The effects of water depth on the growth of two submerged macrophytes in an *in situ* experiment

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**ABSTRACT**

An *in situ* experiment was designed in which *Potamogeton crispus* and *Hydrilla verticillata* were planted in plastic pots 25, 50, 75, 100, 125, 150, 175 and 200 cm underwater to study the effect of water depth on the growth and photosynthetic fluorescence characteristics of the two submerged macrophytes in Lake Gehu, China. The results showed that: 1) Water depth had no significant effect on the germination of both submerged macrophytes. The final germination rate of *P. crispus* turions was higher than 80%, and the final germination rate of the *H. verticillata* winter buds was 100%; 2) Water depth affected the survival rate of both submerged macrophytes, and the seedlings at depths of 150, 175 and 200 cm all eventually died; 3) Water depth altered the morphological characteristics of *P. crispus* and *H. verticillata* seedlings. (4) Increasing water depth significantly affected biomass (*p < .05*), with the biomass initially tending to increase, but then decreasing. The root to shoot ratio of both submerged macrophytes decreased with increasing water depth; 5) Chlorophyll contents of *P. crispus* and *H. verticillata* increased with water depth from 25 to 150 cm; 6) Water depth had an obvious effect on the photosynthetic fluorescence of submerged macrophytes. The \(F_0/F_m\) increased slightly from water depths from 25 to 75 cm, and then decreased significantly when water depth exceeded 100 cm. The \(ETR_{max}\) was significantly different among all treatment groups, and \(ETR_{max}\) was obviously higher at water depths of 25 and 50 cm than at all other depths. These results showed that submerged macrophytes have a limited water depth tolerance range. In Lake Gehu, the recovery of submerged macrophytes will be better in areas with water depths less than 125 cm.

**Abbreviations:** *P. crispus*: *Potamogeton crispus*; *H. verticillata*: *Hydrilla verticillata*; \(F_0\): fixed fluorescence yield; \(F_m\): maximum fluorescence yield; \(F_t\): the apparent fluorescence yield; \(ETR\): electron transport rates; \(ETR_{max}\): maximum electron transport rate; \(F_0/F_m\): maximum light quantum yield; \(RLC\): the fast light response curve

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1. Introduction

Submerged macrophytes occupy a key interface in shallow water habitats, and can be important primary producers in lake ecosystems, which play an important role in the health and stability of the ecosystem (Steffenhagen et al. 2012; Hao et al. 2017; Liu, Hou, et al. 2021). As human activities have intensified, submerged macrophytes in many lakes have begun to decline or have even disappeared, which has disrupted their respective lake ecosystems (Zhou et al. 1997; Qiu and Wu 1998; Zhang et al. 2021). Prioritizing the restoration of submerged vegetation is an effective approach to the ecological restoration of lakes (Hilt et al. 2006; Zhang et al. 2020). In eutrophic lakes, there are many factors that influence the recovery of submerged macrophytes, and water depth is a major factor that affects their distribution and growth (Spence 1982; Ostendorp 1991; Cui et al. 1999; Jin and Guo 2001; Strand and Weisner 2001; Cao Y et al. 2016; Li et al. 2019). Water level regulation is also important to wetland ecosystem management and conservation (Keddy 2010; Poff and Olden 2017; Ersoy et al. 2020; Lan et al. 2020). For example, water depth has been shown to affect the allocation of energy for reproduction as well as reproductive allometry in the submerged macrophyte Vallisneria natans (Li et al. 2017). Submerged macrophytes have morphological plasticity that allows them to adapt to different water regimes, but only within a certain tolerance range (Madsen et al. 2001; Wernberg and Thomsen 2005; Chen et al. 2011; Wu et al. 2012; Wang et al. 2021). Many studies have investigated how the growth of submerged macrophytes is affected by depth, most have utilized experimental simulations or field observations (Riis and Hawes 2002; Nöges et al. 2003; Busch et al. 2004, 2006; Geest et al. 2005; Hu et al. 2006; Gu et al. 2017; ). Water depths of 60–120 cm were shown to be the optimal growth depth range for the conservation and restoration of Potamogeton crispus in Lake Taihu (Zhou et al. 2016). Furthermore, both the number and length of roots of Vallisneria spinulosa were affected by amplitudes, but not frequencies, of water level fluctuations (Ding et al. 2021).

Lake Gehu is an eutrophic lake in the upper reaches of the Lake Taihu basin in China, with an area of 164 km² and an average depth of 1.2 m (Wu et al. 2020). After the ecological reconstruction of the lake, the underwater light environment was improved, which provided favorable conditions for the recovery of aquatic vegetation, especially submerged vegetation. This article selected the pioneer species P. crispus and Hydrilla verticillata as the research objects, both of which are naturally occurring macrophytes in Lake Gehu. Assuming that under the water environmental conditions of Gehu Lake, the maximum water depth that submerged macrophytes can recover is 1.25 m. The effects of water depth on the germination, growth and the photosynthetic fluorescence characteristics of the two submerged macrophytes were studied in situ to provide a theoretical basis and guidance for the reconstruction and scientific management of submerged vegetation.

2. Materials and methods

2.1. Experimental design

The experimental area was located in the northern area of Lake Gehu (31°39′50.18″ N, 119°52′14.10″ E). The total phosphorus, total nitrogen, ammonia nitrogen, permanganate index and chlorophyll a of the water in the study area were 0.089, 2.97, 0.21, 3.00 and 0.03 mg/L, respectively. Stainless steel floats with stainless steel racks were set on the lake surface and pots were suspended at different water depths using nylon cords. Fishing nets have been placed around the experimental system to prevent fish from entering. The buds of the two macrophytes were collected from Gucheng Lake. Selected robust P. crispus
buds (average fresh weight 0.67 g) and winter buds of *H. verticillata* were planted regularly in pots (25 cm diameter × 25 cm depth) with about 15 cm of sediment. Ten buds were planted in each pot. The experimental sediment was collected from the northern lake area, near the experimental float. A total of eight water depth treatments were set up in the range of 25–200 cm with the upper openings of the flowerpots at 25, 50, 75, 100, 125, 150, 175 and 200 cm below the water surface. Six replicates were set up for each treatment, making a total of 48 pots.

**2.2. Sampling and analysis**

**2.2.1. Morphological indexes**

The experiment growth period for *P. crispus* group was from December 2013 to March 2014. One week after the start of the experiment, the germination rate of *P. crispus* was monitored every 2 d. After germination, the morphological indexes of *P. crispus* were measured every 3–5 d, these included plant height, tiller number, internode length, leaf length and leaf width. The growth indicators were measured by gently raising the pots to the surface. The average of each morphological index was calculated for each water depth, for which nine individuals of *P. crispus* were selected at random from the six replicate pots. At the end of experiment, the biomass and root to shoot ratio of *P. crispus* were determined. Then the plants were gently pulled out and brought back to the laboratory where any mud and surface attachments were rinsed off with water. The plants were put into the oven at 105°C, then dried for 24 h at 80°C before being put it in the desiccator to cool and weigh. The experiment with the *H. verticillata* group was conducted in March–September 2014. The morphological indexes and biomass were measured following the same protocols used for the *P. crispus* group.

**2.2.2. Chlorophyll content**

The extraction of the chlorophyll was conducted following the Arnon method (Arnon 1949). After one month of growth, 6 plants were randomly selected from each treatment of each experimental group, and 3–4 of the top leaves of each plant were measured and the average value was calculated. Leaves of *P. crispus* were larger, so four indexes of chlorophyll were measured. Due to the small size of *H. verticillata* leaves, in order to avoid affecting its growth, only one index was measured.

**2.2.3. Photosynthetic fluorescence characteristics**

In the early morning (6:00–8:00), five plants from each group were randomly selected and the first 3–4 leaves below the top of the plant were collected (for the deep-water treatment group, the replicates were brought to the surface and connected with the fluorescent instrument before returning them to the experimental depth) to measure the photosynthetic fluorescence characteristics.

To determine the fixed fluorescence yield (F0) and maximum fluorescence yield (Fm), the underwater saturation pulsed chlorophyll fluorescence instrument DIVING-PAM (WALZ, Effeltrich, Germany) and the data acquisition software win control were used. The measurements were made between 6:00 and 8:00 in the morning, with a starting detection light of 0.15 μmol photon m⁻²s⁻¹ to get F0, and measuring Fm using saturated pulsed light (4000 μmol photon m⁻²s⁻¹, 0.8 s).

The rapid light response curves of the leaves were determined using an after dark adaptation period of 10 s, the leaf clamp was opened and the detection light (0.15 μmol photon m⁻²s⁻¹) was used obtain a F0, then the Fm was obtained using saturated pulsed
light (4000 μmol photon m$^{-2}$·s$^{-1}$, 0.8 s). After 10 s of light exposure, the apparent fluorescence yield ($F_t$ is sometimes expressed as $F_a$ or $F_s$) and $F_m$ at the time of light exposure were measured using the detected light and saturated pulsed light. Finally, eight apparent photosynthetic electron transport rates were calculated ($ETR = \text{Yield} \times \text{PAR} \times 0.84 \times 0.5$) and the optical response curve of the ETR mean was plotted.

2.3. Statistical analysis

Significant differences among the depth groups from 25 to 200 cm, in terms of the average values over time, were determined by one-way ANOVA. All statistical tests were carried out in SPSS version 13.0 for Windows (SPSS Inc., Chicago, IL).

3. Results and analysis

3.1. Germination of submerged macrophytes

$P. crispus$ sprouts germinated at all water depths between 25 and 200 cm, and germination was complete within 7 d of planting. The final germination rate of the shoots in each group was greater than 80%, and there was no significant difference between groups (Figure 1(a)). Winter buds of $H. verticillata$ were also able to germinate in water depths between 25 and 200 cm and germination was complete within 10 d of planting. The final germination rate of winter buds was 100% in all groups and there were no significant differences among groups (Figure 1(b)). These results indicated that the germination of these two submerged macrophytes was not restrained at any of the experimental depths examined in this eutrophic lake.

3.2. Morphological characteristics and biomass of submerged macrophytes

The water depth of the reconstructed area of Lake Gehu significantly affected the morphological characteristics of $P. crispus$. The effect of water depth on plant height in $P. crispus$ was obvious (Figure 2(a)). During the first 70 d of the experiment, the height of $P. crispus$ increased rapidly in all depth groups, however, beyond that time plant heights in the 150, 175 and 200 cm depth groups decreased rapidly and the plants died at 130–140 d. The tiller number of $P. crispus$ decreased with increasing water depth (Figure 2(b)), showing
Figure 2. The morphological characteristics of *P. crispus* at different water depths.
a significant correlation between the two ($p < .01$). The maximum number of tillers in *P. crispus* appeared in the 25 cm depth group, and decreased to 83.00, 78.57, 69.05, 42.86, 33.33, 26.19 and 23.81% of the maximum, respectively, at the depths between 50 and 200 cm. *P. crispus* internodal length was also significantly affected by the water depth gradient (Figure 2(c)). The internodal length of *P. crispus* plants showed a significant prolongation in depths from 25 to 150 cm, but shortened significantly at depths more than 150 cm. Leaf length and leaf width of *P. crispus* appeared to decrease with depth (Figure 2(d,e)), but there was no significant difference among the depth groups. With the increase of water depth, the root to shoot ratio of *P. crispus* significantly decreased ($p < .05$), that is, the proportion of underground biomass decreased (Figure 2(f)). The water depth had a significant effect on the biomass of *P. crispus* ($p < .05$). The biomass peaked at the water depth of 50 cm, and the
second-highest biomass was in the 25 cm treatment. As the water depth increased beyond 50 cm, the biomass of *P. crispus* decreased significantly (*p* < .05; Figure 2(g)).

The water depth in the reconstructed area of the Lake Gehu had a significant effect on the morphological characteristics of *H. verticillata*. Different depths had a significant effect on plant height (Figure 3(a)). During the first 40 d, the height of *H. verticillata* in all groups increased rapidly, but as the experimental time extended, the plant heights in the 150, 175 and 200 cm water depth groups decreased rapidly and plant death occurred on the 55, 85 and 95 d, respectively. The tiller number of *H. verticillata* decreased significantly with increasing water depth (*p* < .01; Figure 3(b)). The tiller number of *H. verticillata* peaked in the 25 cm depth group, and decreased to 87.18, 64.10, 58.97, 51.28, 33.33, 33.33 and 30.77% of the maximum, respectively, in water depths from 50 to 200 cm. The internodal length of *H. verticillata* was also significantly influenced by the depth gradient (*p* < .05; Figure 3(c)). In the depth range of 25–125 cm, internodal length of *H. verticillata* was significantly prolonged, but it decreased at depths over 125 cm. With increased water depth, the root to shoot ratio of *H. verticillata* showed a decreasing trend (Figure 3(d)). The water depth significantly affected the biomass of *H. verticillata* (*p* < .05). The biomass of *H. verticillata* increased at first, but then decreased with increasing water depth, and the biomass peaked at a depth of 75 cm (Figure 3(e)).

### 3.3. Chlorophyll content and photosynthetic fluorescence characteristics of submerged macrophytes

*P. crispus* can adapt to changing light intensities at different depths using phenotypic plasticity, as well as by enhancing chlorophyll content to enhance the light capture...
ability. The chlorophyll content within treatment groups initially increased with depth, but then decreased (Figure 4(a)). The chlorophyll contents of \textit{P. crispus} showed an upward trend from 25 to 150 cm, and it significantly decreased with depth \((p < .05)\).

The water depth had a significant effect on the photosynthetic fluorescence of \textit{P. crispus} (Figure 4(b,c)). Measured on the 30th day, the maximum light quantum yield \(\left(\frac{Fv}{Fm}\right)\) of \textit{P. crispus} leaves initially increased with depth (from 25 to 75 cm), but then decreased with increasing water depth. When the depth of water exceeded 100 cm, the \(\frac{Fv}{Fm}\) of the treatment groups significantly decreased \((p < .05)\). The maximum electron transport rate \(\left(ETR_{\text{max}}\right)\) among treatment groups was also significantly affected \((p < .05)\), with the \(ETR_{\text{max}}\) of the 25 and 50 cm groups being significantly higher than that of other groups.

The chlorophyll content of \textit{H. verticillata} initially increased with depth (from 25 to 125 cm), but then decreased with the chlorophyll content in groups at water depths between 150 and 200 cm, significantly decreasing with depth (Figure 5(a)). The water depth also had a significant effect on the photosynthetic fluorescence characteristics of \textit{H. verticillata} leaves (Figure 5(b,c)). On the 30th day, the maximum light quantum yield \(\left(\frac{Fv}{Fm}\right)\) of the leaves of \textit{H. verticillata} increased from 25 to 75 cm, but then decreased with increasing water depth beyond 100 cm. The maximum electron transfer rates \(\left(ETR_{\text{max}}\right)\) among all treatment groups were significantly different \((p < .05)\). The \(ETR_{\text{max}}\) at water depths of 25 and 50 cm group were significantly higher than those of other groups.

Figure 5. Chlorophyll and photosynthetic fluorescence characteristics of \textit{H. verticillata} at different water depths.
4. Discussion

Water depth is one of the most important ecological factors affecting the growth and reproduction of submerged macrophytes, and fluctuations in depth characterized by magnitude, frequency, timing, duration and rate of change can all affect aquatic vegetation (White and Ganf 2002; Liu et al. 2006; Li et al. 2017). It is generally believed that naturally occurring fluctuations in water level can benefit ecosystems by favoring diversity (Qin et al. 2011; Lan et al. 2020; Ding et al. 2021). In the subtropical monsoon region of China, low water levels in spring provide conditions that best facilitate the germination and growth of submerged macrophytes seedlings. As spring transitions to early summer, the water level and temperature rise gradually, which is matched by continuous macrophyte growth enabling plants to adapt to water level change. However, extreme flooding in summer can severely hinder submerged macrophyte growth.

4.1. High water levels reduce the survival rate of submerged macrophyte seedlings

Light has an important effect on the growth and survival of macrophytes (Strand and Weisner 2001; Li et al. 2006; Wang et al. 2006; Carr et al. 2010; Wu et al. 2012). Submerged macrophytes will not survive when light intensity drops below their photosynthetic compensation point (Ni 2001), especially submerged macrophytes, sufficient light is a key factor affecting their survival. There is a close relationship between the attenuation coefficient, optical transparency and the diffuse attenuation coefficient, which can reflect the distribution of the light field under water in lakes (Zhang et al. 2003; Li et al. 2009). Lake Gehu and other eutrophic lakes have weak underwater light intensity due to low transparency that limits the growth of submerged macrophytes and hinders their recovery. The transparency of the water in the experimental area fluctuated between 30 and 60 cm, the average transparency was 40 cm, and the average euphotic depth was 130 cm. It can be seen that the 50–200 cm depth treatment groups were located below the water transparency depth. This showed that submerged macrophytes had a light compensation range of 0.5–3.0% of full sunshine, which is concerning because submerged macrophytes are unable to adapt to underwater light intensities of less than 1% of the incident light (Van et al. 1976; Jones et al. 2000; Pierini and Thomaz 2004). In this experiment, the water depths of 150, 175 and 200 cm were 3.75, 4.38 and 4.0 times beyond the average transparency depth of the water body, which was deeper than the euphotic depth, which meant that noon time light penetration was less than 1% of full sunshine at these depths. Indeed, the seedlings of *P. crispus* and *H. verticillata* in water depths of 150, 175 and 200 cm all died, likely because there was insufficient light for energy production. Lake Gehu is a typical sub-tropical shallow lake (Wu et al. 2017, 2020), the water level fluctuation is generally small in winter and spring, and high in summer and autumn (Figure 6). In normal years, water level fluctuation has no obvious effect on submerged macrophytes, however, extreme weather events such as flooding can cause severe damage to submerged vegetation. For example, the flooding that occurred in the summer of 1999 created high water levels that resulted in a significant reduction in submerged vegetation coverage.

4.2. Increasing water depth altered the morphology and chlorophyll of submerged macrophytes

Both submerged macrophytes and emergent plants are capable of a variety of morphological responses to water depth changes (Vretare and Weisner 2000; Liu, Hou, et al.
Different plants are adapted to different water depths (Wang et al. 1999). The plant height, internode number, internodal length, number of branches and chlorophyll content of macrophytes were all significantly affected by water depth, which indicated that these macrophytes were able to adapt to different water depths. The submerged macrophytes at shallower water depths had shorter plant height and fewer stem nodes, but the number of branches was greater, indicating increased branching is a growth strategy adopted by macrophytes in response to excessive light. With increasing water depth, the available light for plants decreased, which affected the chlorophyll content of the macrophytes. When light is sufficient, macrophytes need not promote light capture by increasing the chlorophyll content, but as water depth increases, the chlorophyll content must be increased to compensate for the rapid decrease of the light intensity and ensure the plants obtain enough light to sustain growth. However, when the water depth increased even further, the light in the water body became even weaker, resulting in a reduction of leaf activity in the plants, which led to a decrease in the chlorophyll content.

The morphology of the submerged macrophytes was also affected by water depth. In this experiment, plants at greater water depths tended to produce more nodules and longer internodes in order to maximize light capture. By reducing the tiller number, the material usually dedicated to photosynthetic activity was repurposed to increase the height of plants, which led to increases in plant height with water depth at the cost of photosynthetic capacity (Li and Wang 2010; Wu et al. 2012). This is one morphological adaptation strategy adopted by macrophytes in low light conditions. As the light weakens further, the light energy obtained by the plant becomes insufficient for the required increases in the growth of stem nodes, which further limits access to light and restricts the growth of plants, eventually causing death (Chen et al. 2008).

4.3. Water depth significantly affected submerged macrophyte biomass

Biomass is the most important measure of plant growth, indeed, the growth of macrophytes is directly reflected in their biomass (Li and Wang 2010; Liu, Hou, et al. 2021; Liu,
Liu, et al. (2021). Liu, Hou, et al. (2021) found that water level greatly influenced the growth characteristics and biomass of four submerged plants. With increased water depth, *P. crispus* and *H. verticillata* had decreased root to shoot ratios, which reflects increased effort to obtain light, with most of the plants’ energy being invested in aboveground growth. Gafny and Gasith (1999) found that there is an ‘opportunity window’ water depth in which plants profit most from the environmental conditions, resulting in the largest plant biomasses, and plants above or below the ‘opportunity window’ depths will have reduced biomasses. The ‘opportunity window’ reflects the optimum combination of environmental factors like light, water temperature, water depth, etc., at which plants are able to accumulate the most material. During the experiment, the water quality and nutrient availability were homogenous throughout the experimental depth, and the difference in water temperature was small (\(< 2^\circ\text{C}\) ), so the environmental factor exerting the strongest gradient was light. This in situ experiment showed that the biomass of *P. crispus* was the largest at the 50 cm depth, while that of *H. verticillata* was largest at 75 cm, which indicated that the ‘opportunity windows’ of these two species were marginally different.

### 4.4. Water level affected the photosynthetic capacity of submerged macrophytes

Chlorophyll fluorescence kinetics is an important indicator of physiological chlorophyll activity. This measure contains an abundance of information about changes in the photosynthetic process and is regarded as an intrinsic probe of the relationship between plant photosynthesis and the environment (Hu et al. 2007). $Fv/Fm$ reflects the quantum yield of all PS II reaction centers when they are in the open state (Wang et al. 2006). $Fv/Fm$ changes very little when plants are not stressed ($Fv/Fm$ was about 0.8 during normal growth), but decreases significantly during stressful conditions (Zhang 1999). The fast light response curve (RLC) indicates how the electron transfer rate changes with light intensity. In the RLC, the changes in the curve within the first few minutes of illumination are of great importance, and the determination of the RLC can determine the actual photochemical efficiency of the leaves of submerged macrophytes (Schreiber et al. 1997). In this experiment, when the water depth increased, the ETR$_{\text{max}}$ of the submerged macrophyte leaves decreased significantly, which indicated that the photo responsiveness of submerged macrophytes decreased with depth. This showed that the maximum photon production and maximum electron transport rate of the submerged macrophytes decreased with increased water depth, and indicated that the photosynthetic capacity of the plants was inhibited in deep water conditions.

### 5. Conclusion

1. Water depth had no significant effect on the germination of submerged macrophytes.
2. *P. crispus* and *H. verticillata* were able to adapt to weak light environments using adaptive growth strategies and altering plant morphology in depths up to 125 cm. When the water depth exceeded 125 cm, both species were unable to complete their life cycles.
3. Deeper waters inhibited the photosynthetic capacity of these submerged macrophytes.
4. In the environment of Lake Gehu, the recovery of submerged macrophytes will be optimized in areas where the water depth is less than 125 cm.
Disclosure statement

The authors declare no conflict of interest.

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Data availability statement

The data that support the findings of this study are available on request from the corresponding author.

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