

Article

Influence of N:P Ratio of Water on Ecological Stoichiometry of *Vallisneria natans* and *Hydrilla verticillata*

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Abstract: Eutrophication is one of the major threats to shallow lake ecosystems, because it causes large-scale degradation of submerged plants. N:P ratio is an important indicator to estimate nutrient supply to water bodies and guide the restoration of submerged plants. The massive input of N and P changes the structure of aquatic communities and ecological processes. However, the mechanism underlying the influence of changes in N and P content and the N:P ratio of a water body on the growth of submerged plants is still unclear. In this study, we simulated gradients of water N:P ratio in lakes in the middle-lower reaches of the Yangtze River using outdoor mesocosm experiments. Using established generalized linear models (GLM), the effects of total nitrogen (TN) content and N:P ratio of water, phytoplankton and periphytic algae biomass, and relative growth rate (RGR) of plants on the stoichiometric characteristics of two widely distributed submerged plants, *Hydrilla verticillata* and *Vallisneria natans*, were explored. The results reveal that changes in water nutrient content affected the C:N:P stoichiometry of submerged plants. In a middle-eutrophic state, the stoichiometric characteristics of C, N, and P in the submerged plants were not influenced by phytoplankton and periphytic algae. The P content of *H. verticillata* and *V. natans* was positively correlated with their relative growth rate (RGR). As TN and N:P ratio of water increased, their N content increased and C:N decreased. These results indicate that excessive N absorption by submerged plants and the consequent internal physiological injury and growth inhibition may be the important reasons for the degradation of submerged vegetation in the process of lake eutrophication.

Keywords: submerged plants; water N:P ratio; C:N:P stoichiometric characteristics; growth rate; middle-lower Yangtze River reach

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1. Introduction

Submerged plants are important primary producers in lakes and play a unique role in maintaining clean water by competing with algae for light and nutrients [1]. Submerged plants not only support macroinvertebrates and fishes in the lakes but also are important food resources for waterbirds, providing vital ecosystem services [2–4]. However, with the acceleration of industrialization processes, decline and disappearance of submerged plants is occurring worldwide, causing widespread concern [5,6]. Global lake aquatic plants assessment reported that 65% of study sites exhibited a significant reduction in the aquatic vegetation cover [7]. Over the past 20 years, biomass and diversity of submerged plants in China's lakes are in decline due to deterioration of lake ecosystems [6,8,9]. *Vallisneria natans* and *Hydrilla verticillata* are submerged plants that are widely

distributed in lakes in the middle and lower reaches of the Yangtze River. The growth forms and biomass allocation strategies of these two submerged plants are different. *V. natans* is a rosette-type submerged plant with elongated leaves, well-developed roots, and short, upright stems and can tolerate low light [10,11]. *H. verticillata* is an erect submerged plant whose biomass is relatively evenly distributed among leaves, stems, and roots [10]. The biomass ratio of the aboveground and underground parts of *H. verticillata* is greater than that of *V. natans*; therefore, they may have different nutrient absorption and metabolism strategies.

The eutrophication degree in lakes in mid- and low-latitude regions is higher than that in high-latitude regions [12]. In China, the ratio of the number of moderately eutrophic lakes relative to the total number of lakes considered for this study had raised from 31.3% in 2009 to 42.7% in 2018 [13]. Most of the lakes at the middle and lower reaches of the Yangtze River are mesotrophic or eutrophic, leading to a heavy decrease in light penetration [14]. The rapid increase in eutrophication has led to frequent occurrence of cyanobacterial blooms in the watershed. Phytoplankton death and decomposition consumes dissolved oxygen in water, exacerbates the extinction of submerged plants, leads to biodiversity decline and simplification of the biological community structure, and destroys the health of aquatic ecosystems [14–17].

Environmental stoichiometry can strongly affect an organism's stoichiometry [18–21]. This may alter competitiveness of species [22], leading to a shift in species composition [23] and affecting structure, function, and stability of lake ecosystems. Studies have reported that N and P of water column are more important than those of sediment in determining C:N:P stoichiometric signatures of submerged plants [24–26]. The growth process of organisms is essentially a process of accumulating elements (mainly C, N, and P) and adjusting their relative ratios [27]. Based on this, the growth rate hypothesis proposes that C:N:P in organisms lacking P storage mainly depends on the rRNA content [27]. Fast-growing organisms require a large amount of rRNA to participate in the formation of ribosomes to synthesize proteins. Therefore, fast-growing organisms tend to have relatively low C:P and N:P ratios [28]. Some studies have confirmed that growth rate and biostochiometric characteristics of plants were closely related, and they follow the relative growth rate hypothesis [29–32]. In lakes, the addition of N and P increases the net growth rate and nutrient content of cells, so the stoichiometry of N:P ratio and C:P ratio will be reduced [33]. However, reports on the growth rate hypothesis are inconsistent. For example, under N restriction, the N:P ratio of *Daphnia* has no obvious relationship with the growth rate [34]. This inconsistency may be due to the decrease in the amount of anabolism closely related to growth that is used for physiological mechanisms, such as stress response, when organisms are in an N- and P-restricted environment [35]. The large input of N and P changes the structure of nutrient content of water and aquatic community, as the coupling effect between N and P restricts ecological processes. Water N:P ratio has become an important tool for researchers to evaluate the nutrient structure of water bodies and its influence on phytoplankton and submerged plants biomass [36–38].

Studies show that during the eutrophication process, with the increasement of P and N in the water, the submerged plants first show good growth and are resistant to the increase in N loading at moderate P concentrations [39], but as the nitrogen load increases, the biomass of submerged macrophytes decreases due to high concentrations of NH_4^+ and NO_3^- . This exerts toxic effects on aquatic plants [40], decreases the allocation of C, N, and P to the stem [41], and changes the light condition caused by cyanobacteria bloom [39,40,42]. However, when water P and N concentrations are sufficient but not over-excessive, submerged plants still lose biomass [6–9]. It is necessary to consider the influence of water N:P ratio.

To understand how P and N contents in water column influence growth and stoichiometric characteristics of submerged plants, we simulated P and N contents of the lakes in the middle and lower reaches of the Yangtze River by random setting of a gradient of 90 N:P ratios. We assumed that when water N:P ratios increased, the excessive nitrogen

would inhibit the growth of submerged plants. As algae and submerged plants compete for light, nutrients, and space, we performed outdoor mesocosm experiments to explore the effects of N and P contents and N:P ratio of water and phytoplankton and periphytic algae biomass on the stoichiometric characteristics and growth of *H. verticillata* and *V. natans*.

2. Materials and Methods

2.1. Experimental Design

According to the literature summary of the total phosphorus (TP) and total nitrogen (TN) contents and N:P ratio of shallow lakes in the middle and lower reaches of the Yangtze River (Figure 1), the N:P ratio and TP and TN contents of middle-eutrophic lakes are mainly concentrated in the ranges of 9–29 (Table S1), 0.06–0.14 mg/L, and 0.5–3 mg/L, respectively. The median values of TN and TP were 1.38 mg/L and 0.082 mg/L, respectively. The maximum and minimum values of TN were 3.86 mg/L and 0.212 mg/L, respectively; the maximum and minimum values of TP were 0.18 mg/L and 0.024 mg/L, respectively.

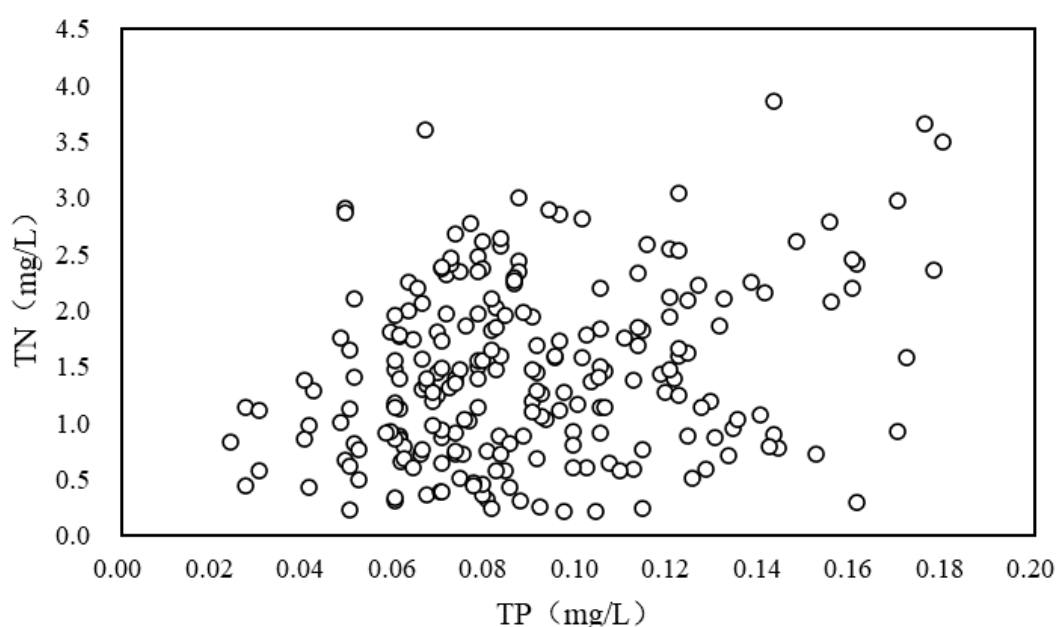


Figure 1. Total phosphorus (TP) and total nitrogen (TN) contents in waters of shallow lakes of the middle and lower reaches of the Yangtze River based on literature data (Table S1).

V. natans and *H. verticillata* were harvested from Poyang Lake and planted in plastic cups separately with the washed river sand as the substrate. Further, they were placed in two 50 L plastic buckets (upper diameter 40 cm, bottom 33 cm, height 41 cm) with purified water after 7 days of adaptation. Overall, 15 cups of *V. natans* or *H. verticillata* with good growth condition and similar weight were put into each 50 L plastic bucket. According to the literature summary of TP and TN contents and N:P ratio in shallow lakes of the middle and lower reaches of the Yangtze River (Figure 1, Table S1), we randomly set each bucket water N:P ratio within the range of 9–29, with TP and TN contents in the ranges of 0.06–0.14 and 0.5–3 mg/L, respectively.

The experiment started on July 1, 2020, and ended on August 9, 2020, lasting for 40 days. The fresh weight of transplanted plants was recorded as the weight at time 0 for relative growth rate calculation. A hand-held multi-parameter water quality meter (HQ40D, Hach Inc., Loveland, CO, USA) was used to measure environmental indicators such as water temperature (T), total dissolved solids (TDS), and oxidation–reduction potential (ORP). During the experimental period, purified water was supplemented

regularly, and NH_4NO_3 and KH_2PO_4 solutions were supplemented according to the nutrient gradient to maintain the initial nutrient level. At the end of the experiment, three *V. natans* and *H. verticillata* plants were randomly selected from each bucket, and a total of 540 plants in 180 buckets were weighed (denoted as the weight at time t_1) and recorded. Further, the plants were dried and ground, and the C, N, and P contents were analyzed. On days 20 and 40 after the start of the experiment, TN and TP contents and periphytic algae and phytoplankton biomass in the water of 180 experimental buckets were measured.

2.2. Laboratory Analysis

At days 0, 20, and 40, the TN, TP, DTN, and DTP contents in water were measured using alkaline $\text{K}_2\text{S}_2\text{O}_8$ digestion UV spectrophotometry and $\text{K}_2\text{S}_2\text{O}_8$ digestion $(\text{NH}_4)_2\text{MoO}_4$ spectrophotometry, respectively. $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, $\text{NO}_2\text{-N}$, and $\text{PO}_4\text{-P}$ contents in water were analyzed using flow analyzer (CleverChem 200+, DeChem-Tech.GmbH, Hamburg, Germany). Hot ethanol method was performed to measure the chlorophyll a of periphytic algae and phytoplankton.

The samples of submerged plants were oven-dried at $80\text{ }^\circ\text{C}$ for 48 h so that constant weight was obtained; further, they were ground into fine powder using a planetary ball mill (Mini Beadbeater-16, Biospec product, Bartlesville, OK, USA) before elemental analyses. The C and N contents of plants were determined using an elemental analyzer (Flash EA 1112 series, CE Instruments, Waltham, MA, USA). P contents of plants were measured using sulfuric acid/hydrogen peroxide digestion and ammonium molybdate ascorbic acid methods [43].

2.3. Data Analysis

The relative growth rate (RGR) of plants can be calculated using Equation (1):

$$\text{RGR} = (\ln W_1 - \ln W_0) / t \quad (1)$$

where RGR is the relative plant growth rate [$\text{mg} \cdot (\text{g} \cdot \text{d}^{-1})$]; W_0 is the fresh weight of the plant at the beginning of the experiment (mg); W_1 is the fresh weight of the plant at the end of the experiment (mg); and t is the experiment time (d).

R 4.1.1 was used to establish GLM models to analyze the relationship of plant C, N, and P contents, C:N ratio, C:P ratio, N:P ratios, water body TN content and N:P ratio, phytoplankton biomass, periphytic algae biomass, and RGR of plants. T-test was used to compare C, N, and P contents of *H. verticillata* and *V. natans*. Reduced chi-squared test was used to analyze whether a nonlinear fitting relationship existed between the indicators. Reduced chi-squared test value was equal to chi-squared test value divided by degrees of freedom. The closer the reduced chi-squared test to 1, the better the fitting effect.

3. Results

3.1. Nutrient Concentrations in Mesocosm System and Stoichiometric Traits of Submerged Plants

The contents of TN, TP, N:P ratio, phytoplankton Chl-*a*, and periphytic algae Chl-*a* in mesocosm systems of *H. verticillata* and *V. natans* are given in Table 1. C and N contents of *H. verticillata* were significantly higher than those of *V. natans*, whereas P content of *H. verticillata* was significantly lower than that of *V. natans* (all $p < 0.05$). The Chl-*a* content of phytoplankton in the *H. verticillata* group was significantly higher than that of the *V. natans* group, and the TP content was significantly lower than that of the *V. natans* group ($p < 0.05$). The C/N ratio, C/P ratio, and N/P ratio of *H. verticillata* were significantly higher than those of *V. natans* ($p < 0.05$). Other environment data are shown in Table S2.

Table 1. Mean values of environmental parameters and stoichiometric traits of submerged plants.

	<i>H. verticillata</i>		<i>V. natans</i>	
	Mean	Standard Error	Mean	Standard Error
Water TN (mg/L)	1.79	0.12	1.60	0.09
Water TP (mg/L)	0.09	0.00	0.10	0.00
Water N:P	22.29	1.26	17.85	1.02
Phytoplankton Chl- <i>a</i> (mg/m ³)	14.41	2.67	13.08	1.13
Periphytic algae Chl- <i>a</i> (mg/m ²)	5.2×10^{-3}	0.01	5×10^{-3}	4.5×10^{-3}
Plant C (mg/g)	0.14	4×10^{-3}	0.13	2×10^{-3}
Plant N (mg/g)	8.98×10^{-3}	2.9×10^{-4}	8.75×10^{-3}	2.1×10^{-2}
Plant P (mg/g)	2×10^{-4}	1×10^{-4}	9×10^{-4}	3×10^{-5}
Plant C:N	17.6	0.6	15.5	0.3
Plant C:P	856.7	65.2	153.4	3.9
Plant N:P	49.7	3.6	10.3	0.3

3.2. Factors Determining Stoichiometric Characteristics of *H. verticillata*

The C:N ratio of *H. verticillata* was negatively correlated with the TN content and N:P ratio of water (Table 2, Figure 2). The N content of *H. verticillata* was positively correlated with water TN content; the reduced chi-squared test value was close to 1, indicating that the nonlinear fitting curve had a good fitting effect (Table 3, Figure 3). The P content of *H. verticillata* was positively correlated with RGR and TN in the water body (Table 4, Figure 4), indicating that with the increase of the TN content in the water body, the P content of *H. verticillata* also increased. C content and the N:P and C:P ratios of *H. verticillata* had no significant correlation with the following five factors: water body TN content, N:P ratio, phytoplankton biomass, periphytic algae biomass, and RGR of plants ($p > 0.05$).

Table 2. Summary of the best model of the relationship between *H. verticillata* C:N and water N:P.

Predictor	Coefficient	Std. Error	<i>t</i> Value	<i>p</i>
Intercept	22.573	1.281	17.623	<0.001
TN (mg/L)	−1.229	0.534	−2.303	0.024
Water N:P	−0.143	0.049	−2.927	0.005
Phytoplankton (mg/m ³)	0.129	0.130	0.991	0.325
Periphytic algae (mg/m ²)	−193.167	268.323	−0.720	0.474
RGR [mg·(g·d ^{−1})]	−61.470	54.298	−1.132	0.262

Bold numbers indicate significant differences ($p < 0.05$).

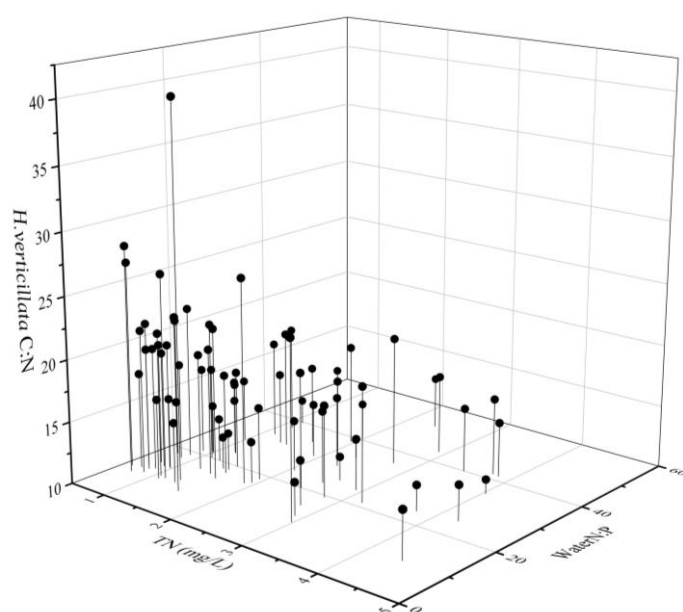


Figure 2. The relationship between *H. verticillata* C:N, water TN, and water N:P.

Table 3. Summary of the best model of the relationship between *H. verticillata* N and water N:P.

Predictor	Coefficient	Std. Error	<i>t</i> Value	<i>p</i>
Intercept	6.833×10^{-3}	7.491×10^{-4}	9.121	<0.001
TN (mg/L)	8.527×10^{-4}	3.122×10^{-4}	2.732	0.008
Water N:P	2.753×10^{-6}	2.853×10^{-5}	0.096	0.923
Phytoplankton (mg/m ³)	-5.350×10^{-5}	7.628×10^{-5}	−0.701	0.485
Periphytic algae (mg/m ²)	8.544×10^{-2}	1.569×10^{-1}	0.544	0.588
RGR [mg·(g·d ^{−1})]	2.199×10^{-2}	3.175×10^{-2}	0.693	0.491

Bold numbers indicate significant differences ($p < 0.05$).

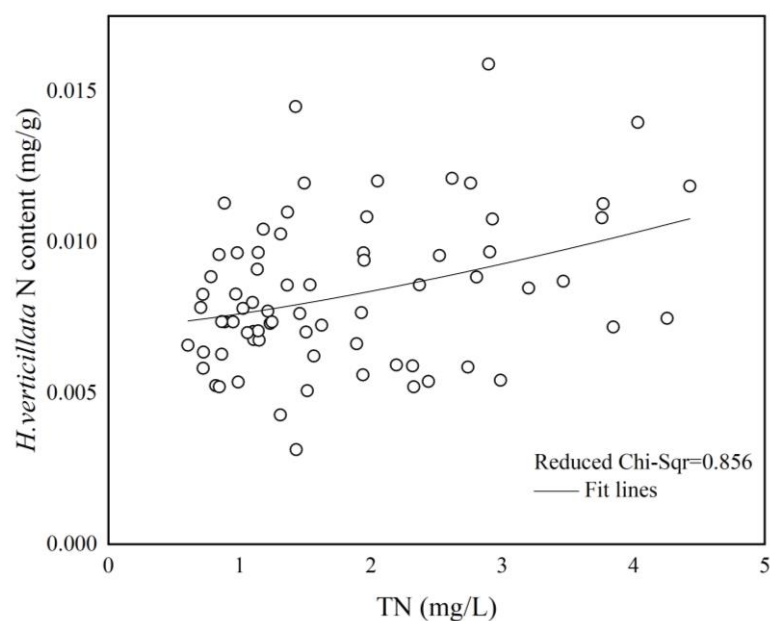
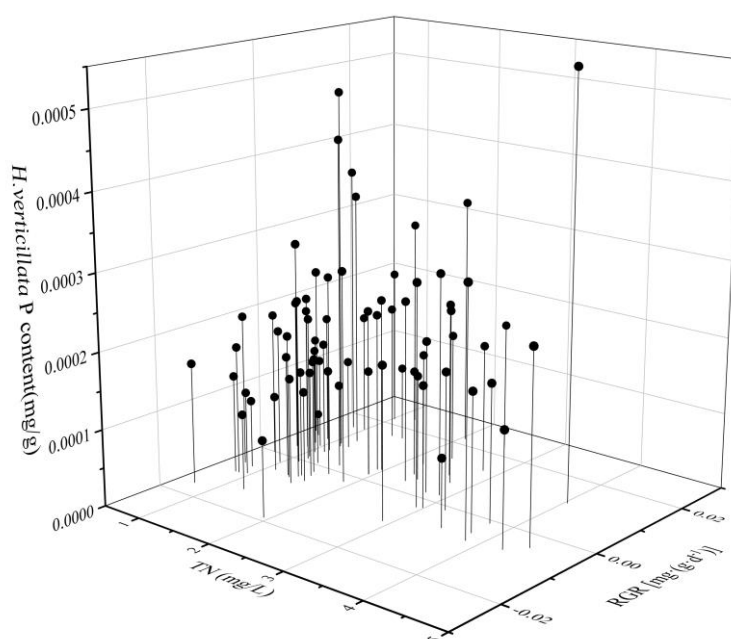


Figure 3. The relationship between *H. verticillata* N and water TN.

Table 4. Summary of the best model of the relationship between *H. verticillata* P and water N:P.

Predictor	Coefficient	Std. Error	t Value	p
Intercept	1.675×10^{-4}	2.689×10^{-5}	6.228	<0.001
TN (mg/L)	2.473×10^{-5}	1.120×10^{-5}	2.207	0.031
Water N:P	-7.076×10^{-7}	1.024×10^{-6}	-0.691	0.492
Phytoplankton (mg/m ³)	-7.101×10^{-7}	2.738×10^{-6}	-0.259	0.796
Periphytic algae (mg/m ²)	4.353×10^{-4}	5.632×10^{-3}	0.077	0.939
RGR [mg·(g·d ⁻¹)]	2.897×10^{-3}	1.140×10^{-3}	2.542	0.013

Bold numbers indicate significant differences ($p < 0.05$).

**Figure 4.** The relationship between *H. verticillata* P, water TN, and relative growth rate (RGR).

3.3. Factors Determining Stoichiometric Characteristics of *V. natans*

C:N ratio of *V. natans* was negatively correlated with TN content and N:P ratio of water (Table 5, Figure 5). The N content of *V. natans* was positively correlated with TN content of water. The reduced chi-squared test value was close to 1, indicating that the fitting effect of the nonlinear fitting curve was good (Table 6, Figure 6). The P content of *V. natans* was positively correlated with RGR of plant (Table 7, Figure 7), and the N:P of *V. natans* was positively correlated with the TN of the water body. The higher the TN of the water body, the higher the N:P of *V. natans*. The reduced chi-squared test value was close to 1, indicating that the fitting effect of the nonlinear fitting curve was good (Table 8, Figure 8). The C:P ratio of *V. natans* was negatively correlated with RGR (Table 9, Figure 9). No significant correlation existed between the C content of *V. natans* and the above five factors ($p > 0.05$).

Table 5. Summary of the best model of the relationship between *V. natans* C:N and water N:P.

Predictor	Coefficient	Std. Error	t Value	p
Intercept	20.100	0.664	30.259	<0.001
TN (mg/L)	-0.362	0.512	-2.662	0.009
Water N:P	-0.096	0.048	-2.008	0.048
Phytoplankton (mg/m ³)	-0.115	0.116	-0.992	0.324

Periphytic algae (mg/m ²)	136.287	266.497	0.511	0.610
RGR [mg·(g·d ⁻¹)]	-21.892	41.237	-0.531	0.597

Bold numbers indicate significant differences ($p < 0.05$).

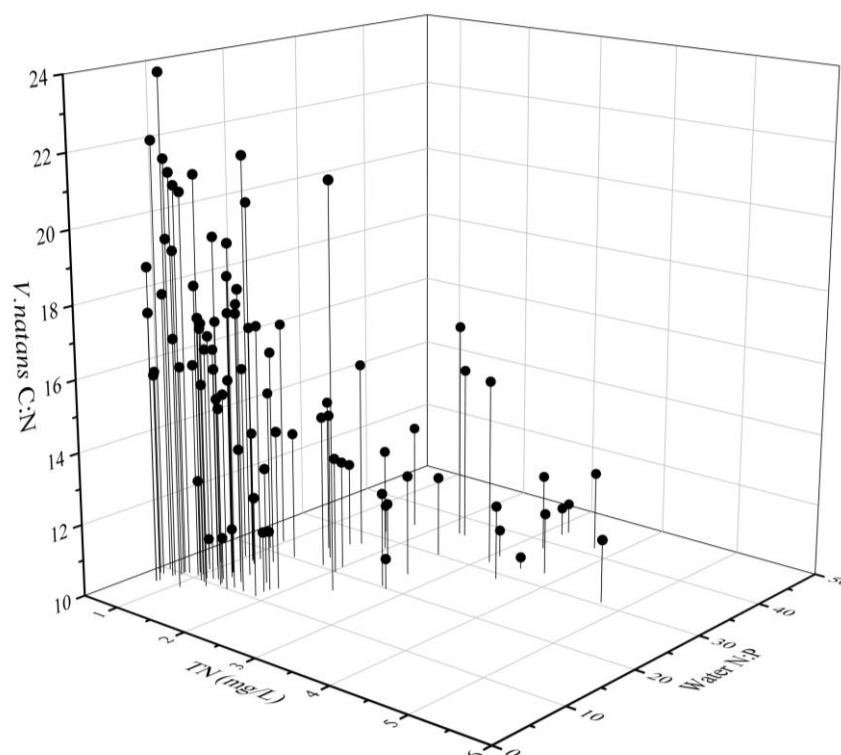


Figure 5. The relationship between *V. natans* C:N, water TN, and water N:P.

Table 6. Summary of the best model of the relationship between *V. natans* N and water N:P.

Predictor	Coefficient	Std. Error	<i>t</i> Value	<i>p</i>
Intercept	6.197×10^{-3}	4.162×10^{-4}	14.890	<0.001
TN (mg/L)	9.825×10^{-4}	3.206×10^{-4}	3.065	0.003
Water N:P	3.251×10^{-5}	3.009×10^{-5}	1.080	0.283
Phytoplankton (mg/m ³)	8.610×10^{-5}	7.254×10^{-5}	1.187	0.239
Periphytic algae (mg/m ²)	-1.235×10^{-1}	1.670×10^{-1}	-0.740	0.462
RGR [mg·(g·d ⁻¹)]	2.339×10^{-2}	2.583×10^{-2}	0.905	0.368

Bold numbers indicate significant differences ($p < 0.05$).

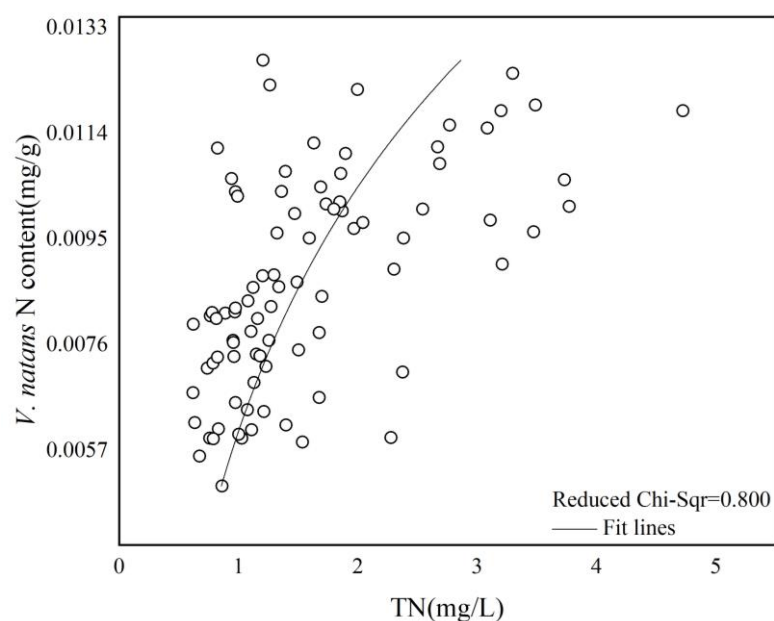


Figure 6. The relationship between *V. natans* N and water TN.

Table 7. Summary of the best model of the relationship between *V. natans* P and water N:P.

Predictor	Coefficient	Std. Error	<i>t</i> Value	<i>p</i>
Intercept	9.103×10^{-4}	6.087×10^{-5}	14.956	<0.001
TN (mg/L)	2.362×10^{-5}	4.688×10^{-5}	0.504	0.616
Water N:P	-4.172×10^{-6}	4.401×10^{-6}	-0.948	0.346
Phytoplankton (mg/m ³)	1.620×10^{-5}	1.061×10^{-5}	1.527	0.131
Periphytic algae (mg/m ²)	-3.116×10^{-2}	2.442×10^{-2}	-1.276	0.206
RGR [mg·(g·d ⁻¹)]	8.342×10^{-3}	3.778×10^{-3}	2.208	0.030

Bold numbers indicate significant differences ($p < 0.05$).

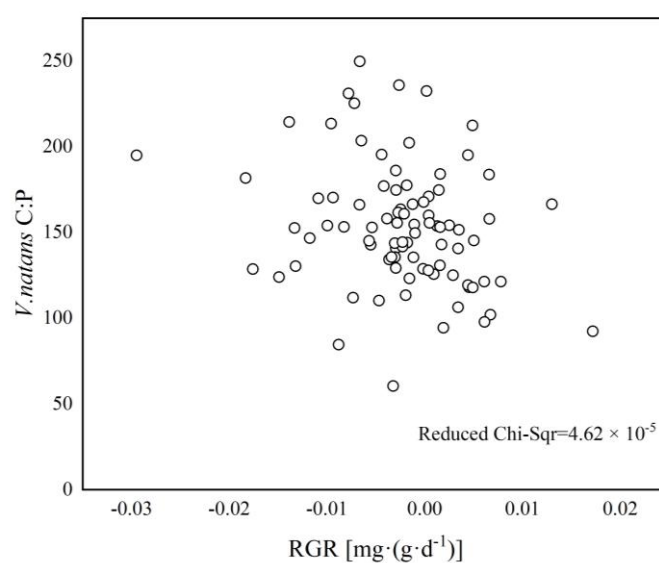
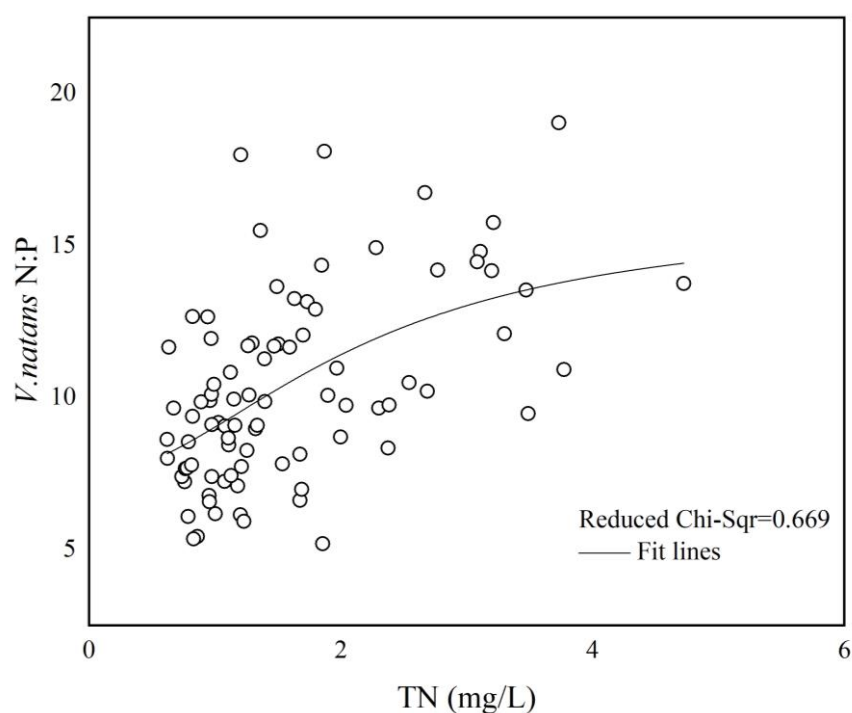


Figure 7. The relationship between *V. natans* P and relative growth rate (RGR).

Table 8. Summary of the best model of the relationship between *V. natans* N:P and water N:P.

Predictor	Coefficient	Std. Error	<i>t</i> Value	<i>p</i>
Intercept	6.909	0.694	9.951	<0.001
TN (mg/L)	1.204	0.535	2.250	0.027
Water N:P	0.065	0.050	1.294	0.199
Phytoplankton (mg/m ³)	−0.057	0.121	−0.468	0.641
Periphytic algae (mg/m ²)	159.002	278.573	0.571	0.570
RGR [mg·(g·d ^{−1})]	−66.161	3.105	−1.535	0.129

Bold numbers indicate significant differences ($p < 0.05$).

**Figure 8.** The relationship between *V. natans* N:P and water TN.**Table 9.** Summary of the best model of the relationship between *V. natans* C:P and water N:P.

Predictor	Coefficient	Std. Error	<i>t</i> Value	<i>p</i>
Intercept	1.518×10^2	9.384×10^0	16.174	<0.001
TN (mg/L)	2.079×10^0	0.229×10^0	0.288	0.774
Water N:P	8.067×10^{-2}	6.785×10^{-1}	0.119	0.906
Phytoplankton (mg/m ³)	-1.262×10^0	1.636×10^0	−0.772	0.443
Periphytic algae (mg/m ²)	1.935×10^3	3.765×10^3	0.514	0.609
RGR [mg·(g·d ^{−1})]	-1.199×10^3	5.826×10^2	−2.058	0.043

Bold numbers indicate significant differences ($p < 0.05$).

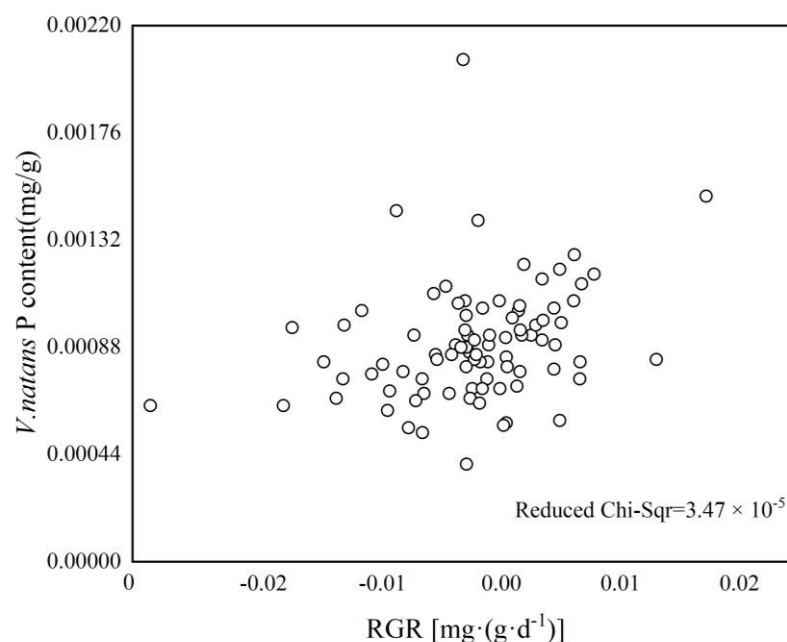


Figure 9. The relationship between *V. natans* C:P and relative growth rate (RGR).

4. Discussion

4.1. The Influence of Water Nutrients on the Stoichiometric Characteristics of Submerged Plants

Water nutrients were the basis of C, N, and P content allocation in submerged plants to meet the needs of rapid growth and reproduction [44,45]. Changes in the nutrient content of a water body affect stoichiometric characteristics of submerged plants and plant community composition [19,21,46,47]. The input of external nutrients trigger change in C:N:P stoichiometric signatures in the aquatic plants. Plants accumulated nutrients in excess of their cellular requirements when their growth was not limited by N and P availability [40,48]. Because of the high concentration of P in water, the C:P and N:P ratios decreased, and intracellular C:N:P stoichiometric signatures of aquatic plants significantly lowered [49]. Bi et al. [50] studied the growth of *Rhodomonas* sp., *Phaeodactylum tricornutum*, and *Isochrysis galbana*; N:P ratios varied within the environmental N:P ratio, and lower N:P ratio promoted the growth of algae [50].

In our study, the mean N:P ratio of *V. natans* was approximately 10.3:1, which was a bit lower than that of plants (11:1) in the River Spey in Great Britain, as reported by Demars and Edwards [50]. Our result was consistent with the studies on the floodplain lakes of eastern China [11] and the middle and lower reaches of the Yangtze River [49]; these studies reported that as the water body TN increased, the N content and N:P ratio of *V. natans* also increased [11,49]. Many studies have reported that freshwater organisms change their N:P and C:P ratios in response to P enrichment [11,35,51]. However, the N:P ratio of *H. verticillata* (49.7:1) was much higher than that reported in previous studies. *H. verticillata* might have the ability to absorb N in water more easily.

In addition, the stoichiometric characteristics of C:N:P in plant tissues depended not only on nutrient supply but also on the availability of light in the water column. The light in the water column could affect the physiology, morphology, and biomass distribution of submerged plants, resulting in large variations in the concentration of C, N, and P and stoichiometry of C:N:P in plants [40,52–54]. N is a constituent element of plant cell proteins and nucleic acid, and it participates in the synthesis of chlorophyll in the chloroplast. Therefore, it is closely related to the ability of plant photosynthesis [55]. The

photosynthetic compensation point and photophobicity of *V. natans* were lower than those of *H. verticillata*. Therefore, *V. natans* could adapt to low-light environments, which resulted in higher N:P ratio in *H. verticillata* than that in *V. natans* [10]. Therefore, the shading effect caused by phytoplankton may have affected the photosynthesis of the plants. In our study, the content of phytoplankton Chl-*a* in the water of the *H. verticillata* planting was higher than that of the *V. natans* planting.

Differences in nutrient absorption and adaptability strategies were observed between *H. verticillata* and *V. natans*. Whereas *V. natans* has roots, *H. verticillata* was a “pseudo-root tip” plant with only whisker-shaped adventitious roots [10]. With lower C input for supporting tissues, the C absorption of *V. natans* was lower than that of *H. verticillata*, which was conducive to its tolerance under low-light stress and was consistent with its low-light photosynthetic compensation point [25,56,57]. In addition, the C:N metabolism level of *V. natans* was lower and carbohydrate storage was higher than those of *H. verticillata* [25,58]. This might be because of *H. verticillata* allocating more C on the stem to stretch its branches to the surface of the water [56,59].

In addition, C:N ratio of *H. verticillata* and *V. natans* decreased with the increase in water TN, and water C:N ratio reflected the high N-based biomass of plant unit C and the decrease in nutrient use efficiency [60]. The same conclusion was obtained while studying the stoichiometric characteristics of algae [61]. Moreover, the phytoplankton biomass is limited by the nutrient concentration and the ratio of limiting nutrients [21]. In our study, the attached algae had no significant effect on the stoichiometric characteristics of the submerged plants, whereas the periphytic algae may be less affected by the nutrient enrichment in the water column [62].

With the increase in TN content of the water body, the N:P of water increased, but C:N of *H. verticillata* and *V. natans* decreased. Low C:N of plants under high N and P environment indicated the overabsorption of N; this led to the accumulation of ammonia nitrogen in tissues, change in nitrogen metabolism, and the production of free amino acids producing physiological toxicity [42]. Soluble sugar accumulates in plant leaves in response to stress, resulting in the decrease in soluble sugar content in plant roots. This affects the production of new buds and finally inhibits the growth of plants [42]. Submerged plants may be resilient to abrupt increases in N loading at moderate TP concentrations; however, after prolonged exposure, a complete collapse occurs [39]. Excessive N content reduces stem strength. When water TN content reached 0.92 mg/L and water TP was 0.12 mg/L, *V. natans* had low ramet counts and biomasses [41]. Excessive N concentration, for example, >5 mg/L, had negative effects on the photosynthetic efficiency and biomass of submerged plants [39,63]. The excessive uptake capacity of submerged plants under rich N and P conditions with high water N:P ratio enhances the decline in growth of submerged plants, which can markedly alter the aquatic ecosystem from a plant-dominated clear state to an algal-dominated turbid state.

4.2. The Relationship between Growth Rate and Stoichiometric Characteristics of Submerged Plants

Fast-growing organisms usually have lower C:P and N:P ratios. The growth rate hypothesis proposes that fast-growing organisms allocate most of their resources to the synthesis of rRNA (high P) instead of protein (high N) [26,64], which explains the positive correlation between the P content and growth rate of *H. verticillata* and *V. natans*. The negative correlation between *H. verticillata* and *V. natans* C:P and N:P ratios and the growth rate was considered to be the conclusion of the growth rate hypothesis [65–68]; this reflects the requirement of P for rRNA and rapid protein synthesis to support rapid growth [28]. Therefore, the higher the N content of the water body, the greater the N:P ratio of *V. natans* and slower its growth rate. The C:P and N:P ratios had no correlation with the growth rate of *H. verticillata*. In the case of vascular plants, tissue N:P ratio was higher when the growth rate was low, and tissue N:P ratio was lower when the growth rate was high [27,41,68]. Therefore, after determining the N:P ratio of water, the tipping point of submerged plant

determined its growth. This would provide a new solution for submerged plant restoration in shallow lakes.

5. Conclusions

In our study, the N:P ratio of *V. natans* was approximately 10.3:1. As TN of the water body increased, the N content and N:P ratio of *V. natans* also increased. However, the N:P ratio (49.7:1) of *H. verticillata* was much higher than that reported in previous studies. *H. verticillata* tended to absorb more N in water. P content of *H. verticillata* and *V. natans* positively correlated with their growth rates. As water TN and N:P ratio increased, N content increased and C:N decreased in *H. verticillata* and *V. natans*. The negative correlation between *H. verticillata* and *V. natans* C:P and N:P ratios and the growth rate was considered to be the conclusion of the growth rate hypothesis. This indicates that excessive N absorption by submerged plants and the consequent internal physiological injury and growth inhibition may be the important reasons for the degradation of submerged vegetation in the process of lake eutrophication. In a middle-eutrophic state, the stoichiometric characteristics of C, N, and P in submerged plants were not influenced by phytoplankton and periphytic algae.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w14081263/s1>, Table S1: Literature summary of TN and TP in lakes in the middle and lower reaches of the Yangtze River in the past decade; Table S2: Main experimental conditions (water quality parameters) [69–165].

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