

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 C<sub>3</sub> invasive species  
18 *Phragmites australis* (Cav.) Trin. ex Steud. and of the C<sub>4</sub> native species *Cyperus malaccensis*  
19 var. *brevifolius* Boeckeler to investigate the effect of C<sub>3</sub> plant invasion on C, N and P  
20 stoichiometry in the C<sub>4</sub> 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  
25 differ, but plants had a lower C:N and much higher N:P ratios than soils. Root C:P and N:P  
26 ratios were lower in the growing season, both in the invasive and the native species. The leaf  
27 C:N, C:P and N:P ratios peaked in summer. The invasive species had lower C:N ratio in  
28 leaves and roots, and higher N:P ratios in all biomass organs and litter than the native species,  
29 an effect related with the higher N-resorption capacity of the invasive species. Interspecific  
30 differences 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 C<sub>3</sub> (*P. australis*) and C<sub>4</sub> (*C.*  
32 *malaccensis*) plants. Our results generally suggested that invasive success in these wetlands  
33 was related to the slow-growth and to the higher resorption capacity of P and N that implied a  
34 conservative use of nutrients, particularly of N, that the results suggested to be limiting.

35

36 **Key words:** Carbon; *Cyperus malaccensis*; Ecological stoichiometry; Invasive species;  
37 Minjiang River estuary; Nitrogen; N:P ratio; N resorption; Phosphorus; *Phragmites australis*;  
38 Plant; Soil; Wetlands.

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58 **Introduction**

59 Tidal estuarine wetlands cover an estimated 12 000 km<sup>2</sup> 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; Wurzbürger 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 Plants, such as *C. malaccensis* with C<sub>4</sub> metabolism traits have been proved to be  
109 frequently in advantage in drier environments with respect C<sub>3</sub> metabolism plants, such as *P.*  
110 *australis* (Wilson et al. 2007; Zand et al. 2006; Kocacinar and Sage 2003). However, less is  
111 known with respect the competitive advantage between these two strategies in wetland areas  
112 with other limiting resources than water. In wetland environments where water is not the  
113 limiting factor, nutrient-use strategy can be crucial in the competitive relationships among  
114 plant species and also in invasive success. To test this hypothesis, we have examined the link  
115 between the invasion of a C<sub>3</sub> monocot with the seasonal variation of the C, N and P  
116 stoichiometry of a C<sub>4</sub> monocot that dominates the subtropical tidal wetlands of the Minjiang  
117 River in China. Our aims were (1) to study the C:N, C:P and N:P ratios of the leaves, stems  
118 and roots and their relationships in the invasive C<sub>3</sub> plant, *P. australis*, and of the native C<sub>4</sub>  
119 plant, *C. malaccensis*, over the year and specially during the growing season, and (2) to  
120 examine the relationships between the success of plant invasion and the nutrient  
121 concentrations and stoichiometries of 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  $4.2 \pm 2.5\%$ .

137 *P. australis* and *C. malaccensis* are the two dominant species of plants. They are typically

138 found in the upper (mid to high) portions of mudflats. *P. australis* is an invasive plant that has

139 invaded this area over the past 30 years, to now become the single most prevalent plant

140 species in the wetland. It mainly invaded the native *C. malaccensis* wetland, typically found

141 in the upper (mid to high) portions of mudflats. *P. australis* grows between April and October,

142 the highest population height is about 2 m, and the density is about 250 m<sup>-2</sup>. *C. malaccensis* is

143 a native plant, typically found in the upper (mid to high) portions of mudflats that grows

144 between April and October, the highest population height is about 1.5 m, and the density is

145 about 1000 m<sup>-2</sup>. Below-ground rhizomes are creeping growth in the topsoil layers.

146 The decomposition rates of the litter of *P. australis* are slower than those of *C.*  
147 *malaccensis* (Tong et al. 2009). Both species are placed in sites with similar flooding intensity,  
148 but despite this, wetland soils in areas dominated by *P. australis* biomass generally have a  
149 lower pH and bulk density and a higher salinity than do areas dominated by *C. malaccensis*  
150 (Jia et al. 2008).

151

152 Sample collection and measurements

153

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



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

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

181

182 Data analysis

183

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

190 plant organs (leaves, stems and roots), litters and soils and performed all these statistical  
191 analyses using SPSS 13.0 (SPSS Inc., Chicago, USA). Pearson correlation analyses identified  
192 the relationships among the C:N, C:P and N:P ratios of the plants, litters and soils of the  
193 estuarine system. We used major axis (MA) and standardized major axis (SMA) (SMATR  
194 package; <http://www.bio.mq.edu.au/ecology/SMATR>) regression to compare the slopes of  
195 the regressions of the relationships among the C:N, C:P and N:P ratios of the plants, litters  
196 and soils.

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

$$199 \text{ NRE} = 100\% \times [(N_{\text{biomass}} - N_{\text{litter}}) / N_{\text{biomass}}]$$

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

202

## 203 **Results**

204

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

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207 C, N and P concentrations varied seasonally in *P. australis* and *C. malaccensis* and in the  
208 litters and soils of the stands dominated by these species (Tables 1 and 2). In general, in  
209 aboveground plant organs (leaf and stems) N and P concentrations were higher in spring and  
210 C:N, C:P and N:P ratios in summer, whereas C concentrations were higher in summer (leaves)  
211 and in autumn (stems) (Table 1). In stem litter, leaf litter, roots and soils, the C, N and P

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

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

221

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

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

234 *malaccensis* ( $P > 0.05$ , SMA test of common slopes, Figs. 2-4).

235

236 N and P resorption

237

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

243

244 Mineralomasses production

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

251

## 252 **Discussion**

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

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

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

273

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

275

276 C:N ratios of litter are generally strongly correlated with the rates of litter decomposition in  
277 wetlands, with lower C:N ratios usually associated with higher rates of decomposition

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

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

294 The invasive plant species in our study is a slower growing species than the native  
295 species (Zhang et al. 2008; Zeng et al. 2009a; Zeng et al. 2009b), suggesting that invasive  
296 success in the Minjiang River estuarine tidal wetland depends on a lower growth rate and a  
297 more conservative use of nutrients. Most studies in environments with no limitation of any  
298 resource such as water, light or nutrients generally find that plant invasion is frequently  
299 dependent on higher rates of nutrient uptake and cycling (Funk and Vitousek, 2007; González

300 et al., 2010; Matzek, 2011; Sardans and Peñuelas 2012), whereas invasive success in  
301 environments with a serious limitation of resources is instead frequently dependent on a more  
302 conservative use of the limiting resource, despite the low number of studies and the  
303 frequently contradictory results (González et al., 2010; Neves et al., 2010; Sardans and  
304 Peñuelas 2012). In this study, the invasive species *P. australis*, interestingly, had a high  
305 capacity to allocate N to photosynthesis enhances invasive success in both nutrient-rich and  
306 nutrient-poor sites (Feng, 2008; Matzek, 2011).

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

316 The average N:P ratios (on a mass basis) were  $14.0 \pm 2.6$  and  $8.1 \pm 1.0$  for *P. australis* and  
317 *C. malaccensis*, respectively, which are from similar to lower than the average N:P ratios  
318 (14-16) of terrestrial plants and aquatic macrophytes and algae in their natural environments  
319 (Elser et al. 2000; Güsewell and Koerselman 2002; Geider and La Roche 2002; Knecht and  
320 Göransson 2004; Sardans et al., 2012). Leaf N:P ratio is often used to represent nutrient  
321 limitation during plant growth (Tessier and Raynal 2003; Wang and Yu 2008). Thus, the foliar

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

342 To summarize, we found low N and P soil availabilities and low soil N:P ratios in the  
343 Minjiang River tidal estuarine wetlands. We observed lower C:N ratios and much higher N:P



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

357 In general C4 plants are considered more conservative and, in general as a group, more  
358 stress tolerant than C3 plants. Plants, such as *C. malaccensis* with C4 metabolism traits have  
359 been proved to be frequently in advantage with respect C3 metabolism plants, such as *P.*  
360 *australis* in drier environments (Zand et al. 2006; Kocacinar and Sage 2003). In general  
361 reductions in water availability affect more to C3 than to C4 plants (Wilson et al. 2007; Luo  
362 et al., 2013), and during dry periods in wetlands C4 plants tend to substitute C3 plants  
363 (Malone et al. 2013). However, less is known with respect the competitive advantage  
364 between these two strategies in wetland areas with other limiting resources than water. Our  
365 results show that the invasive C3 species has more conservative traits such as slow growth rates,

366 higher foliar N:P ratios and higher N nutrient resorption efficiency. In our particular pair of  
367 species we have observed the contrary, the invasive C3 showed values more according with a  
368 conservative strategy than the native C4, at least for the studied traits. In fact, *P. australis* is an  
369 invasive plant that invaded the wetland during the past 30 years and is now the single most  
370 prevalent plant species. Thus in this wetland *P. australis* have reached a high level of invasive  
371 success and the role of stoichiometry differences reported here the highest height and a plant  
372 density about 4 times lower than *C. malaccensis* suggest that other traits, such as the use of  
373 nutrients and the ecological and growth strategy can be underlying the invasive success of *P.*  
374 *australis* even more than the C-fixation metabolism type.

375

## 376 **Conclusions**

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

384

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576 **Table 1.** C, N and P concentrations and ratios (Average  $\pm$  SD) in plants, stem litters and soils.

Variable	Leaf	Stem	Root	Stem litter	Soil
<b>C</b>					
Spring (both species)	410 $\pm$ 20b	400 $\pm$ 16b	326 $\pm$ 45b	386 $\pm$ 17c	19.0 $\pm$ 2.1a
Summer (both species)	430 $\pm$ 4a	406 $\pm$ 19ab	370 $\pm$ 24a	411 $\pm$ 24ab	18.7 $\pm$ 1.4ab
Autumn (both species)	404 $\pm$ 8b	410 $\pm$ 12a	382 $\pm$ 32a	404 $\pm$ 27b	20.0 $\pm$ 1.7a
Winter (both species)	—	409 $\pm$ 9a	367 $\pm$ 35a	417 $\pm$ 23a	17.5 $\pm$ 1.0b
Season	<b>F = 22.2</b> <b>P &lt; 0.001</b>	<b>F = 5.0</b> <b>P = 0.039</b>	<b>F = 8.46</b> <b>P = 0.003</b>	<b>F = 10.2</b> <b>P &lt; 0.001</b>	<b>F = 10.4</b> <b>P &lt; 0.001</b>
<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	<b>F = 4.22</b> <b>P = 0.109</b>	<b>F = 131</b> <b>P &lt; 0.001</b>	<b>F = 0.016</b> <b>P = 0.907</b>	<b>F = 104</b> <b>P &lt; 0.001</b>	<b>F = 3.23</b> <b>P = 0.147</b>
Season $\times$ species	<b>F = 11.4</b> <b>P = 0.005</b>	<b>F = 2.39</b> <b>P = 0.154</b>	<b>F = 3.39</b> <b>P = 0.054</b>	<b>F = 0.878</b> <b>P = 0.480</b>	<b>F = 11.59</b> <b>P &lt; 0.001</b>
<b>N</b>					
	Leaf	Stem	Root	Stem litter	Soil
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	<b>F = 39.8</b> <b>P &lt; 0.001</b>	<b>F = 25.8</b> <b>P &lt; 0.001</b>	<b>F = 2.71</b> <b>P = 0.092</b>	<b>F = 11.6</b> <b>P &lt; 0.001</b>	<b>F = 10.4</b> <b>P &lt; 0.001</b>
<i>P. australis</i> wetland	30.0 $\pm$ 12.6a	10.6 $\pm$ 3.5	9.1 $\pm$ 1.0	8.5 $\pm$ 3.6b	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 $\pm$ 1.6a	2.0 $\pm$ 0.7
Species	<b>F = 69.6</b> <b>P &lt; 0.001</b>	<b>F = 1.38</b> <b>P = 0.306</b>	<b>F = 2.01</b> <b>P = 0.229</b>	<b>F = 185</b> <b>P = 0.013</b>	<b>F = 3.23</b> <b>P = 0.147</b>
Season $\times$ species	<b>F = 4.61</b> <b>P = 0.047</b>	<b>F = 5.48</b> <b>P = 0.032</b>	<b>F = 1.00</b> <b>P = 0.425</b>	<b>F = 2.93</b> <b>P = 0.077</b>	<b>F = 11.5</b> <b>P &lt; 0.001</b>
<b>P</b>					
	Leaf	Stem	Root	Stem litter	Soil
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	<b>F = 407</b> <b>P &lt; 0.001</b>	<b>F = 128</b> <b>P &lt; 0.001</b>	<b>F = 21.3</b> <b>P &lt; 0.001</b>	<b>F = 30.2</b> <b>P &lt; 0.001</b>	<b>F = 1.54</b> <b>P = 0.256</b>
<i>P. australis</i> wetland	1.7 $\pm$ 0.5b	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 $\pm$ 0.5a	1.9 $\pm$ 0.5a	1.1 $\pm$ 0.5	1.0 $\pm$ 0.2a	0.8 $\pm$ 0.3
Species	<b>F = 19.4</b> <b>P = 0.012</b>	<b>F = 543</b> <b>P &lt; 0.001</b>	<b>F = 1.55</b> <b>P = 0.281</b>	<b>F = 52.2</b> <b>P = 0.002</b>	<b>F = 0.039</b> <b>P = 0.854</b>
Season $\times$ species	<b>F = 1.80</b> <b>P = 0.226</b>	<b>F = 25.1</b> <b>P &lt; 0.001</b>	<b>F = 1.91</b> <b>P = 0.182</b>	<b>F = 6.90</b> <b>P = 0.006</b>	<b>F = 0.679</b> <b>P = 0.114</b>
<b>C:N ratio</b>					
	Leaf	Stem	Root	Stem litter	Soil
Spring (both species)	13.6 $\pm$ 2.7b	30.2 $\pm$ 7.3bc	39.9 $\pm$ 2.0a	35.0 $\pm$ 4.9c	8.1 $\pm$ 0.5c

Summer (both species)	18.3±5.5a	43.2±16.5a	41.0±15.8a	47.8±22.1a	8.1±0.9c
Autumn (both species)	17.9±5.1a	33.0±11.9b	37.8±13.3a	42.5±18.9b	11.9±1.6a
Winter (both species)	—	27.1±8.8c	41.1±14.6a	37.9±12.1bc	9.0±2.4b
Season	<b>F = 49.2</b> <b>P &lt; 0.001</b>	<b>F = 25.6</b> <b>P &lt; 0.001</b>	<b>F = 2.54</b> <b>P = 0.106</b>	<b>F = 23.4</b> <b>P &lt; 0.001</b>	<b>F = 164</b> <b>P &lt; 0.001</b>
<i>P. australis</i> wetland	14.6±3.0b	41.7±10.2	40.0±4.4b	52.5±12.8a	8.9±1.8
<i>C. malaccensis</i> wetland	20.6±3.4a	34.6±8.7	47.2±6.6a	37.1±5.5b	9.4±2.4
Species	<b>F = 93.2</b> <b>P &lt; 0.001</b>	<b>F = 2.34</b> <b>P = 0.201</b>	<b>F = 11.2</b> <b>P = 0.029</b>	<b>F = 73.7</b> <b>P &lt; 0.001</b>	<b>F = 0.711</b> <b>P = 0.447</b>
Season × species	<b>F = 1.33</b> <b>P = 0.317</b>	<b>F = 2.06</b> <b>P = 0.190</b>	<b>F = 2.97</b> <b>P = 0.074</b>	<b>F = 11.6</b> <b>P &lt; 0.001</b>	<b>F = 8.52</b> <b>P = 0.003</b>
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	<b>F = 196</b> <b>P &lt; 0.001</b>	<b>F = 120</b> <b>P &lt; 0.001</b>	<b>F = 17.8</b> <b>P &lt; 0.001</b>	<b>F = 8.64</b> <b>P = 0.003</b>	<b>F = 8.20</b> <b>P = 0.003</b>
<i>P. australis</i> wetland	264±71a	609±323a	517±206	981±408a	23.8±3.8
<i>C. malaccensis</i> wetland	206±50b	218±46b	390±142	414±142b	23.2±4.2
Species	<b>F = 24.3</b> <b>P = 0.008</b>	<b>F = 1273</b> <b>P &lt; 0.001</b>	<b>F = 5.08</b> <b>P = 0.087</b>	<b>F = 140</b> <b>P &lt; 0.001</b>	<b>F = 0.045</b> <b>P = 0.843</b>
Season × species	<b>F = 7.33</b> <b>P = 0.016</b>	<b>F = 86.7</b> <b>P &lt; 0.001</b>	<b>F = 0.945</b> <b>P = 0.450</b>	<b>F = 4.00</b> <b>P = 0.035</b>	<b>F = 1.55</b> <b>P = 0.252</b>
N:P ratio	<i>Leaf</i>	<i>Stem</i>	<i>Root</i>	<i>Stem litter</i>	<i>Soil</i>
Spring (both species)	12.5±4.2ab	8.2±2.4b	8.1±1.2c	10.3±1.3c	2.9±0.3a
Summer (both species)	13.9±7.2a	11.4±8.6a	6.3±2.2d	11.8±6.7c	2.8±0.1a
Autumn (both species)	12.0±5.4b	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	<b>F = 5.15</b> <b>P = 0.037</b>	<b>F = 16.2</b> <b>P = 0.002</b>	<b>F = 20.5</b> <b>P &lt; 0.001</b>	<b>F = 18.8</b> <b>P &lt; 0.001</b>	<b>F = 19.8</b> <b>P &lt; 0.001</b>
<i>P. australis</i> wetland	18.0±2.8a	14.1±5.2a	13.1±5.5a	18.5±6.9a	2.7±0.4
<i>C. malaccensis</i> wetland	9.9±0.9b	6.4±0.9b	8.3±2.7b	11.1±3.1b	2.5±0.4
Species	<b>F = 829</b> <b>P &lt; 0.001</b>	<b>F = 35.7</b> <b>P = 0.004</b>	<b>F = 17.9</b> <b>P = 0.013</b>	<b>F = 65.8</b> <b>P &lt; 0.001</b>	<b>F = 1.64</b> <b>P = 0.270</b>
Season × species	<b>F = 1.58</b> <b>P = 0.265</b>	<b>F = 24.7</b> <b>P &lt; 0.001</b>	<b>F = 3.83</b> <b>P = 0.039</b>	<b>F = 3.97</b> <b>P = 0.035</b>	<b>F = 2.10</b> <b>P = 0.154</b>

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578 Different letters within season indicate statistical differences ( $P < 0.05$ ).

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581 **Table 2.** C, N and P concentrations and ratios (Average  $\pm$  SD) in leaf litter.

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

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583 Different letters within season and species indicate statistical differences ( $P < 0.05$ )

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586 **Figure captions**

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

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

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

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

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

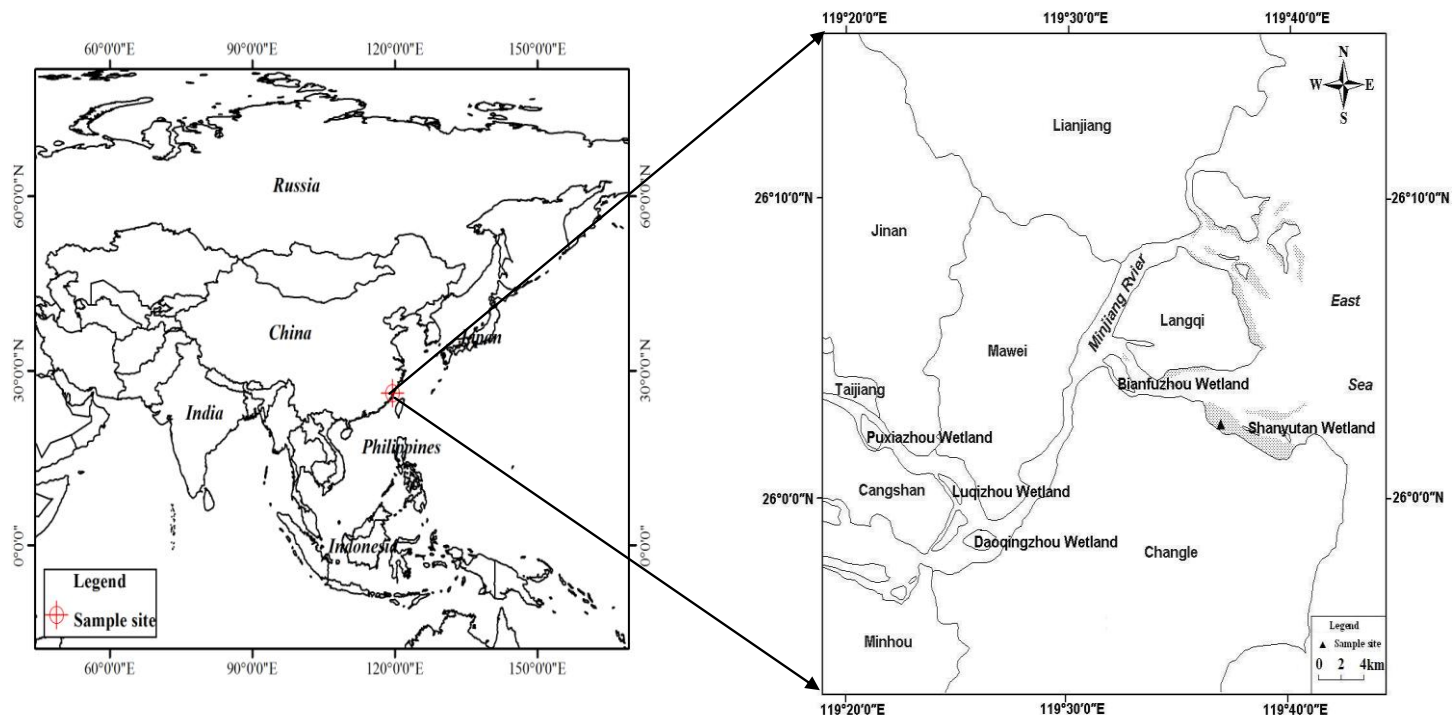
596 **Figure 6:** C (a), N (b) and P (c) contents (mean  $\pm$  S.E., kg ha<sup>-1</sup>) in *P. australis* and *C.*  
597 *malaccensis* in above-, below- and total biomass at the end of growing season. Different  
598 letters indicate significant differences between species ( $P < 0.05$ ).

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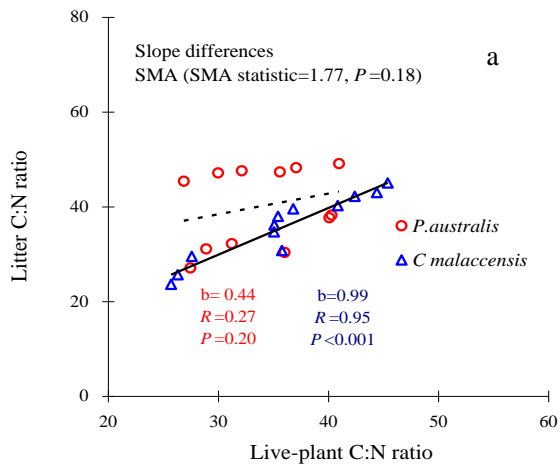
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605 **Fig. 1**

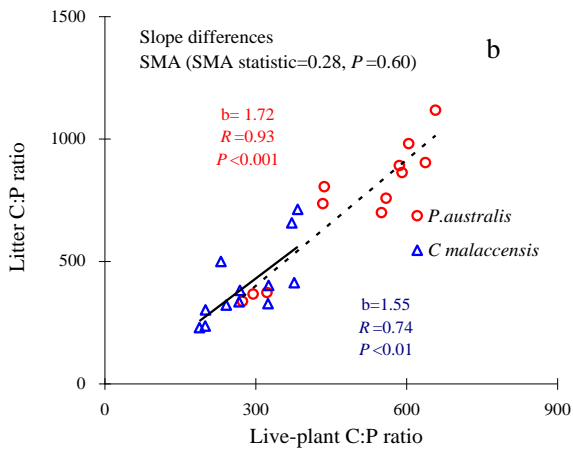
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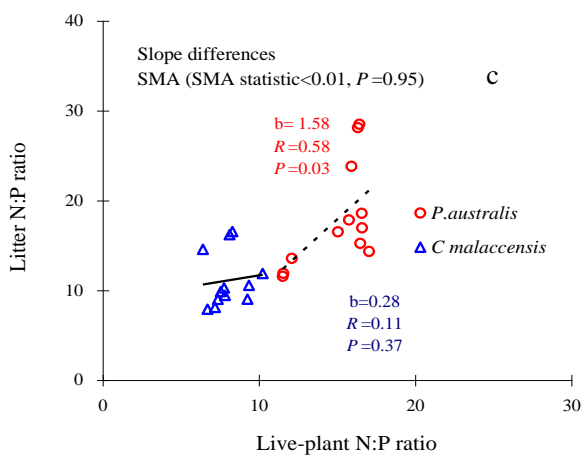




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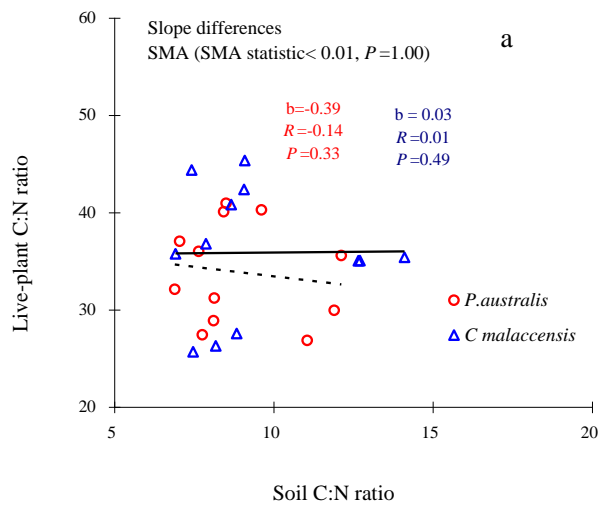
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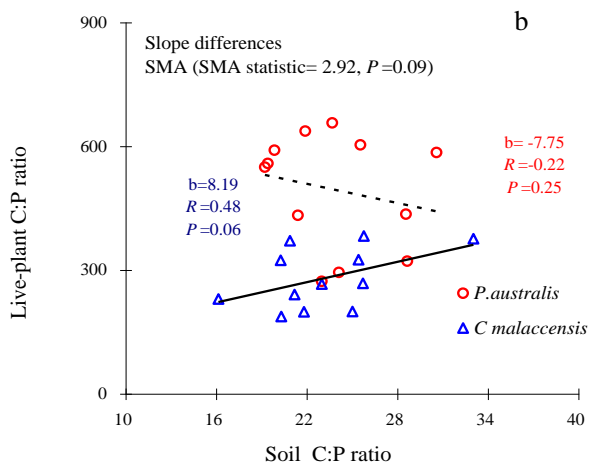
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611 **Fig. 2**

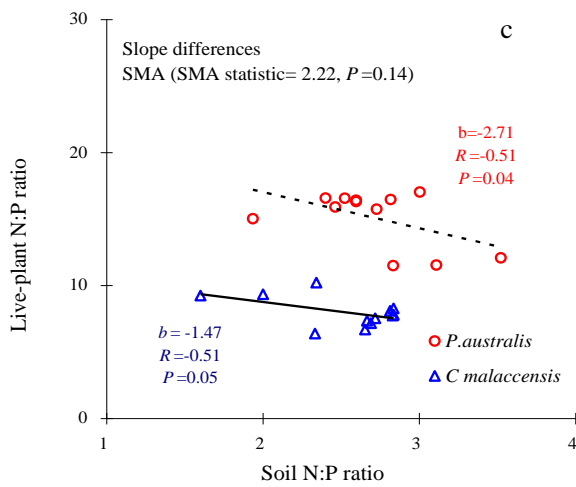
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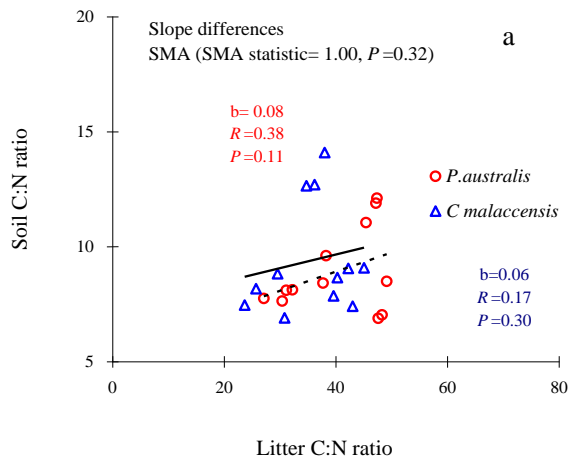


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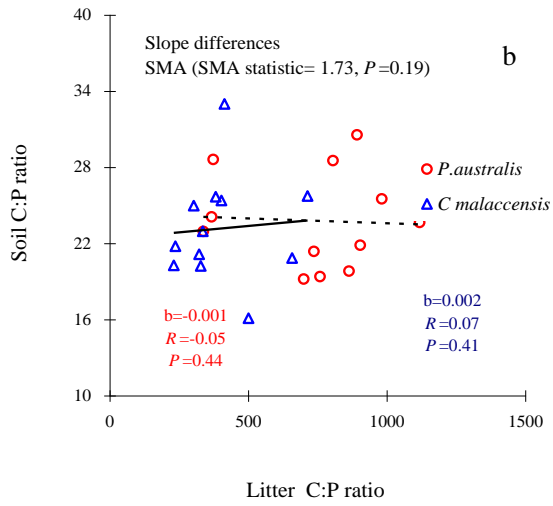


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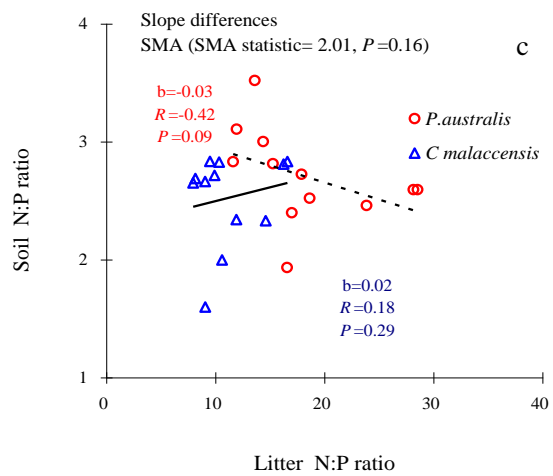
616 **Fig. 3**



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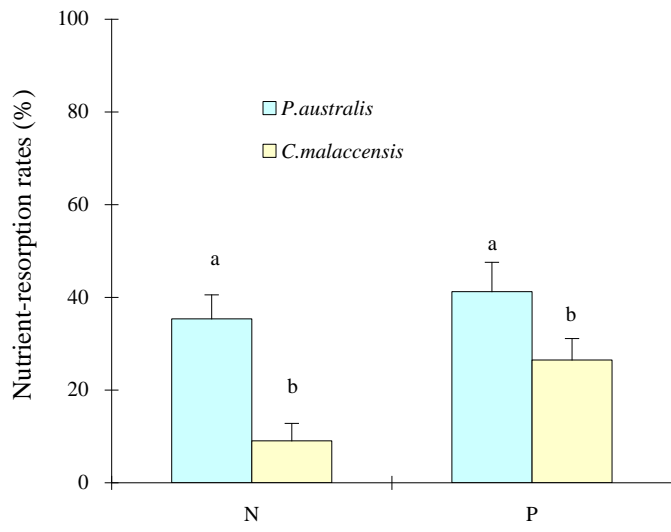
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620 **Fig. 4**

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623 **Fig. 5**

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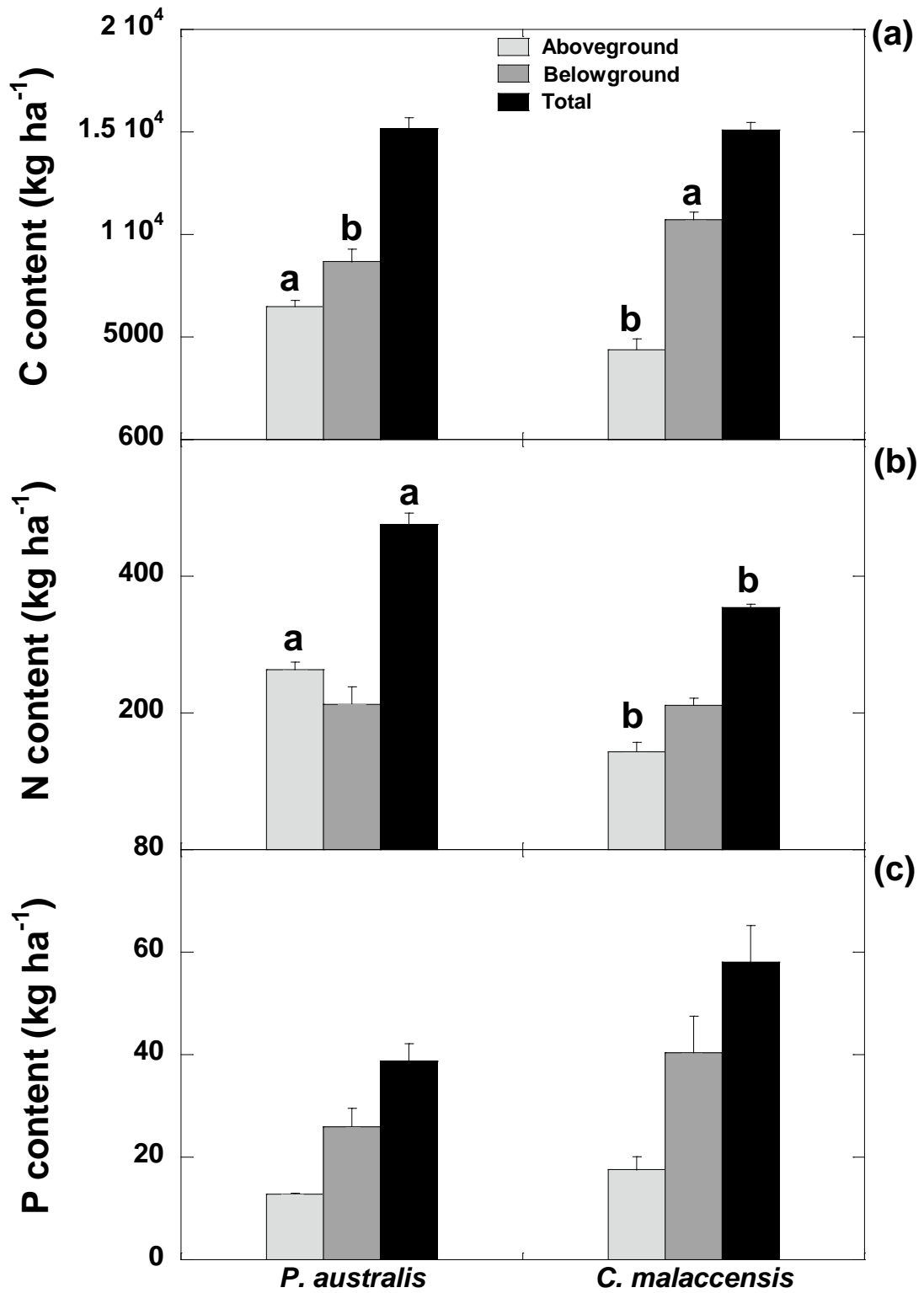
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Figure 6

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