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**

4   Wei Qi Wang[1,2*], Jordi Sardans[3, 4*], Chun Wang[1,2], Cong Sheng Zeng[1,2], Chuan Tong[1,2],

5   Dolores Asensio[3,4] and Josep Peñuelas[3,4]

6   [1]Institute of Geography, Fujian Normal University, 350007 Fujian, China

7   [2]Key Laboratory of Humid Subtropical Eco-geographical Process, Ministry of Education,

8   Fujian Normal University, 350007 Fujian, China[3]CSIC, Global Ecology Unit

9   CREAF-CSIC-UAB, 08913 Cerdanyola del Vallès, Catalonia, Spain.

10   [4]CREAF, 08913 Cerdanyola del Vallès, Catalonia, Spain.

11   Correspondence: Dr W. Q. Wang; email: wangweiqi15@163.com; Dr J. Sardans; email:

12   j.sardans@creaf.uab.es

13

Abstract Tidal estuarine wetlands of China are rich in plant diversity, but several global change drivers, such as species invasion, are currently affecting the biogeochemical cycles of these ecosystems. We seasonally analyzed the carbon (C), nitrogen (N) and phosphorus (P) concentrations in litters and soils and in leaves, stems and roots of the C_3 invasive species *Phragmites australis* (Cav.) Trin. ex Steud. and of the C_4 native species *Cyperus malaccensis* var. *brevifolius* Boeckeler to investigate the effect of C_3 plant invasion on C, N and P stoichiometry in the C_4 plant-dominated tidal wetlands of the Minjiang River. When averaged across seasons, the invasive species *P. australis* had higher N concentrations and lower P concentrations in leaves than the native species *C. malaccensis*. N and P concentrations were lower in litter (stem and leaf) whereas C concentrations in leaf litter were higher in *P. australis* than in *C. malaccensis*. The C, N and P concentrations of the soil also did not differ, but plants had a lower C:N and much higher N:P ratios than soils. Root C:P and N:P ratios were lower in the growing season, both in the invasive and the native species. The leaf C:N, C:P and N:P ratios peaked in summer. The invasive species had lower C:N ratio in leaves and roots, and higher N:P ratios in all biomass organs and litter than the native species, an effect related with the higher N-resorption capacity of the invasive species Interspecific differences in C:N, C:P and N:P ratios may likely reflect the differences in plant morphology, nutrient-use efficiency and photosynthetic capacity between the C_3 (*P. australis*) and C_4 (*C. malaccensis*) plants. Our results generally suggested that invasive success in these wetlands was related to the slow-growth and to the higher resorption capacity of P and N that implied a conservative use of nutrients, particularly of N, that the results suggested to be limiting.

39

40

41

42

43

44

45

46

47

48

49

50

51

52

53

54

55

56

57

Introduction

Tidal estuarine wetlands cover an estimated $12\,000$ km^2 of China's $18\,000$-km coastline (Shen and Zhu 1999; Huang et al. 2006). These tidal wetlands are generally rich in animal and plant biodiversity (Zhou et al. 2006) and are reported to have important biogeochemical roles within the entire estuarine ecosystem (Zeng et al. 2009a,b; Wang et al. 2010a,b; Tong, Wang and Zeng 2010). The Minjiang River estuary in southeastern China is an important tidal wetland ecosystem due to its unique location at the transition between central and southern subtropical climatic zones (Zheng et al. 2006).

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

The elemental composition of plant tissues is tightly associated with the nutrient concentration of litter, which in turn can feed back into the soils (McClaugherty et al. 1985; 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. autralis*, 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 C4 metabiolism traits have been proved to be

109 frequently in advantage in drier environments with respect C3 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 C3 monocot with the seasonal variation of the C, N and P

116 stoichiometry of a C4 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_3 plant, *P. australis*, and of the native C_4

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.

122

123

Materials and methods

Study area

This study was conducted in the Shanyutan wetland (26°01′46″N; 119°37′31″E, Fig. 1), the largest tidal estuarine wetland (approximately 3120 ha) in the estuary of the Minjiang River. The climate in this region is relatively warm and wet, with a mean annual temperature of 19.6 °C and a mean annual precipitation of 1346 mm (Zheng et al. 2006). The soil surface is submerged across the study site beneath 10-120 cm of water for 3-3.5 h during each tidal inundation. Soil surfaces of the entire wetland are exposed at low tide, and the average annual weight percentage of water in soil and soil redox potential are 116.39% and 12.57 mV, respectively, and soil remains flooded at some depths. The average salinity of the tidal water between May and December 2007 was 4.2 ± 2.5‰.

P. australis and *C. malaccensis* are the two dominant species of plants. They are typically found in the upper (mid to high) portions of mudflats. *P. australis* is an invasive plant that has invaded this area over the past 30 years, to now become the single most prevalent plant species in the wetland. It mainly invaded the native *C. malaccensis* wetland, typically found in the upper (mid to high) portions of mudflats. *P. australis* grows between April and October, the highest population height is about 2 m, and the density is about 250 m^{-2}. *C. malaccensis* is a native plant, typically found in the upper (mid to high) portions of mudflats that grows between April and October, the highest population height is about 1.5 m, and the density is about 1000 m^{-2}. 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 ℃ 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    $NRE = 100\% \times [(N_{biomass} - N_{litter}) / N_{biomass}]$

200   where $N_{biomass}$ and N_{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

206

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

223

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 ±

239   9.0% and 9.0 ± 6.6%, respectively, and the rates of P resorption for *P. australis* and *C.*

240   *malaccensis* were 41.2 ± 10.9% and 26.5 ± 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**

253

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

255

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 gC m^{-2} y^{-1}) than

290 for *P. australis* (443.04 gC m^{-2} 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; Gonzàlez

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±2.6 and 8.1±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 tolerants 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

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

Acknowledgements

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

References

410

Adame MF, Virdi, B, Lovelock CE (2010) Effect of geomorphological setting and rainfall on nutrient exchange in mangroves during tidal inundation. Mar Fresh Res 61:1197–1206

Amlin NA, Rood SB (2001) Inundation tolerances of riparian willows and cottonwoods. J Am Water Res Assoc 37:1709–1720

Bai JH, Yang HO, Deng W, Zhu YM, Zhang XL, Wang QG (2005) Spatial distribution characteristics of organic matter and total nitrogen of marsh soils in river marginal wetlands. Geoderma 124: 181–192

Bridgham SD, Pastor J, McClaugherty CA, Richard CJ (1995) Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. Am Nat 145:1–21

Broadley MR, Bowen HC, Cotterill HL, Hammond JP, Meacham MC, Mead A, White PJ (2004) Phylogenetic variation in the shoot mineral concentration of angiosperms. J Exp Bot 55:321–336

Cebrian J (1999) Patterns in the fate of production in plant communities. Am Nat 154:449–468

Cebrian J, Lartigue J (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecol Monogr 74:237–259

Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85:235–252.

Demars BOL, Edwards AC (2007) Tissue nutrient concentrations in freshwater aquatic macrophytes: high inter-taxon differences and low phenotypic response to nutrient supply.

432   Fresh Biol 52:2073–2086

433   Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant-soil system. An Rev Environ

434   Res 30:75–115

435   Elser JJ, Peace AL, Kyle M, Wojewodzic M, McCrackin ML, Andersen T, Hessen DO (2010)

436   Atmospheric nitrogen deposition is associated with elevated phosphorus limitation of

437   lake zooplankton. Ecol Let 13:1256–1261

438   Elser JJ, Fagan WF, Denno RF et al (2000) Nutritional constraints in terrestrial and

439   freshwater food webs. Nature 408:578–580

440   Elser JJ, Acharya K, Kyle M et al (2003) Growth rate- stoichiometry couplings in diverse

441   biota. Ecol Let 6:936–943

442   Feng YL (2008) Photosynthesis, nitrogen allocation and specific leaf area in invasive

443   *Eupatorium adenophorum* and native *Eupatorium japonicum* grown at different

444   irradiances. Physiol Plantarum 133:318-326

445   Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource

446   systems. Nature 446:1079–1081

447   Geider R, La Roche J (2002) Redfield revisited: variability of C: N: P in marine microalgae

448   and its biochemical basis. Eur J Phycol 37:1–17

449   González AL, Kominoski JS, Danger M, Ishida S, Iwai N, Rubach A (2010) Can ecological

450   stoichiometry help explain patterns of biological invasion? Oikos, 119:779–790

451   Güsewell S, Koerselman W (2002) Variation in nitrogen and phosphorus concentrations of

452   wetland plants. Persp Plant Ecol Evol Syst 5:37–61

453   Güsewell S, Verhoeven JTA (2006) Litter N: P ratios indicate whether N or P limits the

454   decomposability of graminoid leaf litter. Plant Soil 287:131–143

455 Hawlena D, Schmitz OJ (2010) Herbivore physiological response to predation risk and

456   implications for ecosystem nutrient dynamics. Proc Natl Acad Sci USA 107: 15505–

457   15507

458 Huang GL, He P, Hou M (2006) Present status and prospects of estuarine wetland research in

459   China. Chin J Appl Ecol 17:1751–1756

460 Huang JY, Zhu XG, Yuan ZY, Song SH, Li X, Li LH (2008) Changes in nitrogen resorption

461   traits of six temperate grassland species along a multi-level N addition gradient. Plant

462   Soil 306:149–158

463 Jia RX, Tong C, Wang WQ, Zeng CS (2008) Organic carbon concentrations and storages in

464   the salt marsh sediments in the Min River estuary. Wetland Sci 6:492–499

465 Jobbágy EG, Jackson R (2001) The distribution of soil nutrients with depth: global patterns

466   and the imprint of plants. Biogeochemistry 53:51–77

467 Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ (2006) Phylogenetic and growth form variation

468   in the scaling of nitrogen and phosphorus in the seed plants. Am Nat 68:E103–E122

469 Kirwan ML, Guntenspergen GR (2012). Feedbacks between inundation, root production, and

470   shoot growth in a rapidly submerging brackish marsh. J Ecol 100:764–770

471 Knecht MF, Göransson A (2004) Terrestrial plants require nutrients in similar proportions.

472   Tree Physiol 24:447–460

473 Kobayashi T, Ryder DS, Gordon G, Shannon I, Ingleton T, Carpenter M, Jacobs SJ (2009)

474   Short-term response of nutrients, carbon and planktonic microbial communities to

475   floodplain wetland inundation. Aquat Ecol 43:843–858

476   Kocacinar F, Sage RF (2003) Photosynthetic pathway alters xylem structure and hydraulic

477   function in herbaceous plants. Plant Cell Environ 26:2015-2026

478   Laungani R, Knops JMH (2009) Species-driven changes in nitrogen cycling can provide a

479   mechanism for plant invasions. Proc Natl Acad Sci USA 106:12400–12405.

480   Liu JQ, Zeng CS, Chen N (2006) Research of Minjiang River estuary wetland. Beijing: Sci

481   Press

482   Lu RK (1999). Analysis methods of soil science and agricultural chemistry. Beijing: Agric

483   Sci Technol Press

484   Luo WT, Jiang Y, Lu XT, Wang X, Li MH, Bai E, Han XG, Xu ZW (2013) Patterns of Plant

485   Biomass Allocation in Temperate Grasslands across a 2500-km Transect in Northern

486   China. PLOS ONE:e71749

487   Malone SL, Starr G, Staudhammer CL, Ryan MG (2013) Effects of simulated drought on the

488   carbon balance of Everglades short-hydroperiod marsh. Global Change Biol 19:2511-2523

489   Matzek V (2011). Superior performance and nutrient-use efficiency of invasive plants over

490   non-invasive congeners in a resource-limited environment. Biol Inv 13:3005–3014

491   McClaugherty CA, Pastor J, Aber JD, Melillo JM (1985) Forest litter decomposition in

492   relation to soil nitrogen dynamics and litter quality. Ecology 66:266–275

493   Meier CL, Bowman WD (2008) Links between plant litter chemistry, species diversity, and

494   below-ground ecosystem function. Proc Natl Acad Sci USA 105:19780–19785

495   Mulder C, Ahrestani FS, Bahn M, Bohan DA, Bonkowski M, Griffiths BS, Guicharnaud RA,

496   Kattge J, Krogh PH, Lavorel S, Lewis OT, Mancinelli H, Naeem S, Peñuelas J, Poorter

497   H, Reich PB, Rossi L, Rusch GM, Sardans J, Wright IJ (2013) Connecting the green and

brown worlds: allometric and stoichiometric predictability of above- and below-ground networks. Adv Ecol Res 49: 69–175

Neves JP, Simões MP, Ferreira LF, Madeira M, Gazarini LC (2010) Comparison of biomass and nutrient dynamics between an invasive and a native species in a Mediterranean saltmarsh. Wetlands 30:817–826

Noe GB, Hupp CR (2007) Seasonal variation in nutrient retention during inundation of a short-hydroperiod floodplain. River Res Appl 23:1088–1101

Northup RR, Dahlgren RA, Mccoll JG (1998) Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback?. Biogeochemistry 421:89–220

Olde Venterink H, Wassen MJ, Verkroost AWM Buiter PCD (2003). Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. Ecology 84:2191–2199

Peñuelas J, Poulter B, Sardans J, Ciais P, van der Velde M, Bopp L, Boucher O, Godderis Y, Hisinger R, Llusia J, Nardin E, Vicca S, Obersteiner M, Janssens IA (2013) Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. Nature Commun 4:2934

Peñuelas J, Sardans J, Llusia J, Owen S, Carnicer J, Giambelluca TW, Rezende EL, Waite M, Niinemets Ü (2010) Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native plant species. Global Change Biol 16:2171–2185

Sardans J, Rivas-Ubach A, Peñuelas J (2012) The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem

520   structure and function: a review and perspectives. Biogeochemistry 111:1-39

521   Sardans J, Peñuelas J (2014) Climate and taxonomy underlie different elemental

522   concentrations and stoichiometries of forest species: the optimum "biogeochemical

523   niche". Plant Ecol 215:441-455

524   Sardans J, Peñuelas J (2012) The role of plants in the effects of Global Change on nutrient

525   availability and stoichiometry in the plant-soil system. Plant Physiol 160:1741–1761

526   Shen H T, Zhu JR (1999) The land and ocean interaction in the coastal zone of China. Mar

527   Sci Bull 18:11–17

528   Sorrell B, Brix H, Schierup HH, Lorenzen B (1997) Die-back of *Phragmites australis*:

529   influence on the distribution and rate of sediment methanogenesis. Biogeochemistry

530   36:173–188

531   Tessier JT, Raynal DJ (2003). Use of nitrogen to phosphorus ratios in plant tissue as indicator

532   of nutrient limitation and nitrogen saturation. J Appl Ecol 40:523-534

533   Tian HQ, Chen GS, Zhang C, Melillo JM, Hall CAS (2010) Pattern and variation of C:N:P

534   ratios in China's soils: a synthesis of observational data. Biogeochemistry 98:139–151

535   Tong C, Liu BG (2009) Litter decomposition and nutrient dynamics in different tidal water

536   submergence environments of estuarine tidal wetland. Geogr Res 28:118–128

537   Tong C, Wang WQ, Zeng CS, Marrs R. (2010) Methane emission from a tidal marsh in the

538   Min River estuary, southest China. J. Environ. Sci Health 45:506–516

539   Townsend A, Cleveland CC, Asner GP, Bustamante MC (2007) Controls over foliar N: P

540   ratios in tropical rain forests. Ecology 88:107–118

541   Vitousek PM, Peter M (1984) Nutrient cycling, and nutrient limitation in tropical forests.

542   Ecology 65:285–298

543 Wang SQ, Yu GR (2008) Ecological stoichiometry characteristics of ecosystem carbon,

544   nitrogen and phosphorus elements. Acta Ecol Sinica 28:3937–3947

545 Wang WQ, Tong C, Jia RX, Zeng CS (2010a) Ecological stoichiometry of characteristics of

546   wetland soil carbon, nitrogen and phosphorus in different water-flooded frequency. J Soil

547   Water Conser 24:238–242

548 Wang WQ, Tong C, Zeng CS (2010b) Stoichiometry characteristics of carbon, nitrogen,

549   phosphorus and anaerobic carbon decomposition of wetland soil of different texture.

550   China Environ Sci, 30:1130–1134

551 Wilson SD (2007) Competition, resources, and vegetation during 10 years in native grassland.

552   Ecology 88:2951-2958

553 Windham L (2001) Comparison of biomass production and decomposition between

554   *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish

555   tidal marshes of New Jersey, USA. Wetlands 21:179–188

556 Wright IJ, Reich PB, Westoby M et al. (2004) The worldwide leaf economics spectrum.

557   Nature 428:821–827

558 Wurzburger N, Hendrick R (2009) Plant litter chemistry and mycorrhizal roots promote a

559   nitrogen feedback in a temperate forest. J Ecol 97:528–536

560 Zand E, Soufizadeh S, Eskandari A (2006) Water stress and nitrogen limitation effects on corn

561   (Zea mays L.) competition with a C3 and a C4 weed. Com Agricul Appl Biol Sci

562   71:753-760

563 Zeng, CS, Zhang LH, Tong C (2009a) Seasonal dynamics of nitrogen and phosphorus in

564   *Phragmites australis* and *Spartina alterniflora* in the wetlands of Min River estuary. Wetl

565   Sci 7:16–24

566   Zeng CS, Zhang LH, Tong C (2009b) Seasonal variation of nitrogen and phosphorus

567   concentrations and accumulation of *Cyperus malaccensis* in Minjiang River estuary.

568   Chin J Ecol 28:788–794

569   Zhang LH, Zeng CS, Tong C (2008) Study on biomass dynamics of *Phragmites australis* and

570   *Spartina alterniflora* in the wetlands of Minjiang River estuary. J Subtrop Resour

571   Environ 3:25–33

572   Zheng CH, Zeng CS, Chen ZQ (2006) A study on the changes of landscape pattern of estuary

573   wetlands of the Minjiang River. Wetl Sci 4:29–34

574   Zhou LJ, Tu YY, Song YC (2006). The biodiversity of wetland and its prevention measures in

575   Min River Estuary. Ecol Sci 25:330–334

Table 1. C, N and P concentrations and ratios (Average ± SD) in plants, stem litters and soils.

Variable	*Leaf*	*Stem*	*Root*	*Stem litter*	*Soil*
C					
Spring (both species)	410±20b	400±16b	326±45b	386±17c	19.0±2.1a
Summer (both species)	430±4a	406±19ab	370±24a	411±24ab	18.7±1.4ab
Autumn (both species)	404±8b	410±12a	382±32a	404±27b	20.0±1.7a
Winter (both species)	—	409±9a	367±35a	417±23a	17.5±1.0b
Season	$F = 22.2$	$F = 5.0$	$F = 8.46$	$F = 10.2$	$F = 10.4$
	$P < 0.001$	$P = 0.039$	$P = 0.003$	$P < 0.001$	$P < 0.001$
P. australis wetland	420±18	419±6a	360±21	424±23a	19.4±2.4
C. malaccensis wetland	410±28	396±16b	363±57	385±20b	18.2±2.1
Species	$F = 4.22$	$F = 131$	$F = 0.016$	$F = 104$	$F = 3.23$
	$P = 0.109$	$P < 0.001$	$P = 0.907$	$P < 0.001$	$P = 0.147$
Season × species	$F = 11.4$	$F = 2.39$	$F = 3.39$	$F = 0.878$	$F = 11.59$
	$P = 0.005$	$P = 0.154$	$P = 0.054$	$P = 0.480$	$P < 0.001$
N	*Leaf*	*Stem*	*Root*	*Stem litter*	*Soil*
Spring (both species)	31.5±7.7a	13.8±2.8a	8.2±0.9	11.2±1.3a	2.4±0.3a
Summer (both species)	22.4±4.4b	8.4±1.2b	8.1±1.1	8.0±1.8b	2.4±0.2a
Autumn (both species)	21.7±5.0b	11.3±1.6ab	9.1±1.3	8.8±1.9b	1.6±0.3b
Winter (both species)	—	13.1±0.6a	8.3±1.9	10.1±1.5ab	2.2±0.3a
Season	$F = 39.8$	$F = 25.8$	$F = 2.71$	$F = 11.6$	$F = 10.4$
	$P < 0.001$	$P < 0.001$	$P = 0.092$	$P < 0.001$	$P < 0.001$
P. australis wetland	30.0±12.6a	10.6±3.5	9.1±1.0	8.5±3.6b	2.2±0.5
C. malaccensis wetland	20.4±6.2b	12.1±5.4	7.8±0.7	10.6±1.6a	2.0±0.7
Species	$F = 69.6$	$F = 1.38$	$F = 2.01$	$F = 185$	$F = 3.23$
	$P < 0.001$	$P = 0.306$	$P = 0.229$	$P = 0.013$	$P = 0.147$
Season × species	$F = 4.61$	$F = 5.48$	$F = 1.00$	$F = 2.93$	$F = 11.5$
	$P = 0.047$	$P = 0.032$	$P = 0.425$	$P = 0.077$	$P < 0.001$
P	*Leaf*	*Stem*	*Root*	*Stem litter*	*Soil*
Spring (both species)	2.6±0.3a	1.8±0.7a	1.0±0.2b	1.1±0.2a	0.8±0.1
Summer (both species)	1.5±0.3b	1.0±0.6c	1.3±0.4a	0.7±0.4b	0.8±0.1
Autumn (both species)	1.6±0.2b	1.3±0.4b	0.6±0.2d	0.7±0.3b	0.8±0.2
Winter (both species)	—	1.9±0.3	0.8±0.4c	0.5±0.2c	0.8±0.2
Season	$F = 407$	$F = 128$	$F = 21.3$	$F = 30.2$	$F = 1.54$
	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.256$
P. australis wetland	1.7±0.5b	0.9±0.7b	0.8±0.5	0.5±0.2b	0.8±0.2
C. malaccensis wetland	2.1±0.5a	1.9±0.5a	1.1±0.5	1.0±0.2a	0.8±0.3
Species	$F = 19.4$	$F = 543$	$F = 1.55$	$F = 52.2$	$F = 0.039$
	$P = 0.012$	$P < 0.001$	$P = 0.281$	$P = 0.002$	$P = 0.854$
Season × species	$F = 1.80$	$F = 25.1$	$F = 1.91$	$F = 6.90$	$F = 0.679$
	$P = 0.226$	$P < 0.001$	$P = 0.182$	$P = 0.006$	$P = 0.114$
C:N ratio	*Leaf*	*Stem*	*Root*	*Stem litter*	*Soil*
Spring (both species)	13.6±2.7b	30.2±7.3bc	39.9±2.0a	35.0±4.9c	8.1±0.5c

	Leaf	Stem	Root	Stem litter	Soil
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	*F* = **49.2**	*F* = **25.6**	*F* = 2.54	*F* = **23.4**	*F* = **164**
	P < **0.001**	*P* < **0.001**	*P* = 0.106	*P* < **0.001**	*P* < **0.001**
P. australis wetland	14.6±3.0b	41.7±10.2	40.0±4.4b	52.5±12.8a	8.9±1.8
C. malaccensis wetland	20.6±3.4a	34.6±8.7	47.2±6.6a	37.1±5.5b	9.4±2.4
Species	*F* = **93.2**	*F* = 2.34	*F* = **11.2**	*F* = **73.7**	*F* = 0.711
	P < **0.001**	*P* = 0.201	*P* = **0.029**	*P* < **0.001**	*P* = 0.447
Season × species	*F* = 1.33	*F* = 2.06	*F* = 2.97	*F* = **11.6**	*F* = **8.52**
	P = 0.317	*P* = 0.190	*P* = 0.074	*P* < **0.001**	*P* = **0.003**
C:P ratio	*Leaf*	*Stem*	*Root*	*Stem litter*	*Soil*
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**	*F* = **120**	*F* = **17.8**	*F* = **8.64**	*F* = **8.20**
	P < **0.001**	*P* < **0.001**	*P* < **0.001**	*P* = **0.003**	*P* = **0.003**
P. australis wetland	264±71a	609±323a	517±206	981±408a	23.8±3.8
C. malaccensis wetland	206±50b	218±46b	390±142	414±142b	23.2±4.2
Species	*F* = **24.3**	*F* = **1273**	*F* = 5.08	*F* = **140**	*F* = 0.045
	P = **0.008**	*P* < **0.001**	*P* = 0.087	*P* < **0.001**	*P* = 0.843
Season × species	*F* = **7.33**	*F* = **86.7**	*F* = 0.945	*F* = **4.00**	*F* = 1.55
	P = **0.016**	*P* < **0.001**	*P* = 0.450	*P* = **0.035**	*P* = 0.252
N:P ratio	*Leaf*	*Stem*	*Root*	*Stem litter*	*Soil*
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	*F* = **5.15**	*F* = **16.2**	*F* = **20.5**	*F* = **18.8**	*F* = **19.8**
	P = **0.037**	*P* = **0.002**	*P* < **0.001**	*P* < **0.001**	*P* < **0.001**
P. australis wetland	18.0±2.8a	14.1±5.2a	13.1±5.5a	18.5±6.9a	2.7±0.4
C. malaccensis wetland	9.9±0.9b	6.4±0.9b	8.3±2.7b	11.1±3.1b	2.5±0.4
Species	*F* = **829**	*F* = **35.7**	*F* = **17.9**	*F* = **65.8**	*F* = 1.64
	P < **0.001**	*P* = **0.004**	*P* = **0.013**	*P* < **0.001**	*P* = 0.270
Season × species	*F* = 1.58	*F* = **24.7**	*F* = **3.83**	*F* = **3.97**	*F* = 2.10
	P = 0.265	*P* < **0.001**	*P* = **0.039**	*P* = **0.035**	*P* = 0.154

577

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

579

580

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

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

582

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

584

585

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 ± S.E., kg ha-1) 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 ($P < 0.05$).

599

600

601

602
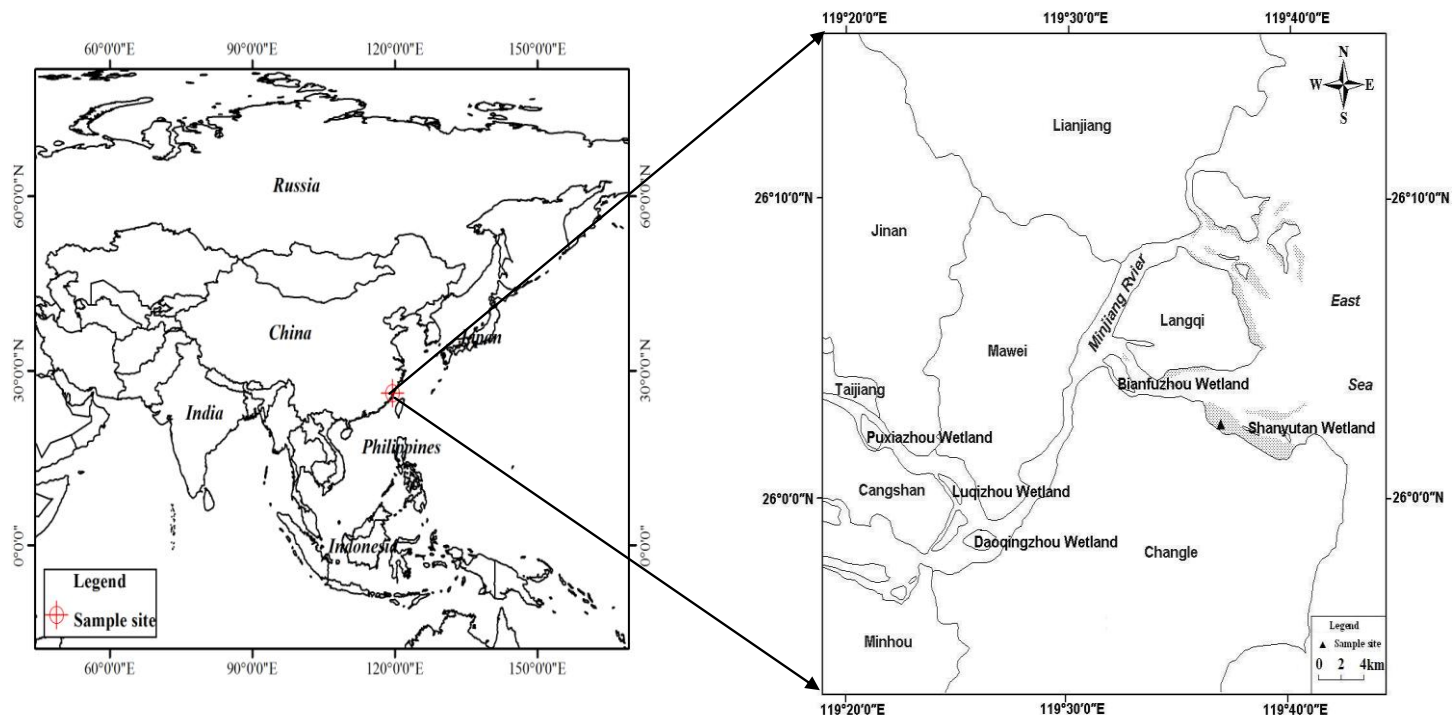
603

604

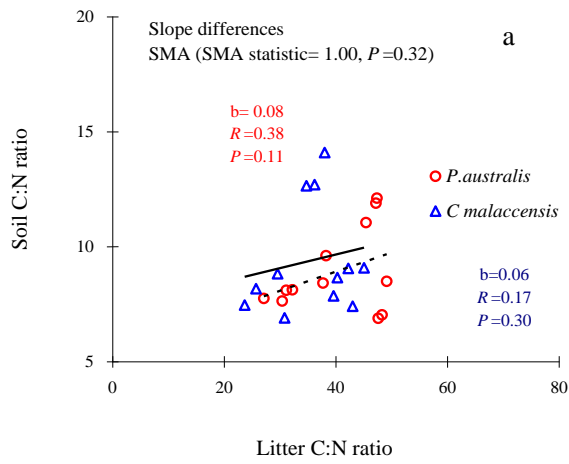605 **Fig.** 1

606

607

608

609

610

Fig. 2

611
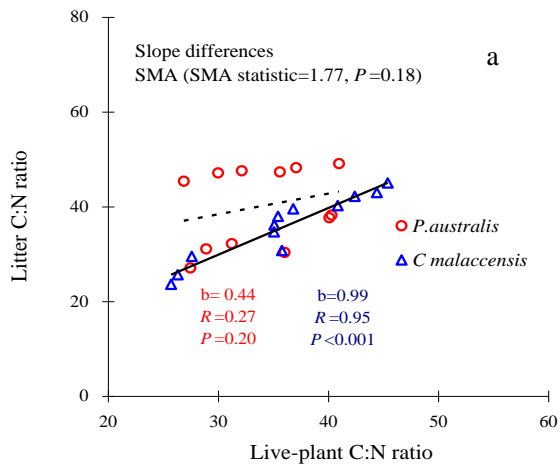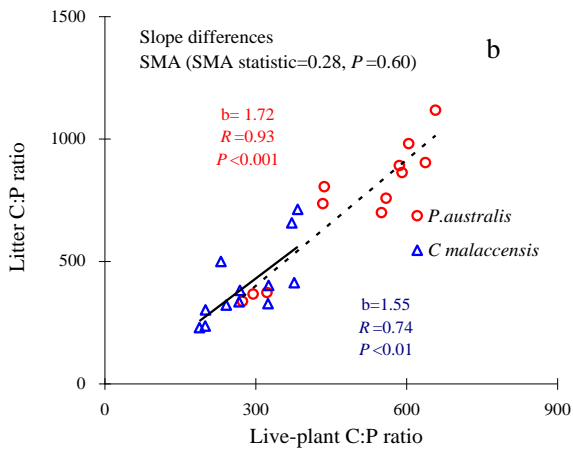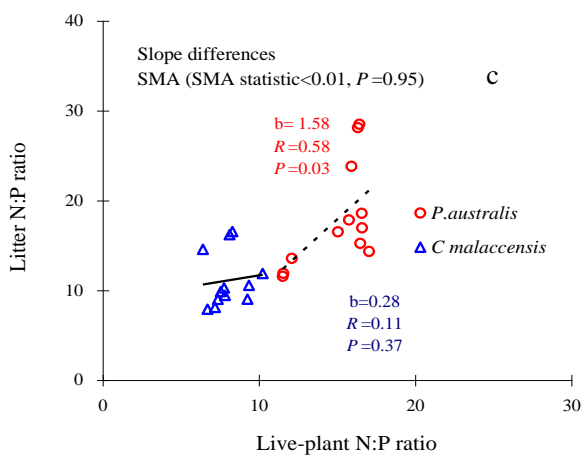
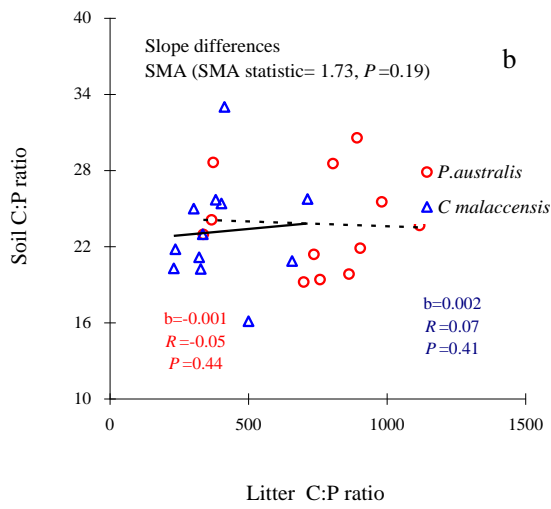612
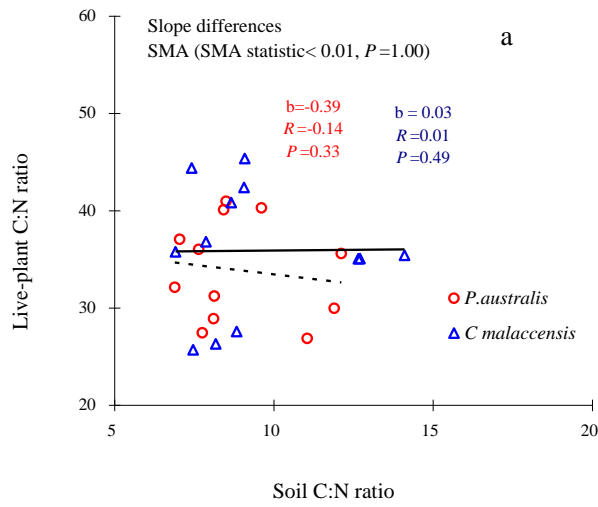
613
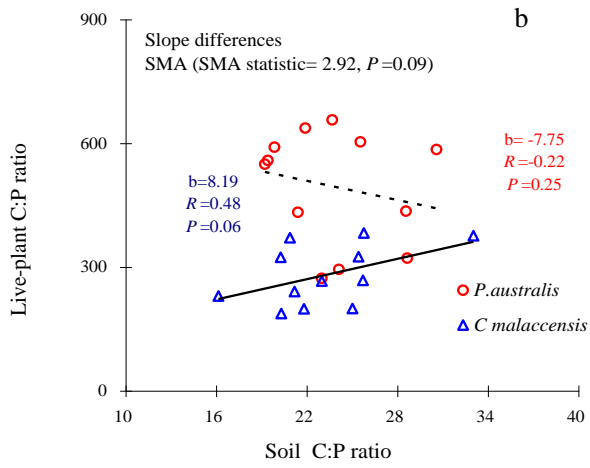
614
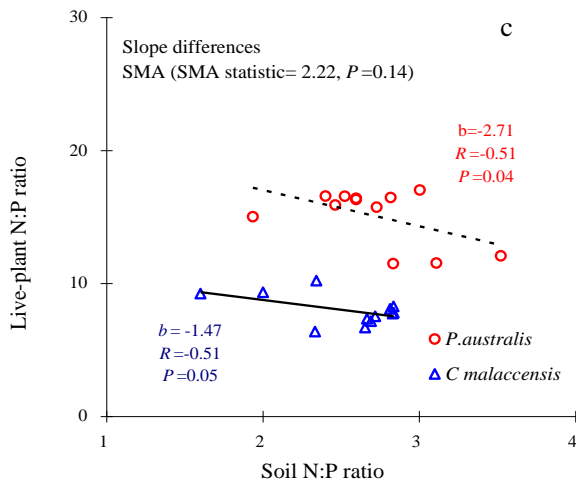
615
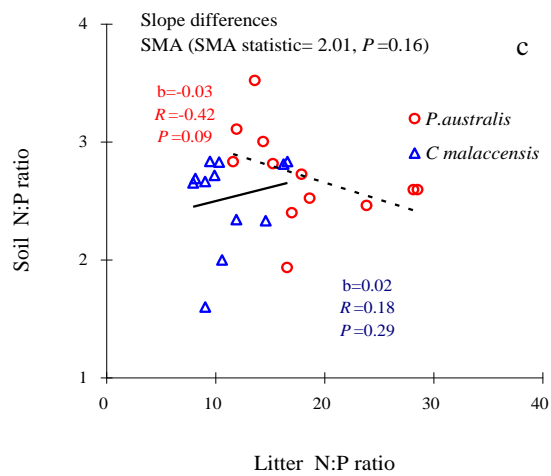
616 **Fig. 3**

617
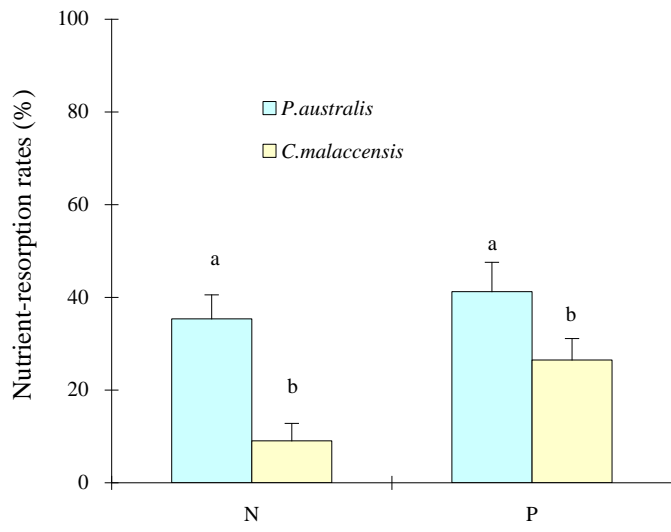

618

619

620 **Fig. 4**

621

622

623   **Fig. 5**

624

625

626

627

628

629

630

631

632

633

634

635

636

642
643
644
645