Storage and release of nutrients during litter decomposition for native and invasive species under different flooding intensities in a Chinese wetland

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ABSTRACT

Projections of climate change impacts over the coming decades suggest that rising sea level will flood coastal wetlands. We studied the impacts of three intensities of flooding on litter decomposition in the native *Cyperus malaccensis*, and the invasives *Spartina alterniflora* and *Phragmites australis* in Shanyutan wetland (Minjiang River estuary, China). Invasive species had larger C, N and P stocks in plant-litter compartments and higher fluxes among plant-litter-soil, which increased with flooding intensity. The litter mass decay rates were correlated with the N:P ratio in remaining litter, consistently with the N-limitation in this wetland. *P. australis* had the highest N release rates (P<0.001) in all flooding intensities, whereas *C. malaccensis* had higher rates of N release than *S. alternifolia* but only at low flooding intensity. At high flooding intensity, the rates of N released (g m^{-2} y^{-1}) were 9.56±0.21, 2.38±0.18 and 1.92±0.03 for *P. australis*, *S. alternifolia* and *C. malaccensis*, respectively. The higher rates of nutrient release from litter decomposition in invasive species provided better nutrient supply during the growing season coinciding with the initial phases of decomposition. Thus, this study shows that invasive species may gain a competitive advantage over the native *C. malaccensis* under the projected scenarios of sea level rises.

Key words: Carbon; China; Climate change; Nitrogen; Phosphorus; Plant invasion; Sea level; Stoichiometry; Wetland.

1.Introduction

Coastal wetlands occupy 5.7 × 10^6 km^2 globally (3.6% of land surface) (Ramsar, 2013), and their soil organic matter and plants are sinks of C and nutrients. They are among the ecosystems most affected by global change (Ramsar, 2013). Several global change drivers, such as changes in land use (Wang et al., 2014; Wang et al., 2015a), species invasion (Wang et al., 2015b,c,d), climate change with the consequent rise in sea level and increased flooding (Schewe et al., 2011; Wang et al., 2016a,b) and/or changes in river flow (Bueh et al., 2003; Grafton et al., 2013) are affecting coastal wetland areas everywhere. Some of the detected consequences of these human driven impacts are the increasing storage of P in wetland areas (both coastal and inner) in industrial and/or intense cropland areas, mainly in emerging economical countries, such as China (Yan et al., 2016). The higher flooding and species invasion currently common in China coastal wetlands can aggravate this situation taking into account that several of these freshwater systems drive their P-rich waters to coastal wetlands. Despite wetlands have been considered a great sink of C, the magnitude of C stored in vegetated coastal systems has been decreasing rapidly over the past century due to human driven activities such as dredging, filling and timber harvest, and also by continuous agricultural expansion and sea level rise related to global warming (Hopkinson et al., 2012). This can be detrimental to global C store capacity since coastal wetlands are currently storing 208.4 C g m^{-2} y^{-1}, and this capacity could be compromised (Lu et al., 2017). These systems continue to be lost globally at rates ranging from 1-7% annually (Hopkinson et al., 2012). This is disturbing because inland wetland are also decreasing in several areas (Bai et al., 2007; Fraser et al., 2012; Dominguez-Beisiegel et al., 2013).

Higher sea levels would be especially critical for wetland ecosystems (Ramsar, 2013). Coastal wetlands occupy 1.2×10^4 km^2 in China (Shen and Zhu, 1999), and a higher sea level will increase flooding in the current coastal wetlands and create new wetlands farther inland. Most coastal areas in China, however, are protected by seawalls, so wetland areas cannot increase in size and will only decrease as the sea level rises (Yang et al., 2014). Changes of the flood conditions in turn can affect litter decomposition by changing the aerobic/anaerobic biogeochemical equilibrium and thereby nutrient inputs and outputs (Tong and Liu, 2009). We lack information, however, on the effect of the duration of daily flooding on litter decomposition and nutrient dynamics. Changes in litter mineralization by species invasion and/or flooding should be better known given the great link between litter decomposition and eutrophication in wetlands (Emsens et al., 2017; Grasset et al., 2017; Pan et al., 2017). Moreover, litter decomposition have a key role in plant growth (Fan et al., 2015) and species succession and community structure (Schrama et al., 2015) in wetlands.

Invasion by plant species in wetland areas has been associated with changes in soil condition, especially elemental composition and nutrient availability (Vourlitis et al., 2011; Wang et al., 2016). Moreover, flooding can affect species distribution and diversity and soil nutrient status (Machado et al., 2015; Wang et al., 2015b; Wang et al., 2016a). Invasive plant species have globally higher N and P concentrations in photosynthetic tissues but not in foliar litter, in comparison to their native competitors. Invasive plants are also associated with higher soil C and N stocks and N, P and K availabilities (Sardans et al., 2017. The differences in N and P concentrations in photosynthetic tissues and in soil total C and N, soil N, P and K availabilities between invasive and native species decreases when the environment is richer in nutrient resources. There are higher nutrient resorption efficiencies in invasive than in native species in nutrient-poor environments, whereas in nutrient-rich sites invasive species tend to take up more nutrients and accelerate plant-soil nutrient fluxes (Sardans et al., 2017). This potential impacts of plant invasion can vary and interact with this increase in flooding and also in a context of currently increasing nutrient loads in the wetland estuaries in countries as China.

Litter is an important pool of C and nutrients in terrestrial ecosystems (Poll et al., 2008; Adair et al., 2008) and is key to recycling in ecosystems by the decomposition of organic matter and release of nutrients (Peng and Liu, 2002). The rate of litter decomposition in wetlands affects the accumulation and retention of C and nutrients (Yin et al., 1994). More C and nutrients are released under faster decomposition rates (Tong and Liu, 2009). Moreover, the rise of nutrient release rates during litter decomposition increases soil activity and soil CO_2 emission, with the potential impact on global warming and water eutrophication (Hobbie et al., 2002; Zhang et al., 2014).The relationships of litter elemental composition and stoichiometry with litter decomposition depend on factors such as litter type, litter quality, climate and soil properties (Hättenschwiler and Jørgensen, 2010; Ott et al., 2012).

Some studies have investigated the impacts of species invasion on litter production and decomposition in riparian floodplain wetland forests, observing that invasive trees accelerate the litter decomposition rates (Bottollier-Curtet et al., 2011; Mitchell et al., 2011; Buzhdygan et al., 2016). Invasive species have also frequently higher litter production than native species (Ellis et al., 1998) and when the invasive species is a N_2-fixing accelerates N cycle (Buzhdygan et al., 2016). Moreover, Warren et al. (2001) studying the litter decomposition of the invasive *P. australis* and of their native competitors along a salinity gradient observed higher litter production in *P. australis*, but the elemental composition and nutrient release were not studied. The possible interactive effect of flooding and species invasion on the changes in litter elemental composition and stoichiometry and the rates of nutrient release during litter decomposition has not been studied in coastal wetlands. We consequently hypothesized that invasive plant species would decompose and release nutrients faster than the native ones, consistent with their higher rates of nutrient cycling via litter decomposition. This higher and faster nutrient cycling via litter decomposition for invasive versus native plants would probably change under different flooding intensities. We also hypothesized that the storage and release of nutrients during decomposition should be correlated with species invasion success and shifts in flooding intensity. Moreover, initial litter C:N:P stoichiometry and their shifts during litter decomposition should also be a key factor controlling the effect of flooding on decomposition.

The Gramineae C_4 species *Spartina alterniflora* Loisel., the Gramineae C_3 species *Phragmites australis* (Cav.) Trin. ex Steud. and the C_4 species *Cyperus malaccensis* var. brevifolius Boeckeler comprise much of the emergent macrophyte biomass in the Minjiang River estuary (Liu et al., 2006). Some stands of the native *C. malaccensis* have been invaded over the past 10 years by *S. alterniflora*, native to North America, and the past 30 years by *P. australis*, native to China but not to this area. The latter is now the most prevalent plant species in the wetland. Some studies have observed that the invasive success of *S. alternifolia* and *P. australis* have been associated with a higher N accumulation capacity in stand biomass linked to a higher biomass production and to a larger N resorption capacity than native species (Tong et al., 2011; Wang et al., 2015b, d). Recent meta data analyses have reported a general trend towards higher soil SOC nutrient concentration and availability related to invasive plant success (Sardans et al., 2017), coinciding with higher soil enzyme activity under invasive than under native plants (Aragon et al., 2015). We hypothesized that in this subtropical wetlands plant invasive success can be related with higher nutrient release from litter during growth period, and that the differences between native and invasive species could be conditioned by the level of flooding. The response of the decomposition and nutrient dynamics of the litters of the invasive and native species to the projected increase in flooding (IPCC, 2014), however, is not known. We should expect a drop in litter decomposition under higher flooding, but several compensatory mechanisms can change this trend. Schmidt et al., (2016) have recently reported a higher litter decomposition in litter decomposition under flooded-anoxic periods due to the higher activity of litter invertebrate activities (mesofauna) under flooded anoxic conditions. Moreover, the possible changes in litter decomposition rates under different plant species-specific communities can also be different. Furthermore, under higher flooding regimes the higher speed of water can contribute to accelerate decomposition by promoting higher physical breaking of litter increasing the surface of litter by mass ratio and thus facilitating the activity of decomposers (Langhans et al., 2008)..

Our general goal was to analyze how flooding rise can affect the C, N and P cycling and release capacity from litter in native and invasive species, and thus discern whether the projected increase in flooding intensity can affect native more than invasive species or vice versa. With this aim, we investigated (i) the changes in litter mass and the cycling of C and nutrients (the remaining in litter and the released from litter) for the litters of invasive and native plants in estuarine tidal wetlands under different flooding intensities (350, 1050 and 1760 hours y^{-1}), (ii) the relationships of litter nutrients cycling with litter elemental composition, and (iii) the possible role and/or relationships of soil C, N and P concentration with litter variables.

2. Material and methods

2.1. Study area

This study was conducted in the Shanyutan wetland (26°01′46″N, 119°37′31″E; Fig. 1), the largest tidal 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 (Wang et al., 2015b). The soil surface of the entire wetland is exposed at low tide, but the soil remains flooded at some depths, normally water table remains permanent from 20 cm of depth (Wang et al., 2015b). In the lowest tidal periods the minimum water table is about 20 cm below the ground. The average annual weight percentage of water in the soil potential is 116% [(soil wet weight - soil dry weight)/soil dry weight · 100] and the soil redox is + 12.6 mV, respectively (Wang et al., 2015b). The sea-walls have a height about 1.5 m, and the length of about 10 km along the Shanyutan wetland. the seawalls is located in the estuary and the coastal area, the function of the seawalls is to prevent the tide and storm surge preventing water invasion and flooding in inland

We studied and compared litter decomposition rates among three mono-specific stands: the native plant *C. malaccensis*, the invasive plant *S. alterniflora* (communities >10 years old) and the invasive plant *P. australis* (communities >30 years old). *S. alterniflora*, *P. australis* and *C. malaccensis* are the three dominant plant species in this estuarine wetland. They are typically found in the upper (mid to high) portions of mudflats. *S. alterniflora* is an invasive plant. Both *S. alterniflora* and *P. australis* mainly invaded the native *C. malaccensis* wetland, typically found in the upper (mid to high) portions of mudflats. Three species are located in sites with similar flooding intensity, but despite this, wetland soils in areas dominated by *S. alterniflora* and *P. australis* generally have a lower pH and bulk density and a higher salinity than do areas dominated by *C. malaccensis* (Jia et al., 2008). *S. alterniflora* grows between April and December, the highest population height is about 2.3 m, and the shoot density is about 300 m^{-2} (Zhang, 2008). *P. australis* grows between April and October, the highest population height is about 2 m, and the shoot density is about 250 m^{-2} (Zhang, 2008). *C. malaccensis* grows between April and October, the highest population height is about 1.5 m, and the shoot density is about 1000 m^{-2} (Zhang, 2008). *C. malaccensis* grows between April and October, the highest population height is about 1.5 m, and the shoot density is about 1000 m^{-2} (Zhang, 2008). The root systems of the three species have similar biomass distributions in the soil profiles, all with substantial biomass below 50 cm but with larger biomass fractions in the 0-15 cm soil layer (Tong et al., 2011)

2.2. Experimental design

C. malaccensis, *S. alterniflora* and *P. australis* litter was collected in February 2012. Three replicates of 20 g of each litter were placed in tightly sealed nylon mesh bags, 20 cm long and wide with a mesh size of 0.3 mm, and allowed to decompose (Wang et al., 2016b). The litter was a mixture of foliar and stem litter in the ratios corresponding to annual foliar:stem litter production ratios of each species. To know the exact proportion of leaf and stem litter in each species, we separated the leaves and the stems litters of each plant to thereafter weigh them. The litterbags were anchored to the substrate and only one side of litterbags contact with the ground. The experiment began in March 2012. Three flooding intensities (low, high and continuous) were tested with the *C. malaccensis*, *S. alterniflora* and *P. australis* litters, decomposing under *C. malaccensis*, *S. alterniflora* and *P. austr*alis habitats respectively and in three different flooding intensities. The three levels of flooding intensity were 350, 1050 and 1760 h y^{-1} for low, high and continuous flooding intensity, respectively. The distance between pure-species stands of different plant species for the same flooding intensity level was smaller than 20 m. The sampled areas were at a minimum distance of 100-150 m among them (Fig. 1). In the lowest tidal periods the minimum water table is located about 20 cm below the ground. Samples were collected from the bags 28, 61, 80, 101, 141, 181, 241, 298 and 370 d after the start of the decomposition experiment. In each sampling time the whole bag was removed from each site. We thus had 3 flood conditions × 3 species × 9 time samplings × 3 replicates=243 samples.

2.3. Sample collection and analysis

The litter from the sample bags was gently washed with water and then oven dried to a constant weight (60 °C for 24-36 h), weighed and then finely ground in a ball mill. The concentrations of C and N of the litters were determined using a Vario EL III Elemental Analyzer (Elementar Scientific Instruments, Hanau, Germany). P concentration of the litters were measured using the molybdate-blue reaction (Lu, 1999) with a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan).

2.4. Soil analyses.

Soil samples were collected in February 2012 in the Shanyutan wetland from communities dominated by *C. malaccensis*, *S. alterniflora* and *P. australis*. Three plots were randomly established in each community. The samples were collected with a small sampler (length, 0.3 m; diameter, 0.1 m) from each of two soil layers (0-10 cm) at the center and both ends of the soil pits. These three samples from each layer were bulked to form one sample per layer. The core samples were air-dried and finely ground in a ball mill after the removal of all roots and visible plant remains for the determination of total soil organic carbon (SOC) concentration, total N and P concentrations, salinity and pH.

Total SOC was determined by $K_2Cr_2O_7$-H_2SO_4 digestion. Total soil N concentration was determined by total Kjeldahl digestion (Buchi Scientific

Instruments, Flawil, Switzerland), and total soil P concentration was determined by perchloric-acid digestion followed by ammonium-molybdate colorimetry and measurement using a UV-2450 spectrophotometer. Soil salinity and pH were measured by a DDS-307 salinity meter (Boqu Scientific Instruments, Shanghai, China) and an 868 pH meter (Orion Scientific Instruments, Waltham, Massashusetts, USA), respectively..

2.5 *Data analysis*

1. Litter mass remaining (%) was calculated by the litter remaining mass / initial litter mass *100%

2. C, N, P remaining in residual litter (%) was calculated by (the litter remaining mass *C,N,P concentration in residual litter) / (initial litter mass *C,N,P concentration in initial litter) *100%

3. C, N, P amount remaining in residual litter (g m^{-2}) was calculated by (the litter remaining mass *C,N,P concentration in residual litter) / (initial litter mass *C,N,P concentration in initial litter) *100%* Actual litter production in situ (g m^{-2})

4. C, N, P ratio was calculated by the litter C ,N,P concentration in initial and residual litter (mass ratio)

5. Accumulated released of C, N, P (g m^{-2}) from litter was calculated as (initial litter mass *C,N,P concentration in initial litter) _- (the litter remaining mass

*C,N,P concentration in residual litter) *100%* Actural litter production in situ (g m^{-2})

6. Accumulated released of C, N, P ratio (g m^{-2}) from litter was calculated as (initial litter mass *C,N,P ratio in initial litter) _- (the litter remaining mass *C,N,P ratio in residual litter) *100%* Actual litter production in situ (g m^{-2}).

We determined thee litter mass loss and the C, N and P concentrations remaining so we can calculate the total amount of C, N and P in the remaining litter. This also allows to know the released amount of C, N and P concentrations and ratios of C, N and P in the part of litter released (mineralized).

2.6. Statistical analyses

We analyzed the effects of species (*C. malaccensis*, *S. alterniflora* and *P. australis*), intensity of flooding (low, high and continuous) and time as fixed factors and litter bag replicates as random factor on the studied response variables by using general linear and generalized mixed models. The dependent analyzed variables were elemental concentrations and ratios of the litter, the relative (% from initial) and absolute amounts of C, N and P that still remains in litter, the relative (% from initial) and absolute amounts of C, N and P that have been released from litter, and the C:N, C:P and N:P ratios of the absolute amounts released in each sampling moment during one year of litter decomposition. We used the "nlme" (Pinheiro et al., 2016) and "lme4" (Bates et al., 2015) R packages with the "lm", "lme", "glm" and "glmer" functions.

We chose the best model for each dependent variable using R^2-adjusted in the case of lm models and Akaike information criteria in the case of glm and glmer models. We used the MuMIn (Barton, 2012) R package in the mixed models to estimate the percentage of variance explained by the model.

We performed multivariate statistical analyses using general discriminant analysis (GDA) with litter elemental concentrations and ratios, and the relative (% from initial) and absolute amounts of C, N and P remaining t that still remains in litter, the relative (% from initial) and absolute amounts of C, N and P that have been released from litter, and the C:N, C:P and N:P ratios of the absolute amounts released in each sampling moment during one year of litter decomposition as independent factors and with time as categorical controlling factor to determine if the overall differences of these variables separated the various flooding intensities and plant species used as dependent variables. We also determined the variance due to time as an independent categorical variable. The GDAs were performed using Statistica 6.0 (StatSoft, Inc. Tulsa, USA). C:N, C:P and N:P ratios were calculated as mass ratios.

3. Results

Litter mass and C, N and P contents remaining in the litter decreased by about 50% during the first 50 days of decomposition (Figs. 2, 3). Flooding intensity generally had a slight effect on the percentage of C, N and P remaining relative to the initial contents during decomposition (Table 1, Fig. 2, 3). Under lower flooding, *C.*

malaccensis had the lowest % of the C, N and P contents remaining after the first year of decomposition but this difference with respect the invasive species disappeared at high and continuous flooding intensity. Under continuous flooding intensity, *P. australis* had lowest % of the N contents remaining after the first year of decomposition (Table S1, Fig. 2, 3). Whereas the initial concentrations of C were initially similar in the litter of the 3 species, the initial concentrations of N were lowest in *S. alternifolia* and the initial concentrations of P were highest in *P. australis* than in the other two species, respectively (Fig. 4 and 5). The C amount remaining and released of C during the studied year and the final C accumulated released were similar in the three species (Fig. 4 and 5). *C. malaccesis* released less C, N and P under a year of decomposition at high and continuous flooding than under low flooding, fact did not observe in both invasive species (Fig. 5). *C. malaccensis* released more N than both invasive species under low flooding intensity whereas *P. australis* released more N under continuous flooding intensity and more P under all flooding intensities than the other both species (Fig. 5). Thus, existed a significant trend in *C. malaccensis* in decreasing the C, N and P release with higher flooding intensity, which was instead not observed in the two invasive species.

Litter C concentrations were significantly higher ($P<0.001$) with respect initial C concentrations after one year of decomposition for all species and flooding environments (Fig. 6). Litter C:N concentration ratios tended to decrease slightly for all species and flooding intensities during decomposition (Fig. 7). The litter C:P concentration ratios first increased, then decreased and increased again during the last 100-150 days for several situations but with the degree depending on the species (Fig. 7). The litter N:P concentration increased during the last 130 days in all three species, mainly under the low- and high-flooding intensities (Fig. 7). The litter N:P ratios in the three species were thus lower in the low-flooding than in the high- and continuous-flooding intensities by the end of the year. The accumulated released C:N, C:P and N:P ratios consequently had the opposite patterns (Fig. S1). The mass remaining was correlated positively with litter C:N ($R=0.54$, $P<0.0001$) and C:P ($R=0.33$, $P<0.0001$) ratios and negatively with litter N:P ratios ($R=-0.28$, $P<0.0001$) during decomposition (Table S2). Furthermore, the analysis of all the data of the absolute contents of C, N and P released after one year of decomposition indicated a general trend of flooding intensity to decrease the release of C, N and P (Table S1).

Comparing the three studied species we observed that the native *C malaccensis* decomposing litter at low-flooding intensity had the lowest % of initial litter mass, C and N concentrations remaining along the 370 days of litter decomposition than invasive species (Table 1, Fig. 2, 3). But these relative faster rates of litter decomposition of *C. malaccensis* at low-flooding were not observed at high- and continuous-flooding intensities (Table 1, Fig 2, 3). Under continuous flooding intensity, the % of initial litter N contents remaining was lowest in *P. australis* than in the other two species communities, and the % of initial P contents remaining were lower in both invasive species than in the native *C. malaccensis* (Fig. 2, 3).

The litter of the native *C. malaccensis* released more C, N and P under the low- than high- and continuous-flooding intensities (Table 1, Fig. 5). This did not happen in the two invasive species.

The invasive *P. australis* produced the most litter (Wang et al. 2015c), which was able to decompose faster and release more C, N and P during decomposition. These findings were observed in absolute terms at all flooding intensities, due to the higher initial contents of the litter, but also in relative terms (lowest % of N initial contents) in continuous-flooding intensity (Table 1, Figs. 2-5). The release of total C, N and P (g released) from the *P. australis* litter was nonetheless less affected by the increases in flooding, followed by *S. alterniflora*, the other invasive species. Thus, *C. malaccensis* had the lowest litter production and capacity to release C, N and P and was most negatively affected by increases in flooding intensity (Table 1, Figs. 2-5). *C. malaccensis* released more N (g) during decomposition than *S. alterniflora* under the low-but not under the high- and continuous-flooding intensities (Fig. 5).

Litter N concentrations for *P. australis* after one year did not differ significantly from the initial concentrations. P litter concentrations in the two invasive species initially tended to remain constant but decreased during the last 140 days for all flooding intensities. Litter P concentration for the native *C. malaccensis* fluctuated more during decomposition and was highest in the low-flooding environment (Fig. 6). The initial litter C:N ratio was highest in *S. alterniflora*, followed by *P. australis* and *C. malaccensis* (Fig 7).The initial litter C:P ratio was lowest in *P. australis* and similar between *S. alterniflora* and *C. malaccensis* (Fig. 7). The initial litter N:P ratio was highest in *S. alterniflora*, followed by *P. australis* and *C. malaccensis*. The ratios were higher by the end of the year for all situations, except for the litter from *C. malaccensis* under the low-flooding intensity.

All species under different flooding intensities were separated among them by the GDA model with mass remaining (MR); litter C, N and P concentrations; C:N, C:P and N:P litter concentration ratios; the percentage of initial amounts of C, the C:P and N:P ratios of the accumulated release from litter, soil salinity, pH and C, N and P as the most significant variables in the GDA model (Tables 1 and 2). Soil strongly loading root 1 (explaining the 78.5% of the total variance), separated the different levels of flooding. Continuous flooded soils had the highest soil P concentrations and the lowest values of C and N concentration and salinity, whereas low flooded soils had the contrary patterns and high flooded soils the intermediate position (Fig. 8). Different species were separated along root 2 (explaining 16% of the total variance) and mainly loaded with litter variables. The litter N and P concentrations were highest and C concentrations lowest in soils under *C. malaccensis*, whereas the contrary patterns were observed in *S. alternifolia* litter with *P. australis* litter in intermediate position. (Fig. 8).

4. Discussion

4.1. Changes in mass, C and nutrients released during litter decomposition of the *three species associated to flooding intensity rises*

The impact of flooding intensity on litter elemental composition and the amounts of C, N and P released and remaining during decomposition was species-specific. Flooding had scarce effects on litter rates of C, N and P release in both invasive species but had a negative effect on litter rates of C, N and P release during the 370 first days of decomposition in native species. Under low-flooding intensity *C. malaccensis* had a higher relative (%) from initial but not absolute (g) release of C, N and P, whereas at high-flooding intensity both invasive species had higher relative (%) and absolute (g) release of P and *P. australis* had also higher relative (%) and absolute (g) release of N. As a result, the litter production of *P. australis* was much higher (remember that the quantity of litter in bags was proportional to litter production of each species) and both invasive species increased the decomposition rates under flooding, they both released higher amounts (g) of C, N and P during litter decomposition, except for N that under the low-flooding intensity was released more under *C. malaccensis* than under *S. alterniflora*. Invasive species had thus similar or even higher rates of C, N and P release during decomposition with higher flooding intensities, whereas the native *C. malaccensis* had the opposite trend. *S. alternifolia* and mainly *P. australis* released more N and P from their litter during the growing season than the native species. This higher rates of litter decomposition and nutrient release were accompanied in both invasive species by higher accumulations of C, N and P, in agreement with the general trend observed in previous studies at various regions (Sardans et al., 2017).This should confer to both invasive species a competitive advantage in an environment where at least one nutrient, N, is limiting in this wetland area (Wang et al., 2015 b,d), and this advantage increased with flooding intensity. The first half of the studied period of litter decomposition, however, coincided with the growing season, so the higher release of N and P in invasive than native species made even more evident the competitive advantage of invasive species.

All these results are consistent with the previous studies conducted in this same wetland area of the estuary of Minjiang River. Despite in this area a previous study observed that *C. malaccensis* had higher root production than *P. australis* (Wang et al., 2015c), in this wetland the overall biomass was higher in *P. australis* and *S. alterniflora* than *C. malaccensis* (Wang et al., 2015b; Tong et al., 2011). Moreover, litter production along the studied area was highest for the invasive *P. australis* (1450 g m^{-2} y^{-1}) followed by *C. malaccensis* (747 g m^{-2} y^{-1}) and *S. alternifolia* (653 g m^{-2} y^{-1}) (Zhang, 2008; Wang et al., 2015c,d). Our experimental results were also consistent with the observed advantage in biomass production and nutrient and C accumulation in biomass of *P. australis* at higher flooding intensities relative to *C. malaccensis* in a previous study in nearby wetland areas of the same river delta (Wang et al., 2015c). This study also reported that the invasive *P. australis* accumulated more C (65% increase in aboveground biomass) and took up more N under high flooding (Wang et al., 2015c). Our results also support the faster decomposition of *P. australis* litter in the Yellow River Delta under long-term than intermediate- and short-term flooding reported by Zhao et al. (2015). A previous study also reported similar findings comparing C, N and P concentrations in soils and in leaves, stems and roots of the invasive species *S. alterniflora* with those of the native species *C. malaccensis* in nearby wetland areas (Wang et al., 2015d). N-resorption capacity, N:P ratios in stems and roots, biomass, absolute growth and biomass N were higher and relative growth rate and litter production were lower in *S. alterniflora* than *C. malaccensis*. The soil C and N concentrations were higher for *S. alterniflora* than *C. malaccensis*, indicating that a conservative strategy, a high N-use efficiency and internal plant control of the N in the ecosystem underlie the invasive success of *S. alterniflora* in this N-limited wetland (Wang et al., 2015d).

The higher litter production and absolute higher release of C, N and P but lower release of C, N and P relative to the initial litter amounts for *P. australis* than the native species under the low-flooding intensity has also been observed in other wetlands (Rothman and Bouchard, 2007). *P. australis*, however, is also able to release amounts of C, N and P similar to the initial litter amounts under high and continuous flooding. Successful invasive species frequently have higher capacities to release N and P due to their faster N and P cycles (Chen et al., 2007; Eppinga et al., 2011) or to higher N and P stocks and fluxes (Windham and Ehrenfeld, 2003; Rothman and Bouchard, 2007) than native species, even though the higher stocks and fluxes of the invasive species have been associated with lower rates of litter decomposition (Liao et al., 2007) than the native species.

In wetland areas with limited water movement, for example with no tidal dynamics or little tidal importance such as in Mediterranean wetlands, an increase in flooding can decrease decomposition, because the higher water availability can initially increase microbial activity and thereby decrease oxygen content and thus slow decomposition (Sanmarti and Menedez, 2007). However, in the studied subtropical coastal wetland, the rapid turnover of water with large daily movements by strong tides should, however, prevent anoxic conditions. Water turnover is positively correlated with the rates of N and P release from litter (Lee and Kim, 2014). High fungal activity during the decomposition of *P. australis* litter, even in submerged conditions (Kominkova et al., 2000), may account for the lack of a negative effect on the rates of decomposition in this species. For some wetland species, flooding can frequently increase the rates of the initial leaching phase of decomposition and the acceleration of overall litter decomposition during subsequent immobilization phases (Neckles and Neill, 1994; Sun et al., 2012). Our results are consistent with those of most previous studies showing that flooding has an important role, but less than species, in the rates of C, N and P release during decomposition and that this role is species-specific, being the slowing nutrient release from litter higher in native than in invasive species.

4.2. Wetland C and nutrient cycles

Despite this higher release of C, N and P by the invasive species, mainly at the high- and continuous-flooding intensities, taking into account the higher production of litter (g m^{-2}) in *P. australis* the total absolute value after a year of decomposition should be similar and in some cases higher, e.g. for P under the intermediate- and continuous-flooding intensities, than in the other two species due to its commented higher litter production. Our results thus suggest that this wetland area would continue to retain nutrients (also with higher biomass and litter production) if *C. malaccensis* were replaced by the invasive species, and mainly by *P. australis*. The large capacity and importance of wetland areas to filter nutrients between river and ocean water (Kao et al., 2003) has become an important issue, especially in a region such as southern China where rivers transport large amounts of N and P from human activities such as intensive agriculture. We observed that the studied soil variables such as total soil P and N concentrations did not change under different species but only under different level of flooding. Thus, in spite of litter accumulated more C, N and P after one year of decomposition under both invasive species in all flooding intensity conditions, at this moment after 10-30 years of invasion success total soil P and N concentrations have not changed significantly. The results suggest that, in the projected scenarios of rises in sea level in which most of the remaining coastal wetlands of the main China estuaries come under progressively higher flooding intensities, invasive species such as *S. alterniflora* and *P. australis* can gain an even more competitive advantage over the native *C. malaccensis* by its better nutrient supply from the decomposition of their litter.

4.3. Wetland stoichiometry and litter decomposition

At stoichiometrical level, the fresh litter N:P ratio in our study, 10-15, clearly suggested N-limitation. Güsewell and Verhoeven (2006) reported an initial litter N:P threshold on a mass basis of ~25 between N- and P-limited decomposability for grasses. In fact the litter N:P increased for all species and flooding intensities during decomposition, with N concentrations tending to continuously increase and P concentrations to remain more or less constant, suggesting that the microbial decomposers retained proportionally more N than P. The analysis of all data (including all species and flooding intensities) indicated that the litter concentrations of N and P were negatively correlated with the mass remaining in the litter, showing that litter with higher N and P concentrations decomposed faster. This relationship, however, was stronger for N than P, and the mass remaining was negatively correlated with the litter N:P ratio. Litter proportionally richer in N than P thus decomposed faster, consistent with the limiting role of N in decomposition previously reported for this area. The accumulation of a nutrient in litter during its decomposition is a good proxy for detecting its limiting role in this biological process (Davis et al., 2003: Güsewell and Verhoeven, 2006). Our results are thus consistent with the importance attributed to the C:N:P ratios of litter for the rates of N and P release during litter decomposition in wetlands (Relmankova and Houdkova, 2006; Güsewell and Freeman, 2005; Manzoni et al., 2010; Sun et al., 2012). Results are consistent with the higher soil P concentrations observed under continuous flooding site because of the litter N:P ratio of litter remaining increase less than under low and intermediate levels of flooding. Then the higher P retention in litter under continuous flooding was associated with higher soil P concentrations under continuous flooding. Moreover, both invasive species had higher C, N and mainly P remaining in litter than the native species. All these results suggest a trend towards higher P accumulation in soils of wetlands if increases the proportion of areas with higher flooding intensity and also the proportion of areas occupied by both invasive species.

5. Conclusions and final remarks

Changes in species composition due to flooding and the arrival of invasive species can thus change the N:P ratio of the plant soil-system throughout decomposition, which may contribute to the global changes in N:P ratios observed in several ecosystems mainly due directly or indirectly to human activities (Peñuelas et al., 2012, 2013) specially in water ecosystems of intense industrial and cropland areas of economical emerging countries (Yan et al., 2016). The results suggest that invasive species such as *S. alterniflora* and *P. australis*, which are already widely distributed, can gain a greater competitive advantage over the native *C. malaccensis* by their better nutrient supply from the decomposition of their litter in high flooding conditions. This should be more probable in the projected scenarios of rises in sea level in which most of the remaining coastal wetlands of the main China estuaries come under progressively higher flooding intensities. This advantage would also be augmented by the higher rates of N and P release in the initial phases of litter decomposition during the growing season, the season with higher demands for N and P. The results highlight the importance of the interactions among the different global change drivers, here species invasion and rise in sea level that according to our results should act accelerating the invasive success against native species. In this case invasive species with higher size and capacity to store N and probably other nutrients take advantage of the increases in flooding intensity. This should provide a higher wetland capacity to act as N and P and probably C sinks, thus preventing eutrophication of coastal areas and helping to mitigate atmospheric CO_2 rising, but also should accelerate the wetland silting and disappearance of native species in wide areas.

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Tables

Table 1.

Linear, mixed and generalized models of the changes in litter elemental composition and released composition during the year of decomposition. The best model was based on the assumption of the normality and homogeneity of residual distributions using Akaike information criteria. Empty boxes corresponding to interactions mean that this interaction was not significant and had been not included in the corresponding analysis.

Dependent variable	**Model**	R^2	**AIC (Akaike value) of the model**	**Independent variables**							
				Fixed							**Random**
				Sp	**Fl**	**T**	**Sp × Fl**	**Sp × T**	**Fl × T**	**Sp × Fl × T**	**Litter bag replicates**
Mass remaining (% initial)	**lm**	**0.66**		**F = 1.54 df = 2 *P* = 0.22**	**F = 0.32 df = 1 *P* = 0.72**	**F = 508 df = 1 *P* < 0.0001**					**No**
Mass remaining (g m^{-2})	**glm**	**0.99**	**3475.5**	**F = 304 df = 2 *P* < 0.0001**	**F = 0.45 df = 1 *P* = 0.64**	**F = 845 df = 1 *P* < 0.0001**		**F = 8.9 df =4 *P* = 0.0002**	**F = 6.4 df =2 *P* = 0.002**		**No**
[C] in remaining litter	**lm**	**0.27**		**F = 15.6 df = 2 *P* < 0.0001**	**F = 5.57 df = 1 *P* = 0.0043**	**F = 59.6 df = 1 *P* < 0.0001**					**No**
[N] in remaining litter	**lm**	**0.82**		**F = 213 df = 2 *P* < 0.0001**	**F = 5.4 df = 1 *P* = 0.005**	**F = 644 df = 1 *P* < 0.0001**	**F = 5.85 df =2 *P* = 0.0002**	**F = 32.6 df =4 *P* < 0.0001**	**F = 4.61 df =2 *P* = 0.011**		**No**
[P] in remaining	**lme**	**0.20**	**-19.62**	**F = 11.6**	**F = 7.64**	**F = 0.24**	**F = 6.17**		**F = 5.08**		**Yes**

litter				df = 2 *P* < 0.0001	df = 1 *P* < 0.0001	df = 1 *P* = 0.62	df =2 *P* = 0.0024		df =2 *P* = 0.0069		
C:N in remaining litter	lm	0.69		F = 147 df = 2 *P* < 0.0001	F = 10.8 df = 1 *P* < 0.0001	F = 248 df = 1 *P* < 0.0001	F = 8.73 df =2 *P* < 0.0001				No
C:P in remaining litter	lm	0.21		F = 10.5 df = 2 *P* < 0.0001	F = 5.33 df = 1 *P* = 0.0054	F = 4.25 df = 1 *P* = 0.040	F = 8.26 df =2 *P* = 0.00035		F = 6.88 df =2 *P* = 0.0012		No
N:P in remaining litter	lm	0.59		F = 15.1 df = 2 *P* < 0.0001	F = 24.0 df = 1 *P* < 0.0001	F = 258 df = 1 *P* < 0.0001			F = 23.1 df =2 *P* < 0.0001		No
C amount remaining (% initial)	lm	0.70		F = 3.13 df = 2 *P* = 0.038	F = 0.177 df = 1 *P* = 0.84	F = 577 df = 1 *P* < 0.0001			F = 3.25 df =2 *P* <= 0.040		No
N amount remaining (% initial)	lme	0.39	2287.8	F = 3.52 df = 2 *P* = 0.031	F = 1.17 df = 1 *P* = 0.32	F = 159 df = 1 *P* < 0.0001					Yes
P amount remaining (% initial)	lm	0.43		F = 1.49 df = 2 *P* = 0.23	F = 0.78 df = 1 *P* = 0.46	F = 198 df = 1 *P* < 0.0001					
C amount remaining (g m^{-2})	glm	0.98	3018.6	F = 343 df = 2 *P* < 0.0001	F = 0.213 df = 1 *P* = 0.81	F = 874 df = 1 *P* < 0.0001	F = 9.45 df =2 *P* = 0.00011		F = 7.14 df =2 *P* = 0.00096		
N amount	lme	0.70	905.83	F = 151	F = 1.7	F = 27.8		F = 32.0			Yes

remaining (g m^{-2})				**df = 2** ***P* < 0.0001**	**df = 1** ***P* = 0.19**	**df = 1** ***P* < 0.0001**		**df = 4** ***P* < 0.0001**			
P amount remaining (g m^{-2})	**glmer**	**0.73**	**273.63**	**F = 70.8** **df = 2** ***P* < 0.0001**	**F = 4.69** **df = 1** ***P* = 0.01**	**F = 127** **df = 1** ***P* < 0.0001**	**F = 8.3** **df = 2** ***P* < 0.0001**				**Yes**
C amount released (g m^{-2})	**lm**	**0.93**		**F = 792** **df = 2** ***P* < 0.0001**	**F = 1.8** **df = 1** ***P* = 0.19**	**F = 1167** **df = 1** ***P* < 0.0001**	**F = 369** **df = 2** ***P* < 0.0001**				**No**
N amount released (g m^{-2})	**lm**	**0.76**		**F = 286** **df = 2** ***P* < 0.0001**	**F = 1.26** **df = 1** ***P* = 0.19**	**F = 180** **df = 1** ***P* < 0.0001**	**F = 32.0** **df = 2** ***P* < 0.0001**				**No**
P amount released (g m^{-2})	**lm**	**0.79**		**F = 393** **df = 2** ***P* < 0.0001**	**F = 0.19** **df = 1** ***P* = 0.82**	**F = 177** **df = 1** ***P* < 0.0001**	**F = 24.7** **df = 2** ***P* < 0.0001**				**No**
C:N released	**lm**	**0.61**		**F = 69.9** **df = 2** ***P* < 0.0001**	**F = 0.26** **df = 1** ***P* = 0.78**	**F = 246** **df = 1** ***P* < 0.0001**	**F = 11.8** **df = 2** ***P* < 0.0001**				**No**
C:P released	**lm**	**0.55**		**F = 19.9** **df = 2** ***P* < 0.0001**	**F = 2.71** **df = 1** ***P* = 0.068**	**F = 281** **df = 1** ***P* < 0.0001**					**No**
N:P released	**lm**	**0.37**		**F = 31.5** **df = 2** ***P* < 0.0001**	**F = 2.95** **df = 1** ***P* = 0.054**	**F = 82.5** **df = 1** ***P* < 0.0001**					**No**

SP=Species, Fl=flooding intensity, T=time after beginning of decomposition, F=Fisher statistic.

Table 2

Squared Mahalanobis distances (SMD, with sigma-restricted parameterization) among all pairwise comparisons among the nine (3 flooding intensities × 3 species) combinations of the GDA.

	Cyperus malaccensis (high flooding)	*Cyperus malaccensis* (continuous flooding)	*Spartina alterniflora* (low flooding)	*Spartina alterniflora* (high flooding)	*Spartina alterniflora* (continuous flooding)	*Phragmites australis* (low flooding)	*Phragmites australis* (high flooding)	*Phragmites australis* (continuous flooding)
Cyperus malaccensis (low flooding)	SMD=150 *P*<0.0001	SMD=523 *P*<0.0001	SMD=113 *P*<0.0001	SMD=248 *P*<0.0001	SMD=615 *P*<0.0001	SMD=29.4 *P*<0.0001	SMD=168 *P*<0.0001	SMD=528 *P*<0.0001
Cyperus malaccensis (high flooding)		SMD=200 *P*<0.0001	SMD=279 *P*<0.0001	SMD=117 *P*<0.0001	SMD=306 *P*<0.0001	SMD=193 *P*<0.0001	SMD=35.2 *P*<0.0001	SMD=222 *P*<0.0001
Cyperus malaccensis (continuous flooding)			SMD=674 *P*<0.0001	SMD=*336* *P*<0.0001	SMD=128 *P*<0.0001	SMD=586 *P*<0.0001	SMD=253 *P*<0.0001	SMD=45.3 *P*<0.0001
Spartina alterniflora (low flooding)				SMD=151 *P*<0.0001	SMD=532 *P*<0.0001	SMD=58.8 *P*<0.0001	SMD=225 *P*<0.0001	SMD=593 *P*<0.0001
Spartina alterniflora (high flooding)					SMD=208 *P*<0.0001	SMD=206 *P*<0.0001	SMD=68.4 *P*<0.0001	SMD=265 *P*<0.0001
Spartina alterniflora (continuous flooding)						SMD=589 *P*<0.0001	SMD=280 *P*<0.0001	SMD=69.1 *P*<0.0001
Phragmites australis (low flooding)							SMD=157 *P*<0.0001	SMD=526 *P*<0.0001
Phragmites australis (high flooding)								SMD=204 *P*<0.0001

Table 3

Statistics (Wilks' λ, F and *P*) of the independent litter variables of the discriminant function analysis among the litters during decomposition. Bold type indicates the statistical significant (P<0.05) of the corresponding variable in the model.

Variable	**Wilks' λ**	**F**	***P***
Mass remaining	**0.726521**	**9.8341**	**< 0.00001**
C concentration mg g^{-1}	**0.721669**	**10.0758**	**< 0.00001**
N concentration mg g^{-1}	**0.591990**	**18.0058**	**< 0.00001**
P concentration mg g^{-1}	**0.624283**	**15.7230**	**< 0.00001**
C:N ratio	**0.742607**	**9.0551**	**< 0.00001**
C:P ratio	**0.877577**	**3.6445**	**0.0005**
N:P ratio	**0.851441**	**4.5583**	**< 0.00001**
C in residual litter (% initial)	**0.789840**	**6.9513**	**< 0.00001**
N in residual litter (% initial)	0.972211	0.7467	0.65
P in residual litter (% initial)	0.934035	1.8451	0.070
C:N of accumulated released	0.951666	1.3269	0.23
C:P of accumulated released	**0.584990**	**18.5339**	**< 0.00001**
N:P of accumulated released	**0.643082**	**14.4997**	**< 0.00001**
Soil C concentration	**0.076160**	**316.9030**	**< 0.00001**
Soil N concentration	**0.797280**	**6.6427**	**< 0.00001**
soil P concentration	**0.069456**	**350.0138**	**< 0.00001**
Soil pH	**0.168842**	**128.6055**	**< 0.00001**
Salinity (mS cm^{-1})	**0.621694**	**15.8973**	**< 0.00001**
Time categorical	**0.438487**	**2.9098**	**< 0.00001**

Figure captions

Fig. 1. Location of the sites of litter decomposition for the flood-gradient habitats.

Fig. 2. Mass remaining (%initial, mean ± SE) during the year of litter decomposition in the species (*C. malaccensis*, circle; *S. alterniflora*, triangle; *P. australis*, diamond) and flooding intensities. Different letters within the graphs indicate statistical differences (P<0.05) between species and flooding intensities.

Fig. 3. Amounts of C (a), N (b) and P (c) in residual litter (%initial, mean ± SE) during the year of litter decomposition for the species (*C. malaccensis*, circle; *S. alterniflora*, triangle; *P. australis*, rhombus) and flooding intensities. Different letters within the graphs indicate statistical differences (P<0.05) between species and flooding intensities.

Fig. 4. Amounts of C (a), N (b) and P (c) in residual litter (g, mean ± SE) during the year of litter decomposition for the species (*C. malaccensis*, circle; *S. alterniflora*, triangle; *P. australis*, rhombus) and flooding intensities. Different letters within the graphs indicate statistical differences (P<0.05) between species and flooding intensities.

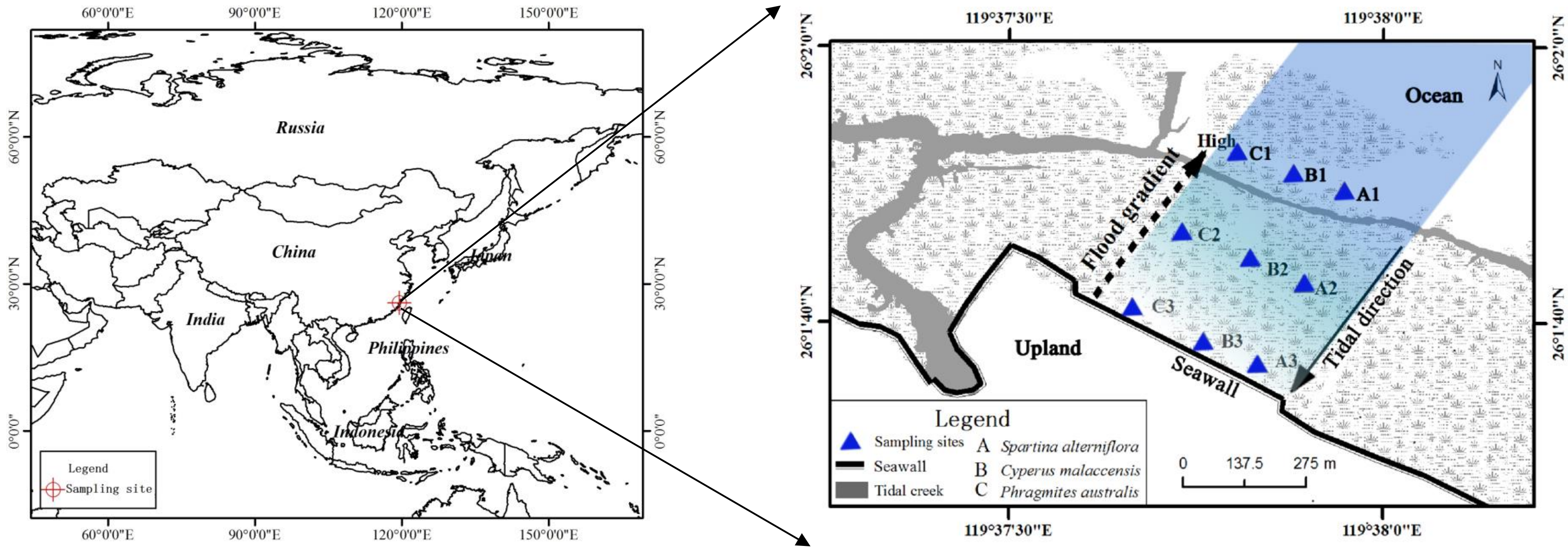
Fig. 5. Accumulated amounts of C (a), N (b) and P (c) released from litter (g, mean ± SE) during the year of litter decomposition for the species (*C. malaccensis*, circle; *S. alterniflora*, triangle; *P. australis*, rhombus) and flooding intensities. Different letters within the graphs indicate statistical differences (P<0.05) between species and flooding intensities.

Fig. 6. C (a), N (b) and P (c) concentrations in residual litter (mg g^{-1}, mean ± SE) during the year of litter decomposition for the species (*C. malaccensis*, circle; *S. alterniflora*, triangle; *P. australis*, rhombus) and flooding intensities. Different letters within the graphs indicate statistical differences (P<0.05) between species and flooding intensities.

Fig. 7. C:N (a), C:P (b) and N:P (c) concentration ratios in residual litter (mean ± SE)

during the year of litter decomposition for the species (*C. malaccensis*, circle; *S. alterniflora*, triangle; *P. australis*, rhombus) and flooding intensities. Different letters within the graphs indicate statistical differences ($P<0.05$) between species and flooding intensities.

Fig. 8. Discriminant general analysis (DGA) of mass remaining (MR); litter C ([C]), N ([N]) and P ([P]) concentrations; C:N ([C:N]), C:P ([C:P]) and N:P ([N:P]) litter concentration ratios; the percentage of initial amounts of C (C), N (N) and P (P), the C:N, C:P and N:P ratios of the accumulated release from litter, soil salinity, pH and C (Soil [C]), N (Soil [N]) and P (Soil [P]) concentration during litter decomposition for the various flooding intensities and species as grouping factors. We also considered the portion of the variance due to time as an independent categorical variable.



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
Sampling site
119°37'30"E
119°38'0"E
26°2'0"N
26°1'40"N
Ocean
N
High
C1
B1
A1
C2
B2
A2
C3
B3
A3
Flood gradient
Tidal direction
Upland
Seawall
Legend
Sampling sites
Seawall
Tidal creek
A Spartina alterniflora
B Cyperus malaccensis
C Phragmites australis
0 137.5 275 m

Fig. 1.

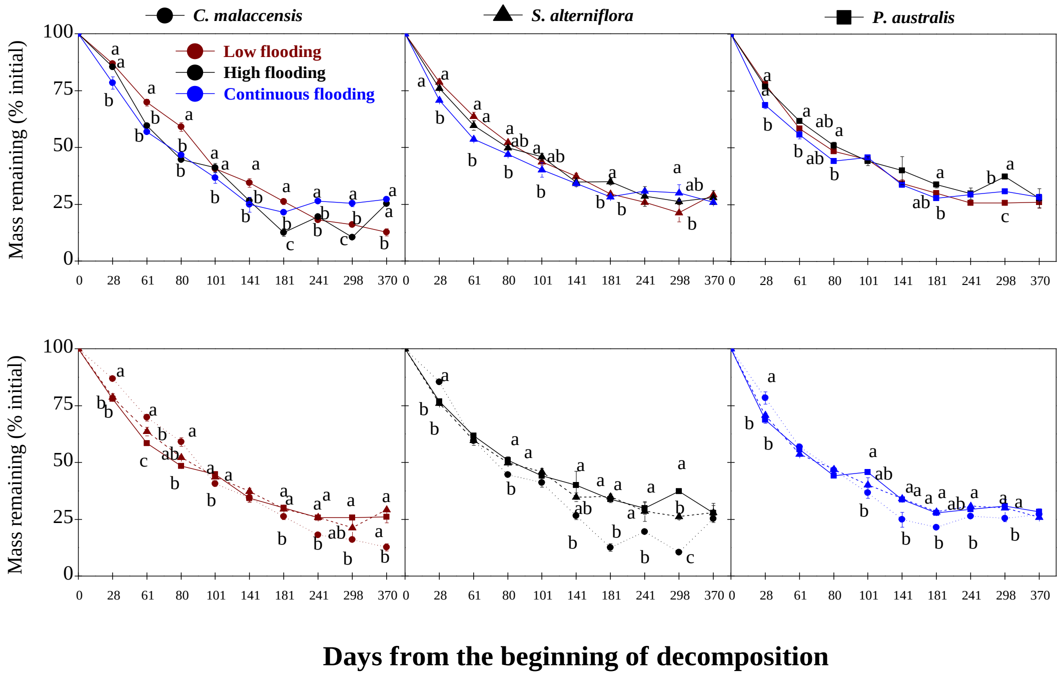

C. malaccensis
S. alterniflora
P. australis
Low flooding
High flooding
Continuous flooding
Mass remaining (% initial)
100
75
50
25
0
0 28 61 80 101 141 181 241 298 370
Days from the beginning of decomposition

Fig. 2.

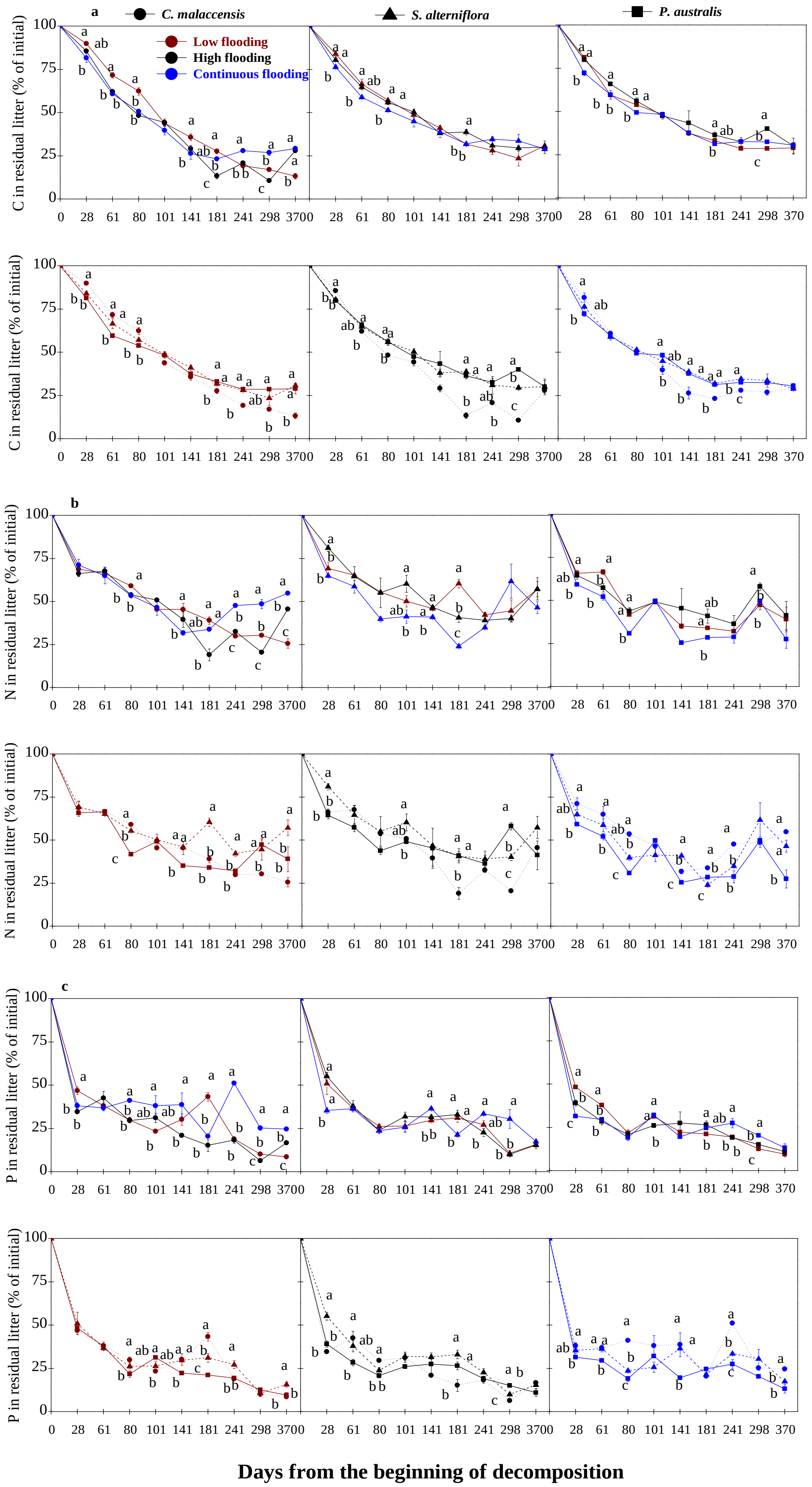

a
C. malaccensis
S. alterniflora
P. australis
Low flooding
High flooding
Continuous flooding
C in residual litter (% of initial)
b
N in residual litter (% of initial)
c
P in residual litter (% of initial)
Days from the beginning of decomposition

Fig. 3.

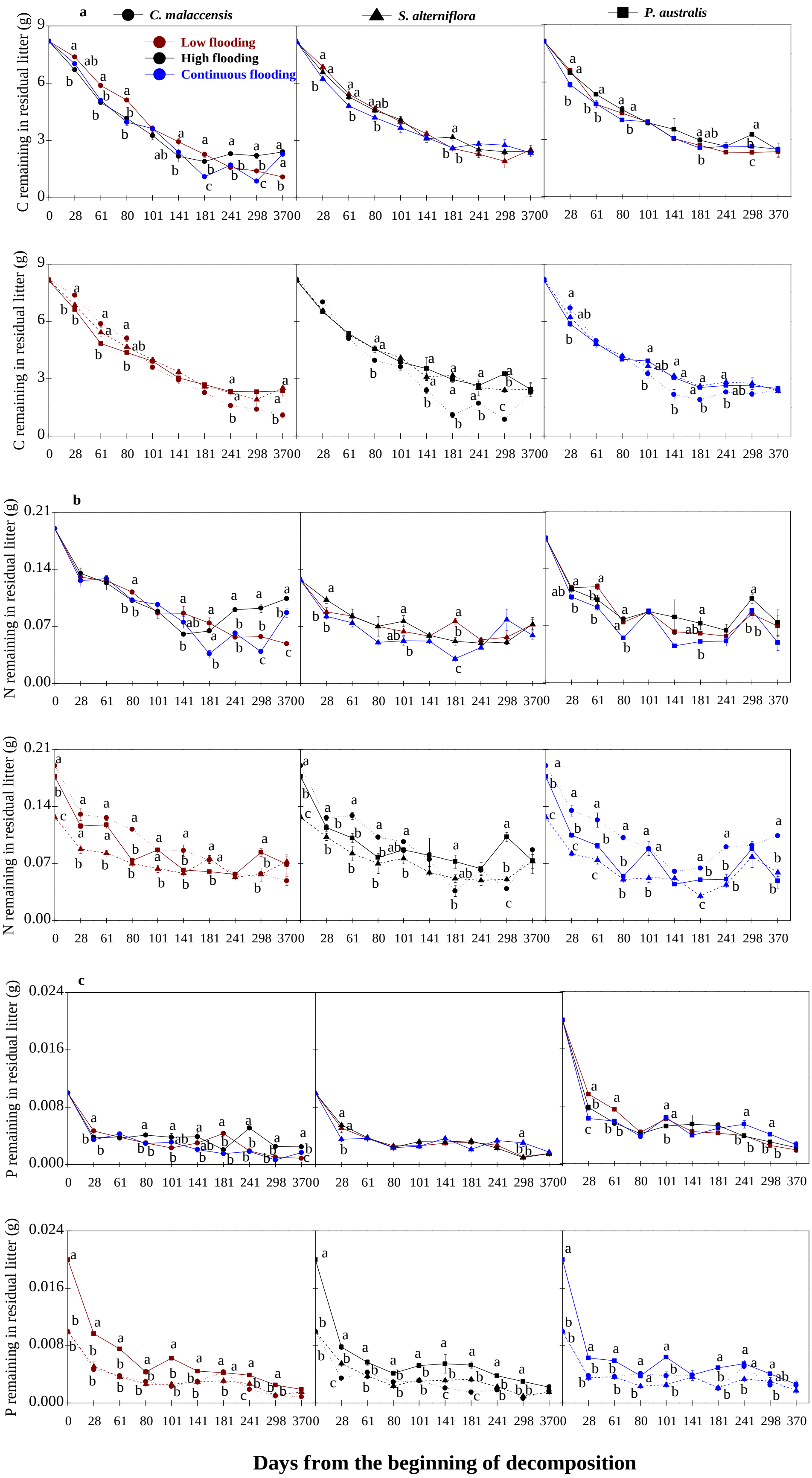

a
C. malaccensis
S. alterniflora
P. australis
Low flooding
High flooding
Continuous flooding
C remaining in residual litter (g)
b
N remaining in residual litter (g)
c
P remaining in residual litter (g)
Days from the beginning of decomposition

Fig. 4.

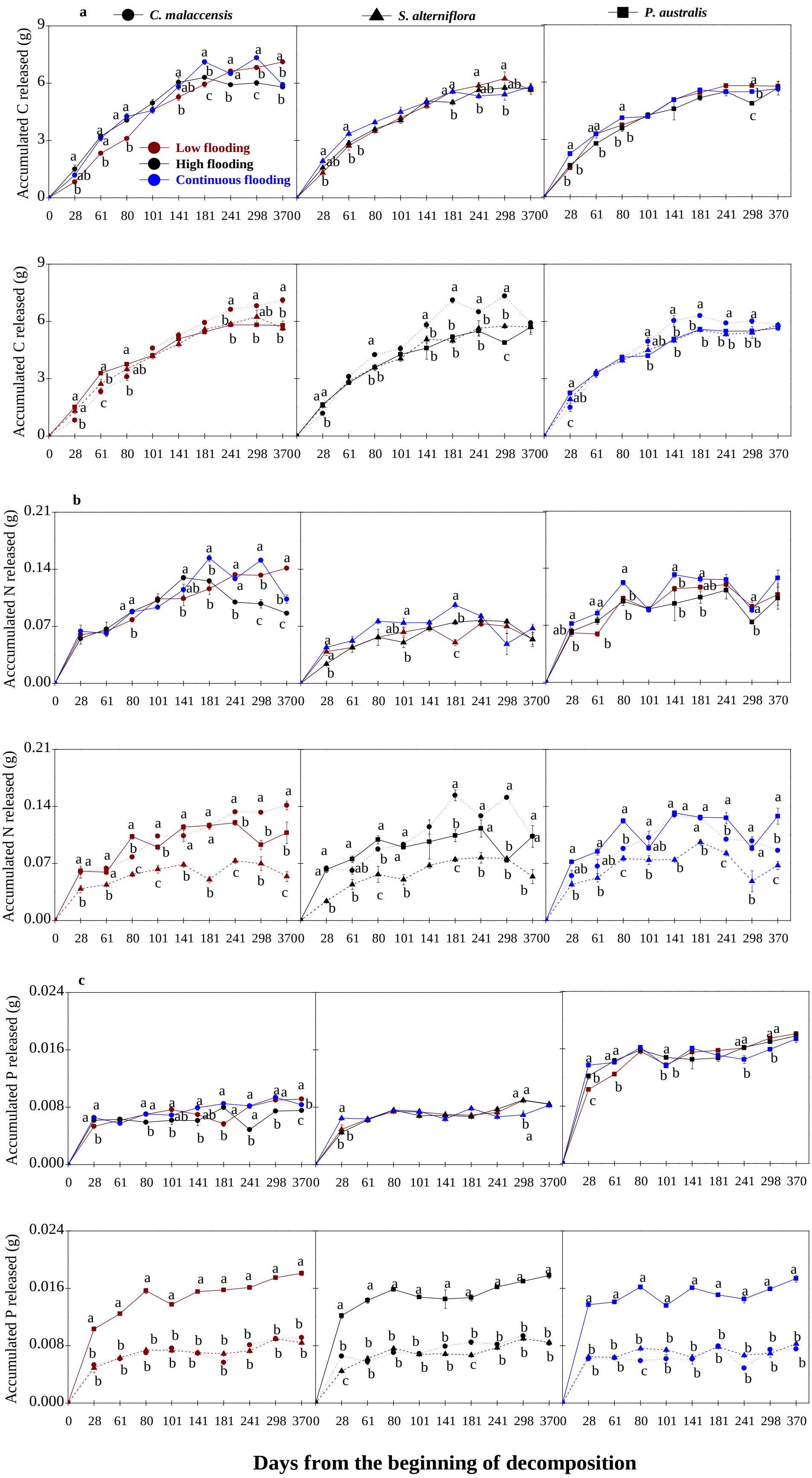

a
C. malaccensis
S. alterniflora
P. australis
Low flooding
High flooding
Continuous flooding
Accumulated C released (g)
b
Acccumulated N released (g)
c
Accumulated P released (g)
Days from the beginning of decomposition

Fig. 5.

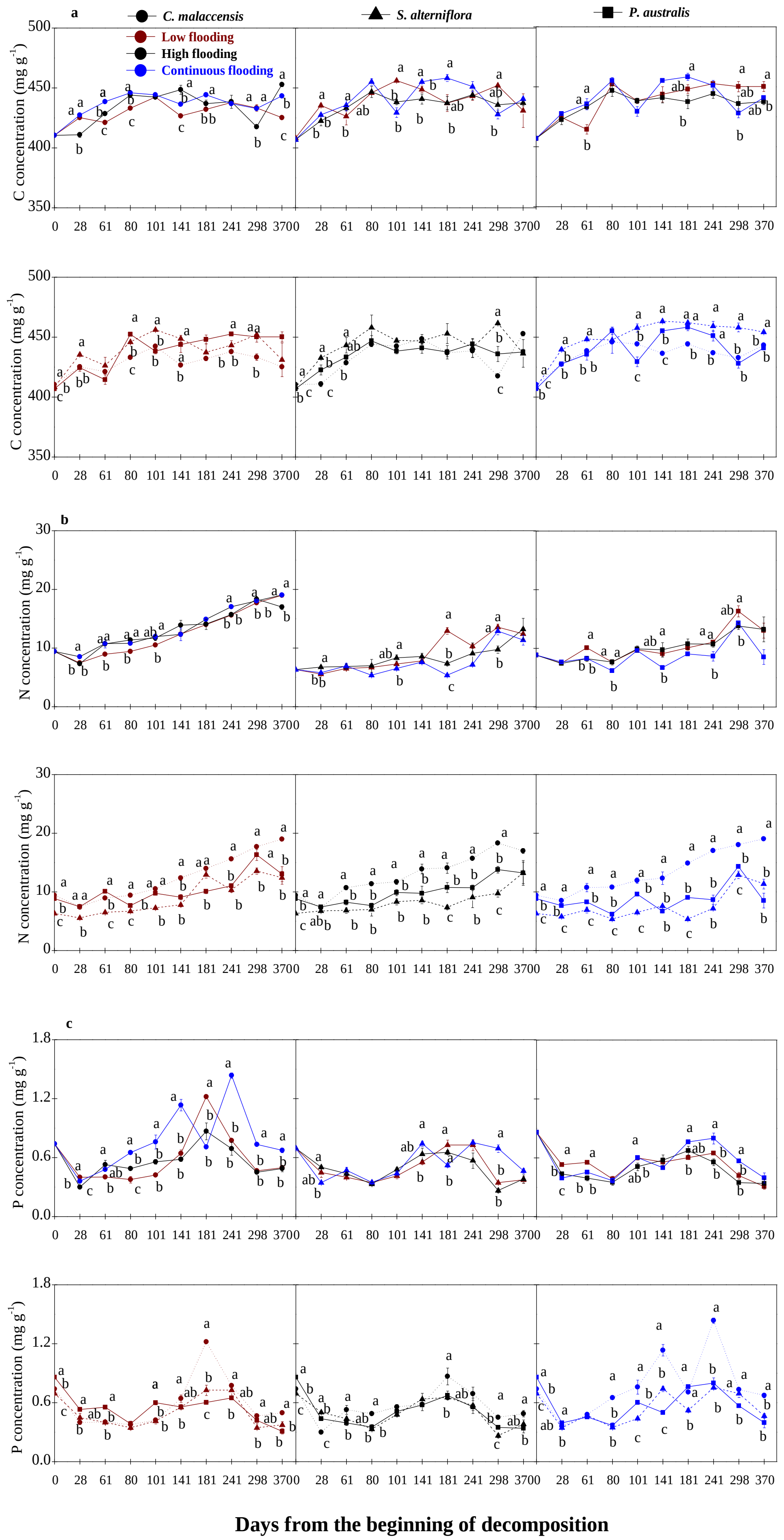

a
C. malaccensis
S. alterniflora
P. australis
Low flooding
High flooding
Continuous flooding
C concentration (mg g-1)
b
N concentration (mg g-1)
c
P concentration (mg g-1)
Days from the beginning of decomposition

Fig. 6.

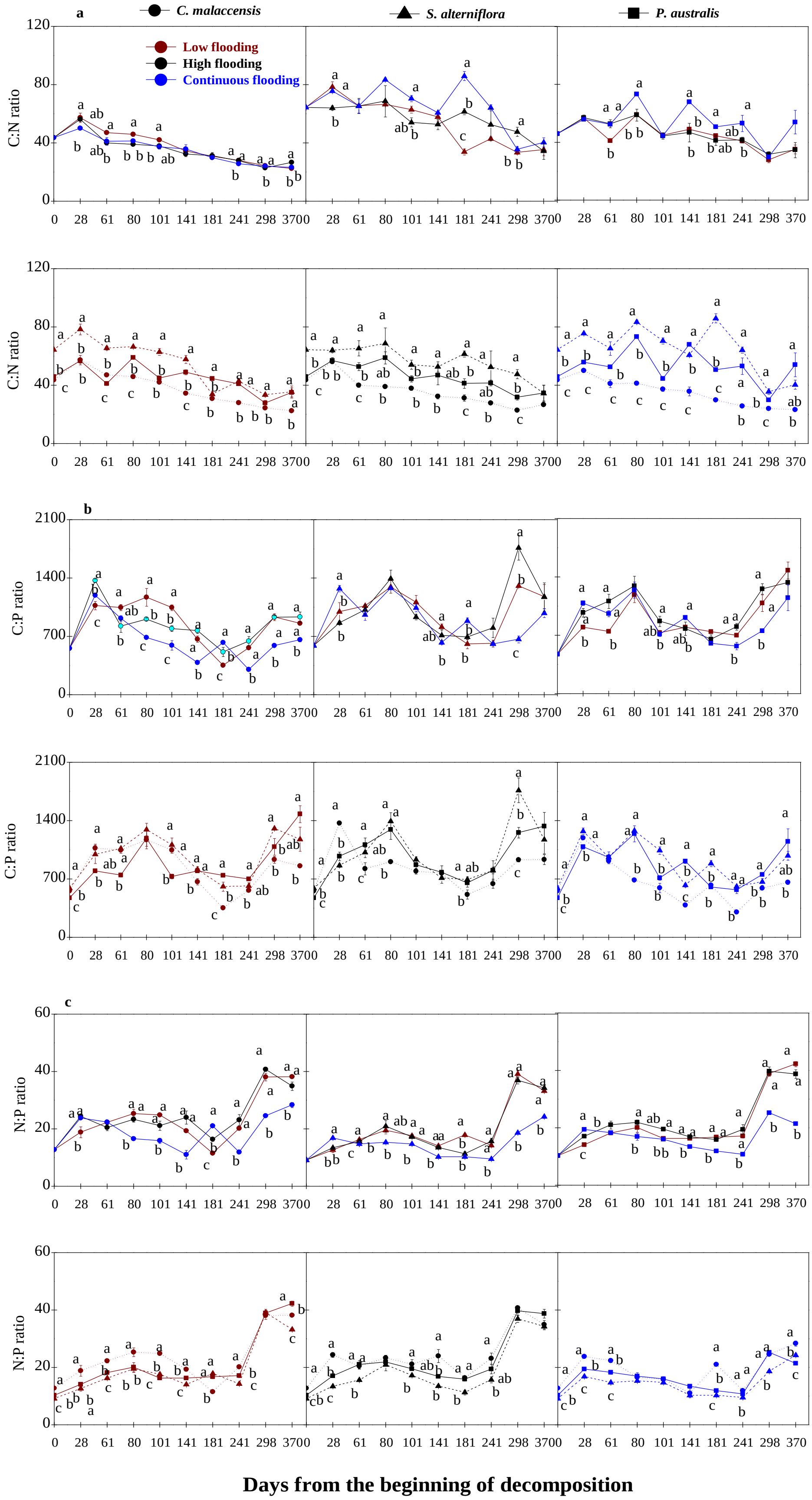

a
C. malaccensis
S. alterniflora
P. australis
Low flooding
High flooding
Continuous flooding
C:N ratio
b
C:P ratio
c
N:P ratio
Days from the beginning of decomposition

Fig. 7.

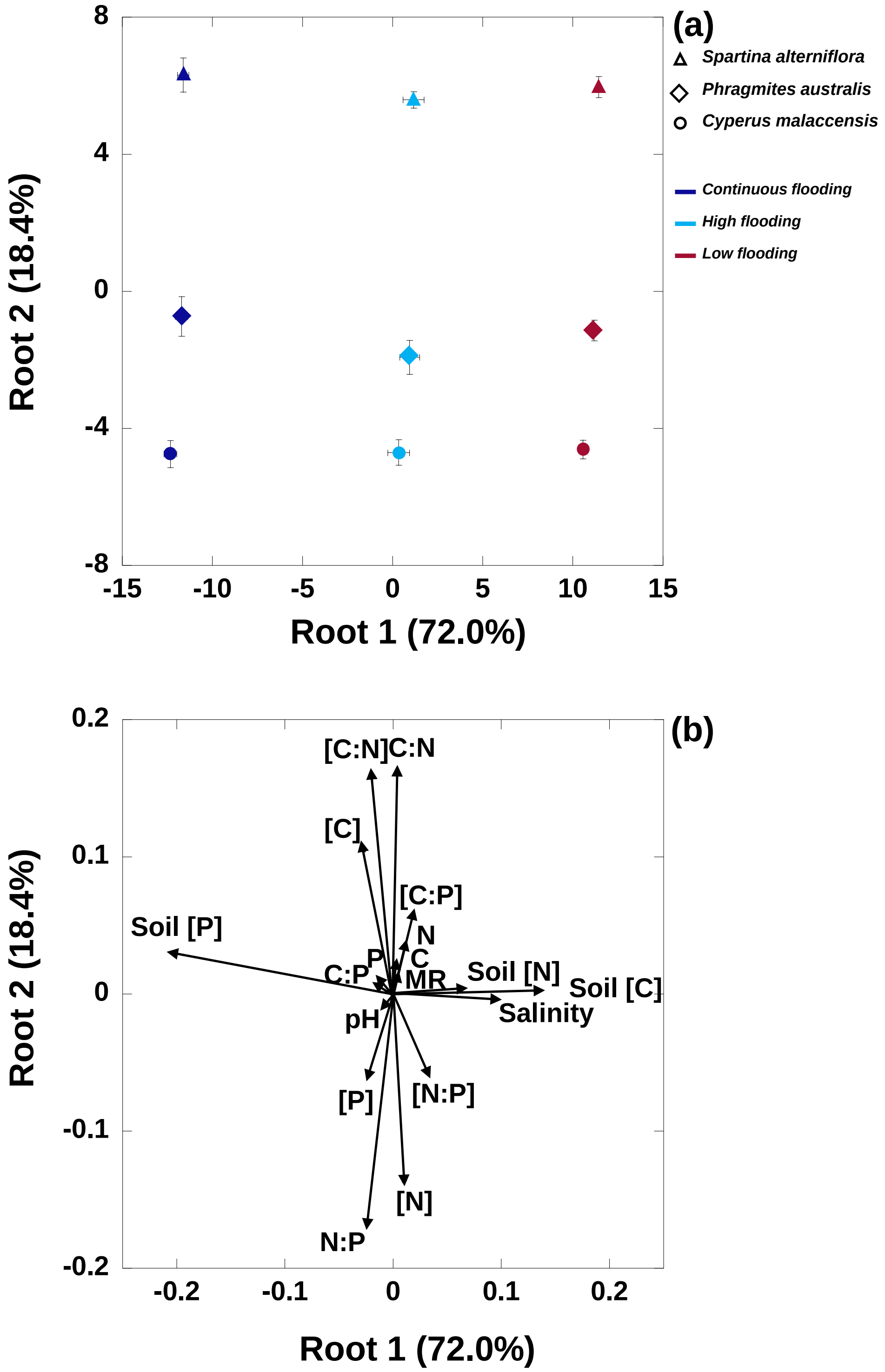

(a)
Spartina alterniflora
Phragmites australis
Cyperus malaccensis
Continuous flooding
High flooding
Low flooding
8
4
0
-4
-8
-15
-10
-5
0
5
10
15
Root 2 (18.4%)
Root 1 (72.0%)
(b)
0.2
0.1
0
-0.1
-0.2
-0.2
-0.1
0
0.1
0.2
[C:N]
C:N
[C]
[C:P]
N
Soil [P]
P
C
C:P
MR
Soil [N]
Soil [C]
Salinity
pH
[P]
[N:P]
[N]
N:P
Root 2 (18.4%)
Root 1 (72.0%)

Fig. 8.