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Plant morphological traits and competition index comparisons of three invasive and native submerged plants

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Abstract – The submerged species Carolina fanwort (*Cabomba caroliniana*) has attracted considerable attention in Lake Taihu Basin (LTB), China. This species was widely used as a garden plant until 2016, when it was identified as invasive. In this study, we conducted a mesocosm experiment to compare the morphological traits, includingtotal dry mass, shoot/root (S/R) ratio, relative growth rate (RGR) and competition index log response ratio (ln *RR*), of *C. caroliniana* and two frequently co-occurring native submerged plants, water thyme (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*). The results demonstrated that *C. caroliniana* did not show more advantageous traits (higher total dry mass, S/R ratio and RGR) or have a lower ln *RR* than *H. verticillata* or *M. spicatum*. We provide a counterexample to commonly accepted thought in which the successful invasion of invasive species may not be explained by outcompeting native plants. Other biotic or abiotic factors that determine the successful invasion of *C. caroliniana* must be studied further.

Keywords: Biological invasion / *Cabomba caroliniana* / competition ability / Lake Taihu Basin

Résumé – Comparaison de leurs caractéristiques morphologiques et de l'indice de compétition de trois plantes submergées envahissantes et indigènes. L'espèce submergée « éventail de Caroline » (*Cabomba caroliniana*) a suscité une attention considérable dans le bassin du lac Taihu (LTB), en Chine. Cette espèce a été largement utilisée comme plante de jardin jusqu'en 2016, date à laquelle elle a été identifiée comme envahissante. Dans cette étude, nous avons mené une expérience en mésocosme pour comparer les caractéristiques morphologiques, y compris la masse sèche totale, le rapport pousse/racine (S/R), le taux de croissance relatif (RGR) et le rapport logarithmique de réponse de l'indice de compétition (ln *RR*), de *C. caroliniana* et de deux plantes submergées indigènes fréquemment co-occurrentes, L'hydrille verticillée (*Hydrilla verticillata*) et le myriophylle à épi (*Myriophyllum spicatum*). Les résultats ont démontré que *C. caroliniana* ne présentait pas de caractéristiques plus avantageuses (masse sèche totale, rapport S/R et RGR plus élevés) ou avait un ln *RR* plus faible que *H. verticillata* ou *M. spicatum*. Nous fournissons un contre-exemple à la pensée communément admise selon laquelle le succès de l'invasion d'espèces envahissantes peut ne pas s'expliquer par la supplantation des plantes indigènes. D'autres facteurs biotiques ou abiotiques qui déterminent le succès de l'invasion de *C. caroliniana* doivent être étudiés plus avant.

Mots clés : Invasion biologique / *Cabomba caroliniana* / capacité de compétition / bassin du lac Taihu

1 Introduction

With the development of economic globalisation, exchanges among different countries and regions have become more frequent, and an increasing number of introduced species have been intentionally or unintentionally brought into new areas (Xu *et al.*, 2006; Hussner *et al.*, 2017; Wu and Ding, 2019). Successful invasive species constitute a minority of introduced species (Nentwig, 2008). However, they have resulted in reduced abundance and diversity of native species in invaded natural habitats and cause harm to human society (Lowe *et al.*, 2000; Goodenough, 2010; Vilà *et al.*, 2011;

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Reshi *et al.*, 2013). Invasive aquatic plants are strong competitors (Lacoul and Freedman, 2006). The successful invasion of an invasive species depends on its specific traits (for instance, functional traits), and successful invaders may have advantageous traits over native species. This thought dates back to *The Genetics of Colonizing Species* by Baker, who is a pioneer in invasion biology (Baker and Stebbins, 1965). Invasive species, normally prone to exhibiting advantageous functional traits over native species, can change the native plant structure and reduce diversity via out competing these plants and/or interfering in competition to exclude native species in biological communities (Hamilton *et al.*, 2005; van Kleunen *et al.*, 2010a; Caplan and Yeakley, 2013; Mathakutha *et al.*, 2019). van Kleunen *et al.* (2010b) also showed that invasive plant species have significantly higher trait values than non-invasive species in a meta-analysis study. In freshwater ecosystems, invasive aquatic plants cause the extinction of native aquatic plants, loss of fish abundance and reduction of benthos, which significantly change freshwater ecosystems (Gallardo *et al.*, 2016; Michelan *et al.*, 2018; Wu and Ding, 2019). Nearly 24% of the plants listed in the *100 of the World's Worst Invasive Alien Species* by the International Union for Conservation of Nature (IUCN) were aquatic plants, which is disproportionate to the area of freshwater habitats (less than 6%) on the earth (Zedler and Kercher, 2004).

By the end of 2016, more than 600 invasive species had been found in China, including nearly 50 of the species identified in the above list (Zhan *et al.*, 2017). The flourishing breeding industries for red swamp crayfishes (*Procambarus clarkia*) and hairy crabs (*Eriocheir sinensis*) have introduced a large number of highly palatable plants, many of which are invasive (Jiang *et al.*, 2011). Additionally, with the increasing prosperity of the aquarium market, a variety of ornamental aquatic plants have been introduced into China (Wang *et al.*, 2016; Yu *et al.*, 2018). Among these, the invasive plant Carolina fanwort (*Cabomba caroliniana*) has been a dominant submerged plant in some areas of the Lake Taihu basin (LTB) (Huang *et al.*, 2020). This plant has only recently been included in the *List of Invasive Species in China* (Ministry of Ecology and Environment (MEE), 2016). Before being listed, it was widely used as a garden wetland plant in ecological restoration, especially in the area downstream of the LTB. Its invasiveness has gained considerable attention; however, it seems there is no conclusion regarding how this invasive plant is successfully invading China.

To our knowledge, no previous competitiveness comparisons have been conducted among *C. caroliniana* and co-occurring native plants. In this study, the morphological traits (total dry mass, shoot/root (S/R) ratio, relative growth rate (RGR) and competitive ability index log response ratio (ln *RR*)) of *C. caroliniana* and two co-occurring species (water thyme (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*)), were evaluated in a mesocosm experiment. As competition will hamper the biomass and growth of plants, comparisons of these associated traits will reflect the relationship among plants (Grotkopp *et al.*, 2002; Wang *et al.*, 2008b; Dawson *et al.*, 2012; Shen *et al.*, 2019). Two questions were posed: (1) Does *C. caroliniana* have more advantageous traits than native species? (2) Can *C. caroliniana* out compete native counterparts within the invaded area?

2 Materials and methods

2.1 Study area

The mesocosm experiment was conducted in the Taihu Laboratory for Lake Ecosystem Research (TLLER) (31.4198°N, 120.2159°E), which is one of the national field stations of the Chinese National Ecosystem Research Network (CNERN) in Wuxi City, Jiangsu Province. Downstream of the Yangtze River, the LTB is one of the most prosperous areas in China. It contains 1/22 of the total population but contributed nearly 1/10 of the gross domestic product (GDP) of China in 2018 (Taihu Basin Authority (TBA), 2019).

2.2 Plant materials

Three commonly co-occurring submerged plants in the LTB, the native *H. verticillata*, *M. spicatum*, and the invasive *C. caroliniana*, were used in this study. Before the experiment began, we conducted an aquatic plant field reconnaissance investigation in the LTB. Sampling quadrats with an area of 1×1 m^2 were randomly selected. The plant coverage was calculated as the species coverage/all species coverage ratio in a sampling quadrat. The results showed that within 1×1 m^2 mature mono-species community quadrats, when the plant coverage was 95% (in freshwater ecosystems, it is rare for plants to show 100% coverage, as gaps among species always exist), the average density of *H. verticillata* was 42/m^2 (estimated density was 44/m^2 for 100% coverage), the average density of *M. spicatum* was 32/m^2 (estimated density was 34 for 100% coverage), and the average density of *C. caroliniana* was 35/m^2 (estimated density was 37/m^2 for 100% coverage). The same plant density was used as high-density treatment (H2M2C2) accordingly to the experiment bucket (basal area = 0.16 m^2 and h = 0.76 m) in the experiment (Tab. 1). Half of the high densities were used as medium-density treatment (HIM1C1) (Tab. 1). In the mono-species treatments (H1, M1 and C1), one shoot of each species was cultivated individually, and for low-density treatment, one shoot of these species was cultivated together (Tab. 1).

2.3 Experimental design

Young shoots of the three species were collected and cultivated at the TLLER for one month. The experiment began on June 20th, 2018. Two factors were set in the experiment: the plant species and density. At the beginning of the experiment, 20 cm of lake sediment from the Lake Taihu was collected, mixed, and then added to each bucket. The lake water was filtered with a sieve and then poured into the buckets to 40 cm (measured from the bottom of the bucket). The lake water parameters were total dissolved nitrogen (TDN) = 0.71 ± 0.11, total dissolved phosphorus (TDP) = 0.052 ± 0.007, dissolved oxygen (DO) = 4.26 ± 0.67 mg/L, conductivity = 395 ± 46 μS/cm and pH = 7.93 ± 1.6 (mean ± S.D.) during the experimental period. The TDN and TDP were measured once aweek, and the other parameters were measured twice a week. Young shoots measuring 20–25 cm from the three species were selected and planted in the

Table 1. Plant density calculation for the mesocosm experiment.

	CK			Low-density	Medium-density			High-density
	H1	M1	C1	H1M1C1	H2M2	M2C2	H2C2	H2M2C2
Hydrilla verticillata	1	0	0	1	2	2	0	2
Myriophyllum spicatum	0	1	0	1	2	0	2	2
Cabomba caroliniana	0	0	1	1	0	2	2	2
Total plants	1	1	1	3	4	4	4	6
Total densities (/m^2)	6	6	6	19	25	25	25	38

Two factors were established: the plant species (*Hydrilla verticillata, Myriophyllum spicatum* and *Cabomba caroliniana*) and the density. In the mono-species treatments (H1, M1, and C1), one shoot from each species was transplanted individually into mesocosms. In the mixed treatments, shoots from the three plant species were transplanted and received mixed treatments (low-density: H1M1C1; medium-density: H2M2, M2C2, and H2C2; and high-density: H2M2C2). The low, medium and high plant densities of the three plant species were evaluated during an aquatic plant field investigation within 1×1 m^2 mono-species quadrats in the Lake Taihu drainage basin. The total densities were calculated according to the bucket basal area (0.16 m^2).

Table 2. Two-way ANOVA results regarding the plant species and density for the plant total biomass, shoot/root (S/R) ratio, relative growth rate (RGR), and competition index ln *RR* during the experiment.

	Plant species			Plant density			Species × density		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Total biomass	2	328.409	<**0.001**	3	8.273	<**0.001**	6	1.099	0.373
S/R ratio	2	8.771	<**0.001**	3	1.077	0.365	6	6.253	<**0.001**
RGR	2	217.639	<**0.001**	3	10.032	<**0.001**	6	3.368	**0.006**
ln *RR*	2	12.061	<**0.001**	3	11.685	<**0.001**	6	4.072	**0.002**

Significance levels of $P < 0.05$ are highlighted in bold.

buckets (Tab. 1). Each treatment had five replicates ($n = 5$), and 40 buckets were used. After one week, all the plants survived, and appeared to have acclimated to the new environment (Li *et al.*, 2015; Li *et al.*, 2016; Huang *et al.*, 2018). The water level in each bucket was then increased to 75 cm (measured from the bottom of the bucket). The plants were harvested when flower buds of *M. spicatum* and *H. verticillata* appeared, which indicated that they had reached the end of vegetative growth on August 4th, 2018.

The plant shoot/root (S/R) biomass ratio was calculated as follows:

S/R ratio = shoot biomass/root biomass;

The relative growth rate (RGR) was calculated as follows (Gillard *et al.*, 2017):

RGR ($mg \cdot g^{-1} \cdot d^{-1}$) = $(\ln r_2 - \ln r_1)/(t_2 - t_1)$;

where r_1 is the initial dry plant biomass at initial time t_1; and r_2 is the dry plant biomass at harvest time t_2. In this study, $t_2 - t_1 = 45$ d.

The competition index log response ratio (ln *RR*) was calculated as follows (Goldberg *et al.*, 1999; Hedges *et al.*, 1999; Weigelt and Jolliffe, 2003):

$$\ln RR = \ln (r_{mono}/r_{mix})$$

where r_{mono} represents the total dry mass of a single plant in a bucket (in the absence of competition, namely, H1, M1 and M1 in this study) and r_{mix} represents the average total dry mass of a plant in a bucket containing more than one plant. A higher ln *RR* indicates more intraspecific and/or interspecific competition intensity.

2.4 Data analysis

A two-way ANOVA was applied with plant species and density as the primary factors to test their effects on plant traits in the competition experiment. When a significant treatment effect was detected, post hoc pairwise comparisons of the means were performed to examine the differences between treatments using Duncan's multiple range test for multiple comparisons.

3 Results

The three species, *H. verticillata*, *M. spicatum,* and *C. caroliniana*, exhibited significant differences ($P < 0.05$) in the plant total dry mass, S/R ratio, RGR and ln *RR*, which indicates the occurrence of significant differences among these plant species (Tab. 2). The plant density had a significant influence ($P < 0.05$) on all the plant trait values except for the S/R ratio (Tab. 2), and the interaction between the plant species and density was significant for all the measured plant trait values except for the total dry mass (Tab. 2).

3.1 Morphological traits

The native plant *M. spicatum* showed a relatively higher total dry mass in the mono-species treatment M1 and low-density treatment H1M1C1 compared with the other

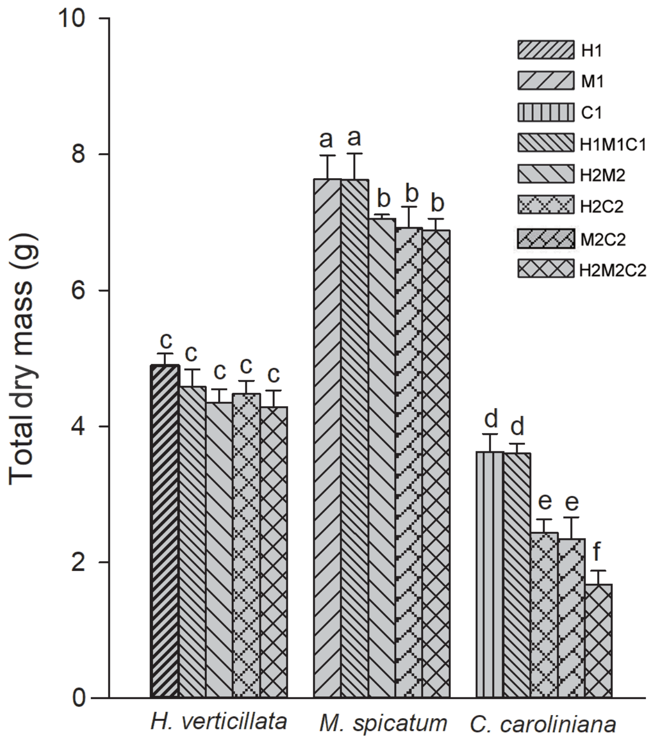

Fig. 1. The plant trait total dry mass of different treatments of *Hydrilla verticillata, Myriophyllum spicatum*, and *Cabomba caroliniana* in the experiment. The values are the means ± SE. Different lowercase letters indicate significant differences among treatments.

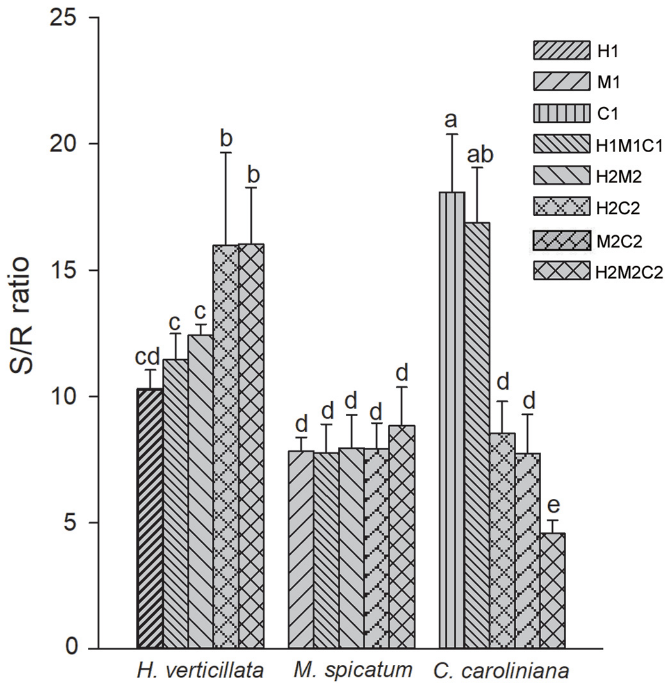

Fig. 2. The Plant trait shoot/root (S/R) ratio of different treatments of *Hydrilla verticillata, Myriophyllum spicatum*, and *Cabomba caroliniana* in the experiment. The values are the means ± SE. Different lowercase letters indicate significant differences among treatments.

treatments. The total dry mass for the native plant *H.verticillata* did not show significant differences, but a decreasingtrend was detected for the invasive plant *C. caroliniana* (Fig. 1).

The highest S/R ratio was obtained for the no competition treatment C1, namely, the treatment that involves one *C. caroliniana* plant, and it decreased with an increase in the plant density (Fig. 2). Conversely, the S/R ratio increased with an increase in plant density for *H. verticillata*, and *M. spicatum* showed a relatively stable fluctuation (Fig. 2).

Myriophyllum spicatum had the highest RGR among all the treatments, followed by *H. verticillata*, while *C. caroliniana* showed a decreasing trend with increasing plant density (Fig. 3).

3.2 Competition intensity

The competition intensity, as measured by the competition index ln *RR,* showed a similar trend among the three plant species (Fig. 4). *Cabomba caroliniana*, as well as the other two plant species had the highest value for the high-density treatment H2M2C2, followed by the medium-density treatments M2C2 and H2C2, while the value for the low-density treatment H1M1C1 was the lowest (Fig. 4).

4 Discussion

4.1 The successful invasion of *C. caroliniana* may not be caused by outcompeting native species

In this study, we found that invasive *C. caroliniana* did not show more advantageous traits or a lower competition index than those of the native *H. verticillata* or *M. spicatum* of the same life-form. The three submerged species can coexist at low density, but high density will lead to competition and result in the inhibition of *C. caroliniana.* This result contradicted previous findings showing that invasive species had more advantageous traits or a higher competitive ability than native species.

As primary producers, biomass accumulation is perhaps the most important manifestation of biological vegetative growth of aquatic plants (Fan *et al.*, 2015; Dalla Vecchia *et al.*, 2020). In this study, *C. caroliniana* did not show a higher total dry mass and a decreasing trend when the density of its native counterparts *M. spicatum or H. verticillata* increased, which indicates that the plant may not win competition by showing high biomass production.Biomass allocation is an adaptive strategy developed by plants in response to ecological factors (Barrat-Segretain, 2001; Wang *et al.*, 2008b). Although *C. caroliniana* have the highest S/R ratio in mono-species treatment C1 (Fig. 2), it shows a decreasing trend when plant density increases, which may indicate that the shoot growth of the plant is suppressed by the two other species while the root is less affected.

Competition is the most common negative interaction among different plants; it is a mutual relationship between two or more plants when the required environmental resources or space are relatively insufficient (Goldberg *et al.*, 1999). Some plants are more efficient in obtaining resources or can occupy more space, thus limiting the survival of other plants (Weigelt and Jolliffe, 2003). Normally, invasive plants are believed to have a higher RGR (Richards *et al.*, 2006; Dawson *et al.*, 2011).

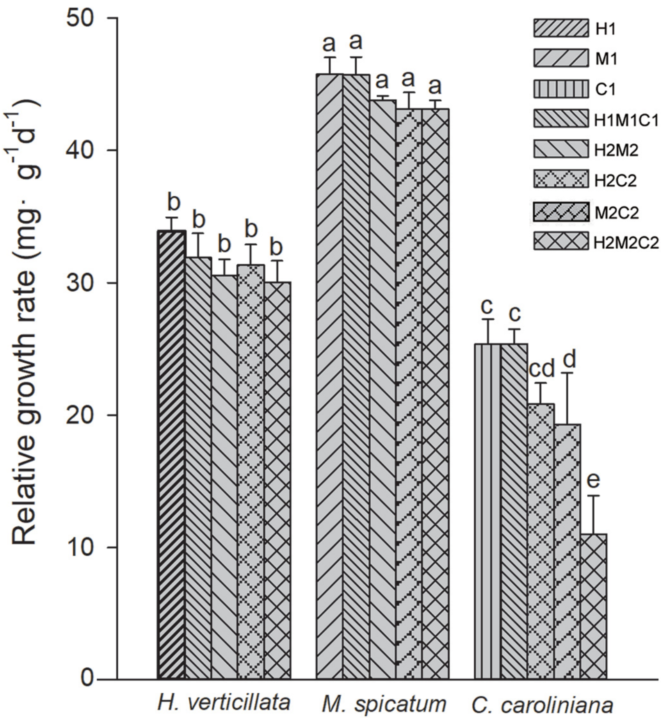

Fig. 3. The plant trait relative growth rate (RGR) of different treatments of *Hydrilla verticillata, Myriophyllum spicatum*, and *Cabomba caroliniana* in the experiment. The values are means ± SE. Different lowercase letters indicate significant differences among treatments.

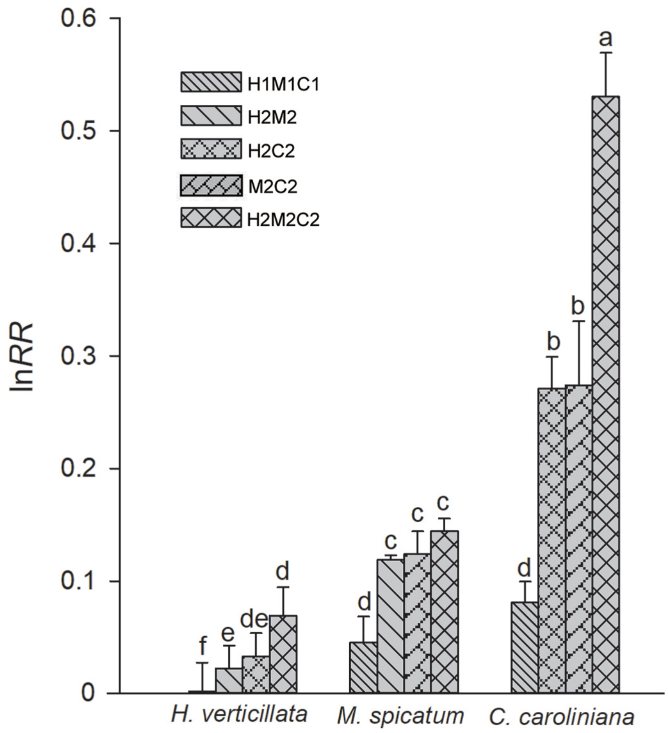

Fig. 4. The plant trait competition index log response ratio (ln *RR*) of different treatments of *Hydrilla verticillata, Myriophyllum spicatum*, and *Cabomba caroliniana* in the experiment. The values are the means ± SE. Different lowercase letters indicate significant differences among treatments.

A recent study also showed that intrinsic growth rates (similar to RGR) are more important than competitive ability, as introduced plants were shown to have higher intrinsic growth rates than those of native plants (Zhang and van Kleunen, 2019). However, we did not record this tendency in *C. caroliniana* (Fig. 4). The less advantageous traits of *C. caroliniana* may indicate that the successful invasion of this plant was not supported by directly outcompeting native plants. This result emphasised its weak competitive ability in invaded habitats, which indicates that other factors, biotic or abiotic factors, affecting the successful invasion of this species should be considered.

4.2 Implications for the control of invasive submerged plants

Submerged plants are probably the most important group of aquatic plants, as they provide the fundamental functions and structures of freshwater ecosystems (Scheffer, 2004; Lacoul and Freedman, 2006). As *C. caroliniana* has been a successful invader in China, it has caused serious and widespread effects (Liu *et al.*, 2018). It seems that no successful removal measures have been identified for the plant, and the only proven successful method is manual removal; during this process, the plant is easily broken into fragments and washed away with the water flow (Fig. 5). Under certain conditions, new populations can be colonized, which may lead to new populations (Ørgaard, 1991; Schooler *et al.*, 2006; Jacobs and Macisaac, 2009; Lima *et al.*, 2014; Bickel, 2015, 2017; Scheers *et al.*, 2019). A realistic and feasible control method for this plant seems difficult.

Myriophyllum spicatum is the most studied aquatic plant species in the scientific literature (Dalla Vecchia *et al.*, 2020). It is a native plant in China but an invasive plant in other countries, especially North America (Gassmann *et al.*, 2006; Li *et al.*, 2016; Hussner *et al.*, 2017; Smith *et al.*, 2021). A large ecological amplitude,low palatability, high nutrient-capturing ability and diverse mechanisms of propagation (seed, rhizome production, and stem segment) enable colonization by this species (Wang *et al.*, 2008a; Bosch *et al.*, 2009; Li *et al.*, 2015; Yu *et al.*, 2016; Son *et al.*, 2017). In this study, we showed that *M. spicatum* has relatively higher values for certain traits and competitive abilities than *C. caroliniana* which may indicate that it is an already quite aggressive species. Other traits of this species and their responses to environmental factors, as well as those of other plant species and herbivores remain to be investigated.

Hydrilla verticillata is native to Asia and is a successful invasive submerged plant throughout the world (Bellinger and Davis, 2017). This plant is adapted to various environmental conditions and has a unique C4 photosynthesis mechanism and a broad ecological amplitude, which causes the suppression of the native aquatic plant community (Bowes *et al.*, 2002; Sousa, 2011). It has been attempted but found to be ineffective as a biological control method for *C. caroliniana* (Schooler *et al.*, 2012). Thus, conducting common-garden experiments with the three plants in invaded and non-invaded areas may be helpful for understandingthe invasion and control of these plants.

Fig. 5. The manual removal of *Cabomba caroliniana* in a river channel (31.4224°N, 120.2165°E) near TLLER in the Lake Taihu Basin. The removal process can produce plant stem fragments (image in the top left corner). Both photographs were taken by the first author.

5 Conclusions

In this study, we conducted a mesocosm experiment to evaluate the morphological traits and competitive ability of the invasive plant *C. caroliniana* and two of its commonly co-occurring native submerged plants *H. verticillata* and *M. spicatum*. In total, *C. caroliniana*did not show more advantageous traits. Thus, we provide a counterexample in which the successful invasion of a submerged species may not be explained by successful competition over native plants. Other biotic or abiotic factors should be explored to explain the widespread distribution of this invasive species.

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