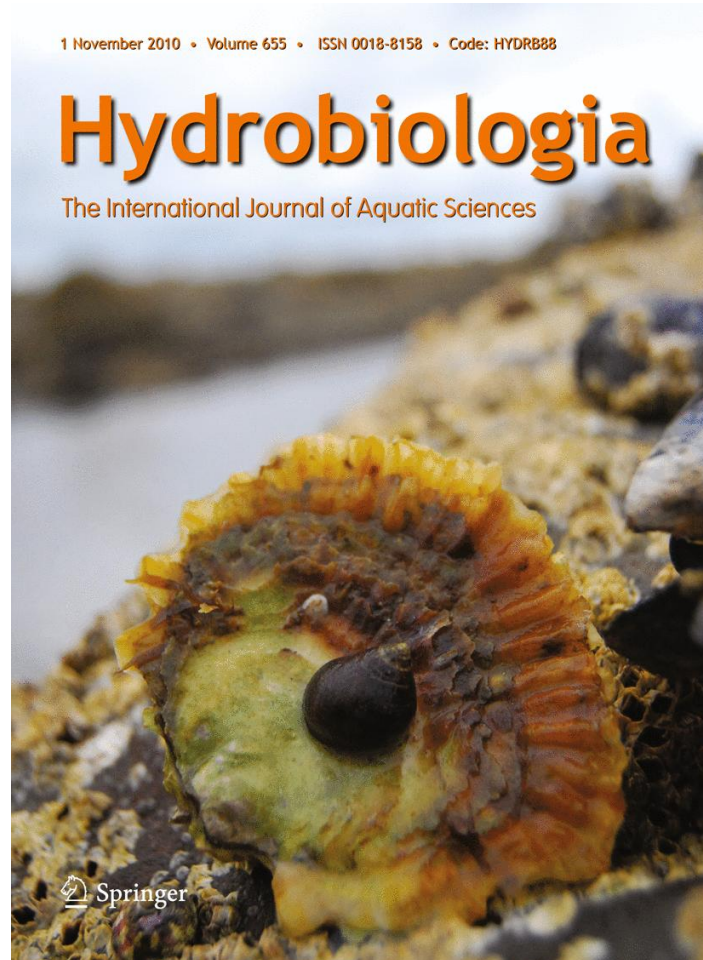


ISSN 0018-8158, Volume 655, Number 1



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Asexual propagations of introduced exotic macrophytes *Elodea nuttallii*, *Myriophyllum aquaticum*, and *M. propinquum* are improved by nutrient-rich sediments in China

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Received: 24 January 2010/Revised: 7 July 2010/Accepted: 3 August 2010/Published online: 17 August 2010
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Abstract An increasing number of recent studies indicate that multiple interacting factors can affect the invasion of plants. However, few studies have focused on asexual propagation and the interaction of propagation with environmental factors that regulate the invasive potential of introduced exotic species in aquatic habitats. This study was designed to investigate the differences in asexual propagation between introduced exotic and non-invasive native aquatic macrophytes in nutrient-poor and nutrient-rich sediments and to test the hypothesis that differences in asexual propagation (stem fragment production) and propagule establishment between introduced exotic and non-invasive native macrophytes are driven by sediment nutrient levels. Three exotic aquatic macrophytes (*Elodea nuttallii*, *Myriophyllum aquaticum*, and *M. propinquum*) recently introduced to China and their non-invasive native counterparts (*Hydrilla verticillata*, *M. oguraense*, and *M. ussuriense*) were used for comparison in nutrient-poor (TN 0.59 and TP 0.03 mg g⁻¹) and nutrient-rich (TN 2.35 and TP 0.10 mg g⁻¹) sediments. After 8 weeks of growth, the exotic species tended to produce more total

biomass, branch biomass and apical shoots and have higher relative growth rate (RGR) than their native counterparts in nutrient-rich sediment. Rooting efficiency and root growth of exotic fragments were higher than that of native counterparts in nutrient-rich sediment, although the survival rates of fragments did not differ between native and exotic species. In addition, superior traits (rooting efficiency and root growth) of exotic species were also observed in nutrient-poor sediment, but to a lesser degree than in nutrient-rich sediment. These results suggest that asexual propagation of these three introduced exotic macrophytes is more effective in nutrient-rich sediment than in nutrient-poor sediment in China.

Keywords Biological invasion · *Elodea* · Fragmentation · *Hydrilla* · *Myriophyllum* · Resource hypothesis

Introduction

Identifying the factors associated with the success of invasive species is helpful in predicting its invasion and controlling such species and to elucidate the interaction between invasive and native species in ecosystems (Pyšek & Richardson, 2007; Funk, 2008). To identify what factors contribute to making a species invasive, researchers have primarily compared performance between invasive and native congeners across environmental conditions (e.g., resource-use

Handling editor: S. M. Thomaz

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efficiency, Funk & Vitousek, 2007; growth plasticity, Funk, 2008). However, our understanding of the characteristics that contribute to invasion is still limited.

The invasion success of an exotic plant species is thought to involve a combination of environmental conditions and plant performance in both terrestrial (Pyšek & Richardson, 2007; Funk, 2008) and aquatic habitats (Maurer & Zedler, 2002; Hastwell et al., 2008). Ecologists have developed many hypotheses to explain the mechanisms that affect the establishment and spread of invasive species (Davis et al., 2000; Daehler, 2003; Blumenthal, 2006; Blumenthal et al., 2009). Among these hypotheses, the resource hypothesis and propagule pressure are well-studied. These two hypotheses are both used to elucidate how invasive species will successfully establish themselves and spread (Davis et al., 2000; Lockwood et al., 2005).

The resource hypothesis predicts that successful invasion by non-native species will result from the enrichment of available resources (e.g., light, nutrients, and water) (Davis et al., 2000). Direct support for the resource hypothesis is growing (Daehler, 2003; Blumenthal, 2006; Blumenthal et al., 2009). For instance, Hastwell et al. (2008) demonstrated that invasive exotic aquatic plants would produce a larger photosynthetic surface area than non-invasive native plants in nutrient-rich environments. In aquatic ecosystems, eutrophication caused by excessive anthropogenic nutrient loading (i.e., phosphorus and nitrogen) has many negative consequences (e.g., algal blooms, oxygen shortages, and loss of biodiversity) and often triggers instability in these ecosystems (Carpenter et al., 1998; Byers, 2002). In addition, eutrophication seems closely related to the invasion success of exotic species (Rahel, 2002). Indeed, several globally submerged weeds (e.g., *Hydrilla* and *Myriophyllum*) are usually more adaptive and competitive than native species under eutrophic conditions bringing them more advantages in resource uptake than native species and resulting in invasion by these species (Ruiz et al., 1999; Chase & Knight, 2006). While the growth of some exotic plants can clearly be facilitated by excess resource availability (e.g. Blumenthal, 2006; Blumenthal et al., 2009; Tanentzap & Bazely, 2009), very few studies have focused on the establishment phase of aquatic macrophytes in freshwater habitats (Lozon & Mac-Isaac, 1997; Byers, 2002).

However, an increase in the availability of resource is not enough to result in invasion. It must coincide with a sustained introduction of new propagules (Davis et al., 2000; Melbourne et al., 2007). As the number of propagules and/or the frequency of release events increases, the probability of a successful invasion increases (propagule pressure, Lockwood et al., 2005). Indeed, sustained pressure by propagules could prevent stochastic extinction of invaders after their initial introduction, even when environmental fluctuations are very high (Melbourne et al., 2007). To date, researchers have focused mainly on the sexual propagules and few experimental studies have addressed the role of the asexual clonal propagule supply on plant invasion. However, clonal plants are regarded as an important component in most ecosystems and the clonality of these species is positively correlated with their invasiveness (Liu et al., 2006). For example, large numbers of invasive plants invade by their asexual clonal propagules in China (44% of 126 invasive plants and 66% of the 32 most invasive plants) (Liu et al., 2006), and some of them have long history of invasion (e.g. *Alternanthera philoxeroides* (Mart.) Griseb., Pan et al., 2007). In addition, the output of propagules from native species may impact the species composition pattern of the local community (Boedeltje et al., 2008). Thus, propagation comparisons must be undertaken between exotic and native species in order to complete our understanding of the role of propagule pressure in plant invasions.

Compared with terrestrial plants, asexual reproduction is more frequent in aquatic plants (Santamaría, 2002). Stem fragments are important for propagation and dispersal in some aquatic plants (Santamaría, 2002). Compared to other means of asexual propagation, fragments have advantages in its easy production and dispersal, long periods of survival and high colonization and regeneration abilities (Riis & Sand-Jensen, 2006). The dispersal of fragments plays an important role in invading and establishing a new habitat for many invasive weeds. The invasions of *Myriophyllum spicatum* L. and *Hydrilla verticillata* (L.f.) Royle in North America (Smith & Barko, 1990; Madsen & Smith, 1999) and *Elodea canadensis* Michx. and *Elodea nuttallii* (Planch.) H. St. John in Europe (Barrat-Segretain et al., 2002) are examples of fragmentation dispersal. However, comparisons of fragment production and

establishment between exotic and native aquatic species are lacking.

In this study, we conducted two experiments. Three introduced exotic aquatic macrophytes in China and their closely related non-invasive native counterparts from two families (Hydrocharitaceae and Haloragaceae) were used for comparisons in nutrient-poor and nutrient-rich sediments, respectively. We hypothesized that nutrient-rich sediment conditions would allow exotic species to grow faster and produce more branches and apical shoots rather than native species and, consequently, increase propagule production potential. Furthermore, nutrient-rich conditions were hypothesized to give exotic propagules advantages in establishment compared to native species.

Materials and methods

Plant material

This study was conducted at The National Field Station of Freshwater Ecosystem in Liangzi Lake, China (30°5′–30°18′ N, 114°21′–114°39′ E). We used three native species: *H. verticillata*, *Myriophyllum oguraense* Miki., and *Myriophyllum ussuriense* (Regel) Maxim., and three exotic species: *E. nuttallii*, *Myriophyllum aquaticum* (Vell.) Verdc., and *Myriophyllum propinquum* A. Cunn. Stem fragments are the dominant means of dispersal for the aquatic plants that we used (Cook, 1990; Madsen & Smith, 1999; Barrat-Segretain et al., 2002). We determined each plant's origin using Flora Reipublicae Popularis Sinicae Tomus I (Wu, 2004). One exotic species and one native species from the same genera or family with similar morphology were compared. Thus, three pairs were established (Table 1). Following Xiong et al. (2008), we collected all individuals of exotic and native species from different populations in Liangzi Lake, and each pair of exotic and native plants was collected from the same site.

Experimental design

Plants were cultivated in mixed mud/sand sediments with defined nutrient level compositions. All the

experiments took place outdoors, and two different experimental set-ups were designed.

Growth traits in response to sediment nutrient level

This experiment lasted for 8 weeks (from May to July 2008) and focused on whether there were differences in nutrient-related growth and asexual propagation (fragments production) between introduced exotic and non-invasive native species. Two different sediment nutrient levels were established by mixing lake sediment with dry clean sand (both mud and sand were obtained from the lake): the nutrient-rich substratum contained 80% dry-weight of lake sediment (final TN and TP concentrations were 2.35 mg g⁻¹ TN, 0.10 mg g⁻¹ TP and 10.28% organic matter), and the nutrient-poor substratum contained 20% dry-weight of lake sediment (final TN and TP concentrations were 0.59 mg g⁻¹ TN, 0.03 mg g⁻¹ TP, and 2.57% organic matter). Each treatment used 30 apical shoots. All apical shoots were collected from multiple parent individuals of similar size cut into equal lengths of 7 cm, and fragment fresh weights were recorded. One apical shoot was planted in a plastic pot (1.75 l) that contained 1 kg (approximately 10 cm depth) of substratum. Consequently, the experiment was conducted in 360 pots and used a total of 360 apical shoots. All pots were then randomly placed in an outdoor pond that was filled to a depth of 60 cm with lake water (TN 0.62 ± 0.05 mg l⁻¹, TP 0.04 ± 0.02 mg l⁻¹ during the experimental period, mean ± s.e.). The pond water was changed weekly to minimize the influences of algal and sediment nutrient dissolution into the water. To prevent shoot competition, the pots were separated by low density white nylon netting. The water temperature and light intensity were recorded every day at noon (water temperature averaged 26.32 ± 2.28°C; light intensity at the water surface averaged 2250 ± 48.63 μmol m⁻² s⁻¹, mean ± s.e.).

Plants were harvested at the end of cultivation. The individual plants were segmented and categorized into roots, main stems, and branches. The fresh weight was measured for each plant individual. Plant tissue samples were dried at 80°C for 72 h and then weighed. Since the production of stem fragments is positively correlated with branch biomass and apical shoot number (reviewed from Madsen, 1997), here we use these two traits to indicate the supply of fragments.

Table 1 Aquatic plant pairs were used in a study comparing growth and establishment traits in sediments with different nutrient levels

Pairs	Species	Status to China	Origin	Introduced region (to worldwide)
Pair 1	<i>Elodea nuttallii</i>	Introduced exotic	North America	Australia, East Asia and Europe ^a
	<i>Hydrilla verticillata</i>	Non-invasive native	Eurasia	North America ^b
Pair 2	<i>Myriophyllum aquaticum</i>	Introduced exotic	South America	Australia, East Asia, Europe, North America and South Africa ^c
	<i>M. oguraense</i>	Non-invasive native	East Asia	–
Pair 3	<i>M. propinquum</i>	Introduced exotic	Australia and New Zealand	Asia ^d
	<i>M. ussuriense</i>	Non-invasive native	Asia	North America ^e

One exotic species and one native species to China from the same genera or family with similar morphologies were paired for comparison

^a Invasive in Europe and Japan (Cook, 1990; Barrat-Segretain et al., 2002) and introduced in China from Japan in 1986 by The Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences (Wei et al., 2007)

^b Invasive in North America (Madsen & Smith, 1999)

^c Invasive in these regions (Sheppard et al., 2005) and have escaped from aquaria in China (Xie et al., 2001)

^d Export from New Zealand as an ornamental plant (Yeates & Williams, 2006)

^e Collected only in British Columbia in North America (Ceska et al., 1986)

Propagule establishment in response to sediment nutrients

This experiment also lasted for 8 weeks (from July to August 2008) and was designed to discover whether sediment nutrients would give the exotic species advantages that increase the establishment of plant fragments compared to their native counterparts. Fragments of each species were apical, unbranched parts that were cut into equal lengths of 7 cm. The fragments were arranged in plastic experimental boxes (35 cm × 25 cm × 10 cm; length × width × height) that contained 2 cm of sediment and 7 cm of lake water. Two sediment nutrient levels were established (sediment compositions identical to the first experiment). The fragments were then placed on the water's surface. For each treatment, three boxes containing ten fragments each ($n = 3$) were randomly placed outdoors. Consequently, the experiment was conducted in 36 experimental boxes and used a total of 360 apical shoots. Lake water (TN $0.73 \pm 0.03 \text{ mg l}^{-1}$, TP $0.06 \pm 0.01 \text{ mg l}^{-1}$ during the experimental period, mean \pm s.e.) was added to the boxes everyday to compensate for evaporation and to maintain a constant water level. Water temperature and light intensity were recorded every day at noon (water temperature averaged $30.38 \pm 1.46^\circ\text{C}$; light intensity at the water surface averaged $2834 \pm 41.22 \mu\text{mol m}^{-2} \text{ s}^{-1}$, mean \pm s.e.).

Three parameters were recorded: (1) survival measured as the percentage of living fragments; (2) rooting efficiency measured as the percentage of fragments that anchored themselves into sediment; and (3) root growth measured as the maximum length of adventitious roots. The fragments were checked twice a week (every 3–4 days) for rooting efficiency and survival, and dead plant material was removed from the boxes. Fragments that successfully rooted were counted and planted into other empty containers next to the experimental boxes (with the same size and sediment nutrient levels, and the roots of fragments were put into sediment) so that their development would not influence other fragments. When a new bud developed and detached from the fragment, it was counted as a new individual and its growth was recorded in the same way as for other fragments. Surviving fragments included fragments floating in water, fragments that anchored themselves into the sediment and fragments that were uprooted. The rooting efficiency of the fragments was expressed as $\text{FN}_R/\text{FN}_O \times 100\%$, where FN_R is the number of fragments rooted into the sediment, and FN_O is the number of original fragments (the value is 10) (Barrat-Segretain & Bornette, 2000). The maximum root lengths of fragments were measured at the end of experiment, including the fragments floating in water and the fragments that rooted in the sediment.

Statistical analyses

In the first experimental design, an additional 30 fragments of each species were used for calculating the water content to obtain the initial dry mass of fragments. Data including plant total biomass, branch biomass, apical shoot number and relative growth rate (RGR) were analyzed using two-way ANCOVAS with species (exotic and native) and nutrient levels as the between-subject main effect and using the initial fragment dry mass as a covariate. The RGR was calculated as $RGR = [\ln(\text{Final Biomass}) - \ln(\text{Initial Dry Mass})]/\text{days}$ (Burns, 2004). In the second experimental design, survival percentages, rooting efficiency percentages, and root lengths were calculated as the mean value of one box. Dead fragments and the fragments that did not produce root were calculated as zero. Data were analyzed using a nested ANOVA with species (exotic and native) and nutrient level as the between-subject main effect, and with experimental boxes nested within nutrient treatments. We used Bonferroni tests to compare levels within factors for significance ($P < 0.05$). All data of the two experiments were transformed using a $\log(x + 1)$ function and then analyzed to satisfy homogeneity of variances or normal distribution of

residuals. All data were analyzed using SPSS 13.0 (SPSS, Chicago, IL, USA).

Results

Plant growth traits

After 8 weeks of growth, initial dry mass was highly correlated with total biomass, branch biomass, apical shoot number, and RGR for both exotic and native species (Table 2). When the initial dry mass was used as a covariate, most the four growth traits were significantly greater for exotic species than for their native counterparts in nutrient-rich sediment (there was only one exception in the apical shoot number in one plant pair) (Fig. 1). In contrast, most of the growth traits were similar between exotic and native species in nutrient-poor sediment. Only branch biomass and apical number in exotic *E. nuttallii* and the total biomass and RGR in *M. aquaticum* were significantly higher than that for native species (*H. verticillata* and *M. oguraense*), respectively (Fig. 1). The effects of sediment nutrients and species on those four traits were significant, and the interactions of sediment nutrient and species were also

Table 2 *F* and *P* values for species (exotic vs. native) and nutrient gradients for total biomass, branch biomass, apical number and RGR (two-way ANCOVAS), using initial dry mass as a covariate

Source	Total biomass			Branch biomass			Apical number			RGR		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
<i>E. nuttallii</i> vs. <i>H. verticillata</i>												
Nutrient	1,112	107.918	<0.001	1,114	118.771	<0.001	1,112	117.711	<0.001	1,112	100.327	<0.001
Species	1,112	13.302	<0.001	1,114	91.896	<0.001	1,112	355.642	<0.001	1,112	7.422	0.007
Initial dry mass	1,112	6.263	0.014	1,114	24.663	<0.001	1,112	32.321	<0.001	1,112	81.353	<0.001
Nutrient × species	1,112	6.639	0.011	1,114	10.800	0.001	1,112	13.138	0.001	1,112	11.081	0.001
<i>M. aquaticum</i> vs. <i>M. oguraense</i>												
Nutrient	1,113	782.344	<0.001	1,113	436.755	<0.001	1,115	141.181	<0.001	1,114	486.000	<0.001
Species	1,113	884.503	<0.001	1,113	75.236	<0.001	1,115	9.175	0.003	1,114	621.386	<0.001
Initial dry mass	1,113	543.965	<0.001	1,113	190.612	<0.001	1,115	67.202	<0.001	1,114	19.256	<0.001
Nutrient × species	1,113	15.512	<0.001	1,113	43.571	<0.001	1,115	0.481	0.489	1,114	29.295	<0.001
<i>M. propinquum</i> vs. <i>M. ussuriense</i>												
Nutrient	1,114	319.380	<0.001	1,114	238.182	<0.001	1,115	187.580	<0.001	1,114	353.957	<0.001
Species	1,114	23.478	<0.001	1,114	37.729	<0.001	1,115	73.804	<0.001	1,114	4.046	0.047
Initial dry mass	1,114	69.192	<0.001	1,114	33.395	<0.001	1,115	13.057	<0.001	1,114	10.989	0.001
Nutrient × species	1,114	13.668	<0.001	1,114	22.102	<0.001	1,115	53.217	<0.001	1,114	13.007	<0.001

All data were transformed with $\log(x + 1)$

significant (there was one exception in the apical shoot number in one plant pair) (Table 2).

Propagule survival

The survival rates of two pairs of plants were extremely high in both sediment nutrient levels. Therefore, there were no significant survival differences between exotic and native species or between sediment nutrient levels in these two pairs (Fig. 2a, b; Table 3). Only one exotic species (*M. propinquum*) had a higher survival rate than its native counterpart;

the fragments of its native counterparts (*M. ussuriense*) did not survive in either sediment during the experiment (Fig. 2c; Table 3).

Propagule rooting efficiency and root growth

Rooting efficiency and root growth differed significantly between species and across sediment nutrient levels. Most of the significant interactions between nutrients and species indicated that differences in rooting efficiency and root growth between exotic and native fragments were significantly influenced by

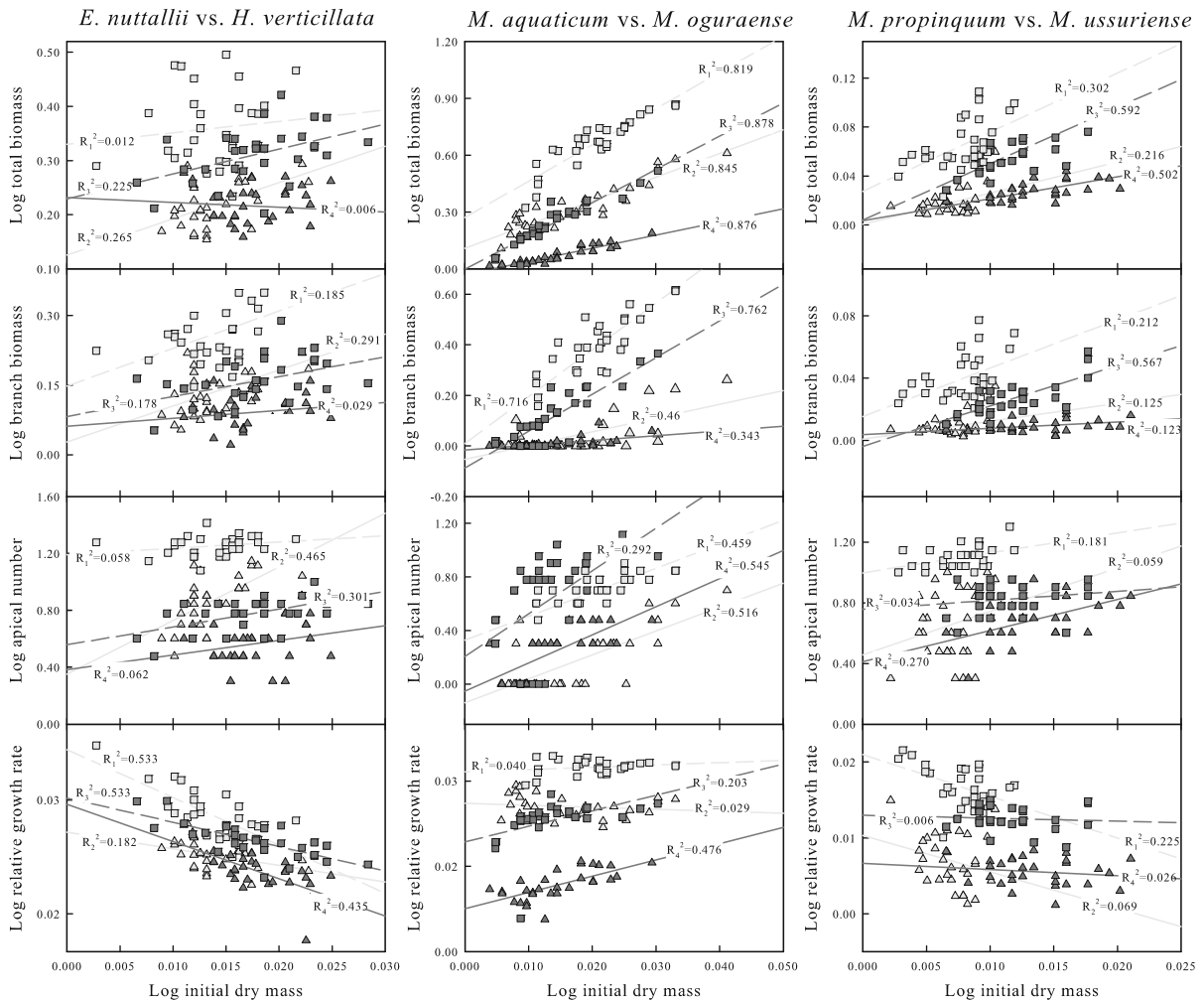


Fig. 1 Regression results showing relationships between fragment initial dry mass and the following traits: total biomass, total branch biomass, apical number, and RGR for the three species pairings, all on a log–log scale. Grey exotic species; dark grey native species; triangle symbols (solid lines) nutrient-poor sediment levels; square symbols (dashed lines)

nutrient-rich sediment levels. R_1^2 and R_2^2 values indicate the regression coefficients for exotic species in nutrient-rich and -poor sediments, respectively; R_3^2 and R_4^2 indicate the regression coefficients for native species in nutrient-rich and -poor sediment, respectively

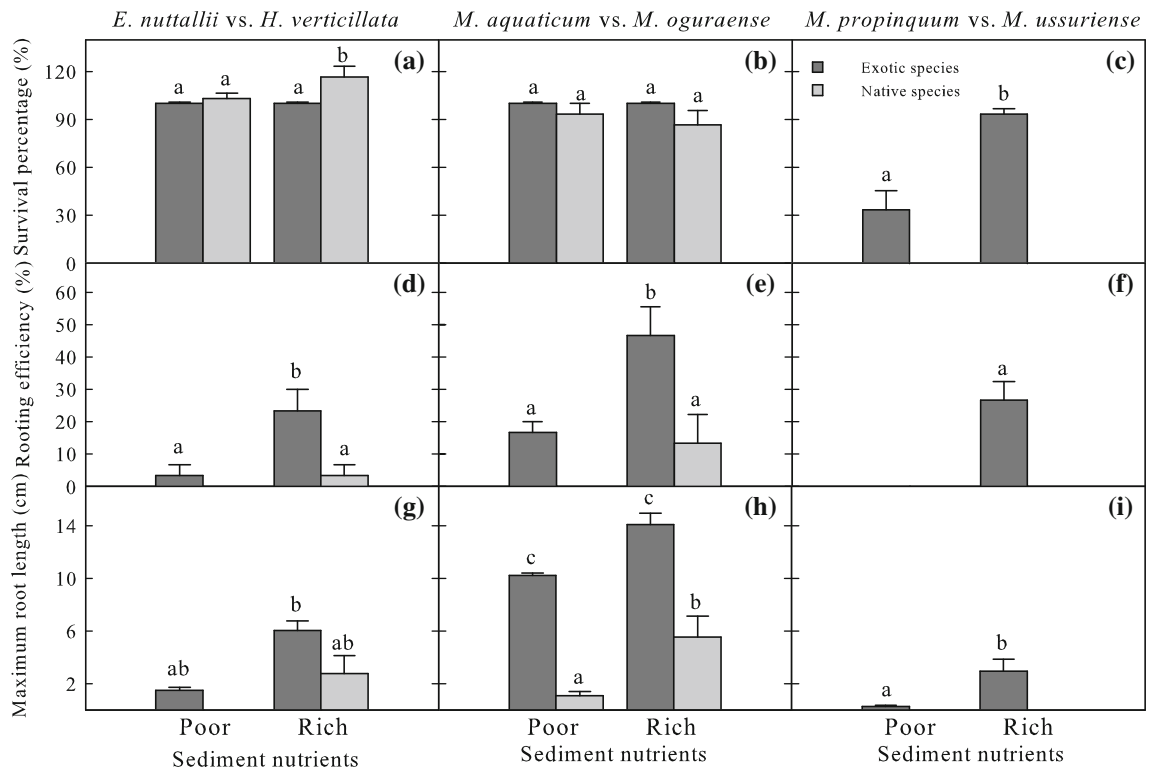


Fig. 2 Mean percentages (\pm s.e.) [survival percentage (a, b, and c) and rooting efficiency (d, e, and f), $n = 3$] and mean root growth per box (cm \pm s.e.) [maximum root lengths (g, h, and i), $n = 3$] between exotic species (dark grey bars) and native species (grey bars) in nutrient-poor and nutrient-rich

sediments. Bars sharing the same letters indicate no significant differences between treatments (Bonferroni test, $P > 0.05$). Survival percentages can be over 100% because detached new buds are counted. All data are log ($x + 1$) transformed

sediment nutrients (Table 3). Rooting efficiency and root growth of the three exotic species were higher than those of the native species in nutrient-rich and nutrient-poor sediments, respectively (Fig. 2b–f; Fig. 2g–i).

Discussion

Many previous studies have determined that soil nutrient levels play an important role in determining invasion success (Daehler, 2003; Funk & Vitousek, 2007). Some extremely invasive aquatic weeds in China (e.g., *Eichhornia crassipes* (Mart.) Solms and *A. philoxeroides*) tend to increase their biomass and clonal propagation in high nutrient environments (Xie et al., 2004; Pan et al., 2006), especially in eutrophic conditions in the field (Xie et al., 2001; Pan et al., 2007). Our results revealed that the growth traits of the exotic species we tested were superior to their native

counterparts in nutrient-rich sediment, but most of the traits were similar in nutrient-poor sediment, which are consistent with previous studies (Daehler, 2003; Blumenthal, 2006). As sediment nutrients increases, exotic species tend to allocate more resources (e.g., nitrogen) to photosynthesis but less resource to defense (due to released from nature enemies), which is likely to cause a growth and reproduction increase in these species (Blumenthal, 2006; Feng et al., 2009). High growth rates may lead to more branch productions which not only increase propagation (fragment) production but also allow these exotic species to be superior to native species when competing for waterborne resources and light (Barrat-Segretain, 2005; Wang et al., 2008). This positive correlation between propagation potential and competitiveness is unique in aquatic habitats, and may explain the rich local abundance and rapid spread of some invasive aquatic plants in nutrient-rich habitats (Boedeltje et al., 2008). Even in nutrient-poor environments,

Table 3 *F* and *P* values for species (exotic vs. native) and sediment nutrients for survival percentage, rooting efficiency, and maximum root length (a nested ANOVA, with experimental boxes nested within nutrient treatments)

Source	d.f.	Survival percentage		Rooting efficiency		Maximum root length	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>E. nuttallii</i> vs. <i>H. verticillata</i>							
Nutrient	1,4	3.336	0.142	9.870	0.035	10.577	0.031
Species	1,4	7.683	0.050	42.195	0.003	13.835	0.020
Nutrient × species	1,4	3.336	0.142	20.439	0.011	<0.001	0.995
Boxes (nutrient)	4,4	1.000	0.500	4.275	0.094	1.818	0.228
<i>M. aquaticum</i> vs. <i>M. oguraense</i>							
Nutrient	1,4	0.370	0.576	37.917	0.004	14.087	0.020
Species	1,4	3.203	0.148	9.585	0.036	86.561	<0.001
Nutrient × species	1,4	0.370	0.576	0.639	0.469	8.353	0.045
Boxes (nutrient)	4,4	1.000	0.500	0.176	0.939	1.732	0.304
<i>M. propinquum</i> vs. <i>M. ussuriense</i>							
Nutrient	1,4	15.802	0.016	78.029	<0.001	16.059	0.016
Species	1,4	96.354	<0.001	78.029	<0.001	31.338	0.005
Nutrient × species	1,4	15.802	0.016	78.029	<0.001	16.059	0.016
Boxes (nutrient)	4,4	1.000	0.500	1.000	0.500	1.000	0.500

All data were transformed with $\log(x + 1)$

however, invasion can still occur occasionally because invasive species use limited resources more efficiently than native species (although on short timescales) (Funk & Vitousek, 2007).

Since we used branch biomass and apical number instead of detached fragments to assess differences in asexual propagule production between exotic and native counterparts, our data did not directly address propagule supplement. Nevertheless, branch biomass and apical number correlate strongly with the abundance of plant asexual propagules (stem fragments) in aquatic macrophytes (Riis & Sand-Jensen, 2006; Madsen, 1997). First, stems could detach from parent plants and turn into fragments, a process which may arise from biotic and abiotic factors (Barrat-Segretain, 1996; Sidorkewicz et al., 2000; Riis & Sand-Jensen, 2006; Xiong et al., 2008). For instance, Pieczyńska (2003) provided direct evidence that *E. canadensis* produced more fragments due to herbivory by snails. Second, because of low production costs and high dispersal rates, fragmentation is a highly suitable means of dispersal in aquatic habitats (Santamaría, 2002). Therefore, the exotic species that we tested (which produced more branches and apical shoots than native counterparts) may increase the propagule pool under high-level nutrient conditions and

potentially increase invasion success in both local habitat and surrounding habitats (Didham et al., 2007).

Although the survival of fragments of two exotic species (*E. nuttallii* and *M. aquaticum*) did not show significant differences compared to their native counterparts in our experiment, it should be noted that all fragments of both plant pairings had extremely high survival rates in both sediment nutrient levels. Our results were still consistent with previous invasive aquatic plant research, which found that the fragments of these species are adapted for propagation and are capable of floating in the water column for days to weeks before settling and rooting (Sidorkewicz et al., 2000; Barrat-Segretain et al., 2002; Chadwell & Engelhardt, 2008). No fragments of native *M. ussuriense* survived in our experiment, which we cannot fully explain. Further work is needed to explain this unexpected result.

All three exotic species in our study had faster root growth and higher rooting efficiency than native species in nutrient-rich sediment, indicating that a faster root growth rate may provide advantages for the rapid settlement of exotic fragments (Barrat-Segretain, 2005). This rooting strategy (sometimes referred to as the 'always-ready' strategy, Barrat-Segretain &

Bornette, 2000) could be affected by nutrient availability (Chadwell & Engelhardt, 2008). It is common that high nutrient availability would increase main root elongation (Potters et al., 2006). However, if the nutrient availability in the field were too low (either due to abundance of pre-existing species or low nutrient conditions), then some fragments of exotic species would not settle and would eventually die, even if they produced roots (Barrat-Segretain et al., 2002; Chadwell & Engelhardt, 2008). In addition, the rooting strategy of exotic species may help, at least in part, to explain why the establishment phases of exotic species are especially facilitated in areas of anthropogenic disturbance (e.g., eutrophic water bodies or some land uses) (Lozon & MacIsaac, 1997). Thus, managing the spread of fragments may seem to be an important way to fight fragment-spreading exotic species in the future (Chadwell & Engelhardt, 2008).

Our results are also consistent with previous research which found that eutrophic conditions may in part enhance the invasion ability of some aquatic plants (Byers, 2002; Thiébaud, 2007). Indeed, most of the exotic species we tested in this study are known to prefer and adapt to nutrient-rich habitats (e.g., Sytsma & Anderson, 1993; Thiébaud, 2007). Thus, these species may achieve competitive dominance over their native counterparts through stronger asexual propagation and establishment abilities under conditions of nutrient enrichment. In addition, eutrophication involves complex interactions, such as algal blooms, loss of biodiversity, and changes of the food web in aquatic ecosystems (Carpenter et al., 1998; Chase & Knight, 2006) that may weaken the resistance of native biota to invasion by exotic species (Byers, 2002). Furthermore, growth and physiology of some invasive species are well-suited to conditions of high algal abundance that occur with eutrophication (Ruiz et al., 1999; Chase & Knight, 2006). Therefore, it is reasonable to speculate that the present eutrophication of China would improve the growth and chances of establishment of these exotic species. For instance, *E. nuttallii* is replacing local submersed macrophytes in the eastern part of China's Taihu Lake where eutrophication is a serious issue (Gu et al., 2005), and *M. aquaticum* is invading Taiwan Island (Li & Hsieh, 1996).

Our study was limited by comparing only three pairs of aquatic species at two different nutrient levels. We did not provide a complete examination of

how exotic species outperform native counterparts in the field. For instance, *H. verticillata* is invading all over North America but not *E. nuttallii* (Madsen & Smith, 1999). A possible explanation for this might be the interactions between resource availability and natural enemy (or pathogen) release (Blumenthal, 2006; Blumenthal et al., 2009). Due to the release of natural enemies (or pathogens), the growth and establishment of exotic species could still be facilitated in high resource environments even where native species are well adapted (Blumenthal, 2006). Future studies on aquatic exotic plants should focus more attention on the multiple interacting factors in the field and involve more species. This study focused only on growth and establishment in one season (summer); additional field or experimental data from different seasons across the year may yield different results (see Barrat-Segretain & Bornette, 2000; Collingsworth et al., 2009). In addition, introduced exotic species generally have an acute phase immediately after their arrival and a chronic phase over time (Strayer et al., 2006). For instance, in Europe, *E. canadensis* is in its chronic phase whereas *E. nuttallii* is in its acute phase (Barrat-Segretain et al., 2002). Therefore, further studies will involve comparing growth responses to different levels of resource availabilities between recently introduced exotic and native species across multiple seasons, and a long-term perspective should be considered when studying impacts of these species.

Conclusion

Previously, few investigators have stated that there are differences between exotic and native species in asexual propagule production that are correlated with resource availability in aquatic habitats. The results presented here supported our hypothesis that sediment nutrients would significantly increase growth traits (growth and potential propagule production) and establishment traits (root growth and rooting efficiency) of exotic species compared to native species. A large propagule pool and high fragment performance may improve the invasiveness of these exotic species (Barrat-Segretain et al., 2002), especially in nutrient-rich habitats. Although the proportion of invasive aquatic weeds is small in China (only 4% of the species on the 'Namelist of 100 alien

invasive species in China' excluding phytoplankton, Xu et al., 2004), their status in aquatic habitats, where large numbers of aquatic plants have been introduced intentionally or unintentionally with many escaping into natural environments, is not encouraging (Xu et al., 2004). It is possible that the three exotic species that we tested may become a potential threat to local aquatic communities if the eutrophication process continues and the spread of stem fragments of exotic species is not controlled. Moreover, great efforts should be made to manage the environmental context to prevent exotic propagules from producing and dispersing.

Acknowledgments We thank Keyan Xiao, Wen Xiong, and Qiang Wang for discussion and comments on the manuscript. We also greatly appreciate Dr. Sidinei M. Thomaz and two anonymous reviewers for valuable comments on an early version of the manuscript. This research was supported by the National Natural Science Foundation of China (30770363 and 30930011).

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