

# A quicker return energy-use strategy by populations of a subtropical invader in the non-native range: a potential mechanism for the evolution of increased competitive ability

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## Summary

1. Many studies testing the evolution of increased competitive ability hypothesis have focused on whether plants from invasive populations of a species show reduced allocation to defence and increased allocation to growth than plants from native populations. But few have attempted to understand ecophysiological mechanisms by which decreased allocation to defence may increase growth.

2. Previously, we found that invasive *Ageratina adenophora* plants increase nitrogen allocation to photosynthesis and reduce allocation to cell walls compared with native *Ageratina* plants, suggesting a shift from defence to growth in invasive populations. Here, carrying this work forward, we measured construction costs and benefits associated with photosynthesis at light saturation to leaves. We hypothesized that invasive *Ageratina* populations might employ a quicker return energy-use strategy by increasing light-saturated photosynthetic rates and photosynthetic energy-use efficiency (PEUE) and by decreasing leaf construction costs.

3. Faster-growing plants from invasive populations (China and India) had significantly higher leaf nitrogen concentrations and specific leaf areas than plants from native populations (Mexico). Inconsistent with our prediction, leaf construction costs were not significantly different between plants from invasive and native populations, but higher light-saturated photosynthetic rates and in turn higher PEUE resulted in a significantly shorter payback time of construction costs, which allowed plants from invasive populations to grow faster.

4. *Synthesis.* Our results indicate that *Ageratina* plants from populations in non-native ranges have a distinct quick return energy-use strategy, a high PEUE and a short payback time but not lower construction costs, which might provide a mechanistic explanation for the commonly observed increase in growth when plants are introduced to new parts of the world. To our knowledge, this is the first study to compare energy-use strategy for plants from invasive and native populations of a noxious invasive species. We cannot exclude some alternative hypotheses for these patterns, such as founder effects, but these ecophysiological differences might provide mechanistic insight for how the evolution of decreased allocation to defence may increase growth and competitive ability.

**Key-words:** benefit–cost analysis, common garden experiment, invasion ecology, leaf construction cost, nitrogen, payback time, photosynthesis, photosynthetic energy-use efficiency, specific leaf area

## Introduction

The evolution of increased competitive ability (EICA) hypothesis is the idea that exotic plants can evolve to decrease

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resource allocation to costly structural and chemical defences in response to the lack of natural enemies in introduced ranges, which allows increased allocation to growth and reproduction, and thus to competitive ability (Blossey & Nötzold 1995). Consistent with the EICA hypothesis, invasive plants often experience lower numbers and impacts of enemies (especially specialists) in introduced ranges than in native ranges (Joshi & Vrieling 2005; Liu & Stiling 2006; Adams *et al.* 2009). Increased growth and decreased defences have been documented for many invasive plants (Bossdorf *et al.* 2005; Joshi & Vrieling 2005; Stastny, Schaffner & Elle 2005; Zou, Rogers & Siemann 2007), but EICA is not a general phenomenon for all invaders (Bossdorf *et al.* 2005; Caño *et al.* 2009).

A number of studies have compared the differences in functional traits between plants from invasive and native populations of alien plants (DeWalt, Denslow & Hamrick 2004; Zou, Rogers & Siemann 2007; Brodersen, Lavergne & Molofsky 2008; Feng *et al.* 2009; Mozdzer & Zieman 2010). Of these plants, higher light-saturated photosynthetic rates ( $P_{\max}$ ) for plants from invasive populations have been found for *Sapium sebiferum*, *Ageratina adenophora* and *Phragmites australis* (Zou, Rogers & Siemann 2007; Feng *et al.* 2009; Mozdzer & Zieman 2010), which might contribute to the increased growth in plants from invasive populations. Feng, Wang & Sang (2007a) found that  $P_{\max}$  is positively correlated with net assimilation rate, one of the determinants of RGR, for *A. adenophora*. Positive correlations between growth rate and  $P_{\max}$  have been demonstrated in invasive plants (Pattison, Goldstein & Ares 1998; Zheng *et al.* 2009).

However, high benefits to leaf performance in terms of  $P_{\max}$  may not necessarily lead to high fitness, as growth and/or reproduction depend on both benefits and costs (Griffin 1994). Leaf construction cost, the glucose needed to form a unit of leaf, is a quantifiable measure of the energy demand for biomass production and is generally associated with growth rate (Poorter & Villar 1997). Lower construction cost has been found for some invasive species relative to natives (Nagel & Griffin 2001; Song, Li & Peng 2009; Osunkoya *et al.* 2010). However, there have been no efforts to date to compare the construction costs between plants from populations of an invasive species from its native range and plants from populations from the non-native range. Understanding construction cost is crucial for understanding mechanistic aspects of resource allocation in plants, and biogeographic comparisons have the potential to shed light on the ecophysiology underlying evolutionarily increased growth in invasive plants.

There is reason to think that invasive plants may benefit from higher benefit–cost ratios than native species in invaded systems. This is because photosynthetic energy-use efficiency (PEUE, the ratio of  $P_{\max}$  to construction cost and a commonly used measure of energy-use strategy) is positively correlated with growth (Nagel *et al.* 2005). Disproportionally higher PEUE has been found for a few invasive species (Funk & Vitousek 2007; Song, Li & Peng 2009; Osunkoya *et al.* 2010). Payback time (days needed to pay back leaf construction cost through photosynthesis) is another measure of energy-use strategy (Williams, Field & Mooney 1989). This reflects plant

energetic benefit during leaf lifetime; leaves with short payback time may gain more carbon or energy during their lifetime than leaves with long-payback time, if they have similar longevities (Chabot & Hicks 1982). However, no study has compared differences in payback time between plants from invasive and native populations or even among invasive and native species in a community.

*Ageratina adenophora* (Sprengel) R. M. King & H. Robinson (syn. *Eupatorium adenophorum*, Asteraceae) is native to Mexico but a noxious invasive perennial forb in Asia, Oceania, Africa, Europe and the USA (Shrestha, Wilson & Gay 2008; Muniappan, Raman & Reddy 2009). *Ageratina* has been spreading extensively in the lower and mid-Himalayan regions of India since its introduction in 19th century (Kaushal *et al.* 2001; Muniappan, Raman & Reddy 2009). *Ageratina* spread into Yunnan Province, south-west China in 1940s from Burma, Laos and Vietnam. It invades pastures, agricultural fields, disturbed forests, roadsides and abandoned fields, reducing native plant species richness in China and India (Inderjit *et al.*, in press). *Ageratina* spreads mainly by seeds that predominantly mature in spring but can also spread vegetatively. Higher photosynthetic rates contribute to higher growth rates for *Ageratina* relative to its native congeners (Zheng *et al.* 2009). Photosynthetic rates of *Ageratina* leaves are not influenced by plant age, but there are substantial photosynthetic costs for reproduction (Wang *et al.* 2005).

In a previous study, we compared the growth and physiological parameters of *Ageratina* plants raised in a common garden from seeds collected from native (Mexico) and non-native (China and India) ranges (Feng *et al.* 2009). We found that *Ageratina* plants from invasive populations had lower nitrogen (N) allocation to cell walls (defence) and higher N allocation to photosynthesis (growth) in comparison with plants from native populations, contributing to increased  $P_{\max}$  and growth (Feng *et al.* 2009). Carrying this work forward, we have used new measurements on the same populations to estimate the costs (construction costs) and the benefits (photosynthesis at light saturation) of building leaves to test the hypothesis that the ratio of benefits to costs is higher for plants from invasive populations than for conspecifics from native populations. Here, we present a novel case for differences in energy-use strategy between native and invasive populations of *Ageratina*.

## Materials and methods

This study represents further analyses of our previous work (Feng *et al.* 2009) and is designed to determine if construction costs and benefits in terms of photosynthesis at light saturation are different among plants from populations in the native and non-native ranges. In addition to the 15 populations used in our previous study, we included one more Chinese population (Jingdong, Yunnan; see Table S1 in Supporting Information) to estimate construction costs and benefits for invasive *Ageratina* populations. Seeds from 16 populations were collected in spring 2006 and were sown in a seedbed on 20 December 2006. When the seedlings were *c.* 10 cm tall, 320 similar-sized seedlings (20 per population) were transplanted to five  $2 \times 2$ -m plots (four seedlings per population per plot) established at a

site fully exposed to the sun. The detailed methodology and experimental conditions are given in Feng *et al.* (2009).

In October 2007 (no plants were producing flowers), we collected the youngest fully expanded leaves of 15 plants per population (one leaf per plant and three plants per plot), and mixed the leaves from each population. We determined leaf area using a Li-3000C leaf area meter (Li-cor, Lincoln, NE, USA), oven-dried leaves at 60°C for 48 h and then finely ground the dried leaves. Specific leaf area (SLA) was calculated as the ratio of leaf area to mass for the 15 mixed leaves. Carbon and N ( $N_m$ ) concentrations of the powdered leaves were determined with a Vario MAX CN Element Analyser (Elementar Analysensysteme GmbH, Hanau, Germany). Ash concentration (Ash) was determined after combusting leaf sample in a muffle furnace at 550°C for 6 h; ash alkalinity was determined acidimetrically (Poorter & Villar 1997). The mineral concentration (Min) of each sample was calculated according to Poorter & Villar (1997) as follows:

$$\text{Min} = \text{Ash-ash alkalinity} \times 30 + \text{nitrate concentration}$$

Construction cost was calculated according to Navas *et al.* (2003) as follows:

$$\text{Construction cost} = [-1.041 + 5.077 \times C / (1000 - \text{Min})] \times [(1000 - \text{Min}) / 1000] + [5.325 \times \text{organic N} / 1000],$$

where C is carbon concentration. Nitrate concentrations were negligible, thus we assumed that organic N =  $N_m$  (Navas *et al.* 2003).

Payback time was calculated after Williams, Field & Mooney (1989). Daily accumulation of photosynthate was calculated as the product of daily duration of photosynthesis and half of the average  $P_{\max}$  of each population, which was used in this study because it was similar to daily mean photosynthetic rate derived from preliminary measurements. Night respiration loss was calculated as the product of length of night and the average respiration rate of each population. Photosynthetic energy-use efficiency (PEUE) was calculated as the ratio of average  $P_{\max}$  of each population to construction costs (Nagel *et al.* 2005; Song, Li & Peng 2009). Average  $P_{\max}$  and respiration rate of each population were calculated with  $P_{\max}$  and respiration rates of five plants (one per plot), measured in a previous study (Feng *et al.* 2009).

In the measurements described above, the mean for each population rather than each sample plant, was used as a replicate because we could not consistently collect 15 uniform leaves from each sample

plant. Preliminary measurements indicated that leaves other than the youngest fully expanded leaves had different construction costs, and thus could not be used to calculate payback time and PEUE because  $P_{\max}$  was measured on the youngest fully expanded leaf.

To further evaluate differences between plants from invasive and native populations in traits involving gas exchange, mass-based  $P_{\max}$ , stomatal conductance ( $G_s$ ) and respiration rate were calculated using area-based values according to the leaf mass per area of each sample plant from Feng *et al.* (2009). Area-based  $G_s$ , intercellular CO<sub>2</sub> concentration and area-based respiration rate (measured after 200 s of dark) were concomitantly recorded when measuring  $P_{\max}$  (Feng *et al.* 2009), but were not presented in our previous study. Furthermore, photosynthetic water-use efficiency and respiration efficiency (respiration cost for photosynthesis) were calculated as the ratios of  $P_{\max}$  to  $G_s$  and respiration rate respectively (Pattison, Goldstein & Ares 1998; Feng, Auge & Ebeling 2007b). To examine the roles of  $N_m$  and  $G_s$  in explaining photosynthetic differences, correlations between  $N_m$ ,  $G_s$  and  $P_{\max}$  were analysed. To explore how SLA and  $N_m$  influence energy-use strategy, we correlated these variables with PEUE, payback time and other related variables.

#### STATISTICAL ANALYSES

Differences between plants from invasive and native populations in  $P_{\max}$ ,  $G_s$ , respiration rate, respiration efficiency, intercellular CO<sub>2</sub> concentration and photosynthetic water-use efficiency were tested using nested ANOVAS, with range as a fixed factor, population nested within range as a random factor, and the altitude of each population as a covariate (Univariate of GLM) (Table 1). Invasive populations were collected at lower altitudes than with the native populations (see Table S1), and altitude can affect the constitutive physiology of plants (see Table S2 and Premoli & Brewer 2007). Differences in other variables, with each population as a replicate, were tested using MANOVA, with range as a fixed factor and altitude as a covariate (Multivariate of GLM) (Table 2). A one-way ANCOVA was used to test the differences between plants from invasive and native populations in the relationship between  $P_{\max}$  and  $N_m$  or  $G_s$  (Fig. 1), with range (invasive versus native) as a fixed factor,  $P_{\max}$  as a dependent variable, and  $N_m$  or  $G_s$  as a covariate. If the difference was significant, we tested for the significance of linear regressions for plants from invasive and native populations separately; otherwise, we pooled data from plants of all populations to test for the significance of regressions. One-way ANCOVA was not carried out for the results reported in Figs 2 and 3 because of small sample sizes. The significance of linear regressions

**Table 1.** Differences between plants from invasive (China and India) and native (Mexico) populations of *Ageratina adenophora* as tested with nested ANOVAS with range as a fixed factor, population nested within range as a random factor, and altitude as a covariate

Variable	Invasive	Native	$F_{1,13}$ (Range)	$F_{13,64}$ (Population)
Light-saturated photosynthetic rate ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	0.307 ± 0.0092	0.212 ± 0.0151	16.334***	1.503
Dark respiration rate ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	0.038 ± 0.0012	0.040 ± 0.0030	0.005	2.763**
Respiration efficiency	8.49 ± 0.340	5.77 ± 0.513	6.300*	1.398
Photosynthetic water-use efficiency ( $\mu\text{mol mmol}^{-1}$ )	48.92 ± 2.681	39.34 ± 4.340	0.092	2.726**
Stomatal conductance ( $\text{mmol g}^{-1} \text{s}^{-1}$ )	7.51 ± 0.485	7.33 ± 1.030	0.439	2.241*
Intercellular CO <sub>2</sub> concentration ( $\mu\text{mol mol}^{-1}$ )	261.8 ± 4.901	282.5 ± 7.429	0.105	2.992**

Mean values ± SE are given (five populations for Mexico or India, six populations for China, and five individuals per population). The type III sum of squares is zero for altitude because the same altitude was used for all sample individuals of each population; thus there is no F-value for altitude.

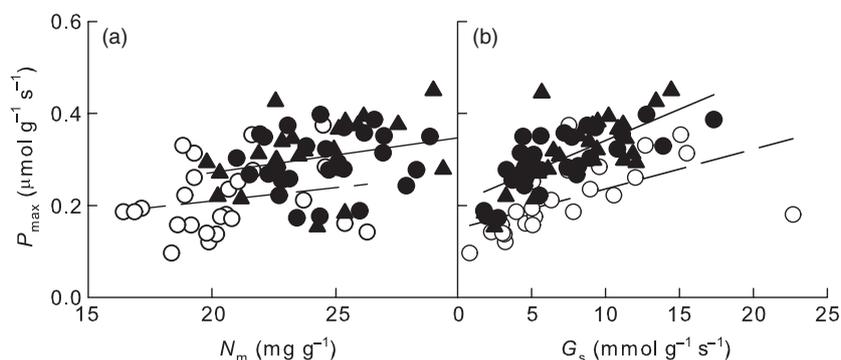
\* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ .

**Table 2.** Differences between plants from invasive (China and India) and native (Mexico) populations of *Ageratina adenophora* from MANOVA with range as a fixed factor and altitude as a covariate

Variable	Invasive	Native	$F_{1,13}$ (Range)	$F$ (Altitude)
SLA ( $\text{cm}^2 \text{mg}^{-1}$ )	$0.194 \pm 0.0046$	$0.165 \pm 0.0056$	13.434**	0.795
Leaf nitrogen ( $\text{mg g}^{-1}$ )	$24.62 \pm 0.408$	$20.58 \pm 0.538$	23.735***	0.044
Carbon ( $\text{mg g}^{-1}$ )	$492.6 \pm 2.18$	$490.2 \pm 1.24$	0.027	2.681
Ash ( $\text{mg g}^{-1}$ )	$83.74 \pm 0.805$	$83.71 \pm 1.695$	0.005	0.012
Mineral ( $\text{mg g}^{-1}$ )	$73.04 \pm 0.920$	$62.71 \pm 1.110$	28.327***	0.211
C:N ratio ( $\text{g g}^{-1}$ )	$20.06 \pm 0.970$	$23.89 \pm 0.677$	31.395***	0.518
CC ( $\text{g glucose g}^{-1}$ )	$1.67 \pm 0.013$	$1.62 \pm 0.005$	1.738	1.922
PEUE ( $\mu\text{mol g}^{-1} \text{glucose s}^{-1}$ )	$0.183 \pm 0.0075$	$0.129 \pm 0.0097$	12.357**	0.010
Payback time (days)	$11.46 \pm 0.191$	$19.07 \pm 1.722$	22.938***	0.008

Mean values  $\pm$  SE are given (five populations for Mexico or India, six populations for China, and one mixed sample of 15 individuals per population). CC, leaf construction cost; C:N ratio, the ratio of leaf carbon to nitrogen; PEUE, photosynthetic energy-use efficiency; SLA, specific leaf area.

\*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ .



**Fig. 1.** Light-saturated photosynthetic rate ( $P_{\max}$ ) as a function of (a) leaf nitrogen concentration ( $N_m$ ; for invasives,  $R^2 = 0.099$ ,  $P = 0.019$ ; for natives,  $R^2 = 0.041$ ,  $P = 0.329$ ) and (b) stomatal conductance ( $G_s$ ; for invasives,  $R^2 = 0.521$ ,  $P < 0.001$ ; for natives,  $R^2 = 0.347$ ,  $P = 0.002$ ) in plants from invasive (China, closed circles and India, closed triangles) and native (Mexico, open circles) populations of *Ageratina adenophora* grown in a common garden. Plants from invasive populations had significantly higher  $P_{\max}$  than plants from native populations at a given value of  $N_m$  (for range,  $F = 10.431$ ,  $P = 0.002$ ; for  $N_m$ ,  $F = 6.485$ ,  $P = 0.013$ ) or  $G_s$  (for range,  $F = 52.209$ ,  $P < 0.001$ ; for  $G_s$ ,  $F = 59.983$ ,  $P < 0.001$ ) based on ANCOVAs with range (invasive versus native) as a fixed factor,  $P_{\max}$  as a dependent variable and  $N_m$  or  $G_s$  as a covariate. Leaf N concentration for each sample plant was taken from a previous study (Feng *et al.* 2009).

between each pair of variables was tested with pooled data from invasive and native populations. We used SPSS 13.0 (SPSS Inc., Chicago, IL, USA) for all analyses.

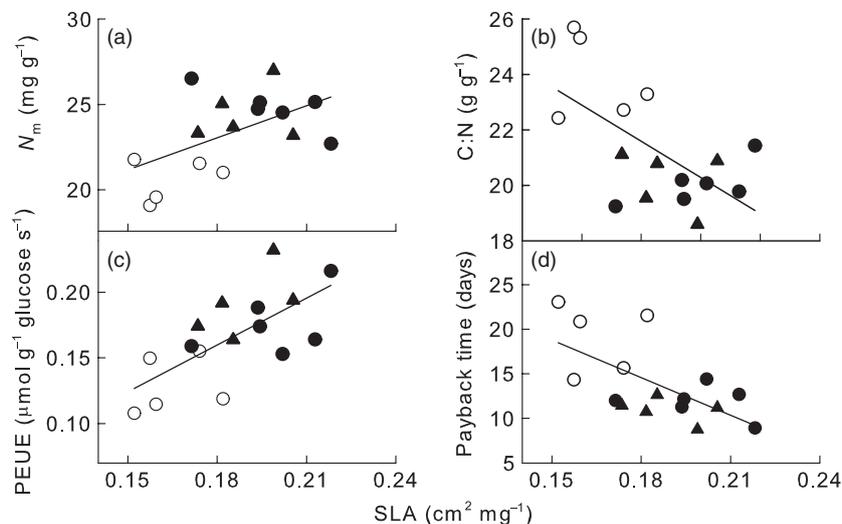
## Results

Plants from invasive populations had 44.8% higher mass-based light-saturated photosynthetic rates ( $P_{\max}$ ), 47.1% higher respiration efficiency (ratio of photosynthesis to respiration), 41.7% higher PEUE, 17.6% higher SLA, 19.6% higher mass-based leaf N concentrations ( $N_m$ ), and 16.5% higher mineral concentrations than plants from native populations (Tables 1 and 2). In contrast, payback time and C:N ratio were 39.9% and 16.0% lower, respectively, for plants from invasive populations than for plants from native populations. Dark respiration rates, stomatal conductance ( $G_s$ ), intercellular  $\text{CO}_2$  concentration, photosynthetic water-use efficiency, leaf construction costs and the concentrations of carbon and ash were not significantly different between plants from invasive and native populations.

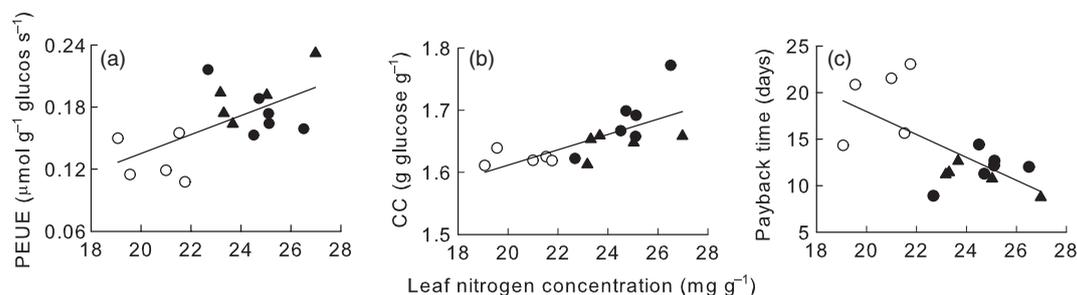
$P_{\max}$  increased linearly with increasing  $N_m$  or  $G_s$ , and plants from invasive populations showed significantly higher  $P_{\max}$  than plants from native populations at a given value of  $N_m$  or  $G_s$  (Fig. 1). Leaf N concentration and PEUE increased significantly with increasing SLA, while C:N ratio and payback time decreased (Fig. 2). Construction cost and PEUE increased significantly with increasing  $N_m$ , whereas payback time decreased (Fig. 3).

## Discussion

Our results indicate that mass-based leaf traits may be more generally useful in comparative studies of invasive plants than area-based leaf traits, perhaps because mass-based traits are determined only by chemical characteristics, whereas area-based traits are determined by both chemical and structural (SLA) characteristics. *Ageratina* plants from invasive populations showed significantly higher mass- (Table 1) and area-based (Feng *et al.* 2009)  $P_{\max}$  than plants from native populations. But the percentage increase in mass-based  $P_{\max}$



**Fig. 2.** (a) Leaf nitrogen concentration ( $N_m$ ;  $R^2 = 0.287$ ,  $P = 0.032$ ), (b) carbon to nitrogen ratio (C:N;  $R^2 = 0.364$ ,  $P = 0.013$ ), (c) photosynthetic energy-use efficiency (PEUE;  $R^2 = 0.467$ ,  $P = 0.004$ ) and (d) payback time ( $R^2 = 0.406$ ,  $P = 0.008$ ) as a function of specific leaf area (SLA) in plants from invasive (China, closed circles and India, closed triangles) and native (Mexico, open circles) populations of *Ageratina adenophora*.



**Fig. 3.** (a) Photosynthetic energy-use efficiency (PEUE;  $R^2 = 0.378$ ,  $P = 0.011$ ), (b) construction cost (CC;  $R^2 = 0.476$ ,  $P = 0.003$ ) and (c) payback time ( $R^2 = 0.425$ ,  $P = 0.006$ ) as a function of leaf nitrogen concentration for plants from invasive (China, closed circles and India, closed triangles) and native (Mexico, open circles) populations of *Ageratina adenophora*.

for plants from invasive populations was much higher (44.8% in the present study) than that in area-based  $P_{max}$  (24.0% in our previous study), which was associated with higher SLA in this study. Due to higher SLA, plants from invasive populations also showed significantly higher  $N_m$  than plants from native populations (Fig. 2a; Table 2), although they had similar area-based leaf N contents (also see Feng *et al.* 2009).

Photosynthesis is highly associated with N content in the photosynthetic apparatus. In our previous study, higher area-based  $P_{max}$  in *Ageratina* plants from invasive populations was attributed completely to higher proportions of leaf N allocated to photosynthesis (Feng *et al.* 2009). Here, we progressed a step farther and found that higher  $N_m$  also contributed to higher mass-based  $P_{max}$  in plants from invasive populations (Fig. 1a). Increased SLA in plants from invasive populations may also contribute to increased mass-based  $P_{max}$  by increasing  $N_m$  (Fig. 2a) and N allocation to photosynthesis (Feng *et al.* 2009). It is important to note that  $G_s$  could not explain the higher  $P_{max}$  in plants from invasive populations, as  $G_s$  and intercellular  $CO_2$  concentration were not significantly different

between plants from invasive and native populations (Table 1). Thus, at a given value of  $G_s$ , mass-based  $P_{max}$  was higher in plants from invasive populations than in plants from native populations (Fig. 1b), indicating higher biochemical capacity for photosynthesis, consistent with higher carboxylation efficiency, maximum carboxylation rates and higher maximum electron transport rates (data not shown).

Higher  $P_{max}$  led to higher respiration efficiency in plants from invasive populations because respiration rates were not significantly different between plants from invasive and native populations (Table 1). Higher respiration efficiency indicates a lower respiration cost for photosynthesis, which would leave more carbon to allocate to growth. Higher  $P_{max}$  also resulted in higher photosynthetic N-use efficiency but not higher photosynthetic water-use efficiency in *Ageratina* plants from invasive populations relative to plants from native populations (Table 1; Feng *et al.* 2009).

Increased SLA of invasive *Ageratina* plants did not lead to decreased leaf construction costs, which may be due to higher  $N_m$  (Fig. 3b) and the expensive energetic costs of proteins,

amino acids and other N-based chemicals (Penning de Vries, Brunsting & van Laar 1974). Even so, plants from invasive populations still had higher benefit–cost ratios; because plants from invasive populations had higher PEUE and returned the investments of nutrients and dry mass in leaves in a shorter time (lower payback time), leaving more resources available for allocation to growth and reproduction. Higher SLA and  $N_m$  in plants from invasive populations contributed to higher PEUE and shorter payback time by increasing  $P_{max}$  (Figs 1a, 2cd and 3ac). These results indicated that invasive *Ageratina* plants were located at the quick-return end of the leaf economics spectrum even though they did not show lower construction costs, inconsistent with the trade-off between cost and benefit (Shipley *et al.* 2006; Zhu & Cao 2010). A quicker return energy-use strategy combined with higher N-use efficiencies and lower respiration cost for photosynthesis may contribute to higher growth in *Ageratina* plants from invasive populations relative to plants from native populations (Nagel & Griffin 2001; Feng, Auge & Ebeling 2007b; Funk & Vitousek 2007; Song, Li & Peng 2009; Zhu & Cao 2010).

The above discussion indicates that higher  $N_m$  and SLA in plants from invasive populations relative to native populations may have important roles in the invasion success of *Ageratina* in subtropical areas with mild, moist climates. Higher  $N_m$  contributed to lower C:N ratios in plants from invasive populations (Fig. 2b), thus facilitating growth (Poorter *et al.* 2004). High SLA may increase leaf area ratio, one of the determinants of RGR, which should contribute to invasiveness (Feng, Wang & Sang 2007a; Zheng *et al.* 2009). High  $N_m$  and SLA also promote leaf turnover, litter decomposition and soil nutrient cycling (Rout & Callaway 2009), perhaps facilitating invasions as invasive plants appear to benefit more from improved nutrient availability than native plants (Daehler 2003).

Increased SLA and  $N_m$  of *Ageratina* plants from invasive populations may be due to the directional selection for genotypes with reduced defences and increased growth by escaping natural enemies in introduced ranges. For *Ageratina*, more than 30 phytophagous insect species and additional pathogens have been found in the native range of Mexico (Fritz Heystek, pers. comm.), many more than we have observed in China and India (Niu *et al.* 2010). As predicted by a refinement of the EICA hypothesis (Müller-Schärer, Schaffner & Steinger 2004), *Ageratina* plants from invasive populations indeed have reduced defences against specialist and generalist enemies (Niu Y.-F., Geng Y.-P., Callaway, R.M. & Feng Y.-P., Y.-F. Niu, Y.-P. Geng, R.M. Callaway & Y.-P. Feng, unpublished data). SLA is negatively correlated with the contents of digestibility-reducing chemicals, such as phenolics, condensed tannins and lignin, and with leaf toughness (Wright & Cannon 2001; Kurokawa & Nakashizuka 2008). Leaf N concentration is not only a measure of nutrient value for herbivores but it is also negatively correlated with the concentration of carbon-based defensive chemicals (Bryant, Chapin & Klein 1983; Coley, Bryant & Chapin 1985). In general, herbivores prefer leaves with high N content and low C:N ratio (Hoffland *et al.* 2000). Thus, in native ranges abundant herbivores might have strong attraction to and impact on *Ageratina* plants with high SLA and  $N_m$

and select for plants with low SLA and  $N_m$ . In contrast, the lack of natural enemies might contribute to selection for plants with high SLA and  $N_m$  in invasive ranges. Testing these hypotheses in common garden experiments would provide a great deal of insight into how invaders may evolve in responses to biogeographical differences in herbivore communities.

Our common garden experiment excluded the confounding effects of environmental factors, but as for almost all biogeographic comparisons of invasive species, we cannot exclude founder effects. In other words, perhaps a population that we did not sample in the native range possessed the traits that we found in populations from the invasive ranges, and this unsampled native population was the source from which invaders derived. Our low replication of native populations is an important caveat for any interpretation of potentially evolved biogeographic differences. However, there were no significant differences between plants from the two invasive ranges (China and India) for any traits measured (see Table S3), and thus the source for *both* invasive ranges would have to be from unsampled native populations. Importantly, for all traits there were no significant differences between plants from India and China. This indicates some generality in the physiological responses to escaping enemies, and that the traits we measured were likely due to invasion *per se*, rather than local adaptation of an invasive to a specific environment. Plants from Indian populations could not have locally adapted to China. Molecular evidence also supports this argument (Duan *et al.* 2005; Gui, Guo & Wan 2007).

Studies of *Ageratina*'s invasion history also indicate that the single population founder effects are unlikely. As an ornamental plant, *Ageratina* was intentionally introduced to several countries, such as England, New Zealand, USA (California and Hawaii), Australia and India in 19th century (Paxton 1849; Webb, Sykes & Garnock-Jones 1988; Shrestha, Wilson & Gay 2008; Muniappan, Raman & Reddy 2009), and multiple introductions appeared to occur in Hawaii and Australia. *Ageratina* introduced to India may have naturally spread into China via Burma. Alternatively, *Ageratina* may have arrived in Singapore by ship and then spread to China (or even to India) via Vietnam, Laos and Burma (Duan *et al.* 2005; Gui, Guo & Wan 2007; Shrestha, Wilson & Gay 2008). *Ageratina* has a rich genetic diversity in China as evaluated by a relatively high Nei's gene diversity index (Duan *et al.* 2005; Gui, Guo & Wan 2007). These studies show evidence for multiple introductions of *Ageratina* to China as well as many other regions, where *Ageratina* has invaded. In addition, the population from Linchang of Yunnan Province, where *Ageratina* was first found in China, is more genetically similar to a population from Sydney, Australia, than to any of 22 populations from China (Duan *et al.* 2005). Considered together, these studies indicate that *Ageratina* from many sources arrived in China during its invasive expansion.

This study is the first to compare plants from invasive and native populations of an invasive plant in terms of energy-use strategy. The results suggest that *Ageratina* plants from invasive populations have a distinct quick return energy-use strategy, which, combined with low-respiration cost for

photosynthesis and high nitrogen-use efficiency, may provide a potential mechanistic explanation for the commonly observed increase in growth when plants are introduced to new parts of the world. To fully assess the generality of the ecophysiological traits found in *Ageratina* from invasive populations and to determine the extent of the competitive advantages provided by these traits, studies of a wide range of invasive species are necessary. However, our results suggest a possible mechanism for the widely studied and often-reported evolution of increased size and competitive ability of invasive plant species.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Information on the 16 sample populations of *Ageratina adenophora*.

**Table S2.** Linear regressions between each variable and altitude (m) for pooled plants from invasive and native populations of *Ageratina adenophora*.

**Table S3.** Differences between plants from China, India and Mexico populations of *Ageratina adenophora* from MANOVA with country as a fixed factor.

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