Effects of Simulated Defoliation on Growth and Photosynthetic Characteristics of an Invasive Liana, *Ipomoea cairica* (Convolvulaceae)

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To better understand the response of *Ipomoea cairica* (Cairo morningglory) to herbivory, the compensatory growth and photosynthetic characteristics of plants were measured after simulated herbivory by leaf trimming at four intensities: 25, 50, 75, and 100% removal, starting from the apex. Defoliation at 25% had no significant influence on plant biomass, but the total biomass (−19 to −66%) and root biomass (−31 to −75%) of the plants decreased significantly when defoliation intensity was ≥ 50% ($P < 0.05$). Photosynthetic rates (P_n) increased with defoliation intensity ($P < 0.01$), and P_n values in the defoliated plants were 10 to 72% greater than those in the control plants, a relationship that could be attributed to a decrease in stomatal limitation (−11 to −34%) and the increase in rubisco content (9 to 18%) as well as higher photosynthetic efficiency and less light energy dissipated as heat. At defoliation intensities up to 50%, plants needed more energy to compensate photosynthetically, which could influence the plant photosynthetic characteristics as well as the allocation of assimilates, resulting in less root development. Since the spread of *I. cairica* depends primarily on clonal growth, smaller roots could limit uptake of nutrients from the soil. These direct and indirect effects indicate that leaf-feeding herbivores may have potential for biological control of *I. cairica* but to have any effect the herbivores would need to consume ≥ 50% of the leaf biomass.

Nomenclature: Cairo morningglory, *Ipomoea cairica* (L.) Sweet.

Key words: Invasive weeds, *Ipomoea cairica*, photosynthetic characteristics, plant biomass.

Control of invasive plant species can be achieved through mechanical or chemical methods and also through reduction of their biomass or leaf area with biological control agents (Brockerhoff et al. 1999). Mechanical removal by cutting down the plants results in resprouting, whereas plant extraction by hand can increase plant density as a result of disturbance. Given that spraying with herbicides is generally inefficient and very expensive, use of biological control is an attractive control option. Often, biological control offers the only safe, economic, and environmentally sustainable solution for weed management (Ma et al. 2003; McFadyen 1998; Zhang and Feng 2007). Studies of the population ecology of a weed are desirable prior to implementation of biological control programs. These studies can identify weaknesses that can be exploited, and may be helpful in deciding which agents should be given priority, how many species should be released, and the sequence and timing of releases, thereby enhancing the success rate of biological control efforts (Hoffmann 1990; Kriticos et al 1999).

Ipomoea cairica (L.) Sweet (Convolvulaceae), or Cairo morningglory, is an extremely fast-growing, sprawling, and perennial liana. Although it is believed to originate from a rather wide area—Africa, Asia, Pacific Islands, and South America (Fang and Staples 1995)—it is recognized as the second worst invasive weed in South China following *Mikania micrantha* Kunth (Li and Xie 2002; Wu and Hu 2004). In China it occurs widely in thickets, roadsides, waste places, cultivated areas, and sunny meadows in Guangdong, Guangxi, Hainan, Fujian, Taiwan, and Yunnan (Fang and Staples 1995; Li and Xie 2002). It forms extensive monocultures, which transform natural habitats, and it is problematic in parks, forests, plantations,

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Management Implications

Studies of the population ecology of a weed are valuable prior to implementation of biological control programs. This study suggested that agents that can consume 50% or more of the leaf biomass should be given priority for *I. cairica* control. It will help to find out a suitable density of insect population in the future. When we use the beetle *Cassida circumdata* to control *I. cairica*, herbivore feeding would need to consume at least 50% of the leaf.

orchards, and tea and nursery gardens (Liang and Lu 2006; Qiu et al. 2007; Shao et al. 2006).

Inundative biological control using naturally occurring species can provide a supplement to natural control and conservation biological control (Sigsgaard 2006). It has been recently reported that *Cassida circumdata* Herbst (Coleoptera: Chrysomelidae), a leaf beetle native to Asia and distributed widely in southern China, feeds only on the leaves of *I. cairica* and could become a potential inundative biological control agent in China (Chen et. al. 2011; Zhao and Chen 2011). Prior to releasing herbivorous control agents, it is desirable to understand how herbivory might influence plant productivity. We observed that in the field *I. cairica* flourishes even when its leaves are eaten by *C. circumdata*. This may be due to low numbers of beetles or low per capita consumption rates, together providing insufficient damage to the plant, raising the question of how much damage was necessary to suppress the growth of *I. cairica* to control it adequately. One way of gauging this threshold is to measure the effects of defoliation on the target plant. Defoliating the plant to simulate herbivory may not reflect accurately the effects of true herbivory, as complex plant responses may not be triggered by tissue removal alone (Baldwin 1990). However, the method has been shown to offer significant insight into the response of plants to herbivory and is widely used in plant physiological studies (Thomas et al. 2008b) and in biological control (Hoffmann 1990; Raghu and Dhileepan 2005; Watt et al. 2007).

Most studies on plant tolerance to herbivory have focused on changes in photosynthesis and reallocation of assimilates as well as nitrogen translocation patterns (Chen et al. 2000, 2003; Li et al. 2003; Strauss and Agrawal 1999; Thomson et al. 2003, 2008a; Yu et al. 1990, 1993). Proposed mechanisms for a plant's compensation for herbivory include increases in photosynthetic rates (Dryer et al. 1991; Houle and Simard 1996; Meyer 1998a) and growth rates (Danckwerts 1993; Oba et al. 2000), prolonged leaf longevity (Thomas et al. 2008b), an enhanced ability to reallocate stored carbon resources (Caldwell et al. 1981; Mabry and Wayne 1997), increased demand for nitrogen (Thomas et al. 2008a), and decreased reproductive capacity (Thomas et al. 2009). However, the degree of compensation depends on the specific plant species, the amount of leaves lost, the area of leaves lost, the mode of herbivore damage, the timing and frequency of herbivory, and environmental conditions (Maschinski and Whitham 1989; Meyer 1998b; Watt et al. 2007). With regard to *I. cairica*, it is still unclear how it might respond to herbivore damage.

In this study, we aimed to gain a better understanding of the susceptibility of this weed to herbivory. We used potted plants to simulate different intensities of herbivore defoliation on *I. cairica*, and studied the effects on compensatory growth and photosynthetic characteristics of the plants. We expected to define suitable defoliation intensities for suppressing *I. cairica* growth and to identify compensatory mechanisms induced by defoliation, and therefore potential control points.

Materials and Methods

Initial experiments were conducted from March 19 to May 18, 2009, and the plant biomass parameters were measured after harvest. Then these experiments were repeated from June 13 to August 12, 2009, and the plant biomass, chlorophyll fluorescence, and gas exchange parameters were measured. The methods of the two experiments were the same. The specific procedures were as follows.

Culture of Plant Materials. Rhizomes from a single clone collected in the Biological Garden at South China Normal University (28°08′N, 113°09′E, elevation 65 m [213 ft] above sea level) were selected as the experimental materials to ensure that all material was genetically identical. To ensure that all material was of similar sprouting potential, rhizomes with similar diameter and of the same age were cut into 8-cm-long (3-in-long) fragments, on which there was at least two nodes. Cuttings were grown in plastic containers (length 50 cm by width 25 cm by height 5 cm) with sand in an artificial climate incubator (day: 28 C [82 F], 65% humidity; night: 23 C, 50% humidity), watered daily, and fertilized with 20% Hoagland nutrient solution (Epstein 1972) per container twice per week.

Ten days after sprouting, regenerated plantlets of similar sizes were transplanted to 18-cm-diam pots with river sand in a naturally lit experimental site in the Biological Garden from where the founding rhizome had originated. Every plantlet was fertilized once every 2 d with 200 ml (6.8 fl oz) of 10% Hoagland nutrient solution, and watered when showing signs of drought. A pergola was constructed for the plants to climb as they grew. The average monthly minimum and maximum temperatures for the experimental period, June to August 2009, were 22 and 28 C, respectively.

Defoliation Treatments. Thirty days after transplanting, plants of similar size were selected for leaf removal. Because

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the leaf blade of *I. cairica* is palmately five- to seven-parted to a base with ovate–lanceolate lobes (5 to 7 cm long, 0.5 to 1cm wide), the cut length was approximately equal to one-quarter, one-half, or three-quarters of the length of each lobe in one leaf, i.e., removal of 25, 50, or 75% leaf area starting from the apex. The entire leaf removal was regarded as 100% of defoliation intensity and plants with undamaged leaves as control. There were five treatments in total (undefoliated control, 25, 50, 75, and 100% leaf area removal), and each treatment had five replicates.

Chlorophyll Fluorescence and Gas Exchanges Measurements. Chlorophyll fluorescence parameters were determined on clear sunny days 1, 7, and 15 d after defoliation. Specifically, chlorophyll fluorescence parameters were first measured in situ with a portable fluorometer PAM-2100 (Walz, Germany) on July 25, 2009. Leaf samples were predarkened for 20 min before measurements of the minimum (F_o) and maximal fluorescence (F_m). The steady-state (F_s) and maximum fluorescence (F_m') in the light-adapted state were measured under the intensity of actinic light of 800 μmol m^{-2} s^{-1}. Partitioning of absorbed light energy was estimated following Demmig-Adams et al. (1996). The fraction of light absorbed in photosystem II (PSII) antennae that is utilized in PSII photochemistry (P) was estimated as $P = (F_m' - F_s)/F_m'$. The fraction of absorbed light energy that is dissipated thermally within the PSII antennae (D) was calculated as $D = 1 - F_v'/F_m'$. The excess excitation energy (E) defined as a fraction of the absorbed light not attributed to P or D and represented the photon energy absorbed by PSII antennae and trapped by "closed" PSII reaction centers was estimated using $E = F_v'/F_m' \times (1 - qP)$. Rubisco content of specific leaf area was estimated as rubisco (g m^{-2}) = ETR × 0.014 (Evans and Poorter 2001), where ETR was total electron transport rate through PSII estimated following Krall and Edwards (1992): ETR = ΦPSII × PPFD × a × 0.5, where PPFD means the photosynthetic photon flux density and a is the leaf absorption that is estimated at 0.84. The factor 0.5 was used based on the assumption of an equal distribution of photons between photosystem I and PSII. Incident PPFD was measured with a quantum sensor (Genty et al. 1989).

Gas exchange parameters were determined using the LI 6400 portable gas exchange system (LI-COR Inc., Lincoln, NE) on days 1, 7, and 15 after defoliation. Measurements commenced at 8:00 A.M. and were completed within 2 h in full sunshine. Light intensity of natural condition ranged from 800 to 1000 μmol m^{-2} s^{-1}, ambient temperature ranged from 28 to 30 C. Carbon dioxide concentration inside the leaf chamber was maintained at 380 cm^3 m^{-3} through the CO_2 controlling system of the LI-6400 attached to a portable CO_2 cylinder. The PPFD of 800 μmol m^{-2} s^{-1} on the cuvette surface was provided by a light-emitting diode source. Before taking readings, leaves were equilibrated under the artificial light conditions in the leaf chamber for at least 10 min. During measurements, the relative air humidity was about 75% and leaf temperature was maintained at 25 C. Measurements were made on the remaining portion of the treated leaves (i.e., 25, 50, and 75% removal) and on the untreated leaves. Measurements were also made on newly emerged leaves on plants from which the entire leaves were removed (100% of leaf removal). When the remaining portion of the treated leaves did not cover the entire chamber (i.e., in some of the 50 and 75% treatments), the leaf area was measured with a portable area meter (CI-203 CID, Inc., Camas, WA) before the leaf was enclosed within the chamber. Net photosynthetic rate (P_n), intercellular CO_2 concentration (C_i), stomatal conductance (G_s), and transpiration rate (T_r) were recorded. The stomatal limitation (L_s) was estimated as $L_s = 1 - C_i/C_a$, where C_a is the atmospheric CO_2 concentration (Berry and Downton 1982; Shao et al. 2009).

Growth Measurements. Because *I. cairica* grows quickly, the plants were harvested for growth analysis 18 d after defoliation on May 18 and August 12, 2009. The leaves, stems, and roots were separated from each plant and dried to a constant weight for at least 48 h at 60 C and then weighed. The biomass ratios were calculated as the biomass of leaves, stems, and roots in proportion to the total biomass. Compensation index (CI) was estimated as CI = the total biomass of the defoliation treatment/the control (Wang et al. 2003). A significant value for CI > 1 is regarded as overcompensation whereas CI < 1 is regarded as undercompensation. A nonsignificant difference is regarded as equal compensation (Thomson et al. 2003; Wang et al. 2003).

Statistical Analysis. All statistical tests were performed using SPSS 11.5 software (SPSS Inc., Chicago, IL). Plant biomass variables and the fluorescence variables were compared using one-way ANOVA, with different defoliation intensity as a single factor, followed by Dunnett's t tests at $P < 0.05$ (the undamaged plants as the control group, compared with four groups of different defoliation intensities). Because the four parameters (P_n, C_i, G_s, and T_r) that were used to evaluate plant photosynthesis were correlated dependent variables, multivariate ANOVA (MANOVA) was used to evaluate the defoliation treatments on the overall photosynthesis, with P_n, C_i, G_s, and T_r regarded as dependent variables and the defoliation intensity as the factor. A multivariate test result and univariate F test for each variable was used to interpret the respective effect. The equality of covariance matrices were tested using Box's M test and the covariance matrices of each group of residuals were considered to be equal when $P > 0.05$. Equality of error variances were tested using Levene's test and the error

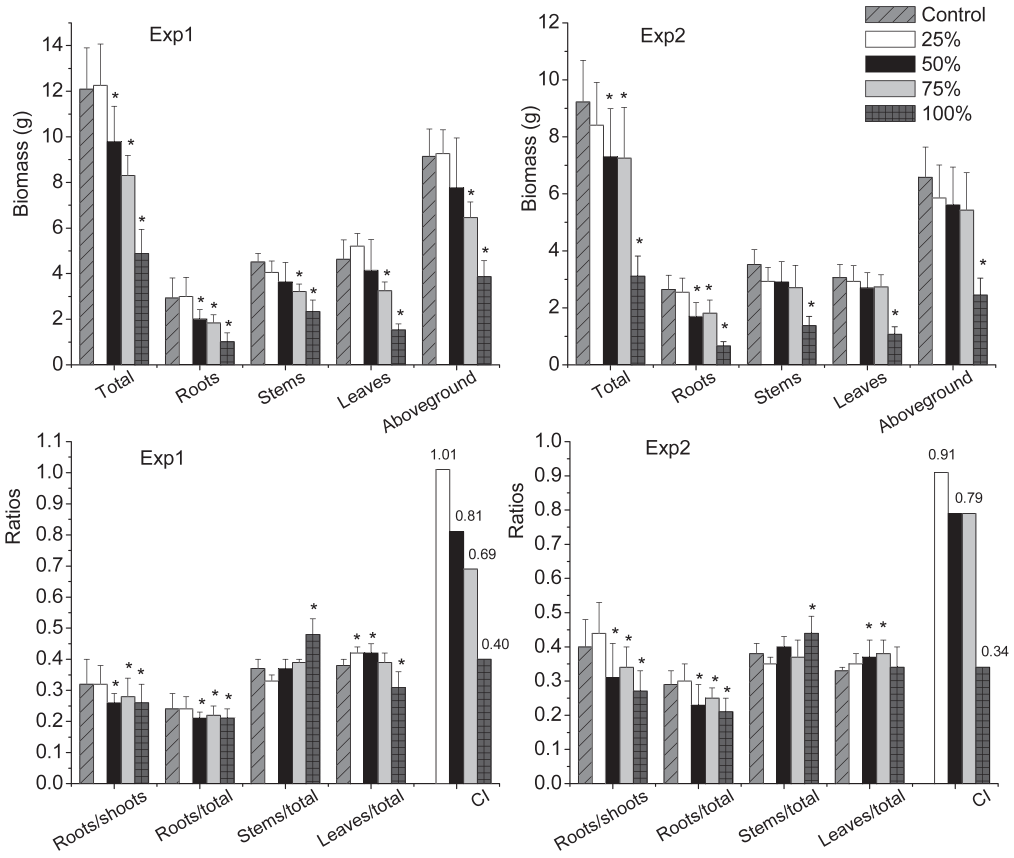

Figure 1. Effects of different defoliation intensities (25, 50, 75, and 100%) on the growth of *Ipomoea cairica* (experiment 1: the initial experiment, 2.19–5.18, 2009; experiment 2: the repeated experiment, 6.13–8.12, 2009; CI - compensation index).

* The mean difference is significant at the 0.05 level, according to the Dunnett's *t* tests (using the undamaged plants as the control group, compared with four groups of different defoliation intensities).

variance of the dependent variable was considered to be equal across groups when $P > 0.05$.

Results

Effects of Defoliation on Plant Biomass. Before defoliation treatments, there were no significant differences in any of the growth variables. Eighteen days after defoliation, the results of the two experiments showed the similar trend. There was a significant difference in plant growth between ≥ 50% defoliation and the control (Figure 1). Plant total biomass (−19 to −60% for experiment 1 and −21 to −66% for experiment 2), root biomass (−31 to −66% for experiment 1 and −36 to −75% for experiment 2), the root to shoot ratio (−4 to −6% for experiment 1 and −6 to −13% for experiment 2), and the root to total biomass ratio (−2 to −3% for experiment 1 and −4 to −8% for experiment 2) decreased significantly when defoliation intensity was ≥ 50%, whereas 25% defoliation resulted in no significant differences in plant biomass when compared with the controls (Figure 1).

Differences in stem biomass, leaf biomass, and aboveground biomass were not significant in 50% treatments as compared to the control, but the ratio of leaf to total biomass was significantly 4% higher than the control (Figure 1). Plants with 50% of leaf removal reduced allocation of biomass to underground parts (−4 to −8%) and increased allocation of biomass to aboveground parts (4 to 7%). CI measurements showed that there was equal compensation in plants with 25% defoliation and undercompensation in plants with ≥ 50% defoliation (Figure 1).

Effects of Defoliation on the Photosynthetic Characteristics. Measurements of the gas exchange parameters (P_n, C_i, G_s, and T_r) showed that defoliation significantly affected photosynthesis in *I. cairica* (Hotelling's trace = 1.32, F = 4.97, df = 16, $P < 0.001$). Tests of between-subjects effects showed that there were significant differences in P_n, C_i, G_s, and T_r in the five treatments (Table 1). The effect of defoliation was largest on Gs, intermediate on P_n and T_r, and least on C_i (Table 1).

After defoliation, P_n (10 to 72%) and G_s (36 to 214%) were significantly higher in plants with ≥ 50% defoliation

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Table 1. Univariate analysis on the gas exchange parameters.

Independent variable	Dependent variables[a]	df1	df2	Mean square	F	Significance
Intensity	P_n	4	65	67.49	9.16	$P < 0.001$
	G_s	4	65	0.17	13.30	$P < 0.001$
	C_i	4	65	3038.84	5.57	$P < 0.01$
	T_r	4	65	37.94	10.05	$P < 0.001$

[a] Abbreviations: P_n, photosynthetic rate; G_s, stomatal conductance; C_i, intercellular CO_2 concentration; T_r, transpiration rate.

treatments than in the control group. There were no significant differences in P_n and G_s between plants with 25% of defoliation and the controls (Figure 2). As the experiment continued, P_n first rose and then fell, while G_s fell continuously (Figure 2). The compensatory photosynthetic response slowed down with the increase of the defoliation time.

With the increasing of defoliation intensities, the fraction of absorbed light utilized in PSII photochemistry gradually increased while the fraction of light energy dissipated thermally greatly decreased (Table 2). The excess excitation energy did not change systematically (Table 2).

Changes of the Stomatal Limitation and Rubisco Content. On the first and the seventh days, plants with ≥ 50% defoliation exhibited significantly lowered stomatal limitation (−26 to −32% in 1 d and −11 to −34% in 7 d) in the plant's leaves (Table 3). At 15 d after defoliation, only the plants with 75 and 100% defoliation exhibited a significantly lower stomatal limitation (−19%) (Table 3). Rubisco content increased with levels of defoliation, being significantly higher in the plants with ≥ 50% defoliation than the control plants at 1 d (9 to 16%) and 7 d (11 to 18%) after defoliation, and significantly (15%) higher than the control in the plants with 100% defoliation on the 15th d after defoliation (Table 3).

Discussion

Accurate selection of biological control agents is a time consuming process and can be costly (McFadyen 1998).

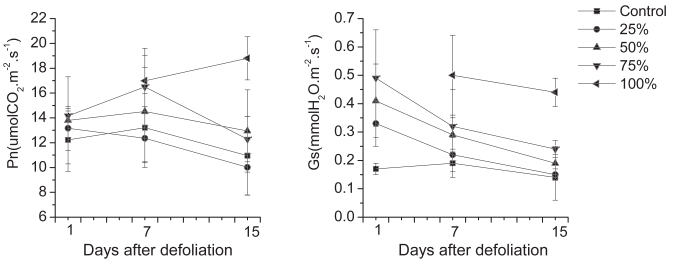

Figure 2. Effects of the different defoliation intensities (25, 50, 75, and 100%) on photosynthetic rate (P_n) and stomatal conductance (G_s) in leaves of *Ipomoea cairica* after defoliation. (Control consists of undamaged plants, means ± SD, $n = 5$).

Simulation of herbivore damage could provide an indication of the likely impacts of candidate biological control agents and help to explain how a weed responds to defoliation (Watt et. al. 2007). Mechanical defoliation experiments have been found to be useful in accurately assessing plant responses to various levels of defoliation (Hjältén 2004; Inouye and Tiffin 2003; Raghu and Dhileepan 2005; Raghu et al. 2006; Wirf 2006), although they may not accurately reflect the full range of effects of herbivores (Lehtilä and Boalt 2004). Simulated herbivory can be applied precisely and does not involve any biosecurity considerations. Real herbivory may be a more direct application of the treatment effect, but it may be difficult to achieve or measure treatment levels or covariates (Watt et al., 2007). In our case, the use of real herbivory damage for *I. cairica* has not yet been approved, but based on the relationship between plant tolerance to herbivore damage and the plant's compensatory ability (Chen et al. 2005; Strauss and Agrawal 1999; Strauss and Murch 2004), the repeated results of our study suggested the following: (1) defoliation does not result in overcompensatory growth of *I. cairica*, (2) the lower defoliation intensity (25%) does not control the plant growth but tends toward equal compensation, and (3) the higher defoliation intensity (50% or greater) can suppress plant growth over the 15-d period we investigated.

Ipomoea cairica's increased photosynthesis when it was treated with high defoliation intensities accords with a well-recognized compensatory response to herbivore damage (Chen et al. 2005; Houle and Simard 1996; Li and Sheng 1996; Li et al. 2003; Meyer 1998b; Thomson et al. 2003). This response could be attributed to the decrease of stomatal limitation, the increase of rubisco content, or both, as well as higher photosynthetic efficiency and less light energy dissipated as heat. Our findings were consistent with those of Thomson et al. (2003) who studied compensation of *Cucumis sativus* L. in relation to herbivory.

Plants can complete their normal life activities only when they can use assimilated products efficiently and can allocate them reasonably (Chen et al. 2005). Under normal circumstance, the assimilates are kept in leaves to meet the needs of the leaf growth, reserved in cellular storage in the leaves, or transported to stems, roots, fruits, or other leaves.

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Table 2. Effects of different defoliation intensities (25%, 50%, 75% and 100%) on the light energy distribution in leaves of *Ipomoea cairica* after defoliation.

Days after defoliation	Proportion of light energy distribution	Control	25%	50%	75%	100%
1	P	51.60%	51.30%	52.70%	57.60%	
	D	47.70%	46.20%	44.70%	39.10%	
	E	0.70%	2.50%	2.60%	3.30%	
7	P	58.30%	59.00%	58.50%	60.30%	64.70%
	D	37.30%	36.40%	36.20%	34.00%	31.40%
	E	4.40%	4.60%	5.30%	5.70%	3.90%
15	P	56.70%	54.30%	59.60%	59.70%	66.50%
	D	37.50%	40.40%	35.00%	33.90%	29.90%
	E	5.80%	5.30%	5.40%	6.40%	3.60%

Abbreviations: P, fraction of light absorbed in photosystem II antennae that is utilized in photosystem II photochemistry; D, fraction of absorbed light energy that is dissipated thermally within the photosystem II antennae; E, excess excitation energy.

The partitioning of assimilates is regulated by source–sink relationships (Gifford and Evans 1981; Thomson et al. 2003), and herbivore feeding or other damage can change both the metabolic production of assimilates and their partition direction (Caldwell et al. 1981; Mabry and Wayne 1997). Defoliation induces a strong sink demand for leaves in source-limited plants (Whigham 1990). The results of this study showed that defoliation intensities up to 50% resulted in the reallocation of assimilates, and plants allocated more energy to leaf tissue to raise the photosynthetic rate, while allocating less biomass to roots. This may be the main reason that the plants undercompensated for the loss of leaf tissue. Defoliation-induced increases in allocation to leaves have also been noted in *Eucalyptus nitens* (H. Deane & Maiden) Maiden (Pinkard and Beadle 1998) and *Buddleja davidii* Franch. (Watt et al. 2007).

In the Chinese context, if the population of *I. cairica* was reduced and herbivory opened up the vegetation canopy, the gaps could be filled with valuable native species such as *Pueraria montana* (Lour.) Merr. var. *lobata* (Willd.) Maesen & S. Almeida or *Paederia scandens* L. When *I. cairica* was planted together with *P. lobata* or *P. scandens*, the total biomass of *I. cairica* reduced by 68.7 and 45.8%, respectively (C. Peng, unpublished data). These native species have rapid seedling establishment and could help suppress *I. cairica*. Community composition is determined by the demographic processes controlling the population size of the component species (Williams et al. 2007). If a balance could be created between the weed and the biological control agent, as well as the surrounding species populations, it is possible to keep the noxious weed at an economically acceptable level, thus helping rebalance ecosystem composition and function.

In conclusion, the decline in root biomass has important implications for the efficacy of defoliation as a control measure, as smaller plant roots suggest a reduced capacity for uptake of nutrients from the soil, which may assist in reducing the invasive spread for the species (Thomas et al. 2008a). Defoliation did not result in the overcompensatory growth of *I. cairica*. Moderate to high levels of defoliation (upwards of 50%) applied over a short duration can suppress plant growth. Although such herbivory greatly increased the photosynthetic efficiency and capacity of *I. cairica*, the net result was undercompensation. Because population expansion in *I. cairica* depends mainly on its clonal growth, which in turn depends on adequate root

Table 3. Effects of different defoliation intensities (25, 50, 75, and 100%) on stomatal limitation and rubisco content in leaves of *Ipomoea cairica* after defoliation (mean ± SD, $n = 5$).

Days after defoliation	Stomatal limitation and rubisco content (g m^{-2})	Control	25%	50%	75%	100%
1	Stomatal limitation	0.31 ± 0.07	0.27 ± 0.03	0.23 ± 0.02[a]	0.21 ± 0.03[a]	—
	Rubisco content	0.68 ± 0.07	0.69 ± 0.11	0.74 ± 0.07[a]	0.79 ± 0.11[a]	—
7	Stomatal limitation	0.38 ± 0.03	0.37 ± 0.06	0.34 ± 0.05[a]	0.34 ± 0.08[a]	0.25 ± 0.02[a]
	Rubisco content	0.55 ± 0.05	0.59 ± 0.05	0.61 ± 0.03[a]	0.63 ± 0.03[a]	0.65 ± 0.02[a]
15	Stomatal limitation	0.36 ± 0.05	0.38 ± 0.08	0.37 ± 0.06	0.29 ± 0.05[a]	0.29 ± 0.03[a]
	Rubisco content	0.54 ± 0.05	0.56 ± 0.01	0.58 ± 0.02	0.57 ± 0.03	0.62 ± 0.02[a]

[a] The mean difference is significant at the 0.05 level, according to the Dunnett's *t* tests (with the undamaged plants serving as the control group, compared with four groups of different defoliation intensities).

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formation (Hu and Wang 2001; Liao et al. 2006; Zhu and Ma 2006), it appears possible that it could be suppressed using inundative biological control with foliar herbivores. Although our results show that the impact of one-off defoliation on plant growth can be significant in the short term, if herbivory is continued, the impacts are likely to increase markedly. Considering the target weed's population ecology (Kriticos et al. 1999) can reveal life stages or processes to target to ensure the greatest impact on weediness from the successful deployment of a biological control agent. In the absence of such a demographic study, if a biological control program is to be undertaken against *I. cairica* using foliar herbivores, then agents that can consume or destroy 50% or more of the leaf biomass in a short duration should be given the highest priority for assessment of control efficacy and suitability for deployment.

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