Effects of Spatial Expansion Between *Phragmites Australis* And *Cyperus Malaccensis* On Temporal Variations And Bioaccumulation of Vanadium In Coastal Marshes of The Min River Estuary, Southeast China

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Abstract

Vanadium (V) plays important roles in physio-ecological processes of marsh plants. To investigate the effects of spatial expansion between native invasive species (*Phragmites australis*, PA) and common native species (*Cyperus malaccensis*, CM) on temporal variations and bioaccumulation of V in coastal marshes of the Min River estuary, *in situ* filed sampling was conducted in PA marsh (PAM, before expansion), CM marsh (CMM, before expansion) and ecotonal marsh (EM, during expansion, marsh plants were denoted by PA' and CM') at different seasons by space-for-time substitution method. Results showed that, over all sampling seasons, the mean V contents in marsh soils ranged from 99.71 to 108.41 $mg\cdot kg^{-1}$ which exceeded its background value in soils of Fujian province (78.3 $mg\cdot kg^{-1}$). The V levels in soils differed among seasons or marshes. Higher V contents in soils of PAM, EM and CMM generally occurred in spring and winter. Over all sampling seasons, the V levels in profiles of EM were much higher than those of PAM and CMM. The temporal variation of V levels in soils of EM might rest with the alterations of soil pH, SOM and plant ecological traits during the spatial expansion. Although the V contents in PA, PA', CM' and CM differed among tissues, both the roots/stems (R/S) and roots/leaves (R/L) ratios were larger than 1 while the stems/leaves (S/L) ratios were less than 1, implying that the values in roots were much higher than those in other tissues. The V levels in tissues differed among species or seasons, which could be interpreted by the differences in ecological traits among plants and the competitive absorption for V by plants during the spatial expansion. Allocations of V in organs differed among seasons or species and roots were the main V stock of plant subsystems. This paper found that the V in soils of the Min River estuary existed enrichment process and the spatial expansion between PA and CM promoted its enrichment in soils and its bioaccumulation by plants.

Introduction

Vanadium (V) is vital beneficial element, which play important roles in many physio-ecological processes of marsh plants (Zhu et al., 2016). Similar to molybdenum (Mo), V is indispensible beneficial element which not only can promote the biological fixation of nitrogen but also can enhance the absorption and utilization of iron (Fe) by plants and eventually influence on the biosynthesis of chlorophyll (Wang and Wei, 1995; Nawaz et al., 2018). However, excessive amount of V might inhibit the adenosine triphosphatase in cell membrane of roots, retard the growth of marsh plants and reduce the absorption of calcium and phosphate by plants (Jiao and Teng, 2008). Marsh soil is the key V stock and the V bioaccumulation by plants not only reflects its bioavailability in soils but also indicates its biogeochemical behaviors in marsh ecosystem (Li et al., 2020a).

Coastal marsh is one of the most sensitive ecosystems where the material-energy exchanges between fluvial ecosystem and marine ecosystem generally occur (Simas et al., 2001). As affected by the mixing of freshwater and seawater, the physico-chemical conditions in environmental medium (e.g., temperature, grain particle, salinity, pH and redox) are greatly and frequently changed (Moran et al., 1996). The coastal marsh is also affected by severe hydrodynamic forces, frequent erosion and deposition and high intensity human activities. All these induce the enrichment and biogeochemical processes of elements in coastal marsh are very complicated (Sun et al., 2017). In the past decade, there has been an ever-increasing interest in discussing the distribution and storage of biogenic elements (e.g., C, N, P and S) (Korol et al., 2016; Herbert et al., 2018; Wan et al., 2020; He et al., 2020) and heavy metals (e.g., Pb, Cu, Zn, Cr and Ni) (Chen & Ma, 2017; Keshta et al., 2020) in plant-soil system of coastal marshes, while information on bioaccumulation of beneficial elements (e.g., V and Co) by plants in coastal marsh is poorly documented.

The Min River estuary, located in the transition region of mid-subtropical zone and south subtropical zone, is one of the biggest rivers flowing into the East China Sea in the Fujian Province of southeast China. The marshes in the Min River estuary distribute along the riverbank or estuary and start from Zhuqi in the west and end in Chuanshi Island in the east, with a total area of 980.6 km^2 (Liu et al. 2006). Shanyutan is the largest marsh in the Min River estuary, where *Scirpus triqueter*, *Phragmites australis*, *Cyperus malaccensis* and *Cyperus compressus* are the most common native plants. Thereinto, *P. australis* and *C. malaccensis* are two dominant vegetations which are widely distributed in intertidal zone. Local historical records showed that *P. australis* (a native invasive species) first colonized the Shanyutan at about 30 ~ 40 years ago due to its dispersal from middle and upper reaches of the Min River (Tong et al., 2011). Thereafter, the marsh originally dominated by *C. malaccensis* is gradually occupied by *P. australis*, resulting in which becomes a single dominant community or even forms an ecotonal community with *C. malaccensis* (approximately 100 ~ 120 meter-wide). The spatial expansion between *P. australis* and *C. malaccensis* actually reflects the competitions of the two species for environmental resources such as light, water and nutrient (Li et al. 2020b). Existing studies have indicated that the spatial expansion of dominant species not only greatly altered the sedimentary environment and the physical or chemical conditions of marsh ecosystem (Ewanchuk et al., 2004), but also significantly influenced the ecological traits of plants and the key biogeochemical processes of elements by exert strong effects on biotic and abiotic variables of marsh (Zhang et al. 2010; Vilà et al. 2011). As jointly affected by hydrodynamic forces, tide and community succession, the biotic and abiotic conditions in ecotonal marsh of the Min River estuary might be more complex (Li et al., 2020a), which directly or indirectly influences the distribution, storage and biogeochemical behaviors of elements in plant-soil system. Although considerable efforts have been conducted in the Min River estuary to investigate the levels of biogenic elements in plant-soil systems of different marshes (Wang et al. 2018; Chen et al. 2018; Zhang et al, 2020), insufficient information is available concerning the bioaccumulation of beneficial elements by plants is still very lacking. Particularly, little is known about the temporal variations of V bioaccumulation by *P. australis* and *C. malaccensis* during their spatial expansion.

In this paper, the influences of spatial expansion between *P. australis* and *C. malaccensis* on temporal variations and bioaccumulation of V in coastal marshes of the Min River estuary were investigated by space-for-time substitution method and three typical marshes (*P. australis*, *C. malaccensis* and ecotonal marshes) were studied. It was hypothesed that the temporal variations of V bioaccumulation in *P. australis* and *C. malaccensis* might be greatly affected by their spatial expansion. Objectives of this paper were: *i*) to explore the temporal variations of V levels in soils of different marshes; *ii*) to investigate the V bioaccumulation in different plants over all sampling seasons; and *iii*) to determine the key factors influencing the bioaccumulation and transference of V in marsh plants.

Study Region And Methods

2.1 Study region

This study was carried out in intertidal zone of the Shanyutan (26°00'36"N ~ 26°03'42"N, 119°34'12"E ~ 119°40'40"E), which is located in the south of the Min River estuary (Fig. 1a), with an area of 893 hm^2 (Zhang et al., 2011). The tide is typical semi-diurnal tide and the mean tidal range is 4.37 ~ 4.46 m (Dai, 2004). During each tidal inundation, the marsh in intertidal zone is generally submerged for 3 ~ 3.5 h. The climate is warm and wet, with a mean annual temperature of 19.6°C and a mean annual precipitation of 1350 mm (Zheng et al., 2006). The marsh soil is dominated by saline soil and the main native vegetations include *P. australis*, *C. malaccensis*, *C. compressus* and *S. triqueter*.

2.2 Study methods

2.2.1 Sample collection

The space-for-time substitution method was used to investigate the influence of spatial expansion between *P. australis* and *C. malaccensis* on temporal variations and bioaccumulation of V in coastal marshes. The *P. australis* (PA) community and *C. malaccensis* (CM) community represented the stage of before expansion, while the *P. australis*-*C. malaccensis* (PA'-CM') community in ecotone represented the stage of during expansion. The elevation and hydrological regime of different communities were similar. Three experimental plots (50 m×50 m) were randomly laid in intertidal zone of the northwest Shanyutan (Fig. 1b). At each plot, three subplots (20 m×20 m) were laid in PA marsh (PAM), ecotonal marsh (EM) and CM marsh (CMM), respectively. Field sampling was conducted at above-mentioned subplots in March, July, October and January in 2016, which represented spring, summer, autumn and winter, respectively.

Aboveground and belowground biomasses were determined using quadrat method (50 cm×50 cm) at spatial scale in each subplot (three replications). The aboveground part of plants in the quadrat was clipped near the ground and the roots were dug out. The height and density of plants were measured, the roots were washed and the stem, leaf and standing litter were separated carefully. All plant samples were washed thoroughly with deionized water and then were oven-dried at 80 °C for 48 h. After the measurement of dry weights, the samples were ground into fine powder. Because the substantial roots (>98%) of *P. australis* and *C. malaccensis* were distributed in 0–60 cm depth (Li et al., 2020a), the V levels in soils of this depth were studied. Three columnar samples (0–60 cm) were obtained from the same position with plant samples. After the columnar samples were extracted, they were divided at 10 cm interval. The soil samples were air-dried, ground and sieved through a 100-mesh nylon sieve.

Soil pH and electrical conductivity (EC) in different depths (at 10 cm interval) were determined *in situ* by portable pH meter (IQ150, Spectrum, USA) and Soil & Solution EC meter (Field Scout, Spectrum, USA), respectively. Three single soil cores (5.0 cm diameter) were sampled from each layer and weighed for soil bulk density (BD) and moisture determination after being oven-dried at 105°C for 24 h. The physical and chemical properties of topsoil in different marshes of the experimental plots were shown in Table 1.

2.2.2 Sample analyses

A 0.0500 (±0.0005) g homogenized sample was digested with 2 mL HNO_3 (70%) and 2 mL H_2O_2 (30%) at 180°C for 15 h. The residue was diluted to 40 mL with deionized water for analyzing V levels by inductively coupled plasma mass spectrometry (XSeries, Thermo Company, USA). Quality assurance and quality control were assessed using duplicates, method blanks and certified reference materials (GBW10020) from the National Research Center for Standards in China with each batch of samples (two blank and one standard for each 20 samples). The recoveries of samples spiked with standards ranged from 83.2–111.2%. Soil organic matter (SOM) was determined by soil nutrient analyzer (TFW, Wuhan Tianlian Apparatus Company, China) and soil particle size was analyzed using a laser particle size analyzer (Mastersizer 2000, Malvern Instruments, UK).

2.2.3 Parameter calculation

The V stock (T_V, mg·m^{-2}) in soil was calculated by the following equation (Wu et al., 2020):

$$T_V = \sum_{i=1}^{n} BD_i \times V_i \times h_i \times 10$$

where BD_i (g·cm^{-3}) is soil bulk density of the *i* layer; V_i (mg·kg^{-1}) is V level in the *i* layer; and h_i is soil depth (10 cm).

The V stocks in tissues of plant (root, stem, leaf and standing litter) (V_i, g·m^{-2}) were calculated according to Li and Redmann (1992):

$V_i = C_i \times B_i$

where C_i (mg·kg^{-1}) is V content in the *i* part; and B_i (g·m^{-2}) is biomass of the *i* part.

Bioconcentration factors [BCF] in relation to the V concentrations in soil was calculated by the ratio $[\text{Element}]_{plant}$ and $[\text{Element}]_{soil}$ (Duman et al. 2007):

$[BCF]_{root} = C_{root}/C_{soil}$

$[BCF]_{stem} = C_{stem}/C_{soil}$

$[BCF]_{leaf} = C_{leaf}/C_{soil}$

$[BCF]_{litter} = C_{litter}/C_{soil}$

where C_{root}, C_{stem}, C_{leaf}, C_{litter} and C_{soil} were the V concentrations (mg kg^{-1}) in root, stem, leaf, litter and soil, respectively.

The V concentration quotients for roots/stems (R/S), roots/leaves (R/L) and stems/leaves (S/L) were calculated according to Dahmani-Muller et al (2000):

$R/S = C_{root}/C_{stem}$

$R/L = C_{root}/C_{leaf}$

$S/L = C_{stem}/C_{leaf}$

where C_{root}, C_{stem} and C_{leaf} were the same as above.

2.2.4 Statistical analyses

Statistical analyses were performed using SPSS 19.0 and Origin 8.5 for Windows. The analysis of variance (ANOVA) test was used to determine if the V levels in soils differed significantly among seasons (or marshes), or the V contents in plants differed significantly among seasons (or tissues) ($p < 0.05$). If ANOVA showed significant differences, multiple comparison of means was undertaken by Tukey's test with a significance level of $p = 0.05$. The stepwise linear regression analysis was used to best predict the variations of V levels in soils of different marshes based on environmental variables. The principal component analysis (PCA) was used as a first exploratory analysis to better visualize the possible environmental gradients determining the variations of V contents in soils of different marshes. In all tests, differences were considered significant only if $p < 0.05$.

Results

3.1 Temporal variation of V contents in soils of different marshes

Dissimilar variations of V content in soils of different marshes were observed over all sampling seasons (Fig. 2). Higher V levels in soils of PAM, EM and CMM generally occurred in spring and winter. The V contents in soils of PAM, EM and CMM between spring and winter, between summer and winter, and between autumn and winter showed significant differences ($p < 0.05$). The variations of V levels in soils also differed among marshes (Fig. 2). With a few exceptions, the V levels in profiles of EM were much higher than those of PAM and CMM. Compared with PAM and CMM, the mean V levels in soils of EM over all sampling seasons increased by 7.2% and 2.2%, respectively. Significant differences of V contents in soils of PAM and CMM occurred in spring ($p = 0.035$) and autumn ($p = 0.003$), while those of PAM and EM were observed in summer ($p = 0.028$) and autumn ($p = 0.009$).

3.2 Temporal variation of V bioaccumulation by plants

3.2.1 Variation of V contents in plants

The V contents in tissues of plants differed among seasons (Fig. 3). The values in roots and leaves of PA or PA' reached the maximums during spring, while those of CM achieved the highest ones in autumn. By comparison, the V contents in roots and leaves of CM' reached the maximums during autumn or winter. The highest V levels in stems of PA' and CM occurred in autumn, whereas those of PA and CM' were observed during winter or spring. The V contents in plants also differed among tissues, and, over all sampling seasons, almost all values in roots of PA, PA', CM' and CM were significantly higher than those in other tissues ($p < 0.05$). The V levels in tissues of PA' were generally higher than those of PA and, similarly, the values in organs of CM' were much higher than those of CM. With a few exceptions, the V contents in tissues of CM' were higher than those of PA' over all sampling seasons.

3.2.2 Transfer and accumulation of V in plants

Dissimilar variations of R/S, R/L and S/L ratios in plants were observed in different seasons (Table 2). The R/S and R/L ratios in PA or CM' reached the maximums in summer, while those in PA' achieved the highest values in spring. The highest S/L ratio in CM and CM' occurred in spring, whereas those in PA and PA' were observed during autumn or winter. With a few exceptions, the R/S and R/L ratios in PA' were lower than those in PA, but the values in CM' were higher than those in CM. Except for spring, the R/S ratios in CM' were higher than those in PA' in other seasons. The R/S and R/L ratios in PA, PA', CM' or CM were larger than 1, while the S/L ratios were less than 1. Over all sampling seasons, the [BCF] in aboveground parts were generally lower than those in roots (Table 3). The [BCF] in roots of PA and PA' reached the maximums in spring, while those of CM and CM' achieved the highest values in winter.

3.3 Variation of V stocks and allocations in plant-soil systems

Similar variations of V stock in profiles of different marshes were observed over all sampling seasons (Fig. 4). The V stocks in soils of EM in the four seasons were much higher than those of PAM and CMM. The higher V stocks in soils of PAM, EM and CMM occurred in winter while the lower values were observed during summer or autumn. The V stock in soils was the main body of total stock in plant-soil system (> 99%) (Table 4). Allocations of V in organs differed among seasons or species. Roots were the main V stock of plant subsystems, which achieved the higher values during spring or winter. Allocations of V in aboveground parts of PA', CM' and CM were the highest in autumn while those of PA reached the maximums in winter.

Discussion

4.1 Temporal variations of V contents in marsh soils

This paper found that the mean V levels in each layer of marsh soils over all sampling seasons ranged from 99.71 to 108.41 mg·kg^{-1} which exceeded its background value in soils of Fujian province (78.3 mg·kg^{-1}) (Chen et al., 1992) but was slightly lower than its background value in terrestrial surface of China (112 mg·kg^{-1}) (Nie, 2011), implying that the V in marsh soils of the Min River estuary existed enrichment process. It was reported that the V enrichment in soils was mainly dependent on parent material and pedogenesis (Li et al., 2020a), and higher V contents generally occurred in soils originated from parent rock with higher V levels (Wang and Liu, 1994). Besides, atmospheric deposition and anthropogenic import also influenced the V enrichment in soils (Chen and Sun, 2020a). In this paper, since the study region located in the National Nature Reserve of the Min River estuary which was strictly protected in recent 20 years, the V levels in marsh soil, to a great extent, rested with its geochemical enrichment process.

This paper indicated that the V contents in soils differed among marshes or seasons (Fig. 2), which might rest with the differences in physical and chemical properties of soils in PAM, EM and CMM. The stepwise linear regression analyses showed that the variation of V levels in soils of PAM could be better explained by soil temperature (x_1) (y=-0.93x_1 + 122.764, R^2 = 0.299, p < 0.001), while those of CMM could be explained by soil temperature (x_1), sand (x_2) and SOM (x_3) (y=-1.093x_1-0.362x_2 + 1.798x_3 + 131.3, R^2 = 0.635, p < 0.001). By comparison, the variation of V contents in soils of EM could be better explained by pH (x_4) and BD (x_5) (y = 6.115x_4-101.983x_5 + 160.575, R^2 = 0.456, p < 0.001). These implied that soil temperature, SOM and pH might be important factors influencing the temporal variations of V levels in soils of different marshes. Previous studies have reported that thermal conditions and SOM significantly affected the adsorption-desorption of metallic ions in marsh soils (Boyer et al., 2018; Li et al., 2020c) and higher SOM contents generally favored for enhancing V adsorption due to its strong complexing capacity (Du Laing et al., 2009; Zhu et al., 2016). In this paper, the variations of soil temperature over all sampling seasons could partly explain the temporal variations of V levels in soils of different marshes. Moreover, the relatively higher SOM contents in EM might also explain its higher V levels in soils (Table 1, Fig. 2). It was also reported that, under acidic condition, metals generally existed in free or ionized state which presented strong mobility (Huang, 2003; Lu and Yan, 2010). The marsh soils in the Min River estuary were acidity and were greatly affected by acid deposition (Pan, 2001; Li et al., 2020c). Although the pH in soils of PAM, EM and CMM showed narrow ranges over all sampling seasons (Table 1), the mobility of V in soils might be increased due to the lower pH values. This conclusion could partly explain the lower V levels in soils of PAM since the lower pH were observed (Fig. 2).

This paper implied that the spatial expansion between PA and CM generally increased the V contents in soils of EM over all sampling seasons (Fig. 2), and, compared with PAM and CMM, the mean values increased by 7.2% and 2.2%, respectively. As shown in Table 1, the physical and chemical properties of soils in EM were greatly altered during the spatial expansion, which might influence the variation of V levels in soils. Similar results were reported by Ehrenfeld (2003) and Chacón et al. (2009) who reported that the alterations of plant species, community structure and ecological traits during alien species invasion significantly affected the physical and chemical properties of soils. Compared with PA or CM communities, both PA' and CM' in ecotone showed higher densities but the former occupied the higher spaces while the latter occupied the lower spaces (Fig. 5b). Just for this reason, the special space combination between PA' and CM' in EM might be more favorable for intercepting the suspended particulate matter in tide. Compared with PAM and CMM, the fine particles (clay and silt) in topsoil of EM increased 13.85% and 29.10%, respectively (Table 1). Simultaneously, considerable V element might be imported into ecotone, resulting in the higher V levels in soils of EM. As shown in Fig. 5, the ecological traits of plants were also greatly altered during the spatial expansion, which might affect the variation of V levels in soils. Previous studies have reported that there were great differences in V absorption and accumulation among vegetations (Nawaz et al., 2018; Li et al., 2020a). Compared with PA or CM communities, both PA' and CM' in ecotone showed lower belowground and aboveground biomasses (Fig. 5a), indicating that the absorption amounts of V by the two plants might be not very high and this, to some extent, could explain the higher V levels in EM soil.

In order to better visualize the possible environmental gradients determining the temporal variation of V contents in soils of different marshes, the principal component analysis (PCA) was conducted (Fig. 6). In PAM, two principle components explained 92.98% of the variance. Principal component 1 (PC1), which explained 87.19% of the total variance, represented the gradient variations of plant height and aboveground biomass. Principal component 2 (PC2), which explained 5.79% of the total variance, showed the gradient variations of plant density, soil temperature and SOM. Further analyses indicated that the V levels showed strong correlation with PC2. By comparison, 84.73% of the total variance of environmental variables in EM was explained by two principle components (PC1 and PC2). PC1 represented the gradient variation of plant height and aboveground biomass, whereas PC2 showed the gradient variation of plant density and belowground biomass. Generally, the V levels showed close correlation with PC2. For CMM, 59.38% and 13.95% of the total variance of environmental variables were explained by PC1 and PC2, respectively. PC1 represented the gradient variations of plant height, aboveground biomass and soil pH, while PC2 showed the gradient variations of plant density and belowground biomass. As a whole, the V levels showed strong correlation with PC1. The above analyses indicated that the temporal variation of V levels in soils of EM, to a great extent, rested with the alterations of pH, SOM and plant ecological traits during the spatial expansion between PA and CM.

4.2 Accumulation and transference of V in marsh plants

This paper implied that the V contents in PA, PA', CM' and CM differed among tissues, and, over all sampling seasons, the values in roots were significantly higher than those in other tissues (Fig. 3). Previous studies have indicated that, as V existed in growing medium, bioaccumulation was a key adaptive strategy for most plants (Saco et al., 2013; Hou et al., 2014). The bioaccumulation for V generally occurred in roots, which was 2 ~ 1000 folds of aboveground parts (Aihemaiti et al., 2020). Moreover, the V in roots could form stable compound with calcium through the chelating and complexating the polar compound in cytoderm, which retarded the transference of soluble vanadium ion and reduced the V bioaccumulation in aboveground parts (Kaplan et al., 1990). In this paper, the R/S and R/L ratios in PA, PA', CM' or CM were larger than 1 (Table 2), implying that the V contents in roots of the four plants were significantly higher than those in aboveground parts. This conclusion could be verified by the higher [BCF] in roots of different plants over all sampling seasons (Table 3). Besides, the S/L ratios in marsh plants were less than 1 (Table 2), indicating that the limited V nutrient transferred from roots to aboveground parts might be preferentially allocated to leaves and this was favorable for the biosynthesis of chlorophyll and the metabolism of carbohydrates in photosynthesis process (Nawaz et al., 2018). It was noting that, over all sampling seasons, the V contents in standing litters were much higher that those in stems and leaves (Fig. 3), which might be dependent on the nutrients (including V) absorbed by plants and the nutrients retained in standing litters (Chen and Sun, 2020b). As mentioned above, the V in living bodies could form stable compound with calcium in cytoderm, which indicated that, as plant withered, the V in these compounds could be stranded in standing litters in large numbers due to their poor mobility.

This paper showed that the V contents in tissues differed among species. Over all sampling seasons, the V levels in tissues of PA' were generally higher than those of PA and, similarly, the values in organs of CM' were much higher than those of CM (Fig. 3). The probable reason was related to the alteration of plant ecological traits and the competitive absorption for nutrients (including V) by different plants during the spatial expansion. Compared to the pure community (PA or CM), the aboveground and belowground biomasses of PA' (or CM') significantly decreased (Fig. 5a), indicating that both the living spaces of PA' and CM' in ecotone were squeezed severely and their competitiveness for nutrient might be intense. Previous studies have found that, in habitat with limited nutrient, the competition advantage of plants generally rested with their conserved utilization for limited resources (Sardans and Peñuelas, 2014; Wang et al., 2018). It was reported that the spatial expansion of PA and CM in the Min River estuary was bi-directional (He et al., 2018) and the competitions between them rested with their ecological adaptation strategies (Li et al., 2020a). In this paper, the V contents and the [BCF] in tissues of CM' were generally higher than those of PA' over all sampling seasons (Fig. 3, Table 3), which indicated that the PA' and CM' in ecotone were very likely adopt different strategies for V absorption and utilization to maintain their competitiveness. Compared to PA, the density of PA' increased but its height, R/S and R/L ratios decreased greatly (Fig. 5, Table 2), implying that the *P. australis* might compete primarily by increasing the number of tillering and transferring the V accumulated in roots to the photosynthetic organ (leaf) preferentially. However, compared with CM, the density of CM' decreased but its height, R/S and R/L ratios generally increased (Fig. 5, Table 2), indicating that the *C. malaccensis* might resist the spatial expansion of *P. australis* by increasing the bioaccumulation of V in roots, decreasing the number of tillering and expanding the space of aboveground parts.

This paper indicated that the V levels in tissues of PA, PA', CM' and CM differed among seasons, which could be better interpreted by the differences in growth rhythm and ecological traits among plants. In this study, the V contents in roots and leaves of PA (or PA') during spring were the highest, while those in summer and autumn were much lower (Fig. 3), implying that, compared to the vigorous growth stage, the roots of PA (or PA') at initial growth stage showed higher V bioaccumulation and higher transference from roots to leaves. By comparison, the V levels in roots and stems of CM (or CM') achieved the higher values in winter (Fig. 3). Previous studies have reported that the aboveground parts of PA (or PA') almost withered in winter, while those of CM (or CM') were not dead and, particularly, stem was the main body of aboveground parts (>94%) (Wu et al., 2020; Li et al., 2020a). Thus, in order to keep alive and enhance the stress resistance for the lower temperatures in winter, the V accumulated in roots of CM (or CM') might be greatly transferred to stems. This paper also indicated that, over all sampling seasons, both the V stocks in roots of PA' and CM' were much higher, but the values in stems and leaves of the former were generally higher than those of the latter (Table 4). As mentioned above, the two plants might adopt different strategies for V absorption and utilization during the spatial expansion. Compared to CM', the PA' in ecotone might preferentially transfer the V in roots to the aboveground parts to maintain its competitiveness, which resulted in the higher V stock in its aboveground parts.

Declarations

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Tables

Table 1

Physical and chemical properties of topsoil in different marshes of the experimental plots over all sampling seasons

Marshes	Grain composition (%)			Soil bulk density ($g \cdot cm^{-3}$)	Soil moisture (%)	Electrical conductivity (EC) ($mS \cdot cm^{-1}$)	pH	Soil organic matter (SOM) (%)	Soil temperature (°C)
	Clay	Silt	Sand						
PAM	16.27 ± 0.52a	54.14 ± 0.22a	29.59 ± 0.73a	0.91 ± 0.02a	46.81 ± 4.68a	1.61 ± 0.19a	5.86 ± 0.79a	5.01 ± 0.96a	22.81 ± 6.78a
EM	15.73 ± 0.09b	64.43 ± 0.65b	19.84 ± 0.74b	0.95 ± 0.02a	48.33 ± 2.95a	1.79 ± 0.34a	6.38 ± 0.98a	5.06 ± 1.30a	22.99 ± 6.84a
CMM	9.76 ± 0.78c	52.33 ± 2.22c	37.91 ± 2.98c	0.89 ± 0.05a	48.51 ± 3.78a	1.88 ± 0.30a	6.45 ± 0.82a	4.69 ± 0.91a	23.38 ± 6.79a

Notes: PAM, Phragmites australis marsh; EM, ecotonal marsh; and CMM, Cyperus malaccensis marsh. Different letters within the same column indicate significant differences at $p < 0.05$.

Table 2
Vanadium concentration quotients for roots/stems (R/S), roots/leaves (R/L) and stems/leaves (S/L) in different marsh plants over all sampling seasons

Vegetations	Ratios	Spring	Summer	Autumn	Winter
PA	R/S	18.70 ± 5.27	25.74 ± 9.35	8.24 ± 0.27	6.83 ± 5.91
	R/L	5.93 ± 0.12	11.92 ± 5.61	3.90 ± 0.13	4.94 ± 2.33
	S/L	0.33 ± 0.10	0.45 ± 0.05	0.47 ± .00	0.92 ± 0.46
PA'	R/S	16.78 ± 5.47	12.96 ± 1.47	1.25 ± 0.59	6.61 ± 0.29
	R/L	6.38 ± 1.69	5.75 ± 1.49	3.13 ± 3.58	3.83 ± 1.07
	S/L	0.42 ± 0.24	0.44 ± 0.07	2.05 ± 1.89	0.58 ± 0.14
CM'	R/S	6.34 ± 1.91	25.79 ± 17.67	10.99 ± 2.02	14.09 ± 1.98
	R/L	5.86 ± 0.40	8.22 ± 4.26	1.93 ± 0.54	NA
	S/L	0.96 ± 0.23	0.34 ± 0.07	0.18 ± 0.08	NA
CM	R/S	4.74 ± 2.54	9.26 ± 3.68	10.49 ± .39	14.00 ± 2.73
	R/L	3.57 ± 2.10	5.15 ± 2.49	4.72 ± 3.86	NA
	S/L	0.74 ± 0.05	0.55 ± 0.05	0.42 ± 0.27	NA

Notes: NA, not available. PA, Phragmites australis; CM, Cyperus malaccensis; PA', Phragmites australis in ecotonal marsh; and CM', Cyperus malaccensis in ecotonal marsh.

Table 3
Bioconcentration factors (BCF) of vanadium in organs of different marsh plants over all sampling seasons

Tissues	Vegetations	Spring	Summer	Autumn	Winter
Roots	PA	0.10 ± 0.02	0.06 ± 0.02	0.06 ± 0.01	0.07 ± 0.04
	PA'	0.19 ± 0.00	0.06 ± 0.03	0.04 ± 0.05	0.07 ± 0.01
	CM'	0.12 ± 0.01	0.12 ± 0.03	0.10 ± 0.03	0.15 ± 0.01
	CM	0.08 ± 0.06	0.10 ± 0.04	0.15 ± 0.07	0.17 ± 0.08
Stems	PA	0.01 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.01
	PA'	0.01 ± 0.00	0.00 ± 0.00	0.03 ± 0.02	0.01 ± 0.00
	CM'	0.02 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
	CM	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
Leaves	PA	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
	PA'	0.03 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.02 ± 0.01
	CM'	0.02 ± 0.00	0.02 ± 0.00	0.06 ± 0.03	0.00 ± 0.00
	CM	0.02 ± 0.00	0.02 ± 0.00	0.04 ± 0.02	0.00 ± 0.00
Standing litters	PA	0.04 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.02 ± 0.01
	PA'	0.08 ± 0.01	0.03 ± 0.00	0.03 ± 0.00	0.04 ± 0.01
	CM'	0.10 ± 0.03	0.04 ± 0.01	0.05 ± 0.02	0.08 ± 0.04
	CM	0.12 ± 0.01	0.06 ± 0.01	0.05 ± 0.01	0.08 ± 0.01

Notes: PA, Phragmites australis; CM, Cyperus malaccensis; PA', Phragmites australis in ecotonal marsh; and CM', Cyperus malaccensis in ecotonal marsh.

Table 4

Stocks and allocations of vanadium in plant-soil systems of Phragmites australis, Cyperus malaccensis and ecotonal marshes over all sampling seasons

Marshes	Vegetations	Seasons	Items	Roots	Aboveground parts		Standing litters	Plant subsystems	Soils (0–60 cm)	Plant-soil systems
					Stems	Leaves				
PAM	PA	Spring	Stock ($mg \cdot m^{-2}$)	14.61 ± 5.40	0.01 ± 0.00	0.02 ± 0.00	3.02 ± 1.12	17.66	55128.19	55145.85
			Percent (%)	82.73 [a]	0.07 [a]	0.12 [a]	17.08 [a]	0.03[b]	99.97 [b]	100
		Summer	Stock ($mg \cdot m^{-2}$)	10.24 ± 0.74	0.19 ± 0.02	0.19 ± 0.00	0.60 ± 0.17	11.22	53090.48	53101.7
			Percent (%)	91.22 [a]	1.70 [a]	1.73 [a]	5.35 [a]	0.02 [b]	99.98 [b]	100
		Autumn	Stock ($mg \cdot m^{-2}$)	8.29 ± 2.19	0.55 ± 0.17	0.23 ± 0.04	1.55 ± 0.22	10.62	50563.73	50574.35
			Percent (%)	78.06 [a]	5.19 [a]	2.12 [a]	14.62 [a]	0.02 [b]	99.98 [b]	400
		Winter	Stock ($mg \cdot m^{-2}$)	8.00 ± 0.80	1.17 ± 1.17	0.03 ± 0.01	1.27 ± 0.20	10.47	62339.20	62349.67
			Percent (%)	76.41 [a]	11.18 [a]	0.32 [a]	12.08 [a]	0.02 [b]	99.98 [b]	100
EM	PA'	Spring	Stock ($mg \cdot m^{-2}$)	13.29 ± 2.68	0.06 ± 0.02	0.07 ± 0.01	2.09 ± 1.05	15.51	58338.40	58353.91
			Percent (%)	85.69 [a]	0.40 [a]	0.45 [a]	13.46 [a]	0.03 [b]	99.97 [b]	100
		Summer	Stock ($mg \cdot m^{-2}$)	8.05 ± 4.96	0.11 ± 0.04	0.19 ± 0.02	1.10 ± 0.18	9.44	56081.76	56091.2
			Percent (%)	85.19 [a]	1.14 [a]	2.00 [a]	11.67 [a]	0.02 [b]	99.98 [b]	100
		Autumn	Stock ($mg \cdot m^{-2}$)	3.66 ± .76	0.94 ± 0.55	0.21 ± 0.06	1.39 ± 0.78	6.20	56207.39	56213.59
			Percent (%)	58.98 [a]	15.23 [a]	3.40 [a]	22.39 [a]	0.01 [b]	99.99 [b]	100
		Winter	Stock ($mg \cdot m^{-2}$)	1.60 ± 0.28	0.08 ± 0.01	0.05 ± 0.02	1.85 ± 0.91	3.58	63632.86	63636.44

Notes: NA, not available. PAM, Phragmites australis marsh; EM, ecotonal marsh; and CMM, Cyperus malaccensis marsh. PA, Phragmites australis; CM, Cyperus malaccensis; PA', Phragmites australis in ecotonal marsh; and CM', Cyperus malaccensis in ecotonal marsh. [a] Percent of plant subsystem; and [b] percent of plant-soil system.

			Percent (%)	44.76 [a]	2.11 [a]	1.37 [a]	51.76 [a]	0.01 [b]	99.99 [b]	100
	CM'	Spring	Stock (mg·m^{-2})	5.52 ± 0.69	0.28 ± 0.16	0.0037 ± 0.00	1.41 ± 0.84	7.21	58338.40	58345.61
			Percent (%)	76.52 [a]	3.88[a]	0.05 [a]	19.55 [a]	0.01 [b]	99.99 [b]	100
		Summer	Stock (mg·m^{-2})	2.79 ± 1.35	0.10 ± 0.08	0.0031 ± 0.0010	0.07 ± 0.01	2.96	56081.76	56084.72
			Percent (%)	94.16 [a]	3.37 [a]	0.10 [a]	2.36 [a]	0.01 [b]	99.99 [b]	100
		Autumn	Stock (mg·m^{-2})	4.80 ± 2.53	0.48 ± 0.09	0.01 ± 0.01	0.16 ± 0.00	5.45	56207.39	56212.84
			Percent (%)	88.13 [a]	8.78 [a]	0.17 [a]	2.92 [a]	0.01 [b]	99.99 [b]	100
		Winter	Stock (mg·m^{-2})	7.02 ± 3.72	0.34 ± 0.10	NA	1.17 ± 0.86	8.53	63632.86	63641.39
			Percent (%)	82.30 [a]	4.01 [a]	NA	13.69 [a]	0.01 [b]	99.99 [b]	100
CMM	CM	Spring	Stock (mg·m^{-2})	6.51 ± 4.53	0.53 ± 0.07	0.01 ± 0.01	4.31 ± 1.62	11.36	57123.13	57134.49
			Percent (%)	57.31 [a]	4.67 [a]	0.09 [a]	37.94 [a]	0.02 [b]	99.98 [b]	100
		Summer	Stock (mg·m^{-2})	8.46 ± 4.26	0.70 ± 0.27	0.01 ± 0.00	1.29 ± 0.62	10.46	50984.14	50994.6
			Percent (%)	80.88 [a]	6.69 [a]	0.10 [a]	12.33 [a]	0.02 [b]	99.98 [b]	100
		Autumn	Stock (mg·m^{-2})	15.95 ± 11.67	1.44 ± 0.79	0.01 ± 0.01	0.92 ± 0.41	18.32	53434.86	53453.18
			Percent (%)	87.07 [a]	7.84 [a]	0.07 [a]	5.02 [a]	0.03 [b]	99.97 [b]	100
		Winter	Stock (mg·m^{-2})	14.94 ± 13.24	0.79 ± 0.19	NA	0.84 ± 0.00	16.57	59525.33	53453.18
			Percent (%)	90.16 [a]	4.77 [a]	NA	5.07 [a]	0.03 [b]	99.97 [b]	100

Notes: NA, not available. PAM, Phragmites australis marsh; EM, ecotonal marsh; and CMM, Cyperus malaccensis marsh. PA, Phragmites australis; CM, Cyperus malaccensis; PA', Phragmites australis in ecotonal marsh; and CM', Cyperus malaccensis in ecotonal marsh. [a] Percent of plant subsystem; and [b] percent of plant-soil system.

Figures

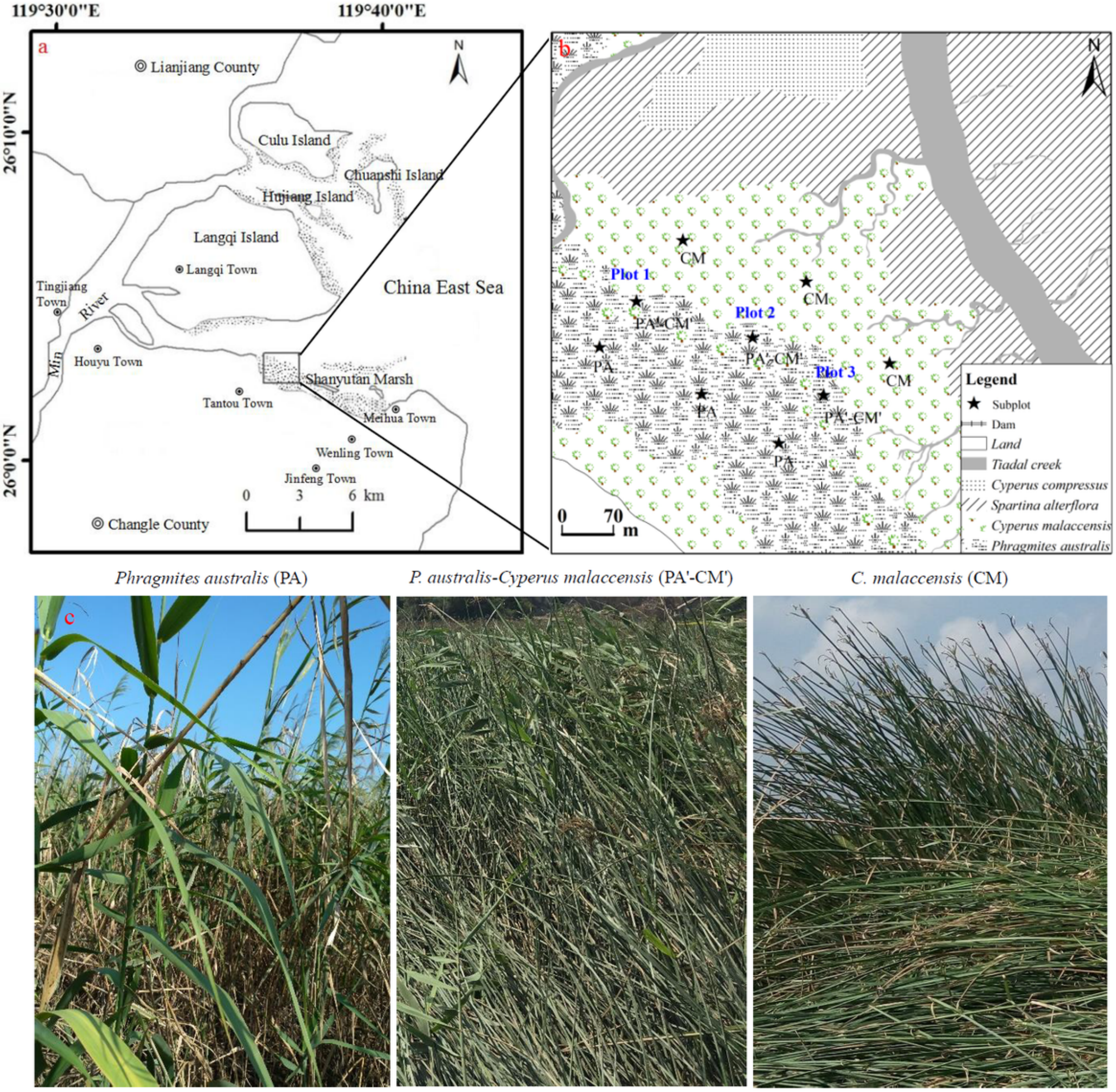

Figure 1

Sketch of the study region (a), the experimental plots (b), and the Phragmites australis, Cyperus malaccensis and P. australis-C. malaccensis communities (c).

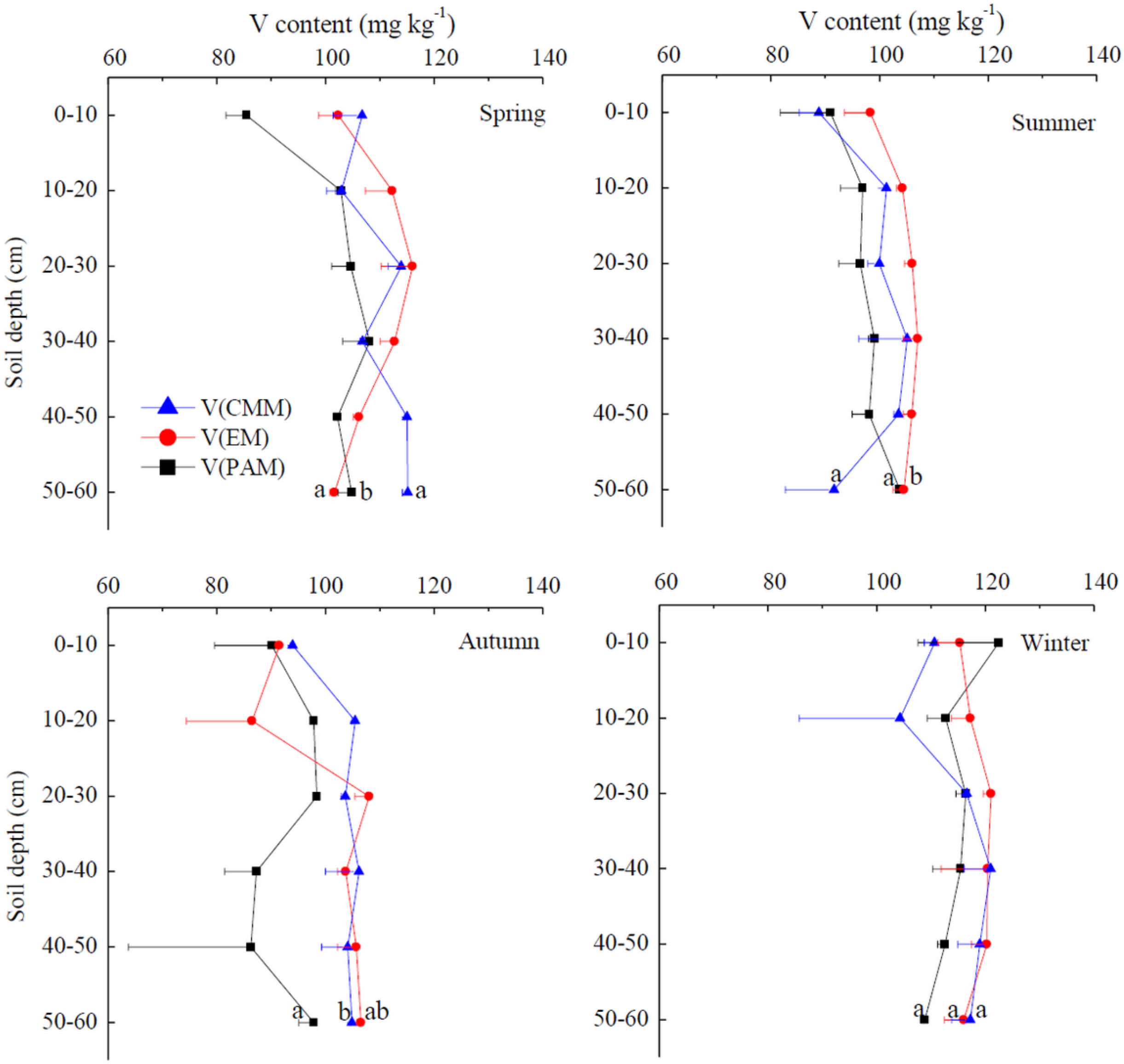

Figure 2

Temporal variations of vanadium content in soils of different marshes over all sampling seasons. PAM, Phragmites australis marsh; EM, ecotonal marsh; and CMM, Cyperus malaccensis marsh. Values with the same letters are not significantly different at p<0.05.

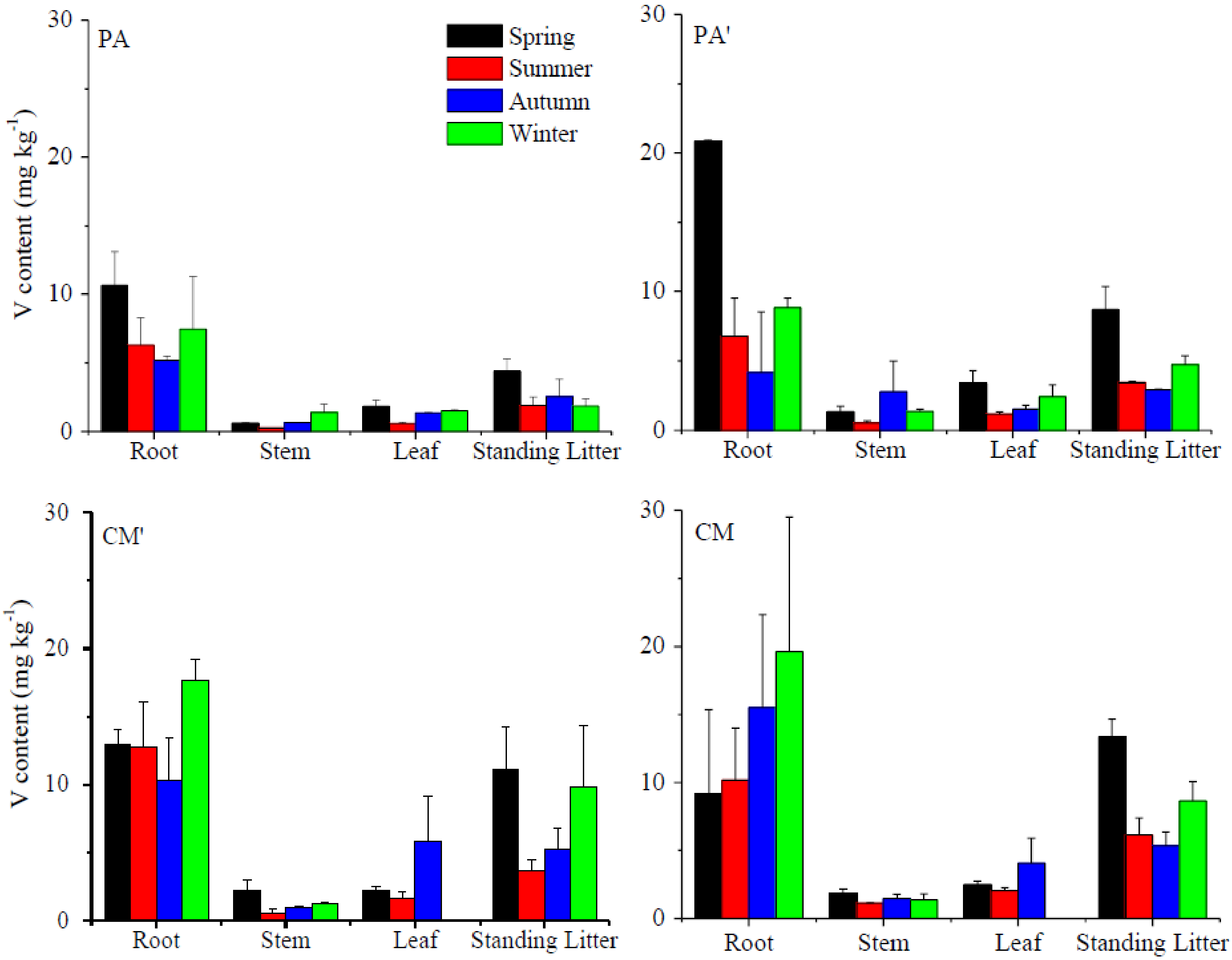

Figure 3

Temporal variations of vanadium content in tissues of different marsh plants. PA, Phragmites australis; CM, Cyperus malaccensis; PA', Phragmites australis in ecotonal marsh; and CM', Cyperus malaccensis in ecotonal marsh.

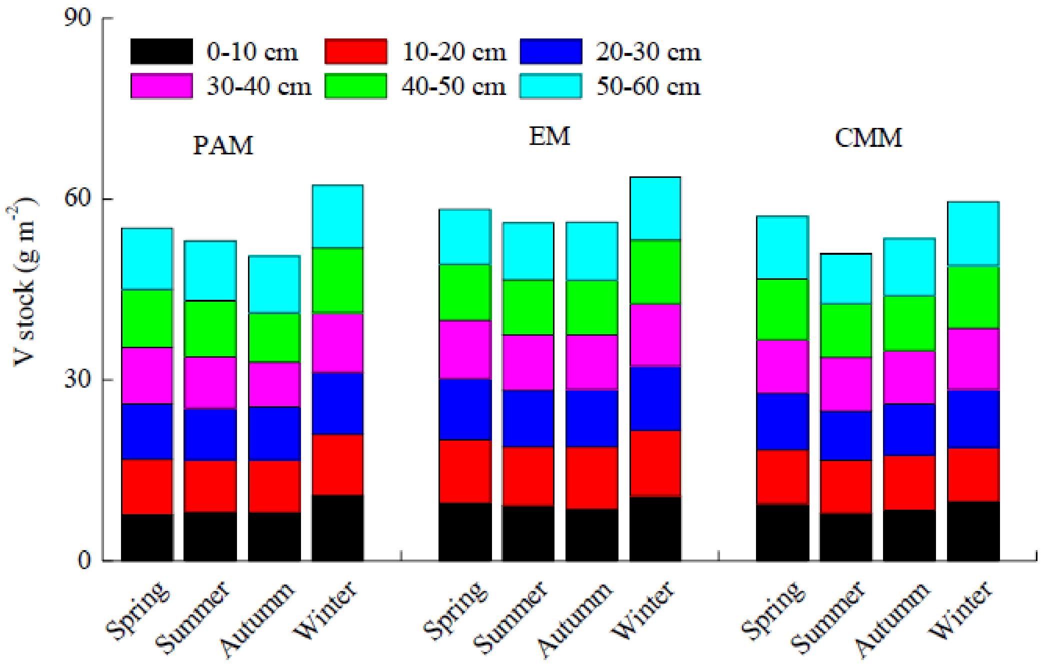

Figure 4

Stocks of vanadium in soils of different marshes. PAM, Phragmites australis marsh; EM, ecotonal marsh; and CMM, Cyperus malaccensis marsh

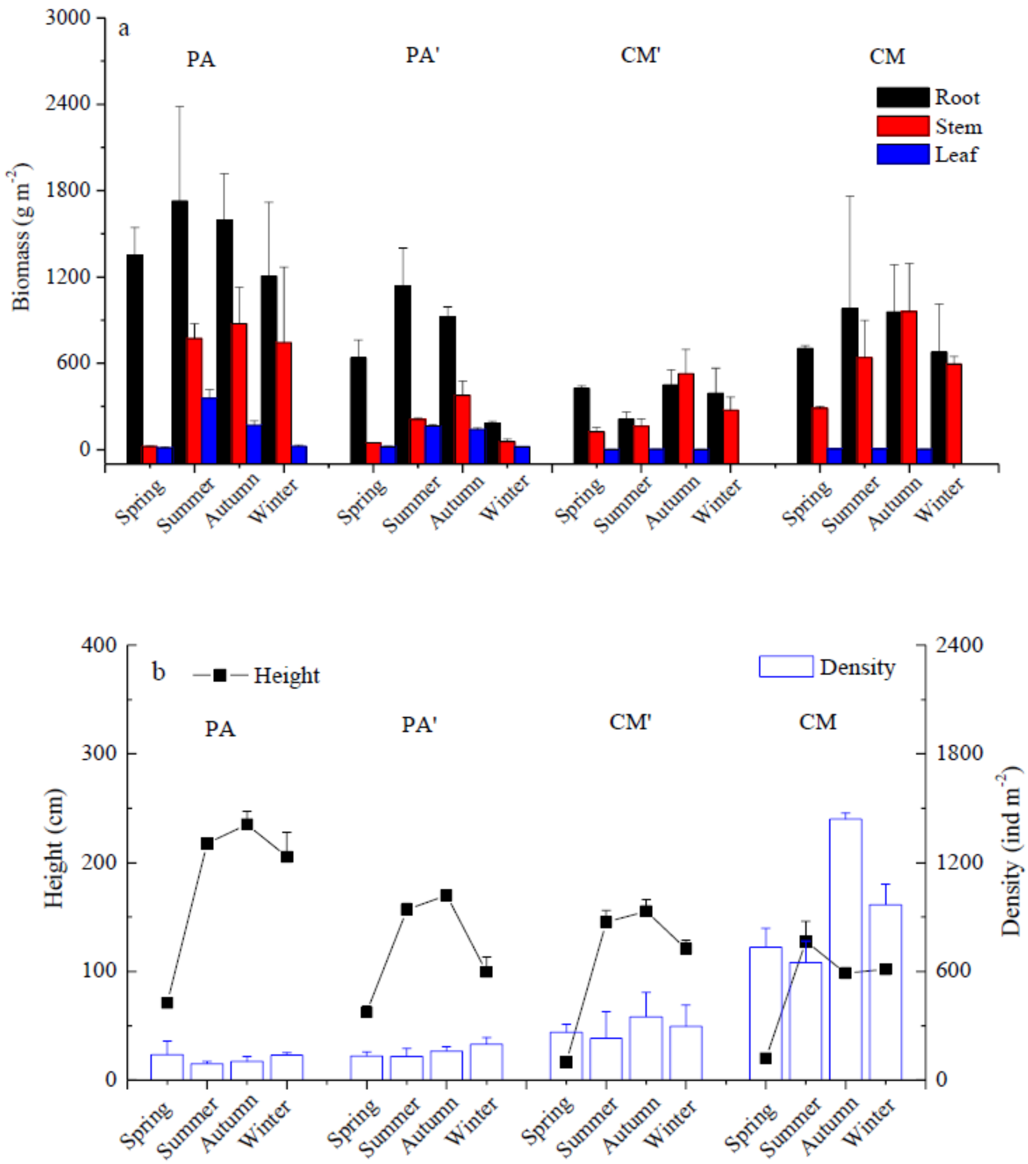

Figure 5

Temporal variations of aboveground and belowground biomasses (a), and heights and densities (b) of different marsh plants. PA, Phragmites australis; CM, Cyperus malaccensis; PA', Phragmites australis in ecotonal marsh; and CM', Cyperus malaccensis in ecotonal marsh.

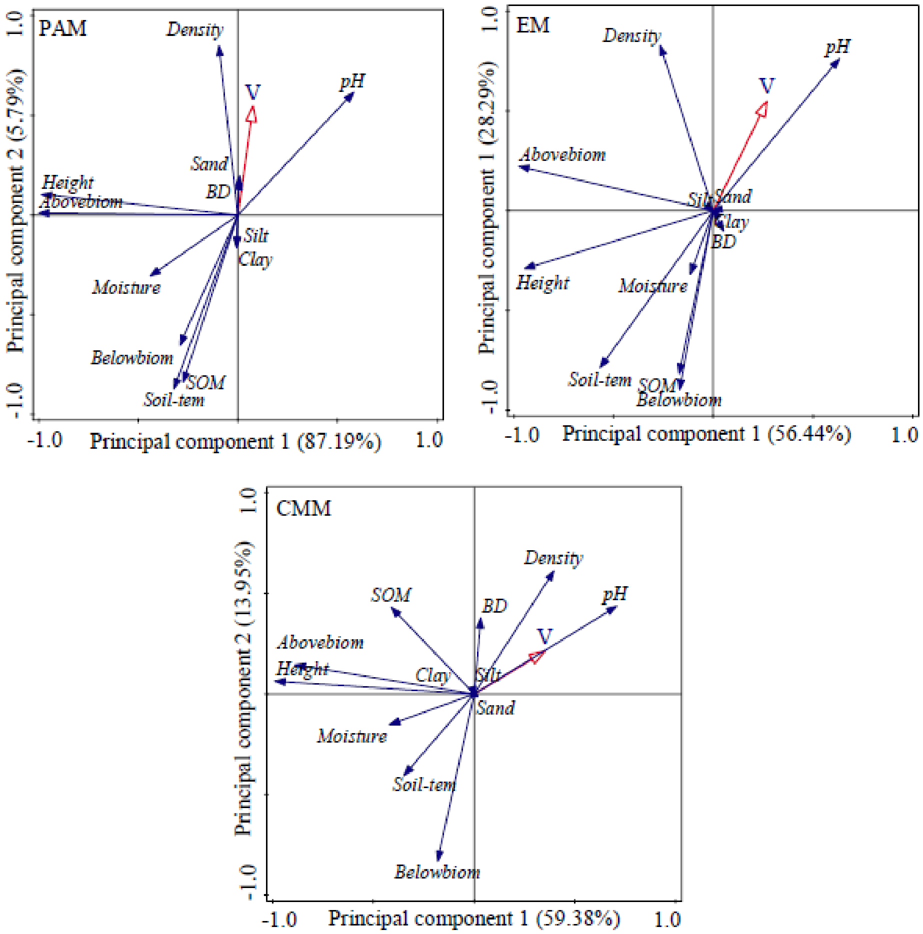

Figure 6

Principal component analyses for vanadium in soils and environmental variables in different marshes. PAM, Phragmites australis marsh; EM, ecotonal marsh; and CMM, Cyperus malaccensis marsh. Soil-tem, soil temperature; Belowbiom, belowground biomass; Abovebiom, aboveground biomass; BD, soil bulk density; and SOM, soil organic matter.