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Responses of growth and photosynthetic fluorescent characteristics in *Ottelia acuminata* to a water-depth gradient

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ABSTRACT

To assess the response of *Ottelia acuminata* to a water-depth gradient, we investigated the plant growth and leaf photosynthesis by setting three water depths (0.5, 1.0, and 1.5 m) *in situ* in Yilong Lake, Yunnan Province, China. The results showed that the growth and photosynthetic fluorescent characteristics of *O. acuminata* exhibited different responses to the water-depth gradient. The plant height, fresh weight, root length, and leaf number of *O. acuminata*, varied significantly with changes in the water depth. With regard to the photosynthetic fluorescent characteristics of leaves, the maximum quantum yield half-saturation light intensity and fluorescence parameter of photosystem II markedly improved with increasing water depth. The increase of photosynthetically active radiation resulted in a decreased photochemical quenching coefficient (qP). In contrast, the nonphotochemical quenching coefficient was relatively high in the leaves of *O. acuminata* in shallow water under high photosynthetically active radiation. The chlorophyll content of the leaves varied significantly with changes in the water depth. Higher chlorophyll a, chlorophyll b, and carotenoid contents were detected in the leaves of *O. acuminata* at the water depth of 1.5 m. The results of the growth and photosynthetic fluorescent characteristics of *O. acuminata* indicate a better protection mechanism against high light in the leaves of *O. acuminata* in shallow water and a higher photosynthetic efficiency, as well as a greater photosynthetic potential, in the leaves of *O. acuminata* in deep water.

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Introduction

The effect of water depth on submerged plants comprehensively reflects multiple influencing factors (e.g. light, temperature, hydraulic pressure, and nutrient salts). Among these, light is the most important environmental factor that plays a decisive role in the growth and spatial distribution of submerged plants (Bornette and Puijalon 2011). Therefore, the effect of water depth on submerged plants can be accurately determined by monitoring plant growth and photosynthetic fluorescent characteristics. In response to the adverse conditions brought about by changes in water depth, submerged plants usually possess the ability to cope with an adverse environmental impact through self-regulation. This is mainly reflected in two aspects: first, the plants deal with the adverse environmental impact by altering their morphological appearance, including leaf length, leaf width, leaf number, and root length; second, the plants deal with the adverse environmental impact through physiological changes, such as activation of the antioxidant system (Chen et al. 2013) and changes in enzyme levels, chlorophyll

content, and photosynthetic rate (Maberly 1993; Strand and Weisner 2001; Spence and Chrystal 2010). Studies concerning the effect of water depth on submerged plants have been conducted mainly in common species of submerged plants such as *Vallisneria spiralis*, *Hydrilla verticillata*, and *Potamogeton crispus*. Research into aquatic plants endemic to China is scarce.

Ottelia acuminata is an endemic, perennial, submerged plant in the family Hydrocharitaceae and is mainly distributed in freshwater habitats below 2700 m in Yunnan, Guizhou, Hainan, and Guangxi (Wang 2011). *Ottelia acuminata* has a high requirement for a water environment and a high dependence on water transparency and light; thus, it can serve as an indicator species for the quality of the water environment. Particularly, water transparency and turbidity can often be inferred based on the growth of *O. acuminata*, owing to the plant's need for transparency. Since the early 1990s, a growing number of studies on *O. acuminata* have been conducted, mainly on the morphological classification (Zhai et al. 2010; Jiang et al. 2005) and nutrient content (Yuan et al. 2009) of the species. In recent years, research has been gradually carried out on the factors that influence and protect *O. acuminata*; however, those studies have mainly focused on heavy metal ions (Zhu et al. 2016), light (Zhao et al. 2014), and seed germination (Wang and Yi 2014). The physiological response of *O. acuminata* to superoxide dismutase (SOD), catalase (CAT), and malondialdehyde (MDA; Chen and Chu 2016) has been investigated, mostly by laboratory simulation experiments. Regarding available data, studies have rarely reported on the photosynthetic fluorescent characteristics in the leaves of *O. acuminata*. Therefore, the present study analyzed the photosynthetic fluorescent characteristics in the leaves of *O. acuminata* in the field to assess the response of this species to different water depths.

The study of the fluorescence characteristics of chlorophyll, which can be used as an internal probe for the relation of plant photosynthesis to the environment, can rapidly, accurately, and noninvasively reflect the physiological conditions of plants in the environment (Küster and Altenburger 2007). In recent years, this probe has been extensively used to study the photosynthetic physiology of terrestrial plants (Redillas et al. 2011), whereas it has been used less frequently in aquatic plants. The emergence of an underwater, saturation, pulse-amplitude-modulated fluorometer (Diving-PAM) has allowed for an increasing number of studies of the *in situ* determination of photosynthesis in submerged plants (Ralph and Gademann 2005; Hussner et al. 2011).

Yilong Lake (longitude 102°28'–102°38' E, latitude 23°28'–23°42' N), one of the nine plateau lakes in Yunnan Province, China, is a typical shallow plateau lake with an area of approximately 31 km² and an average water depth of 1.9 m (Wei and Tang 2014). *Ottelia acuminata* was found to be widely distributed in Yilong Lake in 1980, based on a survey of aquatic vegetation in the plateau lakes in Yunnan by Li (1980). However, this species showed a slight decline in Yilong Lake in 2014, as revealed by a lake-wide survey of aquatic vegetation. In the present study, we investigated the *in situ* growth and photosynthetic fluorescent characteristics of *O. acuminata* in Yilong Lake to provide the theoretical basis and data support for the restoration of the *O. acuminata* communities in this lake.

Methods

In April 2015, *O. acuminata* seedlings with consistent growth were selected from the Yilong Lake demonstration base for the restoration of submerged plants. The seedlings had a plant height of 27 ± 1.5 cm, a leaf number of 7 ± 0.5 , a biomass of 9.8 ± 1.6 g, and a total root length of 110 ± 6 cm.

The demonstration base was a closed lake body enclosed by an earthen dam along the east side of Yilong Lake. The base had an area of 36,350 m², an average water depth of 1.5 m (maximal 2.0 m), and a transparency of 1.55 m.

Table 1. The environmental factors of three water depths in the experiment.

Parameter/depth	0.5 m	1.0 m	1.5 m
TN (mg/L)	2.42	2.53	2.61
TP (mg/L)	0.12	0.14	0.15
Chl.a (mg/m ³)	26.58	24.63	22.82
Light intensity	3.52	2.86	1.48
T (°C)	21.6	21.4	21.3

Experimental design

Three experimental sites were set in the western lake area of Yilong Lake (average water depth = 1.5 m, Secchi depth = 1.2 m). At each site, four bamboo stakes were vertically inserted into the bottom of the lake. Both ends of another four bamboo stakes were fixed to the vertical bamboo stakes, and the horizontal bamboo stakes, which were parallel to the water surface, were used to hang plastic baskets. The selected *O. acuminata* seedlings were grown in nutritional bowls ($h = 10$ cm, $d = 8$ cm), with one plant per bowl. The nutritional bowls were then placed in the plastic baskets (length = 60 cm, width = 48 cm, height = 12 cm), with 45 bowls per basket. The baskets were hung horizontally from the stakes, which were leveled by pulling a nylon rope. At each site, the plastic baskets were hung one of three depths (0.5, 1.0, or 1.5 m) with 24 numbered baskets per depth. Each experimental zone was enclosed using 5×5 mm breeding nets to prevent herbivorous aquatic animals from impacting the experimental results.

The experiment began on 10 April 2015 and lasted 60 days. At the end of the experiment, the *O. acuminata* seedlings were taken from the 120 nutritional bowls held at the different water depths at the three experimental sites (40 bowls were selected at random at each site) to measure the growth and photosynthetic fluorescence parameters.

During the experiment, parameters, including water temperature (T), total nitrogen (TN) and total phosphorus (TP) concentrations, and chlorophyll a (Chl a) content, as well as light conditions at the three water depths, were monitored in the experimental zones at noon every 10 days. The results were then averaged, and the following mean parameter values were obtained for 0.5, 1.0, and 1.5 m, respectively (Table 1).

Parameter determination

The number of leaves was counted. Fresh weight was determined after the plants had been washed with distilled water and dried with absorbent paper. Plant height was measured with a 1 mm precision ruler. The total root length was determined using a root scanner (WinRhizo, Regent Instrument Inc., Ville de Québec, Quebec, Canada).

The chlorophyll content of the leaves was determined by spectrophotometry colorimetry after extraction with 80% acetone (Institute of Plant Physiology and Ecology 1999).

Determination of the photosynthetic fluorescence parameters (Schreiber et al. 1997) began with the measurements made at 7–9 am (9 June 2015) using a Diving-PAM underwater fluorometer and WinControl data acquisition software (Germany). The measurement site of the leaf was first subjected to shading treatment for 20 min using a blade clamp. The blade clamp was then opened, and the measuring light was turned on to obtain the initial fluorescence (F_0). Subsequently, the saturation pulse was turned on [saturation pulse intensity = $4000 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ for 0.8 s] to measure the maximum fluorescence (F_m). There are 120 individuals sampled in the experiment and three experimenters at the same time, and each of which handles 40 samples. The acquisition of experimental data is completed in the shortest time, and the experimental error is reduced as much as possible. Each plant measurement was repeated twice, and the results were used to calculate the variable fluorescence (F_v), the maximum quantum yield (F_v/F_m), and the fluorescence parameter (F_v/F_0).

Calculations were made using the following formulae:

$$F_v = F_m - F_0$$

$$F_v/F_m = (F_m - F_0)/F_m, \text{ and}$$

$$F_v/F_0 = (F_m - F_0)/F_0.$$

Determination of the rapid light response curve began with measurements made at 9–11 a.m. Actinic light was turned on at the light intensity of 0, 60, 152, 286, 431, 631, 840, 1098, and 1263 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$, and the actinic light radiation at each intensity lasted 10 s. After each *photosynthetically active radiation* (PAR), the fluorescence before turning on the saturation pulse was recorded as F_t , and the fluorescence measured after turning on the saturation pulse light was recorded as F_m' . The results were used to calculate the *effective quantum yield* (Yield):

$$\text{Yield} = (F_m' - F_t)/F_m'$$

The photochemical quenching coefficient (qP) was calculated as

$$\text{qP} = (F_m' - F_t)/(F_m' - F_0),$$

and the nonphotochemical quenching coefficient (qN) was calculated as

$$\text{qN} = (F_m - F_m')/(F_m - F_0).$$

The relative electron transport rate (rETR) was derived from the *Yield* and the PAR:

$$\text{rETR} = \text{Yield} \cdot \text{PAR} \times 0.5 \times 0.84.$$

The rapid light response curve was fitted by the least squares method, and the light response curve of the mean rETR was drawn according to the following:

$$P = P_m \cdot (1 - \exp(-\alpha \cdot \text{Ed}/P_m)) \cdot \exp(-\beta \cdot \text{Ed}/P_m)$$

$$\text{rETR}_{\text{max}} = P_m \cdot (\alpha/(\alpha + \beta)) \cdot (\beta/(\alpha + \beta))^{(\beta/\alpha)}$$

$$E_k = \text{rETR}_{\text{max}}/\alpha$$

$$E_m = P_m/\alpha \cdot \ln((\alpha + \beta)/\beta),$$

where P is the electron transfer rate; P_m is the maximum electron transport rate (ETR_{max}); α is the initial slope of photosynthetic curve, which reflects photosynthetic utilization efficiency; β is the photosynthetic suppression parameter; E_k is the half-saturation light intensity, indicating plant tolerance to high light; and E_m is the maximum saturation light intensity.

Data analysis

Statistical analysis and graph plotting were performed using Excel 2007 (Microsoft Corp., Redmond, WA, USA), SPSS 19.0 (IBM SPSS, Somers, NY, USA), and Origin 8.0. All data were tested for normality and homogeneity before analyses. The effects of water depths on the growth and photosynthetic fluorescent characteristics of *O. acuminata* were evaluated by one-way ANOVA and means were compared by Duncan's multiple range test, with the depths as dependent variables, with plant height, total length, leaf number, fresh weight, F_0 , F_m and so on as fixed factors.

Results

Responses of growth to water depth in *O. acuminata*

The growth indicators of *O. acuminata* showed positive responses to water depth. All plant height, total root length, leaf number, and fresh weight varied with changes in water depth. The plant height was significantly higher at 0.5 and 1.0 m than at 1.5 m ($P < 0.05$), but no significant difference was found between the former two groups ($P > 0.05$) (Figure 1). The mean plant height at 1.0 m reached 68.7 cm, which was the highest growth; the lowest plant height appeared at 1.5 m, only 57.2 cm. The roots exhibited a growth trend consistent with that in plant height. The total root length was highest for the 1.0 m group (521.6 cm) and it was lowest for the 1.5 m group (196.5 cm). There were significant differences in total root length between the three groups ($P < 0.05$) (Figure 1). The growth trend of leaf number differed from those of leaf length and root length. At various water depths, the leaf number ranked 0.5 m > 1.0 m > 1.5 m, and significant differences were detected between groups ($P < 0.05$) (Figure 1). The highest leaf number for the 0.5 m group was 27.6. Moreover, the three groups showed significant differences in fresh weight ($P < 0.05$). The fresh weight was highest for the 1.0 m group, with a mean of 31.2 g/plant; lowest for the 1.5 m group, with a mean of 18.3 g/plant; and intermediate for the 0.5 m group, with a mean of 26.8 g/plant (Figure 1).

Responses of photosynthetic fluorescence parameters to water depth

With an increase in water depth, the F_0 and F_m did not vary significantly in the leaves of *O. acuminata* (Duncan test, $p = 0.058$, $n = 2$) (Figure 2). Nonetheless, both the F_v/F_m and F_v/F_0 markedly increased with increasing water depth (Duncan test, $p = 0.039$, $n = 2$), i.e. 1.5 m > 1.0 m > 0.5 m

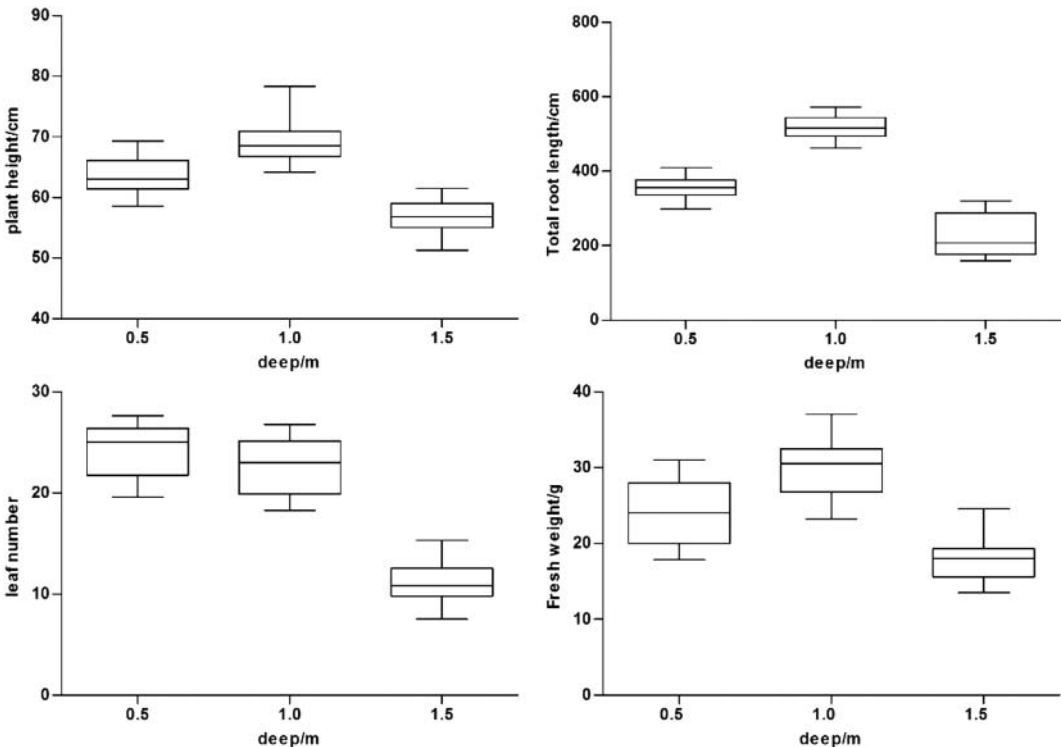


Figure 1. Responses of growth characteristics to water depth in *Ottelia acuminata*.

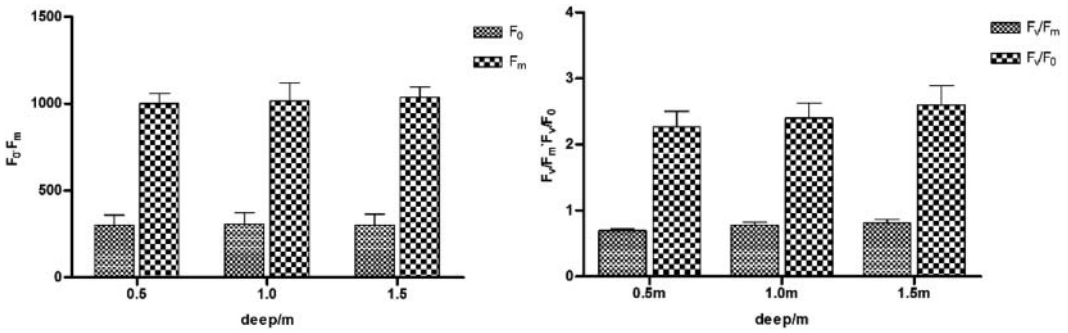


Figure 2. Responses of photosynthetic fluorescent characteristics to water depth in *Ottelia acuminata*.

(Figure 2). It is shown that with the increase of water depth, the ability of the light reaction center to use the weak light increases significantly.

With a continuous increase in water depth, the qP was lower for the shallow water group than for the deep water group under the low PAR treatment, which suggests a higher light-use efficiency in the leaves of the *O. acuminata* in deep water under low light. With a continuous increase of PAR [0–282 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$], a sharp decline was observed in the qP for the 0.5 m group, a slow decline for the 1.5 m group, and a moderate decline for the 1.0 m group (Figure 3). With a further increase of PAR [282–12,352 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$], the qP decline slowed for the 0.5 m group, whereas it accelerated for the 1.5 m group.

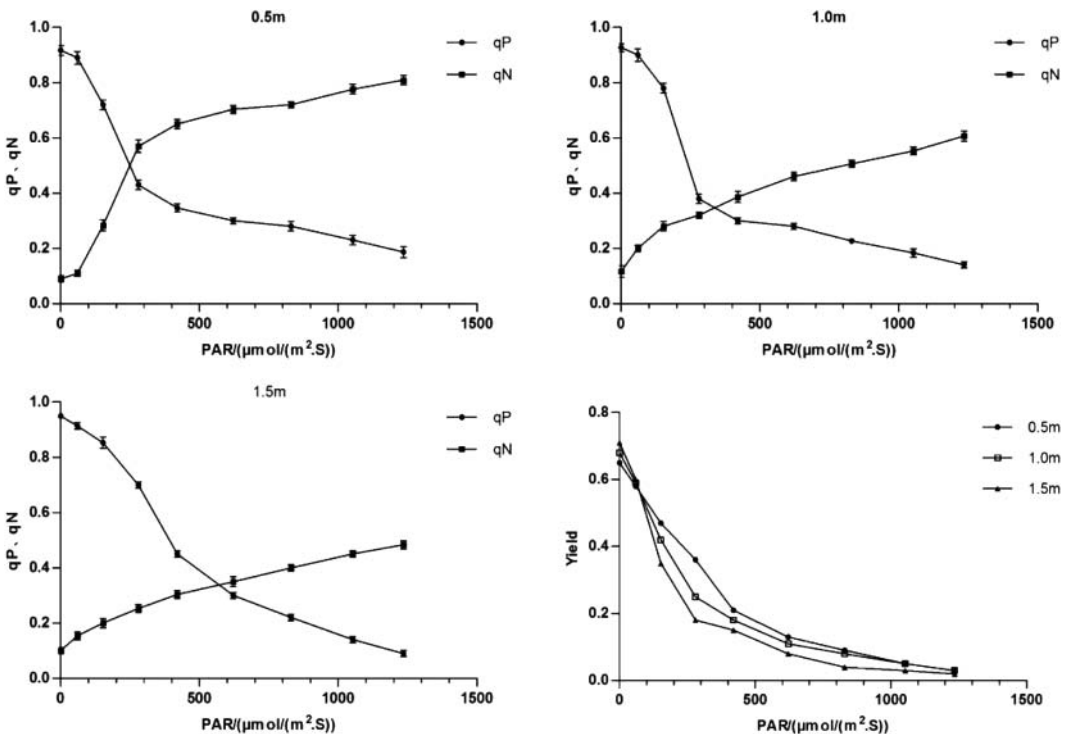


Figure 3. Responses of chlorophyll fluorescence parameters in leaves of *Ottelia acuminata* to water depth.

The qN exhibited the opposite trend to the qP. With a continuous increase of PAR, the qN constantly increased in each treatment group. Different groups had similar qN values under low PAR. When the light intensity was continuously enhanced, the qN rapidly increased in the leaves of *O. acuminata* for the 0.5 m group; the increase was relatively slow for the other two groups, and the group difference was significant (Duncan test, $p = 0.021$, $n = 2$). The highest values were 0.87 for the 0.5 m group, 0.48 for the 1.5 m group, and 0.63 for the 1.0 m group (Figure 3). The above results indicate a higher self-protection ability of leaves in *O. acuminata* against high light in shallow water.

Among the different groups, the Yield showed the same trend of response to water depth in the leaves of *O. acuminata*. With an enhancement of PAR, the Yield declined exclusively. The difference occurred because the decrease was fastest for the 0.5 m group, intermediate for the 1.0 m group, and slowest for the 1.5 m group (Figure 3).

Responses of the light response curve to water depth

Water depth exhibited a significant effect on the light response curve in leaves of *O. acuminata*. α , which reflects photosynthetic efficiency, varied significantly in leaves of *O. acuminata* among the three water depths. The α value was lowest at 0.5 m, intermediate at 1.0 m, and highest at 1.5 m; the difference was significant among the groups ($P < 0.05$) (Figure 4). The $rETR_{max}$ constantly increased with increasing water depth, from 22.935 $\mu\text{mol photons}/(\text{m}^2\cdot\text{s})$ at 0.5 m to 29.324 $\mu\text{mol photons}/(\text{m}^2\cdot\text{s})$ at 1.5 m; the increase was 27.86%, reaching statistical significance ($P < 0.05$) (Figure 4). The E_k exhibited the same trend as the $rETR_{max}$. The E_k value at 1.5 m improved by 44.12% compared with that at 0.5 m; the difference was significant (Duncan test, $p = 0.023$, $n = 2$) (Figure 4). The E_m varied larger with changes in water depth, and significant difference was found between groups (Duncan test, $p = 0.019$, $n = 2$).

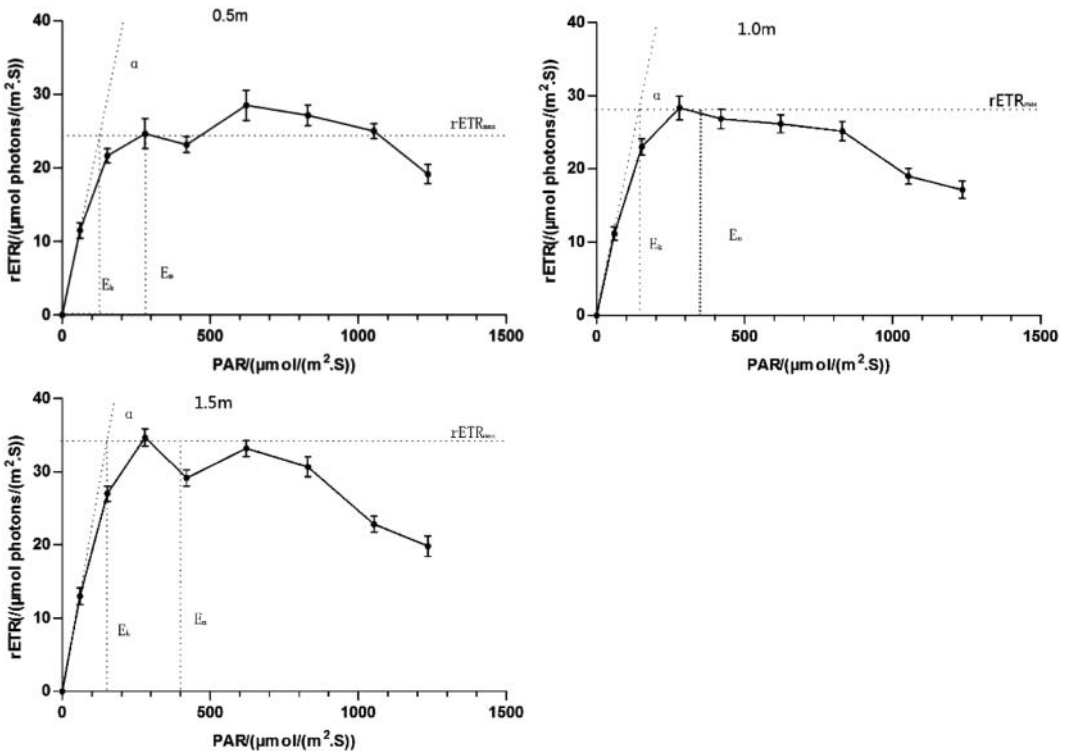


Figure 4. Responses of light response curves of *Ottelia acuminata* leaves to water depth.

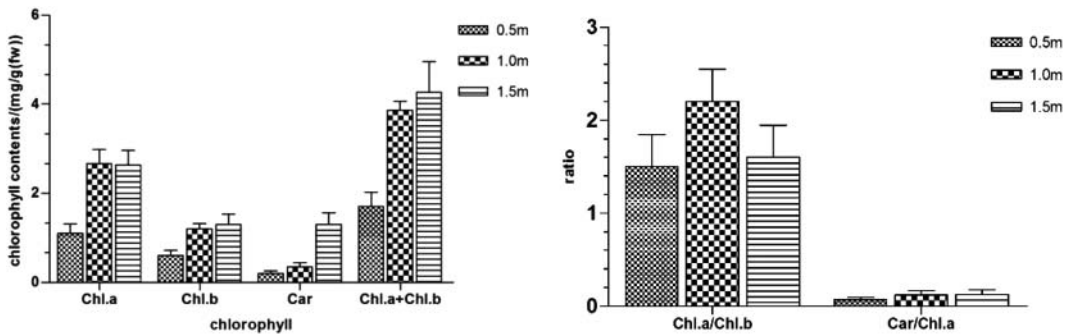


Figure 5. Responses of photosynthetic pigment contents in leaves of *Ottelia acuminata* to water depth.

Responses of photosynthetic pigment contents in leaves of *O. acuminata* to water depth

Photosynthetic pigment contents showed positive responses to water depth in leaves of *O. acuminata*. The lowest Chl a, Chl b, carotenoid (Car), and Chl a + Chl b contents were found at 0.5 m, which showed significant differences compared with the other two groups ($P < 0.05$) (Figure 5). The parameter values were intermediate at 1.0 m and highest at 1.5 m; however, no significant difference was found between the two groups ($P > 0.05$). Comparing the leaves of *O. acuminata* at 1.5 m with those at 0.5 m, we found that the Chl a, Chl b, Car, and Chl a + Chl b contents increased and the differences reached high significance (Duncan test, $p = 0.006$, $n = 2$), by 261%, 203%, 421%, 247%; little change occurred in Chl a/Chl b or Car/Chl a, and no significant difference was found between groups (Duncan test, $p = 0.061$, $n = 2$) (Figure 5). The results showed that the content of chlorophyll increased with the increase of water depth, but the proportion of different kinds of chlorophyll had not changed obviously.

Discussion

Water depth is a major environmental factor that influences plant growth and distribution. Submerged plants have the ability to self-regulate and adapt to the environment; they can adjust the distribution of resources in the plant body for adapting to the environment, which is often manifested as changes in the growth and physiological parameters (Li et al. 2008). Photosynthetic fluorescence parameters in leaves closely relate to photosynthesis in plants and accurately reflect the actual situation of plant photosynthesis in certain circumstances (Guo and Tan 2015). Thus, the growth and photosynthetic fluorescent characteristics of a plant can accurately reflect plant physiology and growth performance at different water depths. In the current study, the results show that water depth has a significant effect on the growth and photosynthetic fluorescent characteristics of *O. acuminata*.

Havens (2003) believed that the water depth is tightly linked to a reduction in light intensity. At a certain water depth, when light intensity has not reached the compensation point for plant growth, submerged plants will change their leaf features and physiological adaptability in response to the changing environment; whereas, in shallow waters, submerged plants often receive high light far above the light compensation point, resulting in high light suppression (Blanch et al. 1998). In the present study, the growth characteristics of *O. acuminata* showed a series of positive responses to water depth. Specifically, due to high light suppression, the plant height at 0.5 m was lower than that at 1.0 m; whereas, at 1.5 m under low light intensity, the growth of *O. acuminata* was subjected to low light suppression, and the highest leaf length was recorded at the 1.0 m water depth. Under high light suppression, *O. acuminata* plants in shallow water showed reduced plant height and increased leaf number to adapt to the high light environment; in deep water, *O. acuminata* plants

showed increased plant height and reduced leaf number to achieve the purpose of photosynthesis. The experimental results indicate that in *O. acuminata*, the response mechanisms of growth characteristics to water depth are similar to those in *V. natans* (Yang et al. 2014).

Changes in F_0 are associated with the initial electronic excitation density of photosystem II (PSII) antenna pigments and chlorophyll content; F_m represents the fluorescence yield when the antenna pigments are completely closed (Barbara et al. 1987). Our results showed that neither F_0 nor F_m varied significantly in response to water depth ($P > 0.05$). This suggests that in an environment with changing water depth, no significant differences occur in the electron density of the PSII reaction center or the fluorescence yield on completely closed antenna pigments in the leaves of *O. acuminata*. When the depth of water is between 0.5 and 1.5 m, and other situations where lake depths are greater need to be discussed in future studies.

F_v/F_m , the maximum quantum yield of PSII, reflects the potential light energy conversion efficiency of the PSII reaction center, and this efficiency is independent of species (Cheng et al. 2014). F_v/F_m changes little under nonstress conditions and measures approximately 0.83 in most higher plants; the value is significantly reduced in plants subjected to environmental stress. In the present study, the F_v/F_m values for the three groups of *O. acuminata* were 0.795 (0.5 m), 0.816 (1.0 m), and 0.831 (1.5 m), indicating an effect of particular stress factors on *O. acuminata* in shallow water. F_v/F_0 reflects the potential activity of PSII. In this study, we observed a significant reduction in the F_v/F_0 at 0.5 m, which indicates a significant increase in the potential activity of the PSII reaction center with increasing water depth ($P < 0.05$).

After being harvested by antenna pigments, light energy is consumed mainly by three competitive pathways: photochemical electron transfer, chlorophyll fluorescence emission, and heat dissipation. Only a small portion of energy is consumed by chlorophyll fluorescence emission, while the majority is consumed by photochemical electron transfer and heat dissipation. qP represents the light energy adsorbed by the antenna pigments of PSII that is used for photochemical electron transfer; this parameter reflects the openness of the PSII reaction center and the number of electrons participating in CO₂ fixation. qN reflects the light energy adsorbed by antenna pigments that cannot be used for electron transfer but consumed in the form of heat. When the antenna pigments of the PSII reaction center adsorb excessive light energy that cannot be dissipated timely, it will cause damage to the photosynthetic structure. Therefore, nonphotochemical quenching is a self-protection mechanism for plant tissue (Van and Snel 1990). The level of qN indicates the self-protection ability of plants against excessive light energy. In the present study, under low PAR, the qP was higher in leaves of *O. acuminata* at 1.5 m; an increase of PAR resulted in a rapid decrease in the qP in deep water and a slow decrease in shallow water. This indicates that when the PAR was low, the PSII reaction center exhibited higher 'openness' and CO₂ fixation ability in leaves of *O. acuminata* in deep water; under high PAR, the trend was the opposite. In light conditions, the qN data in shallow water remained higher than in deep water, i.e. 0.5 m > 1.0 m > 1.5 m, suggesting a better light protection mechanism in the leaves of *O. acuminata* in shallow water. Our observation is in agreement with the result of Yang et al. regarding the response of photosynthetic fluorescent characteristics in leaves of *V. natans* to water depth. Together, these findings prove the common response mechanisms of photosynthetic reaction in *O. acuminata* and *V. natans*. In shallow waters, the leaves of *O. acuminata* possess higher heat dissipation ability and thereby protect the structure of the PSII reaction center against the damage of excessive high-energy electrons. In deep waters, however, the leaves of *O. acuminata* have limited nonphotochemical quenching capacity under high PAR conditions and thus cannot maintain their structural stability through effective heat dissipation, resulting in decreased photosynthetic ability and subsequent growth inhibition. In contrast, the leaves of *O. acuminata* have better light utilization efficiency under low PAR conditions in deep waters. This is an adjustment in the plant physiological structure by *O. acuminata* based on the living conditions, as well as part of the adaptability of plants.

Yield, which indicates the actual photosynthetic efficiency of PSII under light conditions, is the efficiency of a plant for absorbing and supplying photons to the PSII reaction center (Yu et al.

2015). In the current study, the *Yield* under low PAR [$0\text{--}152 \mu\text{mol}/(\text{m}^2\cdot\text{s})$] ranked $0.5 \text{ m} > 1.0 \text{ m} > 1.5 \text{ m}$. With an increase of PAR [PAR $> 152 \mu\text{mol}/(\text{m}^2\cdot\text{s})$], the *Yield* showed a rapid decrease at 1.5 m and a slow decrease at 0.5 m, indicating higher actual photosynthetic efficiency in leaves of *O. acuminata* in deep water under high PAR conditions.

α , which reflects the level of the light-harvesting capacity of leaves, is associated with the light absorption coefficient of leaves and the light utilization efficiency of PSII. In this study, the α value was gradually increased with an increase of water depth, indicating higher light harvesting and light use capabilities of *O. acuminata* in deep water. $r\text{ETR}_{\text{max}}$ and E_k showed the same trends, both of which markedly increased with increasing water depth ($P < 0.05$); this suggests higher electron transfer efficiency and high light tolerance, as well as higher photosynthetic potential in the leaves of *O. acuminata* in deep water.

Chlorophyll is the major pigment for plant photosynthesis, and chlorophyll content reflects, to a certain extent, the photosynthetic capacity of plants (Zhang and Chen 2016). Chl a mainly plays a role in converting light into electrons, whereas Chl b is a major constituent of the light-harvesting pigments in plants; thus, the relative value of Chl a/Chl b reflects the size of the light-harvesting pigment system (Anderson and Aro 1994). Car is a photosynthetic pigment as well as an endogenous antioxidant whose presence is conducive to the protection and stabilization of the structure of light-harvesting complexes (He et al. 2001). In the present study, the chlorophyll contents were significantly lower in the leaves of *O. acuminata* at 0.5 m than at 1.0 and 1.5 m ($P < 0.05$), indicating that the significant increase of chlorophyll content was favorable for the effective absorption of light energy by *O. acuminata* in deep water under low light conditions. However, Chl a/Chl b did not significantly differ with increasing water depth ($P > 0.05$). This suggests that the light-harvesting capacity of the *O. acuminata* leaves did not change greatly at different water depths and that *O. acuminata* improved its photosynthetic capacity in low light conditions only through increasing the Chl a, chl b, and Car contents in the leaves. The Car content varied significantly with increasing water depth ($P > 0.05$), indicating that under high light irradiation, the structure of the light-harvesting complexes was more stable in the leaves of *O. acuminata* in deep water. The leaves exhibited a higher ability to harvest light under high light conditions, which is in agreement with the light-harvesting capacity indicated by α . The Car content is an intrinsic structural factor, and α is the experimental pattern shown due to differences in the Car content.

In summary, we found that the growth and photosynthetic fluorescent characteristics in leaves of *O. acuminata* demonstrated positive responses to water depth. The growth and photosynthetic fluorescence state of plants varied significantly with the various water depths. In shallow water, *O. acuminata* often lived under high light intensity, where it reduced the chlorophyll content in the plant body to attenuate the light harvest and thereby protected photosynthetic structures from damage; on the other hand, the plant maintained high heat dissipation in photosynthesis to protect photosynthetic structures (Zhou et al. 2011). In deep water, *O. acuminata* often lived in a low light environment, where it improved the chlorophyll content in the plant body and reduced heat dissipation to increase the photosynthetic efficiency; the plants commonly had relatively high ETR and E_k as well as high photosynthetic efficiency, but their self-protection ability under high light was lower compared with the plants in shallow water. Thus, *O. acuminata* can adjust the growth and physiological parameters in the growth process based on the habitat conditions to better adapt to the environment and create a more conducive space for growth and development. Therefore, plants grown in different living environments possess particular physical structures adapted to the environment; when the environment changes, the plant has to re-adjust the physical structures. Intense changes in environmental variables may cause growth inhibition and even the death of plants. If the water level suddenly drops, *O. acuminata* plants living in deep water will be exposed to highlight and growth inhibition or death may occur due to a lack of self-protection mechanism under high light. If the water level is elevated, growth inhibition or death may occur in *O. acuminata* in shallow water due to relative low photosynthetic efficiency. This is one of the main reasons why a large amount of *O. acuminata* has gradually declined in plateau lakes in China.

Conclusions

The growth and photosynthetic fluorescent characteristics of *O. acuminata* showed positive responses to water depth. *Ottelia acuminata* changed the growth characteristics and photosynthetic tissue structure with various water depths to adapt to different growing environments.

F_0 and F_m did not vary significantly at the different water depths, whereas F_v/F_m and F_v/F_0 significantly increased with increasing water depth. The α , $E_{TR_{max}}$, and E_K of the light response curve varied significantly at the different water depths, indicating significantly improved photosynthetic efficiency of PSII in leaves of *O. acuminata* in deep water.

No major differences were observed in the light-harvesting capacity in the leaves of *O. acuminata* at the various water depths. *Ottelia acuminata* only increased the Chl a, Chl b, and Car contents in leaves to improve the photosynthetic capacity in low light conditions.

Ottelia acuminata demonstrated different response mechanisms for the water-depth gradient. In shallow water, a better protection mechanism against high light was observed in the leaves of *O. acuminata*, whereas in deep water, a higher photosynthetic potential was observed in the leaves of *O. acuminata*.

Ottelia acuminata can constantly adjust its morphological and physiological conditions with changes in water depth to adapt to complex environments. In the current water environmental conditions, 1.0 m is the optimum water depth for the restoration of *O. acuminata* to Yilong Lake.

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