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# Energetic cost of leaf construction in the invasive weed *Mikania micrantha* H.B.K. and its co-occurring species: implications for invasiveness

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**ABSTRACT.** Construction cost (CC) is a quantifiable measure of energy demand for biomass production and is related to energy-use efficiency. Low construction cost was hypothesized to give invaders a growth advantage by utilizing energy efficiently. The present study examines the energetic cost of leaf construction in the invasive weed *Mikania micrantha* H.B.K. and its five common co-occurring species (*Ageratum conyzoides* L., *Wedelia trilobata* (L.) Hitchc, *Lantana camara* L., *Urena lobata* L. and *Derris trifoliata* Lour.), and provides insight into the success of this invasive weed. *Mikania micrantha* had the lowest leaf construction cost both on a mass basis (leaf $CC_{mass}$, 1.32 g glucose $g^{-1}$) and on an area basis (leaf $CC_{area}$, 28.80 g glucose $m^{-2}$). *Mikania micrantha* dominated the studied community with 60% coverage. The low leaf CC associated with its great abundance indicated that low energetic cost might benefit its spread. Additionally, a higher specific leaf area (SLA) and lower C and N concentrations were found in *M. micrantha*, providing it with another competitive advantage. All the six studied species could be grouped into either an invasive or a native species category. Both the mean leaf $CC_{area}$ and $CC_{mass}$ for the invasive were lower than those for the native species though the mean leaf $CC_{mass}$ was not significantly different. The result indicated that a low energetic cost of leaf construction might generally influence invasive potential. Using discriminant analysis, leaf $CC_{area}$ was identified to be more powerful in distinguishing between invasive and native species. Therefore, leaf $CC_{area}$ might be a valuable index to predict invasiveness and has a meaningful management implication.

**Keywords:** Construction cost; Invasive species; *Mikania micrantha* H.B.K.; Specific leaf area.

## INTRODUCTION

Invasive plants can threaten biodiversity (Dukes and Mooney, 1999) and potentially affect both the structure and function of ecosystems (Vitousek and Walker, 1989; Mack et al., 2000). Biological invasion is estimated to cause approximately $137 billion in global losses every year (Pimentel et al., 2000). Therefore, increasing our understanding of the physiological and environmental factors that influence the invasive potential of plant species is important to facilitate preventative and remediation efforts (Nagel and Griffin, 2001). Previous studies have indicated that specific physiological and morphological characteristics may contribute to the success of invasive species. These include high reproductive allocation, rapid vegetative growth rates, and a high potential for acclimation (Bazzaz, 1986; Rejamanek, 1996). Although many attempts have been made to identify the properties of species that predispose them to become invasive (Lodge, 1993; Carlton, 1996), few generalities have emerged which would allow us to predict which introduced species will be so (Weltzin et al., 2003). However, plant growth is always related to energy processes, and energy can thus be considered a basic unit when comparing organisms (Griffin, 1994). Furthermore, Nagel and Griffin (2001) have proposed construction cost (CC) as a general approach to evaluating invasive potential, reflecting specific growth strategies while allowing for a more general comparison of resource-use efficiency.

Construction cost is a quantifiable measure of energy demand for biomass production (Griffin, 1994). It has been defined as the amount of glucose required to provide carbon skeletons, reductant, and energy for the synthesis of organic compounds (Williams et al., 1987). In general, low CC is associated with high relative growth rates (Lambers and Poorter, 1992; Poorter and Villar, 1997). Even small differences in CC can lead to substantial differences in growth rate (Poorter and Villar, 1997). Previous studies have found lower leaf CC for the invasive vs. native species (Baruch and Gómez, 1996; Baruch and Goldstein, 1999; Nagel and Griffin, 2001; McDowell, 2002), suggesting that invasive species may require less energy and use it more efficiently for biomass construction than co-occurring noninvasive plant species (Nagel and Griffin, 2001).

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*Mikania micrantha* H.B.K. (Compositae), a perennial vine native to tropical Central and South America, is one of the worst weeds in the world (Holm et al., 1977). It has been introduced into southern China since 1910 and widely invades the disturbed forests and plantation crops. In recent years, it has caused significant damage to many native ecosystems (Zhang et al., 2004). The increasing abundance of *M. micrantha* suggests a high competitive advantage over its co-occurring native plants. Wide eco-physiological tolerance (Wang et al., 2004), prolific seed production, fast dispersal by its vegetative propagation (Hu and But, 1994), and allelopathic effects (Shao et al., 2003) have been hypothesized as factors facilitating the spread of this weed.

Since energetic processes may influence plant growth and interspecific competition, a lower CC would be expected to give invaders a growth advantage. However, the number of studies examining construction cost and species invasiveness remains small, and further studies would be useful in determining if a statistical trend toward lower construction costs among invaders is generalizable (Daehler, 2003). The main aims of this study were to evaluate the leaf CC of *M. micrantha* and its co-occurring species, and to provide insight into the success of this invasive weed. Furthermore, the specific leaf area (SLA), leaf nitrogen (N) and carbon (C) concentrations were examined to assess invasive potential and their correlations with leaf construction cost. The relation between construction cost and invasive potential was also discussed.

## MATERIALS AND METHODS

### Study site and plant materials

Plant materials were collected on September 24, 2005 from Qi'ao Island (113˚39', 22˚24'), Zhuhai, China. *Mikania micrantha* had seriously imperiled the banana plantation and disturbed forests at the foot of hills on the island. The study site selected was a shrub area of approximately 250 × 10 $m^2$, which *M. micrantha* had seriously invaded and dominated with a 60% coverage. *Ageratum conyzoides* L. (Compositae), *Wedelia trilobata* (L.) Hitchc (Compositae), *Lantana camara* L. (Verbenaceae), *Urena lobata* L. (Malvaceae) and *Derris trifoliata* Lour. (Leguminosae) were the most abundant species in this area. These species have been found always co-occurring with *M. micrantha* (Wang et al., 2004) and thus were selected as the experimental species. The five species were smothered by *M. micrantha* to different extents, and *L. camara* was especially endangered. Among the six studied species, *L. camara* and *U. lobata* were small shrubs about 1-2 m high while the other four species were all herbs. Additionally, *A. conyzoides*, *W. trilobata*, and *L. camara* were also recognized as invasive species (Li and Xie, 2002), which had spread widely in open habitats and endangered the native crops and plantations.

Within the studied shrub belt, three quadrats (5 m × 5 m) were established approximately 50 m apart, with the first quadrat placed 50 m from the belt edge. In each quadrat, the six selected species were identified. Leaves of herbaceous species were collected from different positions on the branches from 5-10 individuals. Since the amount of shrubby species was limited, all the individuals in the quadrat were collected from about 1-3 individuals per quadrat. For each species, leaves from the same quadrat were mixed into one sample. In total, there were three samples for each species from three quadrats.

### Plant measurements

Fifteen to twenty leaves per species were placed in moistened paper towels to prevent leaf curling, and leaf blade area was determined with a leaf area meter (Li-Cor 3100A, Li-Cor, USA). These leaf subsamples were weighted after being dried at 60°C for 72 h to determine SLA. All dried leaves were ground into a fine powder, homogenized, and then stored with a desiccant to maintain dryness for the subsequent analysis. Leaf carbon (C) and nitrogen (N) concentrations were determined with an elemental analyzer (Vario, Elmentar, Germany). To calculate C and N concentrations per unit area, these values were divided by SLA. Ash content (ASH) was measured by burning preweighted leaf powder samples in a 500°C muffle furnace (Vulcan A-550, Vulcan, UK) for 6 h and weighing the remaining mass. To obtain ash-free heat of combustion ($\Delta$Hc), three 0.5 g pellets of leaf powder from each sample were pressed and combusted using a calorimeter (HWR-15E, Shanghai, China) with correction for nitric acid formation and ignition wire. The $\Delta$Hc values obtained for the triplicate pellets of each sample were then averaged.

Leaf construction cost per unit of mass ($CC_{mass}$, equivalent to grams glucose per gram dry mass) was calculated according to the methods described by Williams et al. (1987) as: $CC_{mass} = [(0.06968\Delta Hc\text{-}0.065)(1\text{-}ASH) + 7.5(k\ N/14.0067)]/E_G$. Where $k$ was the oxidation state of the N substrate (+5 for nitrate or -3 for ammonium) and $E_G$ was the growth efficiency. $E_G$ has been estimated to be 0.87 across species (Penning de Vries et al., 1974). Because the relative proportions of these forms of N utilized by the plants were unknown, we estimated leaf CC as the mean of CC values calculated with each $NH_4^+$ and $NO_3^-$ oxidation state as $k$ for all species. To calculate leaf CC per unit leaf area ($CC_{area}$, equivalent to grams glucose per square meter), these values were divided by SLA.

### Statistical analysis

All calculations and statistical analysis were performed with SPSS 11.5. A one-way model analysis of variance (ANOVA) was performed to compare means between species of leaf CC and other leaf chemical and morphological variables. Mean values were considered to be significantly different if $P \leq 0.05$. Species were compared to determine if means of the dependent variable were significant at the 0.05 probability level with Student-Newman-Keuls (S-N-K) post hoc analysis. Linear regression analysis was used to determine the degree

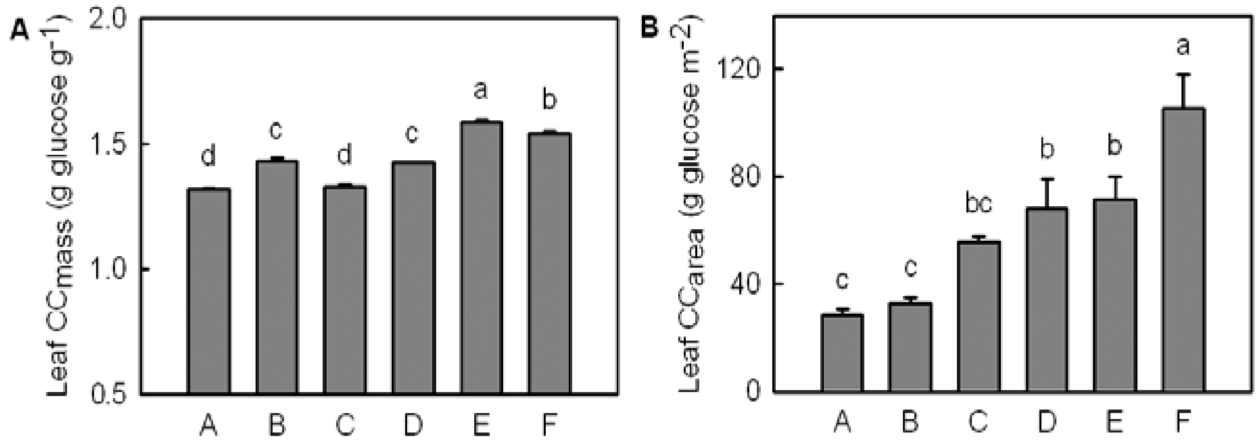


**Figure 1.** Mean leaf construction cost in per unit mass (leaf $CC_{mass}$) (A) and per unit area (leaf $CC_{area}$) (B) of *Mikania micrantha* and its five abundant co-occurring species within the study site. A=*Mikania micrantha*; B=*Ageratum conyzoides*; C=*Wedelia trilobata*; D=*Urena lobata*; E=*Lantana camara*; F=*Derris trifoliata*. Error bars represent 1 SE. Means with a common letter do not differ from each other based on S-N-K post hoc analysis at P=0.05 level.

of association between leaf CC and other leaf variables for all species. An additional discriminant analysis was used to determine whether the measured SLA and leaf $CC_{area}$ could be used to distinguish between invasive and noninvasive species according to McDowell (2002). This analysis was performed for these data by grouping each case of the six species into either an invasive or a native species category. An approximate *F* test was calculated from a transformation of Wilks' lambda to test the equality of group centroids and the distinctness of groups. Standardized canonical discriminant function coefficients were used to determine the relative importance of the input variables of the classification function for predicting group membership. To examine this discriminant analysis graphically, Mahalanobis distances from the category centroid were calculated for each case. The pair of these distances was then plotted for each case, where similar data points would have a similar pair of distances and thus be plotted together as a group.

## RESULTS

### Leaf construction cost

Leaf $CC_{mass}$ was significantly different between species ($F=140.671$, $P<0.001$; Figure 1A) with values ranging from 1.32 g glucose $g^{-1}$ to 1.59 g glucose $g^{-1}$. *Lantana camara* showed the highest leaf $CC_{mass}$ among all species, followed by *D. trifoliata*, and then *A. conyzoides* and *U. lobata*. *Wedelia trilobata* and *M. micrantha* had the lowest $CC_{mass}$. When calculated on an area basis, leaf construction costs also showed significant differences between species ($F=13.698$, $P<0.001$; Figure 1B). The rank of leaf $CC_{area}$ was changed as compared with that of leaf $CC_{mass}$. *Derris trifoliata* showed the highest leaf $CC_{area}$. Overall, it appeared that leaves from *M. micrantha* were the least expensive to construct both per unit mass (1.32 g glucose $g^{-1}$) and per unit area (28.80 g glucose $m^{-2}$) among all studied species.

### Leaf structural and biochemical characteristics

SLA, N and C concentrations of *M. micrantha* and its co-occurring species were examined in this study, and significant differences were found between species (Table 1). In detail, *M. micrantha* exhibited the highest SLA, but the lowest N and C concentrations, especially when the data were expressed as per unit of area. The other three co-occurring invasive species showed a similar trend in SLA, leaf N, and C concentrations.

**Table 1.** Average specific leaf area (SLA), leaf carbon (C) and nitrogen (N) concentrations of invasive *Mikania micrantha* and its five abundant co-occurring species within the study site.

| Leaf variable | *Mikania micrantha* | *Ageratum conyzoides* | *Wedelia trilobata* | *Lantana camara* | *Urena lobata* | *Derris trifoliata* |
|---|---|---|---|---|---|---|
| SLA ($m^2$ $kg^{-1}$) | 46.30±2.96a | 43.54±2.61a | 23.78±0.72b | 22.77±2.57b | 22.27±4.34b | 14.82±1.67b |
| C (%) | 38.89±0.29c | 42.99±1.29b | 39.06±0.37c | 44.67±0.47b | 44.34±1.15b | 48.67±0.60a |
| C (g $m^{-2}$) | 8.48±0.59c | 9.95±0.73c | 16.46±0.58bc | 20.14±2.33b | 21.43±3.93b | 33.23±3.33a |
| N (%) | 2.48±0.10b | 2.40±0.03b | 1.95±0.21c | 2.44±0.04b | 2.50±0.16b | 3.94±0.03a |
| N (g $m^{-2}$) | 0.54±0.01c | 0.55±0.04c | 0.82±0.08bc | 1.10±0.14b | 1.18±0.15b | 2.70±0.32a |

Values are means±1 SE. For each leaf variable, means labeled with the same letter are not significantly different according to S-N-K post hoc analysis at P=0.05 level.

### Correlation between leaf CC and leaf traits

In the present data set, a strong negative correlation ($R^2$ = 0.863, P=0.007; Figure 2A) emerged between SLA and leaf $CC_{area}$ across species, but no significant correlation between SLA and leaf $CC_{mass}$ ($R^2$ = 0.305, P=0.256) was observed. Leaf $CC_{area}$ was positively correlated with both leaf C concentration per unit area ($R^2$ = 0.990, P<0.0001; Figure 2B) and leaf N concentration per unit area ($R^2$ = 0.881, P=0.006; Figure 2C).

### Comparison of leaf CC and SLA between invasive and native species

Taking four invasive species as a group, the mean leaf construction cost was lower than that for the native species. Mean leaf $CC_{mass}$ of the native species was 3.5% higher than that of the invasive species (1.47 g glucose $g^{-1}$ vs. 1.42 g glucose $g^{-1}$; P=0.338; Figure 3A) although it was not significantly different. However, mean leaf $CC_{area}$ of the native species was significantly higher than that of the invasive species (83.05 g glucose $m^{-2}$ vs. 47.29 g glucose $m^{-2}$; P=0.007; Figure 3B). In addition, the mean SLA was significantly lower for the native than for the invasive species (19.29 $m^2$ $kg^{-1}$ vs. 34.10 $m^2$ $kg^{-1}$; P=0.021; Figure 3C).

The discriminant analysis result indicated a good discrimination between invasive and native species when using these variables of leaf SLA and $CC_{area}$ (F=7.163, P=0.028). For *D. trifoliata,* only two samples were available. From a total of 17 cases, only two were misclassified, one native and one invasive case. The data fell into relatively distinct groups (Figure 4). The variable $CC_{area}$ was identified as more powerful for discriminating between invasive and native species because its standardized canonical discriminant function coefficient was larger than that of SLA (1.220 vs. 0.258).

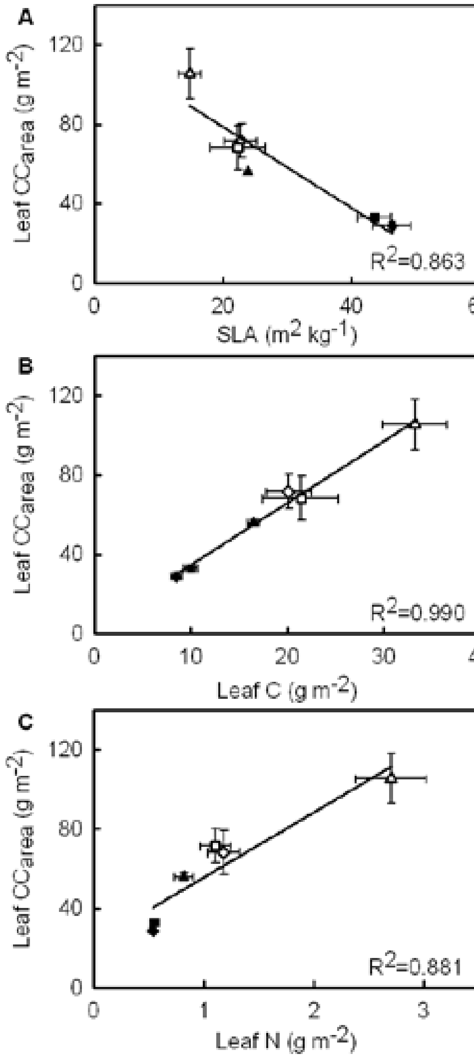


**Figure 2.** The correlation between leaf construction cost per unit area (leaf $CC_{area}$) and specific leaf area (SLA) (A), leaf C concentration (B), leaf N concentration (C), respectively. ◆=*Mikania micrantha*; ■=*Ageratum conyzoides*; ▲=*Wedelia trilobata*; □=*Urena lobata*; ◇= *Lantana camara*; △=*Derris trifoliata*. Error bars represent 1 SE.

## DISCUSSION

Energetic prosperity is likely to influence plant growth. As a quantifiable measure of energy demand for biomass production, the low leaf CC suggests that these species

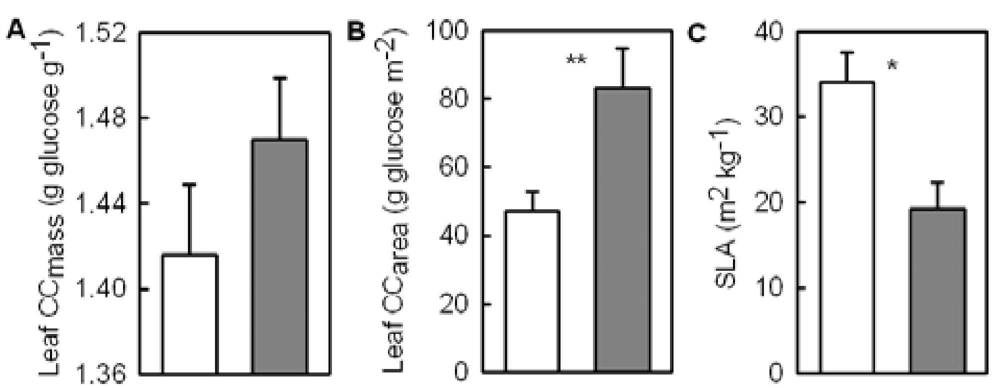


**Figure 3.** Mean leaf construction cost in per unit mass (leaf $CC_{mass}$) (A) and per unit area (leaf $CC_{area}$) (B), specific leaf area (SLA) (C) of the native (*Urena lobata*, *Derris trifoliata*) (filled bars) and the invasive species (*Mikania micrantha*, *Ageratum conyzoides*, *Wedelia trilobata*, *Lantana camara*) (open bars) in the study site. Error bars represent 1 SE. * P < 0.05; ** P < 0.01.

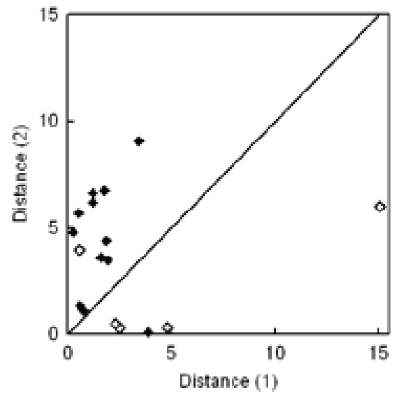


**Figure 4.** Mahalanobis distances calculated from a discriminant analysis, in which all cases from the six species were classified into either an "invasive" (filed diamond) or "noninvasive" category (open diamond) using specific leaf area (SLA) and leaf CC based on unit area (leaf $CC_{area}$) as input variables. The dashed line separates the two categories.

utilize carbon resources more efficiently and expend saved energy on other competitive strategies, such as seed production, biomass productivity, and relative growth rate (Nagel et al., 2004). In the present study, both leaf $CC_{mass}$ and $CC_{area}$ for *M. micrantha* were the lowest among the six species (Figure 1). Meanwhile, *M. micrantha* dominated the studied community with 60% coverage. These results suggest that low leaf CC might have facilitated the successful establishment of *M. micrantha*. At the study site, *L. camara* was damaged most seriously by *M. micrantha*, and this might be attributable to its higher leaf CC (1.59 g $g^{-1}$) than *M. micrantha* (1.32 g $g^{-1}$). The great difference in leaf CC led to substantial differences in competitive ability. *Mikania micrantha* also showed a lower leaf CC than the indigenous close congener *Mikania cordata* (Deng et al., 2004). These results suggest that low leaf CC might be intrinsic to *M. micrantha*, reflect its advantages in energetic cost, and contribute to its successful invasion.

Besides lower leaf construction cost, *M. micrantha* exhibited a higher SLA than its co-occurring species (Table 1). SLA is a plant trait extremely important in the regulation and controlling of plant functions such as carbon assimilation and carbon allocation (Lambers and Poorter, 1992; Reich et al., 1997). With higher SLA, *M. micrantha* could produce larger assimilatory surfaces for a given amount of carbon fixed carbon, indicative of a higher capacity for light interception, which was consisted with its high photosynthetic rates of 21.56 μmol $m^{-2}$ $s^{-1}$ (Wen et al., 2000). Additionally, leaf N and C concentrations of *M. micrantha* were lower (Table 1). Plants with low leaf nutrient concentrations generally tend to use nutrition efficiently (Chapin, 1980). Therefore, these characteristics might provide *M. micrantha* another potential competitive advantage. For *M. micrantha*, though C concentration in leaf was lower (38.89%), more carbon had accumulated in the stems (42.01%, unpublished data), which was expected to facilitate its climbing and spreading.

The present results demonstrate that leaf construction cost was correlated with SLA and leaf N and C concentrations (Figure 2), which suggests that such costs might be inherently determined by chemical composition. Plants characterized by high SLA have thinner leaves and invest less carbon in structural carbohydrates such as cellulose, hemicellulose, and pectin. Additionally, nitrogen and carbon are the respective constituents of protein and secondary compounds (e.g. lignin and tannin) (Coley et al., 1985; Lambers and Poorter, 1992). These compounds are relatively expensive to synthesize (Poorter and Villar, 1997). Therefore, species with high SLA and low N and C concentrations require less energetic cost for construction. The high SLA and low N concentration may also decrease energy loss via respiration (Reich et al., 1998). In the present study, the coordination of the above-mentioned leaf traits was observed in the invasive species. Species with these characteristics always show a high photosynthetic rate and short leaf lifetime, representing a specific growth strategy with quick returns on investment of nutrients and dry mass in leaves (Wright et al., 2004). Therefore, the observed leaf traits could contribute to the success of the invasive species.

The abundant species co-occurring with *M. micrantha* —*A. conyzoides*, *W. trilobata*, and *L. camara*—were also invasive. These species exhibited higher leaf construction costs than *M. micrantha*, which suppressed their invasive potentials. Therefore, these species showed less damage in the studied community. The mean leaf CC was lower for the invasive than for the native species (Figure 3A and 3B), which agreed with previous studies (Baruch and Gómez, 1996; Baruch and Goldstein, 1999; Nagel and Griffin, 2001; McDowell, 2002). These results suggested that low leaf CC might be one of the factors increasing species ability to invade an environment. However, it should be noted that two life forms existed in both the native and invasive groups, and additional comparisons among the same life form species were conducted. Among the four herbs, the native *D. trifoliata* had a higher leaf CC than any of the other three invasive herbs. Between the two shrubs, the native *U. lobata* showed inversely lower leaf CC than the invasive *L. camara*, a result which was inconsistent with the previous study on shrubs (Baruch and Goldstein, 1999). The ambiguous results concerning shrubs were mainly due to the paucity of species and further studies are necessary.

The variation of leaf construction cost was found to be magnified when it was expressed in per unit area rather than in per unit dry mass. In the present study, the mean leaf CC of native species was only 3.5% higher on a mass basis than that of invasive species, but it was 75.6% higher on an area basis. Poorter and Villar (1997) concluded that variation in leaf construction costs on a mass basis was small (within 10%) and due to a balance between various energetic compounds (Chapin, 1989; Poorter and Bergkotte, 1992). The large variations in leaf $CC_{area}$ were due to the leaf area morphological trait. In our study, significant differences in SLA appeared between invasive and noninvasive species (Figure 3C). High SLA is of paramount importance if the invasive species is to establish in disturbed habitats because it is well correlated with the short leaf life-span and fast growth rate (Wright and Westoby, 1999). Hamilton et al. (2005) reported that high SLA was significantly and uniquely correlated with invasion success on a continental scale.

Using leaf SLA and $CC_{area}$ as variables, the discriminant analysis clearly differentiated between the groups of invasive and native species, with 88.2% of original grouped cases correctly classified. Therefore, the two characteristics might be important factors contributing to invasive success. In particular, the variable $CC_{area}$ emerged as a powerful discrimination tool. Nagel and Griffin (2001) proposed that construction cost was a general approach to evaluate invasive potential. The present study suggests that leaf $CC_{area}$ is more preferable for an evaluation of invasive potential because it considers both the energetic cost of biomass construction and leaf area morphology. It also reflects the integrated competitive ability of plants. Energy is a basic unit of comparison between organisms (Griffin, 1994). Therefore, leaf $CC_{area}$ is expected to be a general index to predict invasive potential and has a meaningful management implication. Given the substantial impact of construction cost upon invasive potential, further studies on energy assimilation, investment, and allocation patterns will greatly aid our understanding of the underlying physiological mechanisms of invasive success.

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# 外來入侵種薇甘菊及其伴生種葉片建成成本的比較：對入侵的啟示

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建成成本是定量測定生物量建成所需能量的方法，與植物的能量利用率有關。本文提出假設，較低的建成成本可能有利於外來物種的入侵，並對入侵植物薇甘菊及其 5 種伴生植物（勝紅薊、三裂葉蟛蜞菊、馬纓丹、肖梵天花、魚藤）的葉片建成成本進行了研究，探討其入侵機制。結果表明，薇甘菊具有最低的葉片建成成本，葉片單位質量建成成本（$CC_{mass}$）為 1.32 g glucose $g^{-1}$，葉片單位面積建成成本（$CC_{area}$）為 28.80 g glucose $m^{-2}$。同時，薇甘菊在群落中處於優勢地位，覆蓋率達到 60%。較低的葉片建成成本與薇甘菊在群落中較高的優勢度相聯繫，說明低的能量消耗對其在入侵群落中的成功擴張起到了一定的作用。此外，薇甘菊具有較高的比葉面積（SLA）和較低的葉片碳（C）和氮（N）濃度，為它提供了另外一種競爭優勢。將 6 個物種分為入侵種和本地種兩類，入侵種的平均葉片 $CC_{area}$ 和 $CC_{mass}$ 均低於本地種，意味著較低的葉片建成成本可能是影響外來種入侵的一般性特徵。利用判別分析，SLA 和 $CC_{area}$ 可將所有的物種明確的劃分為入侵種和本地種兩類，並且 $CC_{area}$ 在判別分析中起到較為重要的作用。因此，$CC_{area}$ 可以作為一個有價值的指標用來預測植物的入侵力，在入侵種的管理方面具有重要意義。

**關鍵詞：**建成成本；入侵種；薇甘菊；比葉面積。