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Gas exchange characteristics of the invasive species *Mikania micrantha* and its indigenous congener *M. cordata* (Asteraceae) in South China

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Abstract. In South China, the photosynthetic characteristics of an invasive exotic weed *Mikania micrantha* H.B. Kunth and its indigenous close congener *Mikania cordata* (Burm. f.) B.L. Robinson were studied. *Mikania micrantha* exhibited a greater biochemical capacity for photosynthesis than *M. cordata*, as the former had higher V_{cmax} and J_{max}, which lead to its higher maximum assimilation rate (A_{max}) values. Similar light compensation point, apparent quantum yield (α), and dark respiration (R_d), suggested a similar shade-tolerance. Higher A_{max}, light saturating point, and CO_2 saturating point give *M. micrantha* greater potential to acclimate to brighter environments and a larger pool of available carbon. These differences in photosynthetic characteristics could be a basis for their niche partitioning. The leaf traits of the native and invasive *Mikania* species were as follows: higher construction cost (CC), lower specific leaf area (SLA), as well as lower mass-based leaf N and photosynthetic nitrogen-use efficiency (PNUE) for the native species, but *M. micrantha* had lower area-based leaf N. The higher water use efficiency (WUE) and $\delta^{13}C$ observed in *M. micrantha* was probably due to its high photosynthetic capacity and not to reduced stomatal conductance, explaining the absence of any trade-off between WUE and PNUE.

Keywords: Invasive species, *Mikania*; Nitrogen use efficiency; Photosynthetic characteristics; Specific leaf area.

Introduction

The impact of invasive weeds on native species, communities, and ecosystems has been widely recognized for decades (Elton, 1958; Lodge, 1993; Simberloff, 1997; Vitousek et al., 1997; Mack et al., 2000). However, we still lack a fundamental understanding of the mechanisms by which invasive plants succeed, an understanding that may eventually prove predictive and useful for control efforts (Baruch and Goldstein, 1999; Mack et al., 2000; Kolar and Lodge, 2001). Comparison of closely related invasive and non-invasive congeners that share morphological and life-history traits is an effective approach to identifying mechanisms of invasive plant success (Schierenbeck and Marshall, 1993; Mack, 1996). Distinguishing the ecophysiological traits that confer invasion success (Mack, 1996; Xu et al., 2004) is more precise than working from the concept of an "ideal weed" (Baker, 1965, 1974), which summarizes common attributes of plant invaders from broad surveys (David and Baruch, 2000; Mack, 1996). This latter approach has been widely criticized for its inability to predict the outcome of any specific introduction and for the numerous exceptions to any unique suite of traits expressed by plant invaders (Roy, 1990; Rejmánek, 1995; Rejmánek and Richardson, 1996).

Mikania micrantha H.B. Kunth, commonly known as mile-a-minute, is an extremely fast growing, sprawling, perennial vine and one of the world's most notorious invaders (Holm et al., 1977; Cronk and Fuller, 1995). With its rapid growth, ready rooting at nodes, smothering habit, and prolific seed production, *M. micrantha* rapidly colonizes disturbed habitats, retarding the growth of crops or natural vegetation by competing and producing plant inhibitors. In addition to its native distribution in tropical America, it has spread to Mauritius, India, Sri Lanka, Bangladesh, Southeast Asia, and the Pacific. *Mikania cordata* (Burm. f.) B. L. Robinson is the native congener of *M. micrantha*. They appear to be similar species, as they share similar morphologies and life histories, and their identities have been confused in some documents (Holm et al., 1977; Kong et al., 2000). However, in sharp contrast to *M. micrantha*, *M. cordata* grows slowly and has not been found to be harmful to native plants or habitats in southern subtropical China (Kong et al., 2000). Additionally, while *M. micrantha* can thrive in sunny environments, *M. cordata* can only be found in relatively shady and humid wetlands, and it is more drought-tolerant than (Huang et al., 2000).

It is interesting that *M. micrantha* is not even considered a weed in its native Brazil, but now is a notorious

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weed in Southern China and some Asian and Pacific islands (Holm et al., 1977; Kong et al., 2000). Comparing the ecophysiological traits of the invader *M. micrantha* with those of its native congener can help identify mechanisms of invasive plant success (David and Baruch, 2000). Unfortunately, few studies in this field have been conducted.

The objective of this research was to compare leaf physiological traits of the invasive plant *M. micrantha* with its noninvasive congener *M. cordata* and to provide some basic information on the two *Mikania* species. The physiological mechanisms that underlie these differences may play a role in the success and vigor of the invasive species. This study focuses on instantaneous measurements of photosynthesis and resource costs. The following hypotheses were tested: (1) *M. micrantha* has a higher photosynthetic capacity than *M. cordata* and (2) *M. micrantha* uses resources more efficiently than *M. cordata*. The rate and efficiency with which these species acquire carbon may contribute to their vigor, niche partitioning, and thus their respective levels of invasiveness. In addition to reproductive traits such as abundant small size seeds and high reproductive allocation, high carbon assimilation capacity, fast growth rate, and broad acclimation capacity (Williamson and Brown, 1986; Baruch and Goldstein, 1999) also contribute to the success of an invader plant.

Materials and Methods

At the start of March in 2002, cuts of *M. micrantha* and *M. cordata* were propagated in 2-L pots in a greenhouse at the South China Institute of Botany, Chinese Academy of Sciences, Guanzhou, China (23°08' N, 113°17' E). Each species was planted in 50 pots. The plants were fertilized (Osmocote 20-20-20) and watered to ensure optimum growth conditions. Climate conditions in the greenhouse approximated those outside.

Gas Exchange Measurements

To ensure that all sampled leaves of each species were of similar age and developmental stage, all gas exchange measurements were made on fully expanded sun leaves which numbered sixth from the tip of the stem. One leaf per individual and 6-10 individuals per species were sampled. At the beginning of April, the leaf gas exchange of *M. micrantha* and *M. cordata* were measured with a Li-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA). Light response curves were made with photon flux density (PFD) increases by the sequence 0, 25, 50, 100, 150, 500, 800, 1200, 1500, 2000, and 2500 μmol $m^{-2}s^{-1}$ under $[CO_2]$ of 350 μmol $m^{-2}s^{-1}$ at 25±1°C temperature, 50-55% air humidity and 1.5±0.3 kPa VPD. CO_2 exchange rates in the dark were used as a measurement of dark respiration (R_d, μmol $m^{-2}s^{-1}$) (Bassman and Zwier, 1991; Deng et al., 2002). For the two species, nonlinear regressions of irradiance and net photosynthetic rate (A, μmol $m^{-2}s^{-1}$) were computed to determine light compensation points (LCP, μmol $m^{-2}s^{-1}$), light saturating point (LSP, μmol $m^{-2}s^{-1}$), and apparent quantum yield (α, μmol CO_2 μmol $^{-1}$ photon) (Küppers and Schulze 1985; Deng et al., 2002). Photosynthesis versus intercellular $[CO_2]$ (A/C_i) response curve were measured on intact leaves under a saturating light intensity of 1000 μmol $m^{-2}s^{-1}$ at 25±1°C, 50-55% air humidity, and 1.5±0.3 kPa VPD. Six A/C_i curves per species were measured. Diurnal measurements of net assimilation (A), R_d, and rate of transpiration (E) were made on six plants each of *M. micrantha* and *M. cordata*. Measurements were made on each plant approximately every 2 h from 6:00 to 18:00. Temperature and leaf-to-air vapor pressure deficit (VPD) within the leaf cuvette were allowed to vary with ambient conditions. The diurnal courses were repeated three times during March, April, June, August, and November. Instantaneous water use efficiency (WUE, μmol CO_2 mmol H_2O^{-1}) was calculated as A/E for each measurement (Farquhar et al., 1989). The WUE data were from three diurnal courses measured in June, and the data of stomatal conductance (g_s) versus VPD and A versus VPD were taken from diurnal courses measured in March, April, June, August, and November of 2002.

Curve Fitting and Parameter Calculations

Light response curves were fitted with an empirical model (Küppers and Schulze, 1985; Deng et al., 2002). The equations of Farquhar and Von Caemmerer (1982) were used to fit the A/C_i curves (Poorter and de Jong, 1999). Rubisco activity, V_{max}, was calculated ignoring CO_2 diffusion limitation within the leaf as:

$$V_{cmax} = (A+R_d)\frac{p_i + k_c(1+O/k_o)}{p_i - \Gamma} \qquad (1)$$

for data at low p_i. In this equation A is the rate of CO_2 assimilation, and k_c and k_o are the Michaelis-Menten constants for Rubisco carboxylase and oxygenase, respectively. Γ is the CO_2 compensation point in the absence of non-photorespiratory mitochondrial CO_2 release (R_d), and O is the oxygen partial pressure. R_d was determined from the A/p_i curve near the CO_2 compensation points with the rate at p_i=Γ. Electron transport rate, J, was calculated from data at higher p_i as:

$$J_{max} = (A+R_d)\frac{4p_i + 8\Gamma}{p_i - \Gamma} \qquad (2)$$

The values derived for *Nicotiana tabacum* by Von Caemmerer et al. (1994), K_c=404 μbar, K_o=248 μbar, and Γ=36.9 μbar, were assumed for both species.

To explore the relation of CO_2 transfer conductance from the intercellular spaces to the site of carboxylation (g_w) on calculated Rubisco activity, additional equations are needed (Farquhar and Von Caemmerer, 1982):

$$\frac{\delta A}{\delta p_c} = k = E\ k_{cat}\frac{\Gamma + k_c(1+O/K_o)}{(p_c + K_c(1+O/K_o))^2} \qquad (3)$$

Where the slope of the response of CO_2 assimilation rate to CO_2 partial pressure at the sites of carboxylation, p_c, can be calculated from the Rubisco activity (the product of Rubisco content, E, and Rubisco specific activity, k_{cat}). The parameter *k* can be converted to the slope of the A/p_i curve near the CO_2 compensation point if one has a value for g_w (Evans, 1986; Long and Hällgren, 1987):

$$\frac{\delta A}{\delta p_i} = \frac{k}{1 + k/g_w} \qquad (4)$$

In this way, V_{cmax} can be recalculated ignoring CO_2 diffusion limitations within the leaf:

$$V_{cmax} = \frac{\delta A}{\delta p_i} \frac{(p_i + k_c(1 + O/K_o))^2}{\Gamma + K_c(1 + O/K_o)} \qquad (5)$$

Leaf Analyses

Following the measurements of gas exchange, each leaf was collected and placed in a plastic bag. Leaf area was determined using Delta-T Scan software (Cambridge, CB50EJ, UK). Leaves were then dried for 48 h at 65°C, and masses were measured to the nearest 0.01g immediately upon removal from the oven. Specific leaf area (SLA, $cm^2 g^{-1}$) was calculated as area per unit mass for each leaf. Sample size was about 24-40, 6-10 samples (except for $\delta^{13}C$, which was three samples) for each species were collected for each collection time (March, June and November of 2002).

Construction Cost (CC)

Construction costs were defined as the amount of glucose a plant required to build one gram of biomass (leaf, stem, root), starting from minerals and glucose. Penning de Vries et al. (1974) used this approach first for plants. Each leaf sample was ground to pass through a 0.08 mm sieve and redried. An exact description of the procedures followed for the chemical analyses and the subsequent calculations is given in Poorter and de Jong (1999). Carbon and total nitrogen content were measured with an elemental analyzer (NA1500NC, Fiscons Instruments, UK), and ash content was determined by combustion of plant material in a muffle furnace.

$$CC = (-1.041 + 5.077 C_{om})(1-M) + (5.325 N_{org}) \qquad (8)$$

Where C_{om} is the C content of the organic matter ($g\ g^{-1}$), and M and N_{org} are the mineral and organic N concentrations of the total dry mass ($g\ g^{-1}$), respectively. NO_3^{-1} is assumed to be the N source for the plant, and the cost of protein is lower if the plants utilize ammonium. As the extent to which the study species took up nitrate and ammonium was not known, these construction costs were assumed to be maximum values.

Carbon Isotopic Composition

Healthy fully expanded sun leaves were collected three times (April, June and August), and each time three samples of each species were used for all determinations of $\delta^{13}C$. After oven-drying, samples were ground in a Wiley Mill to pass a size 40 mesh and then further pulverized to submicron particle size using a stainless-steel planetary ball mill. Subsamples of about 1-2 mg were analysed for $\delta^{13}C$ on a MAT 252 Ratio Spectrometer (Finnigan MAT, San Jose, CA).

The isotopic composition of the sample was calculated as:

$$\delta^{13}C\ (‰) = ((R_{sample} - R_{standard})/R_{standard}) \times 1000 \qquad (6)$$

Where R_{sample} and $R_{standard}$ were the ratios of $^{13}C/^{12}C$ in the sample and standard, respectively. Acetanilide, with a carbon isotopic composition of -30.54‰ relative to PeeDee belemite (PDB), was used as a working standard (Farquhar et al., 1989).

Statistics Analyses

Data were analyzed using an Excel package, and statistics tests were carried out using SPSS for Windows, Version 8.0 (Chicago, IL, USA). Nonlinear regression analysis of light and CO_2 response curves were performed with SigmaPlot 5.0 (SPSS Inc.). A critical value of $\alpha = 0.05$ (t-test) was used in testing for significant differences.

Results

Photosynthetic Gas Exchange

Responses to light. As shown in light response curves (Figure 1 and Table 1), the invasive species *M. micrantha* has a higher photosynthetic capacity than its indigenous congener, *M. cordata*. When PFD was higher than 800 $\mu mol\ m^{-2} s^{-1}$, net photosynthetic rate (A) of *M. micrantha* stayed relatively stable, but that of *M. cordata* decreased steadily. The light saturation points of *M. micrantha* and

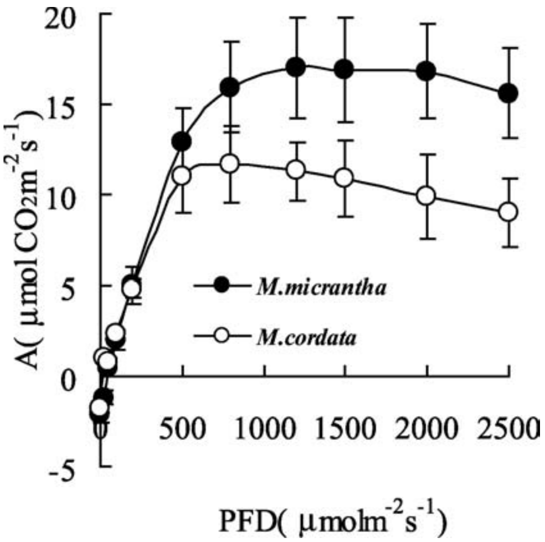

Figure 1. Average light response curves for the invasive *M. micrantha* (filled circles) and for the indigenous *M. cordata* (open circles). Each point is the average of six replicates. Error bars=1 S.E. of means.

Table 1. Average parameters of six irradiance and A/C_i curves for *M. micrantha* and *M. cordata* including light saturating point (LSP), net photosynthesis at saturating irradiances (A_{max}), dark respiration rate (R_d), light compensation point (LCP), apparent quantum yield (α), stomatal conductance (g_s), carboxylation rate (V_{cmax}), and rate of electron transport (J_{max}).

Irradiance response parameter	Species		
	M. micrantha	*M. cordata*	P
LSP (μmol $m^{-2} s^{-1}$)	831±101	465±83	***
A_{max} (μmol CO_2 $m^{-2} s^{-1}$)	16.68±3.71	12.61±1.24	**
LCP (μmol $m^{-2} s^{-1}$)	18.3±5.73	17.7±3.48	ns
α (mol CO_2 mol^{-1} photons)	0.079±0.025	0.080±0.026	ns
R_d (μmol $m^{-2} s^{-1}$)	0.79±0.05	0.78±0.07	ns
g_s (mol H_2O $m^{-2} s^{-1}$)	0.44±0.06	0.31±0.05	**
V_{cmax} (μmol $m^{-2} s^{-1}$)	75±5	56±3	***
J_{max} (μmol $m^{-2} s^{-1}$)	198±29	146±22	***

Values are means ±s.e. at different PFD levels of six light response curves. Symbols indicate the levels of significance of differences according to t-test analyses, ns, *, ** and *** denote non-significant, $P<0.05$, $P<0.01$, and $P<0.001$, respectively. Sample size n=6.

M. cordata were at 831±101 μmol $m^{-2} s^{-1}$ and 465±83 μmol $m^{-2} s^{-1}$ PFD, respectively. *Mikania micrantha* had a higher A_{max} than *M. cordata*, A_{max} values calculated from the light response curves were 16.68±3.71 μmol $m^{-2} s^{-1}$ and 12.61± 1.24 μmol $m^{-2} s^{-1}$, respectively. The average g_s value at different levels of PFD in six irradiance response curves of *M. micrantha* (0.44±0.06 mmol H_2O $m^{-2} s^{-1}$) was higher than that of *M. cordata* (0.31±0.05 mmol H_2O $m^{-2} s^{-1}$). Light compensation points (LCP), dark respiration (R_d), and apparent quantum yields (α) did not differ significantly (Table 1).

Responses to CO_2. The photosynthetic capacity of the invasive plant *M. micrantha* appeared higher than that of the indigenous plant *M. cordata* based on their A/C_i curves (Figure 2). The invasive plant *M. micrantha* had a higher A_{max} than *M. cordata* ($P \leq 0.01$), which was supported by a greater V_{cmax} (75±5 versus 56±3 μmol $m^{-2} s^{-1}$, $P \leq 0.05$), and J_{max} (198±29 versus 146±22 μmol $m^{-2} s^{-1}$, $P \leq 0.01$) than *M. cordata* (Table 1).

SLA, CC, Leaf N and PNUE

The invasive plant *M. micrantha* had a higher mean SLA than *M. cordata* ($P<0.01$, Table 2). The area and mass-based

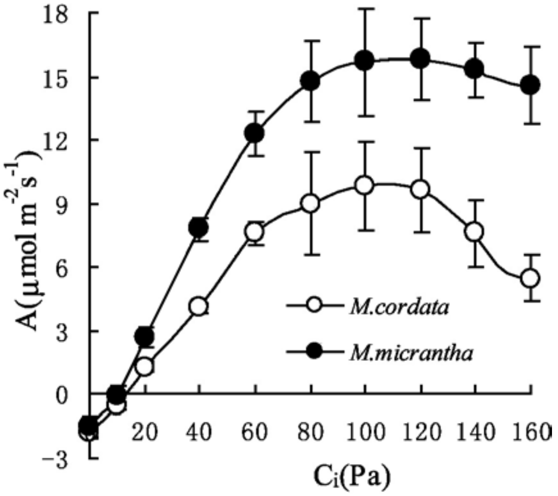

Figure 2. Average A/C_i curves for the invasive *M. micrantha* (filled circles) and for the indigenous *M. cordata* (open circles). Each point is the average of six replicates. Error bars =1 S.E. of means.

Table 2. Average specific leaf area (SLA), leaf nitrogen concentration per unit leaf mass (N), leaf nitrogen per unit leaf area, photosynthetic nitrogen-use efficiency (PNUE), leaf carbon construction costs (CC) on a leaf dry mass, CC on a leaf area basis, and $\delta^{13}C$ for *M. micrantha* and *M. cordata*. Sample size is about 24-40 (except to $\delta^{13}C$, 12 samples), 6-10 samples ($\delta^{13}C$, 3 samples) for each species were collected for each collection time (March, June and November of 2002). Values are means ±s.e. Symbols indicate the same meanings as those in Table 1.

Leaf parameters	Species		
	M. micrantha	*M. cordata*	P
SLA ($cm^2 g^{-1}$)	466.67±6.08	380.45±5.87	**
Leaf N (%)	3.35±0.26	2.85±0.23	**
Leaf N (g m^{-2})	0.72±0.02	0.75±0.01	*
PNUE (μmol CO_2 g^{-1} Ns^{-1})	23.88±3.81	16.93±1.88	***
CC (g glucoseg^{-1} day mass)	1.42±0.02	1.49±0.02	**
CC (g glucose m^{-2})	30.47±0.31	39.31±0.94	**
$\delta^{13}C$ (‰)	- 26.5±0.5	- 28.3±0.6	**

CC of *M. micrantha* were significantly lower than in *M. cordata* ($P<0.01$, Table 2). While area-based leaf N of *M. micrantha* was lower than that of *M. cordata* (Table 2), at all levels of mass-based leaf N, A_{max} per unit leaf mass of invasive *M. micrantha* was higher than in the indigenous *M. cordata* (Figure 3). Both species showed a positive relationship between A_{max} and leaf N. The PNUE, calculated as the ratio of A_{max} to leaf N, was higher for the invasive *M. micrantha* ($P<0.01$, Table 2).

WUE and $\delta^{13}C$ Value

In the morning at about 6:00, both *M. micrantha* and *M. cordata* had similar instantaneous WUE (Figure 4). As VPD increased, however, the invasive *M. micrantha* maintained a higher WUE than *M. cordata*. Although only diurnal courses of WUE and VPD from June are presented here, similar patterns appeared in March, April, August, and November (data not shown). *Mikania micrantha* had fewer negative $\delta^{13}C$ values than *M. cordata* (Table 2) (-26.5‰±0.5‰ and -28.3‰±0.6‰, respectively, $P<0.01$).

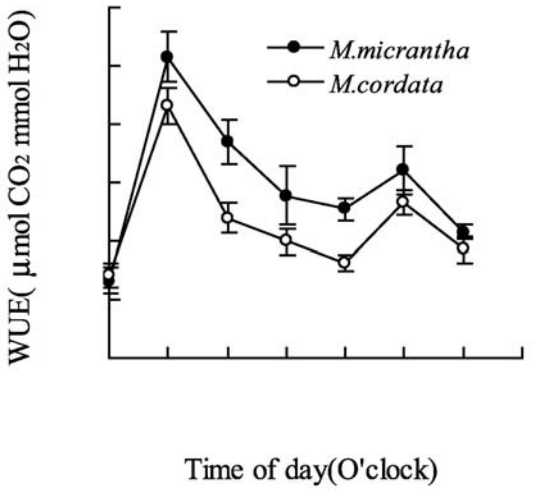

Figure 4. Diurnal course of instantaneous water use efficiency (WUE) of the invasive *M. micrantha* (filled circles) and the indigenous *M. cordata* (open circles). Data are from three diurnal courses measured in June of 2002. Error bars=1 S.E. of the means.

Discussion

Photosynthetic Characteristics and Niche Partitioning

The invasive species *M. micrantha* exhibited much greater capacity for photosynthesis than the indigenous plant *M. cordata*. V_{cmax} and J_{max} were higher in *M. micrantha*, which was consistent with its higher A_{max} values (Table 1). This relatively higher photosynthetic rate was maintained throughout the year (data not shown). The higher A_{max} and higher LSP in photosynthetic irradiance responses give *M. micrantha* a possibility to acclimate to high light environments with a larger pool of available carbon to allocate to reproduction, growth, and respiration. The light response curves of *M. micrantha* and *M. cordata* showed no significant differences in LCP, α, or R_d. These results suggest similar shade tolerances, which field surveys also support. The niche partitioning concept is based on the different responses by species to environmental stress and resource availability. Light may be one resource that is more likely to be associated with the establishment, competition, and expansion of invasive plants than other resources (Hurlbert, 1981). The photosynthetic characteristics of these two *Mikania* species in varying light environments could be a basis for their niche partitioning. While *M. micrantha* can invade a relatively wider light niche, *M. cordata* can only tolerate shaded environments in tropical and subtropical China (Baker et al., 1997; Huang et al., 2000).

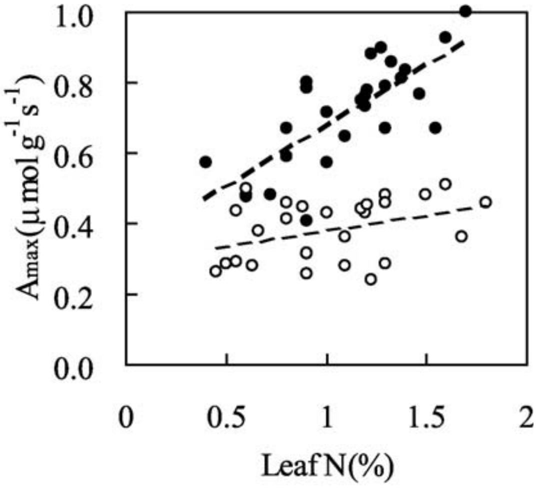

Figure 3. The relationship between maximum photosynthetic rate per unit leaf dry mass (A_{max}) and leaf nitrogen concentration per unit leaf mass (N) for the invasive species *M. micrantha* (filled circles) and indigenous species *M. cordata* (opened circles). Samples were collected after gas exchange measurements in March, April, June, August, and November of 2002.

The invasive *M. micrantha* exhibited a significantly higher saturating CO_2 concentration and CO_2 saturating A_{max} and less decrease in A with CO_2 concentration increasing beyond the saturating point than the native *M. cordata* (Figure 2). These results are consistent with some other studies of invasive plant. For example, *Bromus* species (Huxman and Smith, 2001) and Japanese honeysuckle (*Lonicera japonica*) (Dukes and Mooney, 1999) maintained relatively high A (close to the CO_2 saturating A_{max}) at elevated CO_2 while significant down-regulation of photosynthesis (fell significantly from the CO_2 saturating A_{max}) was observed for the native plant, for example *Eriogonum* (Huxman and Smith, 2001). How the invasive and native plants respond to the long-term rising [CO_2] is still controversial, and it is risky to predict which species will “win” or “lose” in high [CO_2] conditions on the basis of their photosynthetic response in the absence of other species (Dukes and Mooney, 1999).

SLA, Leaf N, PNUE and Construction Cost

In this study, though the area-based leaf N of native *M. cordata* was higher than that of *M. micrantha*, the traits of this pair of native and invasive *Mikania* species followed the patterns described by Baruch and Goldstein (1999): higher CC_{mass} and CC_{area}, but lower SLA and mass-based leaf N and PNUE for the native species (Table 2). The SLA of invasive *M. micrantha* was 22.7% higher than its native congener *M. cordata*. SLA is a plant trait that appears to be extremely important in the regulation and control of plant functions such as carbon assimilation and carbon allocation (Baruch and Goldstein, 1999). By having leaves with high SLA (thin and/or less dense leaves), invasive plants can produce large assimilatory surfaces for a fixed amount of carbon. Due to differences in SLA, the photosynthetic differences between the native and invasive species were significant. The higher A_{max} was likely a result of higher leaf N and higher SLA (Table 2). The relationships between A_{max}, N, and SLA are similar to the interspecific relationships among leaf structure and function described by Reich et al. (1997). Also, the invasive species *M. micrantha*, with its higher SLA, N concentration, and A_{max}, will have higher growth rates than its native congener *M. cordata*, and therefore spread rapidly (data unpublished).

Poorter and Evans (1998) found that high-SLA species achieved rates of photosynthesis as high as low-SLA species with a smaller biomass invested per unit area though the respiration rates were lower. Consequently, photosynthesis on a mass basis is considerably higher for the high-SLA species. Higher SLA species had significantly higher concentrations of total mass-based leaf N and almost invariably higher mass-based PNUE (Poorter and Evans, 1998). Our results were consistent with the views above, with the exception that significantly more area-based photosynthesis was observed in *M. micrantha* (higher SLA) than in its native congener *M. cordata* (lower SLA) (Figure 3). Although with lower area-based nitrogen concentration (Table 2), *M. micrantha* may invest relatively more N in photosynthetic machinery than *M. cordata*. More research is needed to understand the relationship between the amount of leaf N and partitioning of the invasive and indigenous species.

SLA and construction costs for the two species were also consistent with the pattern observed: generally, the cost of a thin leaf (high SLA) is lower than that of a thick leaf (low SLA). Also, SLA was lower and the area-based CC higher in noninvasive species compared with invasive species (Durand and Goldsein, 2001). Still, some exceptions were reported. For example, the SLA of the invasive plant *Rubus* was lower than that of the noninvasive plant in a study by McDowell (2002).

The Absence of Trade-off Between WUE and PNUE

Plants typically exhibit a trade-off between WUE and PNUE because plants that achieve high WUE by closing their stomata may be expected to have high leaf N allocated to photosynthetic enzymes in order to maintain high A under a reduced supply of CO_2. However, if high WUE is obtained without reduced stomatal conductance, then this trade-off may not be observed (Hikosaka et al., 1998; Van den Boogaard and Villar, 1998; McDowell, 2002). It was not observed in *M. micrantha*, and both WUE and PNUE were significantly higher than in *M. cordata*. Using data from diurnal courses done throughout the year, we established responses of stomatal conductance and net photosynthetic rate in the two species to leaf-to-air vapor pressure differences (VPD). Stomatal conductance and A of *M. micrantha* remained significantly higher than in *M. cordata* (Figure 5, P<0.01). Therefore, the WUE observed in *M. micrantha* is probably due to its high photosynthetic capacity and not to reduced stomatal conductance.

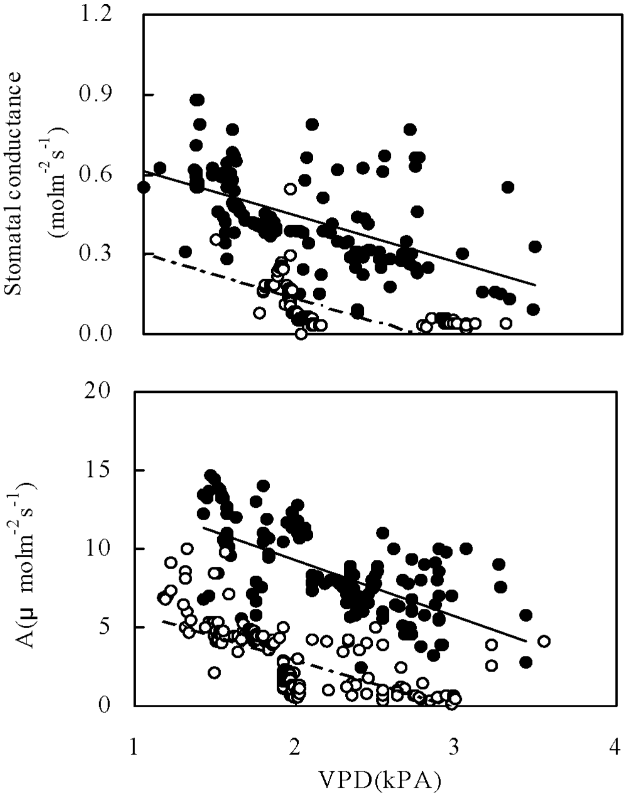

Figure 5. Stomatal conductance versus vapor pressure deficit (VPD) and rate of photosynthesis (A) versus vapor pressure deficit (VPD) of invasive *M. micrantha* (filled circles) and indigenous *M. cordata* (opened circles). Data are from photosynthetic diurnal courses measured in March, April, June, August, and November of 2002.

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華南入侵植物薇甘菊與其同屬本地種假澤蘭的氣體交換特性

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研究了華南地區外來入侵種薇甘菊 *Mikania micrantha* H.B. Kunth 和它的本地同屬種假澤蘭 *Mikania cordata* (Burm. f.) B. L. Robinson 的氣體交換特性。薇甘菊的 Rubisco 活性（V_{cmax}）和電子傳遞速率（J_{max}）比假澤蘭更高，因而表現出更強的最大淨光合速率值（A_{max}），表現出更強的光合能力。二者的光補償點、表觀量子產量（α）和暗呼吸 (R_d) 無顯著差異，意味著它們具有相似的耐陰性。高 A_{max}、光飽和點和 CO_2 飽和點意味著薇甘菊比假澤蘭更易於適應強光環境和積累更多碳同化物。這些光合能力的差異可能是它們產生生態位分異的基礎。兩個種的葉性因數表現出以下的形式：本地種假澤蘭的構建成本（CC）和單位葉面積的氮含量比外來種薇甘菊更高，但葉重比（SLA）以及單位幹重的葉氮含量和光合氮利用率則顯著低於後者。薇甘菊較高的水分利用效率（WUE）和 $\delta^{13}C$ 值更可能歸功於其較強的光合能力而不是減小其氣孔導度，因而導致 WUE 和 PNUE 消長規律的喪失。

關鍵詞：假澤蘭；入侵種；光合特性；葉重比；氮利用率。