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Comparisons of growth, biomass allocation, and morphology of an invasive and two non-invasive varieties of *Bidens pilosa* in Taiwan

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ABSTRACT: Three varieties of *Bidens pilosa* are recorded in Taiwan, among them only *B. pilosa* var. *radiata* is considered an invasive plant, while *B. pilosa* var. *minor* and *B. pilosa* var. *pilosa* are naturalized in Taiwan. To identify traits making var. *radiata* spreading faster than the other two varieties in sympatric areas, we grew these three varieties in summer and in fall and compared their morphology and traits related to growth. We found that all three varieties grew faster in summer than in fall and var. *radiata* grew faster and accumulated more biomass than the other two varieties in summer but not in fall. Further analysis revealed that the proportion of shoot biomass allocating to axillary shoots might contribute to the aforementioned differences. Shoots of all three varieties were capable of producing adventitious roots. However, the growing angle of the lowest axillary shoots was significantly more horizontal in var. *radiata* than in the other two varieties and the secondary axillary shoots were only found in var. *radiata*. Accordingly, the axillary shoots of var. *radiata* would have greater opportunity to contact soil, produce adventitious roots and generate ramets than those of var. *minor* and var. *pilosa*. We concluded that more biomass allocating to axillary shoots and more horizontally-oriented axillary shoots were important traits contributing to the faster growth and better clonal growth potential of *B. pilosa* var. *radiata* than the other two varieties in Taiwan.

KEY WORDS: *Bidens pilosa*, Biomass allocation, Clonal growth, Invasive plant, Leaf character, Shoot allocation, Shoot architecture

INTRODUCTION

Invasive species often cause harmful impacts on biodiversity of ecosystems (Begon *et al.*, 1996) and affect regional economics and society. Thus, invasive biology has become an important subject not only in ecological study but also in economic research (Pimentel *et al.*, 2000). Identifying traits promoting invasiveness might help us finding ways to control and manage the invasive species and to prevent potential invaders being imported. Accordingly, effective action could be taken to reduce their negative effect.

Bidens pilosa L. var. *radiata* Sch. Bip., an annual or perennial herb belonging to Asteraceae, was first collected and documented in 1937 (Sherff, 1937) and recorded in Taiwan in 1984 (Peng *et al.*, 1998; Wu *et al.*, 2004). After its introduction into Taiwan, *B. pilosa* var. *radiata* has become one of the 20 most noxious plants in Taiwan (Chiang *et al.*, 2003). We aimed to understand what makes *B. pilosa* var. *radiata* become an invasive plant in Taiwan. Phylogenetically related plants often share more common traits and require more overlapping resource than unrelated plants (Goldberg, 1987; Rauschert and Shea, 2012). Thus, comparing traits between related invasive and non-invasive plants might be more informative in understanding what makes plants invasive. This approach has been used in many studies (McDowell, 2002; Feng and Fu, 2008; Feng *et al.*, 2008). Two additional varieties of *B. pilosa*, *B. pilosa* var. *minor* (Blume) Sherff and *B. pilosa* var. *pilosa* L., are also found in Taiwan (Peng *et al.*, 1998). Though *B. pilosa* var. *radiata* was introduced into Taiwan later than *B. pilosa* var. *minor* and *B. pilosa* var. *pilosa*, within 30 years, *B. pilosa* var. *radiata* has become a serious invasive plant and dominates over the other two varieties in Taiwan lowlands. So, the question is what makes *B. pilosa* var. *radiata* more dominant than the other two varieties in Taiwan lowlands.

Floral biology and the breeding systems of these three varieties had been studied and it was found that the invasive *B. pilosa* var. *radiata* was self-incompatible while the non-invasive varieties were self-compatible (Huang *et al.*, 2012; Huang and Kao, 2014). In addition to the breeding system, vegetative and life history traits might also play important roles in promoting invasiveness (Zheng *et al.*, 2009; Ordonez *et al.*, 2010; Scharfy *et al.*, 2011). Growth is one of the most relevant traits determining plant performance in the field. Plants have high growth rate would outcompete other sympatric species in resources uptake and become dominant. Many invasive plants were found growing faster and accumulating more biomass than non-invasive plants (Zheng *et al.*, 2009; van Kleunen *et al.*, 2010). Accordingly, traits related to growth are considered important in governing the invasiveness. For example, biomass allocation plays an important role in determining relative growth rate (RGR). It has been found that plants allocating more biomass to aboveground components (with higher shoot/root ratio) might have a higher RGR than those allocating more

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biomass to roots (Wagg *et al.*, 2011; Sorrell *et al.*, 2012). In aboveground components, leaf is the major organ in assimilating carbon for accumulating biomass. Therefore, specific leaf area (SLA = leaf area/leaf dry biomass) is an extremely important trait in regulation and control of plant functions such as carbon assimilation and carbon allocation. Plants with higher SLA would have larger assimilatory surfaces and hence increase the capacity to assimilate CO_2 for a given amount of resources invested in photosynthetic tissues (Lambers and Poorter, 1992; Baruch and Goldstein, 1999). Leaf area ratio (LAR = total leaf area/total plant dry biomass) is another trait affecting carbon assimilation of whole plant. Thus, these are the two major traits contributing to differences in plant growth (Westoby *et al.*, 2002; Wright *et al.*, 2004). Many studies have found significant differences in aforementioned leaf traits between sympatric invasive and non-invasive species, with invasive plants having higher SLA or having higher LAR than non-invasive ones (Pattison *et al.*, 1998; Baruch and Goldstein, 1999; Smith and Knapp, 2001; Hamilton *et al.*, 2005; Leishman *et al.*, 2007; Ordonez *et al.*, 2010; Osunkoya *et al.*, 2010; Scharfy *et al.*, 2011). Accordingly, in this study we compared vegetative aspects, including growth and related traits of these three varieties.

Plant architecture, including the degree of branch and branch angle, would affect light interception and hence might also play an important role in affecting plant growth. It was found that *B. pilosa* var. *radiata* has lateral branches, which can produce adventitious roots (Hsu and Kao, 2014). This ability allows *B. pilosa* var. *radiata* to expand rapidly when its lateral branches touch ground and produce adventitious roots. In a preliminary experiment, we observed that all three varieties of *B. pilosa* had lateral branches but their clonal growth ability seemed different. In addition to compare their ability in producing adventitious roots, in this study we also quantified the plants architecture of these three varieties to evaluate their potential differences in clonal growth.

The objective of this study was to find out the vegetative traits that make *B. pilosa* var. *radiata* more dominant than *B. pilosa* var. *minor* and *B. pilosa* var. *pilosa*. To achieve the objective, we grew the three varieties of *B. pilosa* in summer and in fall, respectively, and compared their vegetative growth, biomass allocation pattern, leaf characters (SLA and LAR), plant architecture and production of adventitious roots. We tested the following two hypotheses: (1) *B. pilosa* var. *radiata* allocates more biomass to shoot and has higher SLA and LAR thus grows faster and accumulates more biomass than the other two varieties during growth period, (2) *B. pilosa* var. *radiata*, with a different branching pattern, has higher clonal growth potential than the other two varieties.

MATERIALS and METHODS

Plant materials

Bidens pilosa L. (Asteraceae) is an annual or perennial herb with erect stems and opposite leaves. Three varieties of *B. pilosa*, *B. pilosa* var. *minor* (abbreviated as var. *minor*), *B. pilosa* var. *pilosa* (abbreviated as var. *pilosa*) and *B. pilosa* var. *radiata* (abbreviated as var. *radiata*), are distributed on roadsides and cultivated fields from low to middle elevations in Taiwan (Peng *et al.*, 1998). The most distinct traits differentiating the three varieties are their ray florets. All three varieties have disc florets, but only var. *radiata* and var. *minor* have ray florets on each capitulum, and the ray florets of var. *radiata* are usually longer than 10 mm, but those of var. *minor* are shorter than 8 mm (Peng *et al.*, 1998).

Seedlings, germinated from achenes collected from central Taiwan (23°26′ N, 120°37′ E, 500 m a.s.l.) where the three varieties growing sympatrically, were transplanted into 4L (18.5 cm×19.5 cm) pots and placed in a greenhouse of National Taiwan University. Six plants for each variety were planted in summer (from 16 June to 11 August, for 56 days) and in fall (from 25 September to 4 December, for 70 days) of 2009, respectively. We harvested plants before they set achenes.

Vegetative growth, biomass allocation and leaf characters

Stem heights and node numbers were measured twice a week after plants producing one to three pairs of leaves. The three varieties have opposite phyllotaxis hence grow two axillary shoots per node. Accordingly, the angles of two axillary shoots growing from the lowest node of main stem were measured on 11 August and 25 November, respectively. The relative growth rate of plant stem height (RGR_{ht}) was calculated as the stem height at harvest/grown days. Plants were dissected into roots, shoots and reproductive organ components at harvest. Shoots were further separated into main shoots and axillary shoots. Leaves growing on main shoots and on axillary shoots were excised and their leaf area was measured with a leaf area meter (Li-3000, Li-Cor, Lincoln, Nebraska, USA) immediately after harvest. Each plant component was dried in an oven at 80℃ over 48 hrs and then weighted. Plant dry weight (DW_{plant}), the relative growth rate of plant dry weight (RGR_{dw}) (= DW_{plant}/grown days), the fraction of biomass of each component (MR), leaf area ratio (LAR = total leaf area/DW_{plant}) and the specific leaf area (SLA = leaf area/leaf dry weight) were calculated. The biomass allocating to main shoots, primary and secondary axillary shoots were calculated as the ratio of biomass of each shoot component to total shoot biomass (the sum of main shoots, primary and secondary axillary shoots).

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Adventitious root

Shoots with two pairs of fully expended leaves were excised from plants with five to six nodes on main stems (n = 10) and immersed into flasks containing 400 ml water on 7 April, 2008. The ability of these shoots to produce adventitious roots was observed. Fifteen days after the treatment (22 April, 2008), the produced roots were harvested and their number and total length were counted and measured. In the following, these adventitious roots were dried in an oven at 80°C over 48 hrs and then their dry weight were measured.

Statistical analysis

Two way analysis of variance (ANOVA) was conducted (general linear model procedure of SAS, release 9.1, SAS Inst. Inc., USA) to determine whether variables were significantly different between two growing seasons and among the three varieties. The difference of adventitious roots among three varieties was analyzed by one way ANOVA. If the null hypothesis was rejected ($p < 0.05$) after the analysis of ANOVA, Student-Newman-Keuls test was used for multiple comparisons.

RESULTS

Vegetative growth and biomass allocation

The results of RGR, total leaf area (LA_{total}), biomass accumulation (DW_{plant}), LAR, biomass allocation (MR) and shoot/root ratio (S/R ratio) of the three varieties grown in summer and fall are presented in Table 1. Plants grown in summer had significantly higher RGR_{dw} than those grown in fall (Table 2). In addition, in comparison of the three varieties grown in summer, var. *radiata* accumulated significantly more biomass than var. *minor* and var. *pilosa* ($F_{2, 15} = 3.74$; $p < 0.05$) (Table 1). However, the three varieties had similar biomass accumulations in fall ($F_{2, 15} = 0.45$; $p = 0.64$) (Table 1).

Similar pattern of biomass allocation to vegetative components was found in these three varieties, with the highest biomass allocated to stems (MR_{stem}> 50% in summer and of 46.2% - 47.9% in fall), the least to roots (MR_{root} of 12.9% - 16.6% in summer and of 9.9% - 16.6% in fall), and intermediate to leaves (MR_{leaf} of 27.1% - 32.1% in summer and of 29.3% - 32.2% in fall) (Table 1). However, when plants grown in different seasons were compared, MR_{stem}, MR_{rep} and S/R ratio of summer-grown plants were significantly different from those of fall-grown plants (Table 2). In all three varieties, summer-grown plants had higher MR_{stem} than fall-grown ones, on the contrast, fall-grown plants had higher MR_{rep} and S/R ratio than summer-grown ones (Table 1). Comparing the biomass allocation among these three varieties at harvest, we found that var. *radiata* allocated proportionally less biomass to reproductive organ (lower MR_{rep}) and more biomass to root (higher MR_{root}) in both experiments (Table 1). Thus, the S/R ratios of var. *radiata* (5.1 in summer and 5.3 in fall) were lower than those of var. *minor* (6.9 in summer and 9.2 in fall) and var. *pilosa* (6.9 in summer and 7.6 in fall) (Table 1).

Table 1. Growth, leaf characters and biomass allocation of three varieties of ***Bidens pilosa***.

Variable	Variety		
	var. *radiata*	var. *minor*	var. *pilosa*
Summer			
RGR_{ht} (mm day^{-1})	12.1 ± 1.0	12.2 ± 0.6	13.5 ± 0.9
RGR_{dw} (mg day^{-1})	215.2 ± 6.7	195.2 ± 7.3	191.8 ± 5.5
LA_{total} (cm^2)	1677 ± 69	1841 ± 90	1479 ± 121
DW_{plant} (g)	12.1 ± 0.4	10.9 ± 0.4	10.7 ± 0.3
LAR (cm^2 g^{-1})	139.1 ± 4.1	168.5 ± 5.5	137.1 ± 9.2
MR_{root} (%)	16.6 ± 1.0	12.9 ± 0.7	13.0 ± 0.9
MR_{stem} (%)	51.2 ± 1.8	52.3 ± 0.8	57.5 ± 2.4
MR_{leaf} (%)	32.1 ± 1.3	31.1 ± 0.9	27.1 ± 1.8
MR_{rep} (%)	0.05 ± 0.04	3.7 ± 0.5	2.4 ± 1.2
S/R ratio	5.1 ± 0.4	6.9 ± 0.4	6.9 ± 0.7
Fall			
RGR_{ht} (mm day^{-1})	7.3 ± 0.8	5.1 ± 0.1	6.6 ± 0.5
RGR_{dw} (mg day^{-1})	139.2 ± 13.0	128.4 ± 8.9	142.0 ± 9.4
LA_{total} (cm^2)	1871 ± 162	2027 ± 134	1953 ± 103
DW_{plant} (g)	9.7 ± 0.9	9.0 ± 0.6	9.9 ± 0.7
LAR (cm^2 g^{-1})	193.9 ± 8.5	227.0 ± 12.2	198.7 ± 10.5
MR_{root} (%)	16.6 ± 1.7	9.9 ± 0.5	11.8 ± 0.7
MR_{stem} (%)	46.2 ± 2.1	47.9 ± 1.3	46.7 ± 1.6
MR_{leaf} (%)	32.2 ± 1.9	31.8 ± 1.2	29.3 ± 1.2
MR_{rep} (%)	5.0 ± 1.2	10.4 ± 1.1	12.2 ± 1.2
S/R ratio	5.3 ± 0.5	9.2 ± 0.6	7.6 ± 0.5

Relative growth rate in shoot height (RGR_{ht}), relative growth rate in dry weight (RGR_{dw}), total leaf area (LA_{total}), plant dry weight (DW_{plant}), the ratio of total leaf area to total plant dry weight (LAR), proportion of biomass allocation to root (MR_{root}), stem (MR_{stem}), leaf (MR_{leaf}) and to reproductive organ (MR_{rep}), and the ratio of aboveground biomass to root biomass (S/R ratio) (mean ± SE, n = 6) of three varieties of *Bidens pilosa* grown in summer and in fall of 2009.

Table 2. Effect of season or/and variety on growth, leaf characters and biomass allocation of ***Bidens pilosa***.

Variable	Season (df = 1)		Variety (df = 2)		Season×Variety (df = 2)	
	F	p	F	p	F	p
RGR_{ht} (mm day^{-1})	116.20	***	1.99	ns	1.67	ns
RGR_{dw} (mg day^{-1})	79.80	***	1.58	ns	1.14	ns
LA_{total} (cm^2)	8.87	**	1.86	ns	0.99	ns
DW_{plant} (g)	12.45	**	1.29	ns	0.90	ns
LAR (cm^2 g^{-1})	65.87	***	8.04	**	0.08	ns
MR_{root} (%)	2.92	ns	15.69	***	1.14	ns
MR_{stem} (%)	22.42	***	1.92	ns	2.03	ns
MR_{leaf} (%)	0.68	ns	4.26	*	0.27	ns
MR_{rep} (%)	75.88	***	14.41	***	3.08	ns
S/R ratio	5.74	*	15.08	***	2.34	ns

Results of two-way ANOVA for the effect of seasons (summer or fall), varieties (three varieties) and their interaction on relative growth rate in shoot height (RGR_{ht}), relative growth rate in dry weight (RGR_{dw}), total leaf area (LA_{total}), plant dry weight (DW_{plant}), the ratio of total leaf area to total plant dry weight (LAR), proportion of biomass allocation to root (MR_{root}), stem (MR_{stem}), leaf (MR_{leaf}) and to reproductive organ (MR_{rep}), and the ratio of aboveground biomass to root biomass (S/R ratio). (ns: not significant at $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.)

Shoot allocation and architecture

In both seasons, all three varieties grew primary axillary shoots but only *B. pilosa* var. *radiata* grew

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Table 3. Shoot biomass allocation of three varieties of ***Bidens pilosa*.**

Variable	Variety		
	var. *radiata*	var. *minor*	var. *pilosa*
Summer			
Main shoot (%)	48.6 ± 2.3	64.8 ± 3.4	64.3 ± 4.5
Primary axillary shoot (%)	50.6 ± 2.2	35.2 ± 3.4	35.7 ± 4.5
Secondary axillary shoot (%)	0.8 ± 0.7	0	0
Fall			
Main shoot (%)	28.8 ± 4.8	29.8 ± 2.0	28.8 ± 1.1
Primary axillary shoot (%)	65.9 ± 3.7	70.2 ± 2.0	71.2 ± 1.1
Secondary axillary shoot (%)	5.2 ± 2.0	0	0

The partition of shoot biomass allocating to main and axillary shoots (mean ± SE, $n = 6$) of three varieties of *Bidens pilosa* grown in summer and in fall of 2009.

secondary axillary shoots (Table 3). Grown in summer, var. *radiata* allocated similar biomass to main shoots and to axillary shoots (primary + secondary axillary shoots), but var. *minor* and var. *pilosa* allocated significantly more biomass to main shoots than to axillary shoots (Table 3). The difference in biomass allocation to main shoots and to axillary shoots among the three varieties grown in summer was not found in those grown in fall. Grown in fall, all three varieties allocated significantly more biomass to axillary shoots than to main shoots. Therefore, the patterns of biomass allocation to main shoots and secondary axillary shoots were significantly different between two growing seasons, among three varieties and had significant interaction between seasons and varieties (Table 4). But biomass allocation to primary axillary shoots only differed significantly between two seasons and had significant interaction between seasons and varieties (Table 4).

In both seasons, the branching angles of axillary shoots growing from the lowest nodes of main stems were significantly lower in var. *radiata* than in the other two varieties (summer: $F_{2, 15} = 11.47$, $p < 0.001$; fall: $F_{2, 15} = 65.60$, $p < 0.0001$) (Fig. 1).

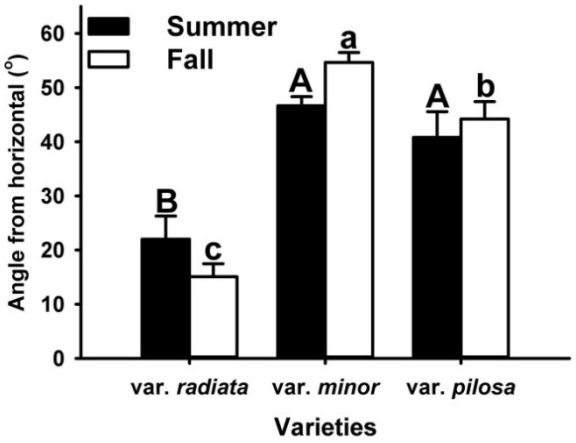


Fig. 1. Growing angles of the lowest axillary shoots of three varieties of ***Bidens pilosa***. The angle from the horizontal (mean ± SE, $n = 6$) of axillary shoots growing from the lowest node of three varieties of *Bidens pilosa* grown in summer (black bar) and in fall (open bar) of 2009. Black bars with different capital letters represent significant difference ($p < 0.05$) among the three varieties in summer, and open bars with different lower cases represent significant difference ($p < 0.05$) among the three varieties in fall.

Table 4. Effect of season or/and variety on shoot biomass allocation of ***Bidens pilosa***.

Variable	Season (*df* = 1)		Variety (*df* = 2)		Season×Variety (*df* = 2)	
	F	*P*	*F*	*P*	*F*	*P*
Main shoot (%)	123.70	***	4.13	*	3.65	*
Primary axillary shoot (%)	133.70	***	1.98	ns	7.17	**
Secondary axillary shoot (%)	4.20	*	8.07	**	4.20	*

Results of two-way ANOVA for the effect of seasons (summer or fall), varieties (three varieties) and their interaction on biomass allocation to main and axillary shoots. (ns: not significant at $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.)

Leaf characters

Summer-grown plants had less total leaf area (LA_{total}) than fall-grown ones. No significant difference was found in total leaf area among the three varieties (Table 1 and Table 2). LAR was significantly different between plants grown in two seasons and among the three varieties (Table 2). All three varieties had significant higher LAR in fall than in summer and var. *minor* had higher LAR than the other two varieties (Table 1 and Table 2).

Comparing leaves grown on main stems, summer-grown plants had more leaf area than fall-grown ones. Comparing leaves grown on axially shoots, fall-grown plants had more leaf area than summer-grown ones (Figure 2A, 2B and 2C). However, a different pattern of leaf area was found between the invasive and non-invasive varieties grown in summer. *B. pilosa* var. *radiata* had more leaf area on axillary shoots than on main stems (Figure 2A) while the other two varieties had more leaf area on main stems than on axillary shoots (Figure 2B and 2C). Among the three varieties only var. *radiata* produced secondary axillary shoots, accordingly, var. *radiata* is the only variety which had leaves on secondary axillary shoots.

SLA were significantly different between leaves of plants grown in two seasons, among the three varieties and among leaf positions (Figure 2D, 2E and 2F). Summer-grown plants had lower SLA than fall-grown ones ($F_{1, 65} = 211.31$; $p < 0.0001$), *B. pilosa* var. *radiata* had lower SLA than var. *minor* and var. *pilosa* ($F_{2, 65} = 31.68$; $p < 0.0001$), and leaves on main stems had lower SLA than those on axillary shoots ($F_{2, 65} = 53.57$; $p < 0.0001$).

The ability of producing adventitious roots

All three varieties were able to produce adventitious roots after their shoots were immersed into water. Shoot segments of var. *radiata* started to produce adventitious roots on 3rd to 4th day, var. *minor* on 4th to 10th day and var. *pilosa* on 4th to 8th day of treatments (Table 5). The biomass of adventitious roots was higher in var. *radiata* than in var. *minor* and var. *pilosa* after shoots immersed into water for 15 days. But no significant differences were found in the number of adventitious roots and total root lengths among the three varieties (Table 5).

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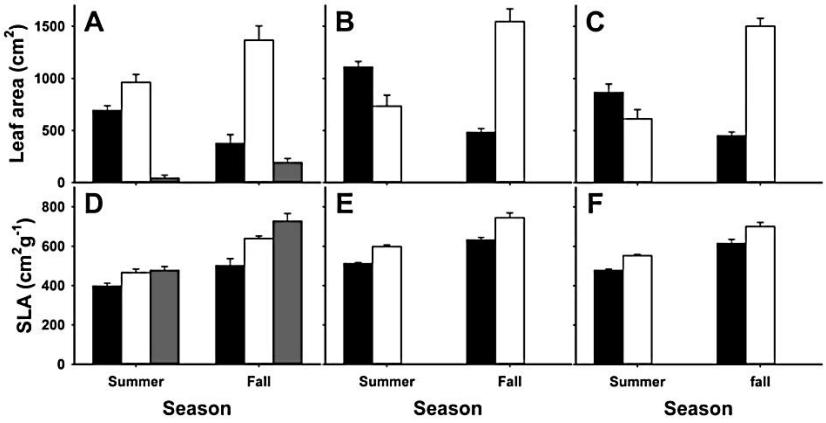


Fig. 2. Leaf area and SLA of three varieties of ***Bidens pilosa***. Leaf area (mean ± SE, *n* = 6) of leaves of var. ***radiata*** (**A**), var. ***minor*** (**B**) and var. ***pilosa*** (**C**) and specific leaf area (SLA) (mean ± SE, *n* = 6) of leaves of var. ***radiata*** (**D**), var. ***minor*** (**E**) and var. ***pilosa*** (**F**) on main stems (black bar), primary axillary shoots (open bar) and secondary axillary shoots (gray bar, which only found in var. *radiata*: *n* = 3 in summer and *n* = 4 in fall, respectively) of ***Bidens pilosa*** grown in summer and in fall of 2009.

Table 5. Production of adventitious root of three varieties of ***Bidens pilosa***.

Variable	Variety			*F*	*p*
	var. *radiata*	var. *minor*	var. *pilosa*		
Days	3.7 ±0.2[b]	5.5±0.6[a]	5.4±0.5[a]	4.68	*
Root number	16.2 ±1.7	12.6±2.1	14.9±1.2	1.12	ns
Total root length (cm)	241 ±25	148±25	198±32	2.85	ns
Total root dry weight (mg)	31.2 ±2.0[a]	17.3±2.4[b]	17.2±2.5[b]	12.34	***

Time for the shoots of the three varieties to produce adventitious roots after being immersed into water (days) and the number, total length and total dry weight of the produced adventitious roots (mean ± SE, *n* = 10) after the axillary shoots of three varieties of *Bidens pilosa* immersed into water for 15 days. The mean ± SE with different lower cases represent significant difference ($p < 0.05$) among the three varieties. (ns: not significant at $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$)

DISCUSSION

Results of this study showed that the three varieties grew faster in summer than in fall (Table 1). Light availability and temperature are two of the important environmental factors affecting plant growth. In Taiwan, the light intensity and air temperature were higher in summer than in fall (Central Weather Bureau, R.O.C.). Accordingly, the differential growth rate might be due to the differences in light availability and/or air temperature of the two seasons. Plants acclimated to low light availability showed increases in leaf area and SLA (Evans and Poorter, 2001; Feng, 2008). Less biomass, more leaf area (Table 1) and higher SLA (Figure 2) found in all three varieties grown in fall than in summer suggested that light availability is a limiting factor for these three varieties grown in fall.

In summer, the invasive var. *radiata* grew faster and accumulated more biomass than the other two varieties. However, this superiority of var. *radiata* over the other two varieties was not found in fall. In general, plants having higher shoot/root ratio would grow faster (Wagg *et al.*, 2011; Sorrell *et al.*, 2012). However, var. *radiata* had the lowest shoot/root ratio among the three varieties and had similar shoot/root ratio between fall and summer, which indicated that the ratio was not the main factor determining the difference in growth rate of the three varieties. LAR and SLA are also suggested as factors affecting plant growth (Westoby *et al.*, 2002; Wright *et al.*, 2004). In comparison to the other two varieties, var. *radiata* did not have higher LAR (Table 1) or SLA (Figure 2) than the other two varieties in summer. Thus, it is unlikely that difference in LAR or SLA contributes to the different growth rate of the three varieties. Photosynthetic rate is another factor that might affect the growth rate. However, in a preliminary experiment, we found that var. *radiata* did not have a higher photosynthetic rate than var. *pilosa* (unpublished data). Then, what could be the factor contributing to their differences in biomass accumulation in summer?

Differences found in the biomass allocation between main shoots and axillary shoots among the three varieties (Table 3) might explain their difference in biomass accumulation in summer. In summer, var. *radiata* allocated significantly more biomass to axillary shoots (Table 3) than the other two varieties. Allocating more biomass to axillary shoots and maintaining more horizontally oriented axillary shoots might help var. *radiata* in increasing light interception hence growing faster and accumulating more biomass than the other two varieties in summer. However, in fall all three varieties increased biomass allocation to axillary shoots and had similar proportion of biomass allocation to axillary shoots which might result in similar light interception among the three varieties. Thus, the advantage of higher light interception of var. *radiata* than the other two varieties in summer disappeared in fall. As a result, the three varieties accumulated similar biomass in fall.

The result that the growth superior of var. *radiata* to var. *minor* and var. *pilosa* was only expressed in summer but not in fall also implied that var. *radiata* would have growth advantage over var. *minor* and var. *pilosa* in habitats with warm and high irradiation conditions. The differential degree of invasiveness of the three varieties

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found in America and in Taiwan supports the implication. For example, var. *minor* and var. *pilosa* are the most invasive varieties in north America (Ballard, 1986; Grombone-Guaratini *et al.*, 2004), while the var. *radiata* is mainly distributed on coastal (Grombone-Guaratini *et al.*, 2004), moist tropical lowlands and eastern coast of Mexico (Ballard, 1986). In Taiwan, var. *minor* and var. *pilosa* are found distributed mainly in middle elevations, but var. *radiata* is an aggressive weed in lowland (Peng *et al.*, 1998; Huang *et al.*, 2015) and loses its dominance in middle elevations (Huang *et al.*, 2015).

Plants capable of clonal growth could develop into large interconnected network, quickly expand horizontally and efficiently colonize the surrounding areas. Accordingly, many invasive species were found having clonal growth ability (Yu *et al.*, 2009). For example, *Spartina anglica*, one of the most widespread and locally abundant invasive plants in North American, spread through clonal growth (Thompson, 1991). A review focusing on population biology of invasive plants also suggested that plant invasiveness was highly related to the ability of vegetative reproduction (Sakai *et al.*, 2001). In this study, we found that all three varieties can produce adventitious roots from shoots indicating their potential of vegetative reproduction. However, among the three varieties, only var. *radiata* had secondary axillary shoots. In addition, var. *radiata* had more horizontally oriented axillary shoots than the other two varieties. The more horizontally oriented axillary shoots would have better chance to contact soil than vertically oriented ones. The horizontally oriented primary axillary shoots would produce adventitious roots and become runners once contacting soil and the secondary axillary shoots would then turn into ramets. These results suggested that var. *radiata* has greater potential than the other two varieties to increase population size by clonal growth. Accordingly, the architecture of var. *radiata* also played an important role in helping the invasive variety increasing population size.

In conclusion, differences in the pattern of biomass allocation between main shoots and axillary shoots among the three varieties might explain the results that var. *radiata* accumulated significantly more biomass than the other two varieties in summer but not in fall. Though all three varieties were capable of producing adventitious roots from their shoots, the growing angle of the lowest axillary shoots was significantly more horizontal in var. *radiata* than in the other two varieties and the secondary axillary shoots were only found in var. *radiata* which conferred var. *radiata* better clonal growth potential than var. *minor* and var. *pilosa*. The aforementioned traits of var. *radiata* and the warm climate and high light intensity provided by the environment played important roles in var. *radiata*'s becoming dominant over the other two varieties and invasive in Taiwan.

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