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Do higher resource capture ability and utilization efficiency facilitate the successful invasion of native plants?

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Abstract The great damage caused by native invasive species on natural ecosystems is prompting increasing concern worldwide. Many studies have focused on exotic invasive species. In general, exotic invasive plants have higher resource capture ability and utilization capacity, and lower leaf construction cost (CC) compared to noninvasive plants. However, the physiological mechanisms that determine the invasiveness of native plants are poorly understood. We hypothesized that native invaders, like exotic invaders, may have higher resource capture ability and utilization efficiency compared to native noninvaders. To test this hypothesis, ecophysiological traits including light-saturated photosynthetic rate (A_{max}), specific leaf area (SLA), photosynthetic nitrogen use-efficiency (PNUE), photosynthetic energy-use efficiency (PEUE), and mass-based and area-based leaf construction cost (CC_{mass} and CC_{area}) were measured. We compared the above traits between three pairs of native invasive and noninvasive native species, and between three pairs of exotic invasive and noninvasive species in Guangzhou, southern China. Our results showed that the native invaders had higher A_{max}, SLA, PNUE, PEUE and lower CC_{mass}, CC_{area}, compared to native noninvaders and that these traits were also found in the exotic invaders. PNUE and PEUE in the native invaders were 150.3 and 129.0% higher, respectively, than in noninvasive native species, while these same measures in exotic invaders were 43.0 and 94.2% higher, respectively, than in exotic noninvasive species. The results indicated that native invaders have higher resource capture ability and resource utilization efficiency, suggesting that these traits may be a common biological foundation underlying successful invasion by both native and exotic invasives.

Keywords Capture · Construction cost · Native invader · Resource utilization · Specific leaf area

Introduction

Exotic plant invasion, one of the most pressing environmental problems, has caused great concern to ecologists worldwide (Mack et al. 2000; Pimentel et al. 2000a). However, recently it was reported that some native species might also become invasive, and the large amount of damage that they cause in natural ecosystems is no less than the damage caused by exotic invasive species (Wright et al. 2004b; Peng et al. 2009). For example, *Lactuca serriola*, one of Europe's native annual herbs, has come to occupy at least 60% of the Netherlands by enlarging its

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geographic range and rapidly broadening its ecological amplitude (Hooftman et al. 2006). In addition, some native lianas in the forests of Panama and across the Neotropics have increased in size and density over the last two decades and are likely to influence stand dynamics in these forests (Phillips et al. 2002; Bragg 2004; Allen et al. 2007). Furthermore, other indigenous plants (e.g., *Humulus scandens* and *Pueraria lobata*) have also threatened forest health and restoration by becoming "plant killers" in Zhejiang Province, southeast China (Li et al. 2006). Any species, whether native or exotic, that grows vigorously and spreads in a region can be qualified as invasive (Valéry et al. 2008). Thus, in this paper we refer to invaders that are native to a region as "native invaders," while we refer to species from outside the native region as "exotic invaders."

The ultimate causes of the invasiveness of exotics are tightly related to the ecological and life history characteristics of species (Kotiaho et al. 2005; van Kleunen and Richardson 2007). High resource capture ability is important for the success of plants involved in interspecific competition (Grime 1974; Shi and Ma 2006). An invasive species can grow very fast, allowing it to kill or displace native species. The degree of invasiveness of exotic invaders has been closely related to a number of ecophysiological traits that promote higher resource capture and utilization efficiency (Nagel et al. 2004; Feng et al. 2008). Previous studies comparing leaf traits of exotic invasive species and native species have shown that invasives have larger SLA than native species (Baruch and Goldstein 1999; Leishman et al. 2007). Exotic invasive species have also been shown to have higher relative growth rates (Pattison et al. 1998; Grotkopp et al. 2002), foliar nutrients and photosynthetic capacity (Baruch and Goldstein 1999; Durand and Goldstein 2001; McDowell 2002; Leishman et al. 2007). It seems likely that exotic invaders often have a higher photosynthetic rate (A), specific leaf area (SLA), photosynthetic nitrogen use efficiency (PNUE), photosynthetic energy use efficiency (PEUE) and low leaf construction cost (CC_{mass} and CC_{area}; Pattison et al. 1998; Baruch and Goldstein 1999; Feng et al. 2008).

Identifying traits that may be associated with invasiveness (Pyšek and Richardson 2007) may improve our ability to predict and control potential invaders, including native invaders. To date, we know much more about exotic invaders than about native invaders, though the damage caused by native invaders is similarly severe. Little is known about the mechanisms underlying native invasion, though a few previous studies have separated native and exotic species into invasive and noninvasive (Lake and Leishman 2004; Leishman and Thomson 2005).

Do native invaders have similar characteristics to exotic invaders, e.g., higher resource capture and utilization efficiency? Our previous studies in Guangdong have shown that many forest ecosystems suffer from the serious damage caused by native invasive plants. There are 39 invasive species on Baiyun Mountain and Xiqiao Mountain in our study site in Guangzhou. Of these, 33 are native to the local region in China and can suppress and cover other dominant trees, ultimately resulting in the death of a large number of local trees (Peng et al. 2009). Successful invasion depends on a number of factors, including the traits of the invaders (e.g., resource capture ability and utilization), resource availability and the condition of the invaded ecosystem. In this paper we focus on the traits of the invaders themselves as a determinant of successful invasion. We hypothesized that native invaders, like exotic invaders, may have higher resource capture ability and utilization efficiency compared to native noninvaders, traits which are beneficial for successful invasion. To test this hypothesis, we compared leaf-level physiological traits (A_{max}, SLA, PNUE, PEUE, CC_{mass} and CC_{area}) of three native invasive (NI) species and three exotic invasive (EI) species with noninvasive controls. All the plants used in the study are common in southern China.

Materials and methods

Study site

This study was carried out in Guangzhou ($23°6'32''$N, $114°15'53''$E), which lies in central-south Guangdong Province, Southern China. The region has a subtropical monsoon climate with a mean annual temperature of 22.8°C (ranging from 0°C in January to 38°C in July or August), a mean annual precipitation of 1,982.7 mm and a relative humidity of 68%. Guangzhou is located on hilly land, and the prevalent soil type is lateritic red soil (Cui et al. 2003). The three study sites were all located in Guangzhou: Baiyun Mountain (a park in Guangzhou), the south campus of Sun

Yat-sen University and Guangzhou Higher Education Mega Center. The sites were separated by a distance of about 20 to 30 km. Detailed information on the vegetation and soil properties of the sites is provided by Guan and Chen (2003). The soil here is latosolic red soil and the soil organic matter content is medium; soil fertility is poor because nutrient elements such as nitrogen (N) and phosphorus (P) are scarce. In the study area, human activities are more intense than in natural forests, thus the vegetation and condition of the forest in the study area differ greatly from natural vegetation. Details of each plant species used in the study are shown in Table 1.

Plant species

Each pair of species was selected from the same family and had a similar life form. To minimize the impact of environmental factors on plant growth, we choose the species of each pair from similar habitats. Although there are many invasive plant species in the studied area, only six of them were found to have the respective noninvasive species pair to meet our standards as controls in this area. Thus, we selected six pairs of plant species that were divided into two groups: invasive (including native invasive, NI, and exotic invasive, EI) and noninvasive (including native noninvasive, NN, and exotic noninvasive, EN; details in Table 1). The three NI species, *Paederia scandens*, *Pueraria phaseoloides* and *Stephania longa*, are perennial vines that grow rapidly and can reach the top of the canopy, causing other plants to die from lack of light. These species have caused severe damage to forest development and function in some areas in Guangzhou (Peng et al. 2009). The three NN species, *Mussaenda pubescens*, *Lablab purpureus* and *Tinospora sinensis*, are widely grown as common species in South China and cause

Table 1 The plant species in the present study

Family	Type	Species	Life form	Location (Guan and Chen 2003)
Rubiaceae	NI	*Paederia scandens* (Lour.) Merr.	Vine	These species were chosen from Baiyun Mountain (a forest park in Guangzhou). The soil is latosolic red soil and the soil fertility is poor
	NN	*Mussaenda pubescens* Ait. f.		
Leguminosae	NI	*Pueraria phaseoloides* (Roxb.) Benth.	Vine	These species were chosen from Guangzhou Higher Education Mega Center. The soil here is latosolic red soil and the soil fertility is poor
	NN	*Lablab purpureus* (Linn.) Sweet.		
Menispermaceae	NI	*Stephania longa* Lour.	Vine	These species were chosen from Sun Yat-sen University. The soil is latosolic red soil and the soil fertility is poor
	NN	*Tinospora sinensis* (Lour.)Merr.		
Convolvulaceae	EI	*Ipomoea cairica* (Linn.) Sweet.	Herb	These species were chosen from Guangzhou Higher Education Mega Center. The soil is latosolic red soil and the soil fertility is poor
	EN	*Pharbitis nil* (Linn.) Choisy.		
Verbenaceae	EI	*Lantana camara* Linn.	Shrub	These species were chosen at full illumination from Guangzhou Higher Education Mega Center. The soil is latosolic red soil and the soil fertility is poor
	EN	*Lantana montevidensis* Briq.		
Oxalidaceae	EI	*Oxalis corymbosa* DC.	Herb	These species were chosen from Sun Yat-sen University. The soil is latosolic red soil and the soil fertility is poor
	NN	*Oxalis corniculata* Linn.		

NI native invasive species, *NN* native noninvasive species, *EI* exotic invasive species, *EN* exotic noninvasive species

no damage to the local ecosystem. In addition, the three EI species, *Ipomoea cairica*, *Lantana camara* and *Oxalis corymbosa*, were compared with the respective noninvasive species *Pharbitis nil*, *Lantana montevidensis* and *Oxalis corniculata*. *Ipomoea cairica*, a perennial herb native to North America, was introduced into China in the 1970s (Lin and Liu 2008). *Lantana camara*, a shrub native to Tropical America, was introduced into China in the middle of the 16th century (Lin et al. 2008). *Oxalis corymbosa*, a perennial herb native to Brazil, was introduced into China in the middle of 19th century (Feng et al. 2008). All of these exotic invasives were introduced as ornamental plants and have been naturalized in the subtropics and tropics of China. These species often form monocultures, causing a serious disruption to the structure and function of the local ecosystem (Huang et al. 2009). *Pharbitis nil* and *Lantana montevidensis* are exotic species. They were introduced into China as ornamental plants but did not cause damage to the local ecosystem. *Oxalis corniculata*, a native perennial herb, is widely distributed throughout China (details of the species are shown in Table 1).

Measurements

Photosynthetic characteristics

Net photosynthetic rate in relation to varying photosynthetic photon flux density (P_n—PPFD curves) was determined on the youngest fully expanded leaves with a Li-6400 Portable Photosynthesis System (Li-6400, Li-Cor, USA). Measurements were made on 2–3 representative leaves on 3–4 randomly selected individuals of each species in a pair over consecutive days from 09:00 to 12:00 am in the field in the summer of 2008. All leaves of the two species in a pair were of similar age and position on the canes. Three replicates for each species were used for each measurement. Light response curves were generated by decreasing PAR. PPFD was decreased in a stepwise fashion from 2,000 to 0 μmol photon m^{-2} s^{-1}. During the measurements, CO_2 concentration, temperature and relative humidity within the leaf chamber were similar to those of ambient conditions. Each leaf was acclimated for 10–25 min to 2,000 μmol m^{-2} s^{-1} mol of PPFD prior to the measurement.

Leaf structural and biochemical characteristics

Around fifty leaves per species were selected, and specific leaf area (SLA, in square centimeters per gram) for each individual was measured using a leaf area meter (Li-3100A, Li-Cor, USA) and leaf dry weight. Leaves were dried for 48 h at 72°C in an oven and weighed. The dried leaves were ground into a fine powder using a micro-plant mill and stored with a desiccant to maintain dryness for subsequent analysis. Leaf N was determined using an azotometer (Kjeltec 2300, Foss, Sweden). Ash content (ASH) was measured by burning 1 g leaf powder samples in a 500°C muffle furnace (Vulcan A-550, Vulcan, UK) for 6 h and weighing the remaining mass, then dividing the ash mass by the sample mass. To obtain the leaf caloric value, ∼0.5 g pellets of leaf powder from each sample were pressed and combusted using a calorimeter (IKA-C2000, IKA, Germany). The same leaf of each sample plant was used if the measurements of photosynthesis and leaf structural and biochemical characteristics were possible (Feng et al. 2008).

Calculation

Photosynthetic characteristics

Entire light response curves were fitted using the standard quadratic equation ($Y = aX^2 + bX + c$). Light-saturated photosynthetic rate (A_{max}, μmol m^{-2} s^{-1}) = $c - (b^2/4a)$ (Wen et al. 2000).

Leaf structural and biochemical characteristics

Specific leaf area (SLA, cm^2 g^{-1}) = leaf area/leaf dry weight. Area-based leaf nitrogen content (N_{area}, g m^{-2}) = N_{mass}/SLA. Leaf construction cost per unit of mass (CC_{mass}, equivalent to grams glucose per gram dry mass) was calculated according to the following equation (Williams et al. 1987): CC_{mass} = [(0.06968ΔHc-0.065) (1−ASH) + 7.5(k N/14.0067)]/EG. Where $ΔH_c$ was ash-free heat of combustion: $ΔH_c$ = Caloric value/(1−Ash content), k was the oxidation state of the N substrate (+5 for nitrate or −3 for ammonium) and EG was the growth efficiency. EG has been estimated to be 0.87 across species (Penning de Vries et al. 1974). Because the form of N utilized by the plants was unknown in our

samples, CC for all species was estimated as the mean of CC values calculated with each NH_4^+ and NO_3^- oxidation state.

Resource use efficiency

Photosynthetic energy use efficiency (PNUE, μmol g^{-1} s^{-1}) = A_{max}/N_{area} (Field and Mooney 1986). Energy use efficiency (PEUE, CO_2 g glucose^{-1} s^{-1}) = A_{max}/CC_{area} (Funk and Vitousek 2007). Water use efficiency (WUE, μmol mmol^{-1}) = A/E (transpiration). Light use efficiency (LUE, μmolCO$_2$ μmol^{-1} proton) = A/PPFD.

Statistical analyses

Independent-sample t tests were conducted to evaluate the differences in resource capture ability and utilization efficiency between each native invasive and noninvasive native pair, and between each exotic invasive and noninvasive pair. Furthermore, the differences between the pooled native invasive and their corresponding noninvasive native species as

well as the differences between the pooled exotic invasive and their corresponding noninvasive species were analyzed with paired t tests All analyses were carried out using SPSS 16.0 (SPSS, Chicago, USA).

Results

The resource capture and utilization properties of NI species

NI species were more efficient in capturing and utilizing resources than were their corresponding NN species (Table 2), and the NI group was more efficient in capturing and utilizing resources than was the NN group (Fig. 1). For family Rubiaceae, the native invader *P. scandens* had higher SLA, PNUE, PEUE and LUE but lower N_{area}, CC_{mass} and CC_{area} than *M. pubescens*. Similarly, for family Menispermaceae and Leguminosae, native invader *S. longa* and *P. phaseoloides* had higher A_{max}, PNUE, PEUE or SLA, but had lower N_{mass}, CC_{mass} and WUE than their controls (Table 2). When the data from the
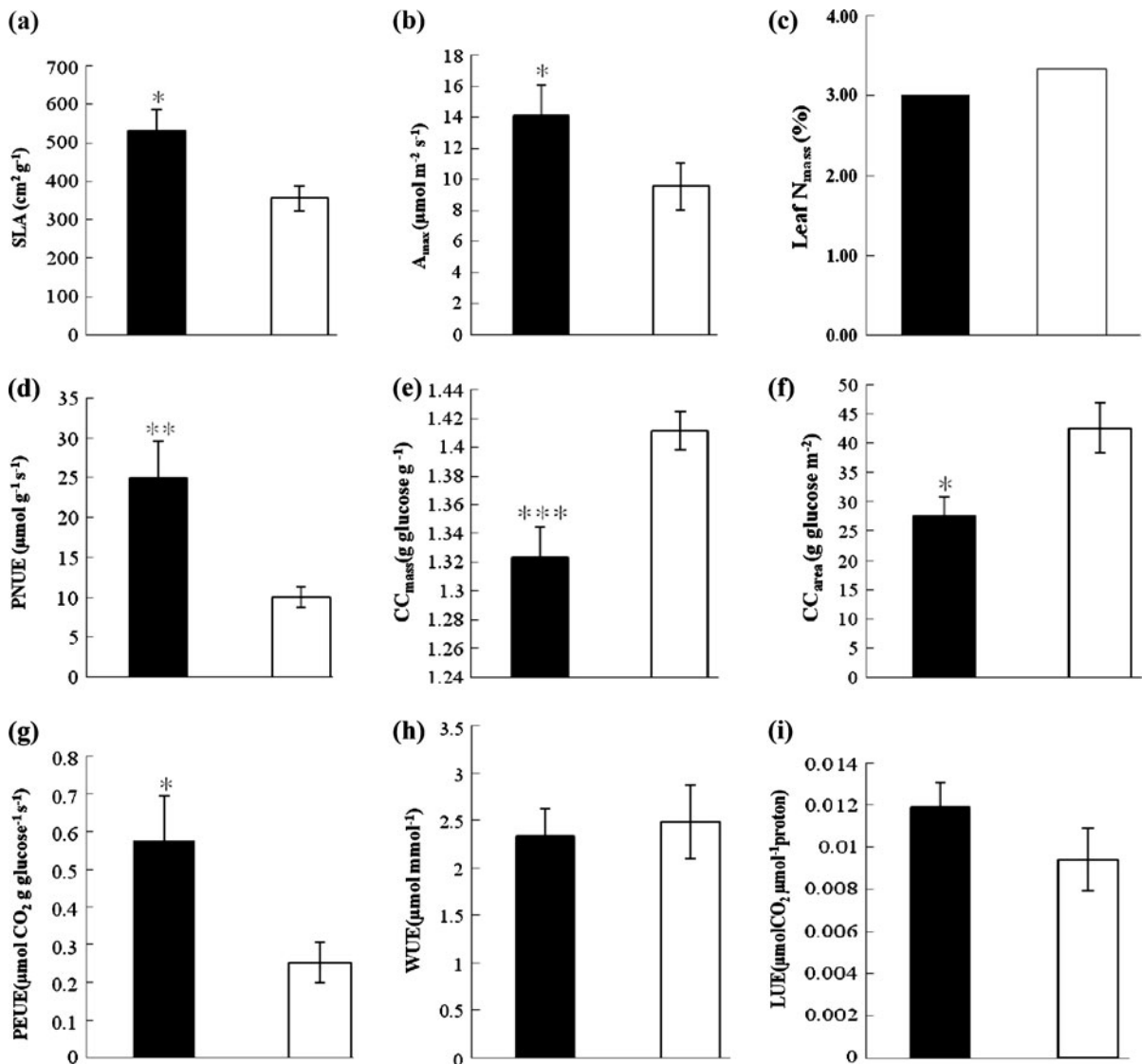
Table 2 The differences between each native invasive and noninvasive native pair in ecophysiological traits according to independent-sample t tests

Variables	Rubiaceae		Menispermaceae		Leguminosae	
	Ps (NI)	*Mp* (NN)	*Sl* (NI)	*Ts* (NN)	*Pp* (NI)	*Lp* (NN)
SLA	609.510 ± 7.323***	244.200 ± 7.323	315.360 ± 9.098	390.3 ± 42.536	667.040 ± 16.174**	431.260 ± 26.052
N_{mass}	2.647 ± 0.043	2.377 ± 0.072	2.7167 ± 0.028**	3.207 ± 0.137	3.673 ± 0.160***	4.413 ± 0.026
N_{area}	0.435 ± 0.005***	0.978 ± 0.065	0.864 ± 0.033	0.834 ± 0.069	0.552 ± 0.037**	1.032 ± 0.071
A_{max}	10.861 ± 1.167	7.812 ± 0.254	12.505 ± 0.560**	5.822 ± 0.931	19.026 ± 5.121	15.084 ± 1.439
PNUE	24.975 ± 2.570**	8.060 ± 0.628	14.492 ± 0.607*	7.246 ± 1.646	35.667 ± 11.705	14.715 ± 1.632
CC_{mass}	1.295 ± 0.005***	1.426 ± 0.005	1.268 ± 0.097*	1.321 ± 0.029	1.407 ± 0.003***	1.438 ± 0.002
CC_{area}	21.252 ± 0.226***	58.612 ± 2.532	40.274 ± 1.130	35.821 ± 3.528	21.118 ± 0.517 **	33.585 ± 2.097
PEUE	0.510 ± 0.050*	0.134 ± 0.009	0.311 ± 0.014*	0.171 ± 0.042	0.911 ± 0.264	0.452 ± 0.049
WUE	2.178 ± 0.389	1.715 ± 0.446	1.554 ± 0.064*	3.755 ± 0.546	3.283 ± 0.312	1.984 ± 0.331
LUE	0.010 ± 0.002*	0.008 ± 0.000	0.012 ± 0.001	0.006 ± 0.001	0.014 ± 0.113	0.015 ± 0.002

All values are expressed as mean ± SE (N = 3 for all of the species)

Native invasive species (NI): *Ps* = *P. scandens*, *Sl* = *S. longa*, *Pp* = *P. phaseoloides*. Native noninvasive species (NN): *Mp* = *M. pubescens*, *Ts* = *T. sinensis*, *Lp* = *L. purpureus*. SLA, specific leaf area in cm^2 g^{-1}; N_{mass}, biomass-based leaf nitrogen content in %; N_{area}, area-based leaf nitrogen content in g m^{-2}; A_{max}, light-saturated photosynthetic rate in μmol m^{-2} s^{-1}; PNUE, photosynthetic nitrogen use efficiency in μmol g^{-1} s^{-1}; CC_{mass}, mass-based leaf construction cost in g glucose g^{-1}; CC_{area}, area-based leaf construction cost in g glucose m^{-2}; PEUE, mean photosynthetic energy-use efficiency in μmol CO$_2$ g glucose^{-1} s^{-1}; WUE, water use efficiency in μmol mmol^{-1}; LUE, light use efficiency in μmolCO$_2$ μmol^{-1} proton

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Fig. 1 a Specific leaf area in $cm^2 g^{-1}$ (SLA), **b** net photosynthetic rate in $\mu mol\ m^{-2}\ s^{-1}$ (A_{max}), **c** biomass-based leaf nitrogen content in % (N_{mass}), **d** photosynthetic nitrogen use efficiency in $\mu mol\ g^{-1}\ s^{-1}$ (PNUE), **e** mass-based leaf construction cost in g glucose g^{-1} (CC_{mass}), **f** area-based leaf construction cost in g glucose m^{-2} (CC_{area}), **g** mean photosynthetic energy-use efficiency in $\mu mol\ CO_2$ g glucose$^{-1}\ s^{-1}$ (PEUE), **h** water use efficiency in $\mu mol\ mmol^{-1}$ (WUE), **i** light use efficiency in $\mu mol CO_2\ \mu mol^{-1}$ proton (LUE) of the native invasive (NI) species (*filled black bars*) and the noninvasive species (*open bars*) in the study site. *Error bars* represent $1 \pm SE$. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

different species was pooled, the NI group showed the same tendency. About 78% of the traits in the NI group were significantly different from those of the NN group, and SLA, PNUE and PEUE in the NI group were significantly higher than those of the NN group (Fig. 1), while N_{area}, CC_{mass} and CC_{area} in the NI group were significantly lower than in the NN group (Table 2; Fig 1). However, N_{mass}, WUE and LUE had no significant differences (Fig. 1).

Resource capture and utilization properties of EI species

Similar to the NI species, EI species had higher resource capture and resource utilization efficiency than the corresponding EN species (Table 3). Likewise, the EI group had higher resource capture and resource utilization efficiency than the EN group (Fig. 2). The exotic invader *I. cairica* had higher SLA

and N_{mass} but lower CC_{area} than exotic noninvader *P. nil*. Exotic invaders *L. camara* and *O. corymbosa* were also more efficient at capturing and utilizing resources because of their higher A_{max}, SLA, PNUE and PEUE but lower N_{area}, CC_{mass} and CC_{area} than their respective controls. Correspondingly, the EI group not only had higher A_{max}, N_{mass}, PNUE, PEUE and LUE, but also had lower CC_{mass} and CC_{area} (Fig. 2) than noninvasive species. The WUE of exotic invaders was not significantly different from that of the noninvasive species.

Discussion

Higher resource capture ability and utilization efficiency has been proposed as one of the potential mechanisms explaining the success of plant invasion (Baruch and Goldstein 1999; Grotkopp and Rejmánek 2007; Funk and Vitousek 2007). With higher resource capture ability and utilization efficiency, invasive species have advantages in competing for sunlight and other resources. Our study illustrated that native invasives, like exotic invasives, have higher resource capture and use efficiency than native noninvasives. In addition, several ecophysiological traits, including high A_{max}, SLA, PNUE, PEUE, and low CC_{mass} and CC_{area}, are tightly related to resource capture and use efficiency. The results suggest that high resource capture ability and utilization efficiency might be the common biological foundation for both exotic invasives and native invasives.

Differences in resource capture ability among plant types

The ability to capture and utilize sunlight plays an important role in plant growth (Durand and Goldstein 2001). SLA is of great importance in regulating and controlling carbon assimilation and allocation (Lambers and Poorter 1992; Reich et al. 1997). A higher SLA has been demonstrated in invasive species vs. noninvasive species (Zou et al. 2007; Grotkopp and Rejmánek 2007), and is thus commonly thought to be associated with invasiveness. Species with greater SLA may increase their capacity to assimilate CO_2 because a larger leaf area could be produced for a given mass of carbon invested in photosynthetic tissues (Lambers and Poorter 1992;

Reich et al. 1997). Consequently, species with high SLA have a greater potential for fast growth than low SLA species. Like SLA, the higher rate of A_{max} may give invasive species a larger potential to accumulate more carbon for allocation to reproduction and growth (Ewe and Sternberg 2003). Based on a broad survey of 280 plant species in different ecosystems, Reich et al. (1997) found that variation in leaf traits among species was strongly related to whole-plant properties. Having a higher SLA and A_{max} may translate into a higher relative growth rate (Davis et al. 2000; Nagel et al. 2004; Grotkopp and Rejmánek 2007).

In the present study, SLA was significantly different among plant types, and the invasives (both EI and NI) had higher SLA than the pairwise noninvasives. The SLA of NI species was 49.3% higher than that of NN species, and the SLA of EI species was 44.2% higher than that of the noninvasives, suggesting that the invaders could produce larger assimilatory surfaces for a given amount of fixed carbon. However, some studies indicate that rapid carbon capture via high SLA may not always be advantageous for invasive plants and the studies highlight the importance of ecological context for each individual species in determining whether particular plant traits will confer an advantage (Pyšek et al. 2009; Leishman et al. 2010). The work by Leishman et al. (2010) has shown that exotic invasive and native species do not have fundamentally different carbon capture strategies, suggesting that differences between exotic invasives and natives may reflect differences in the environmental conditions of the sites where they occur rather than differences between exotic invasives and natives per se. It should be mentioned that Leishman et al. (2010) focused on exotic invasive species and native species in disturbed and undisturbed areas in eastern Australia. By contrast, the present study focused on differences in the traits of not only exotic invasives vs. exotic noninvasives, but also of native invasives vs. native noninvasives in southern China.

In the present study, A_{max} values of the NI and EI species were 47.6 and 26.3% higher than those of the NN species, respectively. This result was consistent with previous studies (Pattison et al. 1998; Baruch and Goldstein 1999; Durand and Goldstein 2001; Feng et al. 2008), which indicated that higher A_{max} might be a significant trait contributing to successful

Table 3 The differences between each exotic invasive and noninvasive pair in ecophysiological traits according to independent-sample t tests
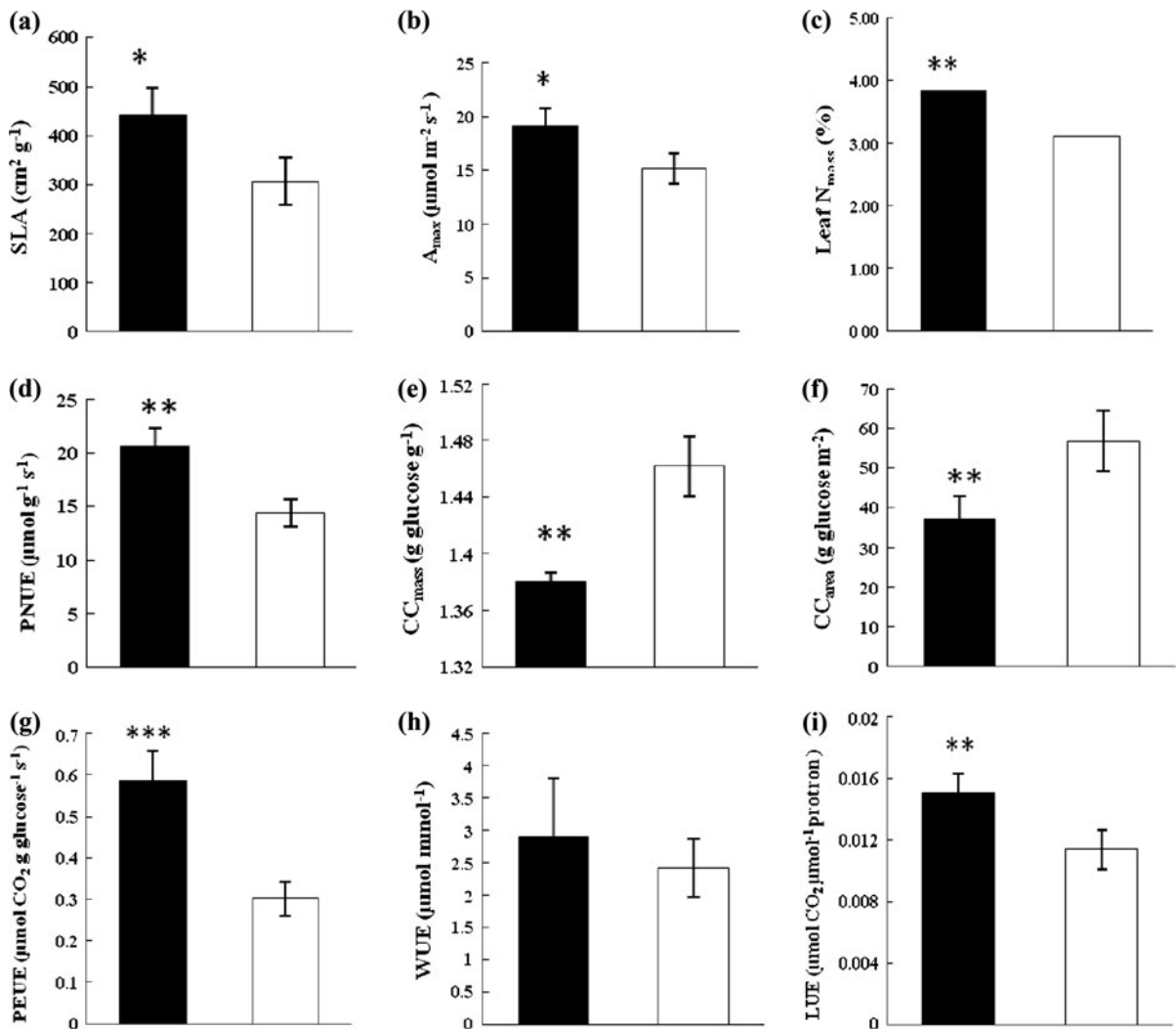
Variables	Convolvulaceae		Verbenaceae		Oxalidaceae	
	Ic (EI)	Pn (EN)	Lc (EI)	Lm (EN)	Oc (EI)	Ocn (NN)
SLA	499.430 ± 48.506*	297.010 ± 10.752	232.620 ± 2.255*	180.400 ± 10.857	589.660 ± 14.313	439.480 ± 104.489
N_{mass}	4.223 ± 0.154***	3.427 ± 0.033	3.237 ± 0.084***	1.943 ± .0219	4.0767 ± 0.177	3.947 ± 0.130
N_{area}	0.866 ± 0.104	1.156 ± 0.045	1.391 ± 0.032**	1.082 ± 0.053	0.691 ± 0.019	1.055 ± 0.331
A_{max}	19.075 ± 3.913	18.589 ± 2.348	22.134 ± 1.311*	16.277 ± 0.787	16.336 ± 1.616	10.681 ± 0.116
PNUE	22.126 ± 3.603	16.211 ± 2.527	15.958 ± 1.218	15.046 ± 0.319	23.574 ± 1.830*	11.865 ± 2.795
CC_{mass}	1.375 ± 0.013	1.380 ± 0.002	1.391 ± 0.009***	1.483 ± 0.007	1.377 ± 0.010***	1.522 ± 0.013
CC_{area}	27.996 ± 2.463**	46.597 ± 1.671	59.798 ± 0.9667**	82.780 ± 4.843	23.385 ± 0.736	40.723 ± 12.801
PEUE	0.684 ± 0.130	0.401 ± 0.059	0.371 ± 0.027*	0.197 ± 0.005	0.704 ± 0.089*	0.307 ± 0.071
WUE	1.385 ± 0.127	1.349 ± 0.114	5.844 ± 1.816	3.982 ± 0.669	1.496 ± 0.124	1.939 ± 0.196
LUE	0.013 ± 0.002	0.011 ± 0.003	0.019 ± 0.002	0.014 ± 0.002	0.013 ± 0.002*	0.009 ± 0.004

All values are expressed as mean ± SE (N = 3 for all of the species)

Exotic invasive (EI) species: $Ic = I. cairica$, $Lc = L. camara$, $Oc = O. corymbosa$, $Mj = M. jalapa$. Exotic noninvasive (EN) species: $Pn = P. nil$, $Lm = L. montevidensis$, $Bs = B. spectabilis$. Native noninvasive (NN) species: $Ocn = O. corniculata$, SLA, specific leaf area in cm^2 g^{-1}; N_{mass}, biomass-based leaf nitrogen content in %; N_{area}, area-based leaf nitrogen content in g m^{-2}, A_{max}, light-saturated photosynthetic rate in μmol m^{-2} s^{-1}; PNUE, photosynthetic nitrogen use efficiency in μmol g^{-1} s^{-1}; CC_{mass}, mass-based leaf construction cost in g glucose g^{-1}; CC_{area}, area-based leaf construction cost in g glucose m^{-2}; PEUE, mean photosynthetic energy-use efficiency in μmol CO$_2$ g glucose^{-1} s^{-1}; WUE, water use efficiency in μmol mmol^{-1}; LUE, light use efficiency in μmolCO$_2$ μmol^{-1} proton

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Fig. 2 a Specific leaf area in cm^2 g^{-1} (SLA), **b** net photosynthetic rate in μmol m^{-2} s^{-1} (A_{max}), **c** biomass-based leaf nitrogen content in % (N_{mass}), **d** photosynthetic nitrogen use efficiency in μmol g^{-1} s^{-1} (PNUE), **e** mass-based leaf construction cost in g glucose g^{-1} (CC_{mass}), **f** area-based leaf construction cost in g glucose m^{-2} (CC_{area}), **g** mean photosynthetic energy-use efficiency in μmol CO_2 g glucose^{-1} s^{-1} (PEUE), **h** water use efficiency in μmol $mmol^{-1}$ (WUE), **i** light use efficiency in μmol $mmol^{-1}$ (LUE) of the exotic invasive (EI) species (*filled bars*) and the exotic noninvasive (EN) species (*open bars*) in the study site. *Error bars* represent $1 \pm SE$. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

invasion by exotic species. Thus, the higher A_{max} together with the higher SLA of NI species might have important implications for their invasion success.

It should be noted that environmental conditions might play an important role in resource capture, which might then affect plant invasion. In our study, a slight difference in growing conditions may have existed that could affect the relationship between plant traits (SLA, A_{max}) and resource capture or invasiveness, though both the invasives and the noninvasives grew under similar conditions

and in the same region, Guangzhou. Future studies should pay more attention to disturbance and growing conditions in addition to the traits of the plants per se.

Differences in resource utilization ability among plant types

The expenditure of energy, in addition to being related to resource capture ability, is also related to plant productivity. Some studies suggest that leaf

construction cost might be considered a general index for predicting invasiveness, as some studies have found that invasive species have a lower cost of leaf construction, irrespective of how they compared with native species or compared with their noninvasive congeners (Baruch and Goldstein 1999; Song et al. 2007; Feng et al. 2008). As a quantifiable measure of energy demand for biomass production, having a low leaf construction cost suggests that these species require less energy to construct biomass and can allot more energy to other competitive strategies, such as seed production, biomass productivity, and relative growth rate, based on a study that researched exotic invasive species and one native species in a desert system (Nagel et al. 2004). Our results showed that both CC_{mass} and CC_{area} of native invasive species were lower than those of noninvasive native species, indicating that lower leaf construction cost may not only be intrinsic to EI species, but may also be an intrinsic property of NI species.

Plants with lower leaf nutrient concentrations generally tend to use nutrition more efficiently (Chapin 1980), but high leaf nutrient concentration, especially N, promotes growth and allows a more efficient use of radiant energy by increasing instantaneous photosynthetic nitrogen use (Field and Mooney 1986). Our results showed that leaf N of NI species was lower than that of NN species, while there was no significant difference in N_{mass} between the pair of Rubiaceae species and no significant difference in N_{area} between the pair of Menispermaceae species. However, the leaf N of EI species was higher than that of noninvasive species, though there was no significant difference in N_{mass} between the pair of Oxalidaceae species, and in N_{area} between the pairs of Convolvulaceae and Oxalidaceae species. Interestingly, in the present study, NI have lower leaf N than the NN controls, while EI have higher leaf N than the noninvasive species. Previous studies suggested that exotic invaders were the result of higher N_{mass} (Baruch and Goldstein 1999; Leishman et al. 2007) and N_{area} (Song et al. 2007; Feng et al. 2008). Leaf nutrient concentration was higher for invasive species in general and also in species-specific comparisons between native and invasive plants. In particular, N was nearly always significantly higher for invasive species. However, few studies have focused on leaf N in native invasive plants. Is it general, like the results in the present study? More attention should be paid to N dynamics of NI species, such as whether lower leaf N for NI species compared with NN species is a general phenomenon.

The lower leaf construction cost of invaders resulted from a higher SLA and lower leaf nitrogen and carbon concentrations (Song et al. 2007). Plants with higher SLA will have thinner leaves and invest less carbon in structural carbohydrates. Additionally, as the respective constituents of many more expensive biochemical plant compounds (Penning de Vries et al. 1974) such as proteins and amino acids (Williams et al. 1987), the concentration of nitrogen was typically positively correlated with leaf construction cost (Griffin et al. 1996). Therefore, with high SLA and low nitrogen concentrations, invasive species may require less energetic costs for construction, and consequently may be more efficient in resource utilization to some extent. In this study, NI species generally had higher SLA, lower leaf N and lower CC than NN species, while EI species had higher leaf N but lower CC than the respective controls. On the whole, it is likely that NI species have the potential for invasiveness no less than EI species.

Differences in resource utilization efficiency among plant types

A plant's efficiency at utilizing resources has implications for its survival, growth and reproductive capacity (Lambers and Poorter 1992; Chen et al. 2005). Light is one of the most important resources for plant growth. LUE of exotic species was higher than that of noninvasive species. LUE of native invaders was 26.6% higher than noninvasive native species, but this difference was not significant, and further studies are needed to confirm it. These results suggest that the invaders may be able to make full use of light, producing more organic matter conducive for their growth, especially the exotic invaders. Furthermore, PNUE is an indicator of resource capture per unit of N investment (Field and Mooney 1986). Plants with high PNUE often have high growth rates (Lambers and Poorter 1992; Schieving and Poorter 1999). Previous studies have shown that the high level of PNUE potentially provides a competitive edge for exotic plants (Ewe and Sternberg 2003; Xu et al. 2007; Feng et al.

2008). In the present study, compared to native noninvasive species, the native invaders had significantly higher PNUE, with a difference that was 3.5 times greater than the difference in PNUE between exotic invasive species and exotic noninvasive ones. The results suggest that PNUE is a common trait in native invasive species and exotic invaders and provides a competitive advantage for successful invasion. Additionally, photosynthesis can be limited by low water availability. Therefore, maximizing A relative to water costs may be another mechanism of invasive plant success (McDowell 2002). However, in our study, there was no significant difference in WUE between invaders and noninvasive species. This may be because that there is typically a trade-off between WUE and PNUE in plants (Van den Boogaard and Villar 1998). Plants achieve high WUE by closing their stomata, which at the same time reduces the supply of CO_2, thereby decreasing the rate of PNUE (Chen et al. 2005). Furthermore, in our study site in Guangzhou, water was not the limiting resource for plant growth as precipitation in the summer is abundant. WUE differences should not be expected under non-stressed conditions; consequently, no significant difference in WUE was observed. PEUE is another useful metric of plant invasion, as it considers both of the supply and demand functions in plant energy budgets (Nagel and Griffin 2004; Funk and Vitousek 2007). With higher PEUE, plants may be better at acquiring resources and competing with native species (Song et al. 2010). This suggests that the dramatically greater PEUE of native invasive species could allow them to assimilate more carbon per unit of energy invested than either of the noninvasive native species measured, which would promote vigorous growth and large areal spread.

Although PEUE provides an instantaneous assessment of energy utilization, the energetic gains and costs are affected by the leaf lifespan when considered over the lifetime of a leaf or plant (Kikuzawa 1991; Kitajima et al. 1997; Nagel and Griffin 2004). Numerous studies have found that leaves with higher PEUE have a shorter leaf lifespan than leaves with lower PEUE (Eamus et al. 1999; Funk and Vitousek 2007). While the leaf-longevity of all the species were not measured in this study, we might speculate that both the native and exotic invaders have shorter leaf lifespans than noninvasive species based on the findings we mentioned above. Species with short leaf lifespans, together with high SLA and A_{max}, can realize higher growth rates (Reich et al. 1997) and may represent a specific growth strategy with quick returns on investment of nutrients and dry mass in leaves (Wright et al. 2004a). However, the importance of resource-use efficiency (RUE) to invasion success might vary across habitats and timescales, based on a broad survey of 19 pairs of phylogenetically related invasive and native species from three habitats in Hawaii where light, water or nutrient availability was limited (Funk and Vitousek 2007). Their findings suggested that high RUE is a plausible mechanism for plant invasion and persistence in low-resource systems, as the invaders were more efficient at using limiting resources than native species on short timescales, but no advantage or disadvantage was evident over long timescales. Thus, further research should be pursued on how resource-use efficiency plays a role in promoting plant invasion under different levels of resource availability and over the long term.

In conclusion, our study provides evidence that native invasive species, like exotic invasive species, have higher A_{max}, SLA, PNUE, and PEUE, and lower CC than native noninvasive species. The results suggest that high resource capture ability and utilization efficiency might be a common biological foundation in plant invasion. Unlike exotic invasives that have higher leaf N, the leaf N of native invasives was lower than in control noninvasives. More attention should be paid to the lower leaf N of native invasive species. In addition, other factors are important for plant invasion such as reproductive efforts, seed dispersal, seedling establishment capabilities, growth and carbon fixation rate, acclimation potential, susceptibility to herbivores and pathogens, phenology, age of reproductive maturity and genetics (Bazzaz 1986; Rejmánek 1996; Williamson and Fitter 1996; Pyšek 1997). Resource capture ability and the utilization efficiency of plants will vary across different species and habitat conditions. Thus, future research should address how these traits act synergistically to promote invasiveness, especially for native invaders. In addition, further comparative studies should be carried out on more species in a wider range of environments to better understand the general traits that play key roles in successful invasions.

References

Allen BP, Sharitz RR, Goebel PC (2007) Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? Forest Ecol Manag 242:17–23

Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia 121:183–192

Bazzaz FA (1986) Life history of colonizing plants: some demographic, genetic and physiological features. Ecol Studies 58:96–110

Bragg DC (2004) Composition, structure, and dynamics of a pine-hardwood old-growth remnant in southern Arkansas. J Torrey Bot Soc 131:320–336

Chapin FS (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260

Chen SP, Bai YF, Zhang LX, Han XG (2005) Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. Environ Exp Bot 53:65–75

Cui GQ, Huang GF, Zhang YB, Liu HW, Au HK, Lin ZL (2003) The present situation, challenge and countermeasure for ecological environment of Guangdong province. Ecol Environ 12:313–316

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Durand LZ, Goldstein G (2001) Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126:345–354

Eamus D, Myers B, Duff G, Williams R (1999) A cost–benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span. Photosynthetica 36:575–586

Ewe SML, Sternberg LSL (2003) Seasonal gas exchange characteristics of *Schinus terebinthifolius* in a native and disturbed upland community in Everglades National Park, Florida. Forest Ecol Manag 179:27–36

Feng YL, Fu GL, Zheng YL (2008) Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive exotic congeners. Planta 228:383–390

Field C, Mooney HA (1986) The photosynthesis-nitrogen relationships in wild plants. In: Givnish TJ (ed) On the economy of plant form, function. Cambridge University Press, UK, pp 25–55

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasions in low-resource systems. Nature 446:1079–1081

Griffin KL, Winner WE, Strain BR (1996) Construction cost of loblolly and ponderosa pine leaves grown with varying carbon and nitrogen availability. Plant Cell Environ 19:729–738

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250:26–31

Grotkopp E, Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. Am J Bot 94:526–532

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. Am Nat 159:396–419

Guan DS, Chen YJ (2003) Status of urban vegetation in Guangzhou City. J Forest Res 14:249–252

Hooftman DAP, Oostermeijer JGB, den Nijs JCM (2006) Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: Spatial distribution and ecological amplitude. Basic Appl Ecol 7:507–519

Huang QQ, Wu JM, Bai YY, Zhou L, Wang GX (2009) Identifying the most noxious invasive plants in China: role of geographical origin, life form and means of introduction. Biodivers Conserv 18:305–316

Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. Am Nat 138:1250–1263

Kitajima K, Mulkey SS, Wright J (1997) Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. Am J Bot 84:702–708

Kotiaho JS, Kaitala V, Komonen A, Päivinen J (2005) Predicting the risk of extinction from shared ecological characteristics. Proc Natl Acad Sci 102:1963–1967

Lake J, Leishman MR (2004) Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conserv 117:215–226

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Leishman MR, Thomson VP (2005) Experimental evidence for the effects of added water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. J Ecol 93:38–49

Leishman MR, Haslehurst T, Ares A, Baruch Z (2007) Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. New Phytol 176:635–643

Leishman MR, Thomson VP, Cooke J (2010) Native and exotic invasive plants have fundamentally similar carbon capture strategies. J Ecol 98:28–42

Li YG, Jin SH, Ai JG (2006) Species, characteristics and control measures of injurious plants in Zhejiang Province. J Zhejiang Forest Coll 23:614–624

Lin C, Liu GK (2008) The research progress of invasive species *Ipomoea cairica*. Subtrop Agri Res 4:177–180

Lin Y, Dai ZC, Si CC, Du DL (2008) A study survey and prospect on invasive condition and invasive mechanism of *Lantana camara* L. J Hainan Nor Univ (Nat Sci) 21:87–93

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology global consequences and control. Ecol Appl 10:689–710

McDowell SCL (2002) Photosynthetic characteristics of invasive and noninvasive species of Rubus (Rosaceae). Am J Bot 89:1431–1438

Nagel JM, Griffin KL (2004) Can gas-exchange characteristics help explain the invasive success of Lythrum salicaria? Biol Invasion 6:101–111

Nagel JM, Huxman TE, Griffin KL, Smith SD (2004) CO_2 enrichment reduces the energetic cost of biomass construction in an invasive desert grass. Ecology 85:100–106

Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117:449–459

Peng SL, Chen BM, Lin ZG, Ye YH, Yu YN, Li JL, Lin HJ (2009) The status of invasive plants in lower subtropical region of China. Acta Ecol Sin 29:79–83

Penning de Vries FWT, Brunsting AHM, Van Laar HH (1974) Products, requirements and efficiency of biosynthesis: a quantitative approach. J Theor Biol 45:339–377

Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, Alexiades M, Cerón C, Di Fiore A, Erwin T, Jardim A, Palacios W, Saldias M, Vinceti B (2002) Increasing dominance of large lianas in Amazonian forests. Nature 418:770–774

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of non-indigenous species in the United States. Bioscience 50:53–65

Pyšek P (1997) Clonality and plant invasions: can a trait make a difference? In: de Kroon H, van Groenendael J (eds) The ecology and evolution of clonal plants. Backhuys Press, Holland, pp 405–427

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in exotic plants: where do we stand? In: Nentwig W (ed) Biological invasions. Springer, Germany, pp 97–126

Pyšek P, Křivánek M, Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90:2734–2744

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Ecology 94:13730–13734

Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. Biol Conserv 78:171–181

Schieving F, Poorter H (1999) Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. New Phytol 143:201–211

Shi GR, Ma CC (2006) Biological characteristics of alien plants successful invasion. Chinese J Appl Ecol 17: 727–732

Song LY, Ni GY, Chen BM, Peng SL (2007) Energetic cost of leaf construction in the invasive weed Mikania micrantha H.B.K. and its co-occurring species: implications for invasiveness. Bot Stud 48:331–338

Song LY, Li CH, Peng SL (2010) Elevated CO_2 increases energy-use efficiency of invasive Wedelia trilobata over its indigenous congener. Biol Invasions 12:1221–1230

Valéry L, Fritz H, Lefeuvre JC, Simberloff D (2008) In search of a real definition of the biological invasion phenomenon itself. Biolo Invasion 10:1345–1351

Van Den Boogaard R, Villar R (1998) Variation in growth and water-use efficiency: a comparison of Aegilops L. species and Triticum aestivum L. cultivars. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys Press, Netherlands, pp 289–308

van Kleunen M, Richardson DM (2007) Invasion biology and conservation biology: time to join forces to explore the links between species traits and extinction risk and invasiveness. Prog Phys Geog 31:447–450

Wen DZ, Ye WH, Feng HL, Cai CX (2000) Comparison of basic photosynthetic characteristics between exotic invader weed Mikania micrantha and its companion species. J Trop subtrop bot 8:139–146

Williams KF, Percival F, Merino J, Mooney HA (1987) Estimation of tissue construction cost from heat of combustion and organic nitrogen content. Plant Cell Environ 10:725–734

Williamson MH, Fitter A (1996) The characters of successful invaders. Biol Conserv 78:163–170

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004a) The worldwide leaf economics spectrum. Nature 428:821–827

Wright SJ, Calderón O, Hernandéz A, Paton S (2004b) Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484–489

Xu CY, Griffin KL, Schuster WSF (2007) Leaf phenology and seasonal variation of photosynthesis of invasive Berberis thunbergii (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. Oecologia 154:11–21

Zou J, Rogers WE, Siemann E (2007) Differences in morphological and physiological traits between native and invasive populations of Sapium sebiferum. Funct Ecol 21:721–730