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Potential Use of Sweet Potato (*Ipomoea batatas* (L.) Lam.) to Suppress Three Invasive Plant Species in Agroecosystems (*Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav.)

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Abstract: Sweet potato (*Ipomoea batatas* (L.) Lam.) is a logical candidate crop to suppress invasive plants, but additional information is needed to support its potential application as a suppressive ground cover. The current study utilized a de Wit replacement series incorporating five ratios of sweet potato grown in the field in combination with one of three invasive plants (*Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav.) in replicated 9 m² plots. Stem length, total biomass, and leaf area were higher for monoculture-grown sweet potato than these parameters for any of the invasive plants grown in monoculture. In mixed culture, the plant height, branch, leaf, inflorescence, seed, and biomass of all invasive plants were suppressed by sweet potato. The relative yield parameter indicated that intraspecific competition was greater than interspecific competition for sweet potato, while the reverse was true for invasive species. The net photosynthetic rate was higher for sweet potato than for *B. pilosa* and *G. parviflora* but not *A. conyzoides*. Superoxide dismutase and peroxidase activities of each of the three invasive plants were reduced in mixture with sweet potato. Our results demonstrated that these three invasive plants were significantly suppressed by sweet potato competition due to the rapid growth and phenotypic plasticity of sweet potato.

Keywords: competitive crops; weed–crop competition; sweet potato; *Ipomoea batatas* (L.) Lam.; *Ageratum conyzoides* L.; *Bidens pilosa* L.; *Galinsoga parviflora* Cav.; antioxidant enzymes; de Wit replacement series

1. Introduction

Biological plant invasions have commanded considerable global attention because they have resulted in serious economic damage, environmental problems, loss of biodiversity, and threatened ecosystem safety and human and animal biosecurity [1,2]. Numerous methods have been developed to manage invasive plant species, but the most effective control is generally achieved using herbicides [3]. Environmental issues stemming from the use of herbicides, along with the frequent occurrence of

herbicide resistance, provide a good rationale for the implementation of alternative control measures [4]. One relatively unexplored alternative is the use of other plant species that can suppress invasive plants, also referred to as competitive cropping or replacement control [5,6]. The use of high-value competitive crop species (e.g., local food and/or cash crops) utilizes the competitive ability of such plants to inhibit exotic plants while simultaneously reducing invasive species damage and enhancing ecosystem health [5–10]. Compared to mechanical or chemical management, control with competitive crops can potentially be more economical, ecological, and sustainable [5]. Moreover, revegetation with high-value crops has been recognized broadly as an important means for both the long-term management of current infestations and the restoration of formerly invaded areas following successful control [11]. Thus, there is an important role for screening potential candidate species for competitiveness against key weeds, mechanisms of competition, and restorative effects [5,12,13].

Three invasive plant species *Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav., belonging to the Asteraceae, have become several of the most destructive weeds in agroecosystems worldwide. *Ageratum conyzoides* is native to Central America and the Caribbean [14], and *B. pilosa* and *G. parviflora* both originated from tropical America [15,16]. These three invasive species are aggressive annual weeds and have similar biological characteristics and habitat preferences, which include erect growth, lack of seed dormancy, high seed germination, rapid growth and development, early flowering, development of multiple generations per growing season, and high fecundity in a wide range of environmental conditions [17,18]. They are common weeds in most temperate, subtropical, and tropical regions of the world, and are widely distributed in various habitats including gardens, greenhouses, arable land, nurseries, roadsides, and wasteland areas. Each of the three invasive plants can quickly become dominant and all can potentially suppress the growth of neighboring plants due to the potential release of allelochemicals into the environment or their rapid growth and/or relatively high seed production over a short growth period [15,19,20]. All three invaded China in the 19th century and are presently among the most destructive invasive plants in temperate, subtropical, and tropical regions of Yunnan Province, Southwest China, causing serious economic and environmental impacts [21].

For integrated management of invasive plants, replacement control through the use of local plant resources has been frequently investigated and applied in recent times. One promising example is the use of sweet potato (*Ipomoea batatas* (L.) Lam.: Convolvulaceae) to control agricultural weeds and invasive plants in natural areas [6,10,22–26]. Native to the American tropics, sweet potato is the seventh most important crop world-wide and the fifth most important crop in developing nations [27]. Sweet potato is rich in polyphenols, vitamin B, calcium, iron, zinc, and proteins, and is tolerant of many diseases and pests [28]. Moreover, its roots, leaves, and shoots are good sources of nutrients and micronutrients for livestock. Sweet potato has been recognized as a very competitive crop against certain weeds because of its rapid growth and canopy formation, and its ability to reproduce asexually. Sweet potato has previously been shown to suppress plant growth, soil nutrient absorption, and reproductive ability of another invasive Asteraceae species *Mikania micrantha* Kunth [6,10]. It has also displayed the ability to reduce the density, frequency, and cover of three invasive weeds *A. conyzoides*, *B. pilosa*, and *G. parviflora* in sweet potato fields [23,29]. Moreover, sweet potato has been noted to have significant allelopathic effects on these three invasive plants [22,24–26,30–33]. However, before sweet potato is utilized to manage these three invasive plants in the field, investigation of the morphological, ecological, and physiological characteristics that confer their competitive interactions is required.

In our previous studies, sweet potato was shown to compete strongly with three invasive plants in question, *A. conyzoides*, *B. pilosa*, and *G. parviflora*, under both field and laboratory conditions [23,26]. However, the mechanisms conferring morphological, ecological, and physiological characteristics that drive the weed suppressive properties of sweet potato are not well characterized. The main objective of this study was, therefore, to examine competitive and physiological interactions of sweet potato with the three invasive plant species (*A. conyzoides*, *B. pilosa*, and *G. parviflora*) utilizing a de Wit replacement series [34] and provide insights on how similar ecological control methods could be applied to other invasive alien species.

2. Materials and Methods

2.1. 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/or temperate monsoon climate. Rainfall averages 1000–1300 mm per year and the annual mean temperature is 14.1 °C. Recently, the range of three studied invasive species has been expanding rapidly within Songming County, where they are now widely distributed in farmlands, wastelands, roadsides, and other disturbed ecosystems [21].

2.2. Study Species

Three invasive species, *A. conyzoides*, *B. pilosa*, and *G. parviflora*, have widely invaded gardens, greenhouses, arable land, nurseries, and wastelands of temperate, subtropical, and tropical regions in Yunnan Province, Southwest China [21]. Seeds from local populations of all three plants were collected in September in 2016 and 2017, dried at room temperature for two months, and then kept in the refrigerator at −4 °C.

Sweet potato is one of the main food and cash crops in tropical and subtropical regions of Yunnan Province [6]. This crop mainly reproduces by asexual means and is usually planted vegetatively. Since 2010, local sweet potato genotypes have been collected and grown in a temperature-controlled glasshouse of the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences.

2.3. Experiment Design and Data Collection

Based on our previous studies and a preliminary evaluation in 2017, the experiment was formally conducted during the April–October growing season in 2018 at the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, in Xiaojie Town, Songming County. To study plant interference, de Wit replacement series experiments [34] have been extensively used in ecological studies of competition between two species of plants (or even for competition between insects), and serve both to detect the existence of and measure the magnitude of competition, as well as to determine the combination of two or more species which maximizes the total yield of a mixture [35]. To set-up a de Wit series, a constant total plant density is maintained, but the proportion in which the two species are grown together is varied from 0% to 100% [36]. The analysis of the results of competition in a de Wit series is based on yield-density responses of plants grown in monoculture or in two-species mixtures [37]. Plant total weight or yield is often used as a measure for determining plant competitive ability or success in competition. Moreover, morphological and physiological modifications or responses under competitive conditions including plasticity of plant height, tillering or branching, production of leaves, flowers and seeds, rate of photosynthesis, and antioxidant enzyme activities of leaves are all important factors affecting the success of a species in competition [38–40].

Seeds of the three invasive plant species and sweet potato tuberous roots (variety SP1) were propagated in the greenhouse starting on 25 April. On 15 June, one-node segments (fresh weight 2.0–2.5 g, 5–6 cm pieces) were taken from central stem portions of the sprouted new shoots (50 days after growing), placed in Hoagland's solution [41], and grown for 5 days. On the 20th of June, seedlings with the same height as the three invasive plants and the sprouts derived from cuttings of sweet potato plants were selected and transplanted. Based on our previous studies on competition of sweet potato and invasive plant *M. micrantha* and field observations, five ratios of sweet potato grown in combination with one of three invasive plants species (in three separate trials with one trial for each invasive plant species: sweet potato versus *A. conyzoides*, sweet potato versus *B. pilosa*, and sweet potato versus *G. parviflora*) were utilized with a total of 180 plants per treatment (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). The plots were arranged in a complete randomized design with 4 replicates utilizing 9 m² plots (3 m × 3 m) for all treatments of each invasive species. 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 October, net photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr) measurements on leaves for sweet potato and the three invasive plant species were conducted mid-month using a Portable Photosynthesis System (LI-COR Biosciences LI6400XT, Lincoln, NE, USA), between 8:00 am and 11:30 am, with a 6400-02 or -02B LED source and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (photosynthetically active radiation). During sampling, air CO₂ concentration, air temperature, and relative humidity (RH) in the chamber were controlled to match ambient air values: 375 \pm 3 ppm CO₂, 25 \pm 1 °C and 65% \pm 10% RH. Measurements were made on a representative leaf randomly chosen on five to six randomly selected individuals of each species.

During peak flowering times in early September, 15 plants of each species were selected randomly and harvested within the central region of each plot. The number and fresh weight of inflorescences and aboveground biomass of all tested plants were measured. On 25 September (97 days after transplanting), seed production of the three invasive plant species was measured in the study plots after flowering had ceased, but prior to seed dispersal. Another fifteen plants of each species were selected randomly and harvested from the interior of each plot. Leaves were clipped and passed through a leaf-area meter (Li-3000A; LI-COR Biosciences, Lincoln, NE, USA) to determine leaf area index. Total shoot length, main stem length, branch number, seed number, seed biomass (fresh weight), and aboveground biomass (fresh weight) were recorded.

For enzyme extracts and assays, leaves were sampled from the four plant species. Leaves weighing 5–6 g were immediately frozen in liquid nitrogen after harvesting. The activities of antioxidant enzymes superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) of leaves were tested and analyzed in the laboratory at the Agricultural Environment and Resources Research Institute of Yunnan Academy of Agricultural Sciences.

2.4. Data Analyses

Relative yield (RY) per plant [34], relative yield total (RYT) [42], and competitive balance index (CB) [43] were calculated from the final biomass for each species in each plot (see equations below). These measurements provided information on the competitive interactions between species in a mixed culture in contrast to growth in monoculture.

Relative yield per plant of species a or b in a mixed culture with species b or a was calculated as:

$$RY_a = Y_{ab}/Y_a \text{ or } RY_b = Y_{ba}/Y_b \quad (1)$$

Relative yield total was calculated as:

$$RYT = (RY_{ab} + RY_{ba})/2 \quad (2)$$

Finally, competitive balance index was calculated as:

$$CB_a = \ln(RY_a/RY_b) \quad (3)$$

where Y_{ab} is the yield for species a growing with species b (g individual^{-1}), 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^{-1}), 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 indicates 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 RY 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 the 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 [42]. Values of CB_a greater than 0 indicate that species a is more competitive than species b [43].

All morphological variables (plant length, branch number, leaf area, inflorescence number, and biomass) and physiological variables (Pn, Gs, Tr, SOD, CAT, and POD) of the three invasive plant species and sweet potato plants were analyzed by analysis of variance (one-way ANOVA) using IBM SPSS 22.0 software (Armonk, NY, USA). If significant differences were detected with the ANOVA, Tukey's honestly significant difference (HSD), post-hoc multiple comparisons, and homogeneity of variance tests were used to detect differences among treatments at a 5% level of significance. Relative yield and RYT from each mixed culture were compared to the value of 1.00 using *t*-tests ($p = 0.05$ or $p = 0.01$), and values of RYT were tested for deviation from 1.0 and values of CB for deviation from 0 using a paired *t*-test.

3. Results

3.1. Plant Growth

In all three invasive plants, the main stem length was much less than the branch length, whereas the main stem length was greater than the branch length for sweet potato, in all treatments (Figure 1A–C, Table S1). *Galinsoga parviflora* had the greatest total shoot length (531.3–785.6 cm per plant) and branch length (484.0–722.0 cm per plant), followed by *B. pilosa* (230.6–373.3 cm per plant for total shoot length and 180.3–312.0 cm per plant for branch length), and the least total shoot (145.4–281.3 cm per plant) and branch length (102.3–222.7 cm per plant) was measured for *A. conyzoides*. In mixed culture, the total shoot length (main stem + branch length), main stem length and branch length of the three invasive plant species were significantly suppressed ($p < 0.05$) with increasing proportions of sweet potato (Figure 1A–C).

The branch number of the three invasive plant species was greater than sweet potato branch number in monoculture. *Galinsoga parviflora* had the greatest branch number (57.3–103.1 per plant), followed by *B. pilosa* (9.4–15.4 per plant) and then *A. conyzoides* (10.4–13.4 per plant). In mixed culture, the branch number of each of the three invasive plant species was significantly suppressed ($p < 0.05$) with increasing proportions of sweet potato, and that of sweet potato was increased markedly with increasing proportions of the three invasive plant species (Figure 1D, Table S1).

Sweet potato leaf area at harvest was much greater than that of the three invasive plant species in all treatments (Table S1, Figure 1E). In monoculture, the leaf area of sweet potato was 62.4 cm², but leaf area was only 10.2 cm² for *G. parviflora*, 12.1 cm² for *B. pilosa*, and 18.1 cm² for *A. conyzoides*. In mixed culture, sweet potato leaf area averaged about 3.5–11.5 times (3.5–4.8 times for *A. conyzoides*, 5.3–7.3 times for *B. pilosa*, and 6.5–11.5 times for *G. parviflora*) that of the three invasive plant species. The leaf area of each of the three invasive plant species progressively declined ($p < 0.05$) with increasing proportions of sweet potato, and that of sweet potato was significantly increased with increasing proportions of invasive plants (Figure 1E, Table S1).

In all treatments, the number of inflorescences for *G. parviflora* (351.4–552.1 per plant) and *A. conyzoides* (94.2–136.1 per plant) was greater than for *B. pilosa* (20.8–44.2 per plant), and *G. parviflora* had the greatest biomass of inflorescences (3.65–5.80 g per plant), followed by *B. pilosa* (2.04–4.22 g per plant) and *A. conyzoides* (1.46–2.55 g per plant) (Figure 1F). The number of seeds of *A. conyzoides* (5184.6–7383.8 per plant) and *G. parviflora* (4581.8–7258.6 per plant) was greater than for *B. pilosa* (719.3–1584.3 per plant), but *B. pilosa* had the greatest biomass of seeds (0.81–1.79 g per plant), followed by *A. conyzoides* (0.62–0.88 g per plant) and *G. parviflora* (0.49–0.79 g per plant). In mixed culture, the number and biomass of inflorescences and seeds of three invasive plants were significantly suppressed ($p < 0.05$) with increasing proportions of sweet potato (Figure 1F–I).

The total biomass of sweet potato was much greater than that of the three invasive plant species in all treatments (Table S1, Figure 1J). In monoculture, the total biomass of sweet potato was 1.10–1.49 higher times than that of the invasive plant species. In mixed culture, the total biomass of three invasive plants (16.42–25.74 g per plant for *A. conyzoides*, 13.42–34.91 g per plant for *B. pilosa*, and 18.88–28.84 g per plant for *G. parviflora*) was increasingly suppressed by increasing proportions of sweet potato (Figure 1J).

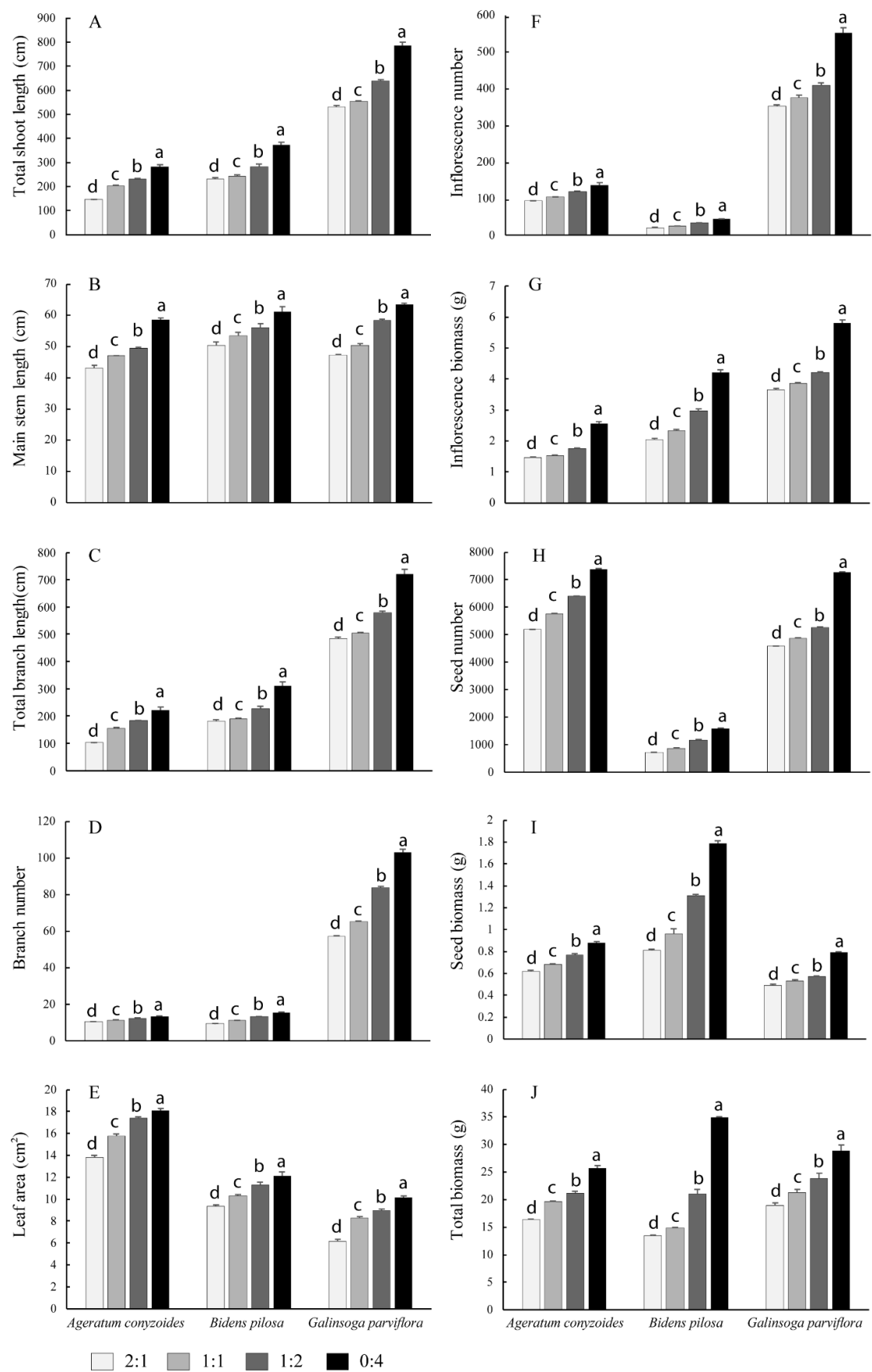


Figure 1. Plant growth comparison of three invasive plants looking at total shoot length (A), main stem length (B), total branch length (C), branch number (D), leaf area (E), inflorescence number (F), inflorescence

biomass (G), seed number (H), seed biomass (I), and total biomass (J) under monoculture and mixed-culture conditions with sweet potato. Different letters represent significant differences at $p < 0.05$.

3.2. Competitive Interactions

The RY of sweet potato and that of the three invasive plant species in different ratios in mixed culture showed that competition between sweet potato and each of the invasive plant species was uneven and favored sweet potato (Table 1). The RY of sweet potato was significantly higher ($p < 0.05$) than 1.0, and the RY of all three invasive plant species was significantly less than 1.0 in mixed culture ($p < 0.05$), showing that intraspecific competition was greater than interspecific competition for sweet potato, and that the opposite was true for each of the invasive plant species. The RYT for each of the three invasive plant species was less than 1.0 in mixed culture (ranging from 0.71 to 0.99), indicating significant competition was taking place between the invasive plant species and sweet potato. The CB index of sweet potato was greater than zero within all ratios in mixed culture. The CB index indicated that sweet potato had the greatest competitive effect on *B. pilosa*, followed by *G. parviflora*. *Ageratum conyzoides* was the least affected by competition with sweet potato but still ranged from 0.34–0.50 with increasing proportions of sweet potato. Overall, sweet potato exhibited greater interspecific competitive ability than the invasive plant species.

Table 1. Relative yield (RY), relative yield total (RYT), and competitive balance (CB) index of sweet potato and three invasive plants (*Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav.) in mixed culture.

Variables		Ratios (Sweet Potato:Invasive Plant)		
		2:1	1:1	1:2
Sweet potato RY	<i>A. conyzoides</i>	1.06 ^{c **}	1.10 ^{b **}	1.16 ^{a **}
	<i>B. pilosa</i>	1.04 ^{c **}	1.10 ^{b **}	1.13 ^{a **}
	<i>G. parviflora</i>	1.08 ^{c **}	1.10 ^{bc **}	1.13 ^{ab **}
Competitive species RY	<i>A. conyzoides</i>	0.63 ^{c **}	0.76 ^{b **}	0.82 ^{a **}
	<i>B. pilosa</i>	0.38 ^{c **}	0.42 ^{b **}	0.60 ^{a **}
	<i>G. parviflora</i>	0.65 ^{c **}	0.74 ^{b **}	0.83 ^{a **}
RYT	<i>A. conyzoides</i>	0.85 ^{c **}	0.93 ^{b **}	0.99 ^{a *}
	<i>B. pilosa</i>	0.71 ^{c **}	0.76 ^{b **}	0.87 ^{a **}
	<i>G. parviflora</i>	0.87 ^{c **}	0.92 ^{b **}	0.98 ^{a **}
CB index for sweet potato	<i>A. conyzoides</i>	0.50 ^{a **}	0.37 ^{bc **}	0.34 ^{c **}
	<i>B. pilosa</i>	0.99 ^{a *}	0.95 ^{b **}	0.63 ^{c **}
	<i>G. parviflora</i>	0.50 ^{a **}	0.41 ^{b **}	0.31 ^{c **}

Data are expressed as the mean. The different letters within the same row mean significant differences within the row comparing the variables among the three ratios at $p < 0.05$. The *t*-test was used to compare each value with 1.0 and 0; * and ** indicate significant differences at the 0.05 and 0.01 levels, respectively.

3.3. Photosynthesis and Enzyme Activities

Photosynthesis and enzyme characteristics varied significantly ($p < 0.05$) among different treatments corresponding to the five ratios of the sweet potato and invasive plant species (Figure 2A, Table S2). In monoculture, the Pn of sweet potato was lower than that of *A. conyzoides* ($5.94 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and higher than that of *B. pilosa* ($11.71 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and *G. parviflora* ($9.19 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and the Gs of sweet potato was greater than that of *B. pilosa* ($0.22 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and less than that of *G. parviflora* ($0.42 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and *A. conyzoides* ($0.32 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$). The Tr of sweet potato was less than that of three invasive plants. In mixed culture, the Pn, Gs, and Tr of each of

the three invasive plant species were significantly suppressed ($p < 0.05$) with increasing proportions of sweet potato (Figure 2A–C).

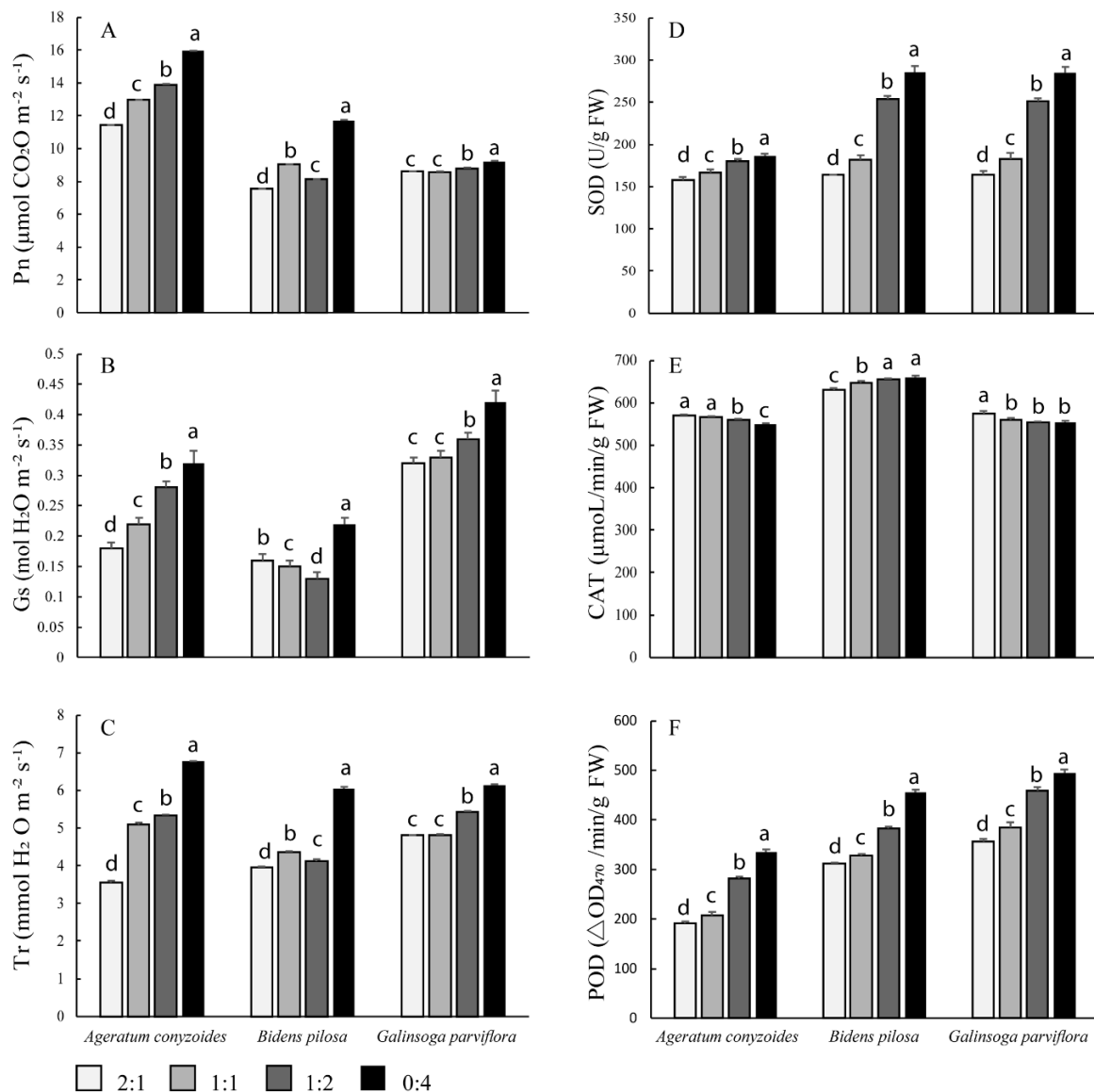


Figure 2. Photosynthetic and antioxidant enzyme properties of three invasive plants under monoculture and mixed-culture conditions with sweet potato. Pn = net photosynthetic rate (A), Gs = stomatal conductance (B), Tr = transpiration rate (C), SOD = superoxide dismutase (D), CAT = catalase (E), and POD = peroxidase (F). The different letters show significant differences at $p < 0.05$.

The antioxidant enzyme activity levels for SOD (157.76–186.33 U/g FW for *A. conyzoides*, 163.71–285.90 U/g FW for *B. pilosa*, and 163.71–284.73 U/g FW for *G. parviflora*) and POD (191.59–334.34 $\Delta\text{OD}_{470}/\text{min/g FW}$ for *A. conyzoides*, 311.79–455.88 $\Delta\text{OD}_{470}/\text{min/g FW}$ for *B. pilosa*, and 357.12–495.42 $\Delta\text{OD}_{470}/\text{min/g FW}$ for *G. parviflora*) in three invasive plant species were significantly lower than that of sweet potato, whereas the CAT activities of invasive plants (549.80–569.59 $\mu\text{mol/min/g FW}$ for *A. conyzoides*, 629.87–660.30 $\mu\text{mol/min/g FW}$ for *B. pilosa*, and 553.76–574.70 $\mu\text{mol/min/g FW}$ for *G. parviflora*) and sweet potato were similar in all treatments (Figure 2D–F, Table S2). The SOD activity of sweet potato was the greatest enzyme activity measured, followed by POD activity. In contrast, CAT activity constituted the greatest enzyme activity seen in each of three invasive plant species. In mixed culture, the SOD, POD, and CAT activity in sweet potato significantly increased ($p < 0.05$).

with decreasing proportions of sweet potato, whereas the SOD and POD activity in each of the three invasive plant species was markedly suppressed with increasing proportions of sweet potato. Except in the case of *B. pilosa*, the CAT activity for *A. conyzoides* and *G. parviflora* was increased with increasing proportions of sweet potato.

4. Discussion

The further development of competitive crops for suppressing invasive plant species in agroecosystems requires a search for crops or cultivars which compete effectively for resources and/or have allelopathic impacts on other plants. This impact on invasive plants could include the ability to exploit light, water, and nutrient resources better for plant growth and/or the release of allelopathic substances [5,6,24]. Compared to local species, invasive plant species generally have a competitive advantage [5,6]. Our current study found that even though invasive plants like *A. conyzoides*, *B. pilosa*, and *G. parviflora* may possess such a competitive advantage over most crops due to their morphological and physiological characteristics, these characteristics do not stand up to the superior attributes of sweet potato. During interspecific competition, morphological characteristics (e.g., leaf shape) and biomass (various other measures of plant size) tend to be the most important measured indexes [5,12]. The total biomass of sweet potato was much greater than that of the three invasive plants in all treatments. In monoculture, the total biomass of sweet potato was 10%–50% greater than the biomass of the invasive species. Although there are some difference for the initial size and weight of sweet potato and the three invasive plant species, because the initial differences were relatively small and because they were grown under similar conditions, differences in final biomass were due to the competitiveness and plant morphology. In mixed culture, the RY of sweet potato was greater ($p < 0.05$) than 1.0 and the RY and RYT for each of the three invasive plant species were significantly less ($p < 0.05$) than 1.0, demonstrating that sweet potato has greater competitive ability compared to the invasive plant species we tested. Comparing the CB index of sweet potato and the CB values for the three invasive plant species, the competitive ability of sweet potato versus the three invasive plant species followed the order *B. pilosa* > *G. parviflora* > *A. conyzoides*.

The three invasive plant species are erect annual herbs whereas sweet potato is an annual or perennial vine, so while all four plants share similar niche at the seedling stage, the niche gradually changes over time when grown together. The three invasive plant species exhibit a high degree of morphological plasticity and an ample capacity for sexual propagation. *Ageratum conyzoides*, *B. pilosa*, and *G. parviflora* all have a relative short growth period such that they can complete their life cycles within 4–5 months, while producing large numbers of seeds, especially *G. parviflora* and *A. conyzoides* [15,18,44]. The life history strategy of sweet potato is different, and the plant mostly reproduces asexually. In fact, most local villagers in Yunnan and many other places only use its root and stem for cultivation. We showed that the number and biomass of inflorescences and seeds of three invasive plants were significantly suppressed ($p < 0.05$) in mixed culture with increasing proportions of sweet potato. The ability to suppress inflorescence and seed production is important in terms of reducing the potential for rapid population growth of the three invasive plant species.

Plant height and tillering or branching are important means by which plants compete with other plants, and also has been considered as a means of pre-empting resources during scramble competition [5]. Although the total branch length and number of branches for the three invasive plant species were much greater than that of sweet potato in all treatments, the main stem length of sweet potato and the invasive plants were relatively similar in monoculture. In mixed culture, the branch number and length of the three invasive plant species were significantly suppressed. The ability of sweet potato to grow its main stem length quickly is key to its competitive ability.

Leaf area provides a major index to measure growth condition and solar energy utilization efficiency of plants [45]. Greater specific leaf area (leaf area per unit leaf mass) may increase carbon assimilation due to more leaf area produced for a given investment in biomass [46]. The present study found that in all treatments, the leaf area of three invasive plants was less than that for sweet potato.

In monoculture, the leaf area of *G. parviflora*, *B. pilosa*, and *A. conyzoides* was only 16%, 19%, and 29% compared to that of sweet potato, respectively. In mixed culture, the leaf area of the three invasive plant species was greatly reduced with increased proportions of sweet potato. A previous study also showed that leaf area of *M. micrantha* was only 21% of that of sweet potato in monoculture, and 70%–90% of *M. micrantha* stems and leaves were covered by sweet potato, greatly reducing *M. micrantha* biomass in mixed culture [6]. Higher rates of photosynthesis connected to higher leaf area can lead to increased growth rates, biomass accumulation and overall production. Higher carbon gain and growth may enable many invasive species to readily outcompete slower growing species by facilitating colonization or resource acquisition [46]. In monoculture, the Pn of sweet potato was less than that of *A. conyzoides* and higher than that of *B. pilosa* and *G. parviflora*; the Gs of sweet potato was greater than that of *B. pilosa* and less than that of *G. parviflora* and *A. conyzoides*. In mixed culture, the Pn of three invasive plants was significantly suppressed with increasing proportions of sweet potato. All these showed that larger leaf area and higher Pn of sweet potato could lead to its higher growth rate and more biomass accumulation in competition with the three invasive plant species.

Antioxidant enzymes are one of the important reactive oxygen detoxifier systems in plant cells, therefore, an increase in antioxidant enzyme activity can be considered an important defense strategy against oxidative stress [47]. Oxidative stress can lead to inhibition of the photosynthesis and respiration processes, and thus, plant growth. The responses of the antioxidant enzymes SOD, CAT, and POD in the development of plant tolerance to extreme environments has been clearly demonstrated [39,40]. However, the enzyme activity observed in each species did not appear to be correlated to competitive response. The *M. micrantha* plants infested by *Bemisia tabaci* Gennadius showed serious damage in the enzymatic protective system since the activities of SOD and CAT significantly decreased, resulting in the reduction of the ability to eliminate active oxygen [48]. The activities of SOD and CAT in the leaves of the invasive plant *Ageratina adenophora* Spreng in mixed culture were significantly higher than those in monoculture, when grown with *Chenopodium serotinum* L [49]. Our study found that SOD or POD enzyme activity levels in sweet potato were both significantly greater than those in the three invasive plant species. Catalase activity of sweet potato and the invasive plants was relatively similar in all treatments. In mixed culture, the activities of SOD, POD, and CAT of sweet potato were significantly increased ($p < 0.05$) with decreasing proportions of sweet potato, and the activities of SOD and POD of the three invasive plant species were markedly suppressed with increasing proportions of sweet potato. Except for *B. pilosa*, CAT activity for *A. conyzoides* and *G. parviflora* was generally increased with increasing proportions of sweet potato. Thus, it is clear that sweet potato can modify its enzyme activities to its advantage via protection against oxidative stress when in competition with other plants, such as the three invasive plant species in our study.

5. Conclusions

These results suggest that plant growth and reproductive ability of three invasive plant species in the Asteraceae, *A. conyzoides*, *B. pilosa*, and *G. parviflora*, were significantly suppressed by sweet potato competition. Sweet potato showed greater plasticity in modifying its growth, including modification of morphological, physiological, and biochemical properties, in comparison to the three invasive plant species we examined. Thus, planting sweet potato may be a promising technique for reducing infestations of invasive plants in agricultural lands or other habitats such as wastelands where suppression of invasive plants is needed. This study also suggests that sweet potato is a suitable ecological management means for other agricultural and environmental weeds, especially such annual plants with short life cycles and relatively short stature. In order to provide a more comprehensive perspective on long-term management of three invasive plants via competition with sweet potato, long-term successional patterns, physiological and biochemical impacts of varying fertilizer levels, and other environmental factors on the relationship among the four species should be further examined.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2073-4395/9/6/318/s1>, Table S1: plant growth of sweet potato looking at total shoot length, main stem length, total branch length, branch

number, leaf area, and total biomass under monoculture and mixed-culture conditions with three invasive plants (*Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav.), Table S2: photosynthetic and antioxidant enzyme properties of sweet potato under monoculture and mixed-culture conditions with three invasive plants (*Ageratum conyzoides* L., *Bidens pilosa* L., and *Galinsoga parviflora* Cav.).

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