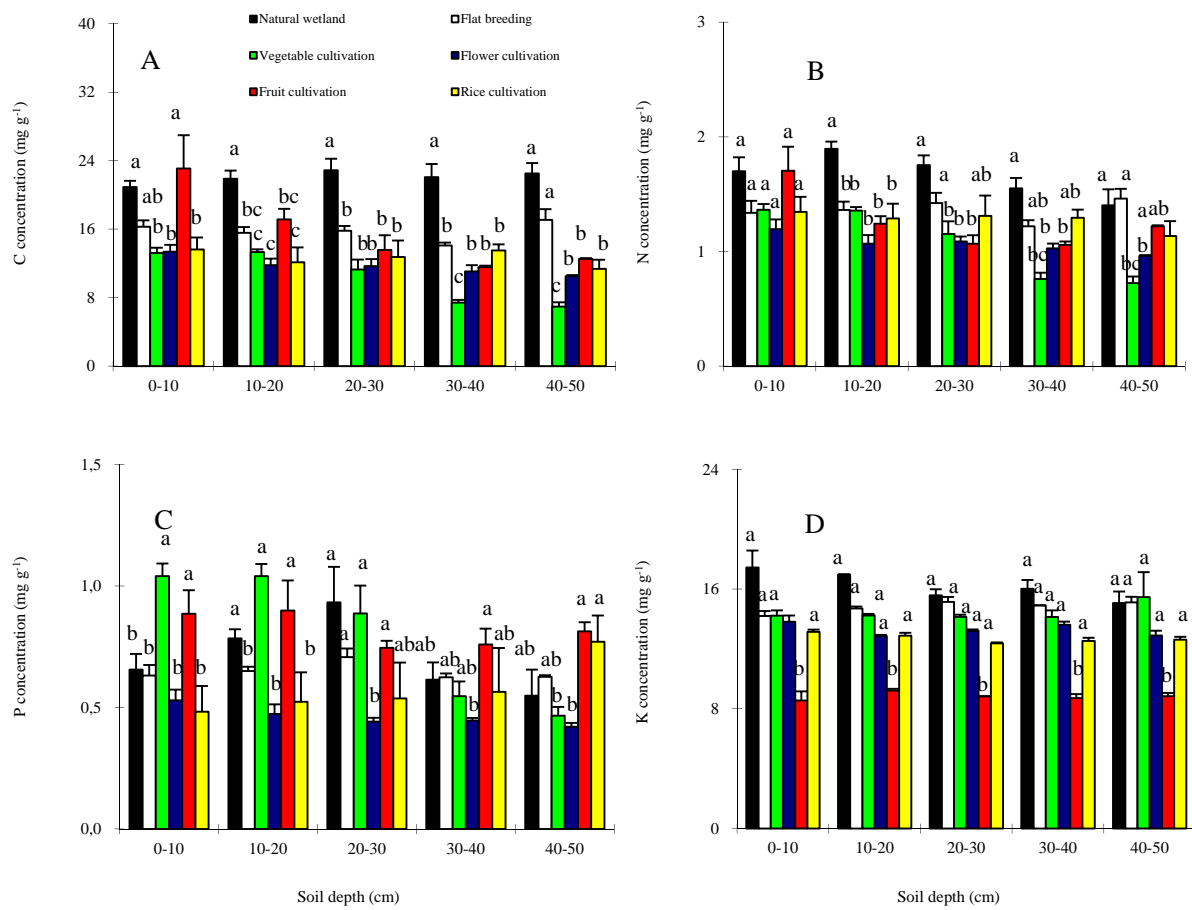
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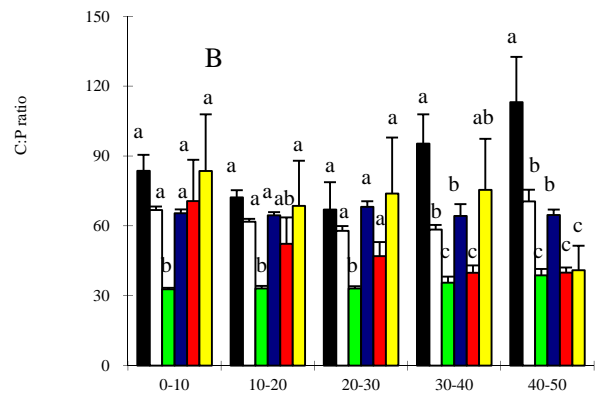
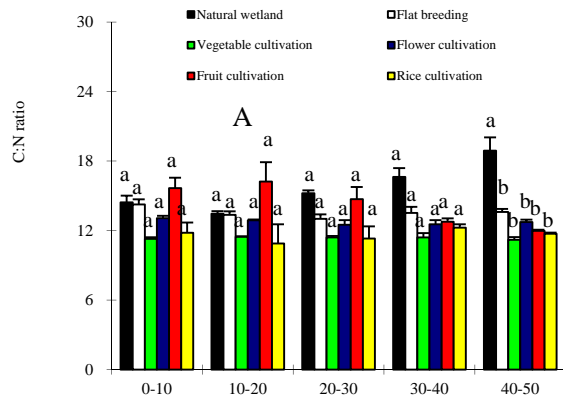


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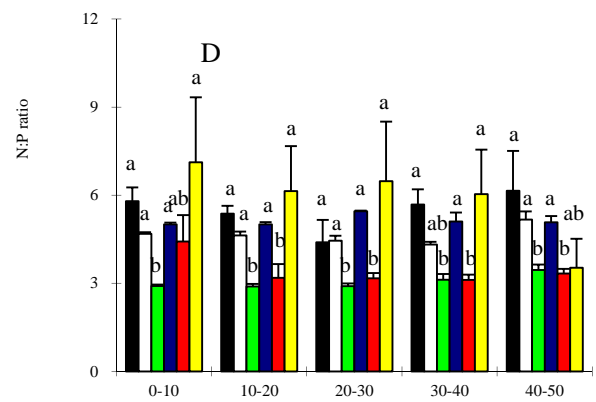
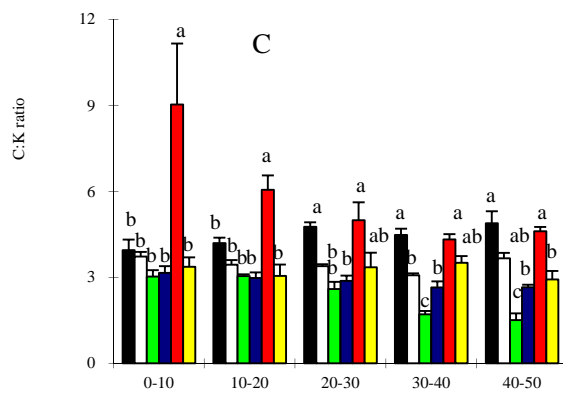
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Fig. S1

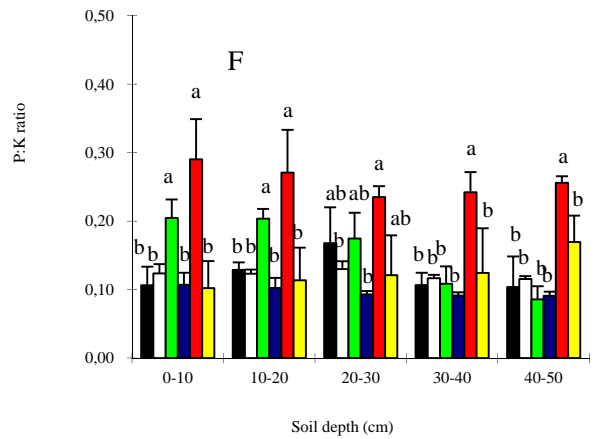
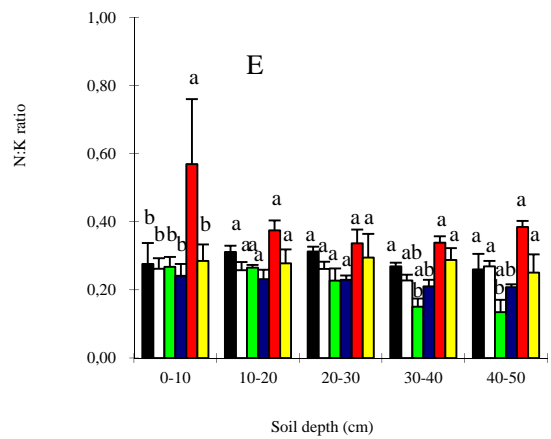
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Fig. S2

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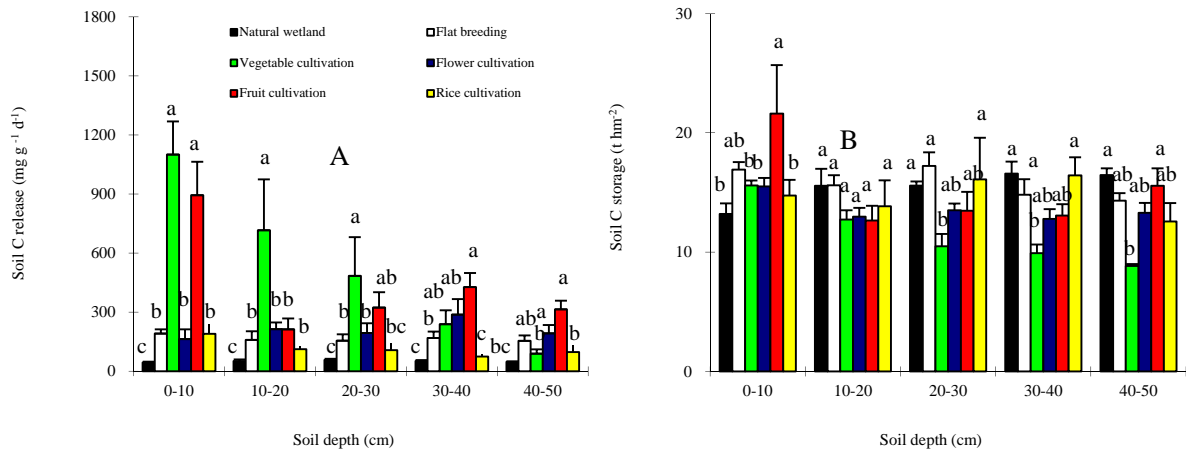
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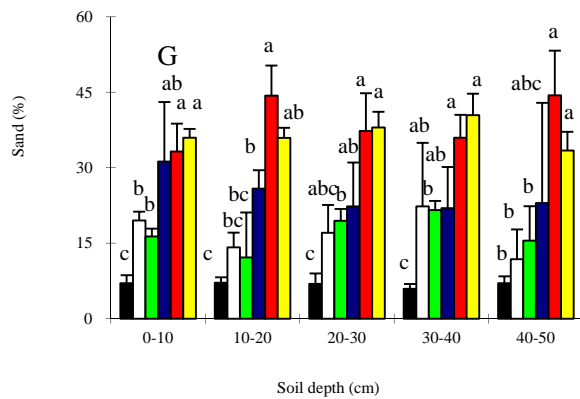
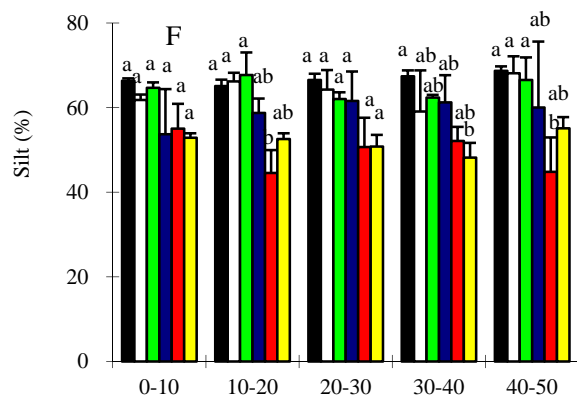
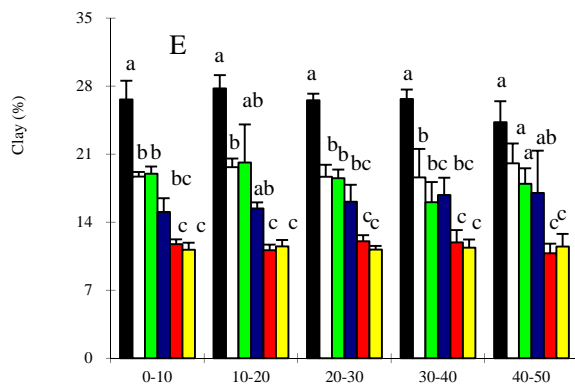
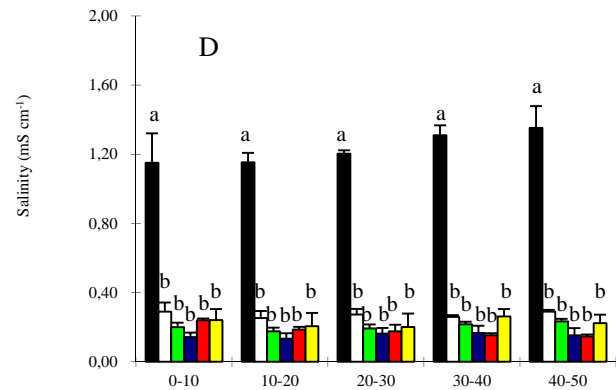
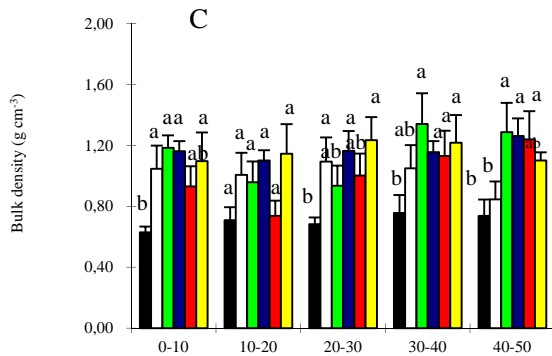
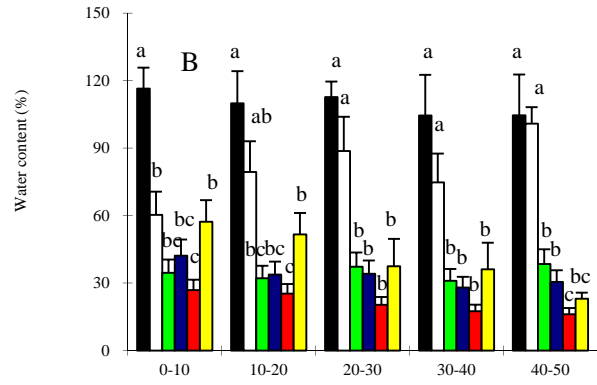
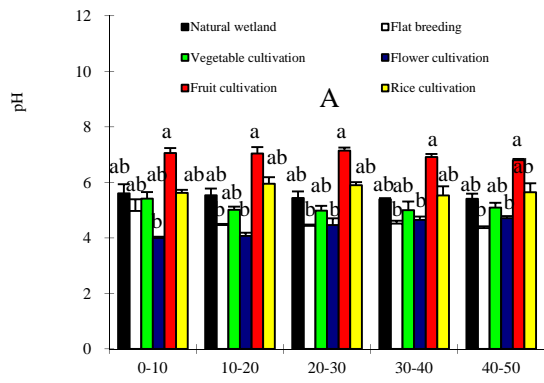
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Fig. S3



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Fig. S4

Highlights

Chinese wetlands are submitted to intense land use changes

The different land uses decrease soil C, N and K concentrations

The different land uses, except rice crops, decrease the soil N:P ratios

Cropland soil management promotes faster nutrient cycles and C emissions

These nutrient imbalances can hinder the natural vegetation regeneration