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Research Article

Ipomoea batatas (sweet potato), a promising replacement control crop for the invasive alien plant *Ageratina adenophora* (Asteraceae) in China

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Abstract

Ipomoea batatas (L.) Lam has been recognized as a very competitive crop against certain farming weeds, but more information is required to support its potential field application. The current study utilized a de Wit replacement series incorporating five ratios of *I. batatas* and *Ageratina adenophora* (Spreng.) R. M. King and H. Rob plants in 9 m^2 plots in 2018. In monoculture, the main stem length, leafstalk length, leaf area, and biomass of *I. batatas* were significantly higher than those of *A. adenophora*. In mixed culture, the plant height, branch, leaf, and biomass of *A. adenophora* were significantly suppressed ($P < 0.05$) by *I. batatas*. The relative yield (RY) of *I. batatas* was significantly higher than 1.0, and the RY of *A. adenophora* was significantly less than 1.0 ($P < 0.05$) in mixed culture, indicating that the intraspecific competition was higher than interspecific competition for *I. batatas*, but the intraspecific competition was less than interspecific competition for *A. adenophora*. The competitive balance index of *I. batatas* demonstrated a higher competitive ability than *A. adenophora*. The net photosynthetic rate (Pn) of *I. batatas* and *A. adenophora* increased gradually from July to September, and then decreased from September to November in all treatments. The Pn of *I. batatas* was higher than that of *A. adenophora* in July and August, less than that of *A. adenophora* from September to November in monoculture, and the Pn of *A. adenophora* was significantly suppressed ($P < 0.05$) with increasing proportions of *I. batatas* in mixed culture after August. The activities of antioxidant enzymes superoxide dismutase, peroxidase and catalase for *A. adenophora* were significantly reduced ($P < 0.05$) with increasing proportions of *I. batatas* in mixed culture. Our results showed that plant growth of *A. adenophora* was significantly suppressed by *I. batatas* competition due to certain morphological and physiological advantages of *I. batatas*. Therefore, *I. batatas* is a promising replacement control candidate for managing the infestations of *A. adenophora*, reducing the soil seed bank and seedlings of *A. adenophora*.

Key words: weed-crop competition, integrated management, morphological suppression, photosynthesis, antioxidant enzymes

Introduction

Ageratina adenophora (Spreng.) R. M. King and H. Rob (Asteraceae), commonly known as crofton weed, is a perennial, semi-shrubby herbaceous plant. Native to Mexico and Costa Rica in Central America, it was purposely introduced into Europe, Australia and Asia as an ornamental plant in past centuries, and now has invaded more than 30 countries and regions (Gui et al. 2009; Wan et al. 2010; Inderjit et al. 2011). As an aggressive competitor, the weed can easily form dense stands that prevent the establishment of other plant species, owing to its rapid growth, abundant clonal growth and strong allelopathic profiles (Qiang 1998; Zheng and Feng 2005). In many areas it is a prevalent weed in both natural ecosystems and agroecosystems.

In China, *A. adenophora* was first introduced from Myanmar into the south Lincang of Yunnan Province in the 1940s (Gui et al. 2008). The weed has successfully invaded eight provinces or regions in China including Yunnan, Guizhou, Sichuan, Guangxi, Xizang, Chongqing, Hubei, and Taiwan, and continues to spread eastward and northward at a rate of 20 km per year (Qiang 1998; Lu and Ma 2004; Wang and Wang 2006). This weed has become one of the worst invasive alien plants in China (Xie et al. 2001). It may invade a variety of habitats, such as roadsides, forest edges, riverbanks, wastelands, crop fields, orchard lands, and other cash forest lands. *Ageratina adenophora* can inhabit a wide range of elevations and has caused tremendous economic losses to agriculture, forestry and livestock, and has severely damaged the ecology and environment of China's native habitats (Sun et al. 2004; Zhu et al. 2007). Furthermore, it is also associated with human and animal health issues, e.g. allergic reactions and acute asthma in response the weed's pollen in humans and consumption of this weed by livestock causing diarrhea, depilation, and even death (Zhu et al. 2007).

In order to manage the spread and damage of *A. adenophora*, extensive research has been recently conducted on chemical control, mechanical removal, biological control, and ecological control in China (Yang et al. 2017). However, due to its high capacity for both sexual and asexual reproduction and morphological plasticity, high compensation capacity, and rapid adaptive evolution (Feng 2008; Zheng et al. 2009), no single control method can effectively alleviate the damage caused by *A. adenophora*, and more comprehensive prevention and control measures must be adopted (Yang et al. 2017). Replacement control technology, utilizing plant competition, represents a promising component of a more holistic, integrated management strategy (Shen et al. 2015). In the past several decades, a large number of greenhouse and fields experiments were conducted to assess the competitive capacity of replacement plants against *A. adenophora* in China and found some suitable candidates of replacement plants (Yang et al. 2017). However, the competitive mechanisms between these replacement plants and *A. adenophora* have not been elucidated.

Ipomoea batatas (L.) Lam (Convolvulaceae), an important cash and food crop widely grown in China, was observed to inhibit farming weeds in the field and under laboratory conditions (Shen et al. 2014, 2015, 2016, 2017, 2018a, b), including *A. adenophora*. Native to the American tropics, *I. batatas* is the seventh most important crop world-wide and the fifth most important crop in developing nations (Jung et al. 2011). *Ipomoea batatas* has been recognized as a very competitive crop against certain weeds because of its rapid growth, rapid canopy formation, and its ability to reproduce asexually (Shen et al. 2014, 2015). This crop has excellent suppression on growth and reproduction ability of invasive plant *Mikania micrantha* Kunth and decreases significantly the density, frequency, and cover of some major farming weeds in Yunnan Province (Shen et al. 2014, 2015, 2016), but information on competition relationship of *I. batatas* and *A. adenophora* is lacking.

Based on excellent inhibition of *A. adenophora* by *I. batatas* seen in field observations, the main objective of this study was to examine the competitive mechanisms of growth, photosynthesis and antioxidant enzymes between *I. batatas* and *A. adenophora* in Yunnan Province, China, and provide a scientific basis for setting up an effective management method utilizing ecological control techniques for comprehensive management of *A. adenophora* in the field.

Materials and methods

Study site

The study site was located in Songming County (25°05′–25°28′N; 102°40′–103°20′E), Yunnan Province, Southwest China. This area is characterized by a subtropical and temperate monsoon climate. Rainfall averages 1000–1300 mm per year and the annual mean temperature is 14.1 °C. Recently, *A. adenophora* has become widely distributed in orchard lands, wastelands, roadsides, forest edges, and other disturbed ecosystems in Songming County (Shen et al. 2012).

Study species

Ageratina adenophora was first noticed invading Yunnan Province in China by way of Myanmar in the 1940s, and has become one of the worst invasive alien species in Yunnan Province, infesting an area of over 300,000 km^2 (Sang et al. 2010). It has invaded a variety of habitats, such as roadsides, forest edges, riverbanks, wastelands, crop fields, orchard lands, and other cash forest lands across a wide range of elevations in the province (Sun et al. 2004; Zhu et al. 2007). The seeds of *A. adenophora* were collected in 2016 and 2017, dried at room temperature for two months and then kept in the refrigerator at −4 °C.

Ipomoea batatas is one of the main food and cash crops in tropical and subtropical regions of Yunnan Province (Shen et al. 2015). This crop mainly reproduces through asexual means and is usually planted by clonal means utilizing 20–50 cm fragments with 3–5 nodes (Sihachakr et al. 1997). Since 2010, various *I. batatas* varieties have been collected and grown in the greenhouse of the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences to research the utility of *I. batatas* as a replacement control crop.

Experiment design and data collection

Based on previous field observation and a preliminary test in 2017, the study was formally conducted during the April–November growing season in 2018 at Experimental Base of the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, in Xiaojie Town, Songming County, utilizing a de Wit replacement series (de Wit 1960). The de Wit replacement series experiments have been extensively used in ecological studies of competition between two species of plants (or even for competition between insects), and serves both to detect the existence of and measure the magnitude of competition, as well as to find the combination of two species which maximizes the total yield of a mixture (Rodríguez 1997). Seeds of the invasive plant species *A. adenophora* and *I. batatas* tuberous roots were propagated in the greenhouse starting April 25th. On June 15th, one-node segments (fresh weight 2.0–2.5 g, 5–6 cm pieces) were taken from central stem portions of relatively young *I. batatas* plants, and then the segments were placed in Hoagland's solution (Hoagland and Arnon 1950) and grown for 5 days. On June 20th, the plant seedlings of *A. adenophora* and the sprouts derived from cuttings of *I. batatas* plants with similar height were selected and transplanted. Based on our previous studies on competition of *I. batatas* and *M. micrantha* (Shen et al. 2015) and field observation, five ratios of *I. batatas* and *A. adenophora* were utilized (4:0 = 180:0 plants, 2:1 = 120:60 plants, 1:1 = 90:90 plants, 1:2 = 60:120 plants, 0:4 = 0:180 plants) while maintaining a constant planting density of 20 plants m^{-2} (0.25 m × 0.20 m space). All plots were arranged in a complete randomized design with 4 replicates utilizing 9 m^2 plots (3 m × 3 m) for each ratio. All plants were distributed evenly within the plot. During the experiment, the plots were weeded by hand and no synthetic fertilizers were used.

From July to November, net photosynthetic rate (Pn) measurements on leaves for *I. batatas* and *A. adenophora* were conducted mid-month using a Portable Photosynthesis System (LI-COR LI6400XT), between 8:00 am and 11:30 am, with a 6400-02 or -02B LED source and 1000 μmol m^{-2} s^{-1} photosynthetically active radiation. During sampling, CO_2 concentration, air temperature and relative humidity (RH) in the chamber were under natural conditions. Measurements were made on a representative leaf randomly chosen on five to six randomly selected individuals of each species.

The experiment was terminated on 20 November 2018 after 153 days since the initial transplanting. Twenty plants of each species were selected randomly and harvested from the interior of each plot. Total shoot length, main stem length, branch number, leafstalk length, leaf area, and aboveground biomass were recorded. Leaves were clipped and passed through a leaf-area meter (Li-3000A; Li-Cor Corp.) to determine leaf area index. For enzyme extracts and assays, leaves were sampled from the two plant species. Leaves weighting 5–6 g were immediately frozen in liquid nitrogen after harvesting. The activities of antioxidant enzymes superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) of leaves were tested and analyzed in the laboratory at the Agricultural Environment and Resources Research Institute of Yunnan Academy of Agricultural Sciences.

Data analyses

Relative yield (RY) per plant (de Wit 1960), relative yield total (RYT) (Fowler 1982) and competitive balance index (CB) (Wilson 1988) were calculated from final biomass for each species in each plot. Relative yield per plant of species a or b (i.e., species a and b represented *I. batatas* and *A. adenophora*) in a mixed culture with species b or a was calculated as $RY_a = Y_{ab}/Y_a$ or $RY_b = Y_{ba}/Y_b$. Relative yield total was calculated as $RYT = (RY_{ab} + RY_{ba})/2$. Competitive balance index was calculated as $CB_a = In(RY_a/RY_b)$. Where Y_{ab} is the yield for species a growing with species b (g/individual), Y_{ba} is the yield for species b growing with species a, Y_a is the yield for species a growing in pure culture (g/individual), Y_b is the yield for species b growing in pure culture. Values of RY_{ab} measure the average performance of individuals in mixed cultures compared to that of individuals in pure cultures. An RY_{ab} of 1.00 indicates species a and b are both equal in terms of intraspecific competition and interspecific competition. An RY_{ab} greater than 1.00 means intraspecific competition of species a and b is higher than interspecific competition, and an RY_{ab} of less than 1.00 implies intraspecific competition of species a and b is less than interspecific competition. Relative yield total is the weighted sum of relative yields for the mixed culture components. An RYT of 1.00 means that both species are competing for the same resources, and one is potentially capable of excluding the other; an RYT of greater than 1.00 means that the two species exploit different resources and therefore do not compete (e.g., due to different root depths); finally, an RYT of less than 1.00 implies that the two species are mutually antagonistic, with both having a detrimental effect on the other (Fowler 1982). Values of CB_a greater than 0 indicate that species a is more competitive than species b (Wilson 1988).

All morphological (plant length, branch number, leaf area, leafstalk length, and biomass) and physiological (Pn, SOD, CAT, and POD) variables of *A. adenophora* and *I. batatas* plants were analyzed by analysis of variance (one-way ANOVA). If significant differences were detected with the ANOVA, Duncan's multiple range tests were used to detect differences among treatments at a 5% level of significance. Relative yield and

Table 1. Plant growth comparison of *Ipomoea batatas* and *Ageratina adenophora* under mono and mixed culture conditions.

Variables		Ratios (*I. batatas* : *A. adenophora*)				
		4:0	2:1	1:1	1:2	0:4
Total shoot length (cm)	*I. batatas*	99.51 ± 2.07d	104.82 ± 1.83c	108.36 ± 1.63b	115.60 ± 2.03a	–
	A. adenophora	–	99.92 ± 2.01d	128.73 ± 1.65c	170.21 ± 2.63b	195.84 ± 3.50a
Main stem length (cm)	*I. batatas*	68.84 ± 1.43d	70.59 ± 1.04c	73.23 ± 0.97b	77.63 ± 1.76a	–
	A. adenophora	–	38.17 ± 0.80d	43.28 ± 0.85c	50.95 ± 1.16b	64.56 ± 1.03a
Total branch length (cm)	*I. batatas*	30.67 ± 1.21c	34.23 ± 0.85b	35.13 ± 0.75b	37.97 ± 1.05a	–
	A. adenophora	–	61.75 ± 1.28d	85.45 ± 1.24c	119.26 ± 1.50b	131.28 ± 3.04a
Branch number	*I. batatas*	8.6 ± 0.2b	10.7 ± 0.1a	10.8 ± 0.3a	11.1 ± 0.4a	–
	A. adenophora	–	10.9 ± 0.4d	13.6 ± 0.9c	17.1 ± 0.3b	20.4 ± 0.7a
Leafstalk length (cm)	*I. batatas*	8.26 ± 0.34b	8.63 ± 0.36ab	9.02 ± 0.08a	9.03 ± 0.07a	–
	A. adenophora	–	2.91 ± 0.18d	3.87 ± 0.15c	4.64 ± 0.08b	5.99 ± 0.16a
Leaf area (cm^2)	*I. batatas*	54.75 ± 1.05c	55.21 ± 0.71bc	56.18 ± 0.74b	57.93 ± 0.70a	–
	A. adenophora	–	12.07 ± 0.40d	21.54 ± 0.84c	27.32 ± 0.94b	32.59 ± 1.29a
Total biomass (g)	*I. batatas*	48.45 ± 0.45d	50.19 ± 0.65c	52.17 ± 0.31b	53.44 ± 0.72a	–
	A. adenophora	–	13.09 ± 0.27d	19.43 ± 0.24c	28.04 ± 0.69b	32.91 ± 0.52a

Data are expressed as mean ± standard deviation. The different letters within same row mean significant differences at $P < 0.05$.

RYT from each mixed culture were compared to the value of 1.00 using t-tests ($P = 0.05$), and values of RYT were tested for deviation from 1.0 and values of CB for deviation from 0 using a paired t-test.

Results

Plant growth

The main stem length of *I. batatas* was higher than that of branch length of *I. batatas* and main stem length of *A. adenophora*, and the main stem length (except at a ratio of *I. batatas* to *A. adenophora* of 0:4) of *A. adenophora* was much lower than that of the branch length of *A. adenophora* in all treatments (Table 1). In mixed culture, the total shoot length (main stem + branch length), main stem length and branch length of *A. adenophora* were significantly suppressed ($P < 0.05$) with increasing proportions of *I. batatas*, and those of *I. batatas* were significantly higher with decreasing proportions of *I. batatas* (Table 1).

The branch number of *A. adenophora* was greater than that of *I. batatas* in monoculture (Table 1). In mixed culture, the branch number of *A. adenophora* was significantly suppressed ($P < 0.05$) with decreasing proportions of *A. adenophora*, and that of *I. batatas* was increased obviously with increasing proportions of *A. adenophora*. The leafstalk length and leaf area of *A. adenophora* were markedly less than those of *I. batatas* in all treatments (Table 1). In monoculture, the mean leafstalk length and leaf area of *I. batatas* were 8.26 cm and 54.75 cm^2, and those of *A. adenophora* were only 5.99 cm and 32.59 cm^2, respectively. In mixed culture, most leafstalk length and leaf area of *A. adenophora* averaged about less half that of *I. batatas*. The leafstalk length and leaf area of *A. adenophora* progressively declined ($P < 0.05$) with increasing proportions of *I. batatas*, and that of *I. batatas* was significantly increased with increasing proportions of *A. adenophora*.

Table 2. Relative yield (RY), relative yield total (RYT) and competitive balance (CB) index of *Ipomoea batatas* and *Ageratina adenophora* in mixed culture.

Variables	Ratios (*I. batatas* : *A. adenophora*)		
	2:1	1:1	1:2
I. batatas RY	1.04 ± 0.01c**	1.08 ± 0.01b**	1.10 ± 0.02a**
A. adenophora RY	0.40 ± 0.00c**	0.59 ± 0.02b**	0.85 ± 0.03a**
RYT	0.72 ± 0.00c**	0.83 ± 0.01b**	0.98 ± 0.03a**
CB index for *I. batatas*	0.96 ± 0.01a**	0.60 ± 0.02b**	0.26 ± 0.02c**

Data are expressed as mean ± standard deviation. The different letters within same row mean significant differences at $P < 0.05$. The t-test was used to compare each value with 1.0 and 0; * and ** indicate significant differences at 0.05 and 0.01 levels, respectively.

The total biomass of *I. batatas* was much greater than that of *A. adenophora* in all treatments. In monoculture, the total biomass of *I. batatas* was higher 1.47 times that of *A. adenophora* (Table 1). In mixed culture, the total biomass of *A. adenophora* was significantly suppressed ($P < 0.05$) with decreasing proportions of *A. adenophora*, whereas the biomass of *I. batatas* was markedly increased with increasing proportions of *A. adenophora*.

Competitive interactions

The RY of *I. batatas* and *A. adenophora* in different ratios showed that the two plants compete strongly (Table 2). The RY of *I. batatas* was significantly higher ($P < 0.05$) than 1.0, and the RY of *A. adenophora* was significantly less ($P < 0.05$) than 1.0 in mixed culture, showing that the intraspecific competition was higher than interspecific competition for *I. batatas*, but the intraspecific competition was less than its interspecific competition for *A. adenophora*. The RYT of *A. adenophora* and *I. batatas* was less than 1.0 in mixed culture (ranging from 0.72 to 0.98) indicating that there was competition between the two plants (Table 2). The CB index of *I. batatas* was greater than zero within all ratios in mixed culture, and the maximum CB index was 0.96. Thus, *I. batatas* has greater both intraspecific and interspecific competitive abilities than those of *A. adenophora*.

Photosynthesis and enzyme activities

Photosynthesis and enzyme characteristics varied significantly ($P < 0.05$) among different treatments corresponding to the five ratios of *I. batatas* and *A. adenophora* (Table 3 and Table 4). The Pn of *I. batatas* and *A. adenophora* increased gradually from July to September, then decreased from September to November in all treatments. The Pn of *I. batatas* in July and August was higher than that of *A. adenophora*, but less than that of *A. adenophora* in September, October and November in monoculture. In July, the Pn of *I. batatas* was significantly higher than that of *A. adenophora*, and there were not much different within treatments for each plant species. Since August, the Pn of *A. adenophora* was suppressed significantly ($P < 0.05$) with increasing proportions of *I. batatas*, and that of *I. batatas* was slightly increased with decreasing proportions of *I. batatas* in mixed culture (Table 3).

Table 3. Net photosynthetic rate (Pn) of *Ipomoea batatas* and *Ageratina adenophora* under mono and mixed culture conditions.

Variables		Ratios (*I. batatas* : *A. adenophora*)				
		4:0	2:1	1:1	1:2	0:4
July	*I. batatas* Pn (μmol CO_2 m^{-2} s^{-1})	11.32 ± 0.40a	11.13 ± 0.52a	11.24 ± 0.33a	11.37 ± 0.38a	–
	A. adenophora Pn (μmol CO_2 m^{-2} s^{-1})	–	8.19 ± 0.09a	8.18 ± 0.06a	8.22 ± 0.09a	8.28 ± 0.07a
August	*I. batatas* Pn (μmol CO_2 m^{-2} s^{-1})	13.43 ± 0.09b	13.74 ± 0.10a	13.84 ± 0.12a	13.81 ± 0.04a	–
	A. adenophora Pn (μmol CO_2 m^{-2} s^{-1})	–	8.97 ± 0.10d	10.07 ± 0.04c	10.88 ± 0.06b	11.26 ± 0.07a
September	*I. batatas* Pn (μmol CO_2 m^{-2} s^{-1})	13.54 ± 0.31a	13.80 ± 0.11a	13.84 ± 0.15a	13.83 ± 0.09a	–
	A. adenophora Pn (μmol CO_2 m^{-2} s^{-1})	–	9.42 ± 0.12d	10.46 ± 0.13c	12.70 ± 0.13b	14.25 ± 0.14a
October	*I. batatas* Pn (μmol CO_2 m^{-2} s^{-1})	11.89 ± 0.10b	12.16 ± 0.07a	12.13 ± 0.09a	12.11 ± 0.12a	–
	A. adenophora Pn (μmol CO_2 m^{-2} s^{-1})	–	7.80 ± 0.06d	8.46 ± 0.05c	8.64 ± 0.13b	13.41 ± 0.11a
November	*I. batatas* Pn (μmol CO_2 m^{-2} s^{-1})	7.49 ± 0.06a	7.51 ± 0.14a	7.52 ± 0.09a	7.43 ± 0.11a	–
	A. adenophora Pn (μmol CO_2 m^{-2} s^{-1})	–	7.21 ± 0.06c	7.37 ± 0.16b	7.46 ± 0.15b	10.34 ± 0.08a

Data are expressed as mean ± standard deviation. The different letters within same row mean significant differences at $P < 0.05$.

Table 4. Antioxidant enzymes superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) of *Ipomoea batatas* and *Ageratina adenophora* under mono and mixed culture conditions.

Variables		Ratios (*I. batatas* : *A. adenophora*)				
		4:0	2:1	1:1	1:2	0:4
SOD (U/g FW)	*I. batatas*	316.26 ± 3.22d	587.69 ± 3.65c	632.95 ± 3.75b	651.66 ± 5.37a	–
	A. adenophora	–	74.84 ± 2.14d	91.43 ± 1.04c	103.07 ± 1.40b	111.02 ± 4.36a
CAT (μmoL/min/g FW)	*I. batatas*	522.44 ± 1.60d	542.23 ± 1.81c	550.78 ± 1.94b	588.37 ± 5.24a	–
	A. adenophora	–	483.99 ± 1.55d	520.03 ± 2.37c	530.21 ± 2.74b	566.37 ± 4.59a
POD ($\triangle OD_{470}$/min/g FW)	*I. batatas*	782.44 ± 2.59d	807.75 ± 3.87c	821.88 ± 3.53b	854.77 ± 3.71a	–
	A. adenophora	–	339.35 ± 3.68d	417.63 ± 3.52c	525.04 ± 4.73b	630.90 ± 6.85a

Data are expressed as mean ± standard deviation. The different letters within same row mean significant differences at $P < 0.05$.

The antioxidant enzyme activities POD and SOD for *I. batatas* were significantly greater than those of *A. adenophora* whereas the CAT activities for *I. batatas* and *A. adenophora* were similar in all treatments (Table 4). In monoculture, the POD activity for *I. batatas* and *A. adenophora* was the greatest, next to CAT activity, and the lowest was SOD activity. In mixed culture, the activities of SOD, POD and CAT for *I. batatas* were significantly increased ($P < 0.05$) with decreasing proportions for *I. batatas*, and the activities of SOD, POD and CAT for *A. adenophora* were markedly suppressed with increasing proportions of *I. batatas* (Table 4).

Discussion

The current study found that morphological and physiological abilities of the invasive plant *A. adenophora* were significantly suppressed by *I. batatas* competition. A successful invasion of alien plants stems from competitive interactions between invasive alien species and native species of the resident communities, involving morphological, ecological and physiological characteristics of the invasive plants (Davidson et al. 2011; Qin et al. 2013). Because both invasive and native plants grow under the same environment and management conditions, the competitive relationship between two species is largely affected by plant density, initial plant size and resource availability (Jiang et al. 2008). Compared to local species, invasive plant species generally have competitive advantages such as higher N allocation to photosynthesis, higher specific leaf area, larger biomass, or more rapid relative growth rate (Lambers and Poorter 1992; Burns 2006; Feng 2008; Jiang et al. 2008). The invasive plant *A. adenophora* may possess such a competitive advantage over many crops and weeds due to its morphological and physiological characteristics, but these characteristics do not stand up to the superior attributes of *I. batatas*.

Competitive plants selected for replacement control should be easy to grow, have high economic value, and the ability to form a high canopy density within a short period of time (Yang et al. 2017). *Ipomoea batatas* is an annual or biennial cash and food crop that exhibits prolific asexual reproduction, rapid growth, and readily forms extensive canopies in farming systems (Shen et al. 2015). Although *I. batatas* is also an alien plant, the risk of invasiveness is very low because its high economic value has already led to its widespread cultivation and the fact it exhibits poor seed production ability or low levels of sexual reproduction in natural conditions. During interspecific competition, morphological characteristics (e.g., leaf shape) and biomass tend to be the most important measured indexes (Keddy et al. 2002; Jiang et al. 2008). Plant species with higher biomass, RY or CB index have stronger competitive ability and are more likely replace neighboring plants (Williams and McCarthy 2001). *Ipomoea batatas* exhibited greater competitive ability than *M. micrantha* and has been shown to suppress plant growth, soil nutrient absorption and reproductive ability of *M. micrantha* as well (Shen et al. 2015, 2016). In monoculture, the total biomass, biomass of adventitious root, leafstalk length, and leaf area of *I. batatas* were all higher than those of *M. micrantha,* and in mixed culture the plant height, branch, leaf, stem node, adventitious root, and biomass of *M. micrantha* were suppressed significantly (Shen et al. 2015). Similarly, this study found that although the total branch length and number of branches for *A. adenophora* were usually much greater than those of *I. batatas*, the main stem length, leafstalk length, leaf area, and biomass of *A. adenophora* tended to be less than those of *I. batatas* in all treatments. In mixed culture, the RY of *I. batatas* was greater than 1.0, and the RY, RYT and CB for *A. adenophora* were significantly less than 1.0, demonstrating that *I. batatas* has greater competitive ability than *A. adenophora*. Because the initial size differences between *I. batatas* and *A. adenophora* were relatively small and they were grown under similar conditions, differences we observed in the final biomass were due to competiveness and plant morphology.

In addition to strong competitive abilities, *I. batatas* was shown to have allelopathic effects on other plants. The extracts from leaves, stems and roots of *I. batatas* strongly inhibited other crops and weeds such as *Ageratum conyzoide* L, *Bidens pilosa* L, *Galinsoga parviflora* Cav, *M. micrantha*, and other species (Harrison and Peterson 1986; Chon and Boo 2005; Xuan et al. 2012; Shen et al. 2017, 2018a, b). Moreover, *I. batatas* was found to contain a large number of allelochemicals such as phenolic acids (Chon and Boo 2005). The large persistent soil seed bank, light sensitive seed germination, and rapid seedling growth of *A. adenophora* have significant implications for any prevention and control measures to deal with the spread of this weed (Li and Feng 2009; Wang et al. 2016). The competitive advantages of *I. batatas* such as rapid seedling growth, long leafstalk length, large leaf area, and allelochemicals released from leaves and roots may generally enable it to inhibit the germination of seeds in the soil seed bank and inhibit seedling growth of *A. adenophora*. Therefore, an optimum replacement control for heavy infestations of *A. adenophora* would be to plant *I. batatas* after *A. adenophora* was dug out and slashed.

In addition to changes in plant biomass and other morphological indicators, plants also respond to competition and changes in the growth environment via adopting various physiological strategies, such as changes in photosynthesis and physiological enzyme activity with different environmental conditions (Burns 2006; Zou et al. 2007; Feng 2008; Zheng et al. 2009). *Mikania micrantha* growth was significantly reduced by *Cuscuta campestris* Yuncker infection due to negative effects of the parasite on host photosynthesis (Shen et al. 2007). Leaf area provides a major index to measure growth condition and solar energy utilization efficiency of plants (Baldwin and Schmelz 1994). Greater specific leaf area may increase carbon assimilation due to greater leaf area production for a given investment in biomass (Lambers and Poorter 1992). The present study found that leaf area of *A. adenophora* was less than that of *I. batatas* in monoculture (only 60%), and the leaf area of *A. adenophora* was greatly reduced with increasing proportions of *I. batatas* in mixed culture. A previous study also showed that leaf area of *M. micrantha* was only 21% of that of *I. batatas* in monoculture, and 70–90% of *M. micrantha* stems and leaves were covered by *I. batatas*, greatly reducing *M. micrantha* biomass in mixed culture (Shen et al. 2015). Higher rates of photosynthesis connected to higher leaf area can lead to increased growth rates, biomass accumulation and overall production (Lambers and Poorter 1992). The Pn of *I. batatas* was higher than that of *A. adenophora* in July and August, less than that of *A. adenophora* from September to November in monoculture, and the Pn of *A. adenophora* was significantly suppressed with increasing proportions of *I. batatas* in mixed culture since August. Thus, larger leaf area and higher Pn of *I. batatas* in the initial seedling period could lead to its higher growth rate and more biomass accumulation in competition with *A. adenophora*.

Antioxidant enzymes are one of the important physiological strategies for plants to response environmental stresses. An increase in antioxidant enzyme activity can be considered an important defense strategy against oxidative stress (Shi et al. 2006). Oxidative stress can lead to inhibition of the photosynthesis and respiration processes and, thus, plant growth. The responses of antioxidant enzymes in the development of plant tolerance to extreme environments has been clearly demonstrated (Jiang and Huang 2001; Ara et al. 2013). *Mikania micrantha* plants infested by *Bemisia tabaci* Gennadius showed serious damages in enzymatic protective system since the activities of SOD and CAT were significantly decreased, resulting in a reduced ability to eliminate active oxygen (Zhang and Wen 2008). The activities of SOD and CAT in the leaves of *A. adenophora* in mixed culture were markedly higher than those in monoculture, when grown with *Chenopodium serotinum* L (Lei et al. 2014). However, our study found that SOD, CAT and POD enzyme activity levels for *A. adenophora* in monoculture were significantly higher than those in mixed culture. This was because the competitive ability of *A. adenophora* was higher than that of *C. serotinum*, but less than that of *I. batatas*. Moreover, the activities POD and SOD for *I. batatas* were significantly greater than those of *A. adenophora* and the CAT activities for *I. batatas* and *A. adenophora* were similar in all treatments. In mixed culture, the activities of SOD, POD and CAT for *I. batatas* were significantly increased with decreasing proportions of *I. batatas*, and the activities of SOD, POD and CAT for *A. adenophora* were markedly suppressed with increasing proportions of *I. batatas*. Thus, it is clear that *I. batatas* has higher plasticity to modify enzyme activities to its advantage via protection against oxidative stress, when in competition with *A. adenophora*.

Conclusions

These results suggest that the growth of *A. adenophora* seedlings is significantly inhibited by *I. batatas* competition. *Ipomoea batatas* shows stronger adjusting mechanisms in terms of morphological and physiological properties compared to *A. adenophora* at the seedling stage. Thus, planting *I. batatas* is a promising replacement technique for reducing infestations of *A. adenophora* in both agricultural and natural areas. Ecological control effects by *I. batatas* on the soil seed bank after mature *A. adenophora* are removed, as well as suppression of other reproductive characteristics of *A. adenophora* warrant further research.

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