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Response differences of *Eichhornia crassipes* to shallow submergence and drawdown with an experimental warming in winter

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Abstract *Eichhornia crassipes* is a noxious weed and is cold sensitive. Water level treatments may affect its overwintering and regrowth capability during warming winter. To test this hypothesis, an experiment was conducted to analyze the effects of different water levels on the survival rates and regrowth of *E. crassipes* under experimental warm winter conditions. Three water levels were set up including drawdown with rooted, shallow submergence with rooted and floating. Regrowth characters including number of ramets, *F*v/*F*m, biomass and biomass allocation were surveyed. The results showed that warming significantly increased survival, ramet numbers and the biomass of plants. Warming also significantly increased *F*v/*F*m in drawdown plants. Water level only impacted plants under warming conditions. Compared to floating plants, drawdown significantly decreased survival but increased total biomass, while submergence led to 100 % survival, significantly higher ramet numbers and increased total biomass. In terms of biomass allocation, the effects of warming were similar for drawdown and submergence cases; it resulted in increased shoot biomass allocation and a lower root mass ratio. Warming only significantly increased the stem mass ratio of floating plants. Our findings suggested that warming help *E. crassipes* successfully overwinter and regrow during the next growing season. Drawdown or shallow submergence cannot effectively control this species but rather promotes its regrowth during warm winters. Thus, this species has the potential to spread with warm winters and frequent water level fluctuations caused by future climate change.

Keywords Invasive · Water level fluctuation · Overwinter · Regrowth · Warming winter · Survival

Introduction

Climate change and invasive species are two of the most pervasive aspects of global environmental change (Rahel and Olden 2008). Over the past 100 years, the mean surface temperature on the earth has increased by 0.6 % and it is estimated to increase by another 3 °C by 2100 (IPCC 2007). Global warming has enabled alien species to successfully spread into new areas where they previously could not survive or reproduce (Hellmann et al. 2008; Walther et al. 2009). In general, warming has been most significant in the winter season (Houghton et al. 1996; McGrath et al. 2013). For example, the increase in the mean temperature was the highest during the winter than other seasons in China from 1951 to 2001; During this time, mean temperatures rose 0.36 °C every

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decade, and this significant increase in winter temperatures will continue in the twenty-first century (Ding et al. 2007). Furthermore, the previous study found that winter warming facilitates the spread of invasive species (Stachowicz et al. 2002). On the other hand, the geographic distribution of some plants is currently limited by cold temperature; if warmer winter temperatures allow plants to overwinter, management will need to be more aggressive and sustained and thus will likely be more expensive (Hellmann et al. 2008).

Global warming could have a significant impact on local and regional climatic regimes, which could in turn impact hydrological cycles leading to more intense frequent floods and droughts (Arnell and Reynard 1996; Allen et al. 2001). Drawdown and submergence will occur more frequently in the future due to climate change. Aquatic macrophytes growing in the littoral zone are sensitive to changes in the water regime (Wantzen et al. 2008). Drawdown and submergence may greatly influence the distribution, density and species composition of aquatic macrophyte communities by promoting or prohibiting survival and growth (Cooke 1980; Valk and Davis 1980; Turner et al. 2005; Fan et al. 2015). However, species have different tolerances to water level disturbances (Schooler et al. 2010), which is species specific. Therefore, more research is needed to understand the effects of winter drawdown and submergence on aquatic macrophytes, especially on invasive macrophytes.

Eichhornia crassipes (Mart.) Solms is a mat-forming, floating aquatic plant native to tropical South America; however, it currently occurs in subtropical and tropical regions worldwide (Gopal 1987; Madsen et al. 1993). Furthermore, it is one of the world's most invasive aquatic plants and is known to have significant negative ecological and socioeconomic impacts (Villamagna and Murphy 2010). Previous studies reveal that the regrowth of *E. crassipes* is inhibited by low winter temperatures (Owens and Madsen 1995); however, the survival rate of this species significantly increases with warmer winter temperatures increasing 1–3 °C compared natural air temperature (You et al. 2013), with the reason that warm winters will allow it to avoid the severe cold; thus, the species is likely to successfully overwinter and expand beyond the subtropical regions in the future (Hellmann et al. 2008; Rahel and Olden 2008; Yang and Everitt 2010). To address the problems, such an expansion will cause, and effective management programs are needed. Mechanical, chemical and biological control methods are commonly used to control this species, but no single method is suitable for all situations (Gopal 1987; Harley 1990; Heard and Winterton 2000; Villamagna and Murphy 2010). The most appropriate management strategy is clearly dependent on how *E. crassipes* responds to different environments (Wilson et al. 2005).

Though *E. crassipes* is a free-floating aquatic macrophyte, it is also occasionally found in wetland situations, such as when it is stranded on mud and appears rooted (Barrett 1980; Madsen et al. 1993; Yang and Everitt 2010). For example, rooted *E. crassipes* was common due to drawdown and seed germination in mud in southern China (Ren et al. 2004; Fan et al. 2013); *E. crassipes* plants were also found rooted on the shore edge of Lake Naivasha's littoral zone (Njambuya and Triest 2010). The free-floating macrophyte assimilates nutrients from the water, while rooted macrophytes mainly obtain nutrients from sediment (Carignan 1982; Barko et al. 1991; Wetzel 2001). Therefore, nutrients in the substrate may influence the survival and growth of *E. crassipes* (Fan et al. 2013; You et al. 2013). With climate change induced fluctuations in water levels, rooted *E. crassipes* now encounters flooded and drawdown conditions and inevitably becomes completely submerged. For example, the overwinter *E. crassipes* rooted on the shore edge of Liangzi Lake were submerged on January 2013, after increasing water level caused by precipitation. Whether these changes in water level inhibit or enhance *E. crassipes* growth and spread is unknown, especially for rooted *E. crassipes*.

Herein, we conducted an experiment to examine the survival, growth and biomass allocation of *E. crassipes* in response to three warm winter water levels in order to test the following hypotheses: (1) Warm winter plants and natural winter plants have different responses to the same water level treatment; (2) Rooted plants show greater performance than floating plants; (3) Drawdown but not submergence would inhibit the plant's survival and regrowth.

Materials and methods

Study site

The experiments were conducted in the National Field Station of Lake Ecosystem of Liangzi Lake, China (30°5′–30°18′N, 114°21′–114°39′E). The climate of this region is a typical subtropical climate, and average winter temperatures range from 3.0 to 7.0 °C (Liu and Yu 2009).

Experimental design

In early December 2013, 500 healthy *E. crassipes* plants were collected from Liangzi Lake and cultivated in concrete pools. 15 days later, 192 plants with a consistent size were chosen (mean fresh biomass 21.6 ± 1.9 g) for further experimentation. The experiments included three water treatments drawdown (where plants were rooted in the lake mud without water), submergence (where plants were firmly rooted in the lake mud and submerged in shallow water 15 cm deep) and floating (where plants were free-floating on water 50 cm deep). The stem bases of all rooted plants were not buried (Fig. 1). Four plants were planted in one aquarium (115 length × 60 width × 60 height cm). Six replicates of each water level treatment were conducted in separate aquariums ($n = 6$). A total of 36 aquariums and 144 plants were used; 18 of these were placed in a greenhouse to simulate the winter warming trend and 18 were placed on an outdoor terrace for the natural, or non-warming treatment. As a result, there were a total of six unique treatments in the experiment. The temperature near the stem base was measured three times a day (at 7a.m., 12 p.m. and 6 p.m.) every 5 days. The mean temperature in the greenhouse (12.4 °C) was significantly higher than that outdoors (5.5 °C) from December 2013 to February 2014 (one-way ANOVA, $F = 40.452$, $P < 0.001$) (Fig. 2). There were no significant differences between the temperatures in the greenhouse and outdoors from March to June (one-way ANOVA, $F = 2.480$, $P = 0.124$) (Fig. 2). The mud was obtained from sediment of Liangzi Lake (N:P = 0.13:0.014 mg g^{-1}) (Fan et al. 2013). The water was obtained from Liangzi Lake (N:P = 0.71:0.04 mg L^{-1}) (Fan et al. 2013). To reduce the influence of algae on plant growth, the water in the aquaria was changed weekly. For the duration of the experiment, the water in each aquarium was kept at a constant level. On March 2, 2014, the submerged plants began to grow above the water surface. The experiment ended on July 2, 2014.

Data collection

Three days before harvesting the plants, minimum ($F0$) and maximum (Fm) fluorescence yields were

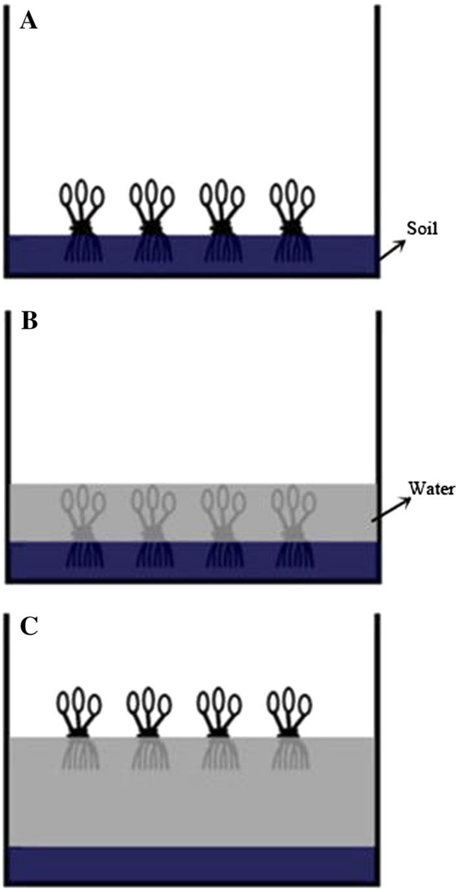

Fig. 1 Sketch of the experimental design. **a** Plants were rooted in the lake mud without water (drawdown), **b** Plants were firmly rooted in the lake mud and submerged in water with a depth of 15 cm (submergence), **c** Plants were free-floating on water with a depth of 50 cm (floating)

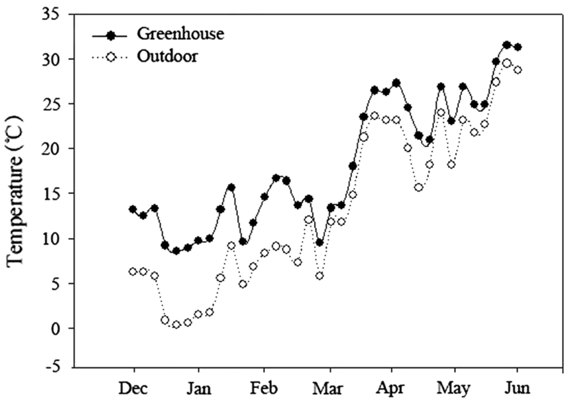

Fig. 2 Mean temperatures from December 2013 to June 2014

measured from five fully developed, healthy leaves in each aquarium. The plants were first adapted to the dark for at least 20 min, which was sufficient time for photosystem II (PSII) reaction centers to open; then, a portable chlorophyll fluorometer (DIVING-PAM, Walz, Effeltrich, Germany) was used in the saturation pulse method (Schreiber et al. 1998) to measure fluorescence. The maximum quantum yield of PSII (Fv/Fm) was calculated as $(Fm - F0)/Fm$. Before harvest, the number of initial plants that survived was tabulated to calculate the survival rate per aquarium. At harvest, the new ramets in each aquarium were counted and categorized as shoots, stems or roots. The biomass was obtained after drying plants in an oven at 70 °C for 72 h to constant weight. Shoot mass ratio (SHMR), stem mass ratio (STMR) and root mass ratio (RMR) were calculated as the ratio between shoot, stem and root biomass and total biomass, respectively.

Data analysis

A one-way ANOVA was performed to examine the differences between the temperature of greenhouse and the outdoor terrace. A two-way ANOVA was used to test the impacts of water level and temperature on survival rate, total biomass, number of new ramets per aquarium, Fv/Fm and biomass allocation of *E. crassipes.* If a significant impact was detected, post hoc pair-wise comparisons of means were carried out to examine the differences between treatments using a Studentized Tukey's HSD for multiple comparisons at the 0.05 significance level. All experimental data were transformed using the log $(x + 1)$ or exp (x) function to ensure homogeneity of the variance or a normal distribution of residuals before being analyzed. All data were analyzed with SPSS 19.0 software (SPSS, Chicago, IL, USA).

Results

Winter survival and regrowth

The survival rate of *E. crassipes* was significantly affected by water level and temperature but not by the interaction between the two factors (Table 1). Warming treatment significantly increased the survival rate of plants with all water levels, while drawdown significantly decreased the survival rate of plants compared with other two water level treatments under warmer environment (Fig. 3a).

Water level, temperature and their interaction had significant impacts on the number of new ramets and total biomass per aquarium, while only temperature had a significant impact on Fv/Fm (Table 1). Warming treatment significantly increased the number of ramets and total biomass of plants with all water levels (Fig. 3b, d). In addition, warming significantly increased the Fv/Fm of drawdown plants (Fig. 3c). Water level had a significant impact on ramet numbers and total biomass of plants under warm conditions but not under natural conditions (Fig. 3b, d). Drawdown had a similar ramets number and a significant higher total biomass compared with floating plants in warm conditions (Fig. 3b, d). Submergence significantly increased ramets number and total biomass compared with drawdown and floating plants in warm conditions (Fig. 3b, d).

Table 1 Effects of water level and temperature on survival rate, regrowth and biomass allocation measures of *E. crassipes*

Trait	Water level (W)	Temperature (T)	W × T
Survival rate	3.320*	89.409***	1.539
Number of ramets	24.794***	145.561***	8.281**
Fv/Fm	1.594	31.790***	1.104
Total biomass	21.383***	158.958***	20.008***
SHMR	13.971***	30.016***	3.750*
STMR	0.621	13.463**	1.863
RMR	4.590*	6.649*	3.603*

The *F*-values derived from two-way ANOVAs are shown

SHMR shoot mass ratio, *STMR* stem mass ratio, *RMR* root mass ratio

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

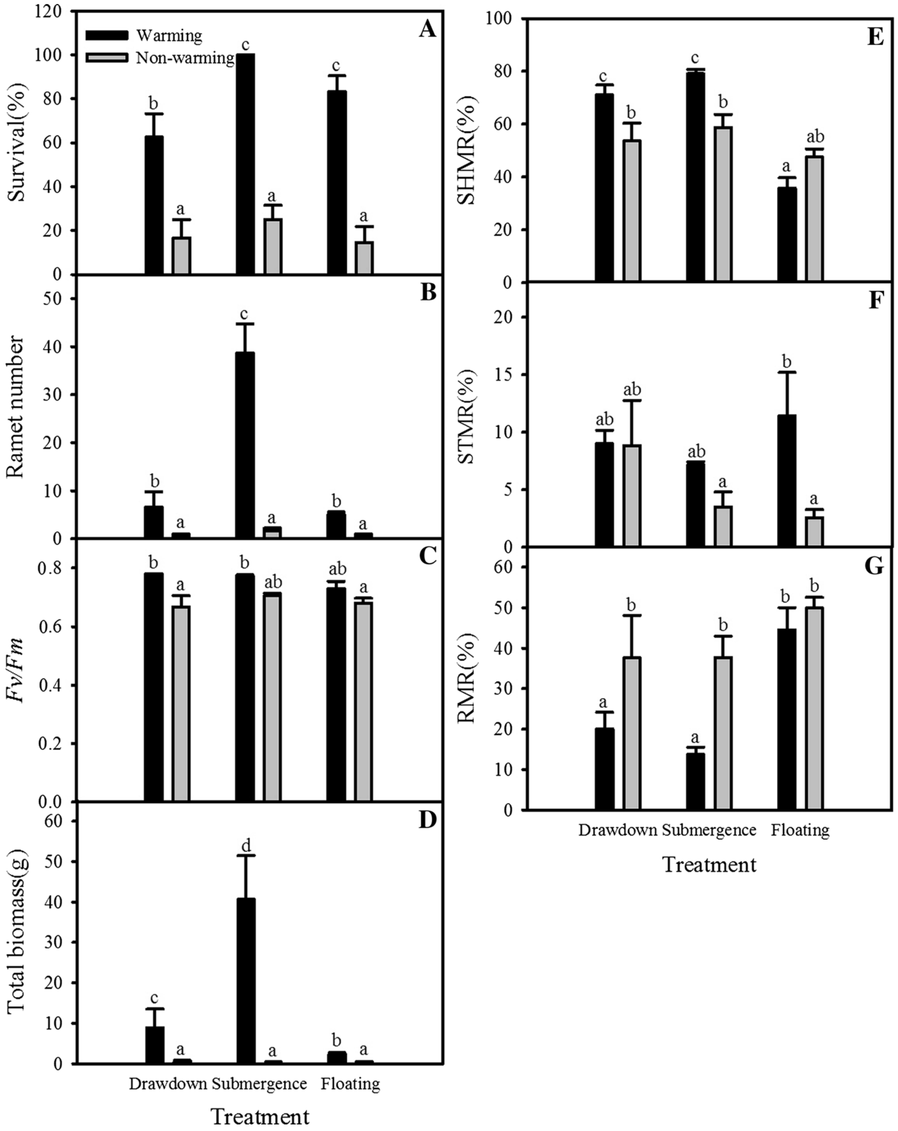

Fig. 3 Comparison of survival rate (**a**), ramet number (**b**), *F*v/*F*m (**c**), total biomass (**d**) and biomass allocation to shoot (**e**), stem (**f**) and root (**g**) of *E. crassipes* among treatments. Data are means ± 1SE. *Bars* sharing the *same letter* are not significantly different at $P = 0.05$

Biomass allocation

Temperature had significant impacts on biomass allocation, which showed that warming increased biomass allocation to shoots and decreased biomass allocation to roots in both the drawdown and submerged plants (Table 1; Fig. 3e, g). However, warming increased biomass allocation to the stems in the floating plants (Fig. 3f). Water level had significant effects on SHMR and RMR in warming condition, except STMR (Table 1; Fig. 3e–g). Biomass allocation to shoots in the drawdown and submerged plants was significantly higher than in floating plants and occurred at the expense of the roots in warm conditions (Fig. 3e, g).

Discussion

Warming temperature significantly improved survival and regrowth of *E. crassipes* in our experiment. This species is a thermophilous aquatic plant (Abbasi and Nipaney 1986; Abbasi 1998), and the survival, growth and clonal integration of *E. crassipes* have historically been limited by low temperatures (Li et al. 1995; Wilson et al. 2005; You et al. 2013), while winter warming buffers the damage caused by low temperatures (You et al. 2013). Therefore, warm temperatures significantly increased the survival rate, number of new ramets and total biomass per aquarium of *E. crassipes* compared with plants that overwintered in the natural environment. On the other hand, the higher number of new ramets and the total biomass of *E. crassipes* per aquarium may positively correlate with the higher Fv/Fm found in warming conditions because decreases in Fv/Fm imply that the photosynthetic efficiency of the leaves is compromised (Baker 2008). This would have inhibited the growth of this species in the low temperature replicates of our experiment. The allocation of biomass to different plant organs depends on the species, ontogeny and the environment in which the plant lives (Poorter and Nagel 2000). In contrast to previous studies that found that biomass allocation to the shoots of floating plants increased with temperature at the expense of the stems (Madsen 1991; Sytsma and Anderson 1993; You et al. 2013), biomass allocation to the shoots of rooted plants increased with warming at the expense of the roots in this study, and warming only increased biomass allocation to STMR of floating plants. The trend of biomass allocation to aboveground components was consistent with previous studies that found that high temperatures increased aboveground growth (Weih and Karlsson 2002); these findings suggest that plants usually partition more biomass to aboveground parts to acquire more carbon resources when the environment is suitable for the promotion of the plant's rapid growth.

Water level had no significant effects on survival rate and regrowth of *E. crassipes* under natural winter conditions (Fig. 3), which confirmed that low winter temperatures are a major limiting factor in the plant's overwintering survival (Wilson et al. 2005). However, this finding is contrary to previous studies, which showed that rooted or buried stem base plants appeared to resist the effects of cold temperatures better than free-floating plants (Owens and Madsen 1995; You et al. 2013). This difference may be caused by the differences in the experiment treatments. For example, drawdown plants were rooted in the lake mud without flood conditions, while submerged plants were firmly rooted in the lake mud and submerged in shallow water 15 cm deep, and the stem base was not buried. However, in other experiments, the stem bases were buried in 10 cm of sediment that was exposed to air (You et al. 2013) and plants were rooted in sediment approximately 30 cm under water (Owens and Madsen 1995). Furthermore, this species has developed the ability to store carbohydrates in its stem base to handle short-term stress or disturbances (Madsen et al. 1993). Protecting the stem base from cold temperatures could enhance the overwinter survival rate of this species by allowing it to store sufficient carbohydrates (Owens and Madsen 1995; You et al. 2013); therefore, because the stem bases of both drawdown and submerged plants were not protected compared to those of floating plants under natural temperature conditions, lower survival rates for rooted and submerged plants were observed in our natural winter temperature treatments. These finding suggest that simply rooting a plant without burying the stem base or completely submerging the stem base in shallow water cannot protect this species from cold temperatures.

In contrast to the natural environment replicates, under warming conditions, both drawdown and submergence had significant impacts on the survival and regrowth of *E. crassipes*, except Fv/Fm (Fig. 3). Fluctuating the water level has been a technique used to manage macrophytes. For example, drawdown is used to control invasive aquatic plants (Poovey and Kay 1998; Thomaz et al. 2006; Silveira et al. 2009; Dugdale et al. 2012; Dugdale et al. 2013). Owens and Madsen (1995) suggested that one appropriate management strategy would be drawdown of water levels in *E. crassipes* populations during cold weather periods, increasing the exposure of plant parts to air temperatures rather than buffered water temperatures. Similarly, in our experiment, drawdown decreased survival in the warm temperature replicates. However, during the latter growth phase, while drawdown had no significant impact on ramet numbers, it led to a higher total biomass compared with floating plants. This finding indicates that drawdown was effective initially in reducing overwinter survival within certain environments but would not affect the population in the long run. Complete submergence is detrimental for nearly all terrestrial plants and results in hampered growth and ultimately causes death for many plant species (Voesenek et al. 2006). Plants use different tactics to avoid the adverse effects of submergence, including underwater photosynthesis, timing of life cycle events and enhanced shoot elongation (Blom and Voesenek 1996; Voesenek et al. 2006). In our experiment, completely shallow submergence in warm water did not result in death of *E. crassipes*, but rather 100 % survival, which is similar to that of another invasive plant, *Alternanthera philoxeroides* (Fan et al. 2015). Some genets and new ramets gradually grew out of the water from submerged *E. crassipes* beginning on March 2. Most new ramets were also rooted in the sediment and thus resulted in the highest rates of later regrowth, including maximum total biomass and ramet numbers.

The regrowth (in terms of number of new ramets and total biomass per aquarium) of rooted plants was greater than that of floating plants in the warm winter treatments of our experiment (Fig. 3b, d). The contribution of roots to total P and N uptake might be dependent on nutrient availability in the sediment relative to the availability in the bulk water of submerged plants (Carignan 1982; Barko et al. 1991). Because the nutrient content of water was significantly lower than that of sediment, rooted plants could obtain more nutrients from sediment than free-floating plants could obtain from water. As a result, rooting in sediment could increase the regrowth of drawdown and submerged plants after overwintering and lead to the observation that growth of rooted *E. crassipes* was increased with higher nutrient level (Fan et al. 2013). Similar to the biomass allocation pattern caused by warming treatments, the rooted *E. crassipes* allocated more biomass to shoots, while the floating plants allocated more to the roots. This finding also mirrored the effect of a change in water nutrient supply (Xie et al. 2004), caused by higher nutrients in sediment and lower nutrient in water.

In conclusion, warming significantly increased the survival and regrowth of *E. crassipes*. Water level had significant impact on *E. crassipes* when it grew in warm environment but not in natural winter environment. Drawdown affect the survival of *E. crassipes* in warm winter temperatures initially, while had no limiting effect on its regrowth post-winter. Complete shallow submergence could not protect *E. crassipes* from cold temperatures when plants grew in natural winter temperatures. However, it also could not inhibit *E. crassipes*, but promote its survival and regrowth in a warm winter environment. The responses of *E. crassipes* to drawdown and shallow submergence could explain why it has expanded widely in various waters and may contribute greatly to its invasiveness in the future as climate change leads to warmer winters and shifting, higher-frequency water level fluctuations. However, our experiment was designed for two temperatures, one drawdown and a shallow submergence treatment only. More fine-tuned experiments are needed to predict warming and water level effects on plant growth, mandatory for the successful management of this invasive species.

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