



# Competition between *Potamogeton malaianus* and *Hydrilla verticillata* in response to different water level conditions

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**Abstract** To explore the effects of different water levels on competition of submerged plants, we selected the canopy submerged plant *Potamogeton malaianus* Miq. and the erect submerged plant *Hydrilla verticillata* (L. f.) Royle as study materials. Four water level gradients (25, 50, 75, 100 cm) were chosen to simulate the hydrological environment of shallow depressions in the main distribution area of submerged plants in the field. The competition between *P. malaianus* and *H. verticillata* under different water levels was investigated by measuring plant height, root length, stem thickness, number of leaves, nodal thrift, nodal spacing, above—ground biomass, below—ground biomass, and canopy whole—plant biomass. The results show that *P. malaianus* and *H. verticillata* increased in height as the water level rose.

In most treatments, above—ground parts grew better than below ground parts. In the 25 cm water level, relative yields (RYs) of the above—and below—ground parts, and whole plant of *P. malaianus* displayed different patterns. At the water level of 25 cm, the RY values of the above—ground part, below—ground part, and whole plant of *P. malaianus* were greater than 1. At the low water level of 25 cm, all treatments had relative yield total (RYT) values greater than 1, and at 50 cm water level, the RYT value of P4H8 was greater than 1. RYT was less than 1 at both 75 and 100 cm at 75 and 100 cm water levels, the growth of each species was limited by the other species. In low water level environments, submerged plants switch from a competitive relationship to a facilitative relationship as the water level decreases (stress increases).

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## Introduction

Submerged plants are macrophytes, all of which are located under the water layer, live in a fixed state, and play an important role in the health and stability of aquatic ecosystems (Søndergaard et al., 2010). As the basis of many food chains and primary producers, submerged plants not only increase spatial ecological

niches, improve underwater light and dissolved oxygen content, provide habitats for organisms, but also play the role of wave elimination and water purification, which is the basis for maintaining the biodiversity of water bodies (Väliranta et al., 2011).

The growth of submerged plants is influenced by both biotic and abiotic factors. Abiotic factors include a variety of environmental factors such as water level, flow rate, light intensity, substrate, and nutrients in the water column (Korschgen et al., 1997; Malkinson & Tielbörger, 2010). Among them, water level is the most critical factor, which mainly affects their growth by reducing light (Ellawala Kankanamge & Kodithuwakku, 2017). It has been suggested that as the water level rises, the ability of submerged plants to obtain light continues to decline, and once the decrease exceeds the upper limit of adaptation (below the light compensation point), submerged plants will not be able to survive. Therefore, the decrease of underwater light resources is an important reason for the widespread disappearance of submerged plants (Collier et al., 2012). In addition, high water levels inhibit the ability of submerged plants to obtain atmospheric O<sub>2</sub> and CO<sub>2</sub>, the material basis for aerobic respiration and photosynthesis, respectively (Yuan et al., 2018). Yin et al. concluded that although *Myriophyllum spicatum* L. could better adapt to the low light environment with continuous high water level, excessive water flooding still had a significant inhibitory effect on its plant height, and long-term exposure to high water level would lead to its death (Yin et al., 2018). Currently, there are many studies on submerged plants at high water levels, while the effects of low water levels on submerged plants cannot be ignored. The low water level exposes submerged plants in shallow water, and plants may die due to water shortage (Li et al., 2019). A lower water level increases the light intensity of the water body, which can lead to low light tolerance. Liu et al., simulated the hydrological environment of shallow depression in the main distribution area of submerged plants in the field, and concluded that the water level of 75 cm is suitable for the growth of *P. malaianus* and *H. verticillate* (Liu et al., 2021).

In addition to abiotic influences, the growth of submerged plants is also affected by biotic factors, including competition, grazing, and attached algae (Foxy & Fort, 2019). Competition is a very important biotic factor, which mainly affects plant growth

through competition for nutrients below—ground and competition for light above—ground. Fabian Sauter suggested that root competition is the main mechanism determining the performance of target plants (Sauter et al., 2021), while the effect of shoot competition has a relatively low effect, although it increases with productivity. This study concludes that the competition of the below—ground parts of plants is greater than that of the above—ground parts, and that the below—ground competition plays an important role in the process of plant growth.

Numerous field studies have confirmed that facilitation and competition between species coexist, and the net effect of the two in the community may change with the relative importance of competition and facilitation mechanisms. It has become a hot topic in studies of population and community ecology to predict how interspecific interactions change with stressful environmental gradients (Grace & Tilman, 1990). A long-standing debate about different approaches to explain competition is between David Tilman and Philip Grime. Grime states that the importance of competition relative to the impact of the environment increases with productivity gradients, while Tilman argues that the intensity of competition is independent of productivity. Bertness and Callaway proposed the stress gradient hypothesis (SGH) (Bertness & Callaway, 1994), which suggests that the relative importance of competition and facilitation may change in opposite directions as the abiotic stress gradient increases (García-Cervigón et al., 2013). Most relevant studies are in line with SGH, such as the studies by Ziffer-Berger et al. (2014) and Li et al. (2018). According to the study by Li et al., competition between *Carex brevicuspis* C. B. Clarke and *Polygonum hydropiper* L. shifted to facilitation as the water level increased, and this facilitation might be regulated by sediment nutrient heterogeneity (Li et al., 2018). At present, relevant studies mainly focus on the effects of water level and competition on plant growth and distribution (Li et al., 2017), and there are many studies on the ecological stoichiometric characteristics of plants under different water levels with different competition patterns among plants (Miao & Zou, 2012; Yuan et al., 2013). However, there are few studies on the competition among different ecotypes under different water levels, especially at low water levels.

The water level is also selective for the type of growth of submerged plants. Middelboe & Markager (1997) found that stalk-supported canopy species (e.g., *M. spicatum* and *P. malaianus*) have leaves that can grow in shallow water where light is relatively more abundant; therefore, such submerged plants can overcome the light-limiting effect of shallow water and can be distributed in areas with shallow water levels, with high light compensation points and high saturation points. In contrast, rosettes have no stalk support and have poor vertical extension, according to the “environmental screening theory” (Poff, 1997), are usually distributed in shallow areas or require low light compensation and light saturation points. At present, there are few studies on the water level competition between canopy and erect submerged plants. According to the life—type characteristics of submerged plants, this paper assumes that the canopy submerged plants and the erect submerged plants are in a facilitative relationship at low water levels, and in a competitive relationship at high water levels.

The purpose of this study was to investigate the effects of water levels on plant-plant competition and facilitation. In this experiment, *P. malaianus* and *H. verticillata* were selected as the materials to study the interspecific competition between two submerged plants at different water levels (25, 50, 75 and 100 cm) using the substitution test method according to a certain gradient. We propose two hypotheses. Hypothesis 1: We assume that the height of the canopy and upright submerged plants will increase with the water level. Hypothesis 2: The competitive intensity of submerged plants decreases with decreasing water level, and the competition intensity decreases with increasing environmental stress, which is consistent with SGH.

## Methods

### Study area

Dongting Lake (8° 44′–29° 35′ N, 111° 40′–113° 10′ E) is the second largest freshwater lake and the most typical river-connected lake in China because of its high water-exchange capacity with the Yangtze River. The lake wetlands are characterized by large seasonal fluctuations in water levels, with complete flooding

from May to October and drought from November to April (Li et al., 2018).

### Plant materials

Two major submerged plants of the Dongting Lake wetlands, *P. malaianus* and *H. verticillata*, were included in this study. *P. malaianus* is a perennial herbaceous submerged plant. It is a dominant species in the submerged vegetation of grass-type lakes in the middle and lower reaches of Yangtze River (Lyu et al., 2021). It occupies an important position in freshwater ecosystems, and can be used as a pioneer species in water ecological reconstruction projects (Qin et al., 2017; Efremov et al., 2019). *H. verticillata* can form large “underwater forests” in water bodies, which play a vital role in the stability of aquatic ecosystem structure and function (Rodrigo et al., 2013). It is one of the preferred plants for the restoration and reconstruction of aquatic ecosystems (Chappuis et al., 2014).

*Potamogeton malaianus* and *H. verticillata* were collected from Dongting Lake and brought back to the experimental station for cultivation. On May 3, 2018, strong seedlings of *P. malaianus* and *H. verticillata* of the same size were selected, about 500 plants each. They were cultured in plastic pots with 15 cm substrate, and then plastic boxes (60 cm×35 cm×20 cm) were placed in an experimental pool (4.0 m×4.0 m×1.1 m) with a water level of 60 cm for seedling culture for 2 weeks. The culture substrate was prepared by evenly mixing river sand and Dongting Lake soil at a ratio of 1:1 (Table 1).

### Experimental design

The experiment was conducted at four water levels (25, 50, 75, and 100 cm), using the substitution series test method (Yuan et al., 2021), with 12 plants per box and five configuration ratios. A completely randomized group experimental design was employed, with the number of *P. malaianus* and *H. verticillata* plants increasing and decreasing by 4, 2, and 4 plants per box, respectively (Fig. 1). On May 17, 20 cm tall seedlings of *P. malaianus* and *H. verticillata* test plants were planted in plastic boxes (60 cm×35 cm×20 cm) with 20 cm substrate in concrete pools (1.0 m×1.0 m×1.1 m). The water levels were 25, 50, 75, and 100 cm, respectively, and each

**Table 1** Substrate nutrient content

Total N (%)	Total P (%)	Total K (%)	Alkaline nitrogen (mg/kg)	Available P (mg/kg)	Available K (mg/kg)	Nitrate nitrogen (mg/kg)	Ammonia nitrogen (mg/kg)	Organic carbon (%)	Organic matter (%)	pH	Eh (mV)
0.09±0.01	0.09±0.01	3.04±0.01	20.87±0.01	10.7±0.03	326.67±0.09	6.97±0.01	6.59±0.01	1.21±0.01	2.09±0.01	7.84±0.05	200.73±0.53

experiment was designed with three replicates, with a total of 60 treatments. The experiment period was two months.

#### Harvest and measurement

The plants were harvested 2 months after planting. Plant height (soil surface to plant tip), node spacing (internode length), and root length (stem base to root tip) were measured with a tape measure; stem diameter, leaf number (number of all leaves above the soil surface), and density (number of plants per square meter) were measured with a vernier caliper. The roots of the plant were carefully dug out by hand, and the sediment was removed by rinsing with tap water. The plants of *P. malaianus* were then divided into leaves, stems, and below-ground parts (rhizomes and roots), and the plants of *H. verticillata* were divided into leaves and below-ground parts. All were oven dried at 80°C for 48 h and weighed. Plant biomass was calculated as the total mass of all tissues.

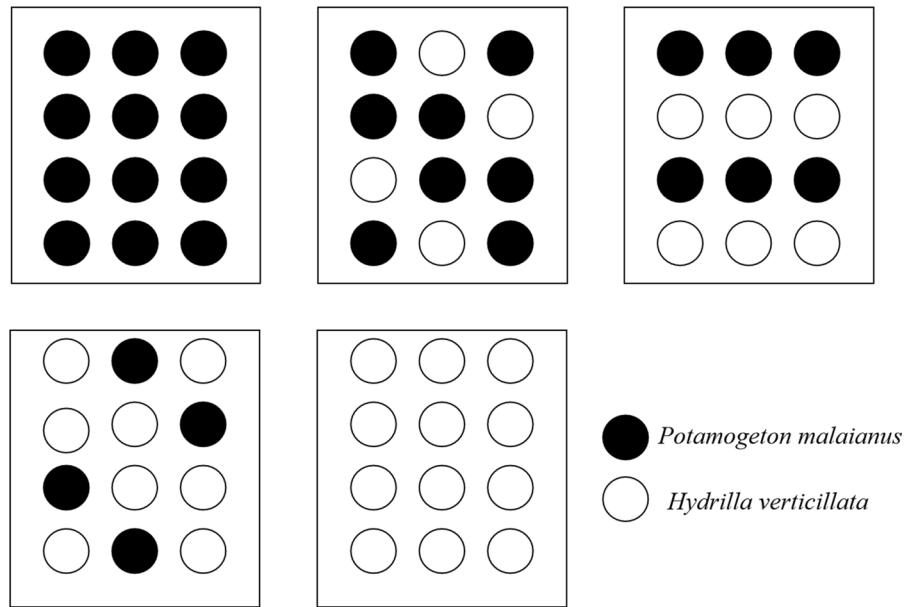
#### Statistical analysis

Relative yield total (RYT), the weighted average of the relative yields (RY) of both plant species, was used to evaluate facilitation or competition between *P. malaianus* (*P*) and *H. verticillata* (*H*). The formula was:

$$RYT_{PH} = (RY_P + RY_H) / 2,$$

where  $RY_P = Y_{PH} / P_P Y_P$ ,  $RY_H = Y_{HP} / P_H Y_H$ , and  $RY_P$  and  $RY_H$  are the relative yields of *P* and *H*, respectively;  $P_P$  is the proportion of *P* in the mixture;  $P_H$  is the proportion of *H* in the mixture;  $P_P + P_H = 1$ ;  $Y_P$  is the biomass of *P* in monoculture;  $Y_H$  is the biomass of *H* in monoculture;  $Y_{PH}$  is the biomass of *P* in the presence of *H*; and  $Y_{HP}$  is the biomass of *H* in the presence of *P* (Hao et al., 2013). When  $RYT = 1$ , the interaction between species is not clear; if  $RYT > 1$ , the interaction among species is positive (facilitation); and if  $RYT < 1$ , the interaction among species is negative (competition). RY measures the average performance of individuals in the mixture compared to that of individuals in the monoculture. Detailed information regarding RY was presented by Fowler (Fowler & Antonovics, 1981).

**Fig. 1** The planting diagram of *Potamogeton malaianus* and *Hydrilla verticillata*



The data were organized by Excel 2010, the graphing was plotted by Origin Pro2018, and the one-way ANOVA was performed by SPSS Statistics 17.0 to test the effect of water level in each competition mode and the effect of competition at each water level. Duncan method was used to conduct multiple comparisons.

**Results**

**Growth pattern**

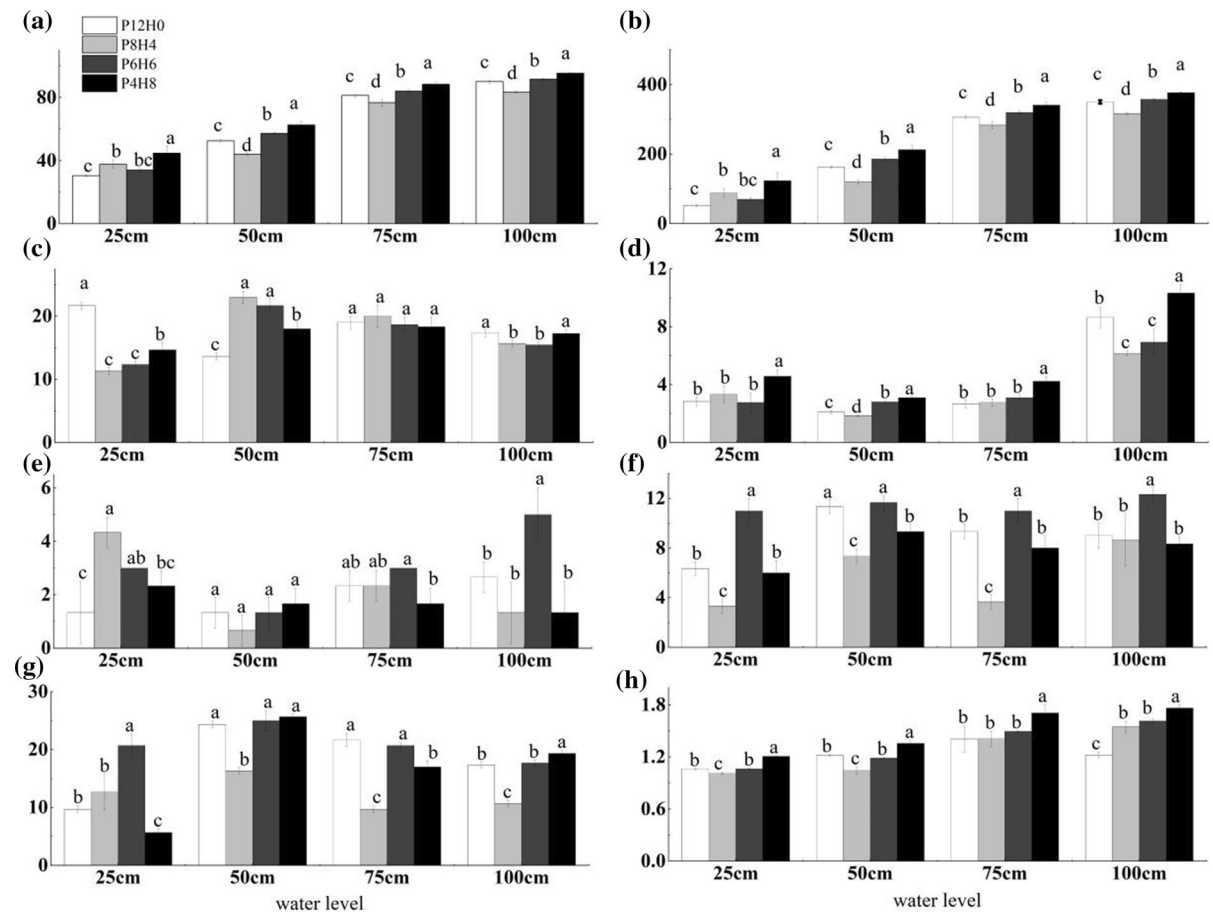
Root length, internode spacing, branch number, node number, leaf number and stem diameter all showed

significant differences among different water level treatments (all  $P < 0.01$ ) (Table 2). Specifically, the higher the water level, the higher the plant height of the two submerged plants (Figs. 2a and 3a). The roots of *P. malaianus* were longer at the water levels of 50 and 75 cm than those at water levels of 25 and 100 cm (Fig. 2c). The number of branches increased significantly at the water levels of 100 and 25 cm (Fig. 2e). The internode spacing was longer at the water level of 100 cm (Fig. 2d), and the number of leaves was larger at the water level of 50 cm (Fig. 2g).

The internode spacing of *H. verticillata* at the water level of 100 cm was higher than other water levels (Fig. 3d) and the number of leaves of *H. verticillata* at the water levels of 50 and 100 cm was larger

**Table 2** Interspecific competition of *Potamogeton malaianus* and *Hydrilla verticillata* under water level

Indicator	<i>Potamogeton malaianus</i>				<i>Hydrilla verticillata</i>			
	Water level		Interaction		Water level		Interaction	
	F	P	F	P	F	P	F	P
Plant height (cm)	2618.29	**	13.39	**	336.49	**	16.03	**
Total root length (cm)	51.85	**	42.95	**	9.66	**	12.55	**
Internode spacing (cm)	401.37	**	9.47	**	24.28	**	18.01	**
Branch number	10.49	**	6.97	**	42.85	**	14.44	**
Node number	34.28	**	5.81	**	29.83	**	37.38	**
Leaf number	163.63	**	36.16	**	23.28	**	10.17	**
Stem diameter (mm)	190.43	**	10.09	**	377.83	**	48.37	**



**Fig. 2** Effect of *H. verticillata* on the growth of *Potamogeton malaianus*. Mean ( $\pm$ SE;  $n=3$ ) (a–c) indicate significant of  $P<0.05$ . P12H0 (*Potamogeton malaianus* 12 plants and *Hydrilla verticillata* 0 plants). P8H4 (*Potamogeton malaianus* 8 plants and *Hydrilla verticillata* 4 plants). P6H6 (*Potamogeton malaianus* 6 plants and *Hydrilla verticillata* 6 plants).

(Fig. 3g). The stem diameter of *H. verticillata* at the water levels of 75 and 100 cm was thicker than other treatments (Fig. 3h). The number of branches of *H. verticillata* at the water level of 50 cm was slightly smaller than that at other water levels, and the number of branches was larger than that at other water levels (Fig. 3e).

#### Relative yield total (RYT)

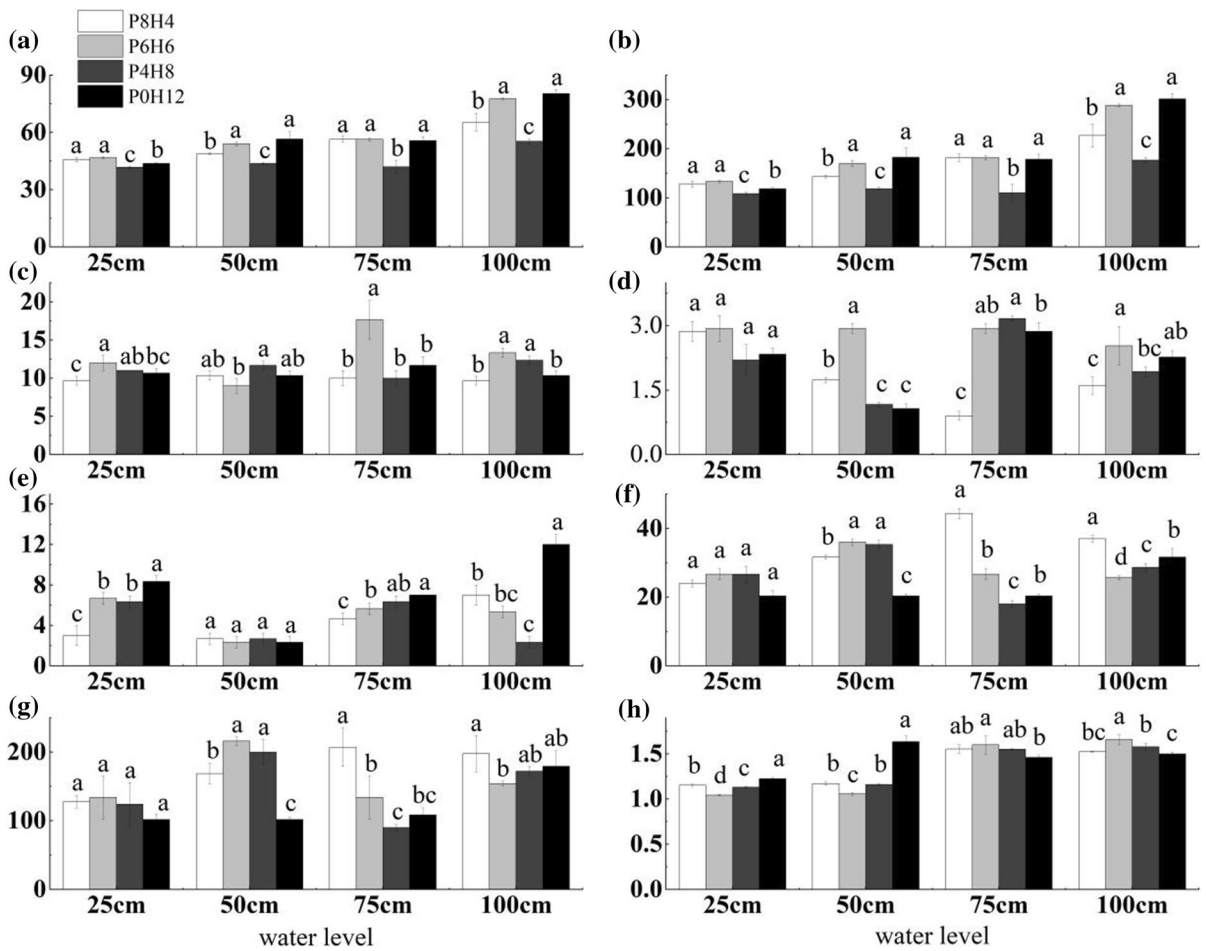
Water level and planting pattern had significant effects on RYT ( $P<0.05$ ). For all treatments at low water level of 25 cm and P4H8 at 50 cm water level,  $RYT>1$ , suggesting that facilitation occurred at the

P4H8 (*Potamogeton malaianus* 4 plants and *Hydrilla verticillata* 8 plants). **a** Plant height (cm); **b** Relative growth rate of plant height (%); **c** Total root length (cm); **d** Pitch (cm); **e** No. of branches; **f** Section number; **g** Number of blades; **h** Stem diameter (mm)

25 cm water level. RYT was less than 1 for all treatments at water levels of 75 and 100 cm, and for P8H4 and P6H6 planting patterns at 50 cm water level, indicating negative competition at water levels of 75 and 100 cm (Table 3).

#### RY relative yields

The RYs of the above-ground part, below-ground part and whole plant of *P. malaianus* and *H. verticillata* were significantly affected by water level, planting pattern, and their interaction (Fig. 4). At the 25 cm water level, RYs of the above-ground part, below-ground part, and whole plant



**Fig. 3** Effect of *Potamogeton malaianus* on the growth of *H. verticillata*. Mean ( $\pm$ SE;  $n=3$ ) (a–c) indicate significant of  $P < 0.05$ . P0H12 (*Potamogeton malaianus* 0 plants and *Hydrilla verticillata* 12 plants). P8H4 (*Potamogeton malaianus* 8 plants and *Hydrilla verticillata* 4 plants). P6H6 (*Potamogeton malaianus* 6 plants and *Hydrilla verticillata* 6 plants).

P4H8 (*Potamogeton malaianus* 4 plants and *Hydrilla verticillata* 8plants). **a** Plant height (cm); **b** Relative growth rate of plant height (%); **c** Total root length(cm); **d** Pitch (cm); **e** No. of branches; **f** Section number; **g** Number of blades; **h** Stem diameter (mm)

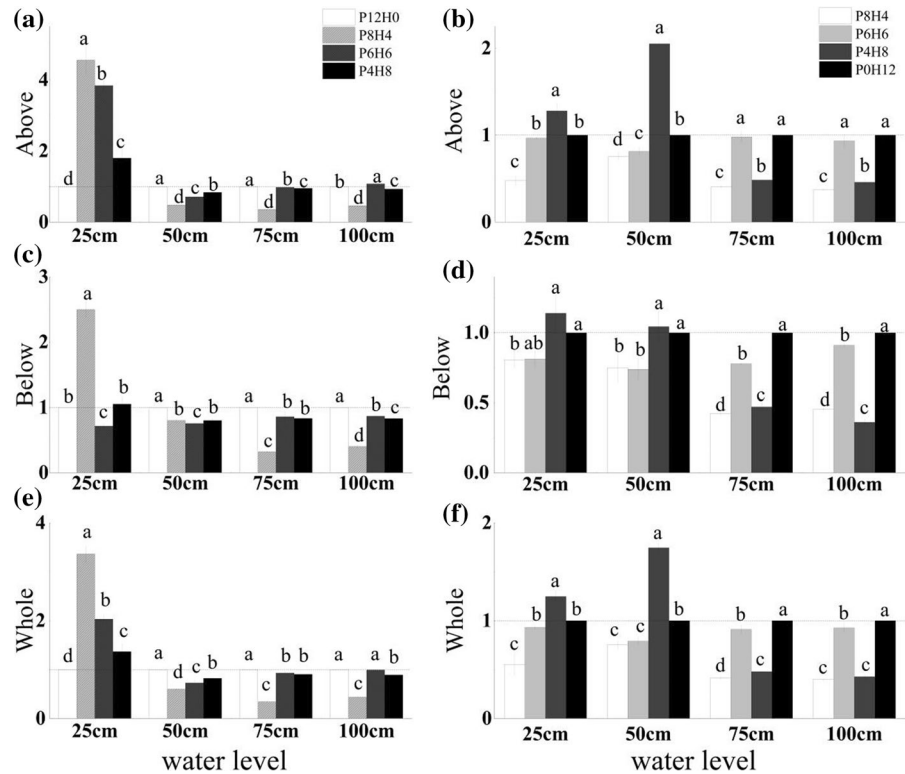
**Table 3** Relative yield total at different water levels

Water level	P12H0	P8H4	P6h6	P4h8	P0H12
25 cm	1 <sup>d</sup>	1.96 $\pm$ 0.07 <sup>a</sup>	1.48 $\pm$ 0.04 <sup>b</sup>	1.31 $\pm$ 0.04 <sup>c</sup>	1 <sup>d</sup>
50 cm	1 <sup>b</sup>	0.68 $\pm$ 0.02 <sup>d</sup>	0.76 $\pm$ 0.03 <sup>c</sup>	1.28 $\pm$ 0.02 <sup>a</sup>	1 <sup>b</sup>
75 cm	1 <sup>a</sup>	0.38 $\pm$ 0.003 <sup>d</sup>	0.92 $\pm$ 0.03 <sup>b</sup>	0.69 $\pm$ 0.002 <sup>c</sup>	1 <sup>a</sup>
100 cm	1 <sup>a</sup>	0.42 $\pm$ 0.01 <sup>d</sup>	0.96 $\pm$ 0.02 <sup>b</sup>	0.66 $\pm$ 0.005 <sup>c</sup>	1 <sup>a</sup>

of *P. malaianus* displayed different patterns. Most values of RY in the above—ground part, below—ground part, and whole plant of *P. malaianus* were  $> 1$  at the water level of 25 cm, indicating that the presence of *H. verticillata* generally facilitated

the growth of *P. malaianus*. However, at the water levels of 50, 75, 100 cm, most values of RY for the above—ground part, below—ground part, and whole plant of *P. malaianus* were  $< 1$ , suggesting

**Fig. 4** Mean ( $\pm$ SE;  $n=3$ ) (a–c) indicate the significance of  $P < 0.05$ . Relative yields (RYs) are illustrated for the above—ground, below—ground, and whole plant of *Potamogeton malaianus* (a, c, e) and *Hydrilla verticillata* (b, d, f)



that the growth of *P. malaianus* was limited by the presence of *H. verticillata* at these water levels.

RY values of the above—ground part, below—ground part, and whole plant of *H. verticillata* in the planting combination of P4H8 at the water levels of 25 and 50 cm were  $> 1$ , and RY values of *H. verticillata* in all the other planting combinations at all water levels were  $< 1$ , indicating that the growth of *H. verticillata* was limited by the presence of *P. malaianus*.

## Discussion

Water level is a decisive factor for the growth and reproduction of submerged plants (Valley & Drake, 2007). Many studies have shown that different water levels have significant effect on the growth, distribution and reproduction of submerged plants (Zhao et al., 2021). Zhu et al. (2012) believe that the biomass, relative growth rate, root anchorage strength, and stem tensile properties of *M. spicatum*, *Ceratophyllum demersum* L., *H. verticillata*, *Potamogeton maackianus* A. Benn., *P. malaianus* decreased with increasing initial water level, suggesting that deep

water can inhibit plant growth and decrease their mechanical resistance.

*H. verticillata* can adapt to different water levels through physiological and morphological changes in the life history (Wei et al., 2013). Wang et al. (2014) and other studies believe that at deep water level, the growth of *H. verticillata* will be inhibited. Gao et al. (2017) simulated the rise of water level and believed that high water level promotes the growth of canopy plants represented by *P. malaianus*, while rising water level is unfavorable for the growth of erect plants represented by *H. verticillata*. This study is consistent with Wang et al. (2014) and Gao et al. (2017). This pilot study is consistent with hypothesis that the plant height of canopy and erect submerged plants increases with rising water levels. The low water levels of 25 and 50 cm inhibited the growth of the plant height of *P. malaianus*, which is closely related with the niche formed by the canopy plants of *P. malaianus*. In order to adapt to growth at low water level, *P. malaianus* has formed an adaptive mechanism to water level changes by increasing the number of nodes and shortening the internode spacing to reduce stress. At the water levels of 75 and 100 cm, *P.*



*malaianus* and *H. verticillata* met their own growth needs by increasing the height and thickening the basal stem to obtain light energy. The water levels of 75 and 100 cm were favorable for the biomass accumulation of the canopy plants of *P. malaianus*. The water level of 25 cm was conducive to the reproduction of *H. verticillata*, and the water levels of 50 and 75 cm were conducive to the biomass accumulation of the erect plants of *H. verticillata*.

The most important consequence of plant competition is the change in biomass. In this experiment, the plant height of *H. verticillata* for P8H4 and P6H6 was greater than that of monoculture plant (POH12) at the water level of 25 cm. This is due to the competing for light resource between the two submerged plants. The canopy plant *P. malaianus* dominates and reduces the sunlight radiation required for photosynthesis of *H. verticillata*. Thus, *H. verticillata* has to increase the height to satisfy its own growth to obtain light, which promotes the growth of plant height (Nunes & Camargo, 2020).

The interrelationship of plants mainly includes two aspects: positive effect and negative effect. They play an important role in regulating plant distribution and community structure, and are one of the main driving forces shaping plant morphology and life cycle formation (Bruno et al., 2003). We examined the effects of water level on the competition and facilitation of *P. malaianus* and *H. verticillata*. Our results suggested that the plant growth of one plant species was limited by the presence of the other plant species when the water level was at 75 and 100 cm. In contrast, at a water level of 25 cm, simulating a low puddle environment, competition shifted to facilitation, consistent with our hypothesis 2. In this experiment, at the water levels of 75 and 100 cm,  $0 < \text{RYT} < 1$ , indicating that the two submerged plants at 75 and 100 cm water levels confronted and competed with each other. *P. malaianus* and *H. verticillata* occupied different ecological niches, showing a certain symbiotic relationship throughout the experiment. This is because the plant height of *P. malaianus* is higher than that of *H. verticillata*. *P. malaianus* are submerged plants that grow upright with a high canopy. *H. verticillata* are submerged plants with small leaves, small stems and a small canopy. These two submerged plants were separated in spatial location and competition between species intensified. Therefore, the two submerged plants showed a competitive relationship. Submerged

plants shift from competitive to facilitative relationships in low water environments (increased stress). The competition among plants is mainly competition for resources in the environment (Trinder et al., 2021). Changes in competitive relationships will affect the allocation of resources among plants, and in turn affect individual growth, population numbers, and community structure (Shen et al., 2020). Combined with the RYT values at 25 and 50 cm water levels, the biomass of *H. verticillata* in the mixed planting system was greater than that under the single planting condition, indicating that the existence of *P. malaianus* promoted the increase of the yield of *H. verticillata*. Combined with the RYT values at 25 and 50 cm water levels, the biomass of *H. verticillata* in the mixed planting system was greater than that of monoculture planting, indicating that the existence of *P. malaianus* promotes the increase of the yield of *H. verticillata*. When environmental conditions are favorable, competition among plants dominates, while when environmental stress is severe, tolerance among plants dominates, and plants tend to allocate most of their resources to the corresponding traits or organs or through morphological and physiological changes to adapt to the environment. However, further research on the tolerance and competitiveness of the low water *P. malaianus* and *H. verticillata* trade-offs is needed to understand this relationship.

## Concluding remarks

*P. malaianus* and *H. verticillata* showed certain sensitivity and plasticity to different water levels and planting patterns, and the interaction of water levels and planting patterns had significant effects on the biomass of *P. malaianus* and *H. verticillata*. Our study supports SGH because plant interactions between *P. malaianus* and *H. verticillata* changed from competition to facilitation as water levels decreased. Interspecific competition under low water levels is beneficial to the growth of submerged plants. Future research could provide insight into the competitive mechanisms of submerged plants.

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**Author contributions** The authors confirm contribution to the paper as follows: study conception and design: XDL, ZYH. Literature search, draft manuscript preparation and critical revision: ZYH, XDL, FL, YHX, YL, XYY.

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**Data availability** Data available on request from the authors.

## Declarations

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

## References

- Bertness, M. D. & R. Callaway, 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9(5): 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4).
- Bruno, J. F., J. J. Stachowicz & M. D. Bertness, 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18(3): 119–125. [https://doi.org/10.1016/S0169-5347\(02\)00045-9](https://doi.org/10.1016/S0169-5347(02)00045-9).
- Chappuis, E., E. Gacia & E. Ballesteros, 2014. Environmental factors explaining the distribution and diversity of vascular aquatic macrophytes in a highly heterogeneous Mediterranean region. *Aquatic Botany* 113: 72–82. <https://doi.org/10.1016/j.aquabot.2013.11.007>.
- Collier, C. J., M. Waycott & L. J. McKenzie, 2012. Light thresholds derived from seagrass loss in the coastal zone of the northern Great Barrier Reef, Australia. *Ecological Indicators* 23: 211–219. <https://doi.org/10.1016/j.ecolind.2012.04.005>.
- Efremov, A. N., B. F. Sviridenko, Y. V. Bolotova, C. Toma & Y. A. Murashko, 2019. Coenocomplex and ecological features of *Hydrilla verticillata* (L. f.) Royle (Hydrocharitaceae) in Northern Eurasia. *Inland Water Biology* 12(1): 57–67. <https://doi.org/10.1134/S1995082919010061>.
- Ellawala Kankanamge, C. & H. Kodithuwakku, 2017. Effect of interspecific competition on the growth and nutrient uptake of three macrophytes in nutrient-rich water. *Aquatic Ecology* 51(4): 625–634. <https://doi.org/10.1007/s10452-017-9640-5>.
- Fowler, N. & J. Antonovics, 1981. Competition and coexistence in a North Carolina Grassland: I. Patterns in undisturbed vegetation. *The Journal of Ecology* 69: 825. <https://doi.org/10.2307/2259639>.
- Fox, A. J. & F. Fort, 2019. Root and shoot competition lead to contrasting competitive outcomes under water stress: a systematic review and meta-analysis. *PLoS ONE* 14: e0220674.
- Gao, F., Y. Zhang, F. Yang, M. J. Ma, Y. X. Gao, D. Wu & Y. R. Ding, 2017. Growth and photosynthetic fluorescence characteristics responses of four submersed macrophytes to rising water level. *Journal of Ecology and Rural Environment* 33: 341–348. <https://doi.org/10.11934/j.issn.1673-4831.2017.04.007>.
- García-Cervigón, A. I., A. Gazol, V. Sanz, J. J. Camarero & J. M. Olano, 2013. Intraspecific competition replaces interspecific facilitation as abiotic stress decreases: The shifting nature of plant–plant interactions. *Perspectives in Plant Ecology, Evolution and Systematics* 15(4): 226–236. <https://doi.org/10.1016/j.ppees.2013.04.001>.
- Grace, J. B. & D. Tilman, 1990. *Perspectives on Plant Competition*. Harcourt Brace Jovanovich, United Kingdom Edition.
- Hao, B., H. Wu, Q. Shi, G. Liu & W. Xing, 2013. Facilitation and competition among foundation species of submerged macrophytes threatened by severe eutrophication and implications for restoration. *Ecological Engineering* 60: 76–80. <https://doi.org/10.1016/j.ecoleng.2013.07.067>.
- Korschgen, C. E., W. L. Green & K. P. Kenow, 1997. Effects of irradiance on growth and winter bud production by *Vallisneria americana* and consequences to its abundance and distribution. *Aquatic Botany* 58(1): 1–9. [https://doi.org/10.1016/S0304-3770\(97\)00014-4](https://doi.org/10.1016/S0304-3770(97)00014-4).
- Li, F., Y. Xie, G. Yang, L. Zhu, C. Hu, X. Chen & Z. Deng, 2017. Interactive influence of water level, sediment heterogeneity, and plant density on the growth performance and root characteristics of *Carex breviscapis*. *Limnologia* 62: 111–117. <https://doi.org/10.1016/j.limno.2016.11.007>.
- Li, F., N. Yang, Y. Lianlian, G. Xie, C. Yang, X. Chen, Hu & Z. Deng, 2018. Competition and facilitation of two wetland macrophytes under different water levels and nutrient-heterogeneous conditions. *Freshwater Science* 35(2): 296–306. <https://doi.org/10.1086/697964>.
- Li, Y., F. Qian, J. Silbernagel & H. Larson, 2019. Community structure, abundance variation and population trends of waterbirds in relation to water level fluctuation in Poyang Lake. *Journal of Great Lakes Research* 45(5): 976–985. <https://doi.org/10.1016/j.jglr.2019.08.002>.
- Liu, X., Z. Hou, Y. Xie, X. Yu, X. Li & J. Zeng, 2021. Influence of water level on four typical submerged plants in wetlands of Lake Dongting. *Journal of Lake Sciences* 33(1): 181–191. <https://doi.org/10.18307/2021.0113>.
- Lyu, R., B. Gu, T. Zhang & Z. Yang, 2021. Simultaneous removal of Cd (II), Ni (II), and Pb (II) from water by a submerged macrophyte pondweed (*Potamogeton malainus*). *Water Environment Research* 93(11): 2637–2647. <https://doi.org/10.1002/wer.1617>.
- Malkinson, D. & K. Tielbörger, 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos* 119(10): 1546–1552. <https://doi.org/10.1111/j.1600-0706.2010.18375.x>.

- Miao, S. L. & C. B. Zou, 2012. Effects of inundation on growth and nutrient allocation of six major macrophytes in the Florida Everglades. *Ecological Engineering* 42: 10–18. <https://doi.org/10.1016/j.ecoleng.2012.01.009>.
- Middelboe, A. L. & S. Markager, 1997. Depth limits and minimum light requirements of freshwater macrophytes. *Freshwater Biology* 37(3): 553–568. <https://doi.org/10.1046/j.1365-2427.1997.00183.x>.
- Nunes, L. S. C. & A. F. M. Camargo, 2020. The interspecific competition of tropical estuarine macrophytes is not density-dependent. *Aquatic Botany* 164: 103233. <https://doi.org/10.1016/j.aquabot.2020.103233>.
- Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16(2): 391–409. <https://doi.org/10.2307/1468026>.
- Qin, L., K. Li, Y. Li, S. Gao, R. Liang & X. He, 2017. Bioaccumulation and tolerance characteristics of *Hydrilla verticillata* (L.F.) exposed to cadmium toxicity. *Fresenius Environmental Bulletin* 26: 2642–2651.
- Rodrigo, M. A., C. Rojo, J. L. Alonso-Guillén & P. Vera, 2013. Restoration of two small Mediterranean lagoons: the dynamics of submerged macrophytes and factors that affect the success of revegetation. *Ecological Engineering* 54: 1–15. <https://doi.org/10.1016/j.ecoleng.2013.01.022>.
- Sauter, F., H. Albrecht, J. Kollmann & M. Lang, 2021. Competition components along productivity gradients—revisiting a classic dispute in ecology. *Oikos* 130(8): 1326–1334. <https://doi.org/10.1111/oik.07706>.
- Shen, N., C. Liu, H. Yu & J. Qu, 2020. Effects of resource heterogeneity and environmental disturbance on the growth performance and interspecific competition of wetland clonal plants. *Global Ecology and Conservation* 22: e00914. <https://doi.org/10.1016/j.gecco.2020.e00914>.
- Søndergaard, M., L. S. Johansson, T. L. Lauridsen, T. B. Jørgensen, L. Liboriussen & E. Jeppesen, 2010. Submerged macrophytes as indicators of the ecological quality of lakes. *Freshwater Biology* 55(4): 893–908. <https://doi.org/10.1111/j.1365-2427.2009.02331.x>.
- Trinder, C. J., R. W. Brooker, H. Davidson & D. Robinson, 2021. Directly quantifying multiple interacting influences on plant competition. *Plant, Cell & Environment* 44(4): 1268–1277. <https://doi.org/10.1111/pce.13944>.
- Väliranta, M., J. Weckström, S. Siitonen, H. Seppä, J. Alkio, S. Juutinen & E.-S. Tuittila, 2011. Holocene aquatic ecosystem change in the boreal vegetation zone of northern Finland. *Journal of Paleolimnology* 45(3): 339–352. <https://doi.org/10.1007/s10933-011-9501-5>.
- Valley, R. D. & M. T. Drake, 2007. What does resilience of a clear-water state in lakes mean for the spatial heterogeneity of submersed macrophyte biovolume? *Aquatic Botany* 87(4): 307–319. <https://doi.org/10.1016/j.aquabot.2007.07.003>.
- Wang, Y., F.-L. Luo, H. Li & F.-H. Yu, 2014. Effects of initial density on biomass, number of nodes and shoot length of 3 kinds of macrophytes. *Wetland Science* 12: 740–746. <https://doi.org/10.13248/j.cnki.wetlandsci.2014.06.009>.
- Wei, H., S. Cheng, H. Tang, F. Zheng, W. Liang & Z. Wu, 2013. The strategies of morphology, reproduction and carbohydrate metabolism of *Hydrilla verticillata* (Linn.f.) royle in fluctuating waters. *Fresenius Environmental Bulletin* 22: 2590–2596.
- Yin, J., F. Yang, Y. M. Zhang, Y. M. Zhu, Y. X. Gao & D. L. Li, 2018. Study on adaptability of two submerged macrophytes for wind-induced wave and high water level stress. *Acta Scientiae Circumstantiae* 38(02): 805–813. <https://doi.org/10.13671/j.hjkxb.2017.0389>.
- Yuan, G., T. Cao, H. Fu, L. Ni, X. Zhang, W. Li, X. Song, P. Xie & E. Jeppesen, 2013. Linking carbon and nitrogen metabolism to depth distribution of submersed macrophytes using high ammonium dosing tests and a lake survey. *Freshwater Biology* 58(12): 2532–2540. <https://doi.org/10.1111/fwb.12230>.
- Yuan, D.-Y., X. Meng, C.-Q. Duan, Z.-H. Wei, W. Gao, J.-J. Chang, X.-J. Lv & Y. Pan, 2018. Effects of water exchange rate on morphological and physiological characteristics of two submerged macrophytes from Erhai Lake. *Ecology and Evolution* 8(24): 12750–12760. <https://doi.org/10.1002/ece3.4703>.
- Yuan, L., J.-M. Li, F.-H. Yu, A. M. O. Oduor & M. van Kleunen, 2021. Allelopathic and competitive interactions between native and alien plants. *Biological Invasions* 23(10): 3077–3090. <https://doi.org/10.1007/s10530-021-02565-w>.
- Zhao, F., X. Fang, Z. Zhao & C. Xiaoli, 2021. Effects of water level fluctuations on the growth characteristics and community succession of submerged macrophytes: a case study of Yilong Lake, China. *Water* 13: 2900. <https://doi.org/10.3390/w13202900>.
- Zhu, G., W. Li, M. Zhang, L. Ni & S. Wang, 2012. Adaptation of submerged macrophytes to both water depth and flood intensity as revealed by their mechanical resistance. *Hydrobiologia* 696(1): 77–93. <https://doi.org/10.1007/s10750-012-1185-y>.
- Ziffer-Berger, J., P. J. Weisberg, M. E. Cablk & Y. Osem, 2014. Spatial patterns provide support for the stress-gradient hypothesis over a range-wide aridity gradient. *Journal of Arid Environments* 102: 27–33. <https://doi.org/10.1016/j.jaridenv.2013.11.006>.

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