PRIMARY RESEARCH PAPER

Differences in leaf nitrogen content, photosynthesis, and resource-use efficiency between *Eichhornia crassipes* and a native plant *Monochoria vaginalis* in response to altered sediment nutrient levels

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Abstract *Eichhornia crassipes* is one of the world's most prevalent invasive aquatic plants, causing significant ecological and socio-economic impacts in introduced areas. In this study, we compared the leaf resource capture- and use-related traits of *E. crassipes* with its confamilial native aquatic plant *Monochoria vaginalis* at three nutrient levels. Our results showed that leaf nitrogen content based on mass, leaf nitrogen content based on area, N:C, photosynthetic rate, specific leaf area, and leaf construction cost of *E. crassipes* increased significantly with increasing levels of nutrition, the mean values of these traits increased 0.55, 0.35, 0.51, 0.43, 0.21, and 0.07 times from low nutrient level to high, respectively. These traits (except for the leaf construction cost) in *M. vaginalis* remained unchanged. At low nutrient level, *M. vaginalis* had a higher leaf nitrogen content, N:C, photosynthetic rate, specific leaf area, and water-use efficiency than *E. crassipes*. At high nutrient level, *E. crassipes* had a higher photosynthetic rate and photosynthetic nitrogen-use efficiency than *M. vaginalis*, suggesting that the invasiveness of *E. crassipes* was dependent on the availability of resources in environment. In addition, our results supported the fluctuating resources hypothesis, indicating that an increased level of nutrients in the environment will increase the invasiveness of *E. crassipes*.

Introduction

Invasive species degrade human health (Juliano & Lounibos, 2005), cause huge economic losses (Pimentel et al., 2005), reduce biodiversity, and alter species composition, structure, processes, and function of the invaded ecosystems (Vitousek, 1990; D'Antonio & Kark, 2002; Svilà et al., 2011). Unfortunately, due to an increase in international commerce, more alien species have been introduced into new habitats (Cohen & Carlton, 1998; Hulme, 2009). In addition, human activities and global changes (such as changes in land-use pattern, nitrogen deposition, and increased atmospheric CO_2) have facilitated such invasions and enhanced their adverse effects (Dukes & Mooney, 1999). Therefore, to improve our ability to control existing invasive species and forecast

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potentially invasive species, it is necessary to determine the mechanisms of invasion and identify the traits that increase the invasiveness of a species.

Resource-use efficiency affects the growth, reproduction, and competitiveness of plants. Vitousek (1986) proposed that, if the life history traits and susceptibility to herbivore pressure are similar between an invasive and a native species, the successful invasive species must either use limited resources more efficiently than the native species or use them at times when they are unavailable to the native species. The traits commonly linked to invasiveness in plants include higher relative growth rate (Pattison et al., 1998; Burns, 2004; Garcia-Serrano et al., 2005; Grotkopp & Rejmánek, 2007; Xie et al., 2010), higher photosynthetic rate (Pattison et al., 1998; Baruch & Goldstein, 1999; Durand & Goldstein, 2001; McDowell, 2002; Funk & Vitousek, 2007), larger specific leaf area (Grotkopp & Rejmánek, 2007; Feng et al., 2008; Osunkoya et al., 2010), lower leaf construction cost (Baruch & Goldstein, 1999; Feng et al., 2007; Osunkoya et al., 2010), and higher photosynthetic nitrogen-use efficiency (Niinemets et al., 2003; Feng et al., 2007; Feng & Fu, 2008; Matzek, 2011). All of these traits are associated with better resource-use strategy, and some traits expressed together to facilitate invasion.

Resource availability can also influence the resource-use strategy of plants. In a resource-rich environment, plants may have a higher relative growth rate, photosynthetic rate and leaf nutrient concentration, while in a resource-poor environment, plants may have a lower relative growth rate, photosynthetic rate, and leaf nutrient concentration (Chapin, 1980; Bloom et al., 1985). Many studies have found that it is rare for invasive plants to consistently outperform native plants; only in resource-rich environments do invasive plants display advantageous traits such as a higher relative growth rate, photosynthetic rate, and specific leaf area (Daehler, 2003; Burns, 2004). Davis et al. (2000) proposed the fluctuating resources hypothesis and concluded that a plant community becomes more susceptible to invasion when there is either an increase in the amount of unused resources or a decreased uptake of the resources by the native plant community. Accordingly, invasive plants have higher resource-use efficiency than native plants only in resource-rich habitats. In contrast, comparing 19 pairs of phylogenetically related invasive and native species, Funk &

Vitousek (2007) found that the invasive plants had a higher instantaneous photosynthetic capacity and photosynthetic nitrogen-use efficiency than the native plants in three habitats in Hawaii in which the light, water, or nutrient availability was limiting to plant growth. Matzek (2011) also found that five invasive pines had a higher relative growth rate, photosynthetic capacity, and photosynthetic nitrogen-use efficiency than five non-invasive pines in a nutrient-limiting environment. Owing to the inconsistent results for the resource-use efficiency of invasive and native plants under different resource conditions, Funk & Vitousek (2007) suggested that more data are needed regarding how the patterns of resource acquisition and usage vary in response to fluctuating resources between invasive and native plants. Some researchers have compared many resource capture- and use-related traits of invasive and native plants under single conditions (Baruch & Goldstein, 1999; Feng et al., 2007; Funk & Vitousek, 2007; Feng & Fu, 2008; Matzek, 2011), but few studies investigated the different patterns of these traits in response to changes in the resource availability. In addition, the plants being studied were all terrestrial plants.

Eichhornia crassipes (Mart.) Solms (Water hyacinth) is one of the world's most prevalent invasive aquatic plants in the monocotyledonous family Pontederiaceae, having significant ecological and socioeconomic impacts in areas of introduction (Villamagna & Murphy, 2010). Many studies have been conducted on *E. crassipes*, mostly focusing on the effect, control, and utilization of the plant, instead of the invasion mechanism. Although some researchers have studied the invasion mechanism of *E. crassipes* (Xie & Yu, 2003; Xie et al., 2004), few studies have compared its traits with phylogentically related plants. Indeed, comparisons with a closely related species are difficult because *E. crassipes* is the only floating species in the family Pontederiacea. Other studies (Parker & Hay, 2005; Xiong et al., 2008) have compared the native herbivore preference for *E. crassipes* with the confamilial aquatic emergent plants *Pontederia cordata* L. and *Monochoria vaginalis* (Burm.f.) Presl, native in North America and Asia, respectively. Although *E. crassipes* is normally a free-floating plant, in some habitats, such as flooded sites, swamps and at the edges of pools, ditches, lakes, and canals, it can root and grow as an emergent plant (Njambuya & Triest, 2010). During seedling stage, *E. crassipes* must root in muddy

banks of waters or in rice field. Because *E. crassipes* has similar leaf structure with *M. vaginalis*, we compared the leaf traits of these two species at three nutrient levels to address the following questions: (i) Does *E. crassipes* differ from *M. vaginalis* in resource capture- and use-related traits? (ii) Does *E. crassipes* display different morphological and physiological patterns compared with *M. vaginalis* in response to changes in nutrient levels? (iii) Does *E. crassipes* achieve a higher photosynthesis and resource-use efficiency than *M. vaginalis* only at high nutrient level?

Materials and methods

Study plants

Originally from South America, *E. crassipes* has invaded more than 62 countries in the tropical, subtropical, and temperate zones of Africa, Asia, North America, and Oceania (Howard & Harley, 1998). *E. crassipes* reproduces both sexually and asexually (data not published) but is spread primarily by vegetative propagation in China. Under the appropriate environmental conditions, *E. crassipes* can reproduce a new ramet in 5 days by cloning; a single plant can produce 140 million daughter plants (28,000 tons of fresh weight) every year, sufficient to cover 140 ha (Ogutu-Ohwayo et al., 1997). Therefore, *E. crassipes* has been considered one of the fastest growing plants on the earth (Abbsi & Nipaney, 1986). In invaded areas, *E. crassipes* can change the hydrological environment, destroy the native animal and plant communities, and reduce the species diversity, thus altering the ecosystem structure and function by disrupting the food chain and nutrient cycling (Villamagna & Murphy, 2010). Accordingly, *E. crassipes* has been listed as one of the 100 most dangerous invasive species by IUCN (Lowe et al., 2000).

The native annual aquatic emergent plant *M. vaginalis* also belongs to the Pontederiaceae family and is distributed in Japan, Malaysia, Philippines, India, Nepal, Bhutan, and the northern and southern provinces of China. *M. vaginalis* is often gregarious and is typically found in flooded sites, swamps, rice fields, and edges of pools, ditches, and canals. *M. vaginalis* reproduces by sexual propagation, flowering in August and September, and fruiting in September and October in China.

Experimental design

This experiment was conducted in The National Field Station of Freshwater Ecosystem of Liangzi Lake, Hubei Province, China (30°50′–30°180′N, 114°210′–114°390′E). A total of 40 clonal ramets of *E. crassipes* and 40 seedlings of *M. vaginalis* were collected in a field population of Liangzi Lake at the end of July. The plants were cultivated in eight circular basins of 36 cm diameter with a sand sediment and 5 cm water depth. One week later, 18 plants of each species with similar weight and height (the mean fresh weight of *E. crassipes* was 8.44 ± 0.36 g, and *M. vaginalis* was 6.61 ± 0.56 g) were transferred to 36 rectangular basins (36 cm length $\times$ 30 cm width $\times$ 15 cm height) filled with approximately 8 cm of sand (from the banks of Liangzi Lake, N:P = 0.13:0.014 mg g^{-1}) and 7 cm depth of water (from Liangzi Lake, N:P = 0.71:0.04 mg L^{-1}). All plants were rooted in sand, and grown under three nutrient levels, with six replicas each. To the high and medium nutrient treatments, 10 and 5 g, respectively, of slow-release fertilizer (containing 16 g N and 8 g P per 100 g) were mixed in sand; no fertilizer was added to the low nutrient treatment. The nitrogen concentration of the three nutrient levels were 0.06, 0.14, and 0.22 mg g^{-1}, similar to the sand, soil, and plant litter sediments of Liangzi Lake, respectively. To facilitate the management of the experiment, six plants in the same treatment were arranged as a group, and six groups were randomly placed on an outdoor cement platform (10 m length $\times$ 8 m width). All plants were exposed to the same intensity and duration of light and were watered daily to maintain a constant water level until they were harvested.

Measurements

At 40 days after planting, all plants (except for *E. crassipes* at the low nutrient level) started inflorescence stage, and their leaf traits were measured (Table 1). The net photosynthetic rate (Pn) and stomatal conductance (Gs) was determined on the youngest fully expanded leaves using a Li-6400 Portable Photosynthesis System (Li-Cor, USA) under a photosynthetic photon flux density (PPFD) of natural light >1,700 µmol m^{-2} s^{-1}, the air temperature was moderate (25–35°C) and the relative humidity ranged between 60 and 70% at 11:00 a.m. to 2:00 p.m. The

Table 1 Definitions and abbreviations of measured traits

Traits	Description	Units
N_{mass}	Leaf nitrogen content based on mass	%
N_{area}	Leaf nitrogen content based on area	g m^{-2}
N:C	Ratio of leaf nitrogen and carbon content on mass	
P_{max}	Maximum photosynthetic rate at saturating light	μmol m^{-2} s^{-1}
SLA	Leaf area per mass	cm^2 g^{-1}
LCC	Leaf construction cost	g cm^{-2}
PUNE	Photosynthetic nitrogen-use efficiency	μmol g^{-1} s^{-1}
WUE	Water-use efficiency	μmol mmol^{-1} s^{-1}

leaves used for the photosynthesis measurements were detached, and leaf area was measured using a Li-3100 Area Meter (Li-Cor, USA) to calculate the light-saturated photosynthetic rate per unit area leaf (P_{max}). From each leaf, 3–5 leaf squares of 1 cm^2 were punched and immediately dried at 70°C for more than 48 h. One leaf square was used to determine the nitrogen content (N_{mass}) and carbon content (C_{mass}) using an element analyzer Euro EA3000 (Euro Vector, Italy). The remaining leaf squares were used to calculate the specific leaf area (SLA). N_{area} was calculated as N_{mass}/SLA. N:C was calculated as N_{mass}/C_{mass}. Photosynthetic nitrogen-use efficiency (PNUE) was calculated as P_{max}/N_{area}. Water-use efficiency (WUE) was calculated as the ratio of P_{max} to Gs. Leaf construction cost (LCC) was calculated according to McDowell (2002).

Statistical analyses

All traits were analyzed using factorial ANOVA, then Duncan tests were used to compare levels within factors for significance ($P < 0.05$). All analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

Results

Differences of traits in species

N_{mass}, N_{area}, N:C, and WUE differed significantly between species and across sediment nutrient levels. The significant interactions between nutrients and

species indicated that differences in N_{mass}, N:C, and WUE between the two species were significantly influenced by sediment nutrients (Table 2). N_{mass} and N:C of *E. crassipes* were lower than those of *M. vaginalis* at each nutrient level (Fig. 1a, c). At the low nutrient level, *E. crassipes* displayed a lower N_{area} and WUE than *M. vaginalis*, but there were no significant differences compared with *M. vaginalis* at the medium or high nutrient levels (Fig. 1b, g).

Table 2 F and P values of the leaf traits for the two species and three nutrient levels (a factorial ANOVA)

| Source	df	F	P
N_{mass}			
Species	1.6	90.465	**<0.001**
Nutrient	2.6	9.673	**0.001**
Species × nutrient	2.6	6.481	**0.005**
N_{area}			
Species	1.6	6.402	**0.017**
Nutrient	2.6	10.538	**<0.001**
Species × nutrient	2.6	1.277	0.294 ns
N:C			
Species	1.6	79.667	**<0.001**
Nutrient	2.6	11.664	**<0.001**
Species × nutrient	2.6	4.524	**0.019**
P_{max}			
Species	1.6	0.665	0.421 ns
Nutrient	2.6	25.833	**<0.001**
Species × nutrient	2.6	10.836	**<0.001**
SLA			
Species	1.6	72.021	**<0.001**
Nutrient	2.6	1.037	0.367 ns
Species × nutrient	2.6	6.744	**0.004**
LCC			
Species	1.6	82.19	**<0.001**
Nutrient	2.6	0.39	0.681 ns
Species × nutrient	2.6	29.828	**<0.001**
WUE			
Species	1.6	6.628	**0.017**
Nutrient	2.6	26.575	**<0.001**
Species × nutrient	2.6	3.848	**0.036**
PNUE			
Species	1.6	9.979	**0.004**
Nutrient	2.6	0.32	0.728 ns
Species × nutrient	2.6	1.001	0.379 ns

Boldface denotes significance, ns denotes no significance

There were no significant differences in P_{max} between the two species. However, among different sediment nutrient levels, P_{max} differed significantly. The significant interactions between nutrients and species suggest that sediment nutrients contribute to the differences of P_{max} between the two species (Table 2). At the low nutrient level, *M. vaginalis* had a higher P_{max} than *E. crassipes*, but these differences become not significant or even reversed at medium and high nutrient levels (Fig. 1d).

SLA, LCC, and PNUE all differed significantly between species, although they remained similar among different sediment nutrient levels (Table 2). SLA of *E. crassipes* was lower than *M. vaginalis* at each nutrient level (Fig. 1e). LCC of *E. crassipes* was lower than *M. vaginalis* at low and medium

Fig. 1 The mean values of *E. crassipes* (*black bars*) and *M. vaginalis* (*gray bars*) in leaf traits at three nutrient levels (*L* low nutrient level, *M* medium nutrient level, *H* high nutrient level)
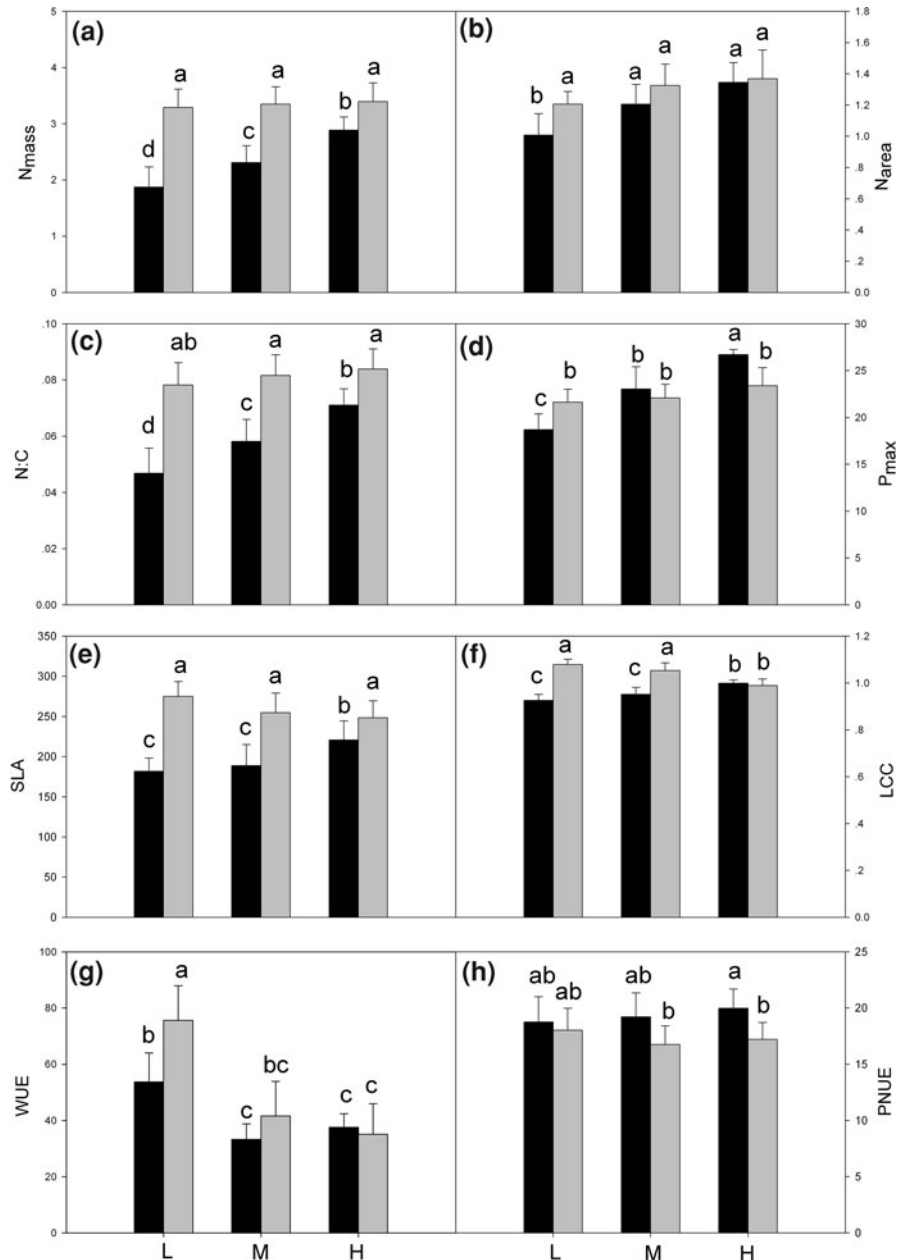
nutrient levels, but was comparable to *M. vaginalis* at high nutrient level (Fig. 1f). Although PNUE differed significantly between the two species, it is much higher only at high nutrient level in *E. crassipes* than in *M. vaginalis* (Fig. 1h).

Trait response patterns to nutrient

As shown in Fig. 1, most traits of the two species differ in response to changes in nutrient levels. N_{mass}, N_{area}, N:C, P_{max}, and SLA of *E. crassipes* increased significantly when the nutrient level increased, whereas those of *M. vaginalis* remained constant at all three nutrient levels. LCC of *E. crassipes* also increased significantly when the nutrient level increased. In contrast, this trait of *M. vaginalis* decreased significantly with increases in the nutrients. WUE of both species decreased significantly when the nutrient level increased, PNUE of both species remained constant at all three nutrient levels.

Discussion

In our study, the resource capture- and use-related traits were markedly different between *E. crassipes* and *M. vaginalis*. *M. vaginalis* had a higher N_{mass} than *E. crassipes* at all three nutrient levels. N_{area} of *M. vaginalis* was also higher than *E. crassipes* at low nutrient level. Previous studies have found that compared with native plants, the invasive plants generally have higher N_{mass} (Baruch & Goldstein, 1999; Leishman et al., 2007) and lower or similar N_{area} (Baruch & Goldstein, 1999; Feng et al., 2007; Leishman et al., 2007; Feng & Fu, 2008). Exceptions, in which N_{mass} of invasive plants was lower or equal to native plants, did exist (Baruch & Goldstein, 1999; Durand & Goldstein, 2001). Because proteins participating in the Calvin cycle and in the thylakoids represent the majority of the leaf nitrogen content, photosynthesis of a leaf correlate positively to these proteins, hence the leaf nitrogen content (Evans, 1989). However, a lower leaf nitrogen content can partially contribute to a high PNUE in invasive plants, owing to an inverse correlation between nitrogen-use efficiency and foliar nitrogen content (Niinemets et al., 2003). Therefore, consistent with this finding, we discovered that *E. crassipes* with a lower leaf

nitrogen content achieved a higher PNUE than *M. vaginalis*.

SLA and LCC are two other important traits representing relative growth rate and resource-use efficiency in plants (Shipley, 2006). Plants with a high SLA and low LCC can produce larger assimilatory surfaces for a given amount of fixed carbon (Baruch & Goldstein, 1999). Furthermore, plants with a high SLA often allocate a higher fraction of the leaf nitrogen to photosynthesis, resulting in a higher PNUE than plants with a low SLA (Poorter & Evans, 1998; Feng et al., 2008). Many researchers found that, compared with native plants, invasive plants often have a higher SLA and lower LCC (Baruch & Goldstein, 1999; Grotkopp et al., 2002; Grotkopp & Rejmánek, 2007; Feng et al., 2007; Feng & Fu, 2008; Feng et al., 2008). However, in our experiment, we found that *E. crassipes* had a lower LCC than *M. vaginalis* only at the low and medium nutrient levels. *E. crassipes* also had a lower SLA than *M. vaginalis* at all three nutrient levels. McDowell (2002) suggested that a lower SLA in invasive species may increase the WUE, which means these plants had thicker, denser leaves, increasing the distance through which water must diffuse thereby leading to water conservation. Since the water was not a limiting factor for these aquatic plants in our study, we suggested that a higher SLA was not always a necessary trait for invasive species. This is consistent with some studies in which SLA of invasive plants was found to be lower than native plants (McDowell, 2002; Feng, 2008).

Many invasive plants were found to have higher P_{max} values than their phylogenetically related native species (Pattison et al., 1998; Funk & Vitousek, 2007; Leishman et al., 2007; Feng & Fu, 2008). Photosynthetic rate is related to various attributes of plant success, including growth, competitiveness, propagation, and resistance to herbivores or pathogens (McAllister et al., 1998). Therefore, P_{max} is an important leaf trait of invasive plants. In our study, *E. crassipes* exhibited a higher P_{max} than *M. vaginalis* only at the high nutrient level, suggesting that it can obtain more energy and achieve higher growth rate to compete with native plants when resources are abundant. Although PNUE of *E. crassipes* was higher compared with *M. vaginalis*, the difference was significant only at the high nutrient level. In introduced areas, due to release from natural enemies, invasive plants will allocate more nitrogen to their

photosynthetic machinery by reducing the nitrogen of cell walls to achieve a higher photosynthetic rate (Feng et al., 2009). In the field, nitrogen is a limiting resource, plants with high PNUE can achieve a higher photosynthetic rate when their leaf nitrogen content is low, it is important to the growth and propagation, therefore, many invasive plants were found to have higher PNUE than their phylogenetically related native and non-invasive species (Niinemets et al., 2003; Feng et al., 2007; Funk & Vitousek, 2007; Matzek, 2011).

There are many different morphological and physiological response patterns to changes in nutrition between *E. crassipes* and *M. vaginalis*. Generally, plants adapted to resource-poor habitats demonstrate a low growth rate, tissue nutrient content, instantaneous photosynthetic rate, and instantaneous PNUE, but exhibit a long leaf lifespan and greater leaf thickness, allowing them to have a longer time to maximize their carbon assimilation per unit resource invested in leaf construction (Chapin, 1980, Bloom et al., 1985). In our study, *E. crassipes* had a decreased photosynthetic rate, leaf nitrogen content, and SLA with decreasing nutrient levels. In contrast, *M. vaginalis* maintained steady values for P_{max}, N_{mass}, N_{area}, N:C, and SLA at all the nutrient levels. In the Liangzi Lake, *E. crassipes* reproduces mainly by clonal propagation, though a few seedlings also were found. Conversely, *M. vaginalis* reproduces by sexual propagation. The carbon and nutrient cost for producing reproductive structures (flowers, fruit, and seed) is generally high because of the high concentrations of nitrogen, phosphorus, and lipids in these organs (Bloom et al., 1985). Therefore, compared with asexual reproduction, sexual reproduction requires more resources from the environment. In a resource-poor environment, plants will increase asexual reproduction and decrease sexual reproduction. For the annual sexually reproducing aquatic plant *M. vaginalis*, a high P_{max} is necessary to support the high energy cost of reproductive structures. Thus, *M. vaginalis* must maintain a high leaf nitrogen concentration to sustain a high photosynthetic rate and a high SLA and LCC to increase its light-capture ability in low nutrient level.

The fact that most traits of *E. crassipes* increased with increasing nutrition suggest that it favors nutrient-rich habitats. Many studies have found that some extremely invasive aquatic weeds tend to increase their biomass, clonal propagation, and propagule

rooting efficiency in high nutrient environments (Xie et al., 2004; Pan et al., 2006; Xie et al., 2010). The increased nitrogen content, SLA, and photosynthetic rate suggest that *E. crassipes* has a higher nutrition capture efficiency, resource use efficiency, and growth rate in high nutrient environments, which contribute to its superior performance compared with co-occurring native plants. Furthermore, although some studies found that invasive plants outperformed native plants in growth rate, P_{max}, resource use efficiency, and tissue nutrient content, in all habitats (Pattison et al., 1998; Durand & Goldstein, 2001), our study suggests that *E. crassipes* did not have leaf trait advantages over the native plant *M. vaginalis* at all three nutrient levels. Only at high nutrient levels, did it achieve significantly higher P_{max} and PNUE than the native species *M. vaginalis*. At the low nutrient level, the native species had significantly higher values in all the studied leaf traits (except PNUE), consistent with previous studies (Daehler, 2003; Xie et al., 2010). Therefore, our results suggest that the success of *E. crassipes* is context-dependent—it outperformed co-occurring native plants only in high nutrient environments. Some studies showed that *E. crassipes* was competitively superior at a range of resource availabilities. For instance, Xie (2003) found *E. crassipes* had a greater biomass and a higher phosphate absorbption rate than native aquatic plant *Hydrocharis dubia* (Bl.) Backer at all three phosphate levels. These different results may reflect the unique characteristics in the species or parameters in the studies. In fact, consistent with our results, *E. crassipes* was rare in Liangzi Lake, a nutrient poor lake (N and P concentrations in water were 0.71 and 0.04 mg l^{-1}; N concentration in sediment was 2.94 and 0.12 mg g^{-1}), and was only present in areas where wastewater was expelled.

Conclusion

After comparing multiple resource capture- and use-related traits of *E. crassipes* with *M. vaginalis* at three nutrient levels, we found the two plants have distinct morphological and physiological response patterns to changes in nutrients. The differences may be due to different strategies of reproduction and help explain the invasiveness of *E. crassipes*. Furthermore, our results supported the fluctuating resources hypothesis,

and found that increasing the nutrient content in sediment will augment the nutrition capture efficiency, resource use efficiency and growth rate of *E. crassipes*. Our results suggest a characteristic of content-dependency of *E. crassipes* invasion and explain the distribution patterns of *E. crassipes* in invaded areas: *E. crassipes* is prevalent in tropical and sub-tropical water bodies in which the water nutrient concentrations are often high due to agricultural runoff, deforestation, and insufficient wastewater treatment (Villamagna & Murphy, 2010).

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