

Potamogeton crispus responses to varying water depth in morphological plasticity and physiological traits

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Abstract

Submerged macrophytes, important primary producers in shallow lakes, play a crucial role in maintaining ecosystem structure and function. By altering a series of environmental factors, especially light intensity, water depth has great influences on growth of submerged macrophytes. Here, by hanging pots statically at water depths of 40, 60, 80, 100, 120, 140, 160, 180, 200, and 220 cm, respectively, we investigated effects of water depths on morphological plasticity and physiological traits of *Potamogeton crispus*. At 40 and 60 cm water depths versus other water depths, *P. crispus* showed lower plant height, larger stem diameter, thicker leaves, and smaller leaf area, leaf length, and specific leaf area. With water depth increasing, the plant height, leaf area, and leaf length gradually increased until 160 cm water depth, while the stem diameter and leaf thickness gradually decreased until 200 cm water depth. In comparison, the plant height, leaf length, and leaf number significantly decreased when the water depth further increased to 180–220 cm. The leaves contained lower concentrations of superoxide dismutase and peroxidase at 100–160 cm water depth, and lower catalase concentrations at 40–140 cm water depth, especially at 80–100 cm. In shallow waters, the concentration of chlorophyll *a* and *b* in leaves were both lower, while the ratio of chlorophyll *a* to *b* was relatively higher. As the water depth of 40–220 cm, the chlorophyll *a* and *b* concentrations increased significantly with increasing water depth, while their ratio gradually decreased. The present study provides new insights into the adaptation strategies of submerged macrophytes to the variation in water levels, and our findings are beneficial for ecosystem construction and management.

Keywords Antioxidant enzyme · Morphological plasticity · *Potamogeton crispus* · Submerged macrophyte · Water depth

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Introduction

In shallow lakes, submerged macrophytes play a major role in maintaining ecosystem structure and function (Søndergaard et al. 2010; Li et al. 2017). They are not only important primary producers but also pivotal in controlling the eutrophication and inhibiting cyanobacterial blooms (Pakdel et al. 2013; Zhou et al. 2016). Thus, submerged macrophytes are widely used in ecosystem reconstruction and ecological remediation (Sayer et al. 2010; Blindow et al. 2014).

Hydrologic regime is a major determinant of macrophyte community structure and productivity in lake ecosystems (Reddy et al. 2004; Ren et al. 2020). By altering a series of environmental factors, especially light intensity, water depth has great influences on growth and metabolism of submerged macrophytes (Chen et al. 2016; 2020). Shallow waters not only compress the living space of submerged macrophytes but generally causes photoinhibition (Winters et al. 2003; Li et al. 2020), while photosynthetic efficiency often declines greatly under low-light conditions in deep waters (Zhang et al. 2014; Min et al. 2019). Therefore, it is imperative to investigate responses of submerged macrophytes to water depths, contributing to hydrology regulation in ecosystem management (Zhang et al. 2014; Liu et al. 2017).

As proxy of plant adaptation to the environment, plant functional traits have aroused wide interest (Wright et al. 2004; Reich 2014; Fu et al. 2014, 2018, 2020). Leaf area represents material and energy exchange between plants and external environments (Yin et al. 2018), specific leaf area is regarded to reflect adaptability and survival strategy of plants (Wright et al. 2004), while leaf thickness indicates plant response to UV-B radiation and plant resource utilization strategies (Zhao et al. 2004; Kitajima and Poorter 2010). Besides morphological traits, physiological traits also reflect plant adaptations to the environment. Therefore, chlorophyll concentration, relating closely to the photosynthesis, can reflect the photosynthetic efficiency and the plant adaptation to changing light intensity (Cao et al. 2018). Antioxidant enzymes can protect plants from reactive oxygen under stress conditions and, thus, are effective indicators characterizing stress intensity (Zhang et al. 2010; Ji et al. 2018). Therefore, the studies, regarding responses of submerged macrophytes to varying water depths in morphological plasticity and physiological traits, would contribute much to revealing plant adaptive strategies and hydrologic management in aquatic ecosystems.

Potamogeton crispus, frequently described as a winter-active species, often sprouts from turions in autumn and grows in winter and spring, at which time most submerged macrophytes remain dormant (Wang et al. 2016; Zhou et al. 2016; Hao et al. 2018). Therefore, temporal niche differentiation makes *P. crispus* become constructive species from winter to spring in several aquatic ecosystems. Moreover, due to high productivity (Rogers and Breen 1980), inhibition on algae

growth (Pakdel et al. 2013; Zhou et al. 2017), and strong nutrient absorption ability (Gao et al. 2009), *P. crispus* generally plays a crucial role in maintaining ecosystem health and stability (Zhou et al. 2016). In previous studies (e.g., Zhou et al. 2016), the water depth was believed to have substantial effects on the growth and reproduction of *P. crispus*. Nevertheless, the response of *P. crispus* at the seedling stage to water level is far from clear, especially in the physiological traits, albeit which is critical for exploring plant adaptive strategies. Here, we measured the morphological and physiological traits of *P. crispus* at water depths from 40 to 220 cm using a pot experiment, and aimed to (1) find the favorable water depth range for *P. crispus*, (2) reveal how *P. crispus* protects from light damage under shallow water conditions, and (3) explore how *P. crispus* adapts to increasing water depths.

Materials and methods

Experimental design

In early November 2018, the turions (vegetative propagules) of *P. crispus* and sediment were collected from Xukou bay located in northeast of the Taihu lake (31°12'47"N 120°28'41"E). After rinsing with distilled water, 500 healthy turions of similar size (8.3 ± 0.5 g) were selected and used for pot experiment. After removing roots, macrofauna, and visible debris, the sediment was sieved (2 mm), mixed thoroughly, and divided into two subsamples. One subsample was used for pot experiment, and the other subsample was milled (<0.25 mm) to measure initial chemical traits. The sediment had the following characteristics: total organic C of 15.50 g kg^{-1} , total nitrogen (TN) of 2.64 mg g^{-1} , total phosphorus (TP) of 0.62 mg g^{-1} , and pH of 5.5.

The pot experiment was performed in a cement pool (300 × 250 × 250 cm) in the Ecological Restoration Experimental Platform of Nanjing Normal University (32°6'27" N, 118°54'19" E). Ten *P. crispus* turions were planted at 2 cm depth at equal spacing in each pot (20 cm diameter, 15 cm height) with 10 cm sediment. Subsequently, all pots were hung in the cement pond filled with tap water exposed to the air for 1 week. In this experiment, ten water level treatments were set up, i.e., the pots were hung at water depths of 40, 60, 80, 100, 120, 140, 160, 180, 200, and 220 cm, respectively, and each treatment was replicated five times. In order to avoid shading each other, the pots were arranged neatly and evenly along a high-to-low water level gradient from south to north. Moreover, all pots were placed more than 30 cm away from the pool wall to reduce boundary effects. Such experiment lasted from November 20, 2018 to January 20, 2019, and tap water was added into the pond when necessary to maintain constant water level throughout the experiment period.

During the experiment, we determined water physical and chemical parameters (including water temperature, pH, conductivity, dissolved oxygen (DO), total dissolved solids, and oxidation reduction potential) weekly at 10 cm height above each pot using a portable water quality analyzer (YSI Pro Plus; Xylem Inc., USA), and meanwhile, 50 mL water was collected to determine the total nitrogen (TN) and total phosphorus (TP) according to the alkaline potassium persulfate digestion method (Hu et al. 2002) and the ammonium molybdate spectrophotometric method (Wang et al. 2009), respectively. Detailed information on water quality indicates that water quality parameters had tiny variations with water levels (Table 1). In addition, the light intensity at each water depth was measured at 11:00–12:00 A.M. by an underwater illuminometer (ZDS-10W-2D; Shanghai Jiahe, China) once a week. Generally, the light intensity decays exponentially after entering the water: $I_z = I_0 e^{-Ez}$, where I_z represents the light intensity (Ix) when the water depth is Z, I_0 the light intensity on water surface, and E the attenuation coefficient of light intensity, which represents the decay rate of light intensity. According to the weekly measurements, the light intensity underwater always exponentially decayed with water depth throughout the experiment period (all $R^2 > 0.973$, Table S1). In general, the decaying light intensity with water depth, as well as the constant water parameters, indicates that the light intensity would take more accountabilities for responses of *P. crispus* growth to water depth in the present study.

Measured parameters and methods

Over the 61-day experiment period, and morphological traits and growth parameters were measured at 5-day intervals. Plant height was measured from the base of the main stem to the tip by a ruler (mm precision), the leaf length and width were obtained by measuring the first fully expanded leaf with a ruler (mm precision), and stem diameter was obtained by

measuring the base of the main stem with a micrometer (0.01 mm precision).

Leaf area, specific leaf area, leaf thickness, and leaf physiological indices were determined at the end of the experiment. Five well-developed healthy leaves were collected from each pot and the leaf area was calculated by image analysis software Motic Images Plus 2.0 after taking a picture with a digital camera. The ethanol extraction method was used to determine the chlorophyll a and b with a spectrophotometer (Cao et al. 2016). Reagent kits provided by Nanjing Jiancheng Biological Technology Co. Ltd were used to determine the enzyme activities. The hydroxylamine method was used to determine the superoxide dismutase (SOD) activities at 550 nm with a microplate reader, peroxidase (POD) activities were determined by catalyzing the corresponding substrate at 420 nm, and catalase (CAT) activities were measured based on the react of ammonium molybdate and hydrogen peroxide at 405 nm. All samples were oven dried at 70 °C for 72 h, and the specific leaf area was calculated as follows: specific leaf area = leaf area/leaf dry mass.

Statistical analyses

All data analyses in the present study were performed in R (version 3.6.1) with an accepted significance level of $\alpha = 0.05$. Generalized additive models (GAM) have flexible forms and can address highly nonlinear and nonmonotonic relationships in ecological data, so we adopted GAM in the “mgcv” package to examine the relationships between the traits and water depth (Table 2). For morphological indicators, GAMs were made only with the last observation data. Plotting was done with the “ggplot” package.

Results

Morphological traits

Morphological traits were significantly affected by water depth, and the effect varied over time (Tables 2 and S2, Fig. S1). At the end of experiment, plant height generally increased as the water depth increased from 40 to 140 cm, but then gradually declined with further increase of water depth (Fig. 1a). The stem diameter significantly decreased with increasing water depth during the incubation period except on the 11th day (Fig. 1b), while the leaf length significantly increased as water depth increased from 40 to 200 cm (Fig. 1c), and the leaf number was often greater at water depth of 40–160 cm (Fig. 1d). As water depth increased, the leaf area and the leaf thickness, respectively, showed an increasing and a decreasing trend, and correspondingly the specific leaf area significantly increased with depth (Fig. 2).

Table 1 Water environmental parameters during the experiment

Parameters	Mean (SD)	Maximum	Minimum
pH	7.93 (0.31)	8.46	7.68
Temperature (°C)	12.1 (2.2)	14.8	10.3
Conductivity (mS cm ⁻¹)	0.344 (0.005)	0.35	0.34
TDS (mg L ⁻¹)	223 (4)	228	220.4
ORP (mV)	249 (7)	258	238
DO (mg L ⁻¹)	10.3 (0.9)	11.2	9.3
TN (mg L ⁻¹)	0.973 (0.012)	0.98	0.96
TP (mg L ⁻¹)	0.029 (0.004)	0.014	0.046

TDS total dissolved solids, ORP oxidation reduction potential, DO dissolved oxygen

Table 2 Effects of water depth on morphological traits and growth parameters of *P. crispus* in GAMs

	edf	Residual.ef	Deviance explained (%)	Adjusted R^2	p value
Plant height	7.715	8.601	93.6	0.913	<0.001
Stem diameter	1	1	80.1	0.794	<0.01
Leaf length	6.662	7.82	91.6	0.89	<0.001
Leaf number	4.375	5.389	88.4	0.864	<0.001
Leaf area	6.95	8.065	97.2	0.963	<0.001
Leaf thickness	4.434	5.459	97.3	0.968	<0.001
Specific leaf area	5.218	6.358	97.8	0.973	<0.001
Chl <i>a</i>	3.437	4.263	93.2	0.922	<0.001
Chl <i>b</i>	2.544	3.164	94.8	0.942	<0.001
Chl <i>a</i> /Chl <i>b</i>	1	1	57.8	0.563	<0.01
CAT	8.891	8.997	99.3	0.99	<0.001
POD	8.918	8.998	99	0.986	<0.001
SOD	8.993	9	99.9	0.999	<0.001

Variables with significant influences are indicated by $p < 0.01^{**}$, $p < 0.001^{***}$

edf estimated degree of freedom, Residual.ef estimated residual degree of freedom

Physiological traits

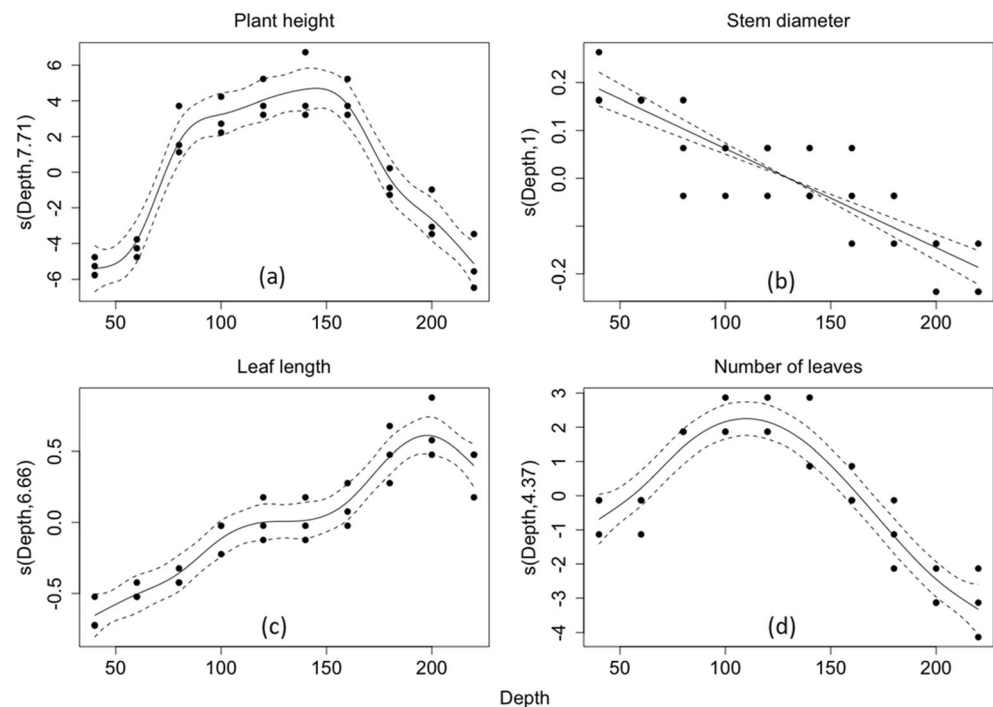
Water depth exerted significant effects on plant physiological traits (Table 2, Figs. 3 and 4). With water depth increasing, the concentrations of chlorophyll *a* and *b* in leaves increased, while their ratios gradually declined (Fig. 3). As the water depth increased from 40 to 140 cm, the activities of SOD, POD, and CAT in leaves generally declined, followed by an increasing tendency with further increase of the water depth (Fig. 4). The activities for all three enzymes were greatest at the water depth of 180–220 cm (Fig. 4).

Discussion

The influence of water depth on morphological traits

In the present study, the morphological traits of *P. crispus* varied among different water depths. Specifically, *P. crispus* showed shorter plant height, larger diameter, thicker leaves, and smaller leaf area, leaf length, and specific leaf area in shallow waters (40–60 cm water depth in the present study). As water depth increased, the plant height, number of leaves, leaf area, and leaf length gradually increased, while the plant

Fig. 1. Responses of plant height, stem diameter, leaf length, and number of leaves to water depth. The number in vertical axis title is the estimated d.f.



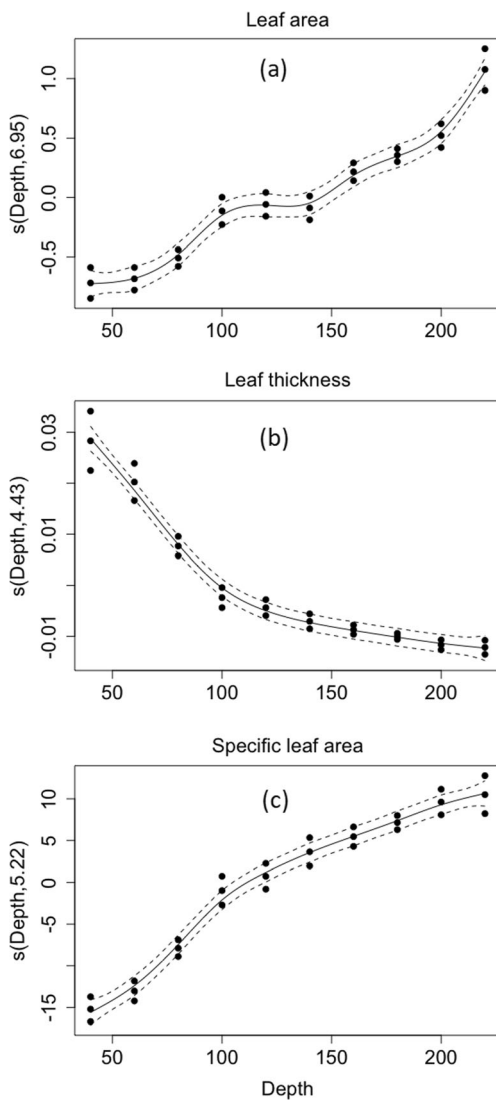


Fig. 2. Responses of leaf area, leaf thickness, and specific leaf area of *P. crispus* to water depth. The number in vertical axis title is the estimated d.f.

diameter and leaf thickness decreased. In comparison, the plant height, leaf length, and leaf number significantly declined as the water depth increased further (180–220 cm in the present study).

In shallow waters, the growth of submerged plants is often inhibited due to not only limited space but also strong illumination. For *P. crispus* leaves, increasing leaf thickness and reducing plant height, leaf area, and specific leaf area are beneficial to avoiding glare damage. Previous studies have shown similar results. For instance, the plant height of *Myriophyllum spicatum* (a canopy-type submerged macrophyte) and *Vallisneria natans* (a rosette-type submerged macrophyte) were lower at 50 cm than at deeper water (Li et al. 2019a, b), *V. natans* had the least leaf length and area when exposed in strong light or planted at water depth less than 60 cm (Chen et al. 2016; Gu et al. 2017), and the specific leaf

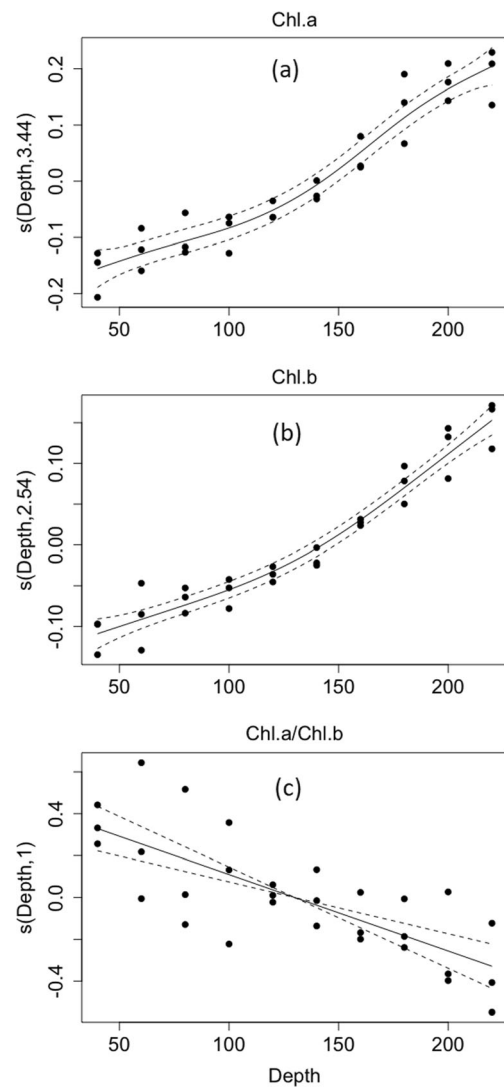


Fig. 3. Responses of chlorophyll a, chlorophyll b, and the ratio of chlorophyll a to b in *P. crispus* leaves to water depth. The number in vertical axis title is the estimated d.f.

area of *Potamogeton maackianus* and *Potamogeton malaianus* were lower at 1.0 m water depth than at 2.5 m water depth (Fu et al. 2012). Together, these findings indicate that submerged plants will adapt to strong light stress by adjusting a series of morphological traits in shallow-water environments.

As the water level rises, the light intensity attenuates, making the light energy gradually become a limiting factor for macrophyte growth. The increase in plant height contributes to shortening the distance between the top leaves and the water surface, which coupled with increased leaf area can help *P. crispus* capture solar energy. In previous studies, *P. crispus*, *V. natans*, and *M. spicatum* were also found to increase in the plant height with water depth increasing (Zhou et al. 2016; Li et al. 2019a, b), and the leaf length, width, and area of *V. natans* always showed increasing trend

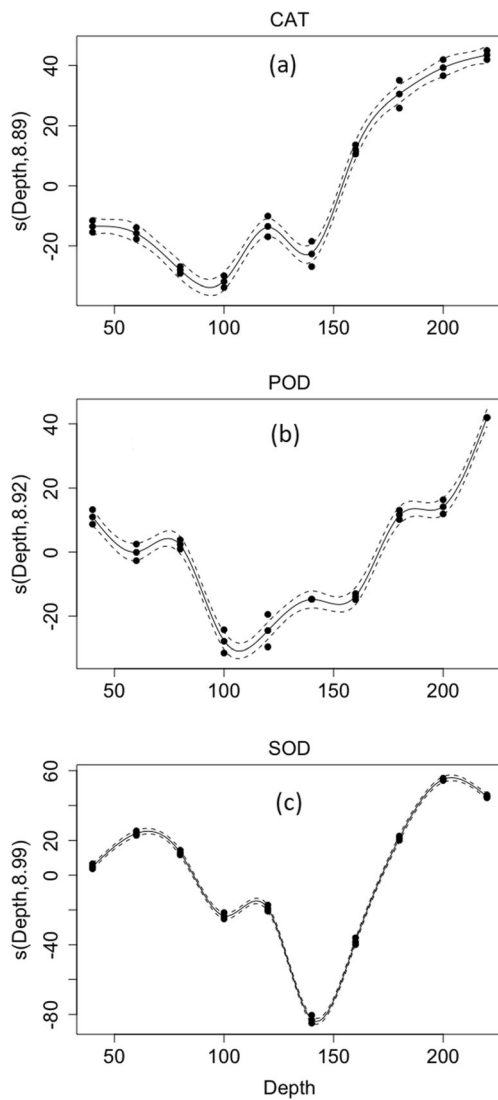


Fig. 4. Responses of catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) in *P. crispus* leaves to water depth. The number in vertical axis title is the estimated d.f.

when the water depth increased from 26 to 170 cm (Gu et al. 2017). In addition, the specific leaf area and leaf number significantly increased with water level, while the stem diameter and leaf thickness responded with a contrary tendency, ensuring resource allocation more reasonable to improve photosynthetic efficiency when the light intensity attenuates. Such inferences have been validated in other submerged plants. For example, *Potamogeton perfoliatus* reduces the stem diameter to cope with the low light stress (Sultana et al. 2010), and the number of *P. crispus* leaves gradually increased in the deep water at the middle and late stages of the experiment. These studies accord with the “optimal partitioning theory,” in that plants preferentially allocate biomass to structures foraging for the most limiting resource (Grime 1977). With resulting light intensity attenuation due to increasing water level, therefore,

the submerged macrophytes will adapt morphological traits and resource allocation to low-light stress.

As the water level further increased to 180–220 cm, nevertheless, the plant height, leaf length, and leaf number of *P. crispus* no longer increased, and even significantly decreased. The rationale behind this phenomenon may lie in that the light intensity in deep water is closed to or even below the light compensation point of *P. crispus*, resulting in a decrease in the capability of adjusting morphological traits and resource allocation. Li et al. (2019a, b) also found a significant decrease in plant height of both *M. spicatum* and *V. natans* at 2.5 m water depth, while He et al. (2009) found that the leaf number significantly decreased when the water depth increased to 180 cm. Moreover, the leaf length, width, and area at 200 cm water depth were found to be less than that at the lower water depths in two studies regarding *V. natans* (Yang et al. 2014; Cao et al. 2016). Together, these results suggest the submerged macrophytes no longer have the ability to make effective morphological adjustment in extremely deep waters or under extremely low-light conditions, where there are generally few macrophytes.

The influence of water depth on physiological traits

In addition to the morphological traits, the water depth also had significant effects on physiological traits of *P. crispus* in the present study. Specifically, the leaves have lower concentrations of SOD and POD at 100–160 water depth, and lower concentrations of CAT at water depths from 40 to 140 cm, especially 80–100 cm. In addition, the concentration of chlorophyll *a* and *b* in leaves were both lower in shallow waters, while the ratio of chlorophyll *a* to *b* was relatively higher. As the water depth increased, the chlorophyll *a* and *b* concentrations increased significantly, while their ratio gradually decreased.

Strong light was found to generally inhibit plant photosynthesis, i.e., the so-called photoinhibition, because of the potential damage of excessive light absorption on plant photosynthetic system (PS) (Kok 1956; Foyer and Noctor 1999). Such rationale can be responsible for the lower chlorophyll concentrations in *P. crispus* leaves in shallow waters in the present study. Another point worth emphasizing is that *P. crispus* leaves contained a higher ratio of chlorophyll *a* to *b* in shallow waters, and previous studies also found similar results when leaves were exposed to high-intensity illumination (Sun et al. 2010; Wei et al. 2018). Such results may be related to the following mechanism. Under strong light, the PS II, containing a lower proportion of chlorophyll *b* relative to PS I (Leong and Anderson 1984; Küster et al. 2004), is easy to be damaged seriously when photoinhibition occurs (Barber 1995; Krause 1988). The rising ratio of chlorophyll *a* to *b* suggests a decreasing in the PS II concentration, making plants escape from optical damage (Anderson and Aro 1994;

Ort et al. 2011, 2015). Therefore, it could be deduced that the submerged macrophytes would adapt the concentration and composition of chlorophyll to the glare from the sun when they grow in shallow waters.

As the water level rises, the light intensity will gradually become a limiting factor for the growth of submerged macrophytes, and no longer a stress factor. The increasing of chlorophyll concentrations in *P. crispus* leaves contributes to the maintenance of photosynthesis in low-light conditions, which is consistent with a study regarding *P. crispus* growth under different light intensities (Cao et al. 2018). In recent studies on *Ottelia acuminata*, *V. natans*, *Hydrilla verticillata*, and *P. maackianus*, the leaf chlorophyll concentrations were also found to generally increase with increasing water depths in a certain range (Zhao et al. 2018; Wei et al. 2018; He et al. 2019; Luo et al. 2019). In addition, the ratio of chlorophyll *a* and *b* in *P. crispus* leaves decreased as water depth increased, while similar trends were also found in previous studies regarding the macrophytes exposed to different light intensities (Sun et al. 2010; Cao et al. 2018). Such trends could be explained by the following reasons. The photosynthetic system mainly consists of two components, i.e., light-harvesting complex and reaction-center complex, and the former contains both chlorophyll *a* and *b*, while the later only contains chlorophyll *a*. Therefore, the decline in the ratio indicates that plants adapt to the decline in light intensity by increasing the proportion of the light-harvesting complex.

In addition to the chlorophyll, antioxidant enzymes also responded sensitively to changing water depths. Under environmental stress, reactive oxygen species would continuously accumulate in plant tissues, and antioxidant enzymes could protect plants by removing these reactive oxygen (Ji et al. 2018). Therefore, the activity of antioxidant enzymes is an important indicator representing plant stress response, which will increase with the stress intensity enhancing (Zhang et al. 2010). In the present study, *P. crispus* always exhibited the lowest antioxidant enzyme activity at moderate water depths, although there were differences in concrete water depth ranges among POD, SOD, and CAT, which indicates that this submerged macrophyte grows in relatively favorable environments. In strong light, photoinhibition would stimulate the generation of reactive oxygen species and superoxide anion radicals during photochemical reactions (Clarke and Johnson 2001). Similarly, the low-light environment, resulting from increasing water levels, would also cause a continuous accumulation of the reactive oxygen species (Song et al. 2017; Li et al. 2020). In our study, the observed increasing activities of antioxidant enzymes could help remove excessive reactive oxygen and radicals, contributing to the balance of reactive oxygen species. Moreover, a recent study regarding *Vallisneria spiralis*

growing at different water depths also found similar trends (Ji et al. 2018; Li et al. 2020). Therefore, increasing antioxidant enzyme activity is one common strategy for submerged macrophytes when they cope with environmental stress, and such mechanism is crucial for their growth and metabolic activity.

In the present study, the morphological plasticity and physiological traits of the aboveground parts help recover the adaptation mechanism of *P. crispus* to the water level in detail. However, the underground part is also essential in plant adaptation to the water level (Hussner et al. 2009; Pan et al. 2014) due to its role in obtaining nutrient and transferring oxygen (Bezbaruah and Zhang 2005; Xie et al. 2006, 2007). Unfortunately, we did not pay close attention to how the roots respond to altered water levels in the present study. In future studies, therefore, a more elaborate design is essential to investigate morphological and physiological responses of *P. crispus* roots to variations of the water level, which would help more comprehensively reveal the adaptive strategy.

Conclusions

In the present study, both morphological and physiological traits of *P. crispus* responded sensitively to varying water levels, which accounts for its adaptive capacity to water depth rising and falling. These traits suggest that *P. crispus* grows well at relatively moderate water depths. In shallow waters, the adjustment in a series of traits contributes to protecting *P. crispus* against optical damage, while that helps obtain more sunlight or relieve the low-light stress in deep waters. However, *P. crispus* showed weak adjustment ability in morphological traits when the water depth crossed a particular threshold. Overall, the present study provides new insights into the adaptation strategies of submerged macrophytes to the variation in water levels, and the finding is beneficial to ecosystem construction and management.

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Authors' contributions L.W. and G.W. conceived and designed the experiments. L.W., X.W., X.H., and Y.G. performed the experiments. L.W. and B.L. analyzed the data and wrote the manuscript. G.W. and X.Z. provided editorial advice. All authors read and approved the final manuscript.

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Availability of data and materials The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Ethics approval and consent to participate Not applicable

Consent for publication Not applicable

Competing interests The authors declare that they have no competing interests.

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