

Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners

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Abstract Comparisons between invasive and native species may not characterize the traits of invasive species, as native species might be invasive elsewhere if they were introduced. In this study, invasive *Oxalis corymbosa* and *Peperomia pellucida* were compared with their respective noninvasive alien congeners. We hypothesized that the invasive species have higher specific leaf (SLA) than their respective noninvasive alien congeners, and analyzed the physiological and ecological consequences of the higher SLA. Higher SLA was indeed the most important trait for the two invaders, which was associated with their lower leaf construction cost, higher nitrogen (N) allocation to photosynthesis and photosynthetic N use efficiency (PNUE). The higher N allocation to photosynthesis of the invaders in turn increased their PNUE, N content in photosynthesis, biochemical capacity for photosynthesis, and therefore light-saturated photosynthetic rate. The above resource capture-, use- and growth-related traits may facilitate the two invaders' invasion, while further comparative studies on a wider range of invasive and noninvasive congeners are needed to understand the generality of this pattern and to fully assess the competitive advantages afforded by these traits.

Keywords Congeneric comparison · Invasiveness · Nitrogen allocation · Nitrogen use efficiency · Photosynthesis · Specific leaf area

Abbreviations

C_i	Intercellular CO ₂ concentration
CC	Leaf construction cost
CE	Carboxylation efficiency
G_s	Stomatal conductance
J_{max}	Maximum electron transport rate
N_A	Total leaf nitrogen content
N_B	Nitrogen content in bioenergetics
N_C	Nitrogen content in carboxylation
P_B	The fraction of leaf nitrogen allocated to bioenergetics
P_C	The fraction of leaf nitrogen allocated to carboxylation
P_{max}	Light-saturated photosynthetic rate
PNUE	Photosynthetic nitrogen use efficiency
RGR	Relative growth rate
SLA	Specific leaf area
V_{cmax}	Maximum carboxylation rate
WUE	Water use efficiency

Introduction

Many species have intentionally been introduced outside their native range for different purposes (Reichard and White 2001; Xu et al. 2006). A few of them have established and spread in their introduced range, becoming invasive species, while most of introduced species are widely cultivated without problems (Williamson and Fitter 1996). Invasive species can alter species composition, structure and function of the invaded ecosystems, and often cause significant environmental damage and huge economic loss worldwide (Pimentel et al. 2000; D'Antonio and Kark 2002; Xu et al. 2006). It is important to predict

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potentially invasive species before introduction to reduce the possibility of introducing new invasive species. Thus, it is necessary to identify the traits that may be associated with invasiveness of alien species. Knowing these traits is also helpful for controlling existing invasive species. However, little is known about these traits and the mechanisms underlying biological invasions (Smith and Knapp 2001; Burns 2004).

For identifying the traits associated with invasiveness, a few ecophysiological comparisons across invasive and native species have been conducted. It has been found that some invasive species have significantly higher light-saturated photosynthetic rate (P_{\max}), photosynthetic nitrogen (N) use efficiency (PNUE), water use efficiency (WUE), and higher specific leaf area (SLA) but lower leaf construction cost (CC) than native species (Durand and Goldstein 2001; Nagel and Griffin 2001; Smith and Knapp 2001; McDowell 2002; Ewe and Sternberg 2003; Niinemets et al. 2003; Feng et al. 2007a; Xu et al. 2007). However, invasive species were not always higher in P_{\max} , PNUE, WUE and SLA (see review of Daehler 2003). For example, 24 photosynthetic comparisons between invasive and native species were reviewed by Daehler (2003): 11 found similar photosynthesis for invasive and native species; seven found higher while six found lower photosynthesis for invasive species. One of the reasons for the inconsistent results in the literature is that most of the studies (20 of the 24 photosynthetic comparisons) compared phylogenetically unrelated invasive and native species. Phylogenetic relatedness may constrain morphological and physiological variations of plants; closely related plants may share more common traits and more overlapping resource requirements than unrelated species (Goldberg 1987). Therefore, comparisons between related invasive and native species are more meaningful in explaining invasiveness of alien species (Harvey and Purvis 1991; Mack 1996; McDowell 2002). Another reason for the inconsistent results is the intrinsic weakness of the approach of invasive and native comparison (Burns 2004, 2006; Grotkopp and Rejmánek 2007). Some native species might be invasive when introduced outside their native range. In this case, comparison between invasive and native species may not elucidate the traits associated with invasiveness, while it may be helpful for understanding why the invasive species outcompete the native species (Burns 2004).

Comparisons across invasive and noninvasive alien species are an effective approach to detect the potential traits associated with invasiveness, while this approach is seldom used (but see Burns 2004, 2006; Grotkopp and Rejmánek 2007; Feng et al. 2007b). Knowing the differences between invasive and noninvasive alien species may help to understand the mechanisms that allow some alien

species to spread rapidly and even dominate communities (Mack 1996; Radford and Cousens 2000; Smith and Knapp 2001). With this approach, it has been found that invasive species have higher relative growth rate (RGR) and SLA than their noninvasive alien congeners (Grotkopp et al. 2002; Burns 2004, 2006; Grotkopp and Rejmánek 2007). However, the higher RGR and SLA were not found for invasive species when compared with phylogenetically unrelated noninvasive alien species (Smith and Knapp 2001; Feng et al. 2007c), indicating again the importance of the relatedness of the compared invasive and noninvasive alien species.

SLA is associated with N allocation to photosynthesis. Poorter and Evans (1998) found that high-SLA species allocate a higher fraction of leaf N to photosynthesis and have a higher PNUE than low-SLA species. Thus, invasive species may allocate a higher fraction of leaf N to photosynthesis than related noninvasive alien species, provided they have a higher SLA. However, few studies determined leaf N allocation to photosynthesis in invasive species (but see Feng et al. 2007a, b), which is an important factor explaining interspecific differences in P_{\max} , PNUE and WUE (Onoda et al. 2004). In a recent study, we found that invasive *Buddleja davidii* allocates a higher fraction of leaf N to photosynthesis than five unrelated native species (Feng et al. 2007a), while in another study, the higher N allocation to photosynthesis was not detected for invasive *Ageratina adenophora* and *Chromolaena odorata* compared to an unrelated noninvasive alien species (Feng et al. 2007b).

In this study, we compared ecophysiological traits of two invasive species with their respective noninvasive alien congeners at a partially shady site. We hypothesized that compared to their respective noninvasive alien congeners, invasive alien species (1) have higher SLA, (2) allocate a higher fraction of leaf N to photosynthesis and (3) have higher P_{\max} , PNUE, and WUE but lower CC. We focused on SLA in this study because of its pivotal roles in determining other variables such as RGR, CC, P_{\max} and N allocation (Reich et al. 1997; Feng et al. 2007a, c). This study is the first that compares ecophysiological traits of two pairs of invasive and noninvasive alien congeners and hence would contribute to the critical evaluation of the role of ecophysiological traits in facilitating alien plant invasion.

Materials and methods

Study site and species

This study was carried out in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (21°56' N, 101°15' E, 600 m above sea level), which is located in

the southern part of Yunnan Province, southwest China. Here, the mean annual temperature is 21.7°C, with a mean of 25.3°C in the hottest month (July) and 15.6°C in the coolest month (January); the mean annual precipitation is 1,557 mm; and the prevalent soil type is latosol.

There are many invasive plant species in the studied area. However, only two of them were found to have noninvasive alien congeners in this area. Thus, in this study, the two invasive species, *Oxalis corymbosa* DC. (Oxalidaceae) and *Peperomia pellucida* (Linn.) Kunth (Piperaceae), were compared with their noninvasive alien congeners, *O. triangularis* cv. *Purpurea* A. St. Hil. and *P. caperata* Yunck., respectively. *Oxalis corymbosa*, a perennial forb, was introduced into China as an ornamental plant in the middle of 19th century; *P. pellucida*, an annual forb, was introduced unintentionally at the beginning of 20th century. Both the invasive species have naturalized in the subtropics and tropics of many countries. They invade crop field, garden, orchard, plantation, wasteland and roadside. *Oxalis triangularis* and *P. caperata*, perennial forbs, were introduced into China more than 10 years ago. They are widely grown as ornamental plants in China and other countries, but are not recognized as invasive species in any country. All the four species are native to tropical America and can propagate sexually and asexually. *Peperomia pellucida* can asexually propagate by forming adventitious roots at stems; the other species can propagate with rhizomes.

Irradiance influences plant growth, morphology, biomass allocation and physiology, including N allocation (Feng et al. 2007b, c). Thus, we compared each invasive and noninvasive alien congeneric species pair at similar irradiance to exclude its influence. Soil conditions, plant age and size (20-cm-tall current year seedlings) were also similar for the invasive and noninvasive alien species of each genus. In October 2006, 11 individuals for each of *O. corymbosa*, *O. triangularis* and *P. pellucida* were chosen at 25% irradiance in a *Murraya exotica*-dominated community beside a road. However, only four individuals were found for *P. caperata*. The invasive species were naturally grown in the community, while the noninvasive species were transplanted to the community 1 month before the study. Light intensity above each sample individual and in an open site was simultaneously recorded in cloudy mornings with quantum sensors and a Li-1400 datalogger (Li-Cor, Lincoln, NE, USA). Relative irradiance above each sample individual was calculated as the ratio of the light intensity above it to that in the open site.

Measurements

Photosynthetic response to intercellular CO₂ concentration (C_i) was determined on the youngest fully expanded leaves

of the field-grown plants with a Li-6400 Portable Photosynthesis System (Li-Cor). Under saturated photosynthetic photon flux density (PPFD) determined by the preliminary experiments, net photosynthetic rate (P_n) was measured at 380, 300, 260, 220, 180, 140, 110, 80, 50 and 0 μmol mol⁻¹ CO₂ in the reference chamber. Relative humidity of the air in leaf chamber was controlled at 55%, leaf temperature at 25°C. Stomatal conductance (G_s), C_i and P_n were recorded when the sample leaf was balanced for 200 s under each PPFD and CO₂ step. In this study, P_n measured at 380 μmol mol⁻¹ CO₂ and 2,000 μmol m⁻² s⁻¹ PPFD was considered as P_{max} and the ratio of P_{max} to G_s as WUE. Afterwards, light- and CO₂-saturated photosynthetic rate (P'_{max}) was detected after 500 s under 2,000 μmol m⁻² s⁻¹ PPFD and 1,500 μmol mol⁻¹ CO₂. Before measurement, samples were illuminated with saturated PPFD provided by the LED light source of the equipment for 5–30 min to achieve full photosynthetic induction. No photoinhibition occurred during the measurements.

Leaf discs with a definite area were taken from each sample leaf, oven-dried at 60°C for 48 h. SLA was calculated as the ratio of leaf area to mass. Leaf N and carbon contents were determined with Kjeldahl (Büchi Auto Kjeldahl Unit K-370, Büchi Labortechnik AG, Zürich, Schweiz) and H₂SO₄/K₂Cr₂O₇ oxidation–FeSO₄ titration methods, respectively. The measurements were performed by the Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. Leaf CC was calculated according to McDowell (2002). The same leaf of each sample plant was used if possible for measurements of photosynthesis, SLA and carbon content and area (N_A)- and mass (N_M)-based N content.

Calculations of P_n–C_i curve-related variables

The P_n–C_i curve was fitted with a linear equation (P_n = kC_i + i) within 50–200 μmol mol⁻¹ C_i. Maximum carboxylation rate (V_{cmax}) and dark respiration rate (R_d) were calculated according to Farquhar and Sharkey (1982) as follows:

$$V_{cmax} = k[C_i + K_c(1 + O/K_o)]^2 / [\Gamma^* + K_c(1 + O/K_o)] \quad (1)$$

$$R_d = V_{cmax}(C_i - \Gamma^*) / [C_i + K_c(1 + O/K_o)] - (kC_i + i) \quad (2)$$

where K_c and K_o were the Michaelis–Menten constants of Rubisco for carboxylation and oxidation, respectively; Γ* was CO₂ compensation point; O was the intercellular oxygen concentration, close to 210 mmol mol⁻¹. The values of K_c, K_o, and Γ* were temperature-dependent (Bernacchi et al. 2001).

Maximum electron transport rate (J_{\max}) was calculated according to Loustau et al. (1999) as:

$$J_{\max} = \left[4 \left(P'_{\max} + R_d \right) (C_i + 2\Gamma^*) \right] / (C_i - \Gamma^*) \quad (3)$$

The fractions of total leaf N allocated to carboxylation (P_C , g g^{-1}) and bioenergetics (P_B , g g^{-1}) of the photosynthetic apparatus were calculated as:

$$P_C = V_{\text{cmax}} / (6.25 V_{\text{cr}} N_A) \quad (4)$$

$$P_B = J_{\max} / (8.06 J_{\text{mc}} N_A) \quad (5)$$

where V_{cr} and J_{mc} are the specific activities of Rubisco ($\mu\text{mol CO}_2 \text{g}^{-1} \text{Rubisco s}^{-1}$) and cyt f ($\text{mol electrons mol}^{-1} \text{cyt f s}^{-1}$), respectively (Niinemets and Tenhunen 1997). Nitrogen contents in carboxylation (N_C) and bioenergetics (N_B) were calculated as the products of N_A and P_C , P_B , respectively.

Statistical analyses

The differences between each invasive species and its noninvasive congener in the variables presented in Table 1 were analyzed with independent-sample t tests. A one-way ANCOVA was used to determine the difference between each invader and its noninvasive congener in the correlation between each pair of the variables presented in Figs. 1, 2, 3 and 4. If the above difference was not significant, the invasive and noninvasive species of the same genus were pooled together and the difference between the two genera was determined further. If the difference between congeners was significant, the difference between the invasive or noninvasive species of different genera was determined further. If the difference between the invasive or noninvasive species of different genera was not significant, the invasive or noninvasive species of different genera were pooled together and the difference between the pooled invasive and the pooled noninvasive species was determined further. All the analyses were carried out using SPSS 13.0 (SPSS, Chicago, IL, USA).

Results

The two studied invasive species had significantly higher P_{\max} , V_{cmax} , J_{\max} , CE, PNUE, P_C , P_B , N_C , N_B and SLA, but lower N_A and CC than their noninvasive alien congeners, respectively (Table 1). Stomatal conductance was significantly higher for invasive *O. corymbosa* than for noninvasive *O. triangularis*, while C_i was similar between the congeners. Invasive *P. pellucida* showed lower G_s and C_i than noninvasive *P. caperata*.

Except *P. caperata* ($P = 0.183$), other studied species showed significant correlation between CC and SLA

($P < 0.001$). Leaf CC decreased exponentially with the increase of SLA (Fig. 1a). *Oxalis triangularis* showed significant correlations between SLA and P_C ($P = 0.003$), P_B ($P < 0.001$) and PNUE ($P < 0.001$); *P. pellucida* exhibited significant correlation between P_B and SLA ($P = 0.007$). However, P_C , P_B and PNUE increased significantly with the increase of SLA for the pooled invasive and noninvasive alien species (Fig. 1b–d).

Photosynthetic N use efficiency was correlated positively with P_C and P_B for all the studied species ($P < 0.05$) except *P. caperata*, in which the correlation between PNUE and P_C was not significant ($P = 0.170$). With the increase of P_C or P_B , PNUE showed similar increase pattern for all the studied species (Fig. 2a, b). *Oxalis corymbosa* ($P = 0.036$) and *P. pellucida* ($P < 0.001$) showed significant correlation between PNUE and P_{\max} , while only *O. triangularis* showed significant correlation between PNUE and N_A ($P = 0.003$). However, PNUE decreased with increasing N_A , but increased with increasing P_{\max} for the pooled invasive and the pooled noninvasive species (Fig. 2c, d). At the same value of N_A or P_{\max} , PNUE was significantly higher in the invasive species than in the noninvasive species.

With the increase of P_C or P_B , P_{\max} also increased significantly for the pooled *Oxalis* and the pooled *Peperomia* species (Fig. 3a, b), although only *P. pellucida* showed significantly positive correlation between P_{\max} and P_C ($P < 0.001$), P_B ($P = 0.007$). At the same value of P_C or P_B , P_{\max} was significantly higher in *Oxalis* than in *Peperomia*. Light-saturated photosynthetic rate was correlated positively with V_{cmax} for all the studied species ($P < 0.01$) except *P. caperata* ($P = 0.598$). Among the four studied species, only *O. corymbosa* ($P = 0.001$) and *P. pellucida* ($P < 0.001$) showed significant correlation between P_{\max} and J_{\max} . With the increase of V_{cmax} or J_{\max} , P_{\max} showed similar increase pattern for all the studied species (Fig. 3c, d).

No studied species showed significant correlation between P_{\max} and N_A ($P > 0.05$). However, P_{\max} increased significantly with increasing N_A for the pooled invasive species, while the correlation between P_{\max} and N_A was still not significant for the pooled noninvasive species (Fig. 4a). *Oxalis triangularis* ($P = 0.006$) and *P. pellucida* ($P < 0.001$) exhibited significant correlation between P_{\max} and G_s . With the increase of G_s , P_{\max} showed similar increase pattern for the pooled invasive and the pooled noninvasive (the outlier was removed for *P. caperata*) species (Fig. 4b). At the same value of G_s , the invasive species showed significantly higher P_{\max} than the noninvasive species, indicating their higher WUE. However, the difference in WUE between *O. corymbosa* and *O. triangularis* was not significant according to independent samples t test (Table 1).

Table 1 The differences between the invasive and noninvasive alien congeners of the two genera according to the independent-sample *t* tests

Variables	<i>Oxalis</i>		<i>Peperomia</i>	
	<i>O. corymbosa</i>	<i>O. triangularis</i>	<i>P. pellucida</i>	<i>P. caperata</i>
SLA (cm ² g ⁻¹)	628.5 ± 47.1***	315.4 ± 24.8	735.2 ± 25.6***	442.9 ± 26.8
CC (g glucose m ⁻²)	15.28 ± 0.97***	27.68 ± 2.42	8.93 ± 0.44***	18.78 ± 1.26
<i>P_C</i> (g g ⁻¹)	0.737 ± 0.116***	0.214 ± 0.031	0.702 ± 0.076***	0.194 ± 0.012
<i>P_B</i> (g g ⁻¹)	0.100 ± 0.005***	0.040 ± 0.005	0.107 ± 0.009***	0.038 ± 0.002
<i>N_C</i> (g m ⁻²)	0.471 ± 0.059**	0.228 ± 0.016	0.288 ± 0.034**	0.166 ± 0.009
<i>N_B</i> (g m ⁻²)	0.066 ± 0.004***	0.042 ± 0.002	0.044 ± 0.004*	0.032 ± 0.000
<i>N_A</i> (g m ⁻²)	0.666 ± 0.040***	1.176 ± 0.108	0.407 ± 0.015***	0.859 ± 0.042
PNUE (μmol g ⁻¹ s ⁻¹)	15.36 ± 1.22***	5.67 ± 0.63	17.52 ± 1.95***	4.75 ± 0.35
<i>P_{max}</i> (μmol m ⁻² s ⁻¹)	10.23 ± 1.16**	5.62 ± 0.14	7.20 ± 0.88**	4.35 ± 0.30
<i>J_{max}</i> (μmol m ⁻² s ⁻¹)	82.73 ± 5.46***	53.35 ± 3.13	54.85 ± 4.97*	40.70 ± 0.25
<i>V_{cmax}</i> (μmol m ⁻² s ⁻¹)	61.15 ± 7.71**	29.57 ± 2.04	37.43 ± 4.40**	21.55 ± 1.14
CE	0.059 ± 0.009**	0.028 ± 0.002	0.037 ± 0.004**	0.020 ± 0.001
<i>G_s</i> (mol m ⁻² s ⁻¹)	0.244 ± 0.018**	0.162 ± 0.001	0.112 ± 0.018	0.207 ± 0.103
<i>C_i</i> (μmol mol ⁻¹)	277.5 ± 8.7	286.2 ± 7.0	245.6 ± 11.2*	304.3 ± 19.9
WUE (μmol CO ₂ mol ⁻¹ H ₂ O)	42.28 ± 4.10	39.52 ± 2.70	69.31 ± 4.79**	32.60 ± 9.30

Species mean values ± SE are given (*n* = 4 for *P. caperata*; *n* = 11 for other species)

SLA specific leaf area, CC leaf construction cost, *P_C* the fraction of leaf nitrogen allocated to carboxylation, *P_B* the fraction of leaf nitrogen allocated to bioenergetics, *N_C* nitrogen content in carboxylation, *N_B* nitrogen content in bioenergetics, *N_A* total leaf nitrogen content, PNUE photosynthetic nitrogen use efficiency, *P_{max}* light-saturated photosynthetic rate, *V_{cmax}* maximum carboxylation rate, *J_{max}* maximum electron transport rate, CE carboxylation efficiency, *G_s* stomatal conductance, *C_i* intercellular CO₂ concentration, WUE water use efficiency

* *P* ≤ 0.05; ** *P* ≤ 0.01; *** *P* ≤ 0.001

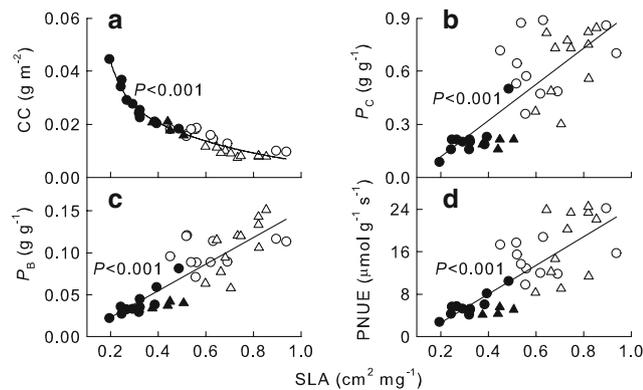


Fig. 1 Leaf construction cost (CC, **a**), the fractions of leaf nitrogen allocated to carboxylation (*P_C*, **b**) and to bioenergetics (*P_B*, **c**), and photosynthetic nitrogen use efficiency (PNUE, **d**) as a function of specific leaf area (SLA) in invasive *Oxalis corymbosa* (open circles) and *Peperomia pellucida* (open triangles), and noninvasive alien *O. triangularis* (filled circles) and *P. caperata* (filled triangles)

Discussion

As expected, *O. corymbosa* and *P. pellucida* had significantly higher SLA than their respective noninvasive alien congeners (Table 1). Higher SLA was also found for other invasive species compared with their noninvasive congeners by Grotkopp et al. (2002), Burns (2006) and Grotkopp and Remánek (2007). In addition, most studies

found that invasive species have higher SLA than their co-occurring native species (Daehler 2003). The higher SLA of the studied invaders may translate to a higher RGR compared to their respective noninvasive congeners, as SLA is the most important determinant of RGR, especially at low irradiance (Shipley 2006; Feng et al. 2007c). The higher *P_{max}* and PNUE of the invaders supported the above prediction. Feng et al. (2007c) found that *P_{max}* is positively correlated with net assimilation rate, which is another factor influencing RGR (Goodger et al. 2006; Shipley 2006). Pattison et al. (1998) found that *P_{max}* is positively correlated with RGR. Species with high PNUE and SLA usually have high RGR (Lambers and Poorter 1992; Reich et al. 1997; Schieving and Poorter 1999). Both RGR and SLA are important in capturing available resources (Grotkopp and Remánek 2007), and the ability to opportunistically capture resources is important for alien plant invasion (Davis et al. 2000). With 29 invasive and noninvasive pine species, Grotkopp et al. (2002) found that both RGR and SLA are positively correlated with invasiveness.

On the other hand, the higher SLA of the two studied invaders contributed to their lower CC (Table 1). Leaf CC decreased exponentially with increasing SLA (Fig. 1a), while in another study, the negative correlation between CC and SLA is linear (Feng et al. 2007a). With lower CC but higher *P_{max}*, the leaves of the two invaders may have

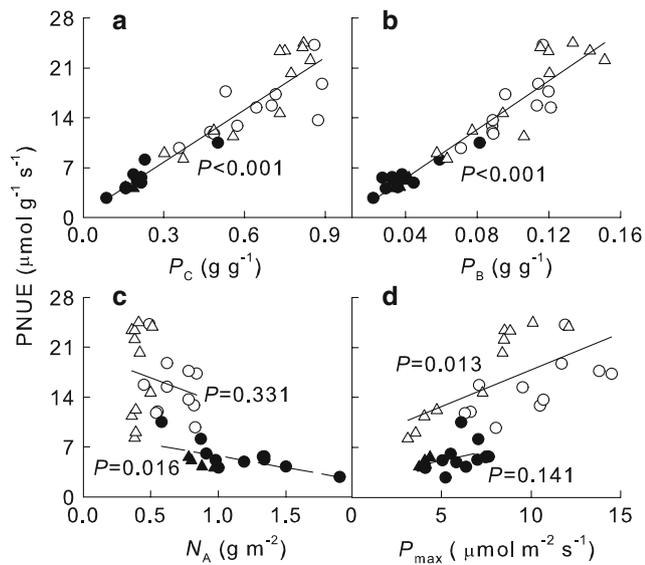


Fig. 2 Photosynthetic nitrogen use efficiency (PNUE) as a function of the fractions of leaf nitrogen allocated to carboxylation (P_C , **a**) and to bioenergetics (P_B , **b**), leaf nitrogen content (N_A , **c**), and light-saturated photosynthetic rate (P_{max} , **d**) in invasive *Oxalis corymbosa* (open circles) and *Peperomia pellucida* (open triangles), and noninvasive alien *O. triangularis* (filled circles) and *P. caperata* (filled triangles). The lines fitted for the invasive and noninvasive alien species are significantly different in plots **c** and **d** ($P < 0.001$) according to the result of a one-way ANCOVA with PNUE as dependent variable, species category (invasive vs. noninvasive) as fixed factor, and N_A and P_{max} as covariate, respectively

shorter payback time than those of their respective noninvasive alien congeners, i.e., they can fix the amount of energy required to construct themselves through photosynthesis in a shorter time, leaving more energy for defense, growth and reproduction. It has been documented that low CC is often associated with high RGR and small difference in CC can lead to big difference in RGR (Griffin 1994; Poorter and Villar 1997). Nagel and Griffin (2001) and Tsialtas et al. (2002) further reported that species with low CC have high field abundances.

Furthermore, the higher SLA of the two studied invaders also contributed to their higher N allocation to photosynthesis (Fig. 1). SLA is the reciprocal of the product of leaf density and thickness. Leaf density is positively associated with the fraction of leaf mass in structural tissue (mainly cell walls). Leaves with high SLA may have lower fraction of leaf mass in structural tissue than leaves with low SLA. Onoda et al. (2004) indeed found that SLA is negatively associated with cell wall mass. Cell walls contain many kinds of proteins, and about 5–10% of the primary cell wall mass is protein (Loomis 1997). Nitrogen allocation to carboxylation and bioenergetics increased significantly with increasing SLA (Fig. 1b, c). Thus, the higher SLA of the two invaders may contribute to their higher N allocation to photosynthesis by reducing N allocation to cell

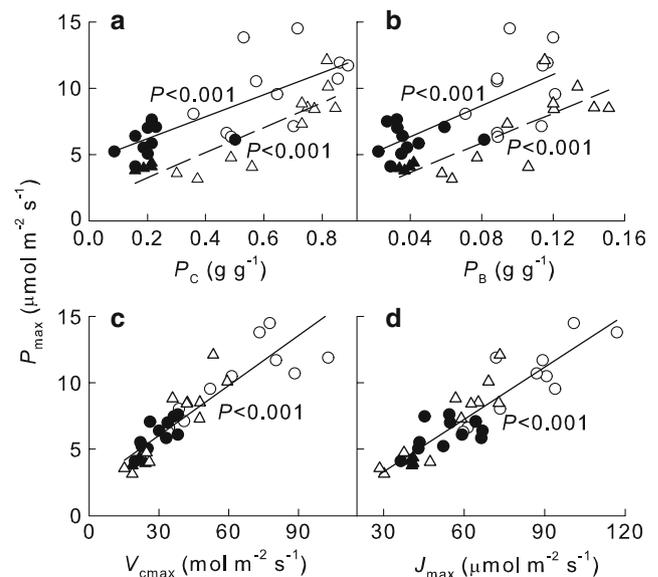


Fig. 3 Light-saturated photosynthetic rate (P_{max}) as a function of the fractions of leaf nitrogen allocated to carboxylation (P_C , **a**) and to bioenergetics (P_B , **b**), maximum carboxylation rate (V_{cmax} , **c**) and maximum electron transport rate (J_{max} , **d**) in invasive *Oxalis corymbosa* (open circles) and *Peperomia pellucida* (open triangles), and noninvasive alien *O. triangularis* (filled circles) and *P. caperata* (filled triangles). The lines fitted for *Oxalis* and *Peperomia* are significantly different in plots **a** and **b** ($P < 0.001$) according to the result of a one-way ANCOVA with P_{max} as dependent variable, genus (*Oxalis* vs. *Peperomia*) as fixed factor, and P_C and P_B as covariate, respectively

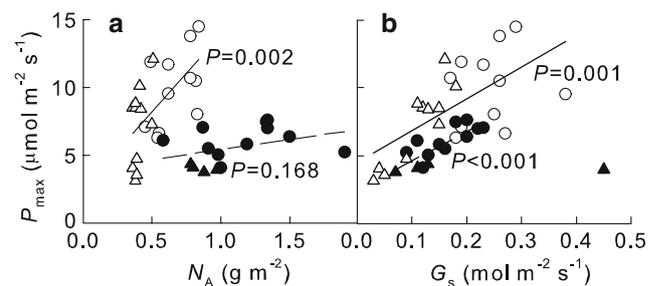


Fig. 4 Light-saturated photosynthetic rate (P_{max}) as a function of leaf nitrogen content (N_A , **a**) and stomatal conductance (G_s , **b**) in invasive *Oxalis corymbosa* (open circles) and *Peperomia pellucida* (open triangles), and noninvasive alien *O. triangularis* (filled circles) and *P. caperata* (filled triangles). The outlier was not included in the correlation between P_{max} and G_s for *O. triangularis*. The lines fitted for the invasive and noninvasive alien species are significantly different ($P < 0.001$) according to the result of a one-way ANCOVA

walls. There is a trade-off between N allocation to cell walls and to photosynthesis. With native species, Takashima et al. (2004) found that SLA is positively correlated with the fraction of leaf N in Rubisco.

The positive correlation between SLA and PNUE (Fig. 1d) may be due to the influence of SLA on N allocation to photosynthesis, indicating that SLA may

influence PNUE by influencing N allocation. It is understandable that increasing N allocation to photosynthesis translates to increasing PNUE. Nitrogen allocation to photosynthesis may influence PNUE by contributing to P_{\max} (Fig. 3a, b), which was positively correlated with PNUE (Fig. 2d). The similar increasing pattern of PNUE with P_C and P_B indicated that the higher PNUE of the two invaders in comparison with their respective noninvasive alien congeners was related to their higher P_C and P_B (Fig. 2a, b). The higher PNUE of the two invaders might also be associated with their lower N_A . At high level of N_A , PNUE is negatively correlated with N_A (Hikosaka and Terashima 1995). In our study, PNUE indeed showed a decreasing trend with increasing N_A , but was significant only for the noninvasive species (Fig. 2c).

Photosynthesis was positively correlated with $V_{c\max}$ and J_{\max} (Fig. 3c, d), which determined N_C [$=V_{c\max}/(6.25V_{cr})$] and N_B [$=J_{\max}/(8.06J_{mc})$] theoretically. The results showed that P_{\max} was directly influenced by N_C and N_B , which are the products of N_A and P_C , P_B , respectively. With lower N_A , the two studied invaders in comparison with their respective noninvasive alien congeners had higher N_C ($V_{c\max}$), N_B (J_{\max}) and therefore higher P_{\max} , indicating that the higher P_C and P_B of the invaders was the main factor explaining their higher P_{\max} (Fig. 3a, b). The higher P_{\max} of the two invaders at the same value of N_A (Fig. 4a) confirmed again the importance of N allocation to photosynthesis in determining P_{\max} . Stomatal conductance was not important in explaining the higher P_{\max} of the two invaders although it was positively correlated with P_{\max} (Fig. 4b). With lower G_s and C_i , *P. pellucida* showed higher P_{\max} compared to *P. caperata* (Table 1). Although *O. corymbosa* had higher G_s than *O. triangularis*, it did not show higher C_i . In addition, P_{\max} exhibited decreasing trend with increasing C_i (data not shown). The results further indicated that the ability to use intercellular CO_2 (associated with N in photosynthesis) was more important than the ability to supply CO_2 (associated with G_s) in explaining the higher P_{\max} of the invaders, thus again confirming the importance of N allocation.

Peperomia pellucida in comparison with *P. caperata* had both higher PNUE and WUE (Table 1), breaking the trade-off between them. The invader increased P_{\max} and PNUE mainly by increasing N allocation to photosynthesis rather than by increasing G_s , and thereby did not reduce WUE. This is different from the situation of invasive *Buddleja davidii*, in which the increased N allocation to photosynthesis and the increased P_{\max} do not completely compensate the negative effect of the increased G_s on WUE (Feng et al. 2007a). However, the increased N allocation to photosynthesis overcompensated the negative effect of the increased G_s on WUE in *O. corymbosa* (Table 1). Durand and Goldstein (2001), McDowell (2002)

and Ewe and Sternberg (2003) also found that invasive species have both higher WUE and PNUE than native species, but they did not give mechanistic explanations to the broken trade-off.

In conclusion, the higher SLA was the most important trait for invasive *O. corymbosa* and *P. pellucida* in comparison with their respective noninvasive alien congeners, which was related directly to their lower leaf CC and indirectly to their higher N content in photosynthesis, biochemical capacity for photosynthesis, light-saturated photosynthetic rate and nitrogen use efficiency by increasing nitrogen allocation to photosynthesis. These traits may contribute to their invasiveness. Higher SLA has also been found for many other invasive species. This easily measured trait might be a predictor of some invasive species and analyzing it before introduction may be useful for reducing the possibility of introduction of new invasive species. Our study is the first that compares ecophysiological traits of two pairs of invasive and noninvasive alien congeners, while few studies have compared life-history traits of invasive and noninvasive congeners. Thus, further comparative studies on more invasive and noninvasive alien congeners at a wide range of environments are necessary for understanding the generality of the patterns found in this study and determining the extent of the competitive advantage provided by these traits. In addition, life-history traits of the invasive and noninvasive congeners compared should be considered in future study, as they may influence ecophysiological traits.

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