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Stoichiometry patterns of plant organ N and P in coastal herbaceous wetlands along the East China Sea: Implications for biogeochemical niche

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Abstract

Background and aims Nitrogen (N) and phosphorus (P) are essential nutrients for plant growth, and their availability and stoichiometry play pivotal roles in trophic dynamics and community composition. The biogeochemical niche (BN) hypothesis claims that each species should have an optimal elemental composition and stoichiometry as a consequence of its optimal function in its specific ecological niche. Little attention, however, has been given to N and P stoichiometric patterns and test the BN hypothesis in coastal wetland communities from the perspective of organ and species-specific comparisons.

Methods We investigated factors responsible for changes in N and P stoichiometry patterns in different functional groups in coastal wetlands and tested the BN hypothesis by evaluating N and P composition in whole aboveground plants and organs.

Results Both plant N and P concentrations were high in coastal wetlands, indicating that N and P were not likely limiting, although the N:P ratio was slightly lower than the ratio reported in global and Chinese terrestrial flora. N and P concentrations and N:P ratios varied strongly between C₃ and C₄ species, among species, and among organs within species. N and P concentrations were not correlated with latitude, mean annual temperature and precipitation, although N:P ratio was weakly correlated with these factors. The differences in N and P concentrations and N:P ratios along the wetland gradients were mainly because of the species-specific community composition of each site.

Conclusions The results are consistent with the BN hypothesis. First, N and P composition is species-specific (homeostatic component of BN), each species tends to maintain its own composition even growing in different sites with different species composition. Second, different species, despite maintaining their own composition, have distinct degree of composition phenotypic flexibility (flexibility component of BN); this different size of “biogeochemical space” was observed when comparing different species living in the same community and the shifts in species BN space and size was observed when comparing populations of the same species living in different sites.

Keywords: Nutrients; Ecological stoichiometry; Biogeochemical niche; Coastal wetlands; Eastern China

Introduction

Ecological stoichiometry focuses on the balance of energy and chemical elements in ecosystems, and is a powerful tool for understanding nutrient biogeochemistry and ecosystemic processes at the individual and ecosystem levels (Elser et al. 2000; Reich and Oleksyn 2004; Elser et al. 2007). Nitrogen (N) and phosphorus (P) are the main limiting elements for terrestrial vegetation (Sterner and Elser 2002; Högberg et al. 2017; Urbina et al. 2017). Their availability and stoichiometric ratios can significantly influence plant growth and community composition (Sterner and Elser 2002; Högberg et al. 2017; Urbina et al. 2017) and can be used to indicate the nutrient dynamics and limitation of vegetation under changing environments (Reich and Oleksyn 2004; Han et al. 2005; Yuan et al. 2011). The N:P ratio in plants, especially in foliar or whole-plants, has been extensively studied at local (Zhang et al. 2016), regional (Sardans et al. 2015), and global (Elser et al. 2007) scales to determine variable patterns and controlling factors. A foliar N:P mass ratio < 14 or > 16 generally indicates an N or P limitation on plant growth, respectively (Koerselman and Meuleman 1996; Wang and Moore 2014). Little information, however, is available on the organ-specific comparisons and whole aboveground plant stoichiometric response to the environment, which is critical for understanding plant productivity and functional diversity (Minden and Kleyer 2014; Yang et al. 2015). Moreover, many studies have also shown that N, P concentrations and N:P ratios have broad biogeographical patterns and vary among all types of ecosystems, such as among or within biomes of various community types like forests and grasslands (Han et al. 2005; Sardans et al. 2011; Yuan et al. 2011; Zhang et al. 2018). However, coastal wetland ecosystems have rarely been studied even though they have extensive spatial heterogeneity and stoichiometric shifts along geographical gradients (Zhang et al. 2013; Sun et al. 2015b).

The biogeochemical niche (BN) hypothesis (Peñuelas et al. 2008; Peñuelas et al. 2010) claims that each species should have an optimal elemental composition and stoichiometry as a consequence of its optimal function in its specific ecological BN. This optimal elemental composition (homeostasis) is mainly because of the long-term evolution of the plant metabolic and physiological functions and morphologies. This, together with the fact that each bio-element has asymmetrical contributions to distinct organisms functions and morphological structures, should make each species a singular evolutionary product, where each species has its optimal overall functionality and morphology, and should tend to have an optimum elemental composition (homeostatic component of BN) (Peñuelas et al. 2008; Peñuelas et al. 2010; Sardans et al. 2015). Moreover, each species should also have some level of flexibility in its elemental composition and stoichiometry, so it can adapt to shifts in current environmental traits because of the evolution of genetic traits responsible for

phenotypic flexibility (flexibility component of BN) (Sardans and Peñuelas 2013; Sardans and Peñuelas 2014; Sardans et al. 2015; Sardans and Peñuelas 2015). The flexibility of the species' BN will influence the quality of plant tissues, which may affect the species' capacity to respond to environmental changes such as seasonality, disturbances, climate change, inter-specific competition, species invasion and N deposition (Peñuelas et al. 2008; Sardans et al. 2015). But this "flexibility capacity" would be different depending on species evolutionary history and the final response to an increasing environmental change may contribute to change the inter-specific competitive relations, and finally the community composition shifts (Peñuelas et al. 2008; Sardans and Peñuelas 2014; Sardans et al. 2015). The study of elemental composition and stoichiometric shifts in plants along an environmental gradient, where species composition progressively changes but where the most abundant species cover a notable range of sites along the gradient and have overlapping distributional ranges, is thus justified for testing the BN hypothesis (Sardans and Peñuelas 2014).

Wetlands are complex environments in terms of spatial and temporal heterogeneity in hydrology and resource supply, which in turn supports complex vegetation structure (Willby et al. 2001). Wetland plants play a key role in biogeochemical cycling (Minden and Kleyer 2014; Mao et al. 2016), and their nutrients availability and stoichiometric ratios can be influenced by various biotic and abiotic factors such as alien invasion (Wang et al. 2015), nutrient availability (Willby et al. 2001), and anthropogenic disturbance (Qu et al. 2014). Through an extensive survey of European wetlands, Willby et al. (2001) found that stress-tolerant or dominant plants had consistently lower nutrient contents and higher N:P ratios, whereas ruderal-dominated plants displayed the opposite pattern. Wang and Moore (2014) investigated the seasonal variation in N, P concentrations and their stoichiometric ratios in ombrotrophic bog peatlands and found that plants exhibit N and P co-limitation and adapted to extremely low nutrient availability by maintaining small nutrient concentrations in photosynthetically active tissues, further suggesting that there is a strong stoichiometric homeostasis in stress tolerant plants (Sardans et al. 2012). Previous studies comparing plant elemental composition in wetland systems have focused mainly on stoichiometric response to the external environment, whereas investigations of organ and species-specific comparisons at regional scales are still pending.

Coastal wetlands are located along the intersection between terrestrial and marine ecosystems and are sensitive to global changes and human activities (Moseman-Valtierra et al. 2011). Nutrient cycling is more complex in coastal wetland ecosystems than in other systems because of frequent human activity and strong hydrodynamic effects (Zhang et al. 2013). Ecological stoichiometry in coastal wetlands has mainly been studied at the level of soil nutrients composition (Zhang et al. 2013; Wang et al. 2014). For instance, Zhang et al. (2013) reported that N and P stoichiometric ratios were spatially heterogeneous in estuarine wetland soils

and that estuarine ecosystems were limited by N and P. Wang et al. (2014) reported that human activities have increased N limitation in an estuarine tidal wetland of the Min River. However, how internal differences between plant organs caused by the functional differentiation of plants in coastal wetlands remains unclear, although some studies have focused on local and foliar levels (Qu et al. 2014; Rong et al. 2015).

China has a coastline approximately 1.8×10^4 km in length and has approximately 5.8×10^6 ha of coastal wetlands accounting for 10.8% of the total area of China's natural wetlands (Sun et al. 2015b). Coastal wetland area, however, has decreased sharply with rapid economic development and frequent human activity (Jiang et al. 2015), which can strongly influence the sustainable development of the coastal zone. Consequently, coastal wetlands are an ideal subject for studying plant N and P stoichiometry, which can provide an important understanding of nutrient dynamics under changing environmental conditions. To our knowledge, no studies have reported N and P stoichiometric patterns from the perspective of plant organs and species-specific comparisons at regional scales and examined key driving factors that affect plant organ elemental composition in coastal wetlands. We hypothesized that (1) both biogeographical and climatic differences affect plant N and P concentrations and N:P ratio patterns at regional scales; and that (2) plant nutrient concentration and stoichiometry in coastal wetland is organ and species-specific, and fits the BN hypothesis.

Materials and Methods

Site description

This study was conducted in 18 coastal wetlands along the East China Sea ($23^{\circ}43'-31^{\circ}38'N$, $117^{\circ}20'-122^{\circ}53'E$), extending for 1,500 km in three coastal provinces in China (Fig. 1). The regional climate is dominated by subtropical monsoons, with an annual mean temperature and precipitation ranging from $15.8^{\circ}C$ to $21.7^{\circ}C$, and from 1,128.9 to 1,900.4 mm, respectively. The dominant plant species in these sites included *Spartina alterniflora*, *Phragmites australis*, *Cyperus malaccensis*, *Scirpus mariqueter*, *Scirpus triqueter*, *Suaeda glauca*, and *Juncellus serotinus*. Detailed locations and geographical characteristics are presented in Fig. 1 and Table S1 (Supplementary material), respectively.

Vegetation sampling and chemical analyses

Plants were collected during the growing seasons from July to September in 2014 and 2015. The distribution of the dominant plant communities had been initially identified based on the published monographs (Zhao 1999). Locations that suffered minimal anthropogenic disturbance and fertilization were chosen for the study sites. Plant species and survey areas were determined according to the topography and plant distribution. One 30×30 m sampling plot (approximately 1 sampling plot per 10,000 hectares) was established for each

community dominated by *S. alterniflora*, *P. australis*, *C. malaccensis*, *S. mariqueter*, *S. triqueter*, *S. glauca*, and *J. serotinus*, respectively. Nine 2 × 2 m (average plant height ≥ 2 m), 1 × 1 m (1 m < average plant height < 2 m), or 0.5 × 0.5 m (average plant height ≤ 1 m) quadrats, were randomly located in each plot. The standing mature and non-senescent aboveground plants were clipped in the three random quadrats, then placed into labeled waterproof envelopes after the mud, litter, and epiphytic algae were removed. A total of 216 whole-aboveground plant samples belonging to 7 species from 72 sampling sites over the 18 coastal wetlands were collected. Geographical information (latitude and longitude) was also recorded at each site using GPS receivers. All field sampling followed an identical protocol to minimize bias due to sampling technique.

The fresh plant samples were washed with tap water, rinsed with deionized water, and then oven-dried at 65 °C to a constant weight for calculating the biomass. The dried samples were divided into stems, leaves, leaf sheaths, and seeds, which were then weighed separately. These dried samples were ground to a powder using a ball mill and passed through a 0.149 mm sieve before elemental analysis. Total N (TN, mg·g⁻¹) concentrations were determined using an elemental analyzer (Elementar Vario MAX, Germany), and total P (TP, mg·g⁻¹) concentrations were measured using a flow injection auto analyzer (Skalar San⁺⁺, Netherlands) after being digested in an HClO₄-H₂SO₄ pretreatment (Bai et al. 2012).

Climatic variables

The climatic data used in this study were obtained from the database of the China Meteorological Data Service Center (<http://data.cma.cn/en>). Mean annual temperature (MAT), mean annual precipitation (MAP), and light duration (LD) were calculated based on 30-year of averaged records (1981-2010) from 18 meteorological stations within or around the study area.

Statistical analysis

The normality of the data was first examined with Kolmogorov-Smirnov tests. The data for N and P concentrations and N:P ratios were mostly non-normally distributed, so geometric means ± standard error were calculated. All data for N and P concentrations and N:P ratios were log₁₀-transformed to normalize the distributions for statistical analysis. The N:P stoichiometric ratios were calculated on a mass basis. Data were analyzed at two levels: (1) all data were used for calculating the N and P concentrations in whole aboveground plants (for individual species) based on the proportion of nutrient concentrations and weight in each organ; and (2) the dataset was subdivided into different photosynthetic pathways (C₃ and C₄), phylogenetic groups (monocotyledons and dicotyledons), and organs (stems, leaves, leaf sheaths, and seeds). The differences in N and P concentrations and N:P ratios among the species, phylogenetic groups, and organs were analyzed by

one-way analysis of variance (ANOVA). Reduced major axis (RMA) regression analyses were used to explore functional allometric relationships between N vs. P because functional rather than predictive relationships were sought (Niklas and Cobb 2005; Niklas et al. 2005; Niklas 2006). The slopes (scaling exponents) of RMA regression curves and Y-intercept of log-log linear functions are designated as α_{RMA} and $\log \beta_{\text{RMA}}$, respectively (see Table 2). Ordinary linear regression analysis was used to describe the relationships between plant stoichiometry and latitude, as well as between stoichiometry and climatic factors. Slopes of relationships between plant elements and climate, as well as between plant elements and latitude, were compared using covariance analysis (Sun et al. 2015a). To overcome the problems caused by the collinearity of climatic factors, we used hierarchical partitioning to explore the contribution of different factors explaining stoichiometric variations (for details, see Heikkinen et al. 2004; Sun et al. 2015a). Statistical significance was set at $P < 0.05$.

Mixed linear models were used to obtain the best model for explaining the maximum variability of the N and P concentrations and N:P ratios for the whole aboveground plants and the various organs with abiotic data, e.g., climate and light duration as independent variables, and site and species as random independent (*lme* function) and fixed (*lm* function) factors. We chose the best model for each dependent variable using Akaike information criteria. We used the MuMIn (Barton 2012) R package in the mixed models to estimate the percentage of the variance explained by the model. We also conducted Tukey's post hoc tests to detect significant differences in the analyses of more than two communities using the "*multcomp*" R package with the "*glht*" function. To determine whether the N and P concentrations and N:P ratios of the organs differed significantly among the species and within species depending on sites, we performed a principal components analysis (PCA) and then an ANOVA for case scores for the species, sites and functional groups (C₃ versus C₄). The PCAs were performed using Statistica 6.0 (StatSoft, Inc. Tulsa, USA). This allows testing the overall significant differences in overall N and P composition in plants depending of species, functional group and sites (homeostasis species-specific component of BN), and also to detect the individual variability in communities of different species and the overall composition shift capacity in comparing different site populations of the same species (flexibility BN component).

Results

Patterns of N and P concentrations and N:P ratios for whole aboveground plants

Plant N and P concentrations and N:P ratios for whole aboveground plants varied markedly across study area. Geometric means ranged from 11.65 ± 0.73 to 21.40 ± 3.95 mg·g⁻¹ for N concentration, from 1.30 ± 0.06 to 3.24 ± 0.36 mg·g⁻¹ for P concentration, and from 4.01 ± 0.42 to 10.18 ± 0.43 for the N:P ratio (Table 1). The

coefficients of variation (CV) for N and P concentrations and N:P ratios were 45.75%, 42.84%, and 31.14%, respectively. The mean N and P concentrations and N:P ratios for all species across all wetlands were $13.28 \pm 0.41 \text{ mg} \cdot \text{g}^{-1}$, $1.76 \pm 0.05 \text{ mg} \cdot \text{g}^{-1}$, and 7.58 ± 0.18 , respectively. The rank of N and P concentrations and N:P ratios differed among the species (Table 1).

The N concentration and N:P ratio was higher ($P < 0.05$, Table 1) in C_3 ($15.46 \pm 1.05 \text{ mg} \cdot \text{g}^{-1}$ and 8.67 ± 0.38 , respectively) than C_4 ($11.69 \pm 0.80 \text{ mg} \cdot \text{g}^{-1}$ and 6.69 ± 0.37 , respectively) plants, but P concentration did not differ significantly between C_3 ($1.78 \pm 0.15 \text{ mg} \cdot \text{g}^{-1}$) and C_4 ($1.75 \pm 0.10 \text{ mg} \cdot \text{g}^{-1}$) plants. N and P concentrations and N:P ratios did not differ significantly between monocotyledon and dicotyledon plants (Table 1).

Patterns of N and P concentrations and N:P ratios in plant organs

For all plant species (Fig. 2d), N and P concentrations were significantly higher in leaves and seeds than stems and leaf sheaths, while the N:P ratio was significantly higher in leaves and leaf sheaths than in stems and seeds. For different species (Fig. 2a, b, c), N and P concentrations were higher in leaves and seeds than stems and leaf sheaths of *S. alterniflora* and *P. australis*, but there were no differences among the organs of *S. glauca*. N concentration and the N:P ratios were higher in the various organs of *P. australis* and *S. glauca* when compared to *S. alterniflora*; whereas the foliar P concentration was significantly higher in *S. alterniflora* than in *P. australis* and *S. glauca*.

Moreover, based on the 95% confidence intervals of RMA regression curves for log₁₀-transformed data, N concentration of each organ-type scaled isometrically (one-to-one) with respect to P concentration (Table 2, Fig. 3a). Across species, whole aboveground plant N levels thus scaled isometrically with respect to whole aboveground plant P (Table 2). For each species, with the exception of *C. malaccensis* and *J. serotinus*, aboveground plant N scaled roughly as the 5/4 power of P (Fig. 3b). For example, the scaling exponent for *S. mariqueter* N vs. P was 1.02 (95% CI= 0.77-1.27), whereas the exponent of N vs. P for *S. triqueter* was 1.45 (95% CI = 1.35-1.92; Table 2).

Differences in N and P composition across plant species

The PCAs of N and P concentrations and N:P ratio for whole aboveground plants, stems, and leaves identified variation among the dominant species along the gradient. The results were separated along the plot formed by the first two PCA axes, which explained 99.0% of the variance for whole aboveground plants (Fig. 4), and 98.8%, and 99.4% in stems and leaves, respectively (data not shown; Fig. 4). Only the distributions for *S. glauca* had some level of overlap in aboveground plant nutrients with *S. triqueter* and *C. malaccensis*, thus

only one (scarcely represented) species overlaps with others. And, only the distributions for *C. malaccensis* partially overlaps with *S. mariqueter* in stem composition ($P = 0.11$ and 0.10 , respectively). When N and P compositions of whole aboveground plants of three of the dominant species co-occurred at three sites along the gradient, *C. malaccensis* and *P. australis* shifted their overall N and P composition depending on the site where they grew; however, this relationship was not observed in *S. alterniflora* (Fig. 5). Each species maintained its elemental identity except for overlap between *P. australis* and *S. alterniflora*, despite the shift within species due to differential grow at the different sites.

Variations in N and P concentrations and N:P ratios with geographical and climatic variables

The N:P ratio for all species decreased linearly as latitude increased and temperature decreased (Fig. 6); however, the individual species N and P concentrations were not correlated with latitude or temperature. P concentration and the N:P ratio had weak positive and negative correlations with MAP, respectively, while N concentration did not correlate with MAP. N and P concentrations were weakly positively correlated with LD across all species, but the N:P ratio only presented a weak negative correlation with LD. Moreover, hierarchical partitioning showed that a substantial fraction of variation in elemental concentrations could be explained by the factors included in our analysis (MAT, MAP, LD, and LAT) from 33% for N to 56% for N:P (Table S2). Most notably, N, P, and N:P were most closely associated with LD. Among all tested factors, on average, LD was the most relevant (Table S2).

The mixed linear models that had climate and LD as fixed factors and site and species as random independent factors indicated that the variability of N and P concentrations and N:P ratios in whole aboveground plants, stems, and leaves was mainly explained by the random factors and by species (Table S3). Linear models with climate, LD, site, and species as fixed factors indicated that species was the main factor that explained the variability in the aboveground and foliar N and P concentrations and N:P ratios, as well as the stem N concentration (Table S3). Moreover, LD was the main factor that explained the variability of the stem P concentration and N:P ratio, even though the species was also an important factor for these two variables.

Discussion

Patterns of N and P concentrations and N:P ratios in China's coastal wetlands

Mean foliar N concentration across all species was $19.7 \pm 0.5 \text{ mg} \cdot \text{g}^{-1}$ (Fig. 2), which was nearly identical to the concentrations reported by Reich and Oleksyn (2004) from a global dataset of 1,280 terrestrial species ($18.3 \text{ mg} \cdot \text{g}^{-1}$) and by Han et al. (2005) for terrestrial species in China ($18.6 \text{ mg} \cdot \text{g}^{-1}$). This value, however, was higher

than the N concentrations reported for other freshwater (9.99 mg·g⁻¹; Mao et al. 2016), ombrotrophic (13.7 mg·g⁻¹; Jiroušek et al. 2011), and minerotrophic (15.1 mg·g⁻¹; Willby et al. 2001) wetland plants (Fig. 7). This discrepancy may be due to a higher N enrichment in Chinese coastal areas. The intensity of N deposition has continued to increase in China, especially in the southeastern coastal areas, and has been accompanied by very high N inputs from upstream runoff and tides (Hu et al. 2017). Elevated N levels can regulate the biogeochemical processing of soil nutrients (Zhang et al. 2016), promote plant growth (Högberg et al. 2017), accelerate the decomposition of litter (Wang and Moore 2014), and ultimately affect plant nutrient dynamics. Moreover, N is easily mineralized at high temperatures by promoting microbial activity, so higher NH₄⁺-N concentrations exist in subtropical wetland soils, which is easily absorbed by plants (Thangarajan et al. 2015).

Foliar P concentration was higher in coastal wetlands (2.06±0.04 mg·g⁻¹, Fig. 2) than previously reported global concentrations (1.42 mg·g⁻¹; Reich and Oleksyn 2004), Chinese terrestrial plants (1.21 mg·g⁻¹; Han et al. 2005), and other inland wetland plants (Fig. 7). There are several reasons why higher foliar P concentrations are found in subtropical coastal wetlands plants. First, coastal marshes have high concentrations of SO₄²⁻, due to their proximity to seawater, which can increase alkalinity and decomposition and mobilize iron (Fe)-associated P by sulfate reduction and its products (sulfide) in coastal wetlands, which can increase the release of P as an endogenous source from sediments to overlying water and is made available to plants (Dierberg et al. 2011). Second, these coastal wetlands are in a subtropical region where high temperatures produce high rates of P mineralization and strong rains cause severe erosion in the river basins, which increase the transport of P from upriver to estuarine areas (Wang et al. 2016). Foliar N:P ratio in these coastal wetlands species was 9.55±0.26 (Fig. 2), which is slightly lower than values reported for an ombrotrophic bog, minerotrophic wetland, non-forested and freshwater wetland (Fig. 7).

Generally, an N:P ratio <14 indicates N limitation, whereas an N:P ratio >16 indicates P limitation (Koerselman and Meuleman 1996). However, both plant N and P concentrations were high in these coastal wetland systems (Table 1), indicating that neither N nor P may be limiting factors for plant growth and nutrition. In this case, N:P ratios are not important for nutrient indicators because neither N nor P are limiting, but from a stoichiometric perspective, when both N and P concentrations in photosynthetic tissues are high, a lower N:P ratio indicates that species with high growth rates are the best adapted for their environment (Sardans et al. 2015; Urbina et al. 2017). This is typical mostly in environments with high perturbation frequencies where ruderal plants have lower N:P ratios (Willby et al. 2001). Additionally, environmental stress such as by anoxic soil conditions, excess salinity, or frequent perturbation, can all favor adaptations to accumulate N and P in biomass as these conditions do not facilitate nutrient uptake. Plants with nutritionally conservative strategies

store the most nutrients in their biomass to ensure nutrient availability and retain these nutrients in their wetland ecosystems. These mechanisms can operate under these conditions because tides, typhoons, and human activities have large and frequent impacts on subtropical coastal wetlands. Furthermore, flooding and salinity can also impede nutrient uptake and result in plant species that retain or accumulate nutrients as a survival strategy. Many processes can release and/or immobilize nutrients in a wetland that is subject to frequent flooding (Vymazal 2007). A high capacity to retain nutrients in biomass and high nutrient use efficiency can thus be good traits for plants that grow in wetland areas.

Moreover, we demonstrated that N concentrations in the organs and whole aboveground plants of sampled plant species were significantly correlated with P concentrations (Table 2; Fig. 3), which may be due to their similar functions (Han et al. 2005). The CV for N:P ratios are less than individual N or P concentrations (Table 1), indicating that N:P ratios within species that grow in coastal wetlands along the East China Sea are stable. This result is in agreement with previous studies that reported homeostatic constraints on the elemental composition of species regardless of the environmental condition (Elser et al. 2000; Han et al. 2005).

Variations of N and P concentrations and N:P ratios in plant organs and functional groups

The differences in N and P concentrations between plant organs are not only affected by basic metabolic demands but also by the functional differentiation and organizational structure of the organs (Minden and Kleyer 2014). N and P concentrations in our study were significantly higher in leaves and seeds than in stems and leaf sheaths, whereas N:P ratios were significantly higher in leaves and leaf sheaths than in stems and seeds (Fig. 2). These findings were consistent with the findings of Sardans and Peñuelas (2015), who also observed lower N:P ratios in stems and branches than in leaves. This may be due to the differences in organ structure and physiology. Minden and Kleyer (2014) suggested that leaves containing many chloroplasts generally have high metabolic and photosynthetic activity and thus contain more N and have higher N:P ratios than other plant organs. Stems may have lower N and P concentrations compared to seeds because stems are only nutrient-transmission channels and therefore, store fewer nutrients; whereas seeds can store more nutrients and thus have higher N and P concentrations and lower N:P ratios (Obeso 2012). Moreover, we also found a strong positive relationship of N, P concentrations and N:P ratios among the different organs (Table S4), which may imply that the organs of plants are interdependent, and general constraints or allocation rules govern the partitioning of nutrients among organs of plants (Kerkhoff et al. 2006).

N concentrations and N:P ratios were higher in C₃ than C₄ plants (Table 1), suggesting that the photosynthetic pathway has an important effect on nutrient cycling. C₄ plants have a higher N-use efficiency

and growth rate than C_3 plants, which leads to the accumulation of plant biomass but less N (Bui and Henderson 2013). Foliar N and P concentrations did not differ significantly between monocotyledonous and dicotyledonous species (Table 1), in contrast to the results reported by Stock and Verboom (2012). Nutrient concentrations may differ greatly between phylogenetic groups, but the patterns can be counterbalanced by species, soil environments, or adaptive strategies (Yang et al. 2015), which impedes the comparison between foliar N and P concentrations in monocotyledons and dicotyledons.

Effects of geography and climate on plant N and P concentrations and N:P ratios

Previous studies suggest that plant N and P concentrations increase linearly with increased latitude and precipitation, or with decreased temperature on national or global scales (Reich and Oleksyn 2004; Han et al. 2005; Zhang et al. 2018). However, our results displayed an inconsistent pattern. N and P concentrations were not correlated with latitude (or MAT) and MAP (Fig. 6), refuting hypothesis 1. These findings may be mainly attributed to a variety of circumstances. First, the ranges in latitude ($23^{\circ}43'N \sim 31^{\circ}38'N$), MAT ($15.81 \sim 21.70^{\circ}C$), and MAP ($1,129 \sim 1,900$ mm) in these coastal wetlands were too small to substantially affect local properties and environmental characteristics. Second, complex hydrological and nutrient conditions caused by periodic flooding and high salinity were so dominant in coastal wetlands (Zhang et al. 2013) that they partially counteracted possible underlying effects of temperature or precipitation and their conventional spatial patterns on plant nutrients. Moreover, plant N and P concentrations showed a weak but positive correlation with LD across the sampling sites, while N:P ratio had a weak negative correlation with LD (Fig. 6), which is consistent with previous findings that the nutrient dynamics of plant leaves and roots are strongly influenced by light availability at a local scale (Walter and Schurr 2005). The most likely reason for this finding is because, according to the carbon (C)-nutrient balance hypothesis, high light availability promotes C fixation, which in turn alters C: N ratios and increases foliar N concentrations (Cronin and Lodge 2003).

In contrast, N:P ratio had weak correlations with geographical and climatic factors, which increased as latitude decreased or MAT and MAP increased; further supporting that stoichiometric homeostasis was well constrained despite the changing environment and nutrient dynamics (Bradshaw et al. 2012). The changes in N and P concentrations and their ratios in the sites along where the gradient occurred were because of the presence of different species at different wetlands rather than because of current climatic differences, as indicated by the mixed linear models (Table S3). This result is consistent with a recent review by Yuan et al. (2017) that discussed the use of natural gradients versus experimental field manipulations at one site, which produced different results for inferring the effects of climate change on soil stoichiometry. The changes we

observed along a climatic gradient were mainly due to the differences in species composition, shaped by long-term evolution, and to interspecific site differences; whereas, the differences in field manipulated experiments are mainly due to intraspecific changes during shorter time scales.

Overall N and P composition in plants: testing the Biogeochemical Niche (BN) hypothesis

Plant elemental composition and stoichiometry have been observed to be related with plant species phylogenetic distances, plant adaptation and response to environmental variables such as climate conditions, N deposition and competitive conditions and finally to terrestrial ecosystems structure and function (Sardans et al. 2012; Sardans et al. 2015). The multivariate analyses indicated that each species had an overall N and P composition identity in whole aboveground plants, stems, and leaves, and that the variability of elemental composition between individuals are higher in some species than in others and that can change in the same species depending of the site where it lives. This different size of “biogeochemical space” was observed when comparing different species living in the same community and the shifts in species BN space and size was observed when comparing populations of the same species living in different sites (Fig. 5). The different elemental compositions in all whole aboveground plants, stems, and leaves was mainly controlled by site and species, suggesting that the species BN shifts in the sense to reach greater distances in PCA space among coexisting sympatric species. This is consistent with the hypothesis that niches shift in the direction that may partially avoid direct competition for the same sources with coexisting species, thus improving the possibilities of different species coexistence. We only used N and P stoichiometry to test the validity of the biogeochemical niche hypothesis, but the sensitivity of our analyses would undoubtedly have been higher if we had also used other important bio-elements such as potassium, magnesium, sulfur, calcium or C. However, our results using two bio-elements identified clear patterns in species nutrient composition and some degree of flexibility in the elemental composition within these species which depended on environmental conditions, consistent with the BN hypothesis (Peñuelas et al. 2008; Peñuelas et al. 2010), approving hypothesis 2.

Uncertainties and future works

In this study, N and P stoichiometric patterns from the perspective of organ and species-specific comparisons along a coastal marsh gradient were reported. These patterns have important implications for our understanding of ecosystemic nutrient dynamics and provide a basis for modeling nutrient cycling from regional to global scales in coastal marshes. However, when the data are scaled up from site-level to regional level, future work needs to carefully consider some uncertainties. First, soil nutrients concentration and availability are important drivers for plant nutrient composition (Castle and Neff 2009; Hao et al. 2015). In this study, we observed that

plant N and P concentrations along the wetland gradients were not correlated with latitude (or MAT) and MAP (Fig. 6). In addition to the influence of species-specific community composition of each site, we speculate that this change may also be influenced by the soil nutrient status of the habitat. In order to identify the relationship between soil nutrients and plant nutrients, the regional soil background nutrient data published in the previous study were used for correlation analysis (Table S5). The results showed that plant nutrients are at least partially controlled by total soil nutrients (Fig. S1), indicating that essential elements do not cycle independently, and plant N and P are closely linked to soil nutrient dynamics. In the future, the collection and analysis of soil-plant system nutrient data altogether should be strengthened, and the number and spatial scale of sampling points should be further expanded.

Second, higher sea levels and saltwater intrusion caused by global warming, accompanied by strong anthropogenic disturbances, could change the hydrothermal conditions and nutrient dynamics in coastal marshes. Thus, future studies need to focus on how these changes (e.g., land-use change, N deposition, and eutrophication) influence stoichiometric characteristics, and whether stoichiometric characteristics in coastal marshes are more flexible than those in other systems. Detailed studies of spatial, temporal, or site-specific coupling, and of the key driving forces that control plant nutrient-cycling, and that can also potentially influence species BN, such as soil nutrients, tidal effect, redox conditions, and salt stress, should also be conducted in coastal marsh ecosystems.

Conclusions

N and P concentrations in the present study were not correlated with latitude (or MAT) and MAP, while N:P ratio was weakly correlated with these factors, partially refuting hypothesis 1. The multivariate analyses indicated that each species had an overall N and P composition identity in whole aboveground, stems, and leaves, and that elemental composition was more flexible in some species than others, their individual population composition as well as the overall population capacity to shift their composition depending on the site ecological traits. These results showed that some plant species could shift their overall N and P composition along the wetland gradient, but species-specific N and P compositions were well maintained along the gradient rather than current biogeographical differences. Therefore, the differences in N and P concentrations and N:P ratios among the sites were mainly due to differences in species composition, and much less to intraspecific differences. These results further support the idea of the BN, approving hypothesis 2.

We also observed that foliar N and P concentration in coastal wetlands was slightly higher, and N:P ratios lower, than those in other freshwater wetlands. In this case, N:P ratios should not be important for nutrient

indicators because neither N nor P are limiting, but from a stoichiometric perspective, when both N and P concentrations in photosynthetic tissues are high, a lower N:P ratio indicates that species with high growth rates are the best adapted for their environment. Moreover, our results also suggested that soil nutrients are the key to determining the status of plant nutrients, and, in the future, large-scale soil-plant system nutrient characteristics and relationships along wetland gradients should be strengthened.

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Table 1 Comparison of N and P concentrations and N:P ratios in various plant groups for whole aboveground plant.

Classification	<i>n</i>	N (mg·g ⁻¹)	P (mg·g ⁻¹)	N:P
<i>Species</i>				
<i>S. alterniflora</i>	87	11.02±0.73a	1.60±0.10a	6.89±0.26a
<i>P. australis</i>	51	13.27±0.79b	1.30±0.06b	10.18±0.43b
<i>C. malaccensis</i>	27	13.96±2.48bc	2.17±0.19c	6.44±1.38ac
<i>S. mariqueter</i>	18	18.25±1.40d	2.34±0.07c	7.79±0.42ac
<i>S. triqueter</i>	15	21.40±3.95e	3.24±0.36d	6.57±0.52ac
<i>S. glauca</i>	15	15.38±3.65cd	2.08±0.25c	7.38±0.45ac
<i>J. serotinus</i>	3	12.83±0.45abcd	3.20±0.24d	4.01±0.42d
<i>Photosynthetic pathway</i>				
C ₃ plant	99	15.46±1.05a	1.78±0.15a	8.67±0.38a
C ₄ plant	117	11.69±0.80b	1.75±0.10a	6.69±0.37b
<i>Phylogeny</i>				
Monocotyledons	201	13.14±0.69a	1.74±0.09a	7.55±0.30a
Dicotyledons	15	15.38±3.65a	2.08±0.25a	7.38±1.08a
All species	216	13.28±0.41	1.76±0.05	7.58±0.18

The number of samples (*n*) and geometric means (mg·g⁻¹) (±SE) are shown. Differences between each group were tested using a one-way ANOVA with an LSD post hoc test of significance. Different letters within each column indicate significant differences at *P* < 0.05.

Table 2 Reduced major axis regression scaling exponents, allometric constants, and their respective 95 % confidence intervals for log10–transformed data of plant N and P concentration (N_T and P_T , respectively)

log Y_2 vs. log Y_1	α_{RMA} (95 % CI)	log β_{RMA} (95 % CI)	r^2	F	P
<i>Organ level</i>					
log N_S vs. log P_S	1.05 (0.93; 1.17)	-0.80 (-0.95; -0.66)	0.5547	188.13	<0.0001
log N_L vs. log P_L	1.36 (1.27; 1.44)	-1.44 (-1.60; -1.28)	0.1310	22.76	<0.0001
log N_{LS} vs. log P_{LS}	1.22 (1.10; 1.34)	-1.12 (-1.28; -0.97)	0.2279	44.58	<0.0001
log N_{SD} vs. log P_{SD}	1.55 (1.48; 1.63)	-1.53 (-1.68; -1.39)	0.4748	136.51	<0.0001
log N_W vs. log P_W	1.03 (0.95; 1.12)	-0.92 (-1.04; -0.79)	0.4810	198.36	<0.0001
<i>Species level</i>					
log N_{SA} vs. log P_{SA}	1.11 (0.98; 1.25)	-0.95 (-1.15; -0.76)	0.6334	146.85	<0.0001
log N_{PA} vs. log P_{PA}	1.22 (1.04; 1.40)	-1.25 (-1.53; -0.97)	0.5668	64.11	<0.0001
log N_{CM} vs. log P_{CM}	1.53 (1.32; 1.74)	-1.41 (-1.76; -1.07)	0.0604	1.61	=0.2165
log N_{SM} vs. log P_{SM}	1.02 (0.77; 1.27)	-0.92 (-1.37; -0.48)	0.4310	12.12	<0.01
log N_{ST} vs. log P_{ST}	1.45 (1.20; 1.70)	-1.42 (-1.89; -0.94)	0.8287	62.89	<0.0001
log N_{SG} vs. log P_{SG}	1.64 (1.35; 1.92)	-1.62 (-2.11; -1.13)	0.5535	16.18	<0.01

N_S = stem N concentration; P_S = stem P concentration; N_L = leaf N concentration; P_L = leaf P concentration; N_{LS} = leaf sheath N concentration; P_{LS} = leaf sheath P concentration; N_{SD} = seed N concentration; P_{SD} = seed P concentration; N_W = N concentration of whole aboveground plant; P_W = P concentration of whole aboveground plant; N_{SA} = N concentration of *S. alterniflora*; P_{SA} = P concentration of *S. alterniflora*; N_{PA} = N concentration of *P. australis*; P_{PA} = P concentration of *P. australis*; N_{CM} = N concentration of *C. malaccensis*; P_{CM} = P concentration of *C. malaccensis*; N_{SM} = N concentration of *S. mariqueter*; P_{SM} = P concentration of *S. mariqueter*; N_{ST} = N concentration of *S. triqueter*; P_{ST} = P concentration of *S. triqueter*; N_{SG} = N concentration of *S. glauca*; P_{SG} = P concentration of *S. glauca*.

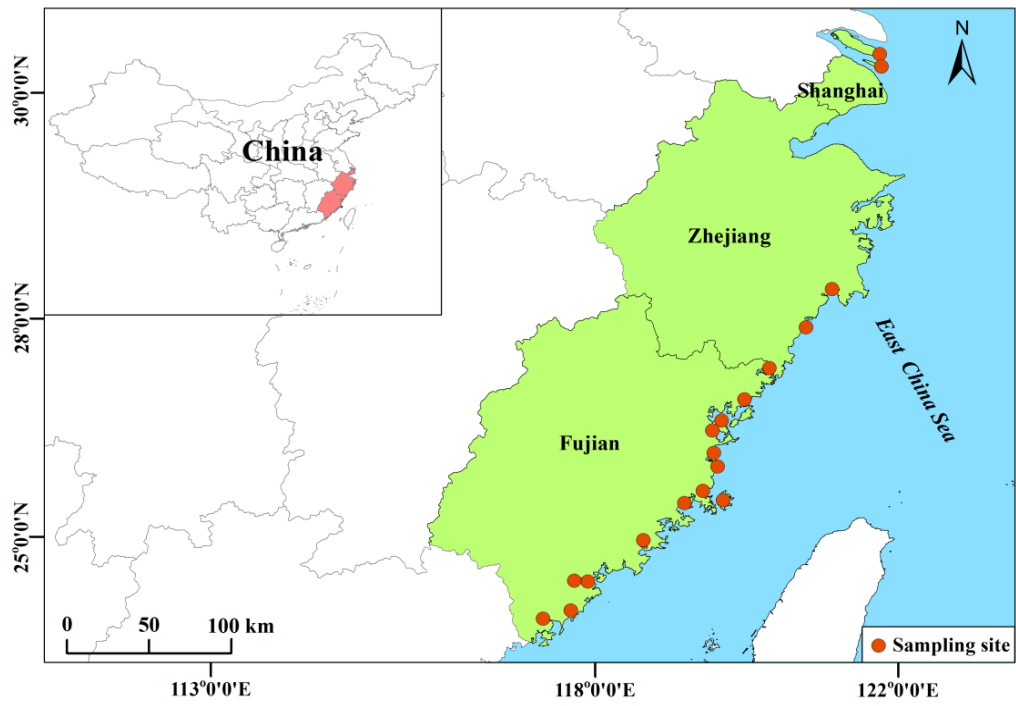


Fig. 1. Locations of the sampled coastal wetlands along the East China Sea, China

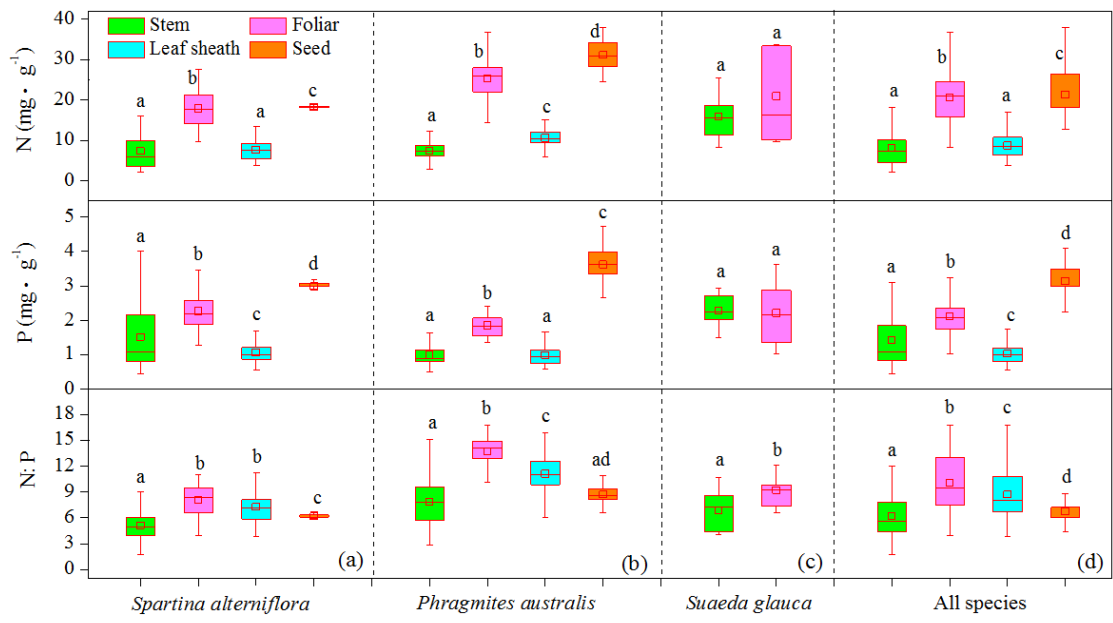


Fig. 2. Box-and-whisker plots showing the N and P concentrations and N:P ratios for the different organs of the observed plant species. Only three species have leaves clearly differentiated from stems and thus that have been analyzed apart from stem. The data points for the species represent the means of the sampling points. Lower letters above each bar indicate significant differences at $P < 0.05$ among the organs from the same species.

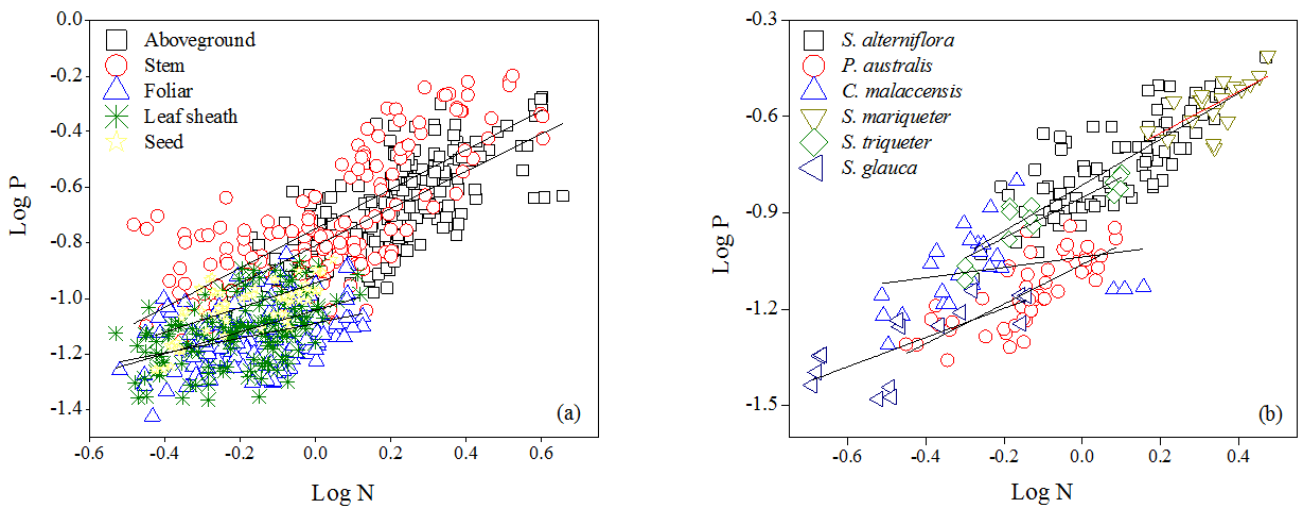


Fig. 3 Log–log bivariate plots illustrating the allometric relationships between N and P concentration for plant organs (a) and species (b). Lines are reduced major axis regression curves (for summary regression statistics, see Table 2) (for details, see Niklas 2006).

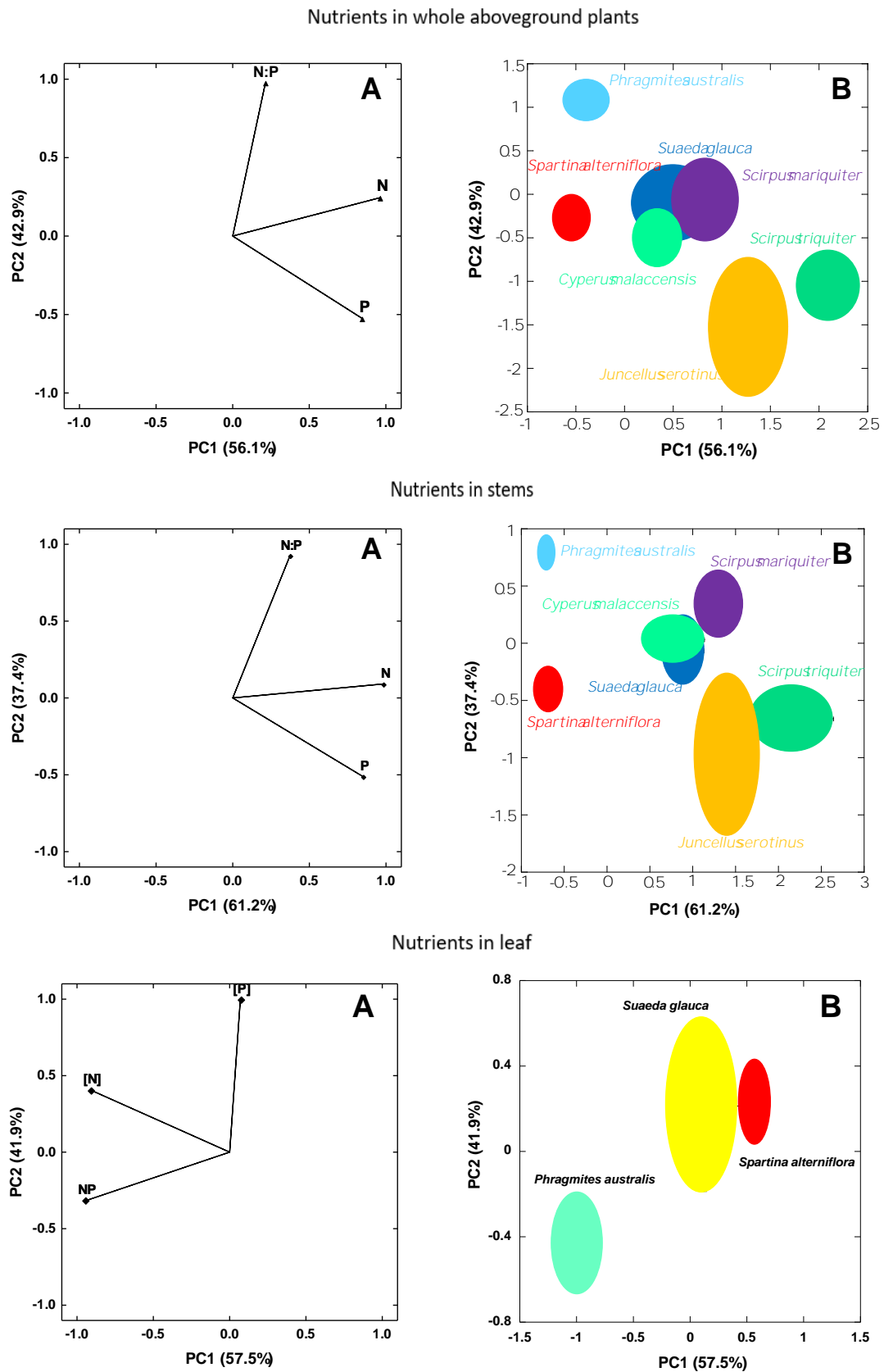


Fig. 4. Principal component analysis of N and P concentrations and N:P ratios (A) and the distribution (mean \pm 95% confidence interval) for whole aboveground plants, stems and leaf along gradient (B), respectively. Only three species have leaves clearly differentiated from stems and thus that have been analyzed apart from stem.

Aboveground nutrient concentrations in three species growing in the same three sites

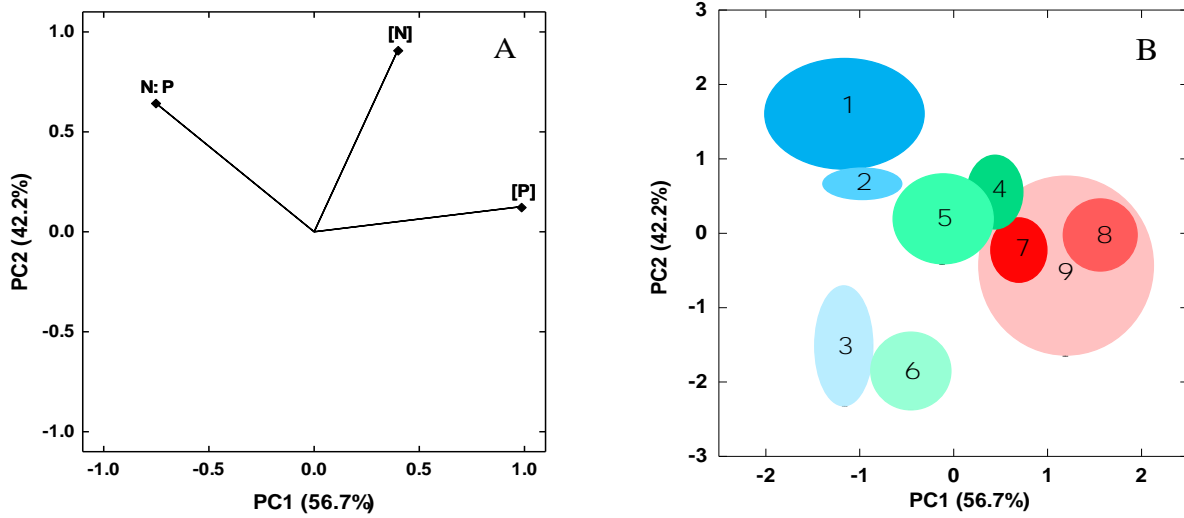


Fig. 5. Principal component analysis of N and P concentrations and N:P ratios for whole aboveground plants (A) and the distribution (mean \pm 95% confidence interval) of three of the dominant species that coincided at three sites along gradient (B). 1, *C. malaccensis* on Changxing Island; 2, *C. malaccensis* in Dongshan Bay; 3, *C. malaccensis* in Sandu Bay; 4, *P. australis* on Changxing Island; 5, *P. australis* in Dongshan Bay; 6, *P. australis* in Sandu Bay; 7, *S. alterniflora* on Changxing Island; 8, *S. alterniflora* in Dongshan Bay; 9, *S. alterniflora* in Sandu Bay.

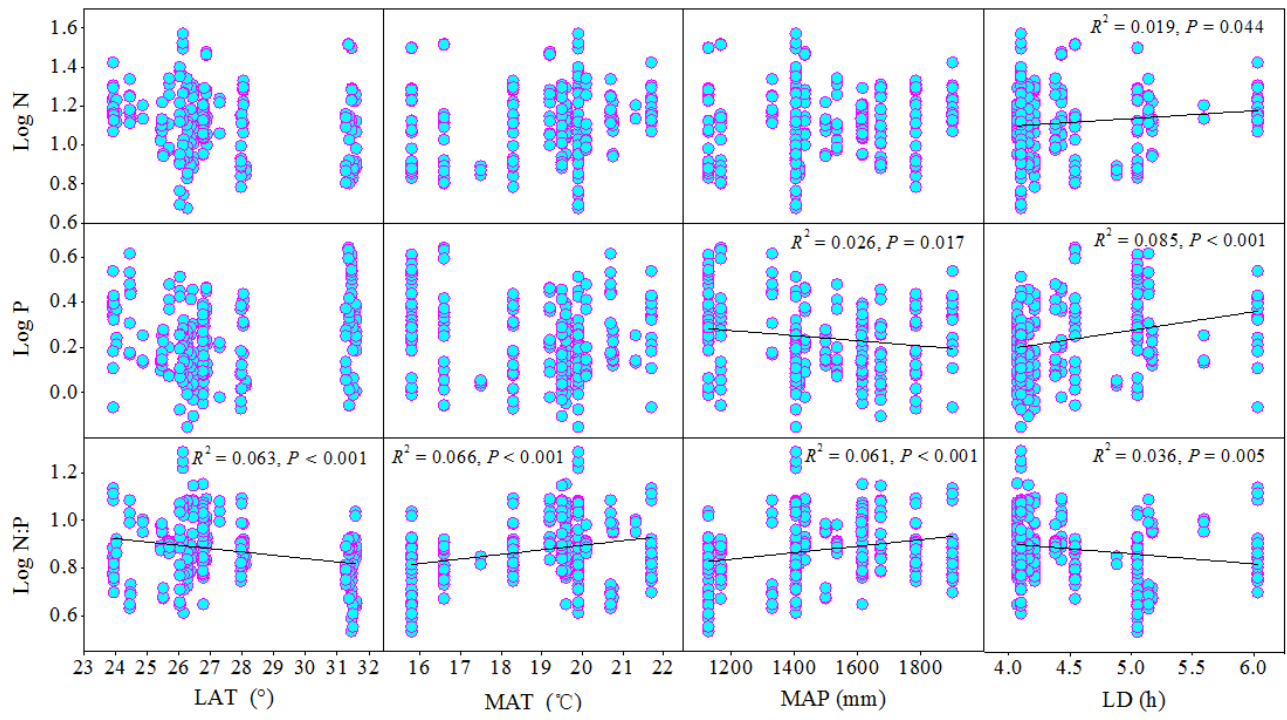


Fig. 6. Relationships between the log₁₀-transformed N and P concentrations and N:P ratios with latitude (LAT), mean annual temperature (MAT), mean annual precipitation (MAP), and light duration (LD) for all species tested. The ordinate data points represent the N and P concentrations and N:P ratios for whole aboveground plants after log₁₀-transformation.

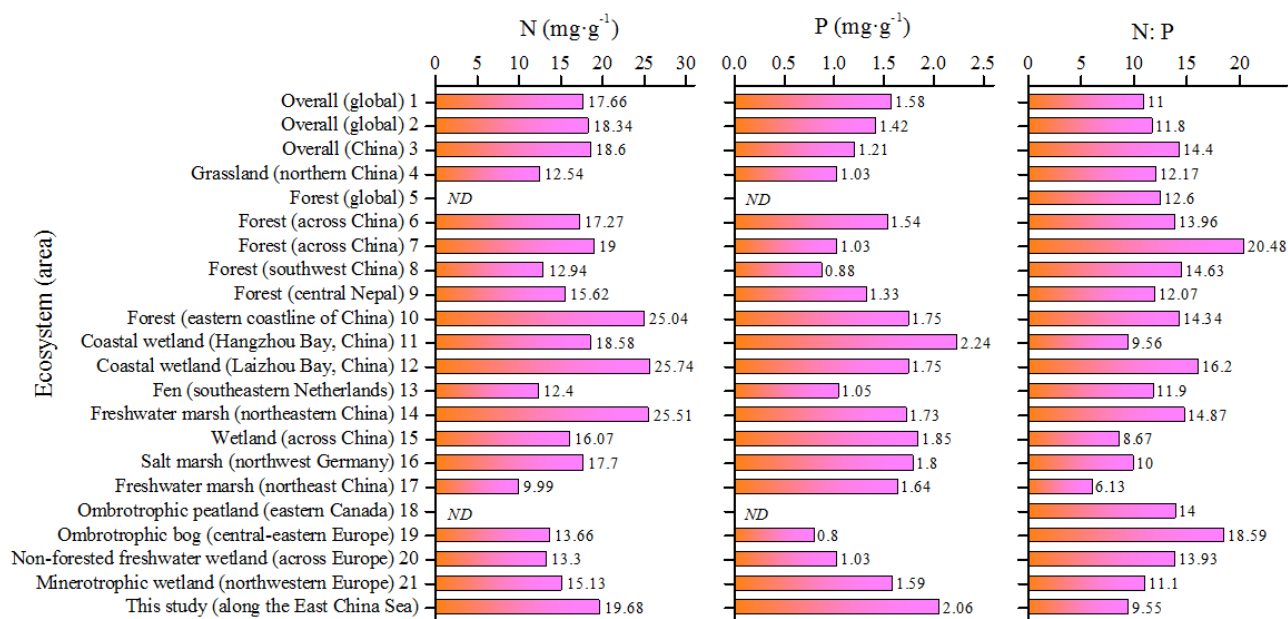


Fig. 7. Foliar N and P concentrations and N:P ratios in plants of coastal wetlands (this study) compared to global and regional data (data from: 1. Elser et al. 2000; 2. Reich and Oleksyn 2004; 3. Han et al. 2005; 4. Lü et al. 2016; 5. Mcgroddy et al. 2004; 6. Wu et al. 2012a; 7. Sun et al. 2015a; 8. Mo et al. 2015; 9. Müller et al. 2017; 10. Zhang et al. 2018; 11. Wu et al. 2012b; 12. Rong et al. 2015; 13. Güsewell et al. 2003; 14. Liu et al. 2015; 15. Hu et al. 2014; 16. Minden and Kleyer 2014; 17. Mao et al. 2016; 18. Wang and Moore 2014; 19. Jiroušek et al. 2011; 20. Güsewell and Koerselman 2002; 21. Willby et al. 2001). *ND* = no data.