**RESEARCH ARTICLE**

# Variation in resource allocation strategies and environmental driving factors for different life-forms of aquatic plants in cold temperate zones

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**Abstract**

1. Resource allocation, including biomass allocation and nutrient allocation between different organs in a plant, reflects the trade-off in partitioning between above-ground and below-ground organs and the growth and adaptation strategies of plants in a changing environment. Although varied resource allocation patterns among different organs in different functional groups of terrestrial plants have been found, few studies have focused on freshwater ecosystems.

2. In this study, to clarify biomass and nutrient allocation strategies and their responses to environmental factors, we collected and analysed 2,162 samples from 262 aquatic plant communities (including emergent plants, floating-leaved plants and submerged plants) in various aquatic habitats in north-eastern China.

3. The results showed that the root/shoot (R/S) ratios of the three aquatic plant life-forms were significantly different, and the trend showed that the ratio values for the three plant life-forms occurred in the following order: emergent plants > floating-leaved plants > submerged plants. There were obvious scaling relationships between above-ground biomass, N (or P or N:P ratios) and below-ground biomass, N (or P or N:P ratios), but their scaling exponents changed among different aquatic plant life-forms. The allocation of biomass and nutrients between different organ responses to environmental factors was not consistent for the different life-forms of aquatic plants. The partial least squares path model revealed that plant stoichiometric characteristics are important direct drivers of biomass production. Climate conditions, water properties and soil nutrients indirectly affect biomass through effects on plant stoichiometric characteristics.

4. *Synthesis*. Our study demonstrates that global climate change may affect water properties and soil nutrients, influence plant stoichiometric characteristics and affect aquatic plant growth, further altering aquatic plant community structure and biogeochemical cycles.

**KEYWORDS**
aquatic plant ecology, ecological stoichiometry, north-eastern China, plant organ, plant–climate interactions, resource allocation strategies, scaling relationship

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Jingwen Hu and Hongwei Yu contributed equally to this work.

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# 1 | INTRODUCTION

Resource allocation is an important way to reflect plant growth and adaptation strategies and includes the allocation of not only biomass but also nutrients between different organs in a plant, and it varies with plant functional groups and environmental conditions (Bazzaz, 1997; Kerkhoff et al., 2006; Reich et al., 2008; Sardans & Peñuelas, 2013). Plant internal biomass allocation reflects the trade-off in partitioning between above-ground biomass (AGB) and below-ground biomass (BGB), which can be affected by species traits, phylogeny and external environmental conditions (Fan et al., 2019; Poorter et al., 2012; Reich et al., 2014; Yang et al., 2010, 2018). The allocation of BGB relative to AGB is usually expressed as the root/shoot ratio (R/S), which reflects the distribution of photosynthetic products in below-ground and above-ground organs (Mokany et al., 2006).

Resource allocation strategies among different plant organs are an important topic in the study of plant adaptation to the environment, and scaling, isometric or allometric relationships have widely been used to analyse biomass partitioning between above-ground and below-ground organs (Cheng & Niklas, 2007; Enquist & Niklas, 2002; McCarthy & Enquist, 2007; Yang et al., 2010). Previous studies have shown that the allocation of biomass between different organs is isometric within plants, and the biomass partitioning model does not significantly change with phylogenetic and ambient conditions (Enquist & Niklas, 2002). A similar isometric scaling relationship between AGB and BGB has been verified in forest ecosystems (Cheng & Niklas, 2007); moreover, a study on biomass allocation in grassland ecosystems on the Tibetan Plateau supports isometric theory, which suggests that there is an isometric relationship between AGB and BGB at the community level. Additionally, the scaling exponent is not significant between different topographic features (temperate and alpine) and grassland types (steppe and meadow; Yang et al., 2010). Different allometric relationships of submerged plants have been observed under different light environments, and the reflections vary by species (Fu et al., 2012; Rao et al., 2020). Biomass allocation in different life-forms of aquatic plants remains to be studied.

Carbon (C), nitrogen (N) and phosphorus (P) are the fundamental elements associated with the chemical composition of living organisms, and their concentrations and ratios can regulate the growth of plants and directly reflect plant adaption to environmental changes (Ågren, 2004; Elser et al., 2007; Sterner & Elser, 2002). The allocation pattern of N and P usually plays a crucial role in different parts of plants because N and P availability can limit plant growth (Sterner & Elser, 2002), and their allocation in different organs reflects the adaptation of plants in a changing environment (Kleyer & Minden, 2015; Reich et al., 2008; Zhang et al., 2019; Zhao et al., 2016). Under different pressures, plants need to balance the nutrient distribution of each organ, and the distribution strategy changes with changes in the external environment (Liu et al., 2020; Minden & Kleyer, 2014; Zhang et al., 2019). Furthermore, the contents of elements in different organs may vary strongly among species, and they vary with the growth rate and organ form and function (Kleyer & Minden, 2015; Minden & Kleyer, 2014; Zhang et al., 2019; Zhao et al., 2016). Specifically, knowledge of nutrient partitioning and the N–P relationship among plant organs is helpful in understanding the stoichiometric adaptation mechanism of plants (Minden & Kleyer, 2014; Reich et al., 2008), which is closely related to the flows of energy and nutrient cycling in ecosystem processes (Sterner & Elser, 2002). According to the plant economics spectrum theory, there is a certain correlation between N and P contents in different plant organs (Reich et al., 2014; Yang et al., 2014; Zhao et al., 2016). The scaling relationship has been widely used to analyse the N and P contents and stoichiometric ratio partitioning in plants; the relationship can describe the relative nutrient allocation in different organs across diverse plant species and be used to compare their responses to environmental factors (Reich et al., 2008). The scaling relationships of N and P among plant organs are not invariable but are likely to change with environmental factors, such as temperature and soil nutrients (Yan, Li, et al., 2016; Yang et al., 2014).

Biomass allocation usually involves relationships among major plant organs, and the allocation scheme mainly depends on allocation to metabolically active or structural tissues and their stoichiometric composition (Kleyer & Minden, 2015; Minden & Kleyer, 2014). On the basis of the growth rate hypothesis (GRH), the rate of change in biomass is related to higher P contents and lower C:P and N:P ratios (Ågren, 2008; Yu et al., 2012). For example, the growth of annual biomass and leaf tissue C, N and P contents are heavily related to the total mass in the above-ground parts of plants (Mulder et al., 2013; Sardans & Peñuelas, 2013). Concurrently, the contents of N (or P) in different tissues are closely related in terrestrial plants, and they are strongly relevant to vegetation gross primary productivity (Tang et al., 2018). Although there have been some studies on the stoichiometric geographical pattern of aquatic plants (Gong et al., 2018; Wang et al., 2015; Xia et al., 2014), these studies mainly focus on leaves, and few studies have paid close attention to the stoichiometric traits in different organs of aquatic plants; thus, whether a scaling relationship exists in aquatic plants is still unknown.

Plant resource allocation is influenced by species characteristics, phylogeny and environmental factors (Poorter et al., 2012; Yang et al., 2010, 2018). In terrestrial ecosystems, plant growth is limited by many environmental factors, and previous studies have suggested that plants will allocate relatively more biomass to above-ground organs when light or $CO_2$ is limited but allocate more biomass to roots when the restricting factors, such as water and nutrients, are below-ground (Poorter et al., 2012). In terrestrial plants, biomass allocation to roots decreases with increasing nutrient availability, and increased root biomass is usually accompanied by decreasing tissue nutrients (Enquist & Niklas, 2002; Poorter et al., 2012; Yang et al., 2010). However, in addition to nutrient availability, water depth (WD) can affect stoichiometric allocation among different organs of submerged plants due to underwater light intensity limitations, and the effects are species specific (Li et al., 2013). Water-level fluctuation may change the interaction between water and sediment, affecting N and P availability and further changing

the resource allocation strategies of different life-forms of aquatic plants (Lacoul & Freedman, 2006; Li et al., 2013; Qin et al., 2020; Sardans et al., 2011). In addition, under the influence of the aquatic environment, the morphological structure and physiological and ecological processes of aquatic plants are significantly different from those of terrestrial plants (Lacoul & Freedman, 2006; Sardans et al., 2011). Due to their diverse life-forms and phenotypic plasticity, aquatic plants can use different organs to absorb nutrients (Carignan & Kalff, 1980), and the nutrient allocation strategies of different aquatic plant organs may be altered with changes in environmental conditions (Rao et al., 2020; Xu et al., 2020). It is important to research the above-ground and below-ground nutrient distribution strategies of aquatic plants. However, due to difficulties in sampling, sufficient attention has not been given to these strategies in aquatic plants (Sterner & Elser, 2002).

North-eastern China is a region at high latitudes with low altitudes; studies have shown that aquatic plants exhibit a high diversity at cold temperate latitudes and the aquatic richness peak was found between 40° and 50°N (Chappuis et al., 2012). A total of 262 aquatic plant communities were surveyed, and 2,162 samples were collected in various natural freshwater ecosystems in north-eastern China to analyse the resource allocation strategy in aquatic plants between various life-forms and different organs. Specifically, we tested the following hypotheses: (a) there are some differences in the resource allocation strategies between above-ground and below-ground organs in different life-forms of aquatic plants; (b) resource allocation strategies of different life-forms of aquatic plants have various responses to environmental factors; and (c) plant biomass allocation is influenced more by plant stoichiometry than by abiotic environmental factors.

## 2 | MATERIALS AND METHODS

### 2.1 | Sampling and chemical measurement methods

To minimize the influence of plant phenology on plant characteristics, field investigations were carried out during the growing season, which is known as the most suitable time for biomass research (Yang et al., 2010). From June to August 2016–2018 in north-eastern China, we conducted a field investigation of aquatic habitats, including lakes, rivers and other water bodies such as streams and ponds (Figure 1). The mean growing season temperature (GST) and mean growing season precipitation (GSP) were obtained from datasets
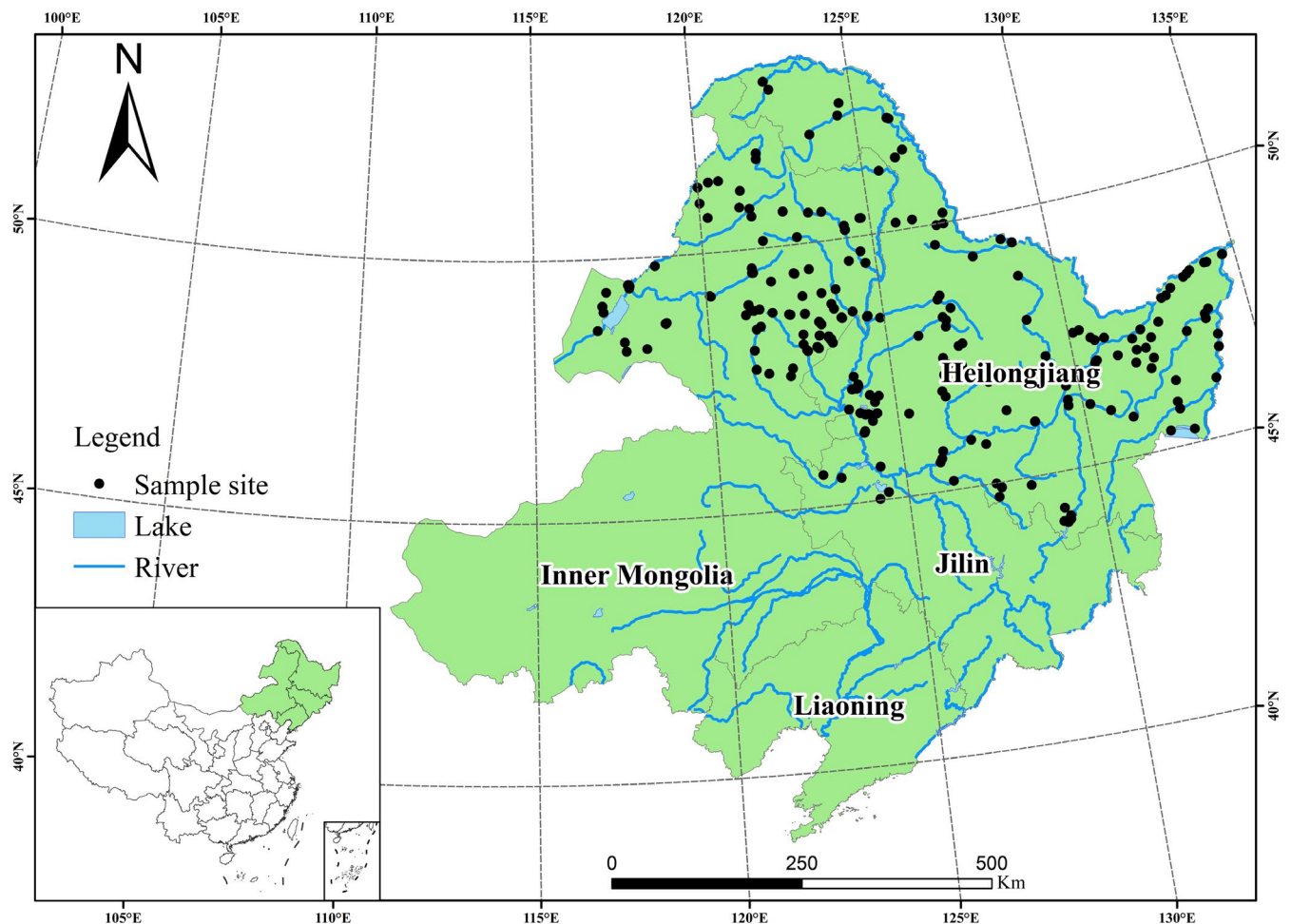


**FIGURE 1** Sample sites in north-eastern China. The samples were collected from June to August 2016–2018

collected by meteorological stations across China (Fang et al., 2001). Using a portable water quality monitor (PROPLUS, YSI, USA), the physical and chemical indexes of water were measured at each site and mainly included water temperature (T), dissolved oxygen (DO), salinity (SAL) and pH; turbidity (Turb) was measured using a turbidity metre (2100Q, HACH, USA). After collecting water samples in clean 500-ml bottles, chemical oxygen demand (COD), nitrate nitrogen ($NO_3$-N), ammonia nitrogen ($NH_4$-N), total nitrogen (WTN) and total phosphorus (WTP) were analysed with a digestion solution for each corresponding parameter and landscape photometry (DR900, HACH, USA; Lv et al., 2018).

According to the characteristics of the habitats (area, WD, velocity, etc.), we mainly used the modified belt transect method to determine the sampling range (Vondracek et al., 2014), and six to twelve $1 \times 1$ m quadrats were set at each site. A total of 262 sites were sampled, and 104 species and 2,162 samples were collected. Aquatic plants were divided into three life-forms, namely emergent plants (EP), floating-leaved plants (FP) and submerged plants (SP; free floating plants were not involved because of the lack of below-ground organization in this study). The five most common species of each life-form are listed in Table S1. We collected whole aquatic plants for each of the three life-forms as much as possible, mainly through deep excavations, artificial dives or rotatable reaping hooks. In each quadrat, we recorded the plant species and determined their fresh weight separately by species. At each site, six to nine intact plants without grazing were sampled randomly for every species. The plants were cleaned carefully and divided into above-ground and below-ground organs, placed in paper envelopes, dried with an air blower and then transported to the laboratory for further analyses. The AGB and BGB were calculated in each $1 \times 1$ m quadrat, the total biomass (TB) was the sum of AGB and BGB and the R/S was calculated as the ratio of BGB to AGB.

Approximately 500 g of sediment was collected from the 0–20 cm layer using a shovel. Three samples were collected at each site and preserved in a polyethylene-sealed bag at each subplot. Plant roots and debris were carefully removed from the sediment samples after air drying, and then the samples were ground into a powder using a mortar and mixed well for elemental analyses. To measure the elements in aquatic plants, the plant samples were cleaned carefully and dried at 65°C for 48 hr and then ground into a powder using a pulverizer and mortar. We used a FLASH 2000 Organic Elemental Analyser (Thermo Fisher Scientific Inc., USA) to measure the C and N concentrations of the plant tissue and sediment. The P concentrations were determined using the molybdate/ascorbic acid method (Jones, 2001). The plant C, N and P concentrations are presented in units of mg/g dry weight, and the C:N, C:P and N:P ratios were calculated on a mass basis for each plant life-form and plant organ.

## 2.2 | Statistical analysis

Before our data analysis, we carried out normality and variance homogeneity tests. Given that the variables were non-normally distributed and did not pass the variance homogeneity test, we used nonparametric tests to compare the differences in biomass allocation and the stoichiometry of aquatic plants among the different life-forms and plant organs (Kruskal–Wallis test; Breslow, 1970). Standardized major axis (SMA) analyses were used to describe the scaling relationships between the above-ground biomass/nutrients and below-ground biomass/nutrients. The regression curve is expressed by the formula $\log Y = \alpha \times \log X + \beta$, where $X$ and $Y$ represent root biomass or nutrients (N, P or N:P ratios) and shoot biomass or nutrients (N, P or N:P ratios), respectively, and $\alpha$ and $\beta$ are the slope (i.e. scaling exponent) and intercept of the regression line respectively (Warton et al., 2006). All statistical analyses were performed using R software (version 3.5.2; R Core Team, 2019). The 'SMATR' package in R was used for the scaling relationship analysis, and likelihood ratio tests were used to compare exponents among different life-forms of aquatic plants (Warton et al., 2012). GLMs were used to analyse the effects of environmental factors on biomass allocation. All environmental factors were incorporated into the model for analysis, the lowest Akaike information criterion (AIC) was considered the best model (Yamashita et al., 2007), and the relative weight of the mean square was the degree of interpretation of the explanatory variables on the response variables. Redundancy analyses (RDAs) were performed to clarify the relationship between plant stoichiometric characteristics and environmental factors, and a Monte Carlo test was conducted to obtain the sequence of importance of variables. Partial least squares path models (PLS-PMs) were constructed to test the direct and indirect effects of climate (GST and GSP), water properties (WD, WTN, WTP, DO, pH and SAL), soil nutrients (soilC, soilN and soilP) and plant stoichiometric characteristics (plant C, plant CN and plant CP) on biomass. The 'PLSPM' package in R was used to construct the path models (Sanchez et al., 2015). Data transformations were applied when necessary to fit the data analysis requirements.

## 3 | RESULTS

### 3.1 | Biomass allocation traits and the effects of environmental factors

According to our field investigation, the average fresh weight of aquatic plants was approximately 1,567.77 g/m$^2$, and there were significant differences in the mean AGB, BGB and R/S values among the three life-forms of aquatic plants (Figure 2). All biomass traits of the emergent plants were significantly higher than those of the floating-leaved plants (Figure 2). With the exception of BGB, the AGB and R/S values of the emergent plants were also significantly higher than those of the submerged plants (Figure 2). With the exception of the R/S ratios, floating-leaved plants and submerged plants showed no significant differences in biomass traits (Figure 2). The GLM analysis showed that the main factors affecting the biomass of aquatic plants were not consistent among the three life-forms (Figure 3). For all aquatic plants and emergent plants, the plant C:N (AbCN and BeCN) ratios and the plant C:P ratios in below-ground organs (BeCP) were
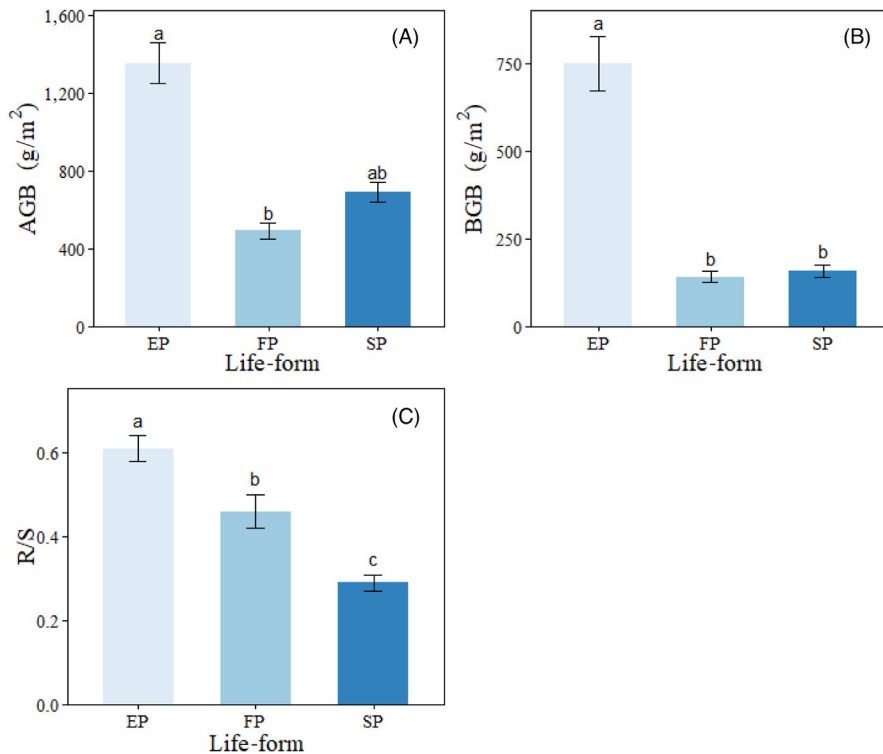
**FIGURE 2** The differences in AGB, BGB and R/S ratios among different aquatic plant life-forms (EP, emergent plants; FP, floating-leaved plants; and SP, submerged plants). Different letters indicate significant differences at the 0.05 level

the key positive factors for the biomass (AGB and BGB) and R/S ratios (Figure 3a,b,e,f,i,j) respectively. For the floating-leaved plants, GST was the principal positive factor affecting the AGB and BGB (Figure 3c,g), and BeCP mainly affected the R/S ratios (Figure 3k). WD had significant positive effects on the AGB and negative effects on the R/S ratios of the submerged plants (Figure 3d,l). The BGB of the submerged plants was mainly affected by the soil C:P ratio (SoilCP; Figure 3h).

## 3.2 | Stoichiometric characteristics and effects of environmental factors

For all collected samples (observations $n = 2,162$), the C, N and P concentrations of the plants varied widely. The mean values of plant C, N and P were $358.99 \pm 60.24$, $19.36 \pm 7.51$ and $3.45 \pm 1.68$ mg/g, respectively, and the mean values of the C:N, C:P and N:P ratios were $21.76 \pm 10.75$, $133.36 \pm 84.49$ and $6.29 \pm 2.59$ respectively. There were significant differences in the stoichiometric traits among the three life-forms and different organs (Table 1). Specifically, there were no significant differences in the C concentrations between the emergent plants and floating-leaved plants, and both had significantly higher C concentrations than submerged plants (Table 1). The submerged plants had the highest N and P concentrations and N:P and the lowest C:N and C:P ratios, while the emergent plants showed the opposite pattern (Table 1). With the exception of the C:N ratios, the C, N and P concentrations and C:P and N:P ratios in the above-ground organs were all significantly higher than those in the below-ground organs (Table 1).

The RDA showed that environmental factors explained 6.18% of the total variation in the stoichiometric characteristics for all data (Figure 4a). The explanation rate for the submerged plants (13.45%) was higher than that for the floating-leaved plants (11.17%) and emergent plants (6.43%) (Figure 4b–d). For all plant samples, WD was the key factor for stoichiometric characteristics, while SAL and soil N:P (SoilNP) had a great influence on stoichiometry (Figure 4e). However, the response of stoichiometry to environmental factors was not consistent among the three life-forms of aquatic plants. DO and SAL had a great influence on the stoichiometry of the emergent plants (Figure 4f). GSP and WD mainly affected the stoichiometric characteristics of both the floating-leaved plants and submerged plants (Figure 4g,h). The stoichiometry of the submerged plants was also greatly influenced by soil nutrients and ratios (SoilNP, SoilP and SoilCP; Figure 4h).

## 3.3 | Scaling relationship between above-ground and below-ground organs

SMA analyses revealed a positive correlation between above-ground and below-ground biomass ($R^2 = 0.74$), and the scaling slopes were significantly different from 1 with 95% confidence intervals, which manifested an allometric relationship ($p < 0.001$; Table 2). However, the trends in the three aquatic plant life-forms were inconsistent, and the slopes of the emergent plants but not the floating-leaved plants and submerged plants were obviously different from 1 (Table 2). There was a significant correlation
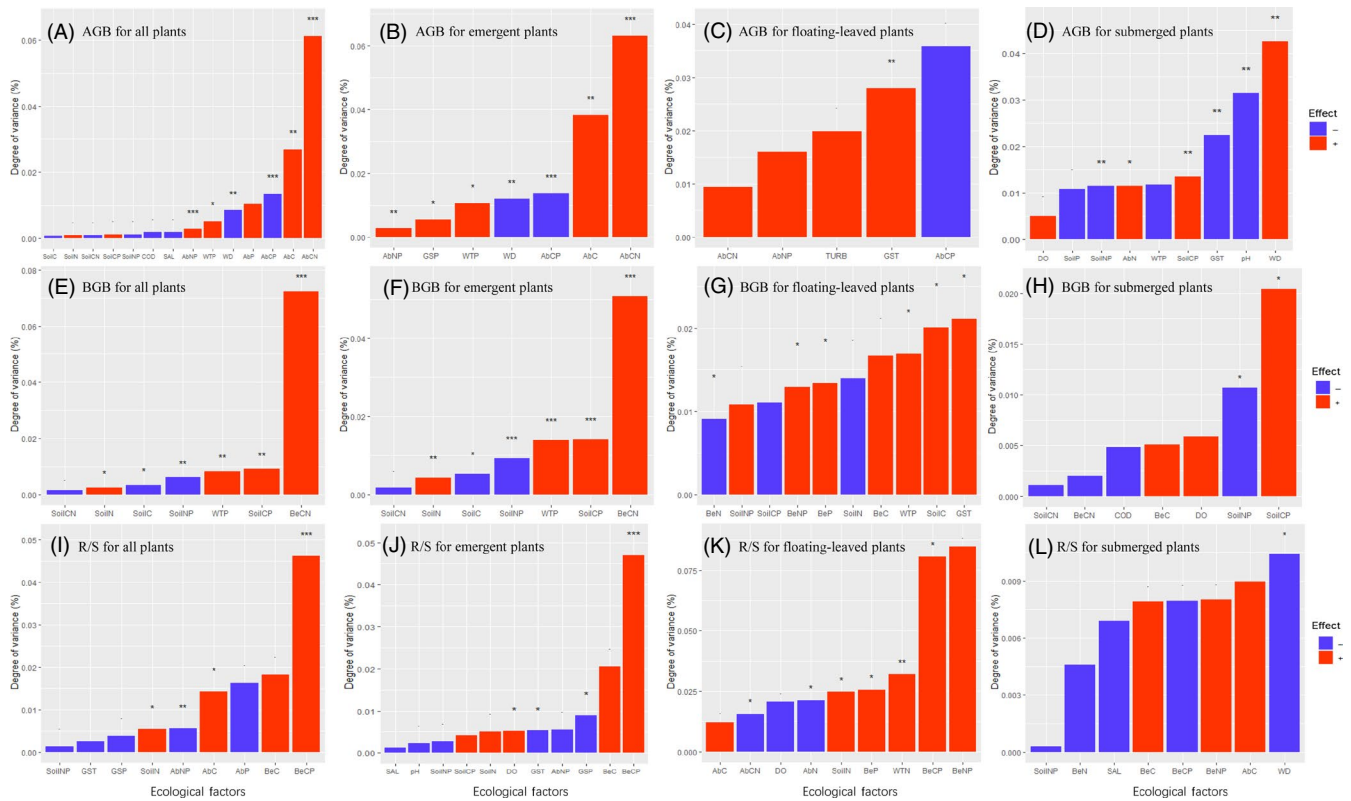
**FIGURE 3** GLMs for the effects of environmental factors and plant elements on the biomass allocation of aquatic plants. The lowest AIC was considered the best model for each GLM. (a) AGB for all plants; (b) AGB for emergent plants; (c) AGB for floating-leaved plants; (d) AGB for submerged plants; (e) BGB for all plants; (f) BGB for emergent plants; (g) BGB for floating-leaved plants; (h) BGB for submerged plants; (i) R/S for all plants; (j) R/S for emergent plants; (k) R/S for floating-leaved plants; and (l) R/S for submerged plants. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$ and $p < 0.1$

**TABLE 1** Plant C, N and P concentrations and C:N, C:P and N:P ratios for different life-forms and organs. The number of samples (*n*), mean value and standard deviation (*SD*) are reported. Different lowercase letters indicate significant differences in mean plant C, N, P, C:N, C:P and N:P between different life-forms ($p < 0.05$), and the different uppercase letters represent significant differences between the two organs ($p < 0.05$)

| Plant group | n | C (mg/g) Mean ± SD | N (mg/g) Mean ± SD | P (mg/g) Mean ± SD | C:N Mean ± SD | C:P Mean ± SD | N:P Mean ± SD |
|---|---|---|---|---|---|---|---|
| Life-form | | | | | | | |
| Emergent plants | 1,300 | 363.3 ± 65.44[a] | 17.11 ± 7.19[c] | 3.19 ± 1.66[b] | 25.09 ± 12.24[a] | 150.91 ± 98.6[a] | 6.1 ± 2.7[b] |
| Floating-leaved plants | 360 | 367.81 ± 47.87[a] | 22.07 ± 6.68[b] | 3.76 ± 1.61[a] | 18.4 ± 5.28[b] | 115.05 ± 46.27[b] | 6.52 ± 2.31[a] |
| Submerged plants | 502 | 341.51 ± 49.95[b] | 23.25 ± 6.59[a] | 3.93 ± 1.62[a] | 15.52 ± 3.85[c] | 101.05 ± 44.33[c] | 6.62 ± 2.48[a] |
| Organ | | | | | | | |
| Above-ground | 1,081 | 392 ± 32.59[A] | 22.38 ± 7.89[A] | 3.62 ± 1.69[A] | 20.7 ± 10.16[B] | 139.59 ± 87.4[A] | 6.86 ± 2.52[A] |
| Below-ground | 1,081 | 325.98 ± 63.38[B] | 16.35 ± 5.68[B] | 3.29 ± 1.65[B] | 22.82 ± 11.23[A] | 127.12 ± 81.05[B] | 5.72 ± 2.54[B] |

between the N content in above-ground and below-ground organs, and the scaling slopes did not show a significant difference when compared to 1, indicating an isometric relationship ($p > 0.05$; Table 2). The N:P ratio but not the P content was significantly different from 1 in the whole data analysis (Table 2). Significant differences among the three life-forms of aquatic plants were found for both P concentrations and N:P ratios (Table 2). The slope of the

emergent plants was significantly higher than that of the floating-leaved plants and submerged plants (Table 2). There were obvious scaling relationships between above-ground biomass, N (or P or N:P ratios) and below-ground biomass (Figure 5a), N (Figure 5b) (or P (Figure 5c) or N:P ratios (Figure 5d)), but their scaling exponents changed among the different life-forms of aquatic plants (Table 2, Figure 5).
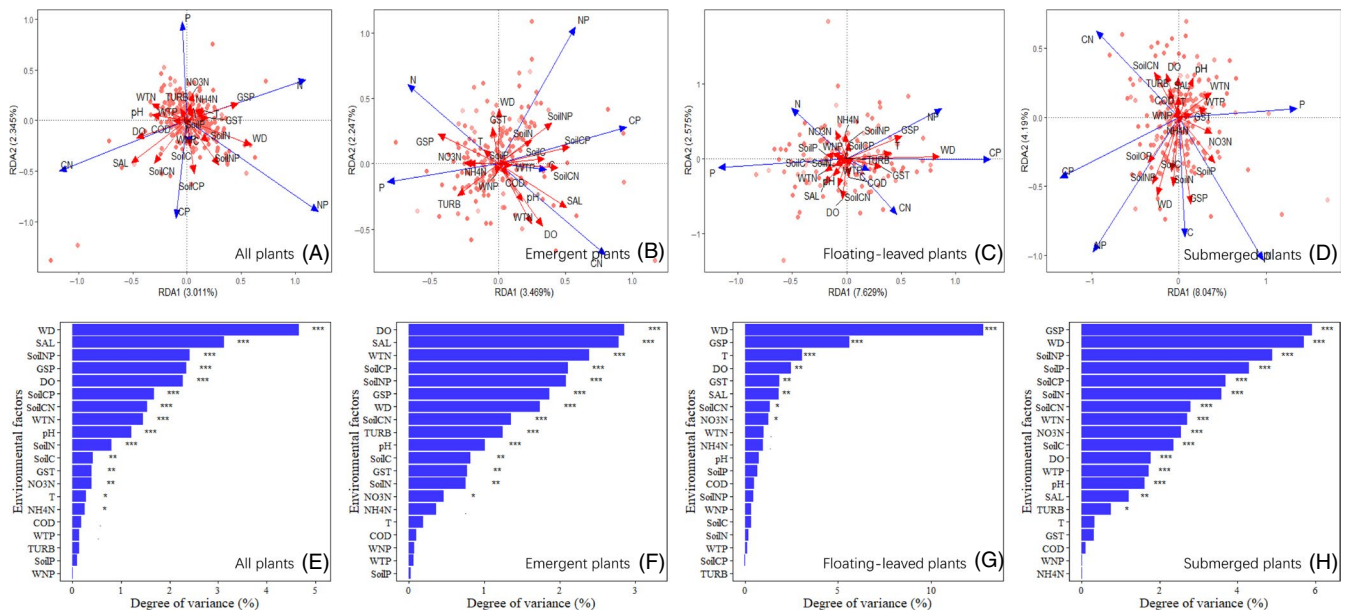
**FIGURE 4** RDA for the effects of environmental factors on the plant element stoichiometry of aquatic plants. a, b, c and d show the RDA plots, and e, f, g and h show the *R* squared of the environmental factors on the plant element stoichiometry of aquatic plants for all plants, emergent plants, floating-leaved plants and submerged plants. Significance levels are indicated by asterisks: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$ and $p < 0.1$

## 3.4 | Partial least squares path models of environments, plant stoichiometric characteristics and biomass

The PLS-PM revealed that the direct effects of climate conditions, water properties and soil nutrients on biomass were not significant; however, climate conditions can obviously affect water properties and soil nutrients and subsequently affect plant stoichiometric characteristics, further influencing plant biomass (Figure 6). Plant stoichiometric characteristics were important direct drivers of biomass production (path coefficient 0.2735), and climate conditions, water properties and soil nutrients had indirect effects on biomass through effects on plant stoichiometric characteristics (Figure 6).

## 4 | DISCUSSION

### 4.1 | Biomass allocation traits and the effects of environmental factors

Internal biomass allocation in plants reflects the trade-off in above-ground and below-ground organs and can be affected by plant characteristics and environmental factors (Fan et al., 2019; Poorter et al., 2012; Yang et al., 2018). Plant roots play an important role in the process of absorbing nutrients and water resources (Cheng & Niklas, 2007; Poorter et al., 2012). Our results revealed that the R/S ratios of the three life-forms were significantly different, and the trend showed that the ratio values occurred in the following order: emergent plants > floating-leaved plants > submerged plants (Figure 2c), which was supported by other previous studies.

For example, some emergent plants, such as *Typha* spp. and *Zizania latifolia*, have a large root structure to fix and support plants (Lacoul & Freedman, 2006). Emergent plants, which are considered to resemble terrestrial plants, are less aquatic than euhydrophytes, such as submerged plants (Cronk & Fennessy, 2001). Floating-leaved plants, such as *Trapa bispinosa Roxb.*, have specialized filamentous lobes that can be suspended to absorb nutrients in water and replace some functions of roots (Lacoul & Freedman, 2006; Li et al., 2011). Although root anchorage plays an important role in the resistance of submerged plants to waves, currents and grazing birds (Schutten et al., 2005), compared with the terrestrial environment, in the aquatic environment where submerged plant growth experiences low light, low oxygen content and poor air permeability, the roots of submerged plants are buried deep in the bottom mud (Li et al., 2013; Rao et al., 2020; Schutten et al., 2005; Xie et al., 2005). In addition, submerged plants can use other organs to absorb nutrients from water, causing root degradation (Carignan & Kalff, 1980), which may lead to the lowest R/S ratios of submerged plants in our study.

The biomass in above-ground organs was significantly positively correlated with that in below-ground organs (Table 2, Figure 5), which was in agreement with the results of previous studies (Cheng & Niklas, 2007; Mulder et al., 2013; Yang et al., 2009, 2018). The allometric and isometric relationship of biomass partitioning has been widely studied (Cheng & Niklas, 2007; Enquist & Niklas, 2002; Liu et al., 2020; McCarthy & Enquist, 2007; Yang et al., 2018). Although an allometric relationship has been observed in many grassland and forest ecosystems (Cheng & Niklas, 2007; McCarthy & Enquist, 2007; Yang et al., 2010), previous studies have also illustrated that plant biomass allocation varies among the different plant types (Fan et al., 2019; Poorter et al., 2012). In our study,

**TABLE 2** Summary statistics for the standardized major axis regression analysis (SMA) of the relationship between above-ground biomass, N (or P, or N:P ratio) and below-ground biomass, N (or P, or N:P ratio), for the three life-forms of aquatic plants (emergent plants, floating-leaved plants and submerged plants)

| Group | n | Scaling exponent | | | | Test for allometry |
| | | $\alpha$ | 95% CI | $R^2$ | p | p |
| --- | --- | --- | --- | --- | --- | --- |
| Biomass | | | | | | |
| All | 1,081 | **0.93** | 0.90–0.97 | 0.74 | <0.001 | <0.001 |
| Life-form | | | | | | |
| EP | 650 | 0.95[a] | 0.92–0.98 | 0.83 | <0.001 | <0.001 |
| FP | 180 | 0.95[a] | 0.85–1.07 | 0.40 | <0.001 | 0.41 |
| SP | 251 | 1.01[a] | 0.94–1.08 | 0.67 | <0.001 | 0.83 |
| N | | | | | | |
| All | 1,081 | 1.03 | 0.96–1.11 | 0.40 | <0.001 | 0.41 |
| Life-form | | | | | | |
| EP | 650 | 1.02[a] | 0.96–1.08 | 0.35 | <0.001 | 0.48 |
| FP | 180 | 0.95[a] | 0.83–1.09 | 0.14 | <0.001 | 0.49 |
| SP | 251 | 1.06[a] | 0.95–1.19 | 0.18 | <0.001 | 0.3 |
| P | | | | | | |
| All | 1,081 | 1.00 | 0.94–1.07 | 0.49 | <0.001 | 0.89 |
| Life-form | | | | | | |
| EP | 650 | 1.06[a] | 1.00–1.12 | 0.50 | <0.001 | <0.05 |
| FP | 180 | 0.85[b] | 0.76–0.96 | 0.40 | <0.001 | <0.01 |
| SP | 251 | 0.84[b] | 0.76–0.93 | 0.37 | <0.001 | <0.001 |
| N:P | | | | | | |
| All | 1,081 | **0.71** | 0.66–0.77 | 0.38 | <0.001 | <0.001 |
| Life-form | | | | | | |
| EP | 650 | 0.90[a] | 0.85–0.96 | 0.37 | <0.001 | <0.01 |
| FP | 180 | 0.65[b] | 0.58–0.73 | 0.38 | <0.001 | <0.001 |
| SP | 251 | 0.67[b] | 0.61–0.74 | 0.42 | <0.001 | <0.001 |

*Note:* Bold letters indicate that the slope ($\alpha$) was significantly different from 1. Letters following the slope ($\alpha$) show the results of the likelihood ratio test among different life-forms of aquatic plants. For each comparison, values with different letters indicate significant differences ($p < 0.05$).

*The likelihood ratio (LR) statistics were 2.56, 1.44, 22.57 and 40.25 for biomass, N, P and N:P respectively.

allometric relationships between the AGB and BGB of emergent plants were found, but the floating-leaved plants and submerged plants showed an isometric relationship (Table 2). Similar to our study, Fan et al. (2019) found that biomass allocation patterns varied significantly among different plant types, and isometric allocation was found in ephemeral plants; however, allometric relationships were verified in ephemeroid and annual plants, which might suggest that biomass allocation patterns are closely related to plant adaptive ecological strategies.

Plant biomass allocation strategies are influenced by many environmental factors (such as light, temperature, water, nutrients and $CO_2$; Liu et al., 2020; Poorter et al., 2012; Reich et al., 2014; Yang et al., 2010) and plant characteristics (such as phylogeny and species category; Fan et al., 2019; Poorter et al., 2012; Yang et al., 2018). Compared with external environmental factors, the stoichiometric characteristics of aquatic plants had a greater influence on biomass allocation. For instance, the C:N ratios in plants were the main factor

affecting plant biomass, and the R/S ratios were mainly affected by the C:P ratios in the below-ground organs (Figure 3), which might indicate that biomass accumulation and the distribution of plants are mainly related to nutrient use efficiency (N or P) (Ågren, 2008; Tang et al., 2018; Yu et al., 2012). Resource allocation strategies change with environmental factors and vary among different plant groups in terrestrial systems (Poorter et al., 2012; Reich et al., 2014; Sardans & Peñuelas, 2013; Tang et al., 2018). Our results also showed that the responses of different life-forms of aquatic plants to environmental factors were not consistent. For emergent plants, C:N or C:P ratios mainly affect their biomass or R/S, and C:N and C:P ratios can reflect C assimilation in response to N and P absorption during the physiological adjustment of plants (Huang et al., 2019; McGroddy et al., 2004). GST is the principal factor affecting the biomass of floating-leaved plants because biomass plasticity in response to changes in temperature may be directly and indirectly altered by nutrient availability (Wang et al., 2019). For submerged plants, WD
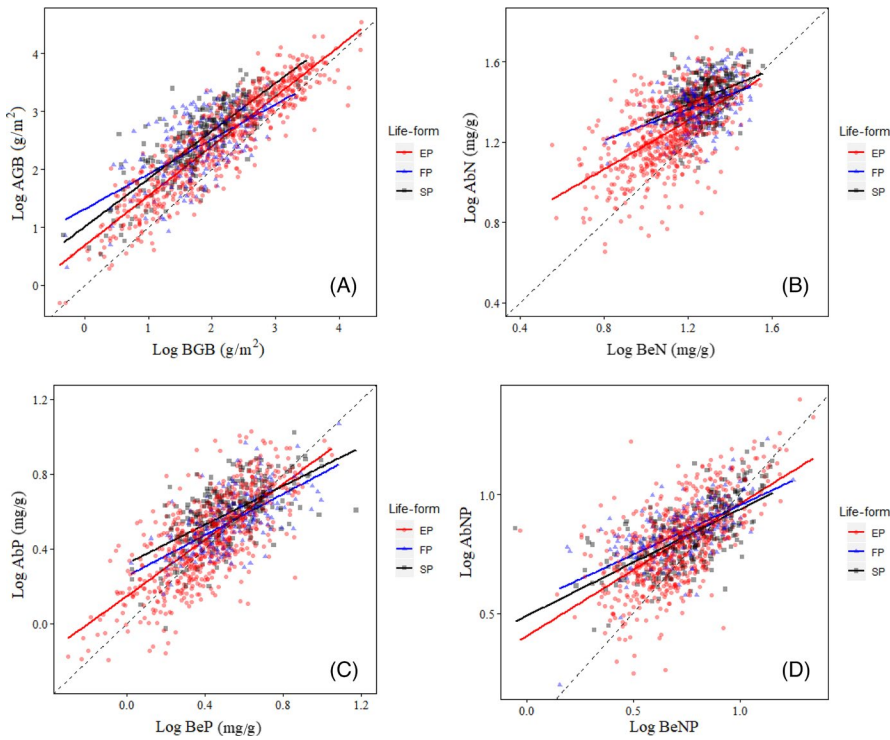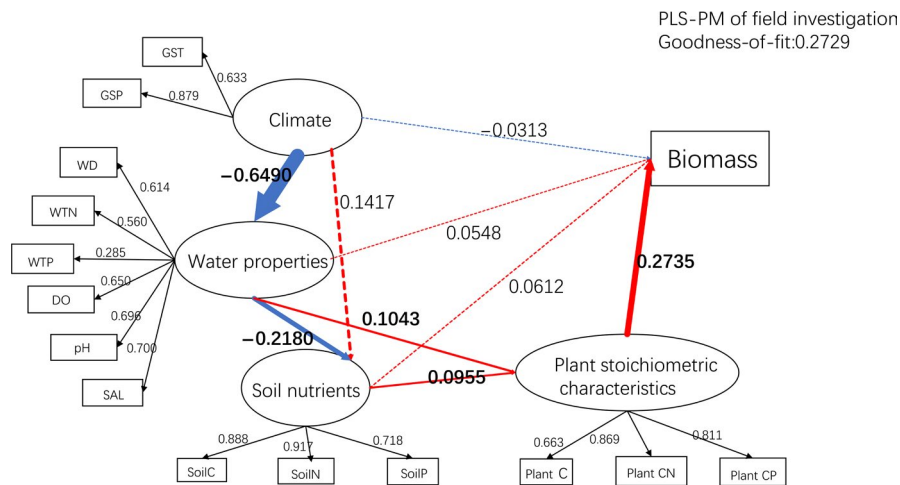
**FIGURE 5** Scaling relationships of above-ground biomass to below-ground biomass (a) and above-ground N (or P, or N:P ratio) to below-ground N (or P, or N:P ratio) (b, c and d) for the different life-forms of aquatic plants (emergent plants, floating-leaved plants and submerged plants). All data were log-transformed before analysis



**FIGURE 6** Partial least squares path models of climate, water properties, soil nutrients, plant stoichiometric characteristics and biomass. The gradual arrow widths are proportional to the strength of the path coefficient. Red and blue lines represent positive and negative pathways, and solid and dotted lines represent significant and non-significant correlations respectively. Correlation significant test at $p < 0.05$ level. Reflective latent variables (black ovals) are indicated by measured variables (black boxes) with their respective loadings shown

had significant positive effects on the AGB and negative effects on R/S (Figure 3), which might be explained by the substantial above-ground growth space provided by WD for submerged plants and the decrease in light availability with increasing WD, phenomena that could affect the biomass allocation of submerged plants (Lacoul & Freedman, 2006; Li et al., 2013). In addition, the BGB of submerged plants was mainly affected by soil C:P (Figure 3). Previous studies have shown that the growth of submerged plants is mainly affected by bottom sediments rather than by water-column nutrients (Carignan & Kalff, 1980; Xie et al., 2005). The C:P ratios in soil are

an effective indicator of organic matter sources and a potential contribution to soil fertility; higher soil C:P ratios indicate a lower available P content in the soil (Elser et al., 2007; Huang et al., 2019). This phenomenon in which restricted resources lead to increased root biomass is consistent with the optimal partitioning theory, which indicates that to maintain a high growth rate in a changing environment, plants should allocate more biomass to organs with the most limited resources (Chapin et al., 1987; Kobe et al., 2010). Therefore, nutrient availability in sediment has profound impacts on the biomass accumulation and distribution of submerged macrophytes.

Different responses to environmental factors by different life-forms of aquatic plants may be due to special ecological adaptation strategies that have developed during the evolution process.

## 4.2 | Stoichiometric characteristics and the effects of environmental factors

The stoichiometric characteristics of aquatic plants show significant differences among different plant life-forms (Gong et al., 2018; Wang et al., 2015; Xia et al., 2014). Our results showed that the C concentrations in the emergent plants and floating-leaved plants were significantly higher than those in the submerged plants, which was consistent with the results of other studies showing that submerged plants have the lowest C concentrations relative to other life-forms of aquatic plants (Gong et al., 2018; Wang et al., 2015; Xia et al., 2014). This finding may have resulted from the lower lignin and cellulose levels in submerged plants due to water buoyancy (Santamaría et al., 2003); however, other stoichiometric characteristics are not consistent across studies with the exception of C concentrations. In our study, compared with the other two life-forms, the submerged plants showed the highest N, P and N:P and the lowest C:N and C:P, while the emergent plants showed the lowest N and P and the highest C:N and C:P, consistent with the results of Xia et al. (2014). Xia et al. (2014) studied eastern China, including some parts of north-eastern China, which may result in a similar pattern of stoichiometric characteristics. However, Wang et al. (2015) showed a lower N and N:P and a higher P and C:N in submerged plants on the Tibetan Plateau, while the highest N and P in floating-leaved plants and the C:N, C:P and N:P in emergent plants occurred in the arid zone of north-western China (Gong et al., 2018). This result may indicate that different life-forms of aquatic plants form various stoichiometric characteristics in response to environmental conditions in different geographical areas. Kerkhoff et al. (2006) found lower nutrient concentrations in roots compared with leaves in seed plants; in our study however, with the exception of the C:N ratios, the C, N and P concentrations and the C:P and N:P ratios in above-ground organs were all significantly higher than those in below-ground organs (Table 1). This result indicates that different organs distribute nutrients in different ways and that photosynthetic organs usually require higher nutrient concentrations due to physiological functions (Minden & Kleyer, 2014; Zhang et al., 2018).

The SMA results revealed that the above-ground and below-ground elements of aquatic plants showed a significant correlation (Figure 5). The scaling slopes of the N content showed an isometric relationship, but the P content and N:P ratios indicated an allometric relationship among the three aquatic plant life-forms (Table 2), which suggested that the responses of the above-ground and below-ground organs to N and P nutrients were not consistent. Kerkhoff et al. (2006) also confirmed that the scaling of N or P is inconsistent among the different organs in woody and herbaceous plants. P-rich rRNA plays an important role in protein synthesis (Sterner & Elser, 2002), which is closely related to plant growth. The results

likely suggest that aquatic plants show greater plasticity to the P distribution than to the N content between different organs in north-eastern China.

The elemental composition and stoichiometric characteristics of aquatic plants are considered to be explained by species (taxon) identity and closely related to the environmental conditions where plants grow (Demars & Edwards, 2007; Gong et al., 2018; Li et al., 2013; Rao et al., 2020; Wang et al., 2015; Xia et al., 2014). For all aquatic plants, WD was the main factor affecting aquatic plant stoichiometry characteristics (Figure 4e). Water-level fluctuation alters gas exchange in water-air interface and light availability for plant photosynthesis (Lacoul & Freedman, 2006; Li et al., 2013); simultaneously, sediment element composition and the interaction between surficial sediments and the water column will change (Qin et al., 2020). Furthermore, SAL and soil N:P also have a great influence on the stoichiometry of aquatic plants (Figure 4e), because increased SAL may create challenges for aquatic plants due to the relationship between water SAL and osmotic stress (Lacoul & Freedman, 2006); in addition, rooted species mainly obtain N, P and other nutrients from sediment, and plant nutrients are closely related to soil nutrient conditions (Lacoul & Freedman, 2006; Peng et al., 2019; Su et al., 2019).

However, the key factors affecting the stoichiometric characteristics of different life-forms of aquatic plants were not consistent. For emergent plants, the stoichiometry was mainly mediated by DO (Figure 4f), which might be explained by the requirement of plants to adjust their stoichiometry to address growth limited by oxygen deprivation as emergent plants grow in anoxic soils (Lacoul & Freedman, 2006; Sterner & Elser, 2002); additionally, oxygen contents may significantly affect nutrient uptake and utilization by emergent plants by affecting the root microbial community (Fang et al., 2019). GSP was important for floating-leaved plants and submerged plants (Figure 4g,h) because precipitation volumes and frequencies may affect hydrologic conditions; some studies, for example, have suggested that floating-leaved plants such as *N. peltata* show different biomass allocation strategies and morphological and anatomical traits that adapt to water-level variation (Li et al., 2011), and the growth performance and stoichiometric characteristics of submerged plants are affected by water levels (Lacoul & Freedman, 2006; Li et al., 2013). Thus, the stoichiometric characteristics of aquatic plants in response to environmental conditions could be affected by the life-forms of aquatic plants produced through phylogenetic evolution.

## 4.3 | Abiotic environmental factors and plant stoichiometric characteristics modulate the biomass of aquatic plants

Plant biomass is usually affected by abiotic environmental factors such as temperature, precipitation, light, nutrients and plant characteristics, including phylogenetic and resource utilization capacity (Liu et al., 2020; Poorter et al., 2012; Reich et al., 2014; Yang et al., 2010, 2018). Our results showed that plant stoichiometric characteristics

were important direct drivers of biomass production (Figure 6). Kleyer and Minden (2015) revealed that C and nutrients allocated to plant organs are closely linked to their biomass and physiological activity, and plant nutrient concentrations and their ratios are closely related to the plant growth rate (Sterner & Elser, 2002). It has been demonstrated that plant N and P concentrations and nutrient allocations in plant tissues are coupled with plant productivity (Tang et al., 2018). Concomitantly, N and P accumulation are imbalanced in human-impacted freshwater ecosystems (Penuelas et al., 2020; Yan, Han, et al., 2016), which could have large effects on the nutrient absorption of aquatic plants and lead to further changes in aquatic plant biomass allocation patterns (Lacoul & Freedman, 2006; Peng et al., 2019). Conversely, environmental conditions (climate, water properties and soil nutrients) indirectly affect biomass through effects on plant stoichiometric characteristics (Figure 6). In grasslands, biomass did not show a significant trend with mean annual temperature but increased with mean annual precipitation, and there was a consistent pattern in AGB and BGB (Yang et al., 2010). Mulder et al. (2013) also determined that the traits of above-ground and below-ground systems can be consistent in the same model. Although climate factors had no obvious direct effect on aquatic plant biomass, they could affect water properties and soil nutrients and then impact plant stoichiometric characteristics, further influencing aquatic plant biomass (Figure 6). Global climate change impacts, such as warming, precipitation and N deposition, and human activities have significantly altered nutrient stocks and the balance of C, N and P in water and the soil environment (Penuelas et al., 2020; Yue et al., 2017). Williamson et al. (2016) have also demonstrated that temperature can alter the C cycle and couple C to N and P in streams. The changes in plant stoichiometric characteristics are closely correlated with the changes in soil and water nutrients (Huang et al., 2019; Peng et al., 2019; Su et al., 2019), and the imbalance of N and P in the environment may alter the C:nutrient ratios of plants that can effectively reflect the physiological regulation of N and P uptake during the C assimilation process, further influencing plant biomass production (Huang et al., 2019; McGroddy et al., 2004; Peng et al., 2019; Tang et al., 2018).

## 5 | CONCLUSIONS

Different life-forms of aquatic plants utilize different resource allocation strategies. The R/S ratios of the three aquatic plant life-forms were significantly different, and the trend showed that the values of the ratios for the three plants were in the following order: emergent plants > floating-leaved plants > submerged plants. The biomass (N, P and N:P) was generally closely correlated between above-ground and below-ground organs, and differences existed between the different life-forms of aquatic plants. The responses of biomass partitioning and nutrient allocation to environmental factors were significantly different among the three life-forms of aquatic plants. Plant stoichiometric characteristics are important direct drivers of biomass production, and environmental conditions (climate, water properties and soil nutrients) indirectly affect biomass through effects on plant stoichiometric characteristics.

Climate change and anthropogenic activities have altered N and P cycling in freshwater ecosystems (Penuelas et al., 2020; Yan, Han, et al., 2016), and as primary producers, aquatic plants play a pivotal role in nutrient biogeochemical cycles linked through the metabolic activity of living organisms (Sardans et al., 2011; Sterner & Elser, 2002). Climate change impacts such as N deposition and precipitation changes and human activities may affect water properties and soil nutrients. These changes influence plant stoichiometric characteristics and affect aquatic plant growth, which may further alter the aquatic plant community composition.

## AUTHORS' CONTRIBUTIONS

J.H., H.Y., C.L. and D.Y. designed the study; J.H., H.Y., Y.L. and J.W. collected the data; J.H. and T.L. analysed the data; J.H., H.Y. and C.L. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

The dataset used for analysis is archived in Dryad Digital Repository https://doi.org/10.5061/dryad.prr4xgxm8 (Hu et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.