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Effects of water regime on the growth of the submerged macrophyte *Ceratophyllum demersum* at different densities

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ABSTRACT

To successfully restore deteriorated lake ecosystems, it is vital to identify influencing environmental factors that impact submerged macrophytes. Planting density and water regime are important factors for submerged macrophytes' growth. While many experimental studies have examined effects of water regime on the growth of some aquatic plant species, very few have tested both planting density and water regime on population, individual, and internode growth of a submerged population. We constructed *Ceratophyllum demersum* populations at two density levels (four and 16 shoot fragments per pot, responding to 96 and 384 plants m^{-2}), subjected to two static water depths (30 and 150 cm) and to low, medium, and high water level fluctuation frequencies (24, 12, and 6 days per fluctuation cycle of water depth change between 30 and 150 cm). Initial density had no significant effect on individuals of *C. demersum*; however, it had a positive effect on population performance. Fluctuation frequency did not affect the growth of *C. demersum*, whereas increasing water depth significantly decreased both individual and internode biomass, and also increased shoot length regardless of comparison level. We therefore conclude that managing water depth and establishing populations with higher plant density may be helpful for the restoration of submerged macrophytes in degraded wetlands.

Introduction

Submerged aquatic plants are among the most important components of many inland waters where they serve as vital components, exerting multiple ecological functions. Examples are the promotion of water purification via increasing water transparency and absorbing potentially polluting nutrients (Engelhardt and Ritchie 2001; Bakker et al. 2010; Li, Zhu et al. 2015), providing food and habitat for other biota (Boamfa et al. 2005; Dibble et al. 2006; Lopes et al. 2007), and consequently increasing freshwater biodiversity (Padial et al. 2009; Liu et al. 2014). Currently, submerged aquatic plants are increasingly disappearing due to environmental degradation such as TaiHu Lake (Borisova et al. 2014; Ejankowski and Solis 2015). Studies have revealed several biotic or abiotic factors that determine growth and adaption of submerged aquatic plants, and plant density (Liu et al. 2014) and water regime (O'Farrell et al. 2011; Zhu et al. 2012) are among the most important factors. Hence, sustainable management and efficient restoration for lake recovery and aquatic vegetation restoration is critically important and is best achieved via the regulation of specific biotic or abiotic factors (Peretyatko et al. 2009), such as plant density and water regime (Zhang, Liu et al. 2014).

Plant density is one of the central determinants of growth and reproduction of plants such as *Potamogeton crispus* (Qian et al. 2014), thus choosing an appropriate initial density for restoration efforts is of vital significance (Demirezen et al. 2007; Liu et al. 2014). Previous studies have demonstrated that the mean biomass of the individual plant is inversely proportional to density (Xie et al. 2006; Bebawi et al. 2014; Li et al. 2014). Consequently, in a densely occupied habitat, self-thinning and competition for often limited resources such as nutrients (Qian et al. 2014), light, or minerals may restrict individual plant growth and even cause an increase in plant mortality (Murrell 2009). For example, fragment colonization by *Myriophyllum spicatum* is improved by large fragments, low density, and nutrient-rich sediments, which contributes to the rapid population expansion of this species (Liu et al. 2014). Furthermore, if there is competition for light, larger individuals may reduce the available light for smaller individuals and result in niche partitioning in submerged macrophytes, for example *C. demersum* and *Ceratophyllum submersum* (Demirezen et al. 2007; Nagengast and Gąbka 2017). Although numerous studies have examined the effects of initial density on plant growth and acclimation of several submerged aquatic plant species to environmental factors, there is little research exploring the effects of specific water regimes on aquatic macrophytes growth with different densities (Demirezen et al. 2007).

The water regime is typically reflected by two aspects, i.e. water average depth and seasonal variability (or fluctuation) (Wang et al. 2016). Water depth can significantly affect the establishment, growth, and distribution of aquatic vegetation (Li et al. 2013; Søndergaard et al. 2013). Generally, a certain level of water depth can give the opportunity for plant growth (Gafny and Gasith 1999), which is clearly conducive to the maintenance of stable macrophyte communities (Geest et al. 2005). However, extremely low or high water levels which are beyond the suitable water depth range of a certain species are both unfavorable for the growth of this aquatic vegetation (Coops et al. 2003; O'Farrell et al. 2011; Zhu et al. 2012). In aquatic ecosystems such as lake or reservoir, a specific water level is often not constantly maintained, but naturally fluctuates both spatially and temporally on scales that are determined by catchment characteristics (both size and geology), the regional climate (e.g. temperate, semi-arid, or arid), precipitation patterns and evapotranspiration, and last by anthropogenic activities as well as climate change (Valk 2005; Beklioglu et al. 2006; Deegan et al. 2007; Zhang, Liu et al. 2014).

Water level fluctuations can affect the growth, distribution, as well as the survival of submerged macrophytes (Sousa et al. 2010; Zhu et al. 2012) both directly and indirectly by affecting the substrate, nutrient, light, water transparency, and gas (Raulings et al. 2010; Zhang, Liu et al. 2014). The effects of water level fluctuation depend on many factors, including fluctuation frequency and amplitude (Yu and Yu 2009; Wang et al. 2014). High fluctuation frequency leads to increased disturbance to plants, which in turn leads to increased nutrient loss and tissue damage (Bornette et al. 2008). Furthermore, increase in the frequency makes plants suddenly re-expose to ambient O_2 levels and normal light conditions, thus it would result in increased production of harmful substances such as reactive oxygen species (Steffens et al. 2013) and acetaldehydes (Boamfa et al. 2005). And these would damage the photosynthetic apparatus. Water regime change can be an efficient treatment for lake recovery and aquatic vegetation restoration in preliminary stage (Zhang, Liu et al. 2014; Ejankowski and Solis 2015). Many previous studies have investigated the effects of water level fluctuations amplitudes on aquatic macrophyte growth (Deegan et al. 2007; Cao et al. 2012; Zhang et al. 2013); however, there are few researches about the effects of water level fluctuation frequency on the macrophytes (Luo et al. 2016), especially when it was crossed with different density.

Based on previous research, we conducted an experiment to test the effects of initial plant density and water regime on submerged macrophyte population. Specifically, we addressed the following questions: (1) Does initial planting density affect the performance of population growth, individual growth, and morphological characteristics of *C. demersum*? (2) Does water regime (i.e. water depth and water level fluctuation frequency) affect the performance of population growth, individual growth, and morphological characteristics of *C. demersum*? (3) Whether the interaction between

initial planting density and water regimen affected the performance of population growth, individual growth, and morphological characteristics of *C. demersum*? We posed the hypotheses that *C. demersum* would have different response to planting density and water regime in population, individual, and internode growth of a submerged population.

Materials and methods

Materials

The experimental population assembled for this study consisted of the submerged macrophyte *C. demersum* L. (Ceratophyllaceae), which is a type of perennial, submerged clonal plant and each of its shoot fragments can potentially develop into an independent new plant (Zhang, Xu et al. 2014). Furthermore, it is a cosmopolitan species, commonly growing in moderately to highly eutrophic shallow ponds, lakes, and ditches (Keskinkan et al. 2004; Li, Wang et al. 2015). Considering its ability of the removal of heavy metals such as lead, zinc, and copper, it can be used for lake recovery (Keskinkan et al. 2004).

In July 2012, shoot fragments of *C. demersum* were collected from the lakes of the Winter Palace (40°00′15.96″N; 116°18′11.26″E) in Beijing, China. Six hundred and twenty shoots were selected and each was trimmed to a length of 13 cm, with an apical bud but without lateral branches to minimize variations of the initial size. Twenty of the chosen 620 shoot fragments were randomly selected for initial biomass measurements.

Experimental design

The experiment was conducted outdoors at the Cuihu National Urban Wetland Park in the suburb area of Haidian district, Beijing, China on 17 July 2012. We initiated 60 *C. demersum* populations within 60 plastic pots (upper diameter, 23 cm; lower diameter, 23 cm; height, 12 cm) filled 10-cm-deep with wetland sediment, which was collected in the Cuihu wetland park (organic matter: 14.01 ± 1.00 mg g^{-1}, total nitrogen (TN): 0.82 ± 0.07 mg g^{-1}, total phosphorus (TP): 6.71 ± 0.04 mg g^{-1} [mean $\pm$ SE, $n = 3$]). Each pot (or community) was placed into a mesh container (diameter, 25 cm; height, 42 cm) with an open top.

For this experiment, *C. demersum* populations were cultured in two density levels: four shoot fragments per pot formed the low density treatment, resulting in approximately 96 plants m^{-2}; and 16 shoot fragments per pot formed the high density treatment with approximately 384 plants m^{-2}; We designed the experiment according to the filed investigation about the density of *C. demersum* in Cui National Urban Wetland Park (Li, Wang et al. 2015). After seven days of recovery, the constructed populations were subjected to five water regimes: two static water depth treatments (low and high); and three water level fluctuation treatments differing in frequency (low, medium, and high frequency). For the static low and high water treatments (called LS and HS), the water levels from the water surface in the tank to the soil surface in the pot were 30 and 150 cm, respectively. For the low fluctuation frequency treatment (called LF), the water depth gradually changed from 30 cm to 150 cm and then returning from 150 cm to 30 cm at a rate of 10 cm per day (24 days per cycle). In the medium fluctuation frequency treatment (called MF), the water depth gradually changed following the same pattern but at a rate of 20 cm per day (12 days per cycle). For the high fluctuation frequency treatment (called HF), the rate was 40 cm per day, resulting in six days per cycle (Figure 1). Each treatment combination was replicated six times. The water used in the study was obtained from the lake of the park (TN: 0.74 ± 0.03 mg L^{-1}, TP: 0.0015 ± 0.0004 mg L^{-1}) (United intelligence, Beijing, China) (Li, Wang et al. 2015).

The experiment was set up in a randomized-block design with six blocks, in six dependent plastic tanks (diameter, 100 cm; height, 162 cm). Each tank contained 10 constructed

Figure 1. Experimental design. C stands for *Ceratophyllum demersum*. These were five water regimes, LS and HS indicated static low (30 cm) and high (150 cm) water depth, respectively; LF, MF, and HF represented water level fluctuation from 30 cm to 150 cm. then returning from 150 cm to 30 cm at a rate of 10, 20, 40 cm per day, with low, medium, and high frequency, respectively.

populations within 10 mesh containers, and these 10 pots were randomly assigned to 10 treatment combinations. In each tank, all mesh containers were suspended in the water via adjustable ropes that were connected to steel bars, affixed on the top of the tank. The water depth of each community was controlled via adjustment of the length of the rope. There was not any loss of fragments from the plant because *C. demersum* were planted and restricted in mesh container of the pot. For static water depth treatments, the lengths of the ropes remained unchanged during the 48-day experiment; however, for fluctuation treatments, the lengths of the ropes were adjusted (released more or pulled up), according to the changes in the water depth.

The experiment was conducted outdoors in the Cuihu wetland park. During the experiment, we maintained a constant water level by adding tap water into the tanks to compensate for water loss due to evaporation or by removing surplus water from the rain. Because we mainly focus on the effects of the water regime, we use the tap water to maintain the water level. During the experiment, the highest and lowest daily mean air temperature was 31 ± 0.4 and $22 \pm 0.3°C$, respectively. Meantime, we measured light intensity just above and under the water surface, at 90 and 150 cm water depth, respectively, in six tanks using a Li-COR UWQ-4341 sensor on a sunny day. Light intensity just under the water surface, at 30 cm depth, at 150 cm depth was $51.49 \pm 0.88\%$, $26.54 \pm 2.12\%$, $2.29 \pm 0.58\%$ (mean $\pm$ SE; $n = 6$) of that above the water surface.

Harvest and measurements

On 4 September, all surviving plants (survival rate seen in supplementary Table S1) in each pot were carefully harvested with their stems and leaves intact. Number of shoot nodes is a measure of potential clonal growth as every single node can develop into a new plant, and total shoot length is a measure of local vegetative spread (Zhang, Xu et al. 2014; Wang et al. 2016). These two measures were determined during harvest. Since the plants can easily be broken into multiple shoot fragments during the harvest, it was difficult to count the node number and measure the shoot length for all shoot fragments. Thus, a subsample of five shoot fragments was collected per experimental population to count the number of nodes and measure shoot length as well as biomass. We then measured the biomass of the remaining parts of

Table 1. Summary of ANOVAs for the effects of population density and water regime on the growth of the *Ceratophyllum demersum* population (A), growth of the individual plant (B), and corresponding internode indexes (C).

Traits	Density (D)		Water regime (W)		D × W	
	$F_{4,50}$	P	$F_{4,50}$	P	$F_{4,50}$	P
(A) Population level						
Total biomass[a]	**323.72**	**<0.001**	1.83	0.138	0.77	0.549
Total number of nodes[a]	**196.15**	**<0.001**	1.07	0.380	1.52	0.211
Total shoot length[a]	**174.30**	**<0.001**	*3.44*	*0.015*	1.43	0.237
(B) Individual level						
Biomass	1.44	0.235	**3.93**	**0.007**	0.54	0.706
Number of nodes	0.49	0.488	0.83	0.511	1.46	0.228
Shoot length	0.48	0.492	*2.74*	*0.039*	1.35	0.264
(C) Internode indexes						
Internode biomass[a]	0.23	0.631	**4.65**	**0.003**	0.36	0.836
Internode length	0.91	0.344	**5.50**	**0.001**	1.01	0.409

Note: Values are in bold if $P < 0.01$ and in italics if $P < 0.05$. See Figure 1 for graphical representation of data. [a]indicates square root-transformed data.

C. demersum for each population. For biomass measurements, plants were oven-dried at 70 °C for 48 h and then weighed.

Data analysis

Based on data from the subsample of the five fragments per species, number of shoot nodes per unit biomass and shoot length per unit biomass was calculated in each population (Zhang, Xu et al. 2014). Then total number of shoot nodes (or total shoot length) for *C. demersum* in each population (i.e. in each pot) was derived by multiplying biomass with number of nodes per unit biomass (shoot length per unit biomass). We furthermore calculated biomass and shoot length per internode as well as biomass, shoot length, and number of nodes per individual plant.

All data analyses were conducted via SPSS 20.0 software (SPSS, Chicago, IL, USA). To examine the effects of treatment of population density (i.e. low and high) and water regimes (i.e. LS, HS, LF, MF, and HF) on *C. demersum* population and individual indexes, a series of two-way ANOVA was performed. The growth data of the *C. demersum* population (total biomass, number of nodes, and shoot length) were transformed using square root transformations prior to analysis to remove heteroscedasticity.

Results

Effects at population level

Overall, total shoot length, total biomass and total number of nodes all increased significantly with increasing population density (Table 1A; Figure 2). Water regime only exerted significant effects on the total shoot length, but not on the total biomass or total number of nodes (Table 1A; Figure 2). Total shoot length did not differ between the three frequency fluctuation treatments (Figure 2(C)). No significant interaction effect was detected between population density and water regime on the three growth measures (Table 1A).

Effects at individual level

At the individual level, population density exerted no significant effect on any of the three indexes (Table 1B; Figure 3). Water regime significantly affected individual biomass and shoot length, while water level fluctuation frequency had no significant effect (Figure 3). No significant interaction effect was detected for population density and water regime on the three growth measures (Table 1B).
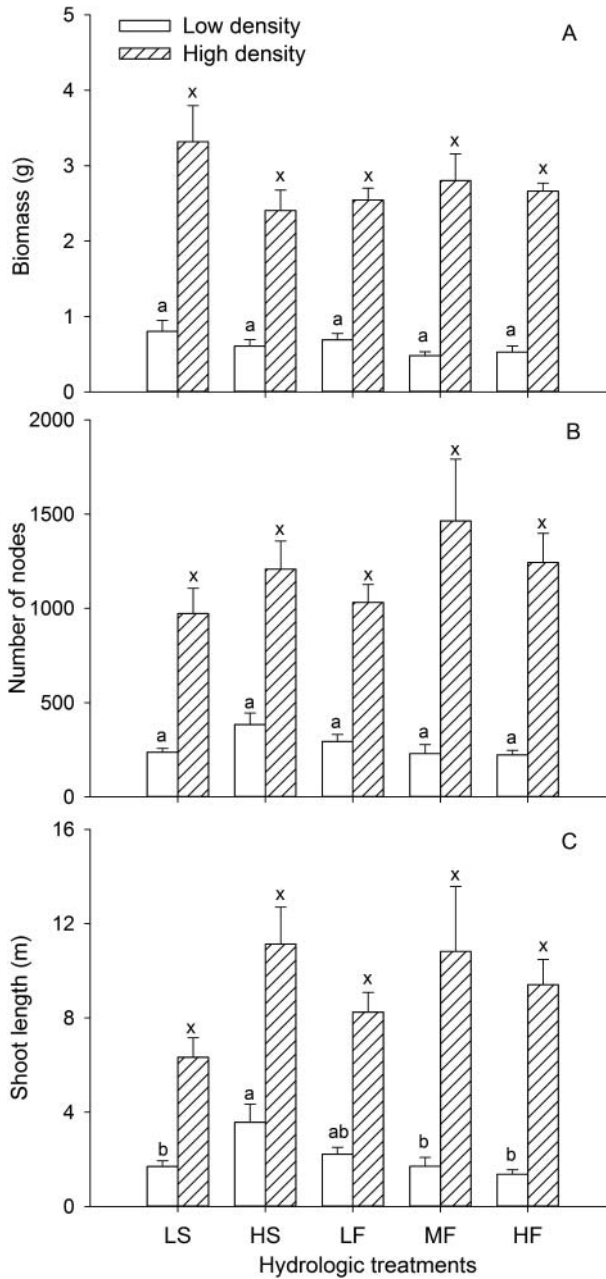
Figure 2. Effects of population density and water regime on growth metrics of the *C. demersum* population (mean ± SE): (A) biomass; (B) number of nodes; (C) shoot length. See Table 1A for a summary of ANOVA results. Means sharing the same letter are not different at $P = 0.05$ within water regimes. Treatment codes are identical to those described in Figure 1.

Effects at internode level

Population density did not affect internode biomass or internode shoot length, while water regime significantly impacted both of these measures (Table 1C; Figure 4). To be specific, internode biomass and internode shoot length revealed the maximal value when subjected to HS treatment and LS treatment, respectively. Nevertheless, fluctuation frequency did not affect any of these indexes.
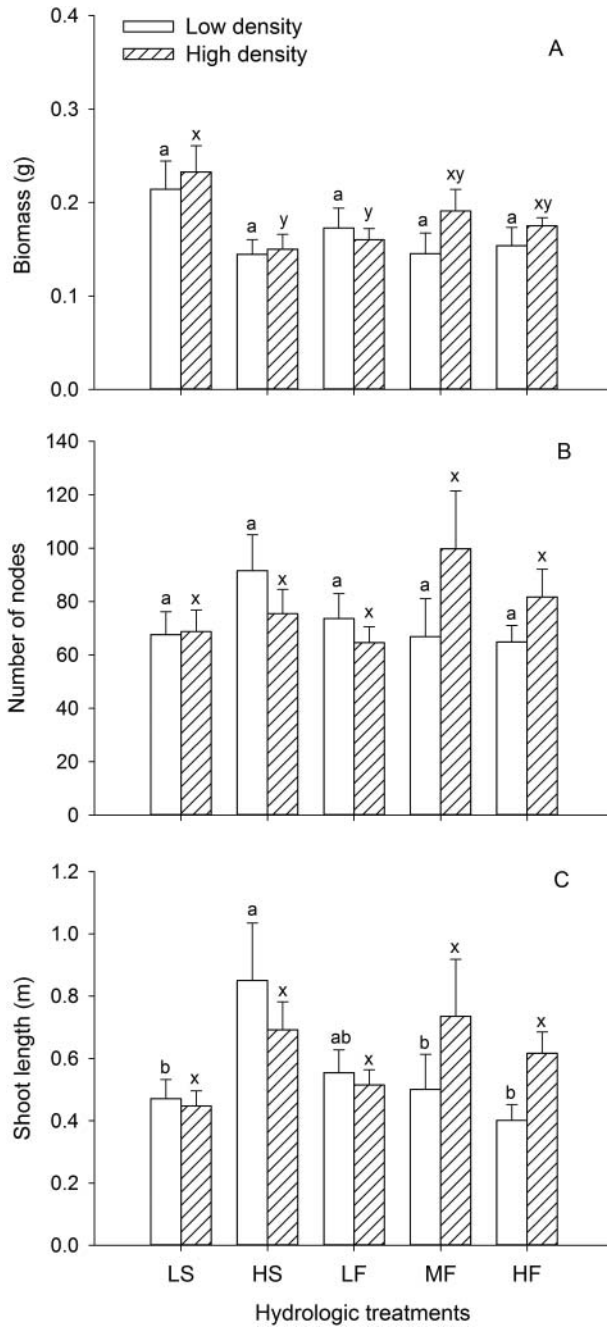
Figure 3. Effects of population density and water regime on growth metrics of *C. demersum* individuals (mean ± SE): (A) biomass; (B) number of nodes; (C) shoot length. See Table 1B for a summary of ANOVA summaries. Means sharing the same letter are not different at $P = 0.05$ within water regimes. Treatment codes are identical to those described in Figure 1.

Discussion

Initial plant density did not significantly affect the individual growth of *C. demersum*, and this contradicts findings of previous studies, which have typically demonstrated that increased plant density can cause a reduction in individual production (Wang et al. 2005; Demirezen et al. 2007). Since the
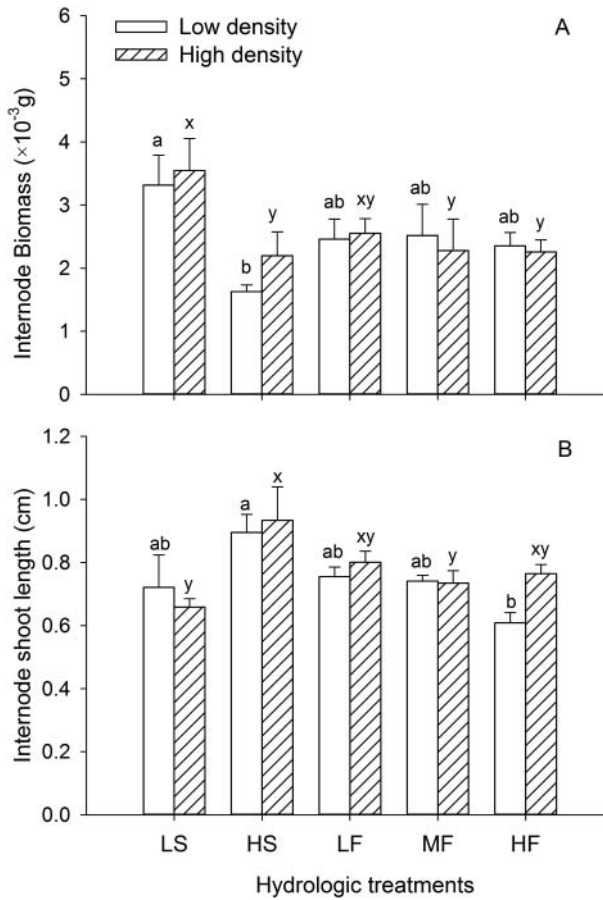
Figure 4. Effects of population density and water regime on (A) internode biomass and (B) internode shoot length. See Table 1C for ANOVA summaries. Means sharing the same letter are not different at $P = 0.05$ within water regimes. Treatment codes are identical to those described in Figure 1.

initial plant density had no significant effect on individual growth, population growth can apparently be enhanced by the initial density. Several potential explanations for this phenomenon are plausible. First, as a rootless species, *C. demersum* modifies its leaves to anchor into the sediment and mostly absorbs nutrients from the water (Foroughi 2011; Xue et al. 2012). Due to this particular life form, lower light intensities and oxygen concentrations for belowground parts in deeper water may not be a key growth limiting factors. Furthermore, the initiation of self-thinning might be determined by root competition (Morris and Myerscough 1991; Morris 2003), whereas *C. demersum* has no roots, making the competition vacant. In addition, *C. demersum* can grow at a higher rate under a relatively low light intensity (Kitaya et al. 2003). As a result, intraspecific competition for light did not restrict the growth. Alternatively, *C. demersum* has long branching stems, whorled palmate dissected leaves, and a relatively high value of fractal dimension (fractal geometry). Previous study has verified a positive relationship between fractal dimension and plant complexity, space inhabiting ability (Dibble and Thomaz 2009). Hence, *C. demersum* can maximize the utilization of an overpopulated space, making the competition for space much less severe. Furthermore, the observed effect may be due to the examined densities not being high enough (Wang et al. 2005) or the time scale not being long enough as the total biomass of the plants increases proportionally with their density and eventually reaches a plateau at ever-higher density (Chu et al. 2008). In summary,

a higher initial density leads to higher yields for *C. demersum* in our experiment and can further help the restoration of the species in lakes or reservoir.

Taking into consideration the water depth, *C. demersum* can markedly elongate the total, individual, and internode shoots with increasing water depth, which agrees with the results of previous studies (Busch et al. 2004; Zhu et al. 2012; Wang et al. 2016). Such a submergence-induced shoot elongation is an important morphological adaptive strategy for *C. demersum* to water depth (Milne et al. 2006; Wang et al. 2014). This strategy may enable macrophytes to stretch towards the water surface from deep water, and thus to maximize the light availability, and ultimately survive (Tobiessen and Snow 1984; Strand and Weisner 2001). This result suggests that deeper water (about 150 cm) benefits the vegetative spread of submerged macrophytes. Apart from the shoot elongation, other macrophytes can typically adjust to a deep static water level and the ensuing limitations in atmospheric carbon and oxygen access in other ways (Deegan et al. 2007), i.e. leaf elongation (Yu and Yu 2009; Zhang et al. 2013) as well as altered resource allocation patterns between aboveground and belowground parts (Vretare et al. 2001; Lytle and Poff 2004; Yang et al. 2004).

Not surprisingly, both individual and internode biomass of *C. demersum* revealed dramatic reductions in response to high levels of water depth, suggesting that the flooding imposed negative effects on them. Generally, submerged macrophytes only grow in their adaptive water depth and show a strong zonal distribution (O'Farrell et al. 2011). These results were most likely because high water levels can induce low light intensities and low dissolved oxygen availability, thus adversely affecting the photosynthetic capacity and the nutrient uptake efficiency of *C. demersum*, consequently reducing plant fitness and growth (Xiao et al. 2007; Huber et al. 2014; Wang et al. 2016). Low water levels are accompanied by sufficient penetration of light to the substratum (Raulings et al. 2010) but restricted shoot growth (Milne et al. 2006), thus supplying *C. demersum* with sufficient light and nutrients for biomass accumulation per internode and production of higher internode biomass in lower water.

In natural habitats, water level fluctuation frequency is a dynamic process that may severely affect submerged macrophyte species both spatially and temporally (O'Farrell et al. 2011; Cao et al. 2012; Luo et al. 2016). To be specific, water level fluctuation frequency can directly modify light availability in the water as well as oxygen availability in the sediment (Raulings et al. 2010; Steffens et al. 2013; Wright et al. 2015), and strongly influencing pathways of nutrient cycling (Pinay et al. 2002), consequently influencing the growth of aquatic macrophytes. In our study, none of the growth metrics of the population, the individual, or the internode was statistically different between any two of the three levels of fluctuation frequency. This suggests that frequency of fluctuation in the water level does not impact the growth of *C. demersum*. This phenomenon can partly be explained by its specific morphological and physiological adaptations to the fluctuation frequency (Yu and Yu 2009; Wang et al. 2016). To be specific, *C. demersum* can produce relatively strong and flexible shoots, which can facilitate its adaption to rapidly changing water levels (Zhu et al. 2012). This is in good accordance with previous studies that reported that the effects of the fluctuation depend on fluctuation amplitude (Deegan et al. 2007; Cao et al. 2012; Zhang et al. 2013), and not on its frequency (Luo et al. 2016). However, other research indicated that water level changes would improve biomass of *C. demersum* in turbid water reservoir (Ejankowski and Solis 2015). The inconsistence may be induced by different water environment such as transparency.

Our results indicate that increasing plant density may promote population growth. However, we can still extend the time scale for the population growth of *C. demersum* in further studies to ensure that an increase in planting density can indeed help to obtain higher yield in the long term. Water level fluctuation frequencies did not impact the growth of *C. demersum* population, while a high level of water depth can decrease the production of the individuals and benefit the vegetative spread due to an increase in shoot length. This indicates that managing water depth may be a helpful strategy for the restoration of submerged macrophytes in degraded wetlands. To specify the effects of fluctuation, it will be essential to establish a corresponding static water depth. In the present study,

water regime treatments cannot include more fluctuation amplitude treatments and static treat-ments, making the results cannot be thoroughly verified. Overall, increasing plant density and man-aging water depth can help the restoration of a submerged macrophyte population especially *C. demersum* and further contribute to the recovery of lakes considering the ability of *C. demersum* to absorb heavy metals.

Disclosure statement

No potential conflict of interest was reported by the authors.

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