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Regulation of climate, soil and hydrological factors on macrophyte biomass allocation for coastal and inland wetlands in China

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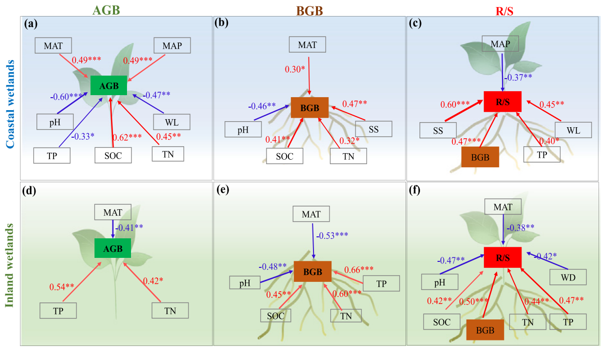
HIGHLIGHTS

- Coastal wetlands have lower root: shoot ratio (R/S) than inland ones in China.
- Spatial variation of wetland R/S was mainly due to that of belowground biomass.
- Soil and hydrological properties explain greater variation of R/S than climate.
- Soil salinity or phosphorus steers coastal or inland R/S in China, respectively.

GRAPHICAL ABSTRACT



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ABSTRACT

Knowledge of root: shoot ratio (R/S) is fundamental for our understanding of carbon allocation and storage in terrestrial ecosystems. Due to the periodic variation of water table and the difficulty of measuring belowground biomass (BGB), macrophyte biomass allocation in both coastal and inland wetlands remains unclear, especially at regional scale. In this study, 131 records of biomass allocation in wetlands were collected to examine general pattern of macrophyte R/S in relation to climate, soil, and hydrological factors in China using model selection and variance decomposition analysis. Our results showed that coastal wetlands supported higher aboveground biomass (AGB, 3.1 kg m^{-2}) but a lower R/S (1.2) than inland ones (1.47 kg m^{-2} and 3.1, respectively). The positive relationships between AGB and BGB and between BGB and R/S in coastal wetlands were significantly different from those in inland wetlands, while only inland wetlands exhibited a significant negative correlation between R/S and AGB ($R^2 = 0.19$, $p < 0.001$). Among climate (i.e., mean annual temperature and precipitation), soil (e.g., pH, salinity, soil organic carbon, soil nitrogen and phosphorus concentration), and hydrological (water level and depth for coastal and inland wetlands, respectively) properties, the latter two groups explained 64% and 31% of spatial variation for inland and coastal R/S, respectively, compared with climate (2.7% and 1.5%, respectively). Specifically, soil salinity was the most important factor in regulating R/S for coastal wetlands, while, for inland wetlands, it was soil phosphorus. This study highlights the importance of hydrology, soil salinity and nutrients on wetland R/S and BGB estimation, which could be incorporated into wetland ecosystem models to improve prediction performance for carbon dynamics and their feedbacks to climate change in the future.

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1. Introduction

Wetlands are one of the most productive ecosystems on the Earth by occupying only 4%–6% of the global land area and harboring 16% - 33% of the world's soil organic carbon (SOC, Bridgham et al., 2006). This critical ecosystem plays an essential role in regulating terrestrial carbon storage and mitigating global climate change (Whiting and Chanton, 2001; Lai et al., 2012). Since water saturation induces oxygen deficit to inhibit organic matter decomposition in wetlands, senescent biomass of aquatic macrophytes becomes an important source for soil carbon storage (Moomaw et al., 2018). However, relative to aboveground biomass (AGB), the measurement of aquatic belowground biomass (BGB) is much more difficult, causing large uncertainty in estimating wetland carbon storage. As a key parameter of biomass allocation, root: shoot ratio (BGB/AGB or R/S), is used widely for the estimation of BGB from the more easily observed aboveground one (Cairns et al., 1997; Mokany et al., 2006). Therefore, the accuracy of R/S for aquatic macrophytes is fundamental for predicting eco-physiological performance and biogeochemical cycles in wetlands (Fritz et al., 2004).

Different from land plants, aquatic macrophytes generally possess relatively well-developed aerenchyma in “roots” (actually including all belowground organs). The pattern of BGB and R/S thus needs to balance oxygen requirement between plant growth, maintenance, and nutrient removal capacity (Pezeshki, 2001; Lai et al., 2012). In addition, litters derived from shoots and roots of aquatic macrophytes are different in subsequent decomposition and nutrient release due to the distinct initial detritus quality (indicating by diverse C/N, N/P and tissue structure, Kao et al., 2003; Fierer et al., 2005; Güsewell and Freeman, 2005), which are directly related to carbon and nutrient cycles. Aquatic macrophytes thus adjust their photosynthate investment between BGB and AGB similarly with land plants to regulate R/S in coping with their habitat properties, mainly including climate, soil, and hydrology (Pan et al., 2020).

During the past decades, numerous studies have investigated effects of climate on pattern of R/S at regional and global scales. For example, the R/S of aquatic macrophytes had a negative correlation with temperature but had a positive one with precipitation (Pan et al., 2020), while R/S of land plants displayed both negative correlations (Mokany et al., 2006). The anoxic condition in wetlands changes hydrothermal effects on biomass allocation, in which root traits (e.g., root length) of aquatic plants in soil matrix balances gas transport capacity with root oxygen consumption (Moomaw et al., 2018; Pan et al., 2020). Meanwhile, climate effects, especially for precipitation, on wetland R/S were reported to be divergent among fresh- and salt-water wetlands, (Murphy et al., 2009; Sosnova et al., 2010; Pan et al., 2020). Therefore, spatial pattern of plant R/S in land might not be applicable for predicting aquatic biomass allocation in wetlands.

Among soil properties, nutrient and salinity are the most important factors for plant R/S in wetlands. Lower nutrient supply (e.g., nitrogen and phosphorus) induces more biomass investment to belowground roots for aquatic macrophytes, modifying root system morphology (e.g., thinner and longer roots, Lorenzen et al., 2001; Xie et al., 2013). Soil salinity inhibits water uptake by roots and the development of macrophytes, resulting in difference of the controlling factors for R/S between saltwater coastal and freshwater inland wetlands (Nielsen et al., 2003; Alldred et al., 2017; Robles-Aguilar et al., 2019). Moreover, soil properties are closely linking with the hydrology in wetlands. For example, the periodic tide for coastal wetlands and rainy season for inland ones considerably influence soil nutrient concentration and vertical distribution. Both water depth for inland wetlands and water level for coastal ones change relative amounts of gas and water in soil (Luo et al., 2010), regulating biomass allocation of aquatic macrophytes. However, the effect of water level or depth on root growth may differ among aquatic macrophytes with different life-forms (e.g., woody vs. herbaceous), depending on plant's competition in shallow water and physiological flooding tolerance in deep water (Sorrell et al., 2012). This is because woody and herbaceous plants have different water competitiveness and flooding tolerance (Bornette et al., 1994; Bornette and Puijalon, 2011; Schile et al., 2014) due to distinct investment in xylem structure (Kramer-Walter and Laughlin, 2017). Therefore, among coastal and inlands wetlands, the pattern of R/S for woody and herbaceous plants and its key influencing factors are inconsistent (Mitsch et al., 2013).

In China, wetlands account for nearly 10% of the global total wetlands, distributing widely and unevenly with two different subtypes: coastal and inland wetlands (Lu and Jiang, 2004). Due to the distinct geographical location, coastal and inland wetlands are generally characterized by diverse properties in soil, climate and/or hydrology (Lu et al., 2017). Coastal wetlands in China stretch across nearly 40 degrees of latitude, extending from temperate, subtropical to tropical climate zones, while inland ones cover a large altitude gradient (tens of meters to more than 5000 m), including riverine, lake, reservoir and fresh marsh (Liu et al., 2020). Although the field-monitored data of plant biomass are increasingly rich in China, the current research still focuses more on resource investigation, utilization, and restoration (e.g., Li et al., 2021; Song et al., 2021). The specific pattern of R/S in coastal and inland wetlands in China, and the controlling factors for plant R/S from climate, soil, and hydrology are still unclear, especially for woody and herbaceous plants (Lu and Jiang, 2004; Song et al., 2006; Lu et al., 2017).

In this study, we compiled 131 records of biomass allocation in China's wetlands, including coastal and inland ones. The key factors determining aquatic macrophytes' R/S were hypothesized to be different among wetland communities. We examined spatial pattern of biomass allocation and the underlying influences from climate, soil and hydrological properties in both coastal and inland wetlands with woody or herbaceous (herb) emergent macrophytes. Our objectives were to (a) address pattern of biomass allocation for emergent macrophytes in both coastal and inland wetlands in China, and (b) probe the key factors of climate (i.e., mean annual temperature [MAT] and precipitation [MAP]), soil (e.g., pH, soil organic carbon [SOC], salinity, nutrients), and hydrological (water level or depth) influencing the pattern of wetland biomass allocation. This study will demonstrate general pattern of biomass allocation and the key controlling factors in China's wetland to improve estimation of wetland carbon storage and management strategies at the regional scale.

2. Materials and methods

2.1. Data sources

Peer-reviewed papers were searched in the Web of Science for English papers and China National Knowledge (CNKI) for Chinese papers using the terms: “China”, “wetland or swamp or reservoir”, and “root: shoot ratio or belowground biomass”. We chose the studies based on the following criteria: (i) experiments were carried out in the field with records of AGB, BGB and R/S for woody or herbaceous (herb) emergent macrophytes; (ii) the studies with the values of AGB for the peak period were used if the AGB was observed monthly; (iii) the observation of BGB used excavation methods; (iv) all the observations of biomass were in natural condition without experimental manipulation; (v) the authenticity of biomass data in the published article could be cross-validated each other or by the graduate students' theses in the same site searched from Thesis & Dissertation Database in CNKI. In total, 117 published papers were selected (Appendix A in Supporting Information). We collected the data of biomass allocation in 131 aquatic plant communities from 45 sites in China (Fig. 1).

In addition to AGB, BGB and R/S, twelve site-related variables were also recorded based on the site information in published papers

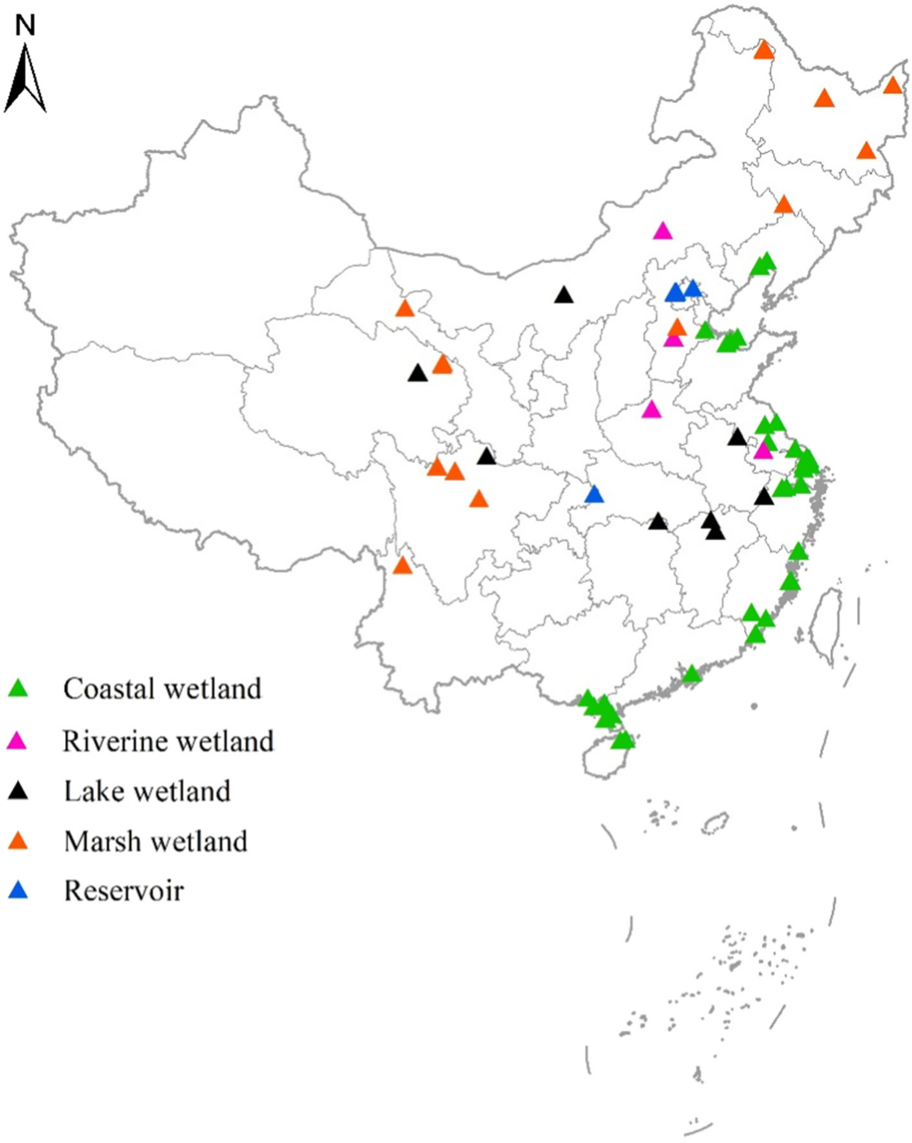

Fig. 1. Site distribution of studies about biomass allocation used in this analysis for coastal and inland wetlands in China. Inland wetlands included riverine, lake, marsh and reservoirs.

or thesis and compiled into the database (Appendix C in Supporting Information). Specifically, they included latitude, longitude, altitude, mean annual temperature (MAT) and precipitation (MAP), soil organic carbon (SOC), soil total nitrogen (TN), soil total phosphorus (TP), soil pH, soil salinity (SS), and water level (WL, level of surface water or ground water for coastal wetlands) or water depth (WD, for inland wetlands). If these 12 variables were not recorded in the selected papers or related theses, we extracted from the nearest meteorological stations in China. The types of wetlands in our study were divided into coastal and inland wetlands, which were directly defined by the published papers. Specifically, inland wetlands include riverine, lake, fresh marsh and reservoir; and coastal wetlands consist of mangrove and coastal marsh.

2.2. Statistical analysis

Analysis of variance (ANOVA) was used to test the impacts of wetland types (i.e., inland and coastal wetlands) and plant life form (i.e., woody and herb plants) on AGB, BGB, and root: shoot ratio (R/S) at significance $p < 0.05$. The relationships among AGB, BGB, R/S, and the properties of climate, soil, and hydrology were analyzed by Pearson correlation analysis. The analysis of covariance (ANCOVA) was used to compare slopes of regression lines and were carried out using SPSS ?thyc=5?> 19.0 package (IBM Company Inc., Armonk, New York, USA). The relative contributions of climate, hydrology, and soil properties for spatial variation of R/S were analyzed by the vegan package in R (http://r-forge.r-project.org/projects/vegan/). The importance of influencing factors (including types of wetlands, and properties of climate, soil and hydrology) on R/S was expressed as the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples) in R.

3. Results

3.1. Vegetation biomass and root: shoot ratio in China's wetlands

Across all 131 aquatic plant communities in this study, the mean AGB, BGB, and R/S were 3.1 ± 3.5 kg m^{-2}, 2.7 ± 4.3 kg m^{-2}, and 1.2 ± 2.3 in coastal wetlands ($n = 72$), and 1.5 ± 3.0 kg m^{-2}, 1.8 ± 3.8 kg m^{-2} and 3.1 ± 3.9 in inland wetlands, respectively ($n = 59$, Fig. 2a, c). Coastal wetlands displayed higher AGB (F =

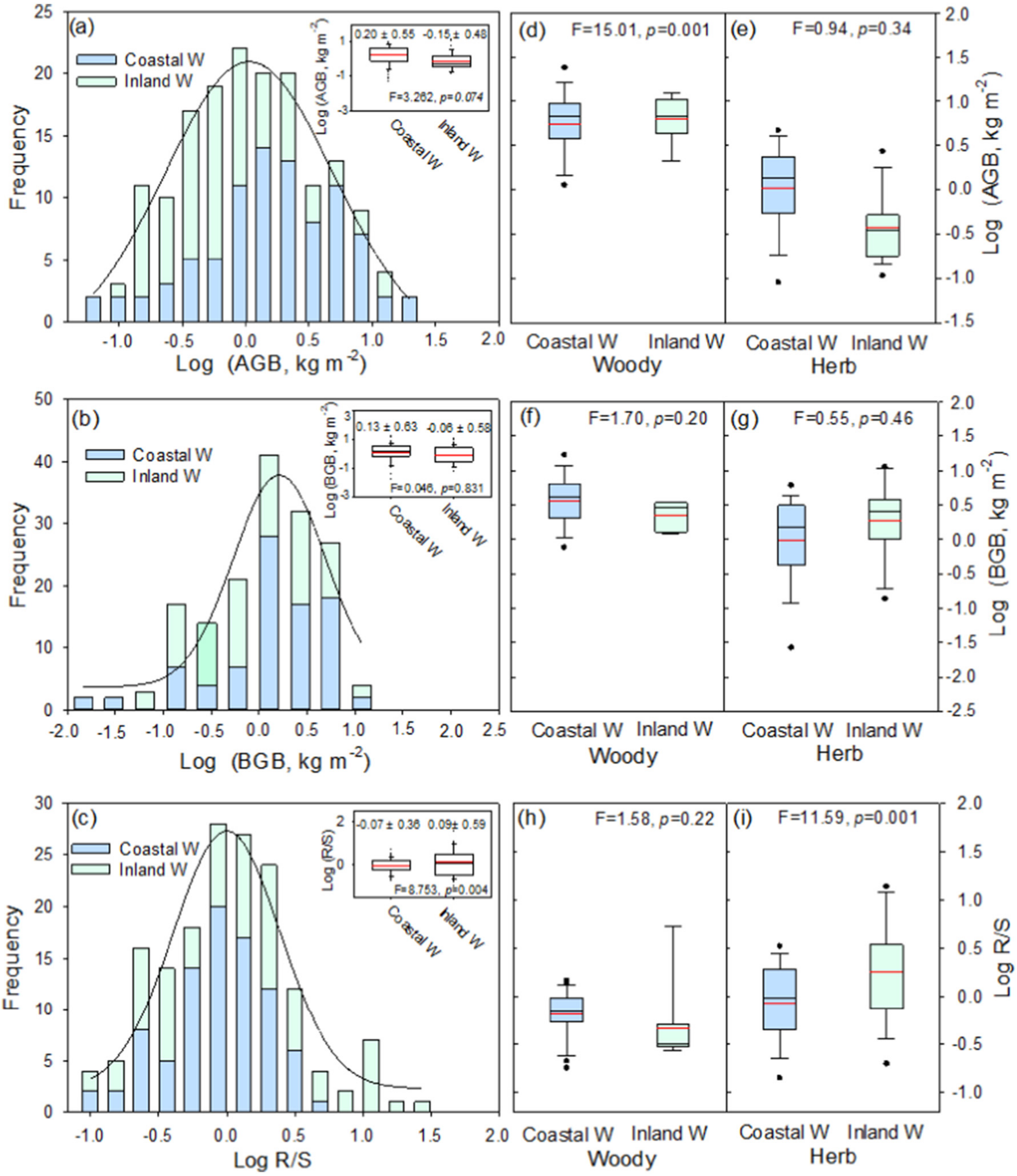

Fig. 2. Frequency distributions of logarithmic transformed (Log 10) aboveground biomass (AGB, a), belowground biomass (BGB, b), and root: shoot ratio (R/S, c) in coastal and inland wetlands (coastal W and inland W). AGB, BGB and R/S in woody and herbaceous (Herb) plants for coastal and inland wetlands were listed in plots d, e, f, g, h and i, respectively.

3.26, $p = 0.074$) but lower R/S ($F = 8.75$, $p = 0.004$) relative to inland ones (Fig. 2a, c, Table 1). Plant life form (i.e., herbs and woody plants) significantly affected AGB, BGB, and R/S ($p < 0.05$, Table 1, Fig. 2d, e, and S1). Relative to herbs, woody plants accumulated greater biomass in both above- ($F = 84.49$, $p < 0.001$) and belowground compartments ($F = 5.23$, $p = 0.024$), with a lower R/S ($F = 8.21$, $p = 0.005$; Fig. S1).

A significant correlation occurred between AGB and BGB and between BGB and R/S for both coastal and inland wetlands (Fig. 3), but these relationships in coastal wetlands were all different from those in inland wetlands ($F = 12.29$, $p = 0.001$; $F = 16.17$, $p < 0.001$; Fig. 3a, b). Coastal BGB displayed a closer correlation with AGB ($BGB = 1.01AGB^{0.94}$, $R^2 = 0.68$, $p < 0.001$) relative to that in inland wetlands ($BGB = 3.55AGB^{0.45}$, $R^2 = 0.15$, $p < 0.001$; Fig. 3a). The negative correlation between AGB and R/S was only observed in inland wetlands (Fig. 3c).

3.2. Influence of climate on biomass allocation in coastal vs. inland wetlands

The positive correlations of AGB with MAT ($R^2 = 0.24$, $p < 0.01$) and MAP ($R^2 = 0.19$, $p < 0.01$) were detected in coastal wetlands, but not in inland ones (Fig. 4a, b). In addition, MAT displayed a weak positive correlation with coastal BGB ($R^2 = 0.07$, $p < 0.05$, Fig. 4c), and negative ones with R/S in both coastal ($R^2 = 0.16$, $p < 0.01$) and inland wetlands ($R^2 = 0.20$, $p < 0.01$, Fig. 4e). The MAP among coastal wetland exhibited a negative correlation with R/S, explaining 40% variation of it ($p < 0.01$, Fig. 4f).

Table 1
The effects of types of wetlands (coastal wetlands or inland wetlands) and plants (woody or herbaceous) on above-, belowground biomass (AGB and BGB), and root: shoot ratio (R/S).

	Source	df	MS	F	Sig.
AGB	Types of wetlands	1	0.610	3.262	0.074
	Types of plants	1	15.807	84.486	**0.000**
	Types of wetlands ×Types of plants	1	1.043	5.575	**0.020**
BGB	Types of wetlands	1	0.015	0.046	0.831
	Types of plants	1	1.662	5.228	**0.024**
	Types of wetlands ×Types of plants	1	0.895	2.816	0.096
R/S	Types of wetlands	1	0.928	8.753	**0.004**
	Types of plants	1	0.871	8.211	**0.005**
	Types of wetlands ×Types of plants	1	0.097	0.981	0.340

Sig. <0.05 are significant (numbers in bold).

3.3. Influence of soil and hydrological properties on biomass allocation in coastal vs. inland wetlands

For coastal wetlands, both SOC ($R^2 = 0.36$, $p < 0.01$) and soil total nitrogen ($R^2 = 0.12$, $p < 0.05$) displayed positive correlations with AGB, while soil pH ($R^2 = 0.22$, $p < 0.01$) and water level exhibited negative ones ($R^2 = 0.24$, $p < 0.01$; Figs. S2, S3). For coastal wetlands, SOC displayed a positive correlation with BGB ($R^2 = 0.11$, $p < 0.05$; Fig. S2). Coastal R/S displayed negative correlations with both SOC ($R^2 = 0.11$, $p < 0.05$) and soil total nitrogen ($R^2 = 0.10$, $p < 0.05$), while it had positive one with soil salinity ($R^2 = 0.33$, $p < 0.01$) and water level ($R^2 = 0.17$, $p < 0.05$; Figs. S2, S3).

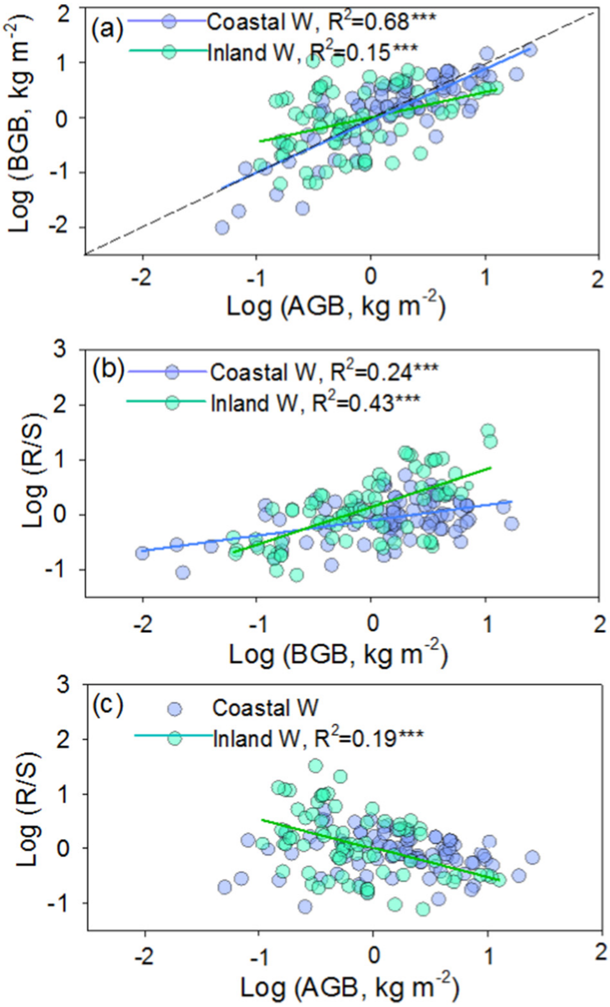

Fig. 3. The relationships of logarithmic transformed (log) AGB vs log BGB (a), log BGB vs log R/S (b), and log AGB vs log R/S (c) for coastal and inland wetlands.

For inland wetlands, soil properties had no relationship with AGB, while soil pH exhibited a negative correlation with BGB ($R^2 = 0.36$, $p < 0.01$; Fig. S2). Inland R/S displayed positive correlations with SOC ($R^2 = 0.59$, $p < 0.01$), soil total nitrogen ($R^2 = 0.21$, $p < 0.05$) and phosphorus ($R^2 = 0.43$, $p < 0.01$), but had negative ones with soil pH ($R^2 = 0.20$, $p < 0.05$) and water depth ($R^2 = 0.25$, $p < 0.01$; Figs. S2, S3).

The most important factors for spatial pattern of R/S among the twelve site-related variables in coastal and inland wetlands were soil salinity and soil total phosphorus, respectively (Fig. 5). Coastal R/S displayed a positive correlation with soil salinity ($R^2 = 0.33$, $p < 0.0001$), while inland R/S exhibited one with soil total phosphorus ($R^2 = 0.42$, $p = 0.002$; Fig. 6a, b). In total, soil properties explained 11.7% and 12.3% variations of R/S for coastal and inland wetlands, respectively (Fig. 7). Soil and hydrological properties together explained 64% and 31% of R/S variation for inland and coastal wetland, respectively (Fig. 7).

4. Discussion

4.1. Spatial variation of vegetation biomass in coastal vs. inland wetlands

Spatial pattern of vegetation biomass generally reflects the underlying effects of the heterogeneous environmental factors, mainly hydrothermal conditions in wetlands (Peregon et al., 2008; Niu et al., 2012). Across China, we found the increasing trend of AGB and BGB with MAT in coastal wetlands from north to south as well as elevating AGB with MAP (Fig. 4a–c). The positive effect of temperature on activities of photosynthesis-related enzymes and net primary production would be the main reason for this positive relationship between MAT and macrophyte biomass (Li et al., 2018). The positive effects of MAP on biomass accumulation were largely due to the closely spatial correlation between MAP and MAT ($R^2 = 0.85$, $p < 0.0001$) in coastal wetlands with low altitudes in this study (Yu et al., 2013; Xiao et al., 2019). Higher MAP generally induces lower plant investment to BGB because of increasing freshwater input by precipitation on soil matrix. Thus, increasing trend of biomass accumulation caused a negative correaltion of R/S with both MAT and MAP in coastal wetlands as the allometric growth between roots and shoots (Fig. 4, Askari et al., 2017).

For inland wetlands, neither MAT nor MAP displayed a significant correlation with AGB or BGB across China (Fig. 4). Inland macrophyte biomass didn't exhibit a significant trend with geographic location (including latitude, longitude and altitude) in this study due to complex distributions of vegetation and the controlling factors (e.g., net radiation, Xiao et al., 2019). The confounding effect from altitudes ranging from 10 m (e.g., Hongze Lake) to 3400 m (e.g., Ruoergai wetland, Shimono et al., 2010) caused considerable differences in vegetation types (e.g., from inland riverine forests to marshes in alpine wetlands, Yu et al., 2013) among inland wetlands. In addition, the regions with higher altitude generally have a lower radiation than those with lower one, limiting growth of plant biomass in inland wetlands (Bhandari and Zhang, 2019). However, R/S in inland wetlands displayed a negative correlation with MAT (Fig. 4), which agreed with the effect of temperature on mass fraction of belowground compartments (Poorter et al., 2012).

4.2. Effects of climate, soil, hydrological conditions on biomass allocation in coastal vs. inland wetlands

The biomass allocation of aquatic macrophytes is usually affected by physical and chemical conditions, including climate, soil, and hydrological properties (Fritz et al., 2004). In this study, the contributions of soil and hydrological properties on macrophytes' R/S were predominant for both inland and coastal wetlands (Fig. 7) relative to that of climate condition (i.e., temperature and precipitation, Fig. 4). For wetlands,

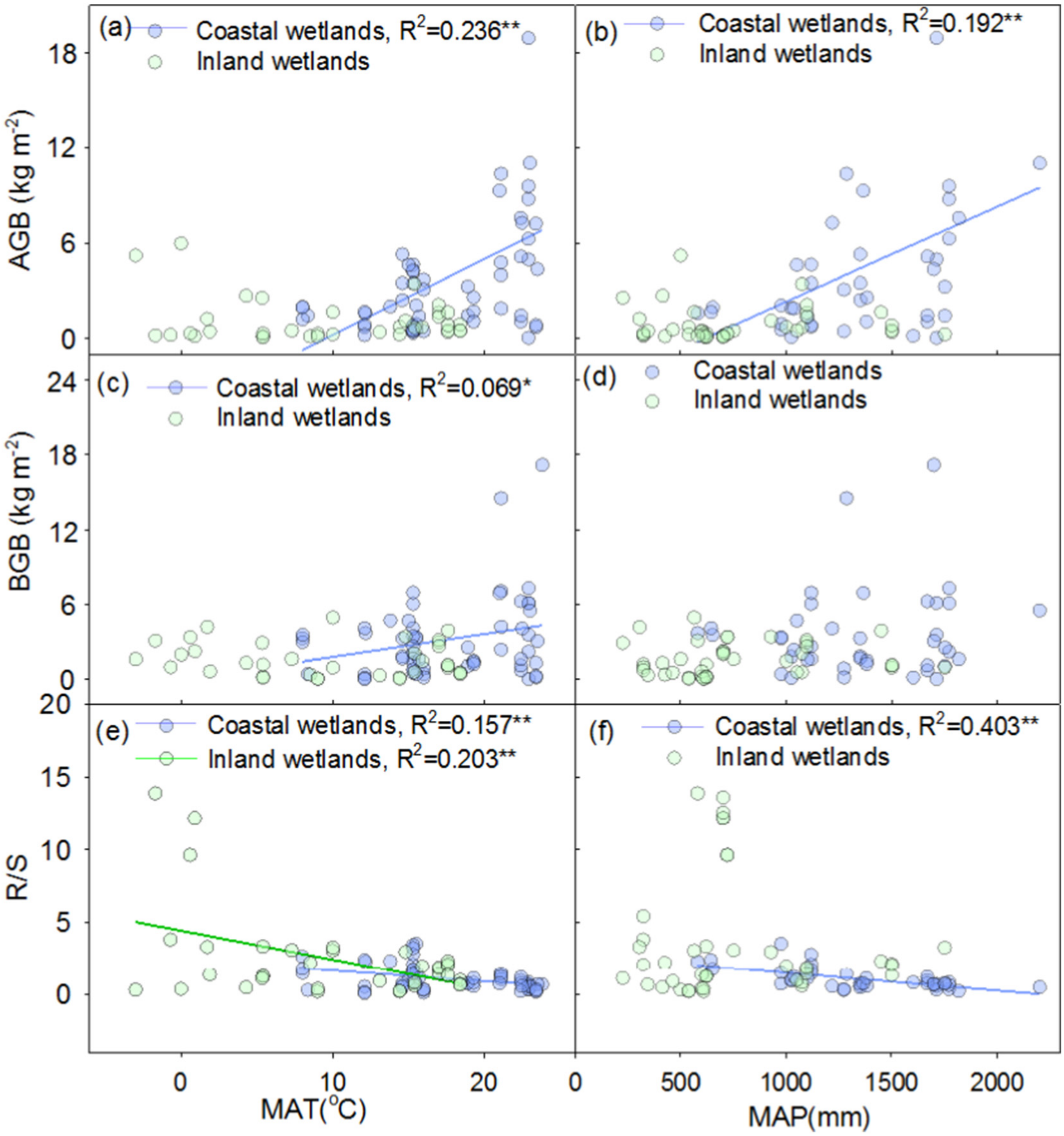

Fig. 4. The correlations of mean annual temperature (MAT, a, c, e) and precipitation (MAP, b, d, f) with AGB and BGB, and R/S. The symbols ** and *** indicate the coefficients are significant at <0.01 and <0.001.

emergent vegetation is generally an important source of organic matter in soil or sediment, while soil organic matter can improve plant growth in turn due to its close relationship with soil fertility (Sahrawat, 2005; Ouyang et al., 2010). However, the positive correlation between soil organic carbon (SOC) and living biomass was found in coastal wetlands but not in inland ones (Fig. S2). With sufficient soil or sediment nutrients, coastal macrophytes would allocate relatively low proportion of biomass to belowground compartments (i.e., non-photosynthetic tissues), resulting in a negative correlation between SOC and R/S (Fig. S2, Shipley and Meziane, 2002). In our study, the negative correlation between MAT and R/S (Fig. 3) and a positive relationship between MAT and SOC occurred (Table 2). Thus, the inhibition of anaerobic environment on organic matter decomposition and the positive effect of MAT on plant production caused the negative relationship of SOC with R/S in coastal wetlands (Zhang et al., 2010).

In inland wetlands, however, the positive correlation was found between SOC and R/S, which could be caused by the similar decreasing tendency of both SOC and R/S with MAT in inland wetlands (Fig. 4 and Table 3). The periodic drought in inland wetlands resulted in the negative effect of MAT on SOC due to the accelerated decomposition (Xiao et al., 2019). Therefore, the spatial positive correlation between SOC and R/S across inland wetlands depends on the underneath linkage with MAT (Rasse et al., 2005; Gross and Harrison, 2019). In addition, soil TN also displayed negative and positive correlations with R/S for coastal and inland wetlands, respectively (Fig. S2), because of the positive correlations between TN and SOC (Tables 2, 3). The coupled carbon and nitrogen cycles in wetland ecosystems (Schlesinger et al., 2011) and nitrogen limitation for primary production in coastal zone would be the main reasons for these results (Fig. S2b, Sundareshwar et al., 2003; Darby and Turner, 2008; Ryan and Boyer, 2012).

In contrast to TN, soil TP was the most important factor for plant biomass allocation in fresh water bodies, displaying a positive correlation with R/S in inland wetlands (Fig. S3, Fig. 6). In order to obtain more available phosphorus from soil, plants allocated more carbohydrates to roots and modified the rhizosphere properties (e.g., increasing root exudation of phosphatase enzymes, H^+ or OH^-) to enhance the phosphorus availability in soil (Shen et al., 2018; Canarini et al., 2019). For coastal wetlands, TP was also one key factor controlling plant growth and productivity, especially for mangroves (Krauss et al., 2008). However, soil salinity was most critical for coastal R/S (Fig. 6), being consistent with the previous studies (e.g., Yang et al., 2009; Luo et al., 2013; Wang et al., 2014; Alldred et al., 2017). Soil salinity had been indicated

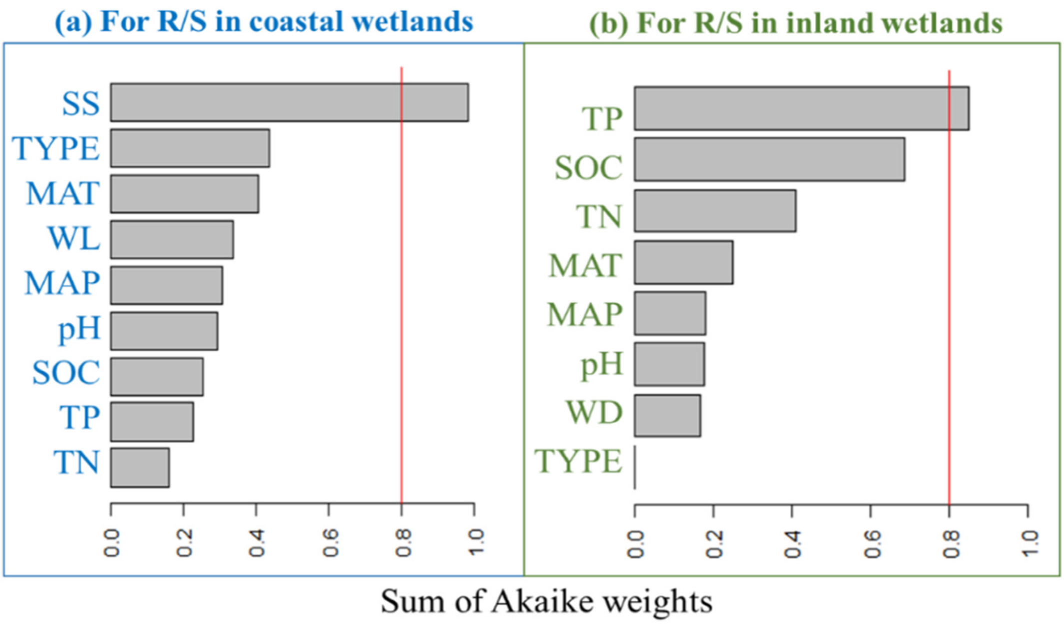

Fig. 5. The importance of influencing factors, including types of wetlands (TYPE), MAT, MAP, soil organic carbon (SOC), soil total nitrogen, phosphorus (TN and TP), salinity (SS), water level or depth (WL or WD) and pH, on R/S for coastal (a) and inland (b) wetlands was expressed as the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples) in R.

to affect root activities through inhibition of mycorrhiza fungi colonization (Saint-Etienne et al., 2006), which was associated with decrease of aboveground biomass for aquatic plants (Nielsen et al., 2003). Even for a certain species, the R/S had been demonstrated to be higher at high salinity (López-Hoffman et al., 2006). The positive relationship between soil salinity and R/S (Fig. 3) potentially reflected a compensation (a great investment of biomass into roots) to balance the root function in resource resorption from sediments (Boyer et al., 2001; Kobe et al., 2010).

Coastal wetlands are bordered on the sea and always restricted by the flood tide of seawater, while water depth directly affects plant growth in inland wetlands due to seasonal waterlogged (Whigham and Simpson, 1978; Twilley and Rivera-Monroy, 2005). We thus selected only water level or depth as the proxy of hydrological property for hydrology properties for coastal and inland wetland, respectively. The pattern of R/S for aquatic macrophytes was significantly affected by water level or depth in both coastal and inland wetlands (Fig. 7). Water depth (or water level) affects fluxes of matter and energy via influencing oxygen and light availability for wetlands (Robinson et al., 1997; Vann and Megonigal, 2003). Inland aquatic plants in those sites with higher water depth generally support a great proportion of shoot biomass to improve light capture, causing a decreasing trend of R/S (Fig. S3, Edwards et al., 2003). However, coastal aquatic plants in sites with higher water level are usually characterized with a greater R/S to absorb available moisture and adapt to tidal wave (Fig. S3, Zhou et al., 2018). The great contributions of hydrological properties for variation of macrophyte R/S could also be explained by the intimate relationship between SOC and water level (or water depth) and between soil TN and water depth in inland wetlands (Tables 2, 3). In addition, the water depth (or water level) has significant effect on the dominance of woody or herb plants in wetland vegetation community (Zhou et al., 2018; He et al., 2019). Woody plants generally have higher biomass accumulation in both AGB and BGB, and a lower R/S relative to herb plants (Fig. S1), because of the weight of trunk in trees and mangroves. Herb R/S in coastal wetlands was significantly lower than that in inland ones (Fig. 2), causing the greater AGB in this study.

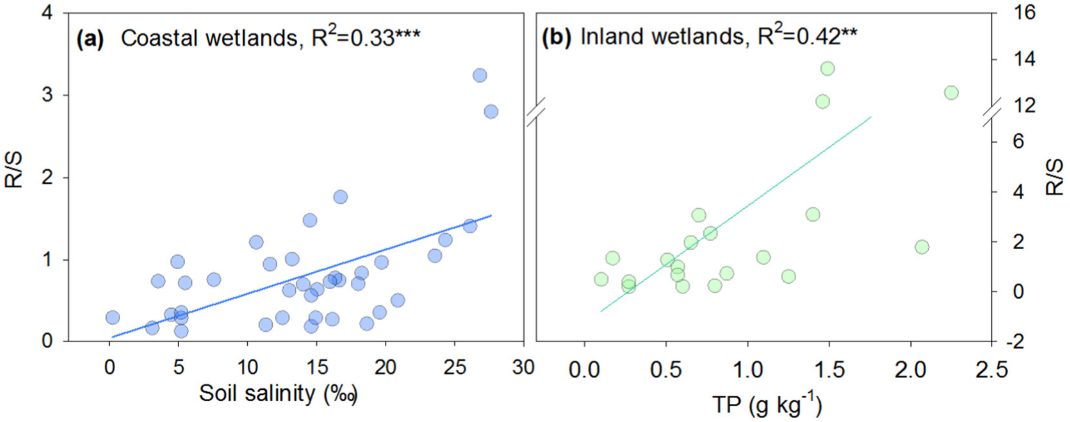

Fig. 6. The correlations of coastal-wetland SS (‰, a) and inland-wetland soil TP (b) with R/S. The symbols ** and *** indicate the coefficients are significant at <0.01 and <0.001.

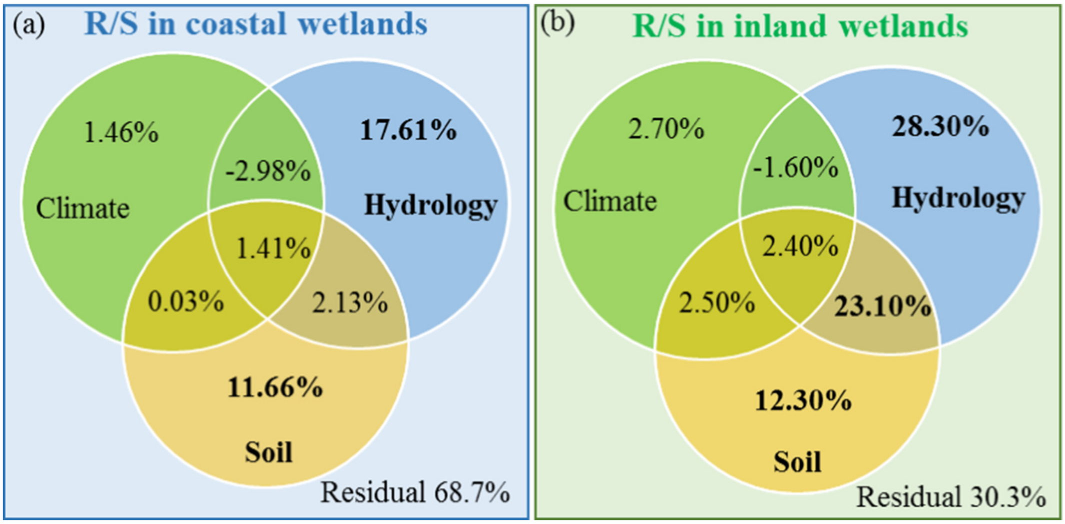

Fig. 7. The contributions of three groups of explanatory variables (including climate condition, hydrology properties, and soil properties) for R/S for coastal (a) and inland wetlands (b). Climate condition (Climate) including MAT and MAP; Hydrology properties (Hydrology) including subgroups of wetlands (i.e., riverine, lake, marsh, and reservoir in inland wetlands; and, mangrove and saltmarsh in coastal wetlands), and WL for coastal wetlands or WD for inland wetlands; Soil properties (Soil) including SOC, TN, TP, SS and pH.

4.3. Implications for model development and prediction in a changing climate

As a critical parameter in simulating carbon cycle in terrestrial ecosystem and biosphere-climate change feedback, R/S is often used for estimating root biomass from the more easily obtained aboveground biomass (Mokany et al., 2006; Gregory et al., 2007). However, the reliability of R/S for wetland vegetation would be greatly challenged by global change, including increasing air temperature, sea level rise, and non-point source pollution derived by land-use change (e.g., nitrogen and phosphorus from agriculture, Moomaw et al., 2018). Our research's outcomes have substantial possibilities to insight the pattern of wetland vegetation that will be helpful for wetland model development and future experiments in a changing climate. First, our results showed greater contributions of soil and hydrological properties relative to that of climate (Fig. 7) on spatial variation of macrophytes' R/S. Current wetland ecosystem models did not separately consider effects of climate, soil and hydrological factors on terrestrial C storage. The findings can be integrated into the framework of wetland models to improve model development and performance (King and Price, 2006; Byrd et al., 2016), especially in the context of global change. Specifically, the quantified correlations of soil salinity, nutrients and water level in coastal wetland, or water depth in inland ones with macrophytes' R/S (Figs. 5–7) could be directly used in setting model parameters and equations (e.g., in Source, Pathway, Receptor, and Consequence, SRRC model, Zhou et al., 2018) to predict wetland C dynamics in the future.

Second, we found that soil salinity and soil total phosphorus were the key controlling factors on macrophytes' R/S for coastal and inland wetlands, respectively (Figs. 5, 6), suggesting importance of wetland-type classification in belowground biomass estimation using aboveground data. Due to the increase in R/S induced by the external inputs of nutrients (e.g., phosphorus from agricultural non-point sources) in inland wetlands, total biomass should be estimated with the combination of AGB and regional environment change (Fig. S2, Schile et al., 2014; Byrd et al., 2016). Furthermore, rising sea level caused by global climate change would induce salinization of freshwater wetlands, and the key controlling factors of biomass allocation would change from soil nutrients to salinity subsequently (Herbert et al., 2015). Model simulation of wetland carbon cycle should thus change from inland to coastal wetlands. Third, the most records of AGB we used in this synthesis were the peak values in each case study, generally in summer and autumn, while the peak BGB generally occurred in winter (Zhou et al., 2018). The season variation of macrophytes' R/S in coastal and inland wetlands should be frequently investigated in the field (Yang et al., 2020). Therefore, the decline trend of R/S with temperature and the underlying negative effect on SOC (Fig. 3, Zhou et al., 2015) should be applied with caution because of the time lag of peak biomass between above- and belowground compartments.

Table 2
The correlation coefficient between variables for coastal wetlands (AGB, aboveground biomass; BGB, belowground biomass, R/S, root/shoot ratio; MAT, mean annual temperature; MAP, mean annual precipitation; WL, water level; SS, soil salinity; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus).

Coastal wetland	AGB	BGB	R/S	MAT	MAP	pH	WL	SS	SOC	TN	TP
AGB		***	ns	***	***	***	**	ns	***	**	*
BGB	**0.76**		***	*	ns	**	ns	**	**	*	ns
R/S	−0.20	**0.47**		ns	**	ns	**	***	ns	ns	*
MAT	**0.49**	**0.30**	−0.21		***	***	ns	ns	***	ns	ns
MAP	**0.49**	0.21	**−0.37**	**0.85**		**	*	ns	***	*	ns
pH	**−0.60**	**−0.46**	0.01	**−0.66**	**−0.50**		ns	ns	***	ns	ns
WL	**−0.47**	−0.10	**0.45**	−0.31	**−0.36**	0.05		ns	*	ns	ns
SS	0.12	**0.47**	**0.60**	0.27	0.08	−0.30	0.01		*	ns	ns
SOC	**0.62**	**0.41**	−0.17	**0.57**	**0.52**	**−0.66**	**−0.37**	**0.40**		**	ns
TN	**0.45**	**0.32**	−0.18	0.13	**0.33**	−0.24	−0.25	−0.12	**0.49**		ns
TP	**−0.33**	0.06	**0.40**	−0.10	−0.29	0.14	0.23	0.32	−0.22	0.05	

The symbols*, ** and *** indicate the coefficients are significant at <0.001, 0.01 and <0.05; ns indicates ≥0.05.

Table 3
The correlation coefficient between variables for inland wetlands (AGB, aboveground biomass; BGB, belowground biomass, R/S, root/shoot ratio; MAT, mean annual temperature; MAP, mean annual precipitation; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus; WD, water depth).

Inland wetland	AGB	BGB	R/S	MAT	MAP	SOC	pH	TN	TP	WD
AGB		***	ns	***	ns	ns	ns	*	**	ns
BGB	**0.86**		***	***	ns	**	**	***	***	ns
R/S	0.03	**0.50**		***	ns	**	**	**	**	*
MAT	**−0.41**	**−0.53**	**−0.38**		***	**	*	**	ns	ns
MAP	−0.12	−0.10	0.05	**0.67**		ns	ns	ns	ns	ns
SOC	0.27	**0.45**	**0.42**	**−0.45**	−0.10		***	***	ns	**
pH	−0.22	**−0.48**	**−0.47**	**0.34**	−0.15	**−0.56**		***	ns	ns
TN	**0.42**	**0.60**	**0.44**	**−0.52**	−0.20	**0.95**	**−0.63**		ns	*
TP	**0.54**	**0.66**	0.47	−0.01	0.25	0.25	−0.34	0.20		ns
WD	−0.08	−0.29	**−0.42**	0.18	−0.22	**−0.49**	0.18	**−0.39**	−0.34	

The symbols *, ** and *** indicate the coefficients are significant at <0.001, 0.01 and <0.05; ns indicates ≥0.05.

5. Conclusions

Patterns of macrophytes' R/S are important for characterizing wetland structure and functions, as processes of carbon, oxygen and nutrients at water-sediment (or at water-soil) interface are affected by biomass allocation. In this study, we found coastal wetlands had higher AGB and lower R/S than inland ones, while woody macrophytes supported greater biomass and lower R/S than herbs across China. The correlations between AGB and BGB, and between R/S and BGB among coastal inlands were significantly different from those among inland wetlands. The spatial variation of wetland R/S across China was mainly explained by soil and hydrological properties, being reflected in importance of inland soil phosphorus and coastal soil salinity. Our results indicated the spatial variation of R/S in China was mainly caused by that of BGB, which would be the main source of uncertainty in regional carbon-stock estimation in wetland ecosystems. This study highlights importance of wetland types and macrophyte life forms and regulation of soil salinity, nutrients, and hydrological properties for wetland R/S across China, which should be considered in regional biomass estimation of wetland vegetation in the future climate.

CRediT authorship contribution statement

Lingyan Zhou: Conceptualization, Visualization, Writing – original draft. **Wei Yan:** Methodology, Investigation. **Xiaoying Sun:** Data curation. **Junjiong Shao:** Software. **Peipei Zhang:** Investigation. **Guiyao Zhou:** Investigation. **Yanghui He:** Visualization, Investigation. **Huiying Liu:** Writing – review & editing. **Yuling Fu:** Conceptualization, Resources, Supervision. **Xuhui Zhou:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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