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

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ABSTRACT

Projections of climate change impacts over the coming decades suggest that rising sea levels will flood coastal wetlands, moving the range of wetlands inland from the current coastline. The intensity of flooding in wetland areas will thus increase, with corresponding impacts on soil properties and coastal ecosystems. We studied the impacts of two levels of water inundation on the concentration and stoichiometry of soil carbon, nitrogen, phosphorus and sulfur in areas dominated by the native C_3 species *Scirpus triqueter* L., the native C_4 species *Cyperus malaccensis* var. *brevifolius* Boecklr. and the invasive Gramineae C_3 species *Phragmites australis* (Cav.) Trin. ex Steud in the Shanyutan wetland areas of the Minjiang River estuary in China. Comparison of the communities dominated by these three species in high- and low- water flood habitats showed that flooding enhanced anaerobiosis and salinity and altered the carbon and nitrogen plant-soil cycles. Higher flooding favored the invasive species more than the two native species. The invasive *P. australis* accumulated more carbon (65% increase in aboveground biomass), and took up more nitrogen under high flooding than did *C. malaccensis* and *S. triqueter*. The more conservative use of soil resources, particularly the limiting nutrient N, appeared to underlie the higher capacity of the invasive species to tolerate higher flooding intensity. Increases in flooding may thus enhance the success and expansion of the invasive *P. australis* to the detriment of the native plant species in these Chinese wetlands.

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

1. Introduction

Global change can affect ocean levels (Schewe et al., 2011; Mendelsohn et al., 2012; Piecuch and Ponte, 2014), river flows (Bueh et al., 2003; van Vliet et al., 2013; Grafton et al., 2013) and water stoichiometry (Sardans et al., 2012; Sardans and Peñuelas, 2014) that in turn can affect community structure and function (Peñuelas et al., 2012; 2013). Rising sea levels could be especially critical for wetland ecosystems (Ramsar, 2013). In China, a higher sea level would flood the current coastal wetlands and create new wetlands farther inland. However, most coastal areas in China, included the studied estuary, are protected by seawalls, so wetland areas cannot increase in size, and this is why the areas of these wetlands will only decrease as the sea level rises (Yang et al., 2014). As an example, with a 0.5 m rise in sea level, the Liaohe delta would lose 3530 km^2 (Xiao et al., 2003) and the Changjiang River estuary would lose 20% of its area (Ji et al., 1994).

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

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

Coastal wetlands occupy 5.7×10^6 km^2 globally (Ramsar, 2013; Mitsch and Gosselink, 2007) and 1.2×10^4 km^2 in China (Shen and Zhu, 1999; Huang et al., 2006). They are cradles of biodiversity upon which countless species of plants and animals depend for survival (Ramsar, 2013). Furthermore, wetlands are among the world’s most productive environments and provide a wide array of benefits, such as mitigation of pollution (Destandau et al., 2013), provision of bird habitats (Fairbairn and Dinsmore, 2001), and reduction of hurricane storm surges (Barbier et al., 2013). Coastal wetlands are also a sink of C as peat and plant matter (Ramsar, 2013; Mitsch and Gosselink, 2007).Wetlands continue to be among the ecosystems most affected by global change, and yet we lack information on the effect of water fluxes during tides and the differences of daily flooding time on their abiotic and biotic environments (Ramsar, 2013; Mitsch and Gosselink, 2007). A better knowledge of the resulting soil C, N, P and S ecological stoichiometries in wetlands would provide decision makers with the necessary information for developing effective methods to enhance the potential capacity of these ecosystems to fix C and reduce the emission of greenhouse gases (Peñuelas et al., 2013). Moreover, determining the cycles and balances of C, N, P and S and the fertility of the soil could improve our understanding of the impacts on potential wetland uses and regenerative capacities.

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

2. Material and methods

2.1. Study area

This study was conducted in the Shanyutan wetlands (26°01′46″N, 119°37′31″E; Fig. 1), the largest tidal wetland area (approximately 3120 ha) in the Minjiang River estuary. The climate in this region is relatively warm and wet with a mean annual temperature of 19.6 ºC and a mean annual precipitation of 1346 mm (Zheng et al., 2006). The average salinity of the tidal water from May to December 2007 was 4.2 ± 2.5 ‰. *Scirpus triqueter* L. and *Cyperus malaccensis* var. *brevifolius* Boecklr. are the most widespread native plant species (Liu et al., 2006) in the area. *P. australis* has invaded the wetlands over the past 30 years and is now the most prevalent plant species. These three species can grow in both high-flood and low-flood habitats. Currently, *S. triqueter*, *P. australis* and *C. malaccensis* are the three primary plant species in the upper (mid to high) portions of mudflats in the Minjiang River estuary (Liu et al., 2006). *S. triqueter* is a native species, C_3 monocot. *S. triqueter* is short (0.6 m), has a vestigial leaves with marginal importance in photosynthetic function, a stick to aboveground base stem, and a belowground crawl stem. *Phragmites australis* is an invasive species, C_3 monocot, a tall plant (2 m during last growth stage) with one leaf on each node of the aboveground stem. *C. malaccensis* is a native species, C_4 monocot, is shorter (1.5 m) than *P. australis*, and has a degenerated leaf, a stick to aboveground base stem and a belowground crawl stem. In our study, the high-flood habitats are located on average at 5.2 meters above sea level and flooded by intermediate tides about 240 days per year and are submerged beneath 10-120 cm of water for 0.5-4 h during each tidal inundation. The low-flood habitats are located on average at 5.6 meters above sea level and are flooded only during spring tides, about 80 days per year, submerged beneath 10-50 cm of water for 0.5-2 h during each tidal inundation. At low tide, the soil surfaces of both the low- and high-flood habitats of the entire estuarine wetlands are exposed, but the soil remains flooded in some low areas.

2.2. Collection and analysis of plant and soil samples

Samples were collected in October 2007 from *S. triqueter, P. australis* and *C. malaccensis* dominated community in the high- and low-flood habitats (Fig. 1). Three replicate plots were randomly established in each community at each flood regime. Plant samples were collected from a consistent height. Each replicate consisted of a large quadrat (10 × 10 m) in each plot and sampled the aboveground and belowground biomass from three randomly selected sub-quadrats (1 × 1 m). All plant material was gently washed with water and then oven-dried to a constant mass (80 ºC for 24-36 h) and weighed. The plant biomass of each community was determined by summing the above- and below ground biomasses. The first 0.6 m of the soil profile in a 1x1m area were excavated. This depth was chosen because most root biomass of all studied species (>80%) is located in the first 60 cm of soil depth. Samples were collected with a small sampler (length, 0.3 m; diameter, 0.1 m) from each of six soil layers (0-10, 10-20, 20-30, 30-40, 40-50 and 50-60 cm) at the center and both sides of the soil pit. These three samples were combined to form one sample per layer. A total of 108 soil samples (three communities × two flood regime × six soil layers × three replicates) were thus collected. In the laboratory, the soil samples were air-dried, roots and visible plant remains were removed and the soil was finely ground in a ball mill to 0.15 mm.

Total soil organic-C content was determined by the $K_2Cr_2O_7$-H_2SO_4 digestion method (Sorrell et al., 1997; Bai et al., 2005), dissolved organic-carbon (DOC) content was determined by extraction with deionized water and measured using a TOC-V CPH total carbon analyzer (Shimadzu Scientific Instruments, Japan) and total soil N concentration was analyzed in a K370 Kjeldahl unit (Buchi Scientific Instruments, Switzerland) by NH_3 distillation of soil acid digests (Kjeldahl, 1883; Wang et al., 2014a). NH_4^+ and NO_3^- were extracted with 2 mol L^{-1} KCl. NH_4^+ concentration was determined by the indophenol-blue method using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Japan). NO_3^- concentration was determined by the zinc-cadmium reduction method using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Japan), although NO_3^- concentration data were low and not accurate for the *S. triqueter* community, so we excluded these data from our analysis to avoid errors. Total soil P concentration was determined by perchloric-acid digestion and measured using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Japan), total S concentration was determined by the next steps, first, by magnesium-nitrate digestion and evaporated to dryness at 70 ℃ on a hot plate, and then the residue was placed in heat oven at 300℃ overnight. After this digestion, in a second step, the residue was digested with nitric acid on a water bath, in order to oxidized sulphur to sulphate. Finally, al the resulting sulphate was measured by the barium-sulfate turbidity method and given as total S (g of S kg^{-1} soil, D.W.). Available-S was determined by phosphate and acetic-acid extraction and measured by the barium-sulfate turbidity method (Lu, 1999).

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

2.3. Determination of soil-C content

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

$$C_S = \sum_{j=1}^{n} c_{\mathrm{m}} \times \rho_{\mathrm{b}} \times D$$

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

2.4. Statistical analyses

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

We also performed multivariate discriminant function analysis (DFA) to determine the importance of total soil C, N, P and S concentrations; DOC, NH_4^+, NO_3^- and available-S concentrations and total soil C:N, C:P, N:P, C:S, N:S and P:S ratios in the separation of the each replicate sampled at both flood regimes for the three communities. DFA is a supervised statistical algorithm that derives an optimal separation between groups established a priori by maximizing between-group variance while minimizing within-group variance (Raamsdonk et al. 2001). DFA is thus an adequate tool for identifying the variables most responsible for the differences among groups. The DFAs were performed using Statistica 6.0 (StatSoft, Inc. Tulsa, Oklahoma, USA).

3. Results

3.1. Effects of flood regimes

The general linear models indicated that total soil C, N, P and S concentrations (Table 1), salinity, soil available-S and soil NH_4^+ concentrations, N:P and C:P ratios and pH and soil-water, clay and silt contents were significantly higher at the high-flood level of all three communities (Figs. 2-4), whereas soil NO_3^- concentrations sand content and bulk density were lower.The soil C:N ratio were lower in the high-flood than the low-flood habitat for the *S. triqueter* community in the most soil layers (Fig. 3). Sand content (Fig. S1) and C:S, N:S and P:S ratios (Fig. 3) were lower in the high-flood than the low-flood habitat for the *P. australis* and *C. malaccensis* communities. Soil DOC concentration and the C:N ratio differed between the flood habitats (Fig.4), but not equally in the three communities. The high-flood habitat had higher soil-C content across all soil depths in the *S. triqueter* community but lower levels in the upper soil layers in the C. *malaccensis* and *P. australis* communities (Fig. 4). The soil C:N ratios were lower in the high-flood than in the low-flood habitat for the *S. triqueter* community in most soil layers (Fig. 3). There was a significant interaction between community x flooding in most studied variables (Table S1). In *S. triquiter* flooding increased soil C, N and P concentrations, silt and clay content and decreases soil C:N ratio in most soil layers, whereas it had no effect in the other two community species (Table S1, Fig 2-4, Fig S1). The DFA analysis indicated that both species community composition and flood regime explained a significant part of the variance of the overall soil elemental and physicochemical traits. The soils properties were more similar in the *P. australis* and *C. malaccensis* communities relative to the *S. triqueter* community. The *S. triqueter* soils were affected more by flooding (Fig. 5). The squared Mahalanobis distances of community × flood regime for the soil parameters differed significantly (Table 1). Soil-water content, salinity and pH; total-C, DOC, nitrate and sulfate concentrations in the soil solutions and the total soil P:S ratio separated the community × flood regimes (Table 2, Fig. 5).

3.2. Correlation analyses

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

3.3. Plant biomass

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

4. Discussion

4.1. General effects of flooding

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

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

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

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

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

Under *S. triquiter* community we observed higher C stocks in the high-flood than the low-flood habitat in all soil layers whereas in *C. malaccensis* and *P. australis*, contrary to expected, we observed lower accumulation of C in the high-flood than the low-flood habitat in the upper soil layer which suggested a lower capacity of C mineralization (oxidation) the higher the flooding intensity. The results observed in soils under *S. triquiter* showing that C content increased as the water content increased, were consistent with the findings of a previous study (Nomura et al., 2013) and with the higher anaerobic conditions in saturated soil. Increasing soil anaerobiosis is the most probable cause of C concentration increases (Tiemann and Billings, 2009). Furthermore, the flooding with seawater increased soil salinity more in the high-flood habitat, and salinity can contribute too, as observed in soils under *S. triquiter.* The release of soil C has also been negatively correlated with soil salinity (Setia et al., 2010; Setia et al., 2011) because higher salinity inhibits the growth and activity of soil microorganisms due to osmotic stress and inhibits C mineralization (Rietz and Haynes, 2003). This effect of flooding also depends of the species community: soils of the *S. triqueter* community had lower C:N ratios under high flooding regime, whereas the soils of the *C. malaccensis* and *P. australis* communities had stable C:N ratios under different regimes of flooding, showing that soil mineralization was less affected by flood regime. Notably the soil under the *S. triquiter* community presents the lowest concentrations of total N and P and also of N:P ratio. This was related with the fact that this species was the species-community with lowest aboveground accumulation both under high and low flooding intensity. The differences in soil N:P ratio among different flooding intensities and communities were due more to N than to P differences, which is consistent with the previously commented N limiting role observed in these wetlands. Low N:P ratios when both N and P concentrations are high had been associated to high mineralization rates in soil (Hartman and Richardson, 2013; Li et al., 2014). But the low soil N:P ratios of soils under *S. triquiter* communities were associated to higher C soil accumulation, suggesting a lower soil mineralization than under other communities. In the frame of the growth rate hypothesis, high growth rates and metabolic activity of soil microbes are expected at low N:P ratios but only when N and P contents are high. Our findings appear to be consistent with the model of cellular metabolism described by the biological stoichiometry theory claiming that biomass is limited by N needed to build proteins, in turn limited by the high P demands of ribosomes, and hence at low N and P concentrations, N becomes more critical. In any case, when both concentrations are low, the soil mineralization processes are limited (Hartman and Richardson, 2013). The high N:P ratios thus favor relatively low growth rate when N and P are low, and the low N:P ratios favor high relative growth rates and production activity when N and P are both abundant (Agren 2004). When flooding intensity was higher, some general trends in soil C and nutrient cycles appeared in all communities. For example, the concentration of soil NH_4^+ was higher and the concentration of NO_3^- was lower, but also differences in function of the plant species appeared. Under high flooding intensity, the plant:soil C and N ratios were higher in the *P. australis* community, were relatively stable in the *C. malaccensis* community and were lower in the *S. triqueter* community.

The total biomass of *S. triqueter* did not differ significantly between the high- and low-flood habitats. The total biomass of *P. australis* was significantly higher in the high-flood than the low-flood habitat. Moreover, biomass was significantly higher for *P. australis* than for *S. triqueter* and *C. malaccensis* in the high-flood habitats but only higher than for *S. triqueter* in the low-flood habitats. The higher *P. australis* biomass in the high-flood habitat was accompanied by lower soil-C content in upper soil layer. High flooding in the *C. malaccensis* community was associated with lower biomass and with lower soil-C content in upper soil layer, and high flooding in the *S. triqueter* community had no apparent effect on biomass but was associated with much higher levels of soil-C content. The *P. australis* community under high flooding intensity had more aboveground biomass (by aprox. 55%) than under low flood intensity whereas there was a slight lower soil C contents in the upper soil layers under high flooding intensity than under low flooding intensity showing that flooding tends to high overall C content in this ecosystem. Contrarily, in the *C. malaccensis* community, flooding enhancement was related to lower aboveground biomass (aprox 60%) and lower C contents in soil until 20 cm depth, showing a trend towards a lower of C content in this ecosystem related to flooding enhancement. In the *S. triqueter* community, flooding enhancement had no apparent effects on aboveground biomass but was related to higher soil C contents in all studied soil layers, showing a trend to higher C content under high flooding intensity than under low flood intensity in this ecosystem. These results show that flooding enhancement can favor the growth of *P. australis* and decrease that of *C. malaccensis*. The results thus suggest that further flooding enhancement will favor *P. australis* spread and higher accumulation of biomass and C per surface unit. Soil C input and respiration are frequently positively correlated (Dias et al., 2010; Carbone et al., 2011; De Deyn et al., 2011), indicating that soil respiration can be correlated with plant productivity (Caprez et al., 2012). This correlation can help to interpret our asymmetrical results of flooding enhancement in different species-community. The decrease of soil C content in high-flooding versus low-flooding observed under *C. malaccensis* could be related to the lower aboveground biomass and soil C concentrations observed in this species-community under high-flooding. The lower C concentration in upper soil layers observed in *P. australis* communities under high-flooding regime was more difficult to understand, and contrary to the expected. High N uptake capacity and N-use efficiency of this species has been observed in other study in this same estuary (Wang et al., 2014). Thus according with the previously commented relationships of plant productivity and soil biological activity, the most consistent explanation is that under high soil moisture, a greater N uptake capacity by higher N solubilization could favor aboveground biomass and thereafter plant capacity to improve mineralization processes (by root enzymes, exudates,..), fact that warrants future research.

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

5. Conclusions

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

Higher regimes of flooding favored the invasive species *P. australis* over the native species *C. malaccensis* and *S. triqueter*. *P. australis* was able to accumulate more N and C in its biomass, but the native species were not. This higher capacity of *P. australis* to tolerate increased flooding was associated with its higher capacity to take up N. The success of *P. australis* in other Chinese wetlands has also been associated with a more conservative and efficient use of N in these N-limited ecosystems.

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

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

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Table 1

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

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

Table 2

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

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

Figure captions

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

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

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

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

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

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

the community effect on plant biomass.

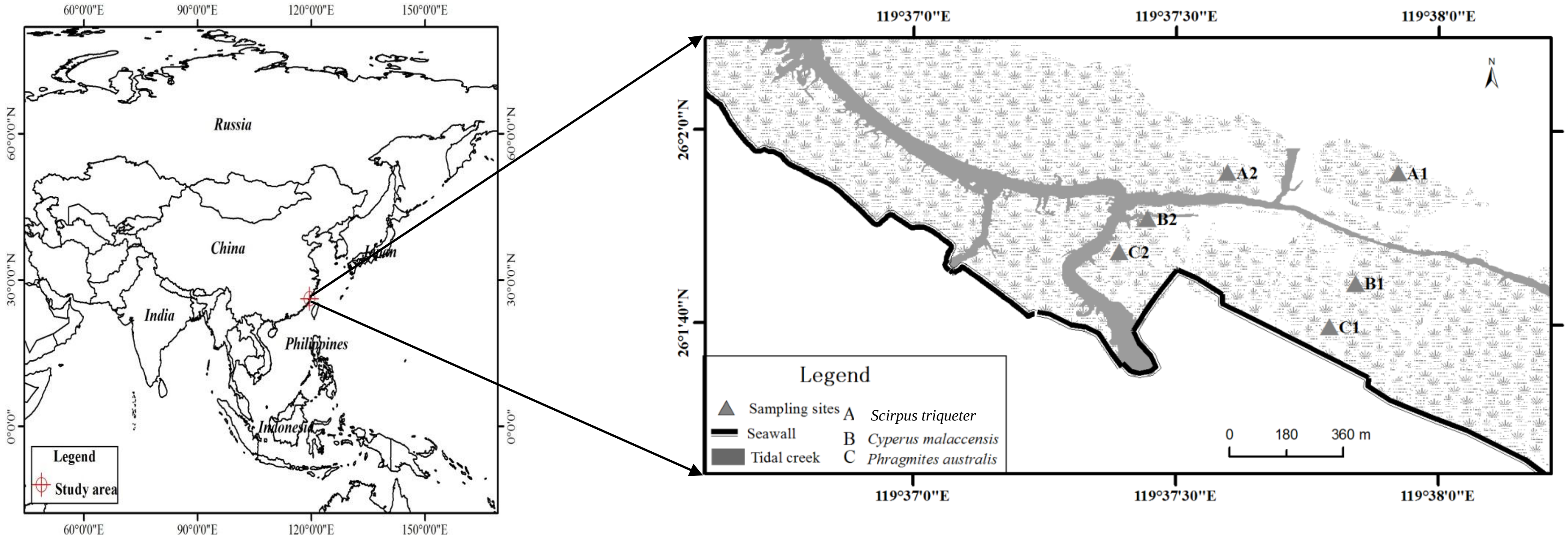
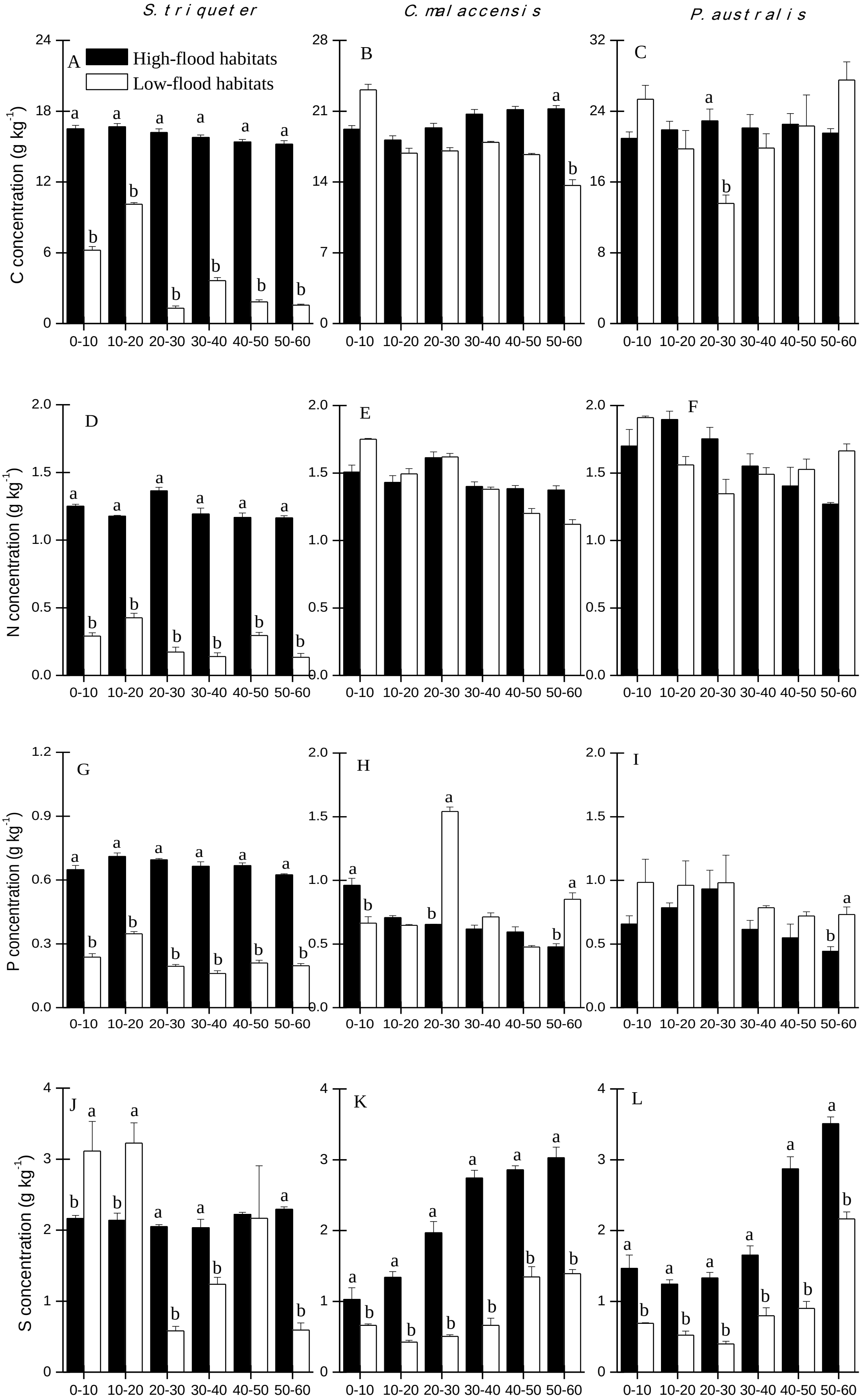

60°0'0"E
90°0'0"E
120°0'0"E
150°0'0"E
60°0'0"N
30°0'0"N
0°0'0"
Russia
China
Japan
India
Philippines
Indonesia
Legend
Study area
119°37'0"E
119°37'30"E
119°38'0"E
26°2'0"N
26°1'40"N
N
A1
A2
B1
B2
C1
C2
Legend
Sampling sites
Seawall
Tidal creek
A Scirpus triqueter
B Cyperus malaccensis
C Phragmites australis
0 180 360 m

Fig. 1


S. triqueter
C. malaccensis
P. australis
High-flood habitats
Low-flood habitats
A
B
C
D
E
F
G
H
I
J
K
L
C concentration (g kg-1)
N concentration (g kg-1)
P concentration (g kg-1)
S concentration (g kg-1)
0-10
10-20
20-30
30-40
40-50
50-60
0
6
12
18
24
7
14
21
28
8
16
24
32
0.0
0.5
1.0
1.5
2.0
0.3
0.6
0.9
1.2
1
2
3
4
a
b

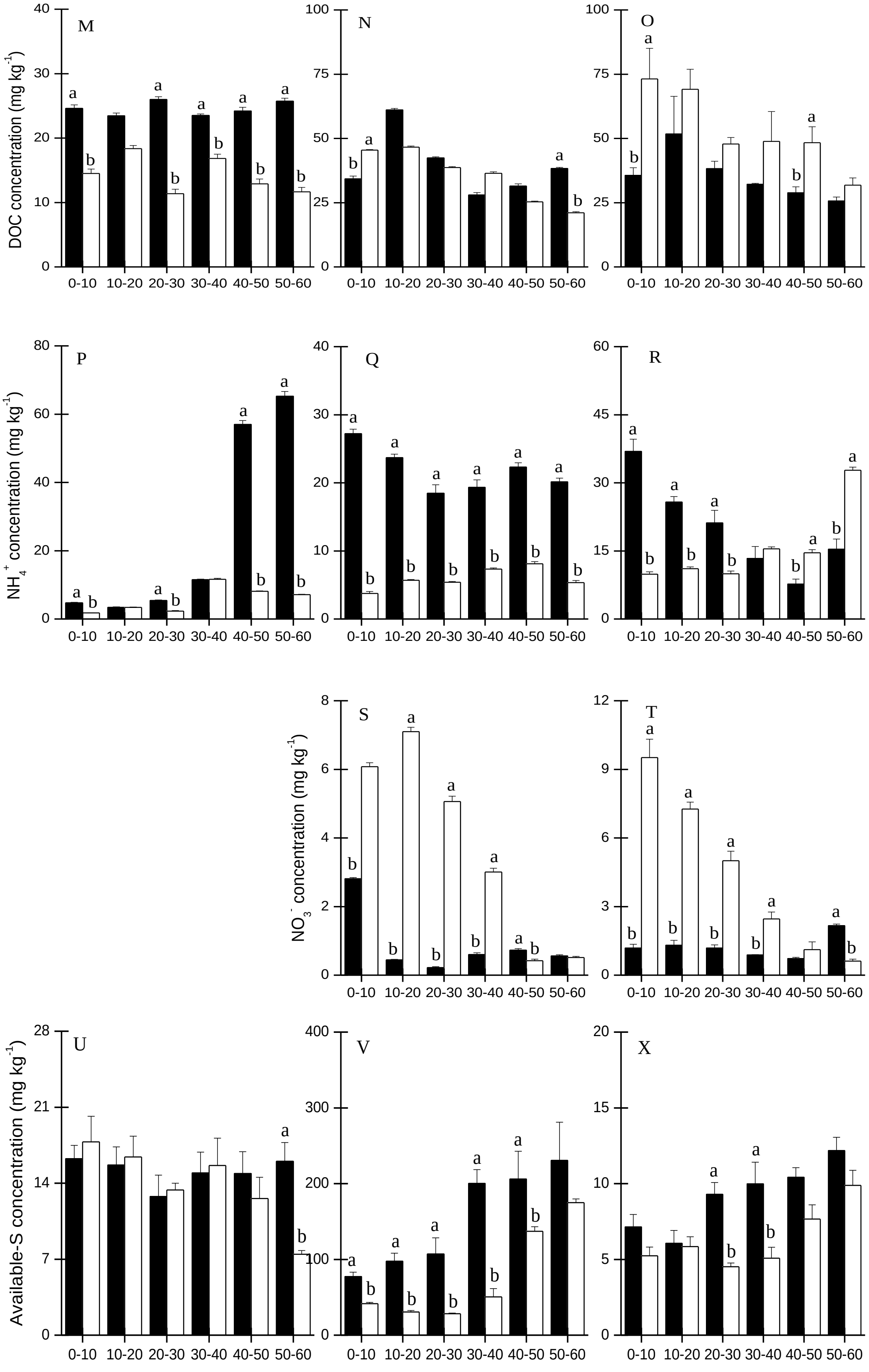
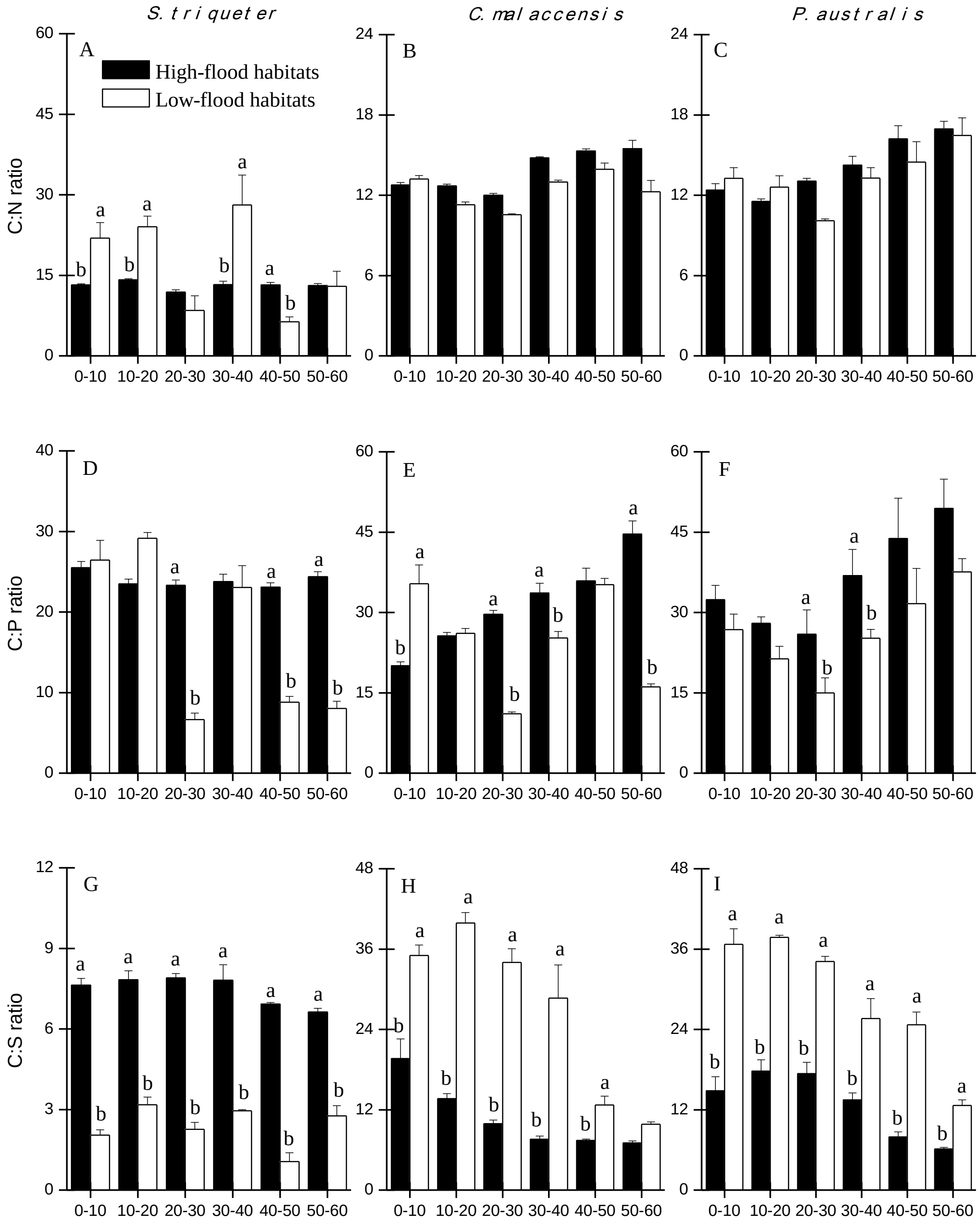

M
N
O
P
Q
R
S
T
U
V
X
DOC concentration (mg kg^{-1})
NH_4^+ concentration (mg kg^{-1})
NO_3^- concentration (mg kg^{-1})
Available-S concentration (mg kg^{-1})
0-10
10-20
20-30
30-40
40-50
50-60
Soil depth (cm)
0
10
20
30
40
25
50
75
100
60
80
15
45
2
4
6
8
3
9
12
7
14
21
28
200
300
400
5
a
b

Fig. 2

S. triqueter
C. malaccensis
P. australis
A
B
C
D
E
F
G
H
I
High-flood habitats
Low-flood habitats
C:N ratio
C:P ratio
C:S ratio
0-10
10-20
20-30
30-40
40-50
50-60

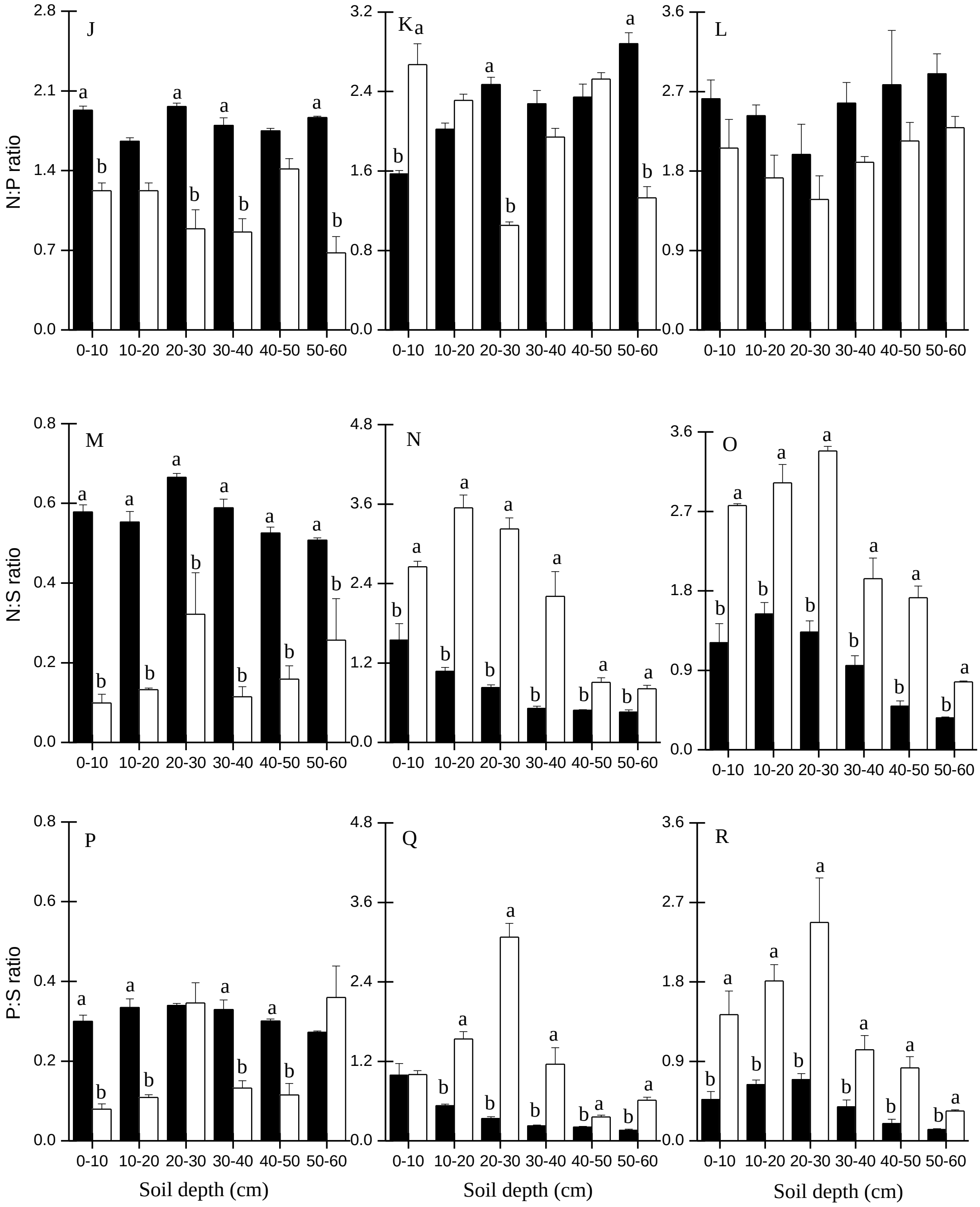

J
K
L
M
N
O
P
Q
R
N:P ratio
N:S ratio
P:S ratio
0.0
0.7
1.4
2.1
2.8
0.8
1.6
2.4
3.2
0.9
1.8
2.7
3.6
0.2
0.4
0.6
0.8
1.2
2.4
3.6
4.8
0-10
10-20
20-30
30-40
40-50
50-60
a
b
Soil depth (cm)

Fig. 3

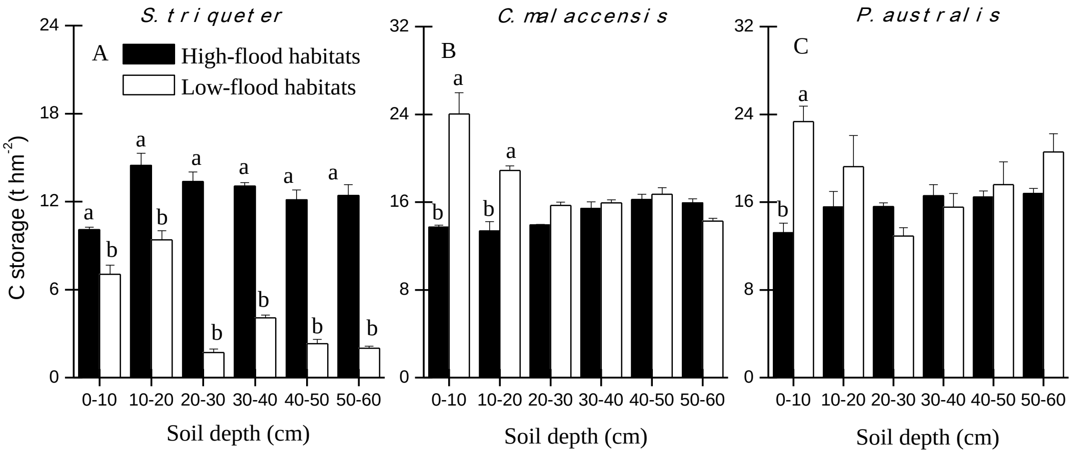

S. triqueter
C. malaccensis
P. australis
A
B
C
High-flood habitats
Low-flood habitats
C storage (t hm^{-2})
0
6
12
18
24
0
8
16
24
32
0
8
16
24
32
a
b
a
b
a
b
a
b
a
b
a
b
b
a
b
a
b
a
0-10
10-20
20-30
30-40
40-50
50-60
Soil depth (cm)
Soil depth (cm)
Soil depth (cm)

Fig. 4

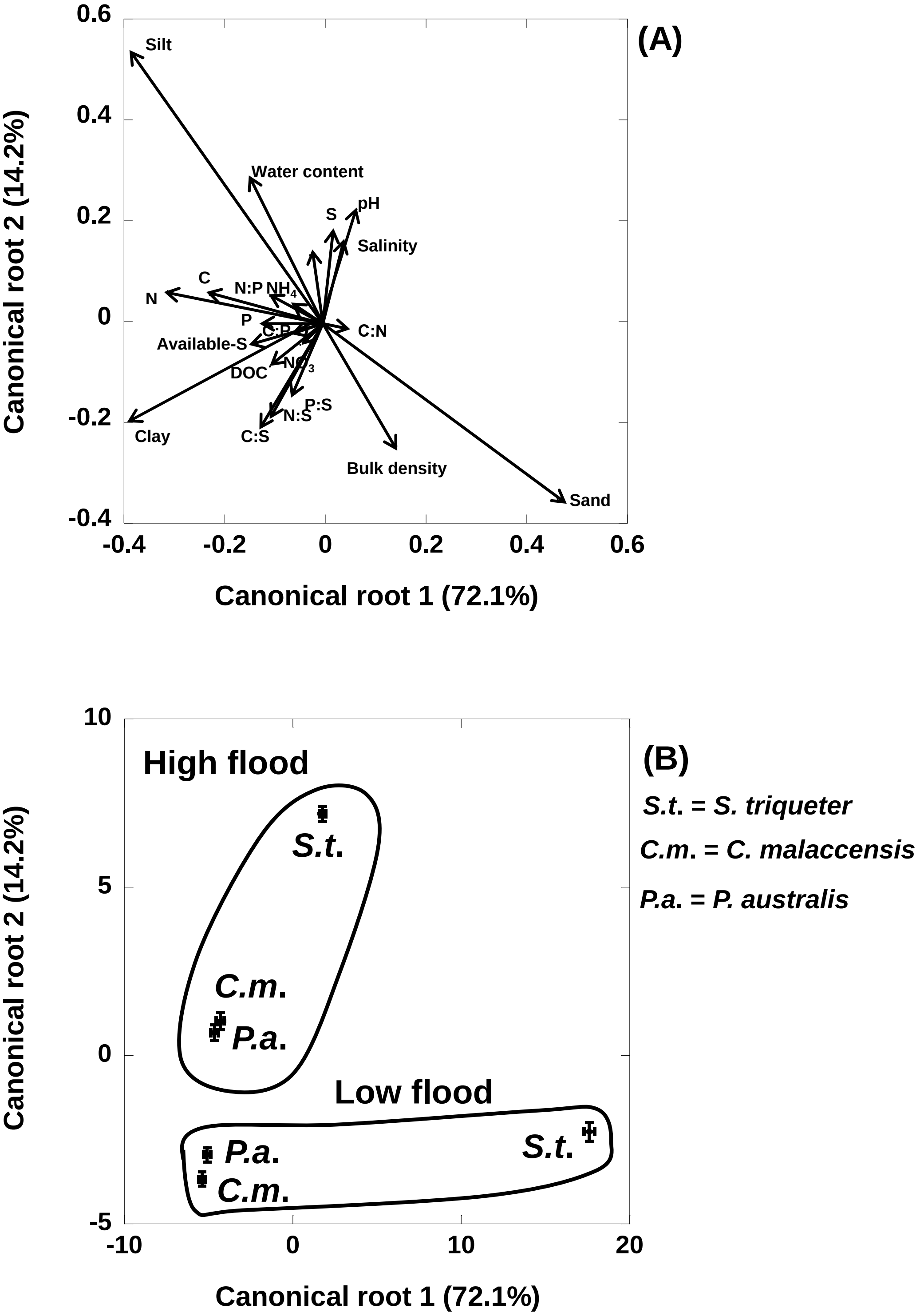

(A)
Silt
Water content
S
pH
Salinity
C
N
N:P
NH4
P
C:P
Available-S
C:N
DOC
NO3
P:S
N:S
C:S
Clay
Bulk density
Sand
0.6
0.4
0.2
0
-0.2
-0.4
-0.4
-0.2
0
0.2
0.4
0.6
Canonical root 2 (14.2%)
Canonical root 1 (72.1%)
(B)
S.t. = S. triqueter
C.m. = C. malaccensis
P.a. = P. australis
High flood
S.t.
C.m.
P.a.
Low flood
P.a.
C.m.
S.t.
10
5
0
-5
-10
0
10
20
Canonical root 2 (14.2%)
Canonical root 1 (72.1%)

Fig. 5

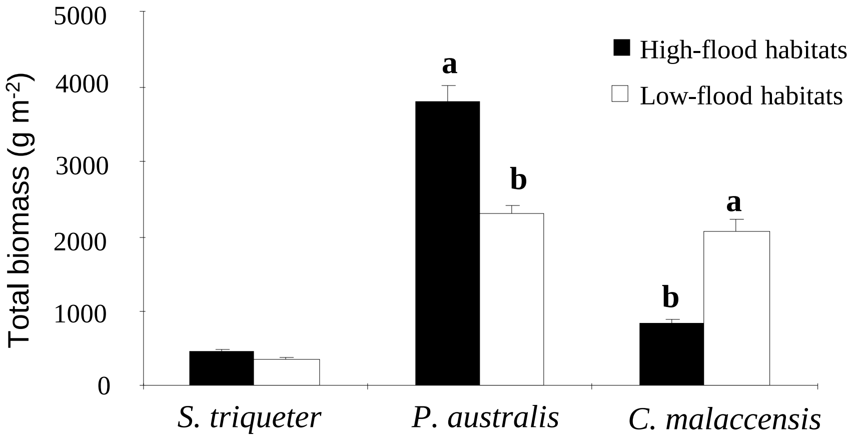

5000
4000
3000
2000
1000
0
Total biomass (g m-2)
■ High-flood habitats
□ Low-flood habitats
a
b
a
b
S. triqueter
P. australis
C. malaccensis

Fig. 6