Elodeid Species as Nursery Beds for the Successful Seed Restoration of *Vallisneria spiralis* L.

Elodeid species as nursery beds for the successful seed restoration of *Vallisneria spiralis* L.

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ABSTRACT

Submerged aquatic vegetation (SAV) is often difficult to restore due to their low seedling survival rates. Therefore, we hypothesized that the elodeid macrophytes serve as effective "nursery" areas to promote success for seedlings of other SAV. However, the high density of the elodeid community may inhibit the establishment of other SAV. An experiment was conducted to explore this "nursery effect" as a restoration approach to increase the success of seed restoration. Two elodeid species were pre-planted into mesocosms to create three levels of "nursery beds" i.e., bare, sparse (approx. 100 g m^{-2}) and dense (approx. 200 g m^{-2}). Seeds of *Vallisneria spiralis* were then placed into these beds to test the seed germination and growth of *V. spiralis* seedlings. After three months, seed germination was lower in the bare treatment than in the sparse and dense treatments. The growth of *V. spiralis* seedlings was greater in the sparse treatment than in the bare and dense treatments. These results revealed that the established elodeid bed had a positive effect on the seed restoration of *V. spiralis* but that the restoration efficiency was significantly reduced by the high-density cover of the elodeid community.

INTRODUCTION

The damage of aquatic ecosystems has caused decline of submerged aquatic vegetation (SAV) worldwide and become a global ecological problem (Blindow 1992, Scheffer *et al.* 1993, Qiu *et al.* 2001, Sand-Jensen *et al.* 2008, Lu *et al.* 2012). For instance, a decrease in SAV can greatly diminish the abundance or survival of species that rely on the protective cover of SAV beds (e.g., juvenile fish and various invertebrates) and degrade water quality due to increases in algal blooms and nutrient loading (Scheffer *et al.* 1993, Eriksson and Weisner 1999, Jones and Sayer 2003, Smith 2003, Danger *et al.* 2008). In response to losses of SAV, restoration efforts have been attempted using either whole plants or seeds, and in recent years, there has been an increased emphasis on the use of seeds due to the potential for increasing the cost-effectiveness for large restoration areas (Orth *et al.* 1994, Ke and

Li 2006, Marion and Orth 2010a). However, compared with terrestrial plants, little is known about the factors affecting the initial establishment of aquatic plants from seeds (Titus and Hoover 1991, Orth *et al.* 2000, Ailstock *et al.* 2010).

In aquatic ecosystems, one of the primary causes of the decline of SAV is eutrophication due to excessive anthropogenic nutrient loading (i.e. nitrogen and phosphorus). Eutrophication has resulted in enhanced algal growth, increased water turbidity, and thus reduced light availability to SAV (Scheffer *et al.* 1993, Salgado *et al.* 2010, Arthaud *et al.* 2012). Similarly, the establishment of new SAV beds from either seeds or transplants requires good water quality conditions, including proper light conditions in the water column (Kemp *et al.* 2004, Ke and Li 2006, Dobberfuhl 2007). A variety of biotic and abiotic factors can influence seed dispersal (Harper 1977, Santamaría 2002, van den Broek *et al.* 2005) and eventual establishment as seed-

lings (Chambers and MacMahon 1994). In restoration systems, seedlings established from seeds are likely to be considerably more vulnerable to stressful environmental conditions compared to established plants, because the newly established seedlings may lack substantial stored reserves to support growth and are easy targets for herbivores due to their small size (Ailstock *et al.* 2010). Therefore, the development of strategies to efficiently utilize seeds in restoration attempts, given a limited seed supply, requires a better understanding of both the processes that limit seed germination and seedling establishment at potential restoration sites and the characteristics of sites that maximize seedling yield.

Fast-growing elodeid species, such as *Myriophyllum spicatum* L. and *Elodea nuttallii* (Planch.) H. St. John, can survive under poor water quality conditions. In fact, the growth and physiology of these submerged macrophytes are well-suited to the conditions of high algal abundance that occurs with eutrophication (Ruiz *et al.* 1999, Chase and Knight 2006). The established beds of elodeid species (referred to as called "nursery bed" after Hengst *et al.* 2010) can alter their environment by reducing nutrients and turbidity, creating a microenvironment that further increases the quality of the habitat and allows other SAV to colonize. Melton (2002) introduced *Potamogeton perfoliatus* L. and *Potamogeton pectinatus* L. into established elodeid species (*Ruppia maritima*) beds and concluded that transplants were more successful in bare areas within elodeid-vegetated sites compared to non-vegetated sites. However, whether established elodeid species beds aid in the successful restoration of SAV through seeds remains unclear.

Vallisneria spiralis L. is a submerged macrophyte that is widely distributed in shallow lakes in the middle and lower Yangtze River Plain in China (Xiao *et al.* 2006, Xiao *et al.* 2011) as well as in many places in Europe (e.g., France, Germany and Poland) (Hussner 2012). This species not only provides food and habitat for crabs and fish but also maintains good water quality (Li *et al.* 2009). However, due to lake eutrophication since the 1980s, the distribution and abundance of *V. spiralis* have been limited, such as southwest and southern China (Hong and Li 2000),

particularly in the middle and lower catches of the Yangtze River, China (Ye *et al.* 2007). The loss of *V. spiralis* has prompted considerable research to identify causal conditions that lead to this loss and to develop effective restoration methods (Qiu *et al.* 2001, Ye *et al.* 2009). Reasons for the decline remain uncertain, but research suggests that the decline is linked to serious of natural and/or anthropogenic disturbances, such as eutrophication, flooding, and herbivory (Ye *et al.* 2007). Therefore, developing effective restoration strategies for *V. spiralis* is of both scientific and practical interest, especially for restoration involving the early stages of its seed germination and development.

In this study, we evaluated the effect of established *M. spicatum* and *E. nuttallii* (two elodeid species) on seed germination and seedling development of submerged macrophyte *V. spiralis* as it transitions from its initial reliance on stored nutritional reserves to photosynthetic competency. These two elodeid species are common in lakes in the Yangtze River Basin (as well as in many lakes in southwest and southern China) and coexist with *V. spiralis* in submerged communities (Hong and Li 2000, Ye *et al.* 2007, Xiao *et al.* 2011). In addition, these two species can tolerate low-light environments, such as eutrophic waters (Smith and Barko 1990, Gross *et al.* 2003); therefore, they are widely used for eutrophic lake restoration in China (Qiu *et al.* 2001). Two hypotheses were tested in this study: (1) elodeid species can indeed be used as "nursery beds", and their presence will have a positive effect on the establishment of *V. spiralis* from seeds; and (2) the effect of elodeid species on the establishment of newly germinated seedlings is density dependent given that *V. spiralis* requires proper light conditions in the water column to germinate. More specifically, we ask question at what density begins inhibitory effect?

MATERIALS AND METHODS

Study area and mesocosm experimental design

The study was conducted at an experimental site of Nanjing Forestry University in Jurong City, Jiangsu Province, China (31°59′N,

119°14'E). *Vallisneria spiralis* seeds were collected from a population growing in Taihu Lake, Jiangsu (31°30'N, 120°30'E).

From October to November 2011, matured fruits of *V. spiralis* were harvested, cleaned, and dried. The fruits were stored at 4°C until the experiment was performed. In mid-March 2012, 600 apical shoots (*ca.* 30 cm long) of *M. spicatum* and *E. nuttallii* were collected from Taihu Lake (sediment total nitrogen, TN: 1.29 mg g^{-1}; total phosphorus, TP: 0.64 mg g^{-1}). The shoots were transplanted into containers filled with clean sand and 20 cm of pond water (TN: 2.56 ± 0.74 mg l^{-1}; TP: 0.15 ± 0.01 mg l^{-1}, mean ± SE, n=21) and then placed in a greenhouse (water temperature: 21.03 ± 2.48°C; *in situ* irradiance: 1,563 ± 40.22 μmol photons m^{-2} s^{-1}, mean ± SE, n=14) for approximately two weeks until the plants displayed well-developed root systems. The apical shoots of the two elodeid species (1.82 ± 0.75 g wet weight and 19.18 ± 0.55 cm in length, mean ± SE, n=480) were planted in 16 mesocosms (100 cm in length × 50 cm in width × 60 cm in height) that contained local sediment (sand-clay mixture, 15 cm deep) and pond water. An additional eight mesocosms were filled with local sediment and pond water, and no apical shoots were planted (bare treatment). These 24 mesocosms were left *in situ* until the experiment began. After one week, seeds (200 seeds in each mesocosm) of *V. spiralis* were planted on the sediment surface in each mesocosm.

A mesocosm study was conducted during a three-month period from April to July 2012 to test the effect of elodeid species on seed germination and seedling establishment of *V. spiralis*. The experimental treatments were performed using a complete randomized design to separate microsite effects from the treatment effects. The experimental design included three treatments: unplanted control treatment (bare), sparse (low-density established cover; 20 apical shoots per mesocosm: approximately 100 g m^{-2}), and dense (high-density established cover; 40 apical shoots per mesocosm: approximately 200 g m^{-2}). The dense treatment approximates conditions occurring in high-density natural populations of *M. spicatum* and *E. nuttallii* in Taihu in the spring (He *et al.* 2008). To maintain the dif-

ferences between sparse and dense treatment, we cut the new growing branches of each elodeid plant weekly throughout the experimental period. To maintain a constant water level, pond water was added to each treatment daily. This experiment was replicated a total of eight times.

At the beginning and harvest of the experiment, the nutrient concentrations (TN and TP) both in water and in the sediment of each mesocosm were measured using Hach˙ test kits (2714100 and 2742645) and a spectrophotometer (Hach® Company, Loveland, USA). The following water quality variables were also recorded weekly for each mesocosm before the final harvest: dissolved oxygen (DO), chlorophyll *a* (Chl-*a*) concentration, pH, surface light intensity (0.5 cm under water surface), and water light intensity. All variables (except surface light intensity) were measured at a depth of 25 cm. For the Chl-*a* analysis, a 550 ml water sample was filtered by a GF/F filter, and the residue was measured using the acetone method for Chl-*a* concentration (Smoot *et al.* 1998). The light attenuation coefficient (K_d) was calculated using the formula proposed by Kirk (1994): K_d = -1/*z* ln*E(z)/E(0)*, where *z* is the measurement depth (0.25 m), *E(z)* is the water light intensity at a depth of 0.25 m, and *E(0)* is the subsurface light intensity.

The total number of seedlings per mesocosm was recorded after three months. Seedling growth was measured as the length of the longest leaf. The leaf width of the three longest leaves and the total connected stolon clone number per plant were recorded for each individual plant. All plants within each replicate mesocosm were then harvested and separated into belowground and aboveground portions. The dry weights of the various parts of the plants were measured after drying at 80°C for 48 h.

Statistical analysis

To determine the effects of the elodeid species community on seed germination, seedling establishment (maximum leaf length, mean leaf width, number of clones, and root-to-shoot ratio), and water quality (TN, TP, Chl-*a*, light attenuation, DO, and pH), one-way analysis of variance (ANOVA) tests were conducted

for each response variable. A Duncan multiple comparison test was used to compare the significance levels within factors (α = 0.05). All data were transformed using the log (x) function to ensure homoscedasticity and normality of the residuals and were analyzed with SPSS 19.0 (SPSS, Chicago, IL, USA).

RESULTS

The established bed of elodeid macrophytes significantly affected water quality after the three-month treatment. The presence of the two elodeid species *M. spicatum* and *E. nuttallii* strongly decreased the TN, TP, and Chl-*a* concentrations and limited light attenuation in the water column (Table 1). In addition, the increase of established macrophytes increased DO concentration but had no effect on the water pH (Table 1).

The presence of elodeid species increased germination of *V. spiralis*. The most beneficial effects were observed at low densities of the elodeid species in the sparse treatment (Fig. 1). Overall, 30–80% of the *V. spiralis* seeds germinated when placed on the sediment surface (Fig. 1A). The treatments significantly influenced the seed emergence of *V. spiralis* ($P <0.001$). For the bare treatment, only 43% of the *V. spiralis* seedlings emerged on average, whereas an average of 71% and 65% of the *V. spiralis* seedlings emerged for the sparse and dense treatments, respectively (Fig. 1A). For the bare treatment, many germinated seeds floated (approximately 15%) when the seedlings emerged. At the final harvest, the total biomass and plant biomass of the *V. spiralis* seedlings differed significantly among the treatments ($P <0.001$). Greater accumulations of total biomass and plant biomass were observed in the sparse treatment compared with the bare and dense treatments (Fig. 1B and C).

By the end of the three-month growth period, the maximum leaf length ($P <0.001$), leaf width ($P <0.001$), numbers of clones ($P = 0.018$), and root-to-shoot ratios ($P <0.001$) were different among the three treatments. Seedlings of *V. spiralis* in the three treatments had attained maximum leaf lengths of over 30 cm by the end of the experiment (Fig. 2A). The seedling maxi-

mum leaf length was significantly greater for plants grown in the dense treatment than for those grown in the bare and sparse treatments, whereas the leaf width was greater for plants grown in the sparse treatment than for those grown in the bare and dense treatments (Fig. 2A and B). Plants grown in sparse conditions had a higher number of clones than plants grown in bare and dense conditions (Fig. 2C). However, the root-to-shoot ratio was higher in plants grown in the bare treatment than those grown in the sparse and dense treatments (Fig. 2D).
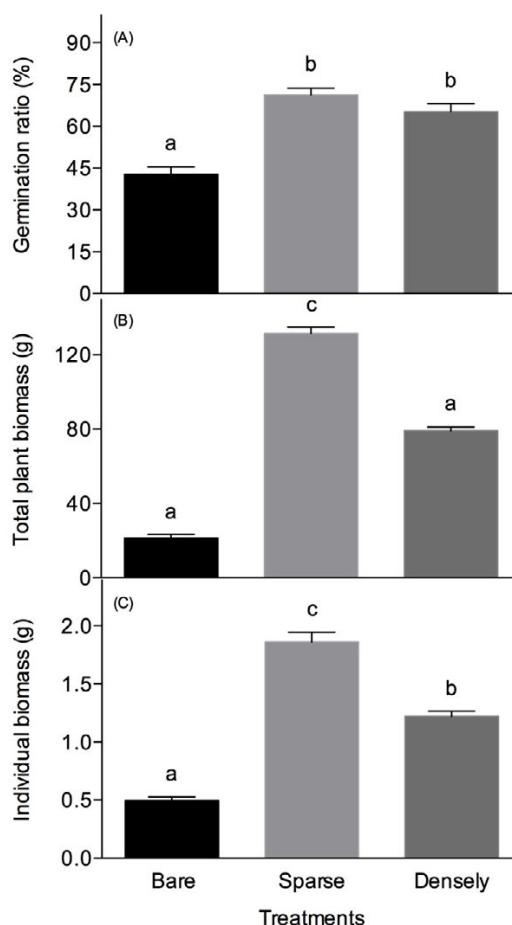

Fig. 1. Mean ± SE (n=8) of *Vallisneria spiralis* (A) seed germination, (B) total biomass, and (C) plant biomass for the bare, sparse, and dense elodeid bed treatments over a three-month experimental period. Bars with different letters represent statistically significant differences ($P <0.05$, one-way ANOVA with Duncan multiple comparison test). All data were transformed using the log (x) function.

Table 1. Summary of water quality characteristics (mean ± SE) for the three elodeid bed treatments (bare, sparse, dense). Different letters indicate significant differences based on Duncan's post-hoc test. n = 8.

Characteristics	Bare	Sparse	Dense
Initial experiment			
Sediment total nitrogen (mg g^{-1} DW)	0.46±0.05[a]	0.44±0.02[a]	0.45±0.06[a]
Sediment total phosphorus (mg g^{-1} DW)	0.13±0.02[a]	0.13±0.01[a]	0.12±0.01[a]
Water column total nitrogen (mg L^{-1})	2.08±0.17[a]	2.10±0.13[a]	2.06±0.18[a]
Water column total phosphorus (mg L^{-1})	0.22±0.13[a]	0.22±0.11[a]	0.24±0.11[a]
Chl-a (µg L^{-1})	5.17±0.56[a]	6.59±0.79[a]	5.26±0.73[a]
Light attenuation coefficient (K_d) m^{-1}	6.28±0.17[a]	6.34±0.20[a]	6.31±0.12[a]
DO (mg L^{-1})	4.41±0.26[a]	4.45±0.38[a]	4.42±0.32[a]
pH	7.62±0.54[a]	7.68±0.33[a]	7.78±0.27[a]
Experiment harvest			
Water column total nitrogen (mg L^{-1})	2.25±0.37[a]	2.12±0.56[a]	1.25±0.11[b]
Water column total phosphorus (mg L^{-1})	0.30±0.33[a]	0.32±0.41[a]	0.08±0.01[b]
Chl-a (µg L^{-1})	12.46±1.23[a]	8.82±1.32[b]	3.36±0.95[c]
Light attenuation coefficient (K_d) m^{-1}	4.96±0.50[a]	2.69±0.56[b]	1.23±0.52[c]
DO (mg L^{-1})	6.46±1.05[a]	11.66±1.05[b]	17.46±2.05[c]
pH	7.82±0.38[a]	7.24±0.68[a]	7.89±0.40[a]
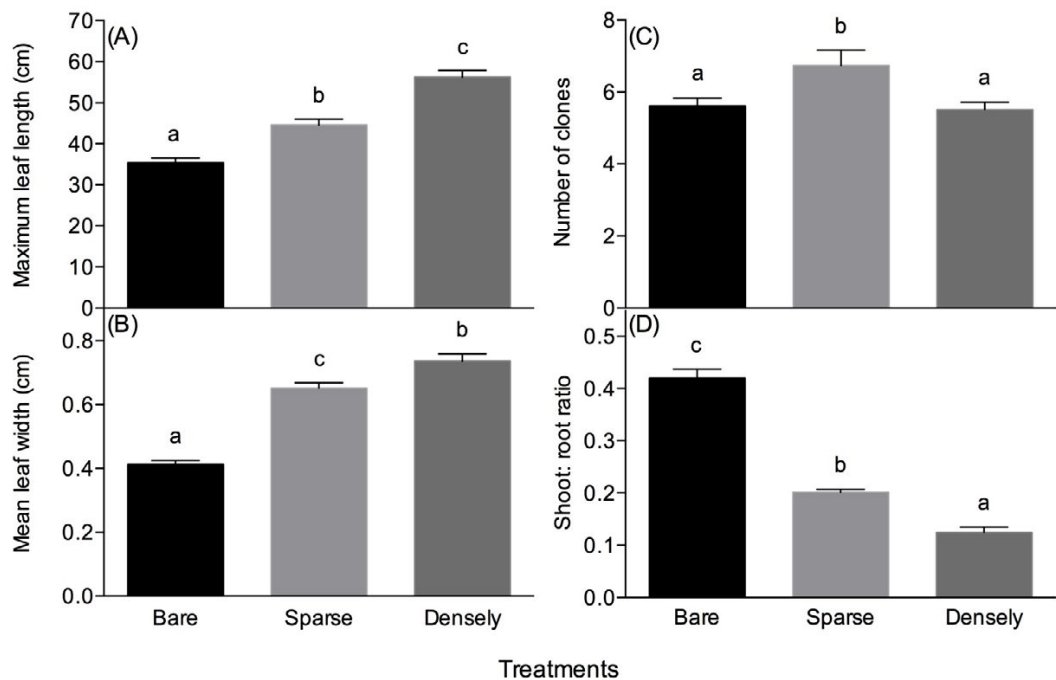
Fig. 2. Mean ± SE (n=8) of *Vallisneria spiralis* (A) maximum leaf length, (B) mean leaf width, (C) number of clones, and (D) root-to-shoot ratio for the bare, sparse, and dense elodeid bed treatments over a three-month experimental period. Bars with different letters represent statistically significant differences (P <0.05, one-way ANOVA with Duncan multiple comparison test). All data were transformed using the log (x) function.

DISCUSSION

The results of the mesocosm experiment revealed that, in line with the proposed hypotheses, elodeid species can be used as "nursery beds" and their presence has a positive effect on the seed establishment of *V. spiralis*. Additionally, *V. spiralis* seeds placed within a low-density (sparse) established elodeid species bed tended to produce more seedlings than seeds placed in a high-density (dense) elodeid bed or in bare sediment. Our results suggest that although elodeid species have positive effects on the restoration of SAV through seed utilization, these effects are density dependent. The results contribute to our understanding of the processes that limit seed germination and establishment in SAV and provide insight into how restoration strategies involving SAV seeds should be conducted. Most of the studies on submerged macrophyte seed germination and seedling growth have been based on various field observations and restoration efforts (Orth and Moore 1983, Jin *et al.* 2006, Lu *et al.* 2012). However, these studies are confounded by the highly variable water quality characteristics of aquatic habitats, making correlations between SAV seedling growth and water quality difficult. In contrast, mesocosm experimental systems, such as the one used in this study, allow environmental conditions to be tightly controlled and are an absolute requirement for identifying the biological potential of SAV seed germination and seedling growth (Ailstock *et al.* 2010). Recent attempts for the restoration of SAV using seeds have mainly focused on the development of practical procedures for propagation and seedling establishment (Qiu *et al.* 2001, Ye *et al.* 2011, Lu *et al.* 2012). Unlike these previous studies, the present study has focused on the creation of a microenvironment that is favorable for seedling growth (see also Ke and Li 2006, Hengst *et al.* 2010).

Many factors, such as climatic events and eutrophication, have contributed to the decline of SAV in aquatic systems, with the most notable factor being reductions in light availability associated with increased eutrophication and/or suspended solids and plankton (Scheffer and van Nes 2007, Best *et al.* 2008, Orth *et al.* 2010). Therefore, the first step to restore SAV is to create a microenvironment that increases the light availability to support plant survival and growth (Koch 2001). In our experiment, the established elodeid species significantly decreased the water turbidity and light attenuation, which may support the initial establishment of *V. spiralis*. However, the total biomass and plant biomass of the final harvested *V. spiralis* for the dense treatment were lower than those for the sparse treatment. The results are in line with those from a previous study that suggested that *V. spiralis* can coexist with other submerged elodeid species (*M. spicatum*) as long as conditions are not worsened by their presence (i.e., by creating a heavily shaded environment) (Xiao *et al.* 2011). In addition, shading by other organisms, such as phytoplankton and/ or epiphyton, may also strongly limit macrophyte growth in natural submerged plant restoration efforts (Jones *et al.* 2002, Jones and Sayer 2003).

Submerged macrophyte dominance can maintain a clear water state through various buffering mechanisms, such as fast growth, bicarbonate utilization, luxuriant uptake of nutrients, and allelopathy. In addition, the SAV provide refugia for macroinvertebrates, which are highly efficient harvesters of phytoplankton/epiphyton (Neckles *et al.* 1993, Li *et al.* 2008, 2009). In the present study, the established *M. spicatum* and *E. nuttallii* significantly decreased the Chl-*a* concentration in the water column, which may result from the allelopathic effect of these two submerged macrophytes (Erhard and Gross 2006, Hilt and Gross 2008). Furthermore, the variation in DO concentrations among treatments may reflect increased biological activity because a high density of established submerged macrophytes may cause an increase in oxygen production.

The sediment bottom environment can have an important impact on plant reestablishment from dormant propagules (Ailstock *et al.* 2010, Hengst *et al.* 2010, Marion and Orth 2010b). Sediment anoxia resulting from the anaerobic degradation of organic matter affects plants by regulating respiration and phytotoxin production (Koch *et al.* 1990, Holmer and Bondgaard 2001, Wu *et al.* 2009). Anoxic conditions can suppress net photosynthesis and thus inhibit bio-

mass production in aquatic plants (Xie *et al.* 2009). In our experiment, the root biomass of *V. spiralis* was higher in the bare treatment than in both of the established macrophyte treatments (sparse and dense), indicating root escape from the anoxic environment in the bare treatment. Similar results suggesting that stem or root elongation is an essential mechanism of adaptation to oxygen deprivation observed by previous studies (Wu *et al.* 2009, Cao *et al.* 2012). In addition, due to strong competition with established macrophytes under dense treatment, *V. spiralis* tended to allocate more resources to shoot growth, leading to longer and wider leaves (Xiao *et al.* 2006, Wang *et al.* 2008).

Seed germination and establishment can be affected by underwater movement (which may be caused be waves); substantial movement during this critical period can lead to seedling loss (Titus and Hoover 1991, Irfanullah and Moss 2004). For instance, in natural habitats, the soft sediments of eutrophic lakes are likely to be an important factor in seedling anchorage failure during/after restoration (Schutten *et al.* 2005). Approximately 15% of newly germinated seedlings became buoyant and floated to the water surface in the bare treatment in our experiment. However, no seedlings floated in the established elodeid species treatments, most likely because the seedlings were better anchored as the root system developed and there was less underwater movement in these treatments.

In China, the restoration of SAV in various water bodies has resulted in mixed outcomes and has focused mainly on restoration in bare, previously-vegetated areas (Qiu *et al.* 2001, Jin *et al.* 2006, Jiang *et al.* 2008, Lu *et al.* 2012) or same-species restoration within a bed (Ke and Li 2006, Dai *et al.* 2012a, b). However, seeds of submerged macrophytes appear to be able to survive long periods in the sediment (survive for decades in some extreme cases, de Winton *et al.* 2000). It is possible that established elodeid species can gradually create improved growth conditions, allowing not only the newly restored seeds of submerged macrophytes but also the seeds in the sediment (seed bank) to germinate (Qiu *et al.* 2001, Lu *et al.* 2012). In addition, our study was limited by only conducting experiments in small mesocosms. We did not perform a comprehensive examination of how other factors (e.g., wind and herbivory effects) in the natural eutrophic aquatic habitats may interact with elodeid species to determine the likely success of SAV seed restoration. For instance, a recent study revealed that over a wide range of environmental conditions, aquatic grazers significantly reduced the establishment and growth of macrophytes (Veen *et al.* 2013). Therefore, in future studies regarding the effect of "nursery beds" on SAV seed restoration, large-range field experiments should be considered. Nevertheless, our findings suggest that the restoration of SAV in aquatic habitats from seeds should be supported by decision makers and that the use of "nursery beds" with certain characteristics (i.e., established elodeid species of a certain density) will play an important role in the success of future restoration efforts. Furthermore, the results are of major relevance with regard to planning future SAV restoration projects in China.

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