

Research Article

Increased suppressive effect of *Ipomoea batatas* (sweet potato) on *Mikania micrantha* (mile-a-minute) under high fertilization levels

Shicai Shen^{1,#}, Gaofeng Xu¹, Yanxian Yang^{1,#}, Xiaofen Yu¹, Diyu Li¹, Shaosong Yang¹, Guimei Jin¹, Shufang Liu¹, David Roy Clements², Aidong Chen¹, Fudou Zhang^{1,*}, Xiaocheng Zhu³ and Leslie A. Weston³

¹Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, 650205 Kunming, Yunnan, China

²Biology Department, Trinity Western University, 7600 Glover Road, Langley, V2Y 1Y1 British Columbia, Canada

³Graham Centre for Agricultural Innovation, Charles Sturt University and NSW Department Primary Industries, Wagga Wagga, New South Wales 2678, Australia

Author e-mails: fdzh@vip.sina.com (FZ), shenshicai2011@aliyun.com (SS), xugaofeng1059@163.com (GX), yxyx99@163.com (YY), 2543757367@qq.com (XY), 504073481@qq.com (DL), yshaos@163.com (SY), jgmbly2006@126.com (GJ), lshufang80@163.com (SL), clements@twu.ca (DC), 15825288855@163.com (AC), XZhu@csu.edu.au (XC), leweston@csu.edu.au (LW)

[#]Shicai Shen and Yanxian Yang contributed equally to this work

*Corresponding author

Citation: Shen S, Xu G, Yang Y, Yu X, Li D, Yang S, Jin G, Liu S, Clements DR, Chen A, Zhang F, Zhu X, Weston LA (2020) Increased suppressive effect of *Ipomoea batatas* (sweet potato) on *Mikania micrantha* (mile-a-minute) under high fertilization levels. *Management of Biological Invasions* 11(3): 560–575, <https://doi.org/10.3391/mbi.2020.11.3.14>

Received: 15 December 2019

Accepted: 12 May 2020

Published: 13 July 2020

Handling editor: Anna Gazda

Thematic editor: Catherine Jarnevic

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Abstract

It has been demonstrated that *Ipomoea batatas* (L.) Lam (sweet potato) has greater soil nutrient absorption ability when grown in association with the invasive plant *Mikania micrantha* Kunth (mile-a-minute), but the competition interaction of the two plant species under different fertilization levels is not well characterized. The current study utilized a de Wit replacement series incorporating three ratios of *I. batatas* and *M. micrantha* densities and four different fertilizer levels in 16 m² plots. In mixed culture, the total shoot length, branch, leaf, and biomass of *M. micrantha* were significantly suppressed ($P < 0.05$) by *I. batatas*. With increasing fertilization, total shoot length, branch, leaf, and biomass of *I. batatas* and *M. micrantha* were significantly increased, but at a greater rate for *I. batatas* than for *M. micrantha*. Relative yield parameters demonstrated that intraspecific competition was less than interspecific competition and that *I. batatas* had a higher competitive ability than *M. micrantha* under different fertilization levels. Fertilization significantly impacted the photosynthetic rate (Pn) of these species in June and July, whereas density ratio had greater effect on Pn of both species in August and September. Growth rates of *I. batatas* were markedly higher than those of *M. micrantha* in July and August, but less than those of *M. micrantha* in June and September. The concentrations of soil organic matter, and available N, P, and K in *M. micrantha* infested soil were significantly greater ($P < 0.05$) than soils where *I. batatas* was grown in monoculture, and fertilization levels were reduced by the presence of *I. batatas* in mixed culture. With increased fertilization, soil nutrient absorption increased, at a greater rate for *I. batatas* than for *M. micrantha*. Our results demonstrated that *I. batatas* could gain greater competitive advantage from enriched fertilization levels than *M. micrantha*. If *I. batatas* is incorporated into cropping system rotations, optimal fertilizer levels could be designed using information from our study to produce high *I. batatas* yields in addition to the benefits of suppressing invasive plants like *M. micrantha*.

Key words: competitive interactions, growth suppression, net photosynthetic rate, soil nutrients

Introduction

Biological invasions have altered biogeographical distribution and caused serious economic damage, environmental problems, loss of biodiversity, and threatened ecosystem safety and human and animal biosecurity (Simberloff et al. 2013; Blackburn et al. 2014). Due to particular geographical features and recent rapid economic and societal development, China is now among the countries most affected by serious biological invasions (Xie et al. 2001). There are 488 invasive alien species present in China that have caused considerable economic losses, amounting to US\$14.5 billion annually (Xu et al. 2006, 2012). Therefore, there is an urgent need to develop better management techniques and measures for ecological control of invasive alien species.

Management of invasive alien plants through replacement control via planting beneficial plant species that displace invasives has been widely explored and applied in the past several decades. One promising option for reducing invasive populations is by planting competitive high value species such as local crops, cash crops or even native species (Sher et al. 2002; Jiang et al. 2008; Li et al. 2015; Shen et al. 2015a). Whereas traditional biocontrol generally involves attack on the invasive plant by pathogens or insects, replacement control takes advantage of superior growth qualities of particular plants in the suppression of exotic plants, while at the same time providing benefits to the health of the local ecosystem (Jiang et al. 2008; Li et al. 2015). This replacement control can be considered more sustainable both economically and ecologically compared to mechanical or chemical control methods (Jiang et al. 2008).

Mikania micrantha Kunth (Asteraceae), known as mile-a-minute, is a rapidly growing vine native to Central and South America listed among the top 10 worst weeds and 100 worst invasive species on a worldwide basis (Lowe et al. 2001; Zhang et al. 2004). Its adventive range includes tropical Asia, the Pacific Islands, the Indian Ocean Islands, and Florida, USA (Zhang et al. 2004; Manrique et al. 2011; Day et al. 2012, 2016). The range of habitats it invades include various agroecosystems and natural ecosystems (e.g., riparian areas and forests), as well as disturbed areas such as roadsides (Zhang et al. 2004; Shen et al. 2013). This invasion leads to economic losses, loss of biodiversity and various other environmental impacts such as reductions in native plant and animal populations and alteration of soil nutrient cycles and microbial communities (Zhang et al. 2004; Zan et al. 2000; Li et al. 2006a, b; Shen et al. 2015b). The unique biological characteristics of *M. micrantha*, including both sexual and asexual reproduction, adaptability, high capacity for compensation, and rapid growth (Lian et al. 2006; Wang et al. 2008; Shen et al. 2012) present serious challenges for land managers and scientists.

One promising replacement control alternative for managing the invasive *M. micrantha* recently reported in China is *Ipomoea batatas* (L.) Lam

(Convolvulaceae) (Shen et al. 2015a, 2016, 2018). *Ipomoea batatas* is a crop native to Central America that is currently grown widely, ranking seventh among worldwide food crops, and fifth in developing countries (Jung et al. 2011). The *I. batatas* vine is propagated vegetatively using stem cuttings or roots (Mohanraj and Sivasankar 2014). The growth pattern and niche of *I. batatas* is similar to that of *M. micrantha* as both grow as clambering vines (Shen et al. 2015a). When grown with *M. micrantha* as part of a cropping system, *I. batatas* has been observed to suppress the growth and reproduction of *M. micrantha* (Shen et al. 2015a, 2016). Specifically, *I. batatas* was found to produce greater total biomass, adventitious root biomass, leafstalk length and leaf area than *M. micrantha* in monoculture, and this superior growth resulted in the suppression of *M. micrantha* by *I. batatas* in terms of its stem length, adventitious roots, branches, stem nodes, leaf area and biomass (Shen et al. 2015a). Moreover, *I. batatas* utilises soil resources more efficiently than *M. micrantha* when the plants are grown together (Shen et al. 2015a). However, the competitive interactions of *I. batatas* and *M. micrantha* under different fertilization levels are not well defined.

Building on previous studies (Shen et al. 2015a, 2016), the current research examined the influence of fertilization levels on competitive and physiological interactions of *I. batatas* and *M. micrantha* in Yunnan Province, China. Our approach was to utilize a de Wit replacement series, growing *M. micrantha* and *I. batatas* together, varying the densities of each. De Wit replacement series are useful for studying competition between two plant species, and are capable of evaluating the nature of the competition between competitors (Rodríguez 1997). The objectives of the study were to further elucidate the mechanisms of competition between *I. batatas* and *M. micrantha* under different fertilization levels and explore more sustainable management methods for *M. micrantha* in fields utilizing competitive crops.

Materials and methods

Study site

The study was conducted at the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, located in Xiaojie Town, in Songming County (25°05'–25°28'N; 102°40'–103°20'E), Yunnan Province, Southwest China. The climate is referred to as subtropical and temperate monsoon. The mean annual temperature is 14.1 °C with an average rainfall of 1000–1300 mm per year (Shen et al. 2019a). The experiment site (25°21'N; 103°06'E) is generally in a maize-wheat rotation and no herbicide was used in the previous crop. The elevation is 1920 m and the mean annual rainfall is 697 mm.

Study species

The invasive species, *M. micrantha* is widely distributed in in Dehong Prefecture, Baoshan District and Lincang District of Yunnan Province, both in subtropical and tropical areas (Shen et al. 2013). It was considered a prevalent weed in both natural ecosystems and agroecosystems (Zhang et al. 2004) and has infested a variety of habitats, such as roadsides, forest edges, riverbanks, wastelands, crop fields, orchard lands, and other cash forest lands in the province (Shen et al. 2013). *Mikania micrantha* plants were collected for experimentation from a population in Longchuan County, Dehong Prefecture and maintained in the Agricultural Environment and Resource Research Institute greenhouse of the Yunnan Academy of Agricultural Sciences, China.

In Yunnan Province, *I. batatas* is a major food and cash crop throughout many different growing areas, ranging from temperate to tropical (Shen et al. 2015a). Like *M. micrantha*, *I. batatas* has been collected and propagated in the Agricultural Environment and Resource Research Institute greenhouse, since 2010.

Experiment design and data collection

We separately set up a de Wit replacement series (de Wit 1960) in 2017 and 2018 during the same growing period but different sites at the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences in Songming County. To provide comparability of the data obtained in different years and at different sites, the two experiment sites were just 100–150 m apart, with nearly identical soil and climatic conditions. Moreover, the farming systems (the cropping, irrigation system and management process) were the same at both sites because of the uniform management rules at the YAAS Institute in Songming County.

On May 10, one-node segments (fresh weight 2.0–2.5 g, 5–6 cm pieces) were taken from central stem portions of relatively young plants, for both *I. batatas* and *M. micrantha* greenhouse propagated plants. For 10 days, the segments were immersed in Hoagland's solution (Hoagland and Arnon 1938). Subsequently resulting sprouts with similar height were selected and transplanted into 16 m² plots (4 m × 4 m). A combination of three ratios of *I. batatas* and *M. micrantha* plants were studied in the following ratios: 1:0 (320:0 plants), 1:1 (160:160 plants), and 0:1 (0:320 plants) at four different fertility levels (0, 75, 150, 225 kg/ha). In each treatment, a total of 320 plants were grown at three ratios of *I. batatas* and *M. micrantha* while maintaining a constant planting of 20 plants m⁻² (0.25 m × 0.20 m space) in each plot. All plants were distributed uniformly within the plot. Fifteen days after transplanting on May 20th, the four fertilization regimes (0, 75, 150, 225 kg/ha) from compound fertilizer (15% N, 15% P₂O₅, 15% K₂O) were applied only once (on June 4th). All plots were arranged in a complete randomized block

design with four replicates per ratio and per fertilization level (total $n = 4$ replicates \times 3 ratios \times 4 fertilization levels = 48). A 1.5 m border was constructed between plots and each plot was fenced with 0.35 m high glass panels to prevent the plants from climbing beyond the plots.

From June to September, from leaves of both *I. batatas* and *M. micrantha*, net photosynthetic rate (Pn) readings were taken mid-month, between 8:00 and 11:30 am, via a Portable Photosynthesis System (LI-COR Biosciences LI6400XT, Lincoln, Nebraska, USA) with a 6400-02 or -02B LED source and 1000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ photosynthetically active radiation. Observations were also made of the CO_2 concentration in surrounding air, air temperature and relative humidity (RH) in the chamber, at the same time photosynthetic readings were made. Photosynthetic readings were taken from 3–4 representative young leaves (as the top third leaf, top fourth leaf, top fifth leaf or top sixth leaf) chosen randomly from 15 individuals of each species per plot.

The experiment was terminated on September 25, 128 days after transplanting. Measurements were taken from twenty plants of each species that were randomly selected from the interior of each plot and harvested. Recorded parameters were: main stem length, branch length (total branch length not including the main stem), branch number, leafstalk length, leaf area, and aboveground biomass (fresh weight). Total shoot length was calculated as main stem length plus branch length. A leaf-area meter (Li-3000A; LI-COR Biosciences Lincoln, Nebraska, USA) was used to acquire the leaf area index for each of the sampled plants.

Prior to the experiment, twenty soil samples (0–10 cm) were taken randomly at the site, and mixed to provide a composite sample. This procedure was replicated four times and used as a control to benchmark soil contents prior to evaluation of plant fertilization impacts on the experimental plants. To examine the interaction effects of the two plant species on soil characteristics under different fertilization levels, twenty random soil sampling points 0–10 cm in depth were collected from each plot, and soil samples from each plot were mixed and treated as one composite sample. All soils were transported to the laboratory under cooled conditions as soon as possible, where they were removed litter and organic matter (including the roots and skeleton), grounded, sifted through a 2 mm sieve, and then air-dried at room temperature for analysis of soil chemical characteristics. Soil analysis was conducted at the Soil Analysis and Detection Center of the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, China. The parameters evaluated were pH, soil organic matter, available N, available P, and available K.

Data analyses

A one-way ANOVA using sites and years as factors was performed to test if year and site had a significant impact on the experiment. No significant year and site effect was found among all data ($P > 0.05$), therefore data were

Table 1. Two-way ANOVA results of effects of density ratio, fertilization level and their interaction on plant growth of *I. batatas* and *M. micrantha*.

Variables		Fertilization level		Density ratio		Interaction	
		F value	Partial eta squared	F value	Partial eta squared	F value	Partial eta squared
Total shoot Length (cm)	<i>I. batatas</i>	1420.744**	0.994	717.795**	0.968	10.995**	0.579
	<i>M. micrantha</i>	287.322**	0.973	9633.687**	0.998	28.753**	0.782
Main stem length (cm)	<i>I. batatas</i>	727.151**	0.989	1316.849**	0.982	23.853**	0.749
	<i>M. micrantha</i>	17.940**	0.692	4411.283**	0.995	8.896**	0.527
Total branch length (cm)	<i>I. batatas</i>	1157.045**	0.993	69.948**	0.745	0.534 ^{ns}	0.063
	<i>M. micrantha</i>	352.687**	0.978	5267.726**	0.995	22.349**	0.736
Branch number	<i>I. batatas</i>	791.437**	0.990	116.571**	0.829	7.950**	0.498
	<i>M. micrantha</i>	76.790**	0.906	1126.838**	0.979	0.229 ^{ns}	0.028
Leafstalk length (cm)	<i>I. batatas</i>	365.456**	0.979	644.208**	0.964	8.799**	0.524
	<i>M. micrantha</i>	8.804**	0.524	428.881**	0.947	2.694 ^{ns}	0.252
Leaf area (cm ²)	<i>I. batatas</i>	916.374**	0.991	653.763**	0.965	8.112**	0.503
	<i>M. micrantha</i>	34.726**	0.813	3307.924**	0.993	0.955 ^{ns}	0.107
Aboveground weight (g)	<i>I. batatas</i>	2236.420**	0.996	15177.484**	0.998	37.960**	0.826
	<i>M. micrantha</i>	61.940**	0.886	84368.120**	1.000	22.354**	0.736

ns, * and ** indicate $P > 0.05$, $P \leq 0.05$ and $P \leq 0.01$, respectively.

combined across the growing years and site. Relative yield (RY) per plant, relative yield total (RYT) and competitive balance index (CB) 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 *M. micrantha* and *I. batatas* in a mixed culture with species b or a calculated as $RY_a = Y_{ab}/Y_a$ or $RY_b = Y_{ba}/Y_b$ (de Wit 1960). Relative yield total was calculated as $RYT = (RY_{ab} + RY_{ba})/2$ (Fowler 1982). Competitive balance index was calculated as $CB_a = \ln(RY_a/RY_b)$ (Wilson 1988). Soil property parameters (pH, soil organic matter, available N, available P, and available K) and morphological variables (total shoot length, branch number, leaf area, leafstalk length, and biomass), as well as photosynthetic rate (Pn) of *M. micrantha* and *I. batatas* plants, as rates changed over time, were analyzed by analysis of variance (two-way ANOVA) using IBM SPSS 23.0 software (Armonk, New York, USA). The F and partial eta squared statistics were calculated considering density ratio and fertilization level with their interaction as factors (5% significance level). T-tests ($P = 0.05$) were used to compare relative yield and RYT to 1.00 from cultures with *M. micrantha* and *I. batatas* growing together. RYT values were also tested for deviation from 1.0, and the deviation of CB values from 0 were tested via a paired t-test.

Results

Plant growth

Significant interaction effects ($P < 0.01$) were obtained between density ratio and fertilization level for total shoot length, main stem length and total branch length of *I. batatas* and *M. micrantha* (Table 1). Total shoot length in both species was affected by density ratio and fertilization level, with *I. batatas* most affected by fertilization level and *M. micrantha* most affected by density ratio. *Ipomoea batatas* had longer main stems and *M. micrantha*

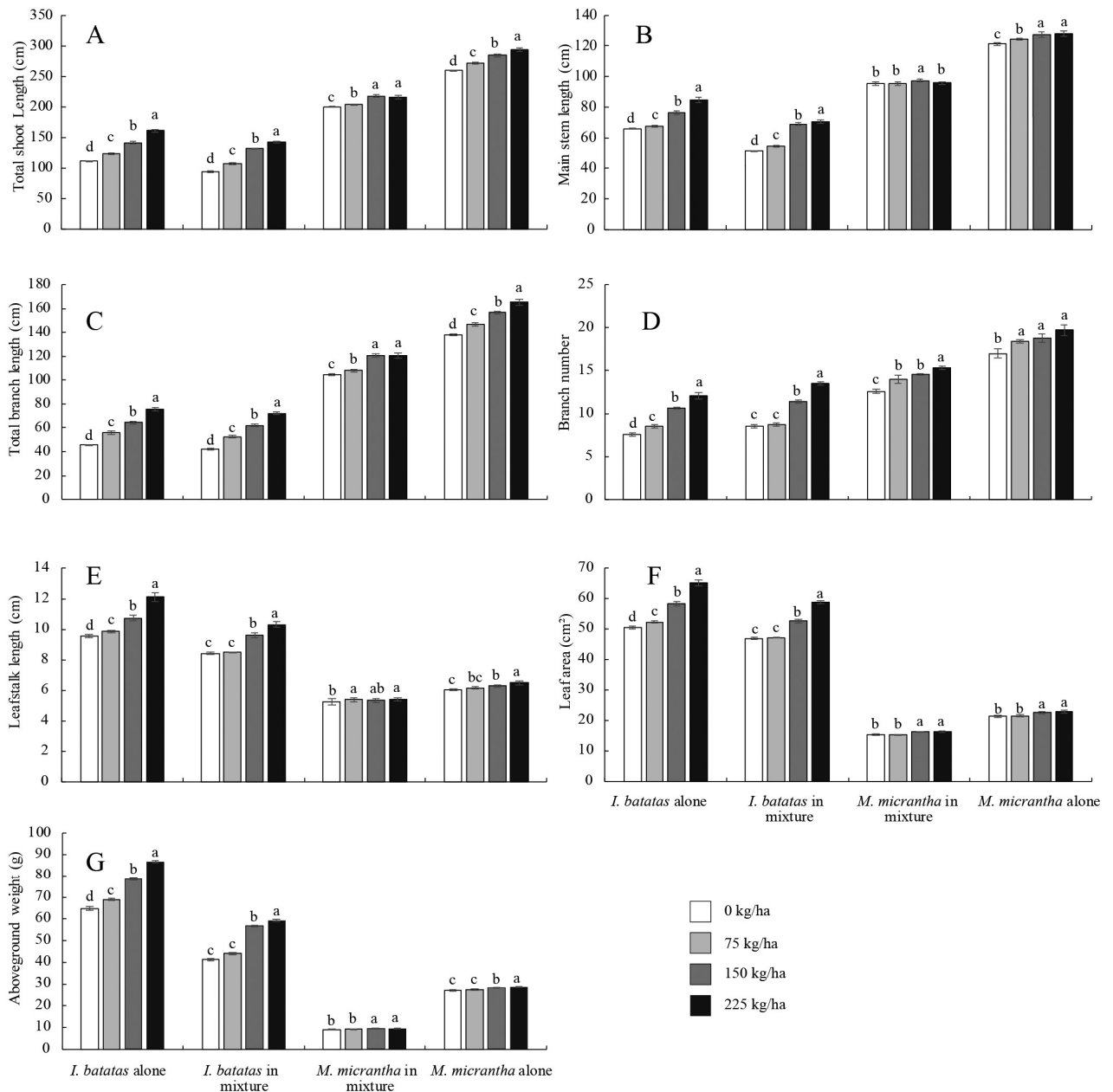


Figure 1. Plant growth comparison of *I. batatas* and *M. micrantha* looking at total shoot length (A), main stem length (B), total branch length (C), branch number (D), leafstalk length (E), leaf area (F), and aboveground biomass (G) under different density ratios and fertilization levels. Different letters represent significant differences at $p < 0.05$.

longer branches (Figure 1A–C). The main stem length of *I. batatas* was much greater than that branch length of *I. batatas* (except at fertilization level 225 kg/ha) among mono and mixed cultures. When grown together, *M. micrantha* total shoot length (main stem + branch length) was reduced significantly by 23–26% ($P < 0.05$), much more than the 7–16% reduction seen in the same parameters for *I. batatas* (Figure 1A–C). Increasing fertilization levels produced increases in the length parameters for both species, but this occurred at a greater rate for *I. batatas* than for *M. micrantha*.

There were no significant interactions between fertilization level and density ratio on branch number, leafstalk length and leaf area of *M. micrantha*, contrary to the pattern seen in *I. batatas* (Table 1). Density ratio and fertilization

Table 2. Relative yield (RY), relative yield total (RYT) and competitive balance (CB) index of *I. batatas* and *M. micrantha* in mixed culture.

Fertilization level (kg/ha)	<i>I. batatas</i> RY	<i>M. micrantha</i> RY	RYT	CB index for <i>I. batatas</i>
0	0.637 ± 0.015c**	0.338 ± 0.006a**	0.488 ± 0.007c**	0.635 ± 0.032c**
75	0.638 ± 0.007c**	0.337 ± 0.007a**	0.488 ± 0.001c**	0.637 ± 0.031c**
150	0.723 ± 0.009a**	0.335 ± 0.003a**	0.529 ± 0.005a**	0.768 ± 0.013a**
225	0.683 ± 0.008b**	0.332 ± 0.003a**	0.508 ± 0.004b**	0.722 ± 0.016b**

Data are expressed as mean ± standard deviation. The different letters within the same column signify 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.

level had a significant effect on branch number and leaf area for both species, fertilization level had greater effect on branch and leaf area of *I. batatas*, and density ratio had higher effect on branch and leaf area of *M. micrantha*. The branch number of *M. micrantha* was higher than that of *I. batatas* (except at fertilization level 225 kg/ha) in all treatments (Figure 1D). In mixed culture, the branch number of *M. micrantha* was significantly suppressed ($P < 0.05$), and the branch number of *I. batatas* was noticeably increased. The leafstalk length and leaf area of *M. micrantha* were markedly less than those of *I. batatas* (Figure 1E–F). In mixed culture, the leafstalk length and leaf area of *M. micrantha* progressively declined ($P < 0.05$), and the inhibition rates were higher than those of *I. batatas*. With proportional increases in fertilization levels, the branch number, leafstalk length and leaf area of *I. batatas* and *M. micrantha* were significantly increased ($P < 0.05$), and the growth rates of *I. batatas* were higher than those of *M. micrantha*.

Aboveground biomass of both species varied significantly with density ratio and fertilization level, and also there was a significant interaction effect ($P < 0.01$) (Table 1). Over all treatments, *I. batatas* exhibited greater aboveground biomass. When grown together, *M. micrantha* biomass was significantly reduced ($P < 0.05$), and these reductions were much greater than the reductions observed for *I. batatas* when grown with *M. micrantha* (Figure 1G). With proportional increases in fertilization levels, the aboveground biomass of *I. batatas* and *M. micrantha* was significantly increased ($P < 0.05$), at a greater rate for *I. batatas* than for *M. micrantha*.

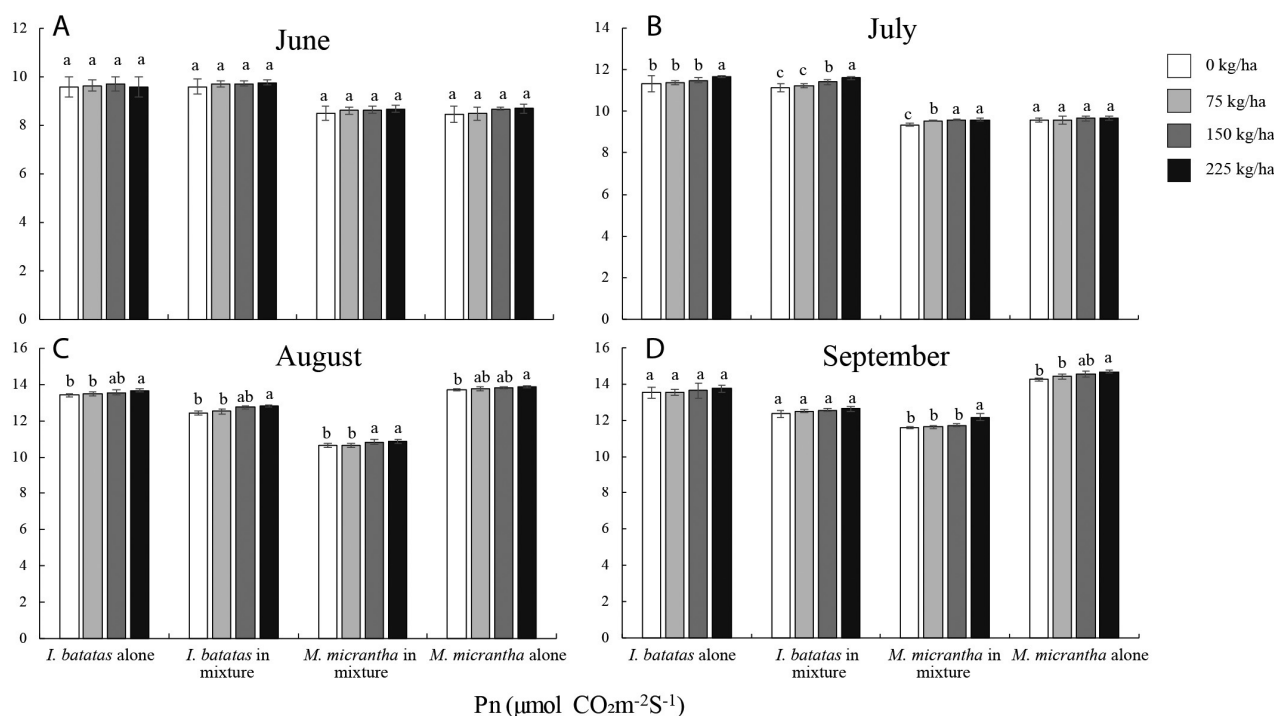
Competitive interactions

Intraspecific competition between *I. batatas* and *M. micrantha* was less than interspecific competition across different fertilization levels, as indicated by an RY value significantly less ($P < 0.05$) than 1.0 for the two species grown together (Table 2). Competition between the two plants was signified by an RYT below 1.0 when grown together (varying from 0.488 to 0.529). Also in mixed culture, the CB index of *I. batatas* was above zero and the maximum CB index was 0.768. With proportional increases in fertilization levels, the RY, RYT and CB of *I. batatas* significantly increased ($P < 0.05$), and the RY of *M. micrantha* gradually declined.

Table 3. Two-way ANOVA results of effects of density ratio, fertilization level and their interaction on net photosynthetic rate (Pn) of *I. batatas* and *M. micrantha*.

Variables	Fertilization level		Density ratio		Interaction	
	F value	Partial eta squared	F value	Partial eta squared	F value	Partial eta squared
June <i>I. batatas</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.312 ^{ns}	0.037	0.500 ^{ns}	0.020	0.198 ^{ns}	0.024
June <i>M. micrantha</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1.704 ^{ns}	0.176	0.112 ^{ns}	0.005	0.212 ^{ns}	0.026
July <i>I. batatas</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	8.507**	0.515	3.147 ^{ns}	0.116	0.277 ^{ns}	0.033
July <i>M. micrantha</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	4.500*	0.360	7.263*	0.232	1.275 ^{ns}	0.137
August <i>I. batatas</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	18.272**	0.695	640.952**	0.964	1.277 ^{ns}	0.138
August <i>M. micrantha</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	7.868**	0.496	8013.318**	0.997	0.696 ^{ns}	0.080
September <i>I. batatas</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1.755 ^{ns}	0.180	189.493**	0.888	0.113 ^{ns}	0.014
September <i>M. micrantha</i> Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	28.368**	0.780	4243.576**	0.994	3.374*	0.297

ns, * and ** indicate $P > 0.05$, $P \leq 0.05$ and $P \leq 0.01$, respectively.


Figure 2. Net photosynthetic rate (Pn) of *I. batatas* and *M. micrantha* looking at June (A), July (B), August (C), and September (D) under different density ratios and fertilization levels. Different letters represent significant differences at $p < 0.05$.

Photosynthesis

The net photosynthesis rate (Pn) of *I. batatas* did not vary by density ratio or fertilization level for either species in June, but by July Pn varied by fertilization level for both species and density ratio for *M. micrantha* (Table 3). The Pn in both species varied significantly in August and September, except in the case of September fertilization level for *M. micrantha*. There was not a significant interactions between density ratio or fertilization level for either species from June to September except in the case of *M. micrantha* in September. The Pn of both species increased gradually from June to September (Figure 2A–D). The Pn of *I. batatas* in June and July was higher than that of *M. micrantha*, but less than that of *M. micrantha* in August and September in monoculture. In June, the Pn of *I. batatas* was significantly

Table 4. Two-way ANOVA results of effects of density ratio, fertilization level and their interaction on soil properties of *I. batatas* and *M. micrantha*.

Variables	Fertilization level		Density ratio		Interaction	
	F value	Partial eta squared	F value	Partial eta squared	F value	Partial eta squared
pH	11.657**	0.493	6.438**	0.263	14.034**	0.701
Organic matter (g/kg)	1062.467**	0.989	148.087**	0.892	9.966**	0.624
Available N (mg/kg)	2836.552**	0.996	1935.007**	0.991	155.771**	0.963
Available P (mg/kg)	1362.711**	0.991	649.966**	0.973	16.761**	0.736
Available K (mg/kg)	8553.181**	0.999	4525.551**	0.996	957.306**	0.994

ns, * and ** indicate $P > 0.05$, $P \leq 0.05$ and $P \leq 0.01$, respectively.

higher than that of *M. micrantha*, with little difference among treatments. From July on, the Pn of *M. micrantha* was suppressed significantly ($P < 0.05$), and the Pn of *I. batatas* declined slightly in mixed culture (Figure 2A–D). The Pn for both *I. batatas* and *M. micrantha* gradually increased with increasing fertilization levels, with the Pn of *I. batatas* increasing at a higher rate than the Pn of *M. micrantha* throughout most of the study duration.

Soil nutrient effects

Soil pH, organic matter, available N, available P, and available K, and nutrient level all varied significantly with density ratio and fertilization level, and their interaction was also significant (Table 4). For the initial soil, pH (CK) was markedly lower than in the four fertilization treatments. However, other parameters for the initial soil were higher ($P < 0.05$) than in the fertilization treatments (Figure 3A). Comparing *M. micrantha* soil and soil for *I. batatas* grown in monoculture, available N, P and K were higher for the former ($P < 0.05$). These parameters decreased significantly in mixed culture (Figure 3B–E). With proportional increases in fertilization levels, the concentrations of organic matter, available N, available P, and available K of *I. batatas* and *M. micrantha* decreased significantly, at a higher rate for *I. batatas* than for *M. micrantha*.

Discussion

The current study found that although the growth of both *I. batatas* and *M. micrantha* was boosted by higher fertilization, *I. batatas* was more sensitive to fertilization level. Furthermore, *M. micrantha* was highly affected by density ratio when grown in combination with *I. batatas*. The photosynthetic rate of *I. batatas* was sensitive to fertilization levels at early growth stages, whereas *M. micrantha* was more affected at later growth stages. Moreover, *I. batatas* benefited more from fertilization levels than *M. micrantha* in terms of increased competitive ability. Fertilizer application is widely used to improve plant vigor and productivity in plant production (Shen et al. 2010; Razaq et al. 2017). If matched to fertilization demands at various plant growth stages, fertilizer availability could also be applied to the ecological management of invasive alien plants. Using fertilization strategically, fertilizer

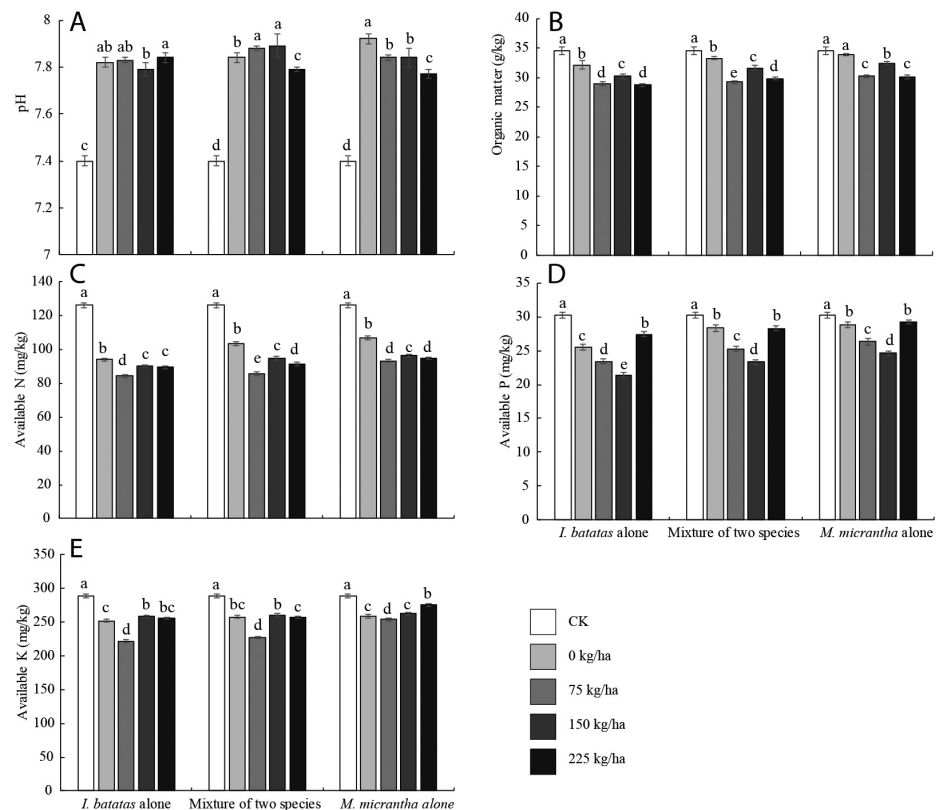


Figure 3. Soil properties looking at pH (A), organic matter (B), available P (C), available K (D), and available K (E) of *I. batatas* and *M. micrantha* soils under different density ratios and fertilization levels. Different letters represent significant differences at $p < 0.05$.

could be applied to deliberately improve the competitive ability of *I. batatas* over invasive plants like *M. micrantha*. The statistical interaction we observed between fertilization level and density ratio indicated that fertility could be successfully manipulated in favor of *I. batatas*.

The competitive performance of invasive plants is generally enhanced with increases in soil fertilization (Tian et al. 2009; Wang et al. 2012; Mattingly and Reynolds 2014). It is generally believed that the application of fertilizations can improve the competitiveness and plant growth of both invasives and natives (Shivega and Aldrich-Wolfe 2017), but the relative effects vary depending on the particular species and other conditions. With increased soil nutrients, the plant growth and competitive effects of two invasive plants *Bromus tectorum* L and *Centaurea maculosa* Lam increased, but the competitive effect of *Poa pratensis* L was unaffected by soil nutrient level (Gao et al. 2014). As a component of cropping systems, *I. batatas* was shown to exhibit an advantage in terms of biomass when grown with several invasive plants, exhibiting superior competitive ability when compared to *M. micrantha*, as well as *Ageratina adenophora* Spreng, *Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav, reducing both their growth and reproduction (Shen et al. 2015a, 2016, 2019a, b). Similarly, the current study found that the competitive balance (CB) index of *I. batatas* was significantly greater than zero and positively correlated with proportional

increases in fertilization levels, indicating that the competitive ability of *I. batatas* was increased proportionately more than that of *M. micrantha*.

In interspecific competition, plant species with similar growth patterns often compete strongly, in terms of competition for water resources, soil nutrients and light (Jiang et al. 2008). When growing in prostrate form, *I. batatas* and *M. micrantha* are very similar morphologically, and occupy a very similar niche (Shen et al. 2015a). Morphological plasticity and the ability to regenerate asexually are hallmarks of the life history strategy of *M. micrantha* (Lian et al. 2006; Wang et al. 2008; Shen et al. 2012). Yet in our study, the presence of *I. batatas* caused reductions in the lengths of main stem, branches, and leafstalks for *M. micrantha*. In scramble competition, branching or tillering has been seen as an important means of pre-empting resources as scramble competition progresses (Jiang et al. 2008). Although the branch number of *M. micrantha* growing alone is greater than that of *I. batatas* growing by itself, the number of *M. micrantha* branches was reduced when the plants were grown together. Fertilization levels increased branch length and other length parameters for both plant species but the rates of increase seen in *I. batatas* were higher than those of *M. micrantha* showing that the shoot length of *I. batatas* was clearly increased more than that of *M. micrantha*.

Leaf area index is a key indicator of plant condition and potential to utilize solar energy efficiently (Baldwin and Schmelz 1994). Specific leaf area also is indicative of carbon assimilation, showing the relationship between investment in biomass to leaf area (Lambers and Poorter 1992). In past studies, the leaf of *I. batatas* was demonstrated to be a key advantage when *I. batatas* was grown with invasive plants. The higher leafstalk length and leaf area of *I. batatas* can readily inhibit the germination of soil seed bank and seedling growth of other competition plants, covering the canopy and blocking sunlight (Shen et al. 2015a, 2019a, b). In the present study, *I. batatas* exhibited longer leafstalks and greater leaf area than *M. micrantha*, and furthermore these parameters were reduced for *M. micrantha* in the presence of *I. batatas*. The extent of the suppression of *I. batatas* is well illustrated by a previous study that found 70–90% of *M. micrantha* stems and leaves were covered by *I. batatas* (Shen et al. 2015a). With proportional increases in fertilization levels, the leafstalk length and leaf area of *I. batatas* and *M. micrantha* in the current study were significantly increased, and increased at a higher rate than those of *M. micrantha*.

Higher leaf area translates into higher rates of photosynthesis and growth, and accumulation of biomass (Lambers and Poorter 1992). In mixed culture, the maximum photosynthesis rate (Pn) of the invasive plant *A. adenophora* was higher than the native plant *Sida szechuensis* Matsuda, but less than two native plants *Brachiaria decumbens* Griseb and *Setaria anceps* Stapf. Moreover, with increased nitrogen fertilizer level, the maximum Pn of *A. adenophora*, *B. decumbens*, *S. anceps*, and *S. szechuensis* (except

the maximum Pn of *A. adenophora* mixed with *S. anceps*) was significantly increased in mixed culture (Tian et al. 2009). Leaf chlorophyll content, photosynthetic rate, transpiration rate, and stomatal conductance of *Ambrosia trifida* L were obviously decreased along with increasing density of *Helianthus tuberosus* L in mixed population (Li et al. 2006a). Previous studies found that the Pn of *I. batatas* was usually higher than invasive plants infesting agricultural fields in early stages, and then the Pn of *A. adenophora*, *A. conyzoides*, *B. pilosa*, and *G. parviflora* at later stages was significantly suppressed with increasing proportions of *I. batatas* in mixed culture (Shen et al. 2019a, b). Similarly, the current study showed that the Pn of *I. batatas* was higher than that of *M. micrantha* in June and July, less than that of *M. micrantha* from August to September in monoculture, and the Pn of *M. micrantha* was significantly suppressed by *I. batatas* since July. The Pn of *I. batatas* and *M. micrantha* gradually increased with increasing fertilization levels, with the *I. batatas* exhibiting a greater response to fertilizer than *M. micrantha*.

Plant competition includes aboveground light competition and belowground water, nutrient and mineral nutrition competition, and the belowground competition is frequently more important and complex (Wilson 1988). It has been shown that some invasive plants can successfully modify soil conditions, changing nutrient availability, enzyme activity, microbial activity, which may pave the way for further invasion (Callaway et al. 2001). Relative to many crop plants, *I. batatas* and *M. micrantha* are quite tolerant of low fertility. *Mikania micrantha* increases soil organic carbon, total N, total K, NO₃-N, NH₄-N, available P, and available K content in invaded habitats, which may be attributed to the superiority of the plant in its interspecific competition (Liu et al. 2012; Li et al. 2006b). However, this advantage of *M. micrantha* was adversely affected when grown in association with *I. batatas*. The soil conditions altered by *M. micrantha* may disproportionately benefit the growth of *I. batatas*. *Ipomoea batatas* needs moderate amounts of N and P, but needs significant amounts of K, and increased P and K availability tends to improve the root accumulation and quality of *I. batatas* (Mukhtar et al. 2010). High root yields of *I. batatas* contribute to high nutrients uptake from the soil, even in soils of low fertility (Onunka et al. 2011). Recent research indicated that *I. batatas* and *M. micrantha* can deplete soil nutrient during their growth, and *I. batatas* has a stronger capacity to consume nutrients than *M. micrantha* in mixed culture (Shen et al. 2015a). Our current research found that with proportional increases in fertilization levels, the organic matter content, available N content, available P content, and available K content of *I. batatas* and *M. micrantha* soils were significantly decreased, but to a greater degree for *I. batatas* soils, revealing that soil absorption of *I. batatas* was clearly increased more than that of *M. micrantha*.

Conclusions

The present study demonstrated that plant growth and photosynthesis of *I. batatas* and *M. micrantha* may be significantly affected by different fertilization regimes. *Ipomoea batatas* growth was particularly sensitive to fertilization level and *M. micrantha* was more negatively affected by density ratio. *Ipomoea batatas* could potentially gain greater competitive advantages from increasing fertilization levels by comparison to *M. micrantha*. This advantage was observed in terms of plant growth, photosynthetic characteristics and greater absorption of soil fertilizer. This study also demonstrated that optimal nutrient levels could provide a strategic tool during the replacement control of *M. micrantha* via ensuring the production of vigorous and healthy *I. batatas* plants. If *I. batatas* is incorporated into cropping system rotations, optimal fertilizer levels could be designed using information from our study to produce high *I. batatas* yields in addition to the benefits of suppressing invasive plants like *M. micrantha*. Additional details on the morphological or physiological impacts of varying fertilizer levels (N, P, K) on the relationship between *I. batatas* and *M. micrantha* should be further examined, in particular to better understand how below-ground plant organs are affected. Longer-term studies are needed, given the perennial nature of both *I. batatas* and *M. micrantha*, to study cumulative impacts of proactively incorporating *I. batatas* rotations in cropping systems to suppress *M. micrantha*.

Acknowledgements

This research was supported by the Yunnan Provincial Key Fund Program (2018FA024), the Middle-aged and Young Academic Leader Training Foundation of Yunnan Province (2018HB054 and 2014HB039), the Applied Basic Research Foundation of Yunnan Province (2017FB049), the Ten Thousand Talent Program (Young Top-notch Talent) of Yunnan Province (2019-2023), the National Natural Science Foundation of China (31960569), the Special Foundation for Applied Basic Research of Yunnan Academy of Agricultural Sciences (YJM201802), the State Scholarship Fund of China Scholarship Council (201808530029), the Program for the Innovative Research Team of Yunnan Province (2020-2022), and the Key Research and Development Program of Yunnan Province (2019IB007). We wish to thank Yuhua Zhang from the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences for her great field support. We also thank Dr Anna Gazda and two anonymous reviewers for helpful comments.

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