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RESEARCH ARTICLE

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Underwater light attenuation inhibits native submerged plants and facilitates the invasive co-occurring plant *Cabomba caroliniana*

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Abstract

Aim: Decreasing in the diversity and distribution of native submerged plants have been widely observed in recent decades. Global underwater darkening, which is mainly caused by radiation dimming and a decrease in transparency due to, e.g. eutrophication, has emerged as a general trend that strongly hampers the growth of submerged plants in lakes by decreasing the light available for photosynthesis. However, few studies have attempted to compare the responses of native and invasive submerged plants to underwater darkening. In this study, we aimed to compare the effects of light attenuation on the growth and photosynthesis traits of native and invasive submerged plants.

Location: East China.

Method: Through field investigations and a mesocosm experiment, the responses of functional traits of two representative native [water thyme (*Hydrilla verticillata*), Eurasian watermilfoil (*Myriophyllum spicatum*)] and one invasive [Carolina fanwort (*Cabomba caroliniana*)] plant species to various environmental factors, notably to underwater light attenuation, were studied.

Results: Underwater photosynthetically active radiation (PAR) exerted a substantial effect on the relative coverage and abundance of the three studied submerged plants in their natural freshwater habitats. Invasive *C. caroliniana* showed relatively superior

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growth (total biomass and relative growth rate) and photosynthesis traits (maximum quantum yield of photosystem II F_v/F_m, chlorophyll *a* content, chlorophyll *b* content and the ratio of Chl *a* and *b* contents) compared to the two native plants under low underwater PAR conditions. In contrast, under high underwater PAR conditions, *C. caroliniana* showed the opposite response.

Main Conclusions: Light attenuation inhibits the growth of native submerged plants but facilitates the growth of invasive plant species. Restoration of freshwater lakes by reducing deterioration from underwater darkening (for instance, by reducing of external nutrients loading) may therefore constrain the growth and spread of the invasive *C. caroliniana*.

KEYWORDS
aquatic plants, biological invasion, disturbance, freshwater ecosystems, invasive species management, photosynthetically active radiation

1 | INTRODUCTION

The growth of aquatic plants is affected by biotic and abiotic factors, where the latter seem to have a greater effect (Chambers et al., 2008; Lacoul & Freedman, 2006; Santamaría, 2002). Among the abiotic factors, which include light, temperature, water nutrient contents and sediment characteristics, light is normally believed to be the key limiting factor for the growth, reproduction and distribution of aquatic plants (Bornette & Puijalon, 2011; Eller et al., 2015). For instance, Karlsson et al. (2009) found that the light supply rather than the nutrient supply was the limiting factor of biomass production for aquatic plants in small and nutrient-poor lakes, and Su et al. (2016) found that the growth of submerged plants was primarily limited by low-light stress rather than by nutrient availability in shallow Yangtze floodplain lakes. Recently, increased light attenuation due to air pollution and aerosol loadings caused by anthropogenic activities has been observed in China (Li et al., 2017; Qian et al., 2007; Wang et al., 2012; Wild et al., 2005, 2009). In freshwater ecosystems, a decrease in water clarity due to eutrophication and the increased concentration of suspended particulate matter also lead to underwater darkening (Fang et al., 2022; Li et al., 2021). As a result of global changes, more frequent flooding has occurred in China, resulting in decreasing levels of underwater photosynthetically active radiation (PAR) and increasing levels of water turbidity in freshwater ecosystems (Wu & Ding, 2019). Both the annual average available PAR and the transparency of lakes in China have generally shown a clear decreasing trend in the past few decades, being particularly apparent for lakes in East China, which have experienced more significant declines due mainly to the high levels of water and air pollution (Shen et al., 2022; Zhang et al., 2020). This underwater darkening has many adverse effects: it may significantly reduce species abundances, disrupt food chains and change the energy flows and material circulation paths of freshwater ecosystems (Zhang et al., 2020, 2022).

Invasion by introduced species has been listed as one of the five main threats to freshwater biodiversity worldwide (Dudgeon et al., 2006; Geist, 2011). The invasion process can be conceptualized as a series of obstacles imposed by native plant communities that must be overcome by introduced invasive species (Jacobs & Macisaac, 2009). Successful invasion of introduced species may be because the invasive species have superior functional traits (for instance, physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness) that allow them to outcompete native species or a stronger ability to exploit varied and changing resources (van Kleunen et al., 2010). Furthermore, some invasive species may not be evicting native species but may rather be highly tolerant to environmental stresses that are viewed as disturbances (Golivets & Wallin, 2018). For instance, the invasive aquatic plant *Alternanthera philoxeroides* has higher tolerance or resistance to flooding than native congeners (Chen et al., 2013; Wang et al., 2018), and *Eichhornia crassipes* performs better than native co-occurring plants under high nutrient loading conditions in freshwater ecosystems (Huang et al., 2019). However, few studies have attempted to compare the effects of light attenuation on the growth and photosynthesis traits of native and invasive submerged plants.

Submerged plants are viewed as euhydrophytes, as they are the most representative life-form of aquatic plants, live permanently or frequently under water and are vulnerable to light attenuation (Chen et al., 2016; Lu et al., 2013). They are exposed to the greatest threat from decreasing light attenuation, as they represent the primary trophic level of freshwater ecosystems (Bornette & Puijalon, 2011). Previous studies have focused on the effects of decreasing light intensity on submerged plants (Ma et al., 2022; Shao et al., 2017; Wang et al., 2016; Wersal & Madsen, 2013; Yuan et al., 2020). Under these conditions, the photosynthesis of submerged plants is strongly affected; therefore, their growth is substantially reduced, as reflected in changes in their morphological and physiological traits (Chen et al., 2016). In addition, underwater

darkening, which is viewed as a disturbance, may promote invasion by submerged plants that are less sensitive to light conditions. Underwater darkening may facilitate the growth of invasive submerged plants that adapt to light attenuation, and may be more flexible to the changing environment.

Carolina fanwort (*Cabomba caroliniana*) originated in South America (McCracken et al., 2013; Roberts & Florentine, 2022). Because of its beautiful fan-shaped dissected leaves, it was introduced as an aquarium plant and soon escaped as a serious invasive threat to freshwater ecosystems worldwide (Lima et al., 2014; Lu et al., 2018; Roberts & Florentine, 2022). The spread of *C. caroliniana* has caused blockages of waterways and irrigation channels in many areas, resulting in a decrease in the biodiversity of native plants. In China, *C. caroliniana* was first discovered in 1993, probably after its release from aquaria and the ornamental trade (Zhan et al., 2017). Nevertheless, *C. caroliniana* was listed as one of China's most dangerous invasive species in 2016 (Ministry of Ecology and Environment of China (formerly Ministry of Environmental Protection of China), 2016). The potential invasive ability and consequences of its invasion have often been overlooked in the downstream Yangtze River Basin, despite the high richness of invasive plants found in this area (Feng & Zhu, 2010). A field survey of the distribution of aquatic plants in 2018 revealed that *C. caroliniana* was a dominant invasive plant in the lower reaches of the Yangtze River (Huang et al., 2020). Prior to our previous investigations, the species was observed to grow well in low sunlight environments, e.g., in areas shaded by bridges, trees and emergent plants where sunlight is partially blocked. Thus, we inferred that the growth of *C. caroliniana* may be more tolerant to a low light intensity than that of other species.

We conducted a field investigation in 2019 to determine the factors affecting three representative co-occurring plants – two native plants, water thyme (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*), and the invasive plant *C. caroliniana* – and how underwater PAR affects these submerged plant species in their natural freshwater habitats. The native plant *H. verticillata* is extensively distributed in East China and has shown fast growth in ecological restoration projects (Tang et al., 2019; Yin et al., 2019; Yu et al., 2010). *M. spicatum* is a native plant in China and has become invasive in North America (Li et al., 2016; Smith et al., 2021). It has whorled leaves and a high light compensation point (Chambers & Kalff, 1987). We subsequently conducted a mesocosm experiment to elucidate the effect of light attenuation on the three submerged plants and investigate the possible adaptation of submerged plants. Functional traits, including the growth traits of total biomass and relative growth rate (RGR) and the photosynthetic traits of maximum quantum yield of photosystem II F_v/F_m, chlorophyll *a* (Chl *a*) content, chlorophyll *b* (Chl *b*) content and the ratio of Chl *a* and *b* contents, were measured. We hypothesised that (1) light induction exerts a different effect on the native submerged plants, *H. verticillata* and *M. spicatum*, and the invasive *C. caroliniana* and that (2) low light may reduce the growth of *H. verticillata* and *M. spicatum* but facilitate the growth of *C. caroliniana*, which may increase the spread of the plant.

2 | MATERIALS AND METHODS

2.1 | Field investigation

The study area included in this study mainly covers Nanjing, Zhenjiang, Changzhou, Wuxi, Suzhou, Yangzhou, Taizhou and Nantong in Jiangsu Province and Hangzhou, Jiaxing and Huzhou in Zhejiang Province and the mainland Shanghai Municipality (Figure 1). The area, which is among the most developed in China, has experienced a rapid increase in the economy and population since the late 1970s, and many environmental issues have arisen as a result of industrialisation and urbanization (Hou et al., 2020; Zhang et al., 2018).

We conducted field investigations at noon only on sunny days in June and July 2019 in natural freshwater habitats consisting of lakes, ponds, rivers, channels and canals in East China (Figure 1). Sampling quadrats were selected, the dominant plant in each quadrat was *H. verticillata*, *M. spicatum* or *C. caroliniana*, and a polyvinyl chloride frame with an area of $1.0 \times 1.0\ m^2$ was used to mark the boundaries of the quadrats. The geographical coordinates, i.e., longitudes (Long), latitudes (Lat) and altitudes (Alt), of the sampling quadrats were captured with the *GPS status* application for iPhone XR (Apple Inc.). PAR is defined as the solar radiation that plants can use in the process of photosynthesis, and its spectral range is from 400 to 700 nm (McCree, 1971, 1972). The available light in this range is quantified as the photosynthetic photon flux density ($\mu mol\ m^{-2}\ s^{-1}$). Underwater PAR was measured 50 cm below the water surface three times at each sampling site, and we made effort to avoid any interfering reflections or shadows with an Apogee MQ-510 underwater PAR metre (Apogee Instruments, Inc.). Water turbidity (Turb) was determined using a Hach 2100Q portable turbidimeter (Hach Co. Ltd.). Water depth (WD) was measured with a plumb bob. The water properties [pH, dissolved oxygen (DO) and salinity (Sal)] were determined using a YSI multiparameter water quality analyser (YSI Inc.). Water samples were collected in plastic bottles and transferred to the Taihu Laboratory for Lake Ecosystem Research (TLLER) to analyse the nutrient contents in the water [total nitrogen (TN) and total phosphorus (TP)] with a UV–Vis 2450 spectrophotometer (Shimadzu Corp.).

The relative coverage (RC) and relative abundance (RA) of a specific species in each quadrat were measured. The RC was estimated visually, and the RC of a specific species was calculated as the projective coverage of that species divided by the total projective coverage in each quadrat. The coverage is believed to be a key factor influencing the invasiveness of freshwater ecosystems by exotic plants, and it is a useful variable for elucidating the effect of plants on water quality in shallow lakes (Canfield et al., 1985; Jeppesen et al., 1998; Yu et al., 2018). The total number of species was counted, and the

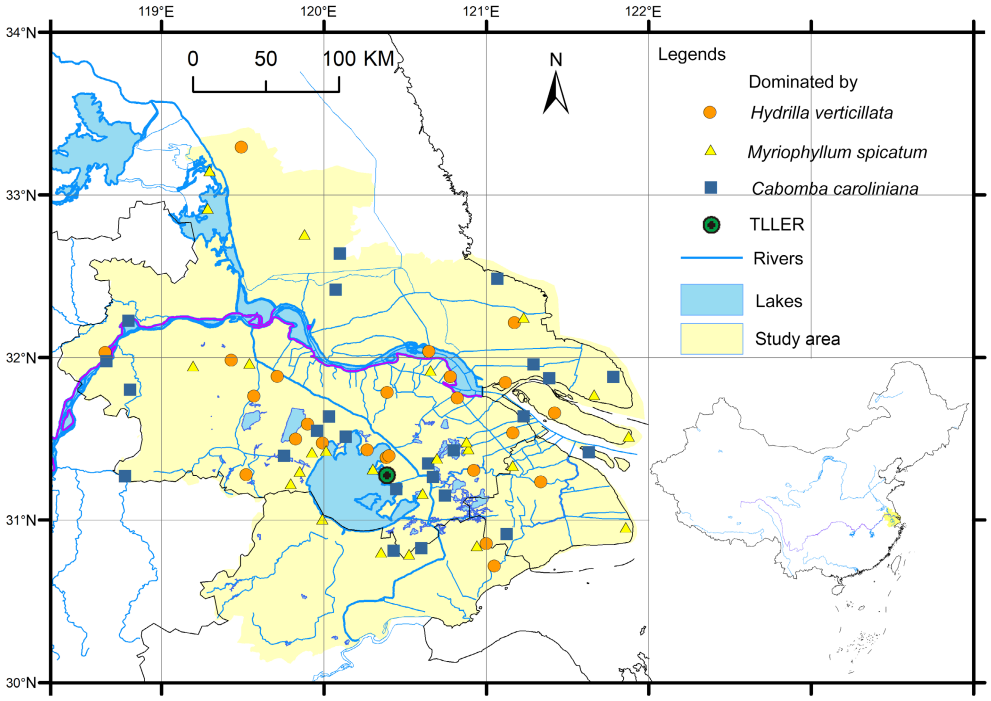


FIGURE 1 Geographical locations of the submerged plant (dominated by *Hydrilla verticillata*, *Myriophyllum spicatum* and *Cabomba caroliniana*) sampling quadrats and the mesocosm experimental site, the Taihu Laboratory for Lake Ecosystem Research (TLLER), East China.

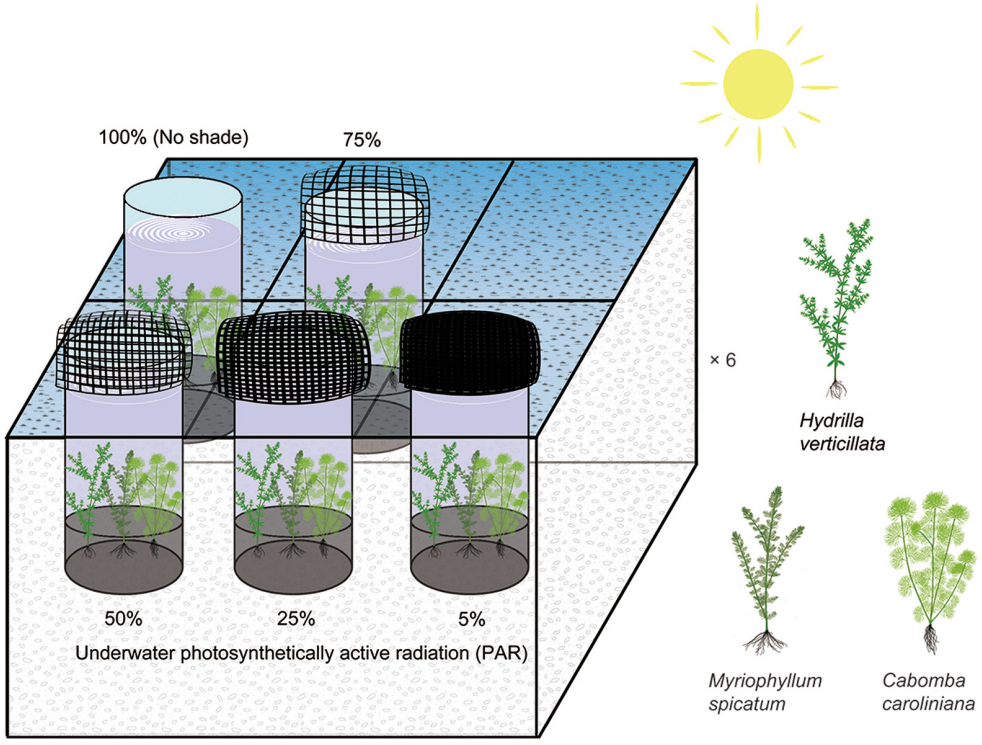


FIGURE 2 Design of the mesocosm experiment. A factorial experiment was established and consisted of different plant species (*Hydrilla verticillata*, *Myriophyllum spicatum* and *Cabomba caroliniana*) combined with different underwater photosynthetically active radiation (PAR) levels [100% (no shade), 75%, 50%, 25% and 5%]. Each experimental setup had six replicates ($n = 6$).

RA of a specific species was calculated as the number of individuals of a specific species divided by the total number of individuals of all the species in each quadrat. The RA of a species is a fundamental aspects of community structure (Molles, 2015). The abundance of invasive species has been shown to be negatively correlated with the alpha diversity and abundance of native species in introduced

ecosystems (Bradley et al., 2019; Lolis et al., 2019). The relative importance value (RIV) of a specific species in a quadrat was calculated as follows:

$$RIV = (RC + RA) / 2.$$

The sample information is listed in the Appendix S1.

2.2 | Experimental design

The mesocosm experiment was conducted at TLLER in 100 L ($h = 0.8$ m and $d = 0.4$ m) cylindrical polyethylene buckets in a pool with a depth of 3.0 m (Figure 2). The polyethylene material can block light from the side of the buckets. We placed all the buckets on steel reinforced bars floating on the surface of the pool, and polypropylene felt cloth was used to cover the top of the buckets when it rained to reduce the effect of the surrounding environment and the temperature change caused by the experimental setup (Figure 2).

Two factors, plant species and light attenuation, were included in the experiment. A decrease in water clarity was not simulated, as maintaining a specific water clarity during the experimental period was too challenging; therefore, we adjusted only light attenuation. Underwater PAR was measured at approximately 12:30 only on sunny days. The light intensity at 50 cm below the water surface was measured, and we used the measured intensity to adjust the underwater PAR levels before the experiment began. We placed multiple black net layers on the top of the buckets to create different underwater PAR levels at 50 cm below the water surface: 100% (no shade), 75%, 50%, 25% and 5% underwater PAR (Figure 2).

Young shoots of the three species were gathered from a pond near TLLER. Then, the shoots were cultivated separately in mud in tanks with water from Lake Taihu for 1 month. Before the experiment, mud was collected from Lake Taihu near TLLER and sieved (with a 40 mesh sieve), and 15 cm of mud was placed in each bucket. Water from Lake Taihu was pumped and filtered with a 64 μm net into each bucket to a depth of 60 cm (measured from the bottom of the bucket). The shoots and roots of three plants (one individual of each species) with similar fresh weights and in good condition were selected for the experiment. One individual of the three plants was planted into the same bucket as one replicate for each underwater PAR treatment on 7 June 2019 (Figure 2). Each underwater PAR treatment had six replicates ($n = 6$). Five extra buckets with one of the three plants were also set up at the same time to measure the initial dry mass when the experiment started after 1 week of cultivation. Although culturing the three species independently is the ideal approach, the results of a previous study (Huang et al., 2021) performed in 2018 showed that competition among the three species under these conditions is relatively low, rendering coculturing acceptable.

After 1 week, the shoots had all survived without aeration, we placed multiple black net layers over the buckets, and the experiment was initiated on 14 July 2019. Five individuals of the three plants with the same experimental setup were collected and dried in an oven for 48 h to measure the initial dry mass. Nineteen sunny days occurred during the experimental period, and only underwater PAR measurements from these sunny days were used in the experiment (Table 1).

TABLE 1 The underwater PAR values measured 50 cm below the water surface in the mesocosm experiment.

	Measured underwater PAR (μmol m^{-2} s^{-1})
100% underwater PAR (No shade)	337 ± 23a
75% underwater PAR	248 ± 21b
50% underwater PAR	151 ± 11c
25% underwater PAR	84 ± 10d
5% underwater PAR	14 ± 2e

Note: Underwater PAR was measured at approximately 12:30 only on sunny days. The data are presented as the means ± SE, and lowercase letters indicate significant differences among the treatment groups ($p < .05$).

Abbreviation: PAR, photosynthetically active radiation.

The experiment ended when the plants in the 5% underwater PAR treatment withered on 26 August 2019. No algal outbreak occurred during the experimental period. The experiment lasted 43 days, after which the plants were harvested by gently removing them from the buckets with shovels and washing them with tap water to remove attached mud. The shoots and roots were separated with a knife and dried in an oven at 60°C for 3 days.

The dominance of *C. caroliniana* in each bucket was calculated as follows:

$$\text{Dominance of } C.\ caroliniana = r_{C.c} / r_{all},$$

where $r_{C.c}$ and r_{all} are the biomasses of *C. caroliniana* and the biomasses of all three species in the same bucket.

The RGR was calculated as follows:

$$RGR\left(\text{mg g}^{-1}\text{ d}^{-1}\right) = \ln\left(r_2 / r_1\right) / \left(t_2 - t_1\right),$$

where r_1 is the initial mass at time t_1, r_2 is the mass at harvest time t_2 and $t_2 - t_1$ is the experimental duration (in this study, $t_2 - t_1 = 43$ days).

Five leaves from each of the three plants were measured after a dark incubation for 20 min (the suggested period is 15–20 min) according to the manual of the handy plant efficiency analyser (PEA) chlorophyll fluorimeter (Hansatech Instruments Ltd.). Initial foliar fluorescence (F_0) and maximum foliar fluorescence (F_m) were measured, and the foliar maximum quantum yield of photosystem II (F_v/F_m) was calculated as follows:

$$F_v / F_m = \left(F_m - F_0\right) / F_m.$$

It is an important index of the quantum efficiency of plant photosynthetic performance, and it is influenced by some stress factors (Demiral & Türkan, 2006; Nobel, 2020).

The contents of Chl *a* and Chl *b* in the third leaf from the apical meristem of each plant of the three species were measured by applying the acetone-ethanol extraction method and were analysed with a UV–Vis 2450 spectrophotometer (Shimadzu Corp.). The ratio of Chl *a* and Chl *b* contents was calculated as follows: ratio of Chl *a* and *b* contents = Chl *a* content/Chl *b* content.

2.3 | Data analysis

All data were tested to determine whether they satisfied the assumptions of a normal distribution (verified by the Shapiro–Wilk test) and homoscedasticity of variances (verified by Levene's test) before conducting the statistical analysis. If the data did not meet these two assumptions, a $\log_{10}(x+1)$ transformation was applied to the data and associated data. Partial least squares path models (PLS-PMs) were constructed to test the effects of geographical variables (Long, Lat and Alt), water properties (WD, pH, DO and Sal), water nutrient contents (TN and TP) and underwater light conditions (PAR and Tur) on the RC and RA of the three plants. PLS-PMs were performed using *R* version 3.6.3 (R Development Core Team, 2020) and the package *plspm* (Sanchez et al., 2015). Nonlinear regression with a Gaussian peak was used to analyse the relationships among the RIVs of the three species with underwater PAR. One-way ANOVA was used to test the difference in the dominance of *C. caroliniana* among the different underwater PAR levels (significance threshold of $p = .05$). Linear mixed models were applied with the plant species and underwater PAR as the fixed factors and the bucket as a random factor to test their effects on plant growth and photosynthetic traits, and post hoc pairwise comparisons of the means were performed to examine the differences between treatments using Duncan's multiple range test at a significance threshold of $p = .05$. The statistical analyses were conducted using SPSS Statistics 26 (IBM Corp.) and SigmaPlot 14 (Systat Software, Inc.) software. Maps were generated using ArcGIS 10.3 (Esri Corp.).

3 | RESULTS

3.1 | Field investigation

Seventy-two aquatic plant quadrats dominated by one of the three plant species (*H. verticillata*, *M. spicatum* and *C. caroliniana*) were collected in East China (Figure 1). The RC of the submerged plant communities was negatively affected by underwater light conditions ($C = -0.83$, $p < .001$) (Figure 3), as were the RAs of the communities

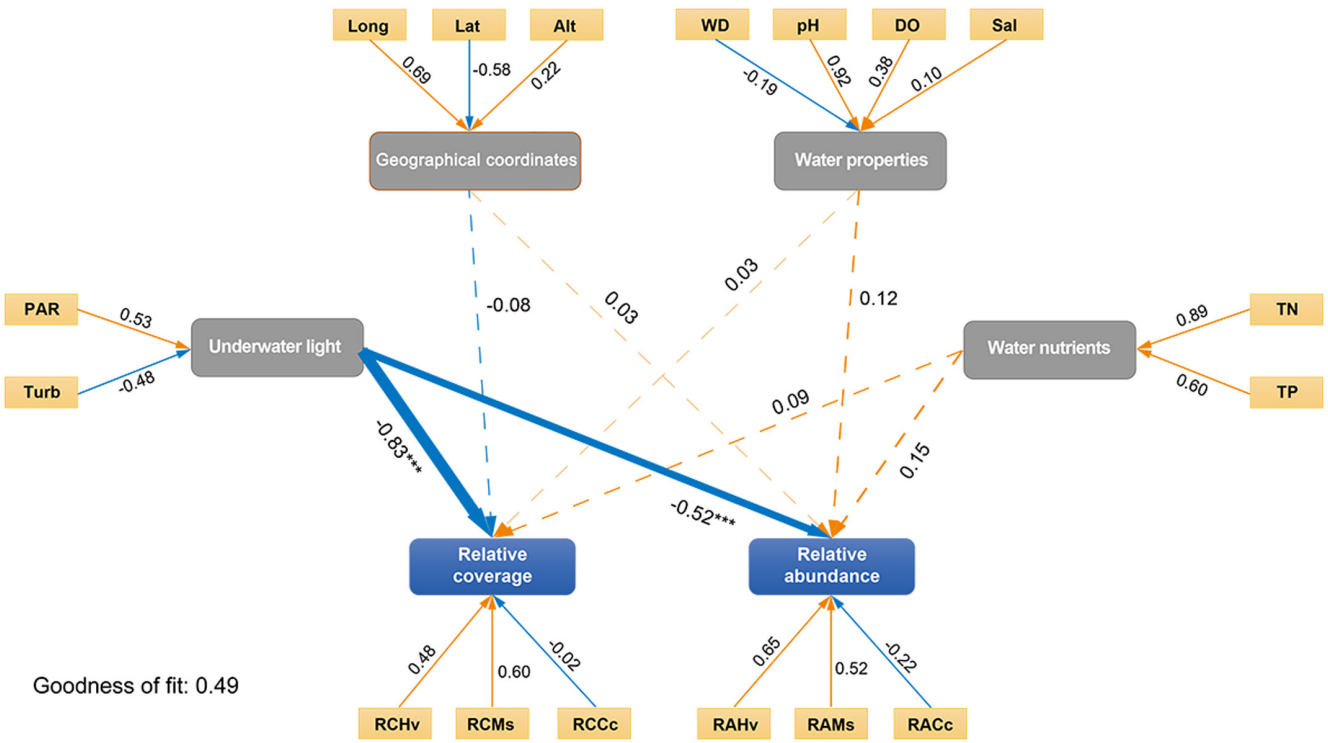


FIGURE 3 Partial least squares path models (PLS-PMs) were constructed to test the effects of underwater light conditions (PAR and Turb), geographical coordinates (Long, Lat and Alt), water properties (WD, pH, Cond, DO and Sal) and water nutrient contents (TN and TP) on the relative coverage (RC) and relative abundance (RA) of the three submerged plants (*Hydrilla verticillata*, *Myriophyllum spicatum* and *Cabomba caroliniana*). The wider arrows indicate stronger path coefficients. The red and blue lines represent positive and negative pathways, and the solid and dotted lines represent significant and nonsignificant correlations, respectively. Significance levels are indicated by asterisks: ***$p < .001$. Reflective latent variables (blue or grey blocks) are indicated by the measured variables (orange blocks), and their respective weights are shown.

($C = -0.52$, $p < .001$) (Figure 3). The underwater PAR (weights of the outer model, $W = 0.53$) contributed positively to the underwater light availability, while Turb ($W = -0.48$) contributed negatively (Figure 3). The geographical coordinates (Long, Lat and Alt), water properties (WD, pH, DO and Sal) and water nutrient contents (TN and TP) exerted positive but insignificant effects on RC (Figure 3). The geographical coordinates (Long, Lat and Alt) had a negative but insignificant effect on the RA, and the water properties (WD, pH, DO and Sal) and water nutrient contents (TN and TP) exerted positive but insignificant effects on RA (Figure 3).

Underwater PAR had the greatest contribution to the RC and RA of the submerged plant communities, and the relationship of the RIVs of the three species with underwater PAR is shown in Figure 4. The *RIV*s of *H. verticillata* and *M. spicatum* displayed an increasing trend with increasing underwater PAR in natural freshwater habitats, which indicated that increasing underwater PAR facilitated the growth of these two native plants and that a relatively high underwater PAR did not threaten their survival in East China (Figure 4). The RIVs of *C. caroliniana* showed an increasing trend with PAR but peaked at an underwater PAR of appr. 200 μmol m^{-2} s^{-1}, followed by a decrease, indicating that a high PAR may inhibit the growth of this species in East China (Figure 4).

3.2 | Experimental results

3.2.1 | Measured underwater PAR values in the mesocosm experiment

Underwater PAR had a significant effect on the RC and RA of the three co-occurring plants in the field investigation. We therefore conducted a mesocosm experiment to elucidate the effect of light attenuation on the three plants, focusing on their adaptation to low light conditions. The measured underwater PAR levels in the different underwater PAR level treatment groups in the mesocosm experiment revealed significant differences in light attenuation among the experimental designs (Table 1).

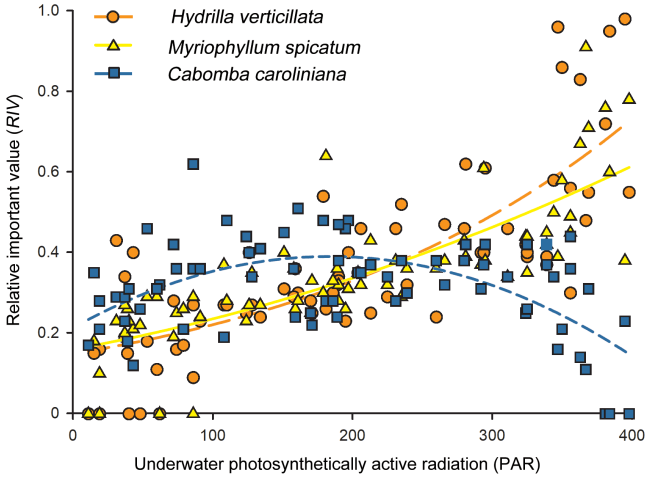


FIGURE 4 Relative importance values (RIVs) of *Hydrilla verticillata* ($r^2 = .619$, $p = .137$), *Myriophyllum spicatum* ($r^2 = .627$, $p = .107$) and *Cabomba caroliniana* ($r^2 = .312$, $p = .101$) in response to underwater photosynthetically active radiation (PAR). The function was created with the Gaussian peak equation ($f(x) = y_0 + a \times \exp(-0.5 \times ((x - x_0)/b)^2)$).

3.2.2 | The effect of light attenuation on different plant species

The two growth traits, total biomass and RGR, differed significantly among the three species ($p < .05$) (Table 2). Underwater PAR also had a significant effect ($p < .05$) on both traits (Table 2), and the interaction effects of plant species and underwater PAR were also significant ($p < .05$) (Table 2).

Except for the Chl *a* content, other photosynthetic traits, including the maximum quantum yield of photosystem II F_v/F_m, Chl *b* content and the ratio of Chl *a* and Chl *b* contents, differed significantly among the three species ($p < .05$), while underwater PAR exerted a significant effect ($p < .05$) on all four photosynthetic traits (Table 2). The interaction between plant species and underwater PAR did not have a significant effect on any of the photosynthetic traits except for F_v/F_m (Table 2).

3.2.3 | Variations in functional traits of submerged plants in response to light attenuation

The highest dominance of *C. caroliniana* was recorded in the 25% and 50% underwater PAR treatments, followed by the 5% and 75% underwater PAR treatments (Figure 5). These results showed that decreasing underwater PAR facilitates the dominance of *C. caroliniana*, but not the dominance of *C. caroliniana* under the extreme 5% underwater PAR treatment.

The growth traits, namely, total biomass and RGR, of all three species showed a similar response to the underwater PAR level (Figure 6a,b). The highest total biomass was recorded for *M. spicatum* in the 100% underwater PAR treatment, followed by *M. spicatum* in the 75% underwater PAR treatment; total biomass then decreased sharply with decreasing underwater PAR for *M. spicatum* (Figure 6a,b). The total biomass and RGR of the native species *H. verticillata* were much lower than those of the other species in response to almost all treatments. *Cabomba caroliniana* exhibited weaker variation with changes in light than the two native species (Figure 6a,b). Thus, compared with *M. spicatum*, it had lower values in the 100% and 75% underwater PAR treatments, whereas it performed better in the 50% and 25% treatments (Figure 6a,b).

The highest level of the photosynthetic trait F_v/F_m was observed for *M. spicatum* in response to the 100% underwater PAR treatment, and the ratio decreased sharply with decreasing underwater PAR (Figure 7a). *Hydrilla verticillata* showed a tendency similar to that of *M. spicatum* (Figure 7a). *Cabomba caroliniana* exhibited a relatively stable fluctuation with lower values than *M. spicatum* in the 100%

TABLE 2 Results of the linear mixed model with plant species (PS) and underwater PAR level (PAR) for the plant growth and photosynthetic traits of *Hydrilla verticillata*, *Myriophyllum spicatum* and *Cabomba caroliniana*.

	Plant species (PS)		Underwater PAR (PAR)		PS × PAR	
	F	*p*	*F*	*p*	*F*	*p*
Growth traits						
Total biomass	71.952	**<.001**	79.992	**<.001**	20.606	**<.001**
RGR	25.537	**<.001**	51.655	**<.001**	6.432	**<.001**
Photosynthetic traits						
F_v/F_m	11.424	**<.001**	60.394	**<.001**	3.617	**.001**
Chl *a*	0.722	.489	12.397	**<.001**	1.058	.402
Chl *b*	4.027	**.022**	8.233	**<.001**	1.010	.436
Ratio of Chl *a* and *b*	3.799	**.027**	20.589	**<.001**	0.964	.471

Note: Significant values ($p < .05$) are highlighted in bold. PS and PAR were applied as fixed factors, and the bucket was applied as a random factor in the linear mixed model.

Abbreviations: Chl, chlorophyll; RGR, relative growth rate.

and 75% underwater PAR treatment groups and higher values in the 50% and 25% underwater PAR treatment groups (Figure 7a).

The level of the photosynthetic trait Chl *a* showed a similar decreasing trend with decreasing underwater PAR levels in all three species (Figure 7b). With the exception of the 100% underwater PAR treatment, the Chl *b* content showed an increasing trend with decreasing underwater PAR levels in all three species (Figure 7c). The ratio of Chl *a* and Chl *b* in the native species (*M. spicatum* and *H. verticillata*) exhibited a relatively sharp decrease with decreasing underwater PAR levels, but a more stable decreasing trend was observed for *C. caroliniana* (Figure 7d).

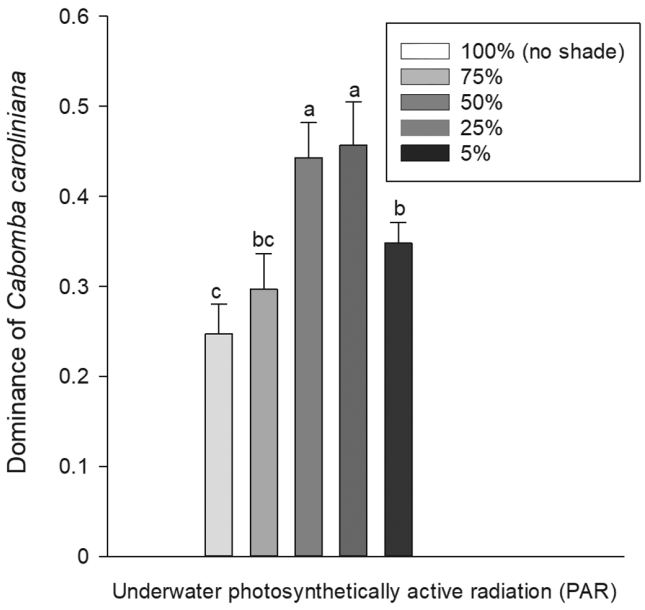


FIGURE 5 The dominance of *Cabomba caroliniana* relative to underwater photosynthetically active radiation (PAR). The values are presented as the means ± SE ($n = 6$). Different lowercase letters indicate significant differences among treatment groups ($p = .05$).

4 | DISCUSSION

In the field investigations, we found that water turbidity and underwater PAR were the main factors affecting the relative coverage and abundance of submerged plants, including two native species, *H. verticillata* and *M. spicatum*, and an invasive species, *C. caroliniana*. Subsequently, we conducted a mesocosm experiment to explore the responses of the functional traits of the three species to different levels of underwater PAR. The performance of *C. caroliniana* was superior to that of the two native species at low underwater PAR, indicating a better ability of this species to attenuate light. However, under extremely low underwater PAR conditions (5% underwater PAR treatment), both the growth and photosynthetic ability of all three plants were severely constrained.

4.1 | The high tolerance of *C. caroliniana* to light attenuation may facilitate its invasiveness under low underwater PAR stress

Photosynthesis is fundamental for the production of plants, and plants can change their photosynthetic pigments to acclimate to environmental changes (Decoteau, 2005). Water bodies have a strong ability to absorb light, which leads to an exponential reduction in the underwater light intensity. Therefore, the light conditions in water bodies are usually insufficient for submerged plants, and light becomes a limiting factor for their growth and distribution. Submerged plants rely on underwater radiation to synthesize photosynthetic pigments, and their biomass and primary productivity are sensitive to light availability (Zhang et al., 2017). Almost all submerged plants have evolved survival strategies as shade plants to adapt to limited light (Bornette & Puijalon, 2011; Chambers et al., 2008). They have relatively low light saturation and compensation points (Santamaría, 2002). The photosynthetic traits of *C. caroliniana* were generally disadvantageous compared to those of *M. spicatum* in response to the high underwater PAR treatments. However, the

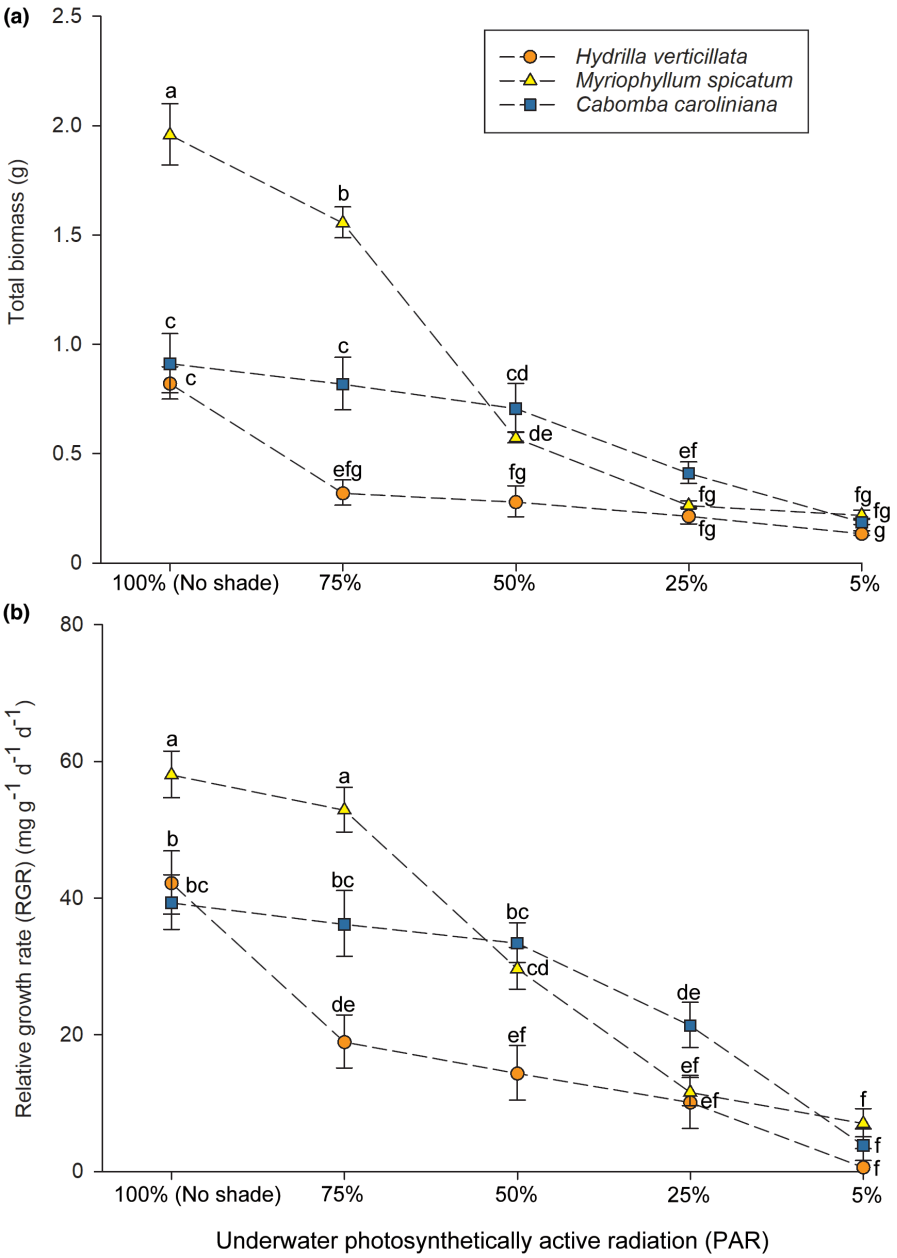


FIGURE 6 Growth traits (a) total biomass and (b) relative growth rate (RGR) of *Hydrilla verticillata*, *Myriophyllum spicatum* and *Cabomba caroliniana* relative to underwater photosynthetically active radiation (PAR). The values are presented as the means ± SE ($n = 6$). Different lowercase letters indicate significant differences among treatment groups ($p = .05$).

performance of *C. caroliniana* was better and more stable than those of *M. spicatum* or *H. verticillata* in response to the low underwater PAR (for instance, 50%, 25% and 5% underwater PAR) treatments. According to a previous study, *C. caroliniana* does not have a better competitive ability than native co-occurring submerged plants (Huang et al., 2021), but it is relatively resistant to herbivory by grass-feeding snails (Huang et al., 2022). In this study, we provide new insights into the possible invasion mechanism of *C. caroliniana* under low underwater PAR levels, which may improve the ability to predict its invasion.

Chambers (1987) concluded that the dominant form in submerged plant communities is the one that best exploits the environment under controlled conditions. Competition among aquatic plants is high since they often form mono-species communities (Engelhardt & Ritchie, 2001). The succession of aquatic plant communities, especially those of submerged plants, is a long-term process. Once formed, a community is difficult to invade; conversely, if invasive plants form a stable community, they become more difficult to remove (Bornette & Puijalon, 2011). Underwater darkening may be considered a disturbance to the growth and photosynthetic capacity of submerged plants (Ma et al., 2022; Xiao et al., 2007). Underwater darkening may result in the loss of native submerged aquatic plants, as these plants are highly adapted to their environment. Under these light attenuation conditions, the native submerged plants did not perform well, as judged both from the results of our field investigation and the mesocosm experiment, thus providing empty niches for invasive species. The expansion of invasive plant species may lead to the invasion of the empty niches left by native aquatic plants requiring high light conditions. Therefore, if underwater darkening continues, submerged plants that are not suitable for or sufficiently tolerant of growth under these conditions may vanish, and plants that are suitable for these

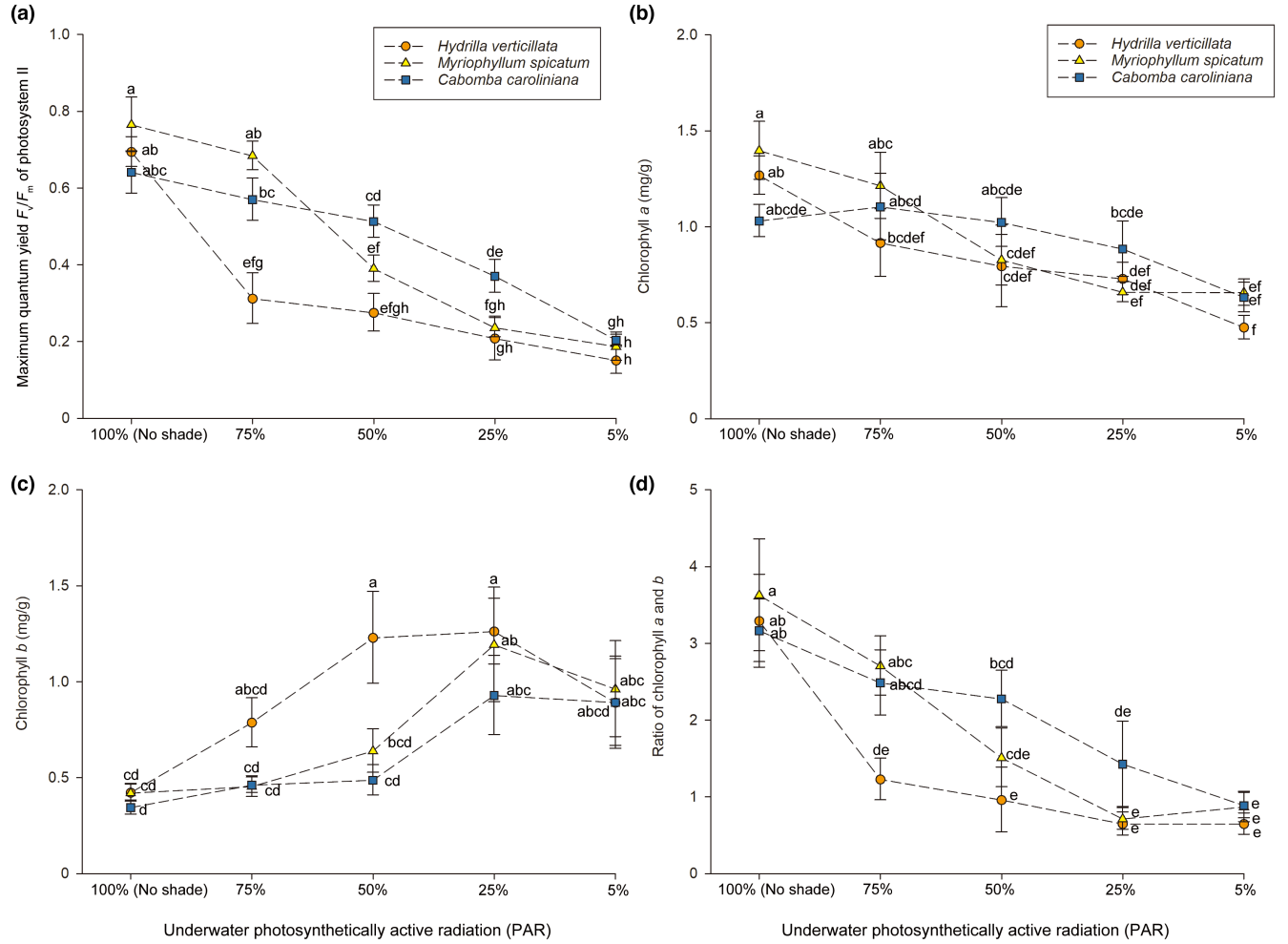


FIGURE 7 The levels of the photosynthetic traits of (a) the maximum quantum yield of photosystem II F_v/F_m, (b) chlorophyll *a* (Chl *a*), (c) chlorophyll *b* (Chl *b*) and (d) the ratio of Chl *a* and *b* of *Hydrilla verticillata*, *Myriophyllum spicatum* and *Cabomba caroliniana* relative to underwater photosynthetically active radiation (PAR). The values are presented as the means ± SE ($n = 6$). Different lowercase letters indicate significant differences among the treatment groups ($p = .05$).

conditions (typically invasive plants, as shown in this study) may prosper. Accordingly, we found that in habitats with a low underwater PAR and high turbidity, *C. caroliniana* often formed monospecies communities, while *C. caroliniana* always co-occurred with native species in habitats with a high underwater PAR and low turbidity. With the increasing trend of radiation dimming and decreasing water clarity, the distribution of *C. caroliniana* may expand.

4.2 | Possible methods for controlling *C. caroliniana* and implications for lake restoration

To date, *C. caroliniana* has become a dominant species in areas of the downstream Yangtze River Basin, such as northern Zhejiang Province, southern Jiangsu Province and parts of Shanghai Municipality, and it has spread even further into the middle and upper reaches of the Yangtze River in China. The restoration of submerged vegetation dominated by invasive plants to the native plant community is a challenge, and only a few lasting successful cases of restoration have been reported thus far. Previous studies, e.g., Schooler (2008), showed that shade can be used to create bare patches in dense *C. caroliniana* infestations, and a 99% shade treatment was suggested to be successful in completely eliminating this plant within 120 days. Nguyen et al. (2021) found that shading from the floating-leaved plant *Nymphoides indica* successfully reduces the growth and flowering of *C. caroliniana*. The 5% underwater PAR treatment used in the present study provided similar evidence. Although the 5% underwater PAR treatment successfully controlled the growth and photosynthesis traits of *C. caroliniana*, it also caused the mortality of other submerged plants. Therefore, shading may not be viewed as an appropriate restoration method.

In China, a motto states that "lucid waters and lush mountains are invaluable assets," and actions have been taken based on this realization; thus, the restoration of freshwater ecosystems has attracted considerable attention, which has led to important action steps. Maintaining water clarity and a low water level is crucial for aquatic plant restoration (Yang et al., 2021). As shown in the present study, the restoration of high underwater PAR conditions does not suit *C. caroliniana*. Therefore, the ecological restoration of aquatic habitats that relies on the reconstruction of aquatic vegetation is

a feasible strategy, but it must be based on habitat transformation. After ecological restoration is completed, water bodies can maintain low turbidity and a high underwater PAR, and natural restoration of aquatic vegetation can be achieved. This restoration may constrain the growth and spread of invasive plants.

5 | CONCLUSIONS

Through field investigations and a mesocosm experiment, the responses of representative native (*H. verticillata* and *M. spicatum*) and invasive (*C. caroliniana*) plants to environmental factors, particularly underwater light attenuation, were studied. We found that light attenuation reduced the growth of native submerged plants but had less of an effect on invasive species. Thus, light attenuation may facilitate the growth and spread of invasive plants, as the disturbance created by light attenuation may be viewed as a resource for the growth of submerged plants. The invasive species *C. caroliniana* is well adapted to light attenuation, indicating that it could spread and become dominant in East China under changing environmental conditions. Our results indicate that if water bodies maintain low turbidity and a high underwater PAR after ecological restoration, the dominance of native aquatic plant vegetation will be achieved, thus constraining the growth and spread of invasive plants.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All relevant data are contained in the manuscript's Appendix S1 and permanently archived at the Dryad Digital Repository (https://doi.org/10.5061/dryad.8w9ghx3r7).

PEER REVIEW

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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