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# Nutrient addition delivers growth advantage to *Hydrilla verticillata* over *Vallisneria natans:* a mesocosm study

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**Abstract –** Nutrient availability can affect both the morphology and the nutrient uptake strategies of submerged macrophytes, with different species responding differently to increases in nutrient levels. A 98-day mesocosm experiment was conducted to investigate the responses of co-cultured *Hydrilla verticillata* and *Vallisneria natans* to nutrient enrichments of 3.0 mg N/(L · week) and 0.2 mg P/(L week), mimicking external loading. Water samples were collected every 2 weeks for measuring nutrient and total suspended solid (TSS) concentrations and biomass of phytoplankton (Chl *a*). Dry biomasses of roots and shoots of both species were measured at the end of the experiment. Results showed that under nutrient-enriched conditions, both species reduced the ratio of root to shoot growth and increased nutrient storage per unit of biomass. However, only *H. verticillata* exhibited enhanced growth and nutrient storage, as well as a lower root: shoot ratio and greater shoot biomass than seen in *Vallisneria*. Our findings demonstrate that nutrient enrichment of the water column can invoke morphological plasticity in both *H. verticillata* and *V. natans*, but when both species grow together, the growth advantage goes to the former.

**Keywords:** Submerged macrophyte / nutrient availability / morphological plasticity / biomass

**Résumé – L'ajout d'éléments nutritifs procure un avantage de croissance à *Hydrilla verticillata* par rapport à *Vallisneria natans* : une étude en mésocosme.** La disponibilité des éléments nutritifs peut influer à la fois sur la morphologie et sur les stratégies d'absorption des éléments nutritifs des macrophytes submergés, les différentes espèces réagissant différemment à l'augmentation des niveaux de nutriments. Une expérience en mésocosme de 98 jours a été menée pour étudier les réponses d'*Hydrilla verticillata* et de *Vallisneria natans* co-cultivées à des enrichissements nutritionnels de 3.0 mg N/(L · semaine) et 0.2 mg P/(L · semaine), imitant un apport externe. Des échantillons d'eau ont été prélevés toutes les deux semaines pour mesurer les concentrations de nutriments et de matières en suspension totales (MES) et la biomasse du phytoplancton (Chl a). Les biomasses sèches des racines et des pousses des deux espèces ont été mesurées à la fin de l'expérience. Les résultats ont montré que dans des conditions enrichies en nutriments, les deux espèces réduisaient le rapport entre la croissance des racines et celle des pousses et augmentaient le stockage des nutriments par unité de biomasse. Cependant, seule *H. verticillata* présentait une croissance et un stockage de nutriments améliorés, ainsi qu'un rapport racine:pousse et une biomasse de pousse plus importants que ceux observés chez *Vallisneria*. Nos résultats démontrent que l'enrichissement en éléments nutritifs de la colonne d'eau peut induire la plasticité morphologique chez *H. verticillata* et *V. natans*, mais que lorsque les deux espèces grandissent ensemble, l'avantage de la croissance va à la première.

**Mots clés:** Macrophyte submergé / disponibilité des nutriments / plasticité morphologique / biomasse

## 1 Introduction

Submerged macrophytes play an important role in the trophic status and ecosystem functions of shallow lakes (Jeppesen *et al.*, 1998; Yu *et al.*, 2016). Light and nutrient availability are two key factors affecting the growth and community structure of submerged macrophytes in such systems (Chambers, 1987). Light is often a limiting factor affecting the submerged plants, especially those growing close to the sediment surface. Macrophytes take up and accumulate the nutrients required for growth, maintenance and

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*Corresponding author: `wetlandxfz@163.com` reproduction from both sediment and the water column (Chambers *et al.*, 1989; Madsen and Cedergreen, 2002) and are able to adapt their nutrient acquisition strategy through morphological plasticity and biomass allocation (Mantai and Newton, 1982; Idestam-Almquist and Kautsky, 1995). Some develop acclimation mechanisms or adaptations, allowing then to extract resources from adjacent environments. Phenotypic plasticity might include the environmentally dependent expression of phenotypes that alter physiological processes or morphology, and the morphological plasticity in aquatic plants is often considerable (Sultana *et al.*, 2010). The relative importance of roots and shoots for nutrient uptake may vary between environments (Barko and James, 1998; Eugelink, 1998). An increase in nutrient availability in the water column has previously shown to result in reduced root biomass and a lower root:shoot ratio in submerged macrophytes (Cronin and Lodge, 2003; O'Connell *et al.*, 2015; Dülger *et al.*, 2017). These changes reflect a reduced need for energetically costly underground roots when ample nutrients can be gleaned from the water column (Portielje and Roijackers, 1995). Shoot growth is also an adaptation to the reduced light availability associated with dense phytoplankton development and elevated trophic states (Paerl *et al.*, 1990; Song *et al.*, 2017). In a nutrient-rich system, shoots become more important in terms of both nutrient acquisition and light harvesting.

Plants are known to exhibit species-specific plasticity in biomass allocation (Grime *et al.*, 1986; Husáková *et al.*, 2018). Different species favor their own nutrient conditions (Ozimek *et al.*, 1993; Cao *et al.*, 2011; Mei and Zhang, 2015) and adopt appropriate strategies for nutrient uptake (Langeland, 1996; Xie *et al.*, 2005; Zhang *et al.*, 2007) according to their morphology. Madsen *et al.* (2001) made a simple classification of aquatic macrophyte morphology, describing them as either meadow formers: plants with a basal meristem and biomass equally distributed over depth, such as *Vallisnaria natans* (Lour.); or canopy formers: plants with an apical meristem and biomass distributed mostly at the top of the plant, such as *Hydrilla verticillata* (L.f.) Royle. Generally speaking, canopy formers are better adapted to more fertile environments with turbid waters (Chambers, 1987; Chambers and Kalff, 1987).

*V. natans* and *H. verticillata* commonly coexist in nature and are commonly used in efforts to restore aquatic ecosystems in China (Qiu *et al.*, 2001; Xie *et al.*, 2006). The two species are significantly different in growth forms: *V. natans* is relatively low growing, does not form a canopy and depends on light penetrating down near the sediment for growth. Its root is relatively well developed and a significant proportion of nutrient can be absorbed from the sediment. *H. verticillata*, on the other hand, often forms a dense mat, or canopy, at the water surface. Its root is less developed than that of *V. natans*, and a significant proportion of its nutrient needs can be absorbed from the water (Langeland, 1996). It was hypothesized that increased availability of nutrients would confer a growth advantage on the canopy-forming *H. verticillata* over *V. natans*, due to its more adaptive morphology in nutrient-rich conditions. Specimens of both *H. verticillata* and *V. natans* were established in eight mesocosms and their responses to addition of N and P were recorded to evaluate the effects of the nutrient. The results may provide useful information for future plant management and nutrient control in aquatic ecosystems.

## 2 Material and methods

### 2.1 Plant materials

*H. verticillata* (L.f.) Royle and *V. natans* (Lour.) Hara were originally collected from Huizhou West Lake in Huizhou, Guangdong Province, China, and subsequently raised in the laboratory of Jinan University for several years. Apical shoots (10 individuals per mesocosm) of *H. verticillata* (22 cm in length), often used in the restoration of eutrophic shallow lakes, were separated from the mother plant, washed with distilled water and weighed to determine initial fresh weight before experiments. Whole plants (10 individuals per mesocosm) of *V. natans*, each also about 20 cm in length, were selected, washed and weighed before experimentation.

### 2.2 Experimental mesocosm setup

The mesocosm experiments were carried out in eight 200 L circular plastic tanks (60 cm × 50 cm × 85 cm) containing rainwater and a 15 cm deep layer of sediment. Sediment was collected conveniently from eutrophic Ming Lake at Jinan University, in Guangzhou, China; it was then dried, sieved to remove coarse particles and large benthic invertebrates and mixed to ensure homogeneity before being added to the mesocosms (Zhang *et al.*, 2014). Rainwater was collected locally between April 8 and May 8, 2017, and analysis indicated levels of total nitrogen (TN) of 0.94 mg/L, total phosphorus (TP) of 0.01 mg/L and chlorophyll a (Chl *a*) at 0.0 mg/L.

Each of the eight mesocosms was planted with 10 apical shoots of *V. natans* and 10 *H. verticillata* side by side. After marcophytes were transplanted into the sediment, the mesocosms were placed under natural sunlight and allowed to equilibrate for 3 weeks, after which nutrient levels were 0.45 mg/L TN and 0.01 mg/L TP. At the start of the experiment, four of the mesocosms began to be supplemented with nutrients of 3.0 mg N/(L week) as $KNO_3$ and 0.2 mg P/(L week) as $NaH_2PO_4$ in order to mimic external loading (Jin, 2003). The remaining four mesocosms were maintained as controls with no nutrients added. The whole experiment lasted for 98 days throughout summer. Water temperature was 23–28 °C during the experimental period.

### 2.3 Sampling and analysis

Samples of 1 L water were collected from each mesocosm every 2 weeks for analysis of TN, TP and phytoplankton biomass (Chl *a*). Chl *a* was determined spectrophotometrically after ethanol extraction at room temperature, according to Jespersen and Christoffersen (1987). TN was determined using an alkaline potassium persulfate digestion-UV spectrophotometric method (Clesceri *et al.*, 1999). TP was determined following the ammonium molybdate spectrophotometric method after digestion with $K_2S_2O_8$ solution (APHA, 1992). Total suspended solid (TSS) samples were collected by filtering 300–500 mL water using Waterman GF-F filters (Glass fiber, pore size 0.7 μm), which were then dried and weighed. Light intensity at the sediment surface was measured between 9:00 a.m. and 11:00 a.m. local time on each sampling day using an underwater irradiance meter (ZDS-10W, Shanghai Jiading Xue Lian Meter Factory).

After finishing the experiments, all macrophytes were collected separately for aboveground biomass (shoots) and belowground biomass (roots), washed through a 1 mm mesh sieve and oven-dried at 80 °C to constant weight to determine the dry weight of both shoots and roots. The plant phosphorus (P) contents of the different species were ascertained as described in Bassett *et al.* (1978). Plant nitrogen (N) contents were determined by the Dumas combustion method using an automated CN analyzer. Nutrient contents were recorded as milligram nutrient per gram dry weight and total stored nutrients were calculated by multiplying the content values (mg/g) by plant biomass (g).

### 2.4 Statistics

Differences in water qualities between treatments were compared by repeated measures ANOVAs, with time as the repeated factor. An LSD test was used to detect differences within time interval when the overall model was significant. One-way ANOVA was carried out to test differences between treatments in each time interval. Two-way ANOVA was used to estimate significance of plant biomass, nutrient contents and root: shoot ratio variations between mesocosms. For within-subject comparison between each treatment or each species, one-way ANOVA was carried out. One-way ANOVA was also conducted to compare *H. verticillata*:*V. natans* biomass ratio between treatments. All statistics were done using the software SPSS 19.0 (SPSS, USA).

## 3 Results

### 3.1 Water quality

Water TN, TP, Chl *a* and TSS concentrations with different treatments are shown in Figure 1, along with light intensity readings at the sediment surface. Significantly higher TN and TP concentrations were observed in the mesocosms with added nutrient (ANNOVA, $F = 1192.632$, $p = 0.000$; $F = 16.489$, $p = 0.007$). Chl *a* concentrations showed no significant differences between treatments according to repeated measures ANNOVA ($F = 3.393$, $p = 0.115$). TSS and light intensity at the sediment surface were lower in the nutrient supplemented mesocosms than in the control group according to ANNOVA ($F = 6.977$, $p = 0.038$; $F = 7.199$, $p = 0.036$).

### 3.2 Biomass of plant tissues

In *H. verticillata*, all dry shoot biomass ($F = 120.143$, $p = 0.000$), root biomass ($F = 46.452$, $p = 0.002$) and whole plant biomass ($F = 48.850$, $p = 0.002$) increased significantly with nutrient addition (Tab. 1). For *V. natans*, shoot biomass was higher in the supplemented treatment group than in the controls ($F = 9.578$, $p = 0.036$), but there was no significant difference for roots ($F = 0.557$, $p = 0.497$) or whole plants ($F = 4.066$, $p = 0.114$). The shoot biomass of *H. verticillata* was significantly greater than that of *V. natans* in all treatments ($F = 46.779$, $p = 0.000$). Significant interactions in plant

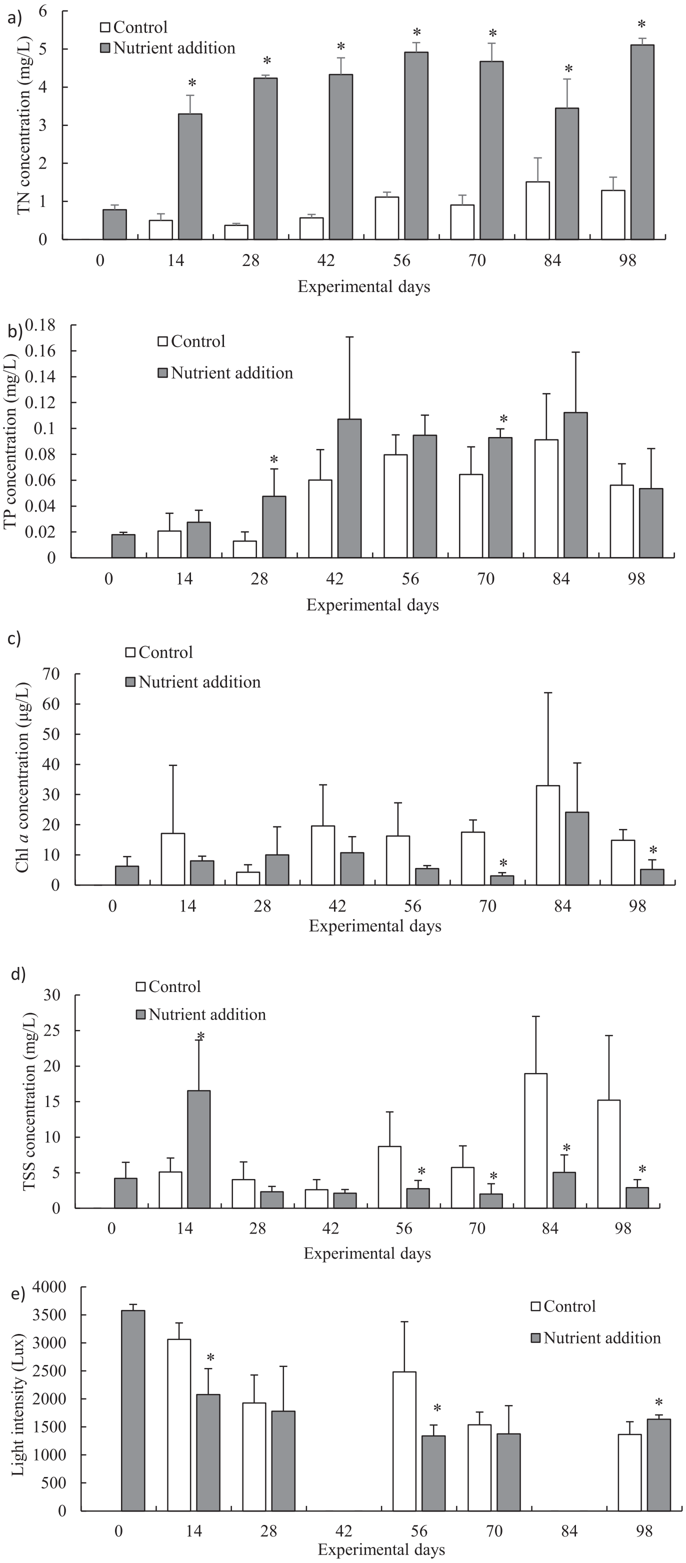

**Fig. 1.** Water TN (a), TP (b), Chl *a* (c) and TSS (d) concentrations and light intensity at the sediment surface (e) in mesocosms with different treatments. Columns marked with * exhibit significant differences using one-way ANOVA between treatments in each time interval ($p < 0.05$).

**Table 1.** Mean (±SD) dry biomass (g) of plant tissues in mesocosms with different treatments after 98 days. Means with * are significantly different ($p < 0.05$).

| | Control | Nutrient treatment |
|---|---|---|
| *H. verticillata* | | |
| Roots | 0.30 ± 0.17 | 1.17 ± 0.15* |
| Shoots | 2.90 ± 1.85 | 22.00 ± 5.02* |
| Whole plants | 3.20 ± 2.01 | 23.17 ± 5.14* |
| *V. natans* | | |
| Roots | 1.03 ± 0.60 | 1.27 ± 0.15 |
| Shoots | 1.13 ± 0.65 | 2.43 ± 0.31* |
| Whole plants | 2.17 ± 1.25 | 3.70 ± 0.46 |
| *H. verticillata: V. natans* | 1.579 ± 0.772 | 6.445 ± 2.302* |

biomass and plant shoot biomass were observed ($F = 31.651$, $p = 0.000$; $F = 32.567$, $p = 0.000$). *H. verticillata*:*V. natans* biomass ratio was higher in the treatment mesocosms than in the controls ($F = 504.412$, $p = 0.000$).

*V. natans* specimens maintained a higher root:shoot ratio than *H. verticillata* ($F = 348.164$, $p = 0.000$) (Fig. 2). Both *H. verticillata* and *V. natans* exhibited reduced root:shoot ratios when supplied with additional nutrients ($F = 43.691$, $p = 0.000$). A significant interaction between species and treatments was observed ($F = 21.676$, $p = 0.002$).

### 3.3 Nutrient content of plant tissues

Nutrient content of plant tissues were presented in Figure 3. The N and P contents of the plant were higher in mesocosms with added nutrient than in the controls ($F = 33.025$, $p = 0.000$; $F = 18.709$, $p = 0.003$). *H. verticillata* showed significantly higher N contents and lower P contents than *V. natans* ($F = 20.990$, $p = 0.002$; $F = 12.822$, $p = 0.007$). No significant interaction between species and treatments was observed ($F = 0.132$, $p = 0.726$; $F = 0.175$, $p = 0.687$).

N and P storage increased significantly in the nutrient-supplemented mesocosms compared to the controls ($F = 42.321$, $p = 0.000$; $F = 71.509$, $p = 0.000$). *H. verticillata* showed significantly higher N and P storage than *V. natans* ($F = 42.321$, $p = 0.000$; $F = 71.509$, $p = 0.000$). Besides, significant interaction between species and treatment was observed ($F = 30.252$, $p = 0.001$; $F = 43.447$, $p = 0.000$).

## 4 Discussion

Morphological plasticity was expressed in both *H. verticillata* and *V. natans* in response to nutrient supplementation, resulting in a reduced root:shoot ratio in both cases. The biomass of *H. verticillata* was significantly higher in the nutrient-added mesocosms than in the controls. Meanwhile, total biomass of *V. natans* showed no significant difference between treatments, although the shoot biomass was higher in the supplemented treatment group than in controls, leading to an increase in the *H. verticillata*:*V. natans* biomass ratio.

Nutrient availability is known to be a crucial factor influencing the morphology, growth and community structure

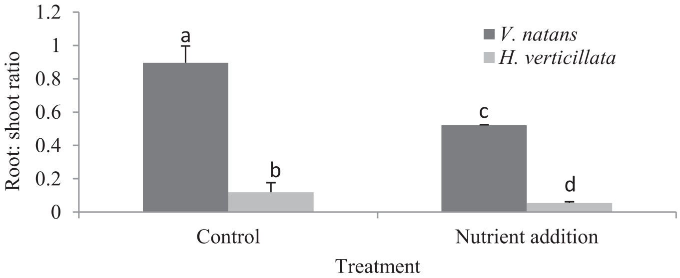

**Fig. 2.** Root:shoot ratio of *V. natans* and *H. verticillata* from different treatments. Columns marked with different letters exhibit significant differences (one-way ANOVA, $p < 0.05$).

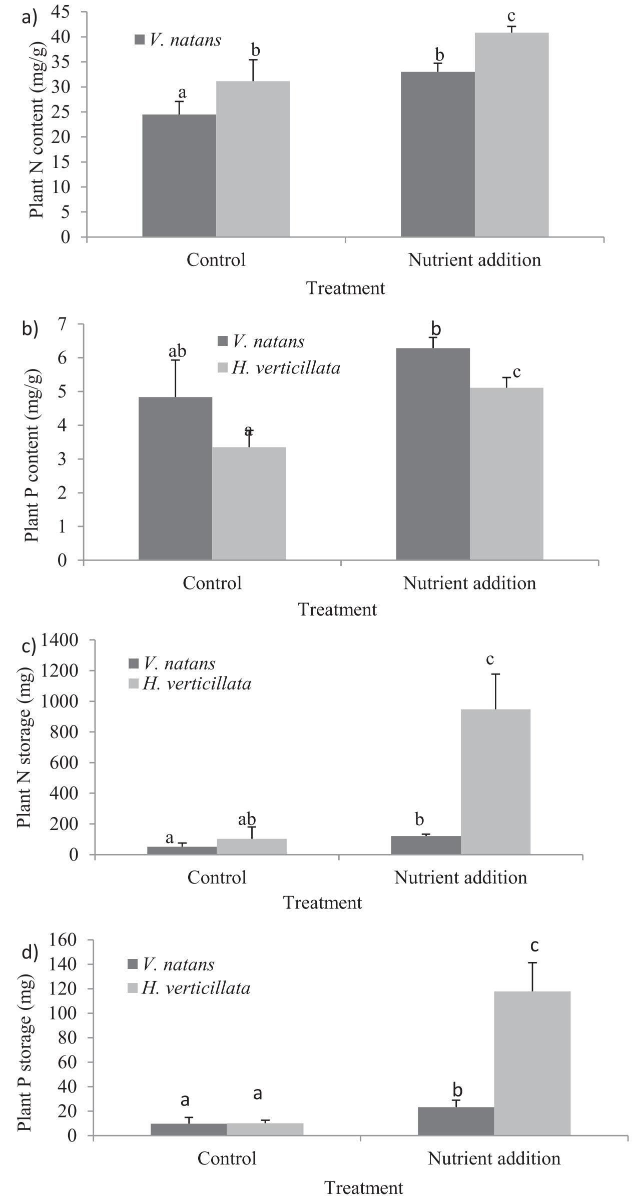

**Fig. 3.** N content (a), P content (b), total N storage (c), total P storage (d) in plant tissues of *H. verticillata* and *V. natans* with different treatments. Columns marked with different letters exhibit significant differences (one-way ANOVA, $p < 0.05$).

of aquatic macrophytes (Chambers, 1987). Such plants are able to assimilate nutrients from sediment via their roots and from the water column via shoots (Denny, 1972), but acquisition strategies vary between species and/or environments (Chambers *et al.*, 1989; Robach *et al.*, 1995; Langeland, 1996; Xie *et al.*, 2005). Increased nutrient availability in the water column can prompt biomass reallocation in order to maximize the uptake potential of shoots (Portielje and Roijackers, 1995; Madsen and Cedergreen, 2002; Cronin and Lodge, 2003; Zhang *et al.*, 2007). In our mesocosms, nutrient loading leads to increased nutrient content in both the experimental species. Both showed a reduced root:shoot ratio in the nutrient treated mesocosms, and the reduction was substantial in *H. verticillata* (Langeland, 1996).

Aquatic macrophytes can show considerable interspecies variation in their capacity for nutrient assimilation (Brisson and Chazarenc, 2009), and the differences can be crucial for interspecies competition and in determining general distribution patterns (Garbey *et al.*, 2004). In our experiment, *H. verticillata* showed a much greater capacity for increased nutrient storage and exhibited a significant growth advantage over *V. natans* when nutrient availability increased.

The addition of nutrients to our experimental mesocosms not only resulted in a direct increase in nutrient availability but also contributed to light limitation, as indicated by reduced light intensity at the sediment surface compared to the control mesocosms. Light availability in aquatic systems can be reduced by increased TSS concentration in the water and/or elevated primary production (James *et al.*, 2004). In our experiments, TSS concentrations declined in the nutrient-supplemented mesocosms compared to the controls, and Chl *a* concentration showed no significant change. However, the significantly increased shoot biomass of both macrophyte species observed in treated mesocosms suggests that shading by macrophytes is likely to cause light stress for neighboring specimens (Arts, 2002).

The responses of aquatic macrophytes to light stress (Van *et al.*, 1976) vary with species and broad type. Canopy forming taxa maximize light harvesting potential mainly by elongating their shoots toward the water surface, while meadow formers invest mainly in photosynthetic adjustments (Chen *et al.*, 2016). Excluding the possibility of light stress due to shading by phytoplankton or periphyton, the increased shoot biomass and shoot elongation of *H. verticillata* is likely to be the main cause of light stress and growth inhibition for *V. natans*. In our experiments, shoots of *H. verticillata* were substantially taller than those of *V. natans*, and in the nutrient treatments these shoots put on seven times more biomass than in the controls. As a meadow former, *V. natans* relies heavily on light being available near the sediment for growth and is more affected by shading than neighboring canopy formers.

In conclusion, the morphology of *H. verticillata* is more adaptive than that of *V. natans* in nutrient-enriched scenarios, resulting in greater biomass and nutrient storage potential. Furthermore, while morphological plasticity is exhibited by both species under nutrient-enriched conditions, when growing side by side, the canopy forming *H. verticillata* takes the growth advantage over the meadow forming *V. natans*. Our results may inform future plant management options for aquatic ecosystems.

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