



Original article

Photosynthesis, growth and foliar herbivory of four *Ardisia* species (Myrsinaceae)

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ABSTRACT

Ardisia elliptica is an understory shrub endemic to Southeast Asia and has become a notorious invasive plant in Florida. In this study, we determined the photosynthetic capacity of *A. elliptica* and phylogenetically related species under four levels of irradiations. In addition, the levels of damage from natural insect herbivory of these four species under common garden conditions were investigated. The results show that *A. elliptica* had the higher photosynthetic capacity and the relative growth rate (RGR) which could be attributed to its high light-saturated photosynthetic rates (P_{max}), relatively low respiratory rate (R_d) and the increasing specific leaf area (SLA) with decreasing irradiation. *A. elliptica* also exhibited high phenotypic plasticity for photosynthetic traits in response to different irradiations including LSPT, P_{max} and RGR. Comparing to its congeners, *A. elliptica* suffered consistently severe damage from natural herbivory. Our results suggest that high photosynthetic capacity and high phenotypic plasticity could enable *A. elliptica* become a nuisance with the absence of natural enemies in introduced habitats, especially in those disturbed environments with high-light conditions.

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1. Introduction

Invasion of non-indigenous organisms into new habitats may substantially threaten native biodiversity, the structure and function of ecosystems, and the productivity of industries such as agriculture and forestry (Walker and Vitousek, 1991; D'Antonio and Vitousek, 1992; Hobbs and Mooney, 1998; Mack et al., 2000). The reason why some species become invasive after being introduced from their native range and which traits allow them to disrupt the systems they are introduced into, remains intensively debated (e.g., Elton, 1958; Callaway and Aschehoug, 2000; Agrawal and Kotanen, 2003; Colautti et al., 2004; Lambrinos, 2004). Several hypotheses have been proposed to interpret biological invasions, e.g., the enemy release hypothesis (Keane and Crawley, 2002) and phenotypic plasticity hypothesis (Williams and Black, 1994; Williams et al., 1995; Sultan, 2000). Knowledge is still critically lacking in the prediction of plant's invasive ability (Baruch and Goldstein, 1999; Mack et al., 2000; but see Richardson and Pyšek, 2006; Theoharides and Dukes, 2007).

Many characteristics have been identified to facilitate the invasion of plants, such as rapid vegetative growth rates, high potential for acclimation (Rejmanek, 1996) and photosynthetic capacity (Baruch and Goldstein, 1999; McDowell, 2002). Among them,

growth is an important index for plants because it implies increased fitness and enhanced survival (Shipley, 2006). Growing fast may give invasive plants the competitive advantage in making resource utilization over other species (Davis et al., 2000; Grotkopp et al., 2002; Burns, 2004, 2006; Grotkopp and Rejmánek, 2007). Additionally, higher specific leaf area (SLA) (Reich et al., 1997; Poorter, 1999; Shipley, 2006; Zheng et al., 2009), low light compensation points (LCPT) (Boardman, 1977), higher light-saturated photosynthetic rates (P_{max}) and lower dark respiration rates (R_d) (Pattison et al., 1998; Durand and Goldstein, 2001; McDowell, 2002; Zheng et al., 2009) have also been found to give invasive species a competitive advantage over noninvasive congeners. However, by comparing the invasive tropical shrub *Clidemia hirta* genotype to its native genotype, DeWalt et al. (2004a) showed that different genotypes between native and introduced of *C. hirta* displayed no significant differences in the relative growth rate (RGR), P_{max} or SLA in different irradiation treatments.

Light is essential to plants but it will become harmful to photosynthetic capacity when absorbed in excess which results in photoinhibition and photodamage. Low light availability also limits the plants to growth. However, phenotypic plasticity ensures plants to have the potential ability to use light efficiently under various environments (Williams and Black, 1994; Williams et al., 1995; Sultan, 2000; Callaway et al., 2003; Funk, 2008). For example, invasive C_4 grass *Pennisetum setaceum* in Hawaii showed high plasticity on photosynthetic rates, SLA, and number of inflorescences (Williams et al., 1995).

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Another important factor that may contribute to invasive plants is escape from natural enemies in the introduced habitat. A series of studies indicate that introduced plant populations are exposed to fewer species of pathogens and insect herbivores (See reviews by Colautti et al., 2004; Hinz and Schwarzaender, 2004; Torchin and Mitchell, 2004; but see Van der Putten et al., 2000), as a result the introduced plant populations are less attacked by pathogens and herbivores than native conspecific populations (DeWalt et al., 2004b; but see Beckstead and Parker, 2003). In the absence of natural enemies, trade-offs between high-light growth and low-light survival may be relaxed (Kitajima, 1994; Walters and Reich, 1999, 2000). Thus, high survivorship may be coupled with fast growth rates, resulting from greater allocation to light interception (SLA) and less allocation to storage (e.g., roots).

Ardisia (Myrsinaceae) is a pan-tropic distributed genus with about 400 species of trees or shrubs (Wu and Raven, 1996). Two species, *Ardisia elliptica* and *Ardisia crenata* which are native to Southeast Asia have been invasive to Florida and Hawaii (FLEPPC, 2005). Escape from gardens via bird and mammal dispersal is probably the main way *A. elliptica* spread to natural areas. *A. elliptica* receives less foliar damage than native congener species and appears to lack specialist herbivores in its introduced habitat (Koop, 2003, 2004). Despite discussions about the invasion of *A. elliptica* were carried on recently, relative little have been reported to interpret why it is not notorious in native range and to better predict the potential ability of its invasion. In this study, we contrasted *A. elliptica* with three congeners which from its native range and surveyed the photosynthesis of them under different irradiations. Otherwise, the leaf damage of each species was also investigated under common garden conditions. We supposed that compared to its congeners, *A. elliptica* 1) shows higher relative growth rate and photosynthetic capacity, 2) adapts easily to different irradiations, and 3) suffers more damage from insect herbivory.

2. Materials and methods

2.1. Study species

We compared *A. elliptica* with three congeners: 1) *Ardisia solanacea* Roxburgh is a shrub or tree reaching 6 m tall and it is native to Southeast Asia including south China at 400–1600 m attitude. 2) *Ardisia virens* Kurz is a shrub or small tree reaching 1–3 m tall. It is native to Southeast Asia at 300–2700 m attitude. 3) *Ardisia chinensis* Benthham is a shrub or subshrub reaching less than 1 m tall. It is also native to Southeast Asia at 300–800 m attitude (Wu and Raven, 1996). Many *Ardisia* species have been introduced from Southeast Asia to Hawaii. Among the four species tested in this study, three species (e.g., *A. elliptica*, *A. solanacea* and *A. virens*) were introduced to Hawaii as ornamental plants about one hundred years ago with only *A. elliptica* being invasive (Langeland and Burks, 1998; FLEPPC, 2005; Daehler and Baker, 2006).

2.2. Irradiance treatment

All the experiments were conducted in the Xishuangbanna Tropical Botanical Garden (XTBG) of the Chinese Academy of Sciences (21°41'N, 101°25'E, 570 m asl, annual mean temperature, 21.5 °C, annual mean rainfall, 1560 mm). Experimental seeds were collected from 3 to 4 year-aged fruiting plants from the living collection of XTBG in December, 2004. Among which, *A. elliptica* was introduced from North Thailand (about 374.4 km away) while the other three species were from nearby forests in Xishuangbanna, south Yunnan, China. Seeds were taken from at least five parent plants of each species, cleaned of pulp, and stored in moist sand at 4 °C for 2–4 weeks. Seeds were germinated in Petri dishes filled

with agar substrate at 30 °C. Before leaf development, each seedling (15 d after radicle emergence) was transferred to a deep pot (20 cm top diameter) containing mixtures of soil and loam. The soil was collected from natural forest near XTBG. Seedlings of each species were then randomly separated into five groups of 20 individuals. One group was harvested to determine initial biomass. Other groups were randomly assigned to one of the four irradiances (100%, 75%, 40%, and 4%), respectively. Seedlings were watered with tap water every day. The irradiance used in this study was created by covering shade houses with different layers of black shade netting, including no netting to create 100% irradiance. We used a LI-COR 6400 gas exchange system (LI-COR, Lincoln, NE) to measure the different treatment of light, and the degrees of different irradiance were 100%, 75%, 40% and 4% respectively. Photosynthetic gas exchange and leaf analysis were measured after seedlings grown under different light treatments for six months.

2.3. Photosynthetic gas exchange measurements and leaf analyses

Responses of net CO₂ assimilation to PPFD were measured with a LI-COR 6400 gas exchange system (LI-COR, Lincoln, NE) on three randomly chosen seedlings from each species and irradiance treatment between 5 and 10 January 2006. Measurements were made on the most recently fully expanded leaf of each plant between 0800 and 1400 h on clear days. Two leaves were measured on each seedling. The order of species measured was random. Light response curves were started after acclimation by decreasing PPFD stepwise in the following order: 1500, 1000, 800, 500, 200, 150, 100, 50, and 20 μmol m⁻² s⁻¹. Light saturation points (LSPT), light compensation points (LCPT), maximum photosynthetic rates (P_{max}) and dark respiration (R_d) were estimated by using nonlinear least squares regression to calculate the values of these parameters that best fit the equations of the von Caemmerer and Farquhar (1981) photosynthesis model (Harley et al., 1992; Wullschlegel, 1993).

All seedlings were harvested and oven-dried at 40 °C until constant mass was reached after photosynthetic gas exchange measurements. Among the 20 seedlings under each treatment, some seedlings of *A. solanacea* died (ten seedlings died for 100% light treatment and 1–3 individuals died for light treatment 75% and 4% respectively). To test the effects of species and irradiance on morphological variables, we took ten seedlings each species each treatment for data analysis. Leaf areas were measured with a LI-3000A leaf area meter (LI-COR, Lincoln, NE). The specific leaf area (SLA) was determined. Relative growth rate (RGR) was determined using the following equation (Evans, 1972).

$$RGR (mg g^{-1} d^{-1}) = [\ln(\text{seedling mass at harvest}) - \ln(\text{initial seedling mass})] / [\text{duration of study (d)}]$$

Dry samples were then sent to the Biogeochemical Laboratory of the Kunming Division of the Xishuangbanna Tropical Botanical Garden for the measurement of carbon (C) and nitrogen (N) contents. The C and N were determined using a wet digestion procedure (Kalra and Maynard, 1991). Instead of 10 duplicates for the analysis of C and N content, we combine 3–4 individuals into one sample, thus we have three samples each species each treatment for chemical analysis.

2.4. Natural herbivory and leaf characteristics

To quantify the damage of herbivory on the four species, natural areas of 20 acres which was recreated in 1996 including all of the four species were sampled in XTBG. The plants grow in XTBG arboretum where with rather dense forest canopy and managed by gardeners without any use of pesticide and chemical fertilizer. Thus

the plants exposing to herbivores are similar to natural forest. For each species, 20 plants of 3–4 year-aged plants were haphazardly selected. Five recently developed mature leaves from different directions (one leaf from the inner tree crown) of each plant were collected to measure consumed leaf area by the LI-3000A leaf area meter (LI-COR, Lincoln, NE) in 2005 December and 2006 September, respectively. Leaf toughness, carbon and nitrogen content of plants per species were measured only in 2005 ($n = 20$). The toughness was surveyed with a punchmeter model designed by Feeny (1970).

2.5. Statistical analyses

Distribution of each variable was normal, though analysis of variance (ANOVA) was used to compare the effects of species and

irradiance on photosynthetic and morphological variables. Because the effects of interactions were significant, one-way analysis of variance was performed to compare the effect of species on photosynthetic and morphological variables for each irradiance treatment. To evaluate the effect of irradiance on the photosynthetic variables and RGR, one-way ANOVA was performed. For the $P_{max}-R_d$ relationship, significant differences between linear regression slopes were tested using one-way ANOVA. To estimate the effect of species on consumed area by herbivory and morphological variables of plants growing in the living collection, one-way analysis of variance was performed. All statistical analyses were carried out using SPSS 13.0 (SPSS Inc., Chicago, IL).

3. Results

3.1. Photosynthetic gas exchange

As expected, species responded typically to variable PPFD, with photosynthesis increasing until saturation (Fig. 1). Both irradiance and species had significant effects on photosynthesis, RGR and SLA in this study according to a two-way ANOVA (Table 1). The interactions between them were also significant for the variables except LCPT.

LSPT and P_{max} of *A. elliptica* were significantly higher than its three congeners (for LSPT and P_{max} , $P < 0.0001$). *A. elliptica* also received higher RGR and SLA than other species (for RGR, $P < 0.0001$. SLA on average among four treatments of these four species are 210.93 ± 12.05 , 160.28 ± 6.68 , 155.38 ± 8.36 , 200.48 ± 10.33 , respectively ($P < 0.0001$)). But *A. elliptica* showed

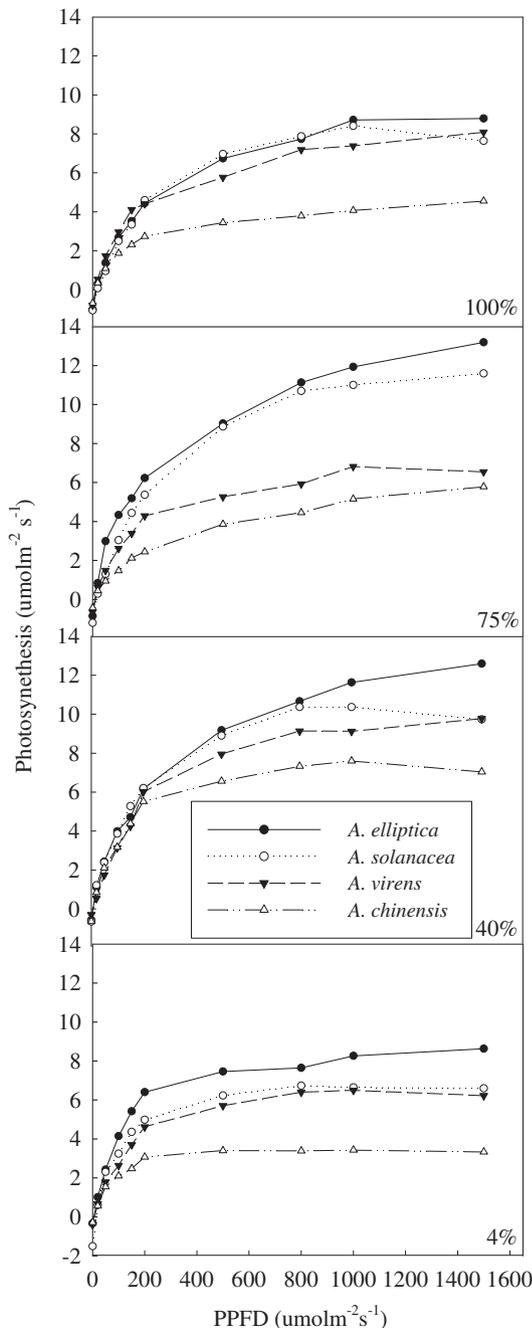


Fig. 1. Leaf photosynthetic rates of the four species grown under four irradiance treatments.

Table 1

Effects of species, irradiance and their interactions on each variable according to a two-way ANOVA (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. LSPT, light saturation points; LCPT, light compensation points; P_{max} , light-saturated photosynthetic rate; R_d , relatively low respiratory rate; RGR, relative growth rate; SLA, specific leaf area).

Variables	Source	Df	MS	F value	P value
LSPT ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Species	3	159,838.89	36.47	<0.0001
	Irradiance	3	118,638.89	27.07	<0.0001
	Species \times Irradiance	9	46,411.11	10.59	<0.0001
	Error	32	4382.29		
	Total	48			
LCPT ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Species	3	158.24	4.71	0.008
	Irradiance	3	311.88	9.28	<0.0001
	Species \times Irradiance	9	40.22	1.20	0.331
	Error	32	33.60		
	Total	48			
P_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Species	3	93.13	115.34	<0.0001
	Irradiance	3	43.92	54.40	<0.0001
	Species \times Irradiance	9	6.99	8.65	<0.0001
	Error	32	0.81		
	Total	48			
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Species	3	0.71	7.65	0.001
	Irradiance	3	0.33	3.54	0.026
	Species \times Irradiance	9	0.26	2.80	0.015
	Error	32	0.09		
	Total	48			
RGR ($\text{g g}^{-1} \text{d}^{-1}$)	Species	3	0.002	101.06	<0.0001
	Irradiance	3	0.000	14.81	<0.0001
	Species \times Irradiance	9	9.88E-005	6.14	<0.0001
	Error	144	1.61E-005		
	Total	160			
SLA ($\text{cm}^2 \text{g}^{-1}$)	Species	3	31,450.66	19.39	<0.0001
	Irradiance	3	76,236.52	47.01	<0.0001
	Species \times Irradiance	9	12,157.21	7.50	<0.0001
	Error	144	1621.87		
	Total	1			

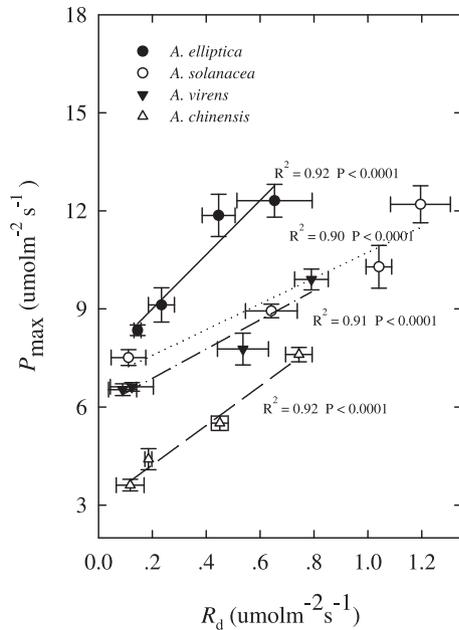


Fig. 2. Relationship between photosynthetic capacity and respiratory rate of four *Ardisia* species under four irradiance treatments. Each point is the mean of three individual plants grown at four irradiances (Mean \pm SE, $n = 3$).

lower LCPT and R_d among four *Ardisia* species (LCPT on average among four treatments of *A. elliptica*, *A. solanacea*, *A. virens* and *A. chinensis* are 6.11 ± 2.03 , 14.57 ± 2.97 , 5.78 ± 2.71 , 8.19 ± 2.17 , respectively ($P = 0.008$). R_d of these four species are 0.33 ± 0.12 , 0.84 ± 0.12 , 0.36 ± 0.12 , 0.34 ± 0.12 , respectively ($P = 0.001$)).

The positive linear relationship between P_{\max} and R_d for all species indicates a leaf-level tradeoff between increased P_{\max} and respiration cost (Fig. 2). However, the slope of the linear relationship of *A. elliptica* was significantly steeper than *A. virens* ($F = 1.788$, $P < 0.05$) and marginally steeper than *A. solanacea* ($F = 1.788$, $P = 0.33$) and *A. chinensis* ($F = 1.788$, $P = 0.14$).

3.2. Plasticity in photosynthetic capacity

Across all four species, irradiance and species influenced photosynthetic characteristics and RGR (Table 1). For *A. elliptica*,

A. solanacea and *A. chinensis*, LSPT increased continuously with the increase of irradiance and peaked at 75% irradiance (Fig. 3). For *A. virens*, LSPT was similar at four irradiances. P_{\max} of *A. elliptica* and *A. solanacea* peaked at 75% irradiance, but for *A. virens* and *A. chinensis*, P_{\max} peaked at 40% irradiance (Fig. 3). RGR of *A. elliptica* was similar among 40–100%, significantly higher than that at 5% irradiance; and for *A. solanacea* and *A. chinensis*, RGR was higher significantly at 40% than that at other three irradiances (Fig. 3). RGR of *A. virens* was not significantly influenced by irradiance.

3.3. Leaf herbivory level and leaf characteristics

For the plants grown under common garden conditions, *A. elliptica* suffered constant significant heavy herbivore damage compared to the three congeners in both 2005 and 2006 (Fig. 4). The leaf toughness of *A. elliptica* was significantly lower than *A. solanacea* and *A. chinensis* but not *A. virens* (Table 2). The leaf C content of the four species did not differ significantly while N content of *A. virens* was significantly higher than the other three species (Table 2).

4. Discussion

In this study, *A. elliptica* exhibited much greater photosynthetic capacity than the three congeners. *A. elliptica* showed higher RGR than its congeners except at 4% irradiance and it displayed higher LSPT, P_{\max} and SLA among the four species under four irradiances. *A. elliptica* also showed relatively higher LSPT and lower LCPT compared with its congeners except full sunlight.

The ability of plants to utilize light is an important determinant of their competitive ability and fitness (Chazdon et al., 1996). High photosynthetic rates have often been suggested as a characteristic shared by plant invaders (Baker, 1974; Bazzaz, 1979). High LSPT and P_{\max} are considered to be advantageous for invasive species (Baker, 1974; Bazzaz, 1979; Reich et al., 1997; Poorter, 1999; Shipley, 2006; Zheng et al., 2009). Low LCPT in the shade is advantageous because it may help maintain a positive carbon balance under low light levels (Boardman, 1977). High SLA also dictates lower carbon cost per unit photosynthetic area which benefits plants during invasion (Pammenter et al., 1986; Williams et al., 1995; Reich et al., 1997; Poorter, 1999; Shipley, 2006).

A significant advantage of *A. elliptica* is that it displays higher photosynthetic capacity under high-light conditions than

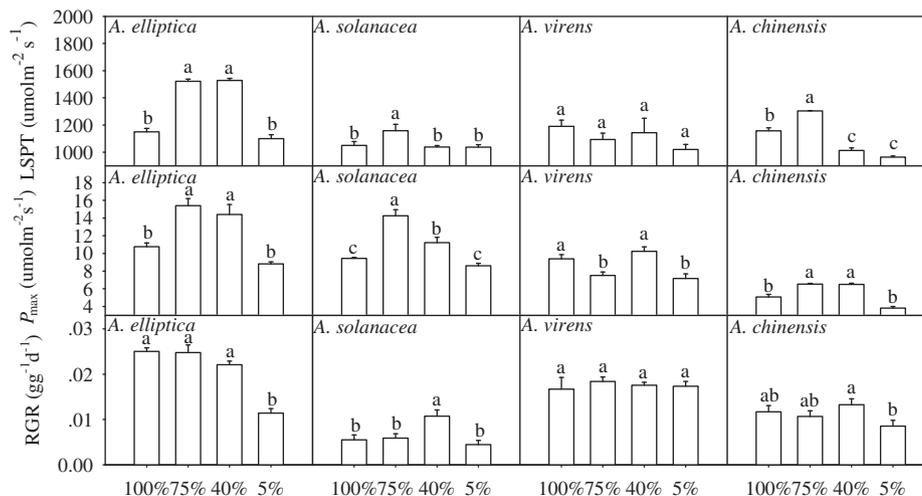


Fig. 3. LSPT, P_{\max} and RGR of four *Ardisia* species under four irradiance treatments. Bars indicate \pm SE ($n = 3$ for LSPT and P_{\max} , $n = 10$ for RGR). Different letters indicate significant differences ($P < 0.05$) among irradiances (LSPT, light saturation points; P_{\max} , light-saturated photosynthetic rate; RGR, relative growth rate).

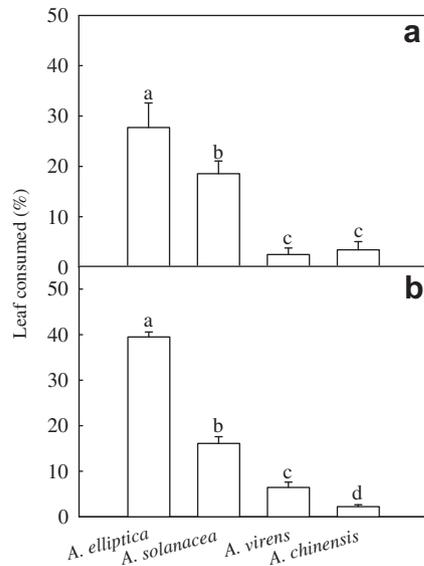


Fig. 4. The leaf area consumed by herbivore from different species in XTBG (a: data collected in 2005, b: data collected in 2006. Mean \pm SE, $n = 20$. Means with a common letter do not differ from other means of the same species ($P < 0.05$)).

congeners (Fig. 1), which is probably ascribed to its high LSPT and high P_{max} , low R_d . Therefore, *A. elliptica* appears to be more efficient at capturing and utilizing light than the other three congeners, particularly in high-light environments. In the present study, *A. elliptica*'s larger range of LSPT and P_{max} compared to its three congeners shows a greater ability to adjust its photosynthetic capacities across a wide range of light environments, indicating that physiological plasticity may be an important component in its invasion success. Physiological plasticity has been considered an important characteristic of invasive species by many studies (Baker, 1974; Williams et al., 1995; Schweitzer and Larson, 1999; Weber and D'Antonio, 1999; Daehler, 2003; Bossdorf et al., 2005; but see Gonzalez and Gianoli, 2004; Brock et al., 2005). Baker (1974) suggested that plasticity can create a "general purpose genotype" capable of invading multiple habitats and is therefore expected to be associated with invasiveness (see also Rice and Mack, 1991; Parker et al., 2003). More recently, Daehler (2003) reviewed studies comparing the plasticity of invasive plant species and native species and concluded that invasive species are generally more plastic and that greater phenotypic plasticity contributes to success as an invader (cf. Leger and Rice, 2003). A limitation of the empirical data supporting greater phenotypic plasticity in invasive species is that they come almost exclusively from comparisons of non-native invasive species with native species whose invasive potential is typically unknown (e.g., Baruch et al., 1985; Pattison et al., 1998; Baruch and Goldstein, 1999; Kolb and Alpert, 2003; Niinemets et al., 2003; also see references in Alpert et al., 2000; Daehler, 2003; but see Gerlach and Rice, 2003; Burns, 2004). Comparison of successful invaders with noninvasive congeners in their native

Table 2

Interspecific differences in leaf characteristics of four *Ardisia* species that were grown under common garden condition for the herbivore experiment (mean \pm SE, $n = 20$). Means showing the same letter are not significantly different ($P < 0.05$).

Species	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)	Toughness (mN)
<i>A. elliptica</i>	459.67 \pm 1.86 ^a	17.8233 \pm 0.59 ^a	3325.11 \pm 127.70 ^a
<i>A. solanacea</i>	472.67 \pm 10.48 ^a	14.8067 \pm 0.431 ^a	6224.78 \pm 300.02 ^b
<i>A. virens</i>	465.67 \pm 9.68 ^a	27.4567 \pm 1.89 ^b	4060.44 \pm 220.19 ^a
<i>A. chinensis</i>	480.67 \pm 7.06 ^a	16.39 \pm 0.33 ^a	6804.85 \pm 410.86 ^b

range would provide a more appropriate test for traits related to invasiveness.

It seems that high photosynthetic capacity and high plasticity alone could not provide a full explanation of invasive success as the invasive species are often not very dominating in their native range (DeWalt et al., 2004a). In our study, *A. elliptica* suffered constant significant heavy herbivore damage compared to the three congeners in both 2005 and 2006 (Fig. 4). At the same time, the leaf toughness of *A. elliptica* was significantly lower than *A. solanacea* and *A. chinensis* but not *A. virens* (Table 2). By comparing survival of larvae by fed different toughness leaves, it has been demonstrated that larvae performance better on soft leaf (Kawasaki et al., 2009). In addition, the leaf C content of the four species did not differ significantly, while N content of *A. virens* was significantly higher than the other three species (Table 2). Nitrogen is considered the most limiting macronutrient for insect herbivores (Mattson, 1980; White, 1993). Increases in foliar nitrogen concentrations have been linked with increased insect density, shorter development time, higher survival rates, and higher fecundity (Mattson, 1980; Cisneros and Godfrey, 2001; Stiling and Moon, 2005; Huberty and Denno, 2006). However, Koop (2003) found that *A. elliptica* experienced less damage by foliar herbivores compared with its native congeners in Florida. The results of our study suggest that *A. elliptica* in their native range may have higher growth rates than congeners as a consequence of more plasticity for photosynthetic capacities. However, herbivore pressure may affect potential growth rates in field conditions (Schierenbeck et al., 1994). This kind of pattern might be found in other invasive species but a sophisticated investigation is critically lacking (Durand and Goldstein, 2001; McDowell, 2002; Williams et al., 1995; DeWalt et al., 2004a). Compared with *A. elliptica*, its congeners also showed relatively more plastic for some leaf traits including RGR. Plasticity of these traits is likely to increase fitness in multiple environments (Burns and Winn, 2006). We speculate that these three congeners also have the potential to be invasive.

Our study was conducted in the XTBG arboretum which is not the same as the native habitats of the *Ardisia* species; the herbivore assembly also might not be the same. However, the differences in herbivores among the four species still could represent the degree of herbivores of the four species in their natural habitats.

Although to provide a full explanation to plant invasion requires a complete investigation on many factors including seed dispersal, susceptibility to herbivores, plant–soil relationships, plant architecture, phenology, genetics and life history characteristics, etc. Our results suggest that higher photosynthetic capacities and phenotypic plasticity coupled with escape from natural enemies may contribute to the invasion of *A. elliptica* in its introduced habitats especially in high-light disturbed habitats.

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