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Performance of the alligatorweed flea beetle, *Agasicles hygrophila*, on nontarget plant species

JUNJIAO LU, LONGLONG ZHAO, NA LI, DONG JIA, YANQIONG GUO, JIANING WEI, RENJUN FAN, AND RUIYAN MA*

ABSTRACT

Alligatorweed flea beetle [*Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae)] has been considered as a biological control agent against the invasive weed, alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb]. The adult development, survivorship, fecundity, larval hatching and the performance of alligator flea beetle adults on target and several nontarget host plants in field conditions were determined in this study. The results showed that alligator flea beetle could feed on a nontarget host plant, *Alternanthera sessilis* (L.) DC., but it did not pupate successfully. Alligator flea beetle could not complete their life cycle on the other plant species.

Key words: *Agasicles hygrophila*, alligator flea beetle, alligatorweed *Alternanthera philoxeroides*, nontarget host plants, weed biological control.

INTRODUCTION

Alligatorweed flea beetle [*Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae)] is an efficient and effective natural biological control agent of alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb (Amaranthaceae)], which is an amphibious perennial plant and native to South America (Julien and Stanley 1999). At present the plant is found in over 20 provinces and regions of China, in diversified habitats from terrestrial to aquatic environments, and causes multiple negative economic effects (Ma and Wang 2005). The flea beetle was first introduced into China in 1987 and has provided control of this exotic aquatic weed in southern parts of China (Wang 1989, Ma et al. 2013).

Biological control is a valuable and environmentally friendly method because infestations of alligatorweed are exacerbated by mechanical control methods, and water supplies are polluted by chemical control methods (Sainty et al. 1998, Strong and Pemberton 2000). There are some cases of damage to nontarget plant species when introduced host-specific biological control agents expand their host range to host shift and attack native organisms (Louda et al. 2003, Andreas et al. 2008). For example, the flower head weevil (*Rhinocyllus conicus* Frölich) was introduced against nodding plumeless thistle (*Carduus nutans* L.) in North America. Unexpectedly, weevils from some nontarget plune thistle (*Cirsium* Mill. spp.) were larger than those from thornless thistle (*Carduus* L. spp.), by 2001, flower head weevil was reported using 22 of the 90+ North American plune thistle (*Cirsium* Mill. spp.) (Pemberton 2000). It is unfortunate that the spread of cactus moth [*Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae)], a biological control agent that was intentional introduced to Nevis Island in the Caribbean against the weedy native prickly pear (*Opuntia* L. spp.), could disrupt interactions between native prickly pear and their associated insects. Some Caribbean iguanid lizards use prickly pear for food, and a variety of native insects are associated with prickly pear (Burger and Louda 1994). Thus recognition of the risks associated with host-shifting and environmental safety of introducing exotic organisms into native ecosystems has increased the emphasis on host specificity of biological agents for invasive weeds (Briese and Walker 2008, Taylor et al. 2007, Paynter et al. 2008).

Previous research has shown that alligatorweed flea beetle larvae and adults preferred strongly the host plant alligatorweed in experiments using 20 representative species for host plant selection tests in laboratory conditions (Lu et al. 2012, Zhao et al. 2013). However alligatorweed flea beetle larval feeding and survival, as well as adult feeding and oviposition did occur on the congeneric species sessile joyweed [*Alternanthera sessilis* (L.) DC.], a native species in the tropical and subtropical regions of China (Lu et al. 2010). The development, survival rates, reproduction and preference in field conditions of alligatorweed flea beetle on other plants were not very clear. The objective of this study was to determine the performance of alligatorweed flea beetle adults on target and nontarget host plants. The adult development, survivorship, fecundity, larval hatching were investigated and measured to evaluate the safety of alligatorweed flea beetle in its novel range.

*First author: PhD and Assistant Research Fellow, College of Agriculture, Shanxi Agricultural University, Taigu Shanxi, 030801, P. R. China. and Institute of Plant Protection, Shanxi Academy of Agricultural Sciences, Taiyuan, Shanxi, 030032, P. R. China, Second to fifth authors: Doctoral Candidates, College of Agriculture, Shanxi Agricultural University, Taigu Shanxi, 030801, P. R. China. Sixth author: Research Fellow, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, P. R. China. Seventh author: Research Fellow Institute of Plant Protection, Shanxi Academy of Agricultural Sciences, Taiyuan, Shanxi, 030032, P. R. China. Eighth author: Professor, College of Agriculture, Shanxi Agricultural University, Taigu Shanxi, 030801, P. R. China. Corresponding author's Email: maruiyan2004@163.com.
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Table 1. List of test plant species for re-evaluating the specificity of *A. hygrophila*.

Order	Family	Test Species	Remarks
Caryophyllales	Amaranthaceae	Alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.]	host plant
		Sessile joyweed [*Alternanthera sessilis* (L.) DC.]	1, 3, 4
		Calico-plant [*Alternanther bettzickiana* (Regel) G. Nichols.]	1, 2
		Common amaranth (*Amaranthus retroflexus* L.)	1, 2
		Callaloo (*Amaranthus tricolor* L.)	1, 2
		Cockscomb (*Celosia cristata* L.)	1, 2
		Globe amaranth (*Gomphrena globosa* L.)	1, 2
	Chenopodiaceae	Sugar beet (*Beta vulgaris* L. S)	3
		Chard (*Beta vulgaris* L. C)	2
		Burning bush (*Bassia scoparia* L.)	2
		Spinach (*Spinacia oleracea* L.)	2, 3
		Lamb's quarters (*Chenopodium album* L.)	2
	Caryophyllaceae	Carnation (*Dianthus caryophyllus* L.)	2
		China pink (*Dianthus chinensis* L.)	2
		Baby's breath (*Gypsophila elegans* Bieb.)	2
	Portulacaceae	Common purslane (*Portulaca oleracea* L.)	2, 3, 4
Capparales	Brassicaceae	Chinese cabbage (*Brassica rapa* L. var. *pekinensis* Lour.)	2
Asterales	Asteraceae	Lettuce (*Lactuca sativa* L.)	2
Solanales	Convolvulaceae	Water spinach (*Ipomoea aquatica* Forssk.)	2
Polygonales	Polygonaceae	Common knotgrass (*Polygonum aviculare* L.)	4

The test plant species were selected according to four criteria:
[1] the species selected based on centrifugal phylogenetic method;
[2] the species selected based on changed economic status or the important agricultural or ornamental plant species;
[3] the plants were tested in the prerelease tests;
[4] the species overlapping in geographic distribution and morphological and ecological similarities.

MATERIALS AND METHODS

Test plant species were selected according to four criteria. First, based on the phylogenetic method of Harris and Zwölfer (1968) and Wapshere (1974) for host specificity testing of biological control agents, the closest relatives of the target weed (plants within the family Amaranthaceae) and less closely related plants in other families within the order Caryophyllales were selected, especially those grown as vegetables and ornamentals. The congeneric species sessile joyweed and calico-plant [*A. bettzickiana* (Regel) G. Nicholson], which has been planted as an ornamental garden plant in China, were selected. Second, plants or vegetables whose economic status has altered, and important agricultural or ornamental plant species were selected for testing, e.g., the species common purslane *Portulaca oleracea* L.) and common amaranth (*Amaranthus retroflexus* L.). Third, plants that were tested in the pre-release tests were selected. Lastly, plant species that overlap in geographic distribution or have morphological or ecological similarities (i.e., life-history, growth pattern) also were selected for testing.

In this study, 20 plant species of eight families and 15 genera were tested (Table 1). The family Amaranthaceae contains many species native to China, including seven species in four genera used in this study. Test plants were obtained as seeds, cuttings, transplants of plants growing naturally in the field, or from nurseries or markets. The plants without pesticides were growing in a greenhouse for the experiments.

The flea beetles were reared using their host plant alligatorweed in a greenhouse, emerging adults within 12 h were collected for the experiments. All experiments were conducted at 26 ± 1 C, 85 ± 5% RH, and with a 12 L/12 D photoperiod in an environmental growth chamber (Safe, PRX-450 C, Ningbo Safe Experimental Instrument Co., Ltd.).

No-choice tests

No-choice tests were conducted using adults and survival rates were recorded. For each test, 10 flea beetle adults (sex ratio was 1 : 1) were enclosed in a glass jar with the experimental plant material, and each test was replicated three times. The host plant alligatorweed and one treatment with no leaves (starvation treatment) were included as controls. The openings of the jars were covered with fine muslin cloth fastened with rubber bands. The leaves excised from test plants were replaced twice a day and kept moist with damp filter paper. The insect survival rates and the consumed leaf area for all test plants were recorded twice a day at 8:00 A.M. and 8:00 P.M.. The adults were monitored until the death of all the flea beetles.

Choice tests

Plants that were fed on by the flea beetles in the no-choice tests were selected for the choice tests. Adult host specificity tests were conducted three times as follows: first, the host species alligatorweed was included in the choice test; second, the host species alligatorweed was absent in the choice test; third, alligatorweed and sessile joyweed were absence in the choice test. The tests were conducted in a round flat-bottomed tub (25 cm in diameter and 10 cm in height) in the environmental growth chamber. About 2 cm by 2 cm leaves excised from the test plants were randomly arranged in the tub. In each test, 10 adults (sex ratio was 1 : 1) were enclosed in a tub and each test was replicated three times. The number of alligatorweed flea beetle adults and the consumed leaf area on each individual test plant were recorded at 24 h. The consumed leaf area was estimated with quadrille paper.

Choice behavior responses of alligatorweed flea beetle adults to the four test plants

A Y-tube olfactometer was used to investigate the behavioral responses of alligatorweed flea beetle adults to the host and nonhost plants. The glass Y-tube olfactometer (internal diameter of 2 cm; length of two arms is 10 cm, length of base tube is 20 cm, angle is 120° between two arms) modified from Ginzel and Hanks (2005) and Wei et al. (2007). The apparatus was placed in a room at 25 to 28 C. The potted plants were placed in a plastic oven bag (40 by 44 cm, Reynolds®, US, with an approximate 7,500 ml in volume). The bag was sealed around each stem approximately 4 to 5 cm above soil surface. The end tubes of the Y were connected to host plant and the other three plants and no plants as control. Using a freshly activated charcoal trap, a stream of filtered and moisturized air was pumped into the bag. The air with emitted plant volatiles was blown in through the Y-tube two arms by a membrane pump (Beijing Institute of Labor Instruments, China) at a rate of 300 ml min^{-1}. Connections between different parts of the set-up consisted of silicone tubing and teflon tubing.

Individual flea beetle adults were collected and starved overnight, then released one at a time within the first cm of the base tube of the olfactometer. If a flea beetle did not choose a side within 5 min, this was scored as a no-choice. A "first choice" was declared whenever the flea beetle moved more than 5 cm into either arm (visually assessed by a line marked on both arms).

Experiments consisted of 30 choices, no choices were discarded. After having tested five flea beetles, the entire set-up was rotated 90° clockwise to avoid any positional effects. Between experiments, all parts of the set-up were cleaned with acetone.

Field adult choice tests

Field choice tests were conducted in large cages (40 cm by 50 cm by 60 cm) for 60 h (8:00 A.M., 1 September 2009 to 8:00 P.M. 3 September 2009) in the field in Taigu, Shanxi province, China. Plants that were fed on by alligatorweed flea beetle in the choice tests were included in these experiments. Test plants grown in pots were moved into the cages and 10 adults (sex ratio was 1 : 1) were enclosed in each cage. Each test was conducted in triplicate. The number of alligatorweed flea beetle adults on individual test plants was recorded at 2, 4, 6, 8, 10, 24, 26, 30, 36, 48, and 60 h. The number of eggs oviposited and the total area of leaf consumed in each test plant were recorded.

Statistical analysis was performed using Microsoft Excel and the SPSS 17.0 statistical package (SPSS Incorporated, Chicago, Illinois). Survival rates and consumed leaf area were compared among plant species using one-way analysis of variance (ANOVA) to test for significant differences. The means were compared using a Tukey test at a significance level of $P = 0.05$. The feeding areas were analyzed after the logarithmic transformation, and if the data were less than 10 mm^2, lg $(x + 1)$ were applied. Arcsine transformations were performed where appropriate on data involving percentages or proportions before analysis (Sokal and Rohlf 1969). A χ^2 test was used to determine the significance of the differences between the numbers of flea beetle choosing each arm of the olfactometer. The preference rate was calculated according to the following formula:

$$\frac{\text{The insects on each tested species}}{\text{The total tested insects in each treatment}} \times 100\%$$

RESULTS AND DISCUSSION

No-choice tests

In no-choice tests, alligatorweed flea beetle adults completed their development on *A. philoxeroides* and sessile joyweed (Table 2). Both plants produced no significant difference on adult survival rates, but showed a significant difference in feeding area (Table 2). All the alligatorweed flea beetle adults that were tested on calico-plant, callaloo (*Amaranthus tricolor* L. syn. A *mangostanus* L.), cockscomb (*Celosia cristata* L.), chard (*Beta vulgaris*. L.), spinach (*Spinacia oleracea* L.), lamb's quarters (*Chenopodium album* L.), carnation (*Dianthus caryophyllus* L.), China pink (*Dianthus chinensis* L.), baby's breath (*Gypsophila elegans* Bieb), lettuce (*Lactuca sativa* L.), water spinach (*Ipomoea aquatica* Forssk.) and common knotgrass (*Polygonum aviculare* L.) died after 10 d. All the alligatorweed flea beetle adults died rapidly at the seventh day after starvation treatment.

The adults fed on 14 of the other 18 plant species under no-choice conditions, but the feeding areas were significantly different from those on alligatorweed and sessile joyweed which could reach as high as 7,018 and 4,982 mm^2 per 10 adults, respectively (Table 2). Alligatorweed flea beetle adults that fed on burning bush [*Bassia scoparia* L. syn. *Kochia scoparia* (L.)Schrad.] and Chinese cabbage (*Brassica rapa* L. var. *pekinensis* Lour.) survived for up to 37 d and 24 d, respectively. Alligatorweed flea beetle adults enclosed with the other tested plant species except alligatorweed and sessile joyweed did not produce any eggs to establish a stable population. Therefore, the other tested plant species did not meet the adult developmental needs of alligatorweed flea beetle.

Choice tests

In multiple-choice tests alligatorweed flea beetle adults were observed on 10 of 16 tested plant species, but not on common amaranth, lamb's quarters, carnation, baby's breath, common purslane, or lettuce. However, they preferred the host plant alligatorweed up to 50%, which more than those to the other tested plant species (Figure 1), though they also attacked sessile joyweed. The feeding areas (Table 3) showed no differences ($P = 0.26$; $P = 0.1$) between alligatorweed and sessile joyweed at 12 and 24 h.

Table 2. Adult survival rate, feeding areas, oviposition and larval hatching of *A. hygrophila*.

Test Species	Survival Rate (%) 1d (M ± SE)	5d (M ± SE)	10d (M ± SE)	Feeding Areas (mm^2/10 adults) (M ± SE)	Oviposition or Not	Larval Hatching or Not
Alligatorweed	100 ± 0 a	100 ± 0 a	96.67 ± 3.33 a	7,018.00 ± 148.99 a	Y	Y
Sessile joyweed	100 ± 0 a	100 ± 0 a	100 ± 0 a	4,982.00 ± 303.44 b	Y	Y
Calico-plant	100 ± 0 a	26.67 ± 6.67 de	0 c	0 d	N	—
Common amaranth	100 ± 0 a	16.67 ± 3.33 de	3.33 ± 3.33 c	18.67 ± 11.20 d	N	—
Callaloo	100 ± 0 a	30.00 ± 5.77 de	0 c	46.67 ± 13.69 d	N	—
Cockscomb	100 ± 0 a	20.00 ± 15.28 de	0 c	11.00 ± 0.58 d	N	—
Globe amaranth	100 ± 0 a	30.00 ± 15.28 de	3.33 ± 3.33 c	125.67 ± 89.93 d	N	—
Sugar beet	100 ± 0 a	70.00 ± 5.77 b	23.33 ± 8.82 bc	525.00 ± 127.64 c	N	—
Chard	96.67 ± 3.33 a	13.33 ± 6.67 de	0 c	38.00 ± 15.10 d	N	—
Burningbush	100 ± 0 a	70.00 ± 0 b	30.00 ± 5.77 b	214.33 ± 25.15 d	N	—
Spinach	100 ± 0 a	43.33 ± 6.67 cd	0 c	1.00 ± 0.58 d	N	—
Lamb's quarters	100 ± 0 a	40.00 ± 5.77 cd	0 c	3.33 ± 3.33 d	N	—
Carnation	100 ± 0 a	0 e	0 c	4.00 ± 2.31 d	N	—
China pink	100 ± 0 a	30.00 ± 0 de	0 c	0 d	N	—
Baby's breath	100 ± 0 a	0 e	0 c	16.00 ± 14.05 d	N	—
Common purslane	100 ± 0 a	43.33 ± 13.33 cd	13.33 ± 8.82 c	164.67 ± 114.17 d	N	—
Chinese cabbage	100 ± 0 a	63.33 ± 3.33 bc	10.00 ± 5.77 c	349.67 ± 47.91 cd	N	—
Lettuce	100 ± 0 a	36.67 ± 3.33 cde	0 c	1.00 ± 1.00 d	N	—
Water spinach	100 ± 0 a	6.67 ± 3.33 de	0 c	0 d	N	—
Common knotgrass	100 ± 0 a	40.00 ± 5.77 cd	0 c	0 d	N	—
CK	100 ± 0 a	33.33 ± 12.01 cde	0 c	0 d	N	—

Note: Oviposition status was observed 3 d after alligatorweed flea beetle adults being enclosed with tested plant species.
Means in the same column followed by the same letters are not significantly different, $P > 0.05$.

In multiple-choice with the absence of alligatorweed assays, alligatorweed flea beetle occurred on 12 of 15 tested plant species and not on baby's breath, lamb's quarters, or carnation, but they preferred the wall of the pot and sessile joyweed more than the other tested plant species (Figure 1). There were significant differences in feeding areas (Table 3) at 12 h ($F_{(3,8)} = 33.55$; $P < 0.01$) and 24 h ($F_{(3,8)} = 25.09$; $P < 0.01$). The adults fed only on sessile joyweed at 12 h and 170.67 mm^2 at 24 h, but just a little on the other three species.

Alligatorweed flea beetle adults preferred the wall of pot more than any tested plant species in absence of alligator-

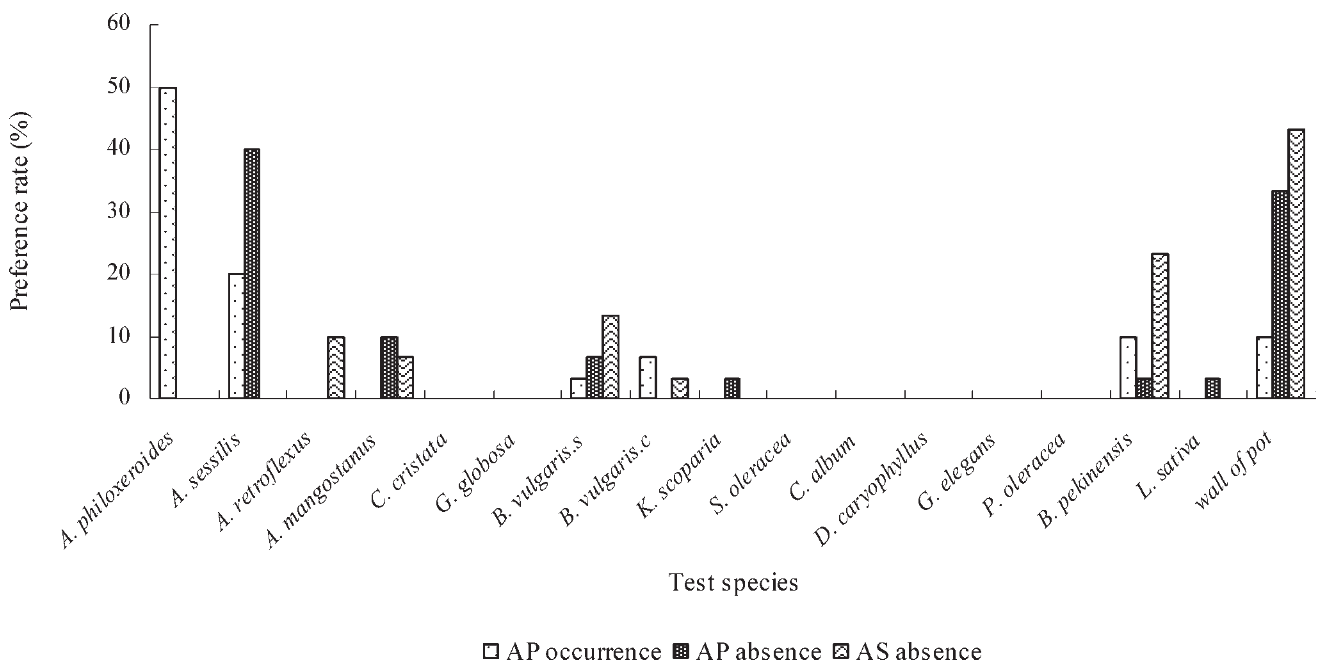

Figure 1. Preference of alligatorweed flea beetle adults at 24 h in choice tests. Note: AP occurrence refers to alligatorweed flea beetle adults with alligatorweed occurrence; AP absence refers to alligatorweed flea beetle adults in the absence of alligatorweed; AS absence refers to alligatorweed flea beetle adults in the absence of alligatorweed and sessile joyweed.

Table 3. Feeding areas (mm^2/10 adults) of plant species by *A. hygrophila* adults.

Test species	Presence of Alligatorweed		Without Alligatorweed		Without Alligatorweed and Sessile Joyweed	
	12 h (M ± SE)	24 h (M ± SE)	12 h (M ± SE)	24 h (M ± SE)	12 h (M ± SE)	24 h (M ± SE)
Alligatorweed	93.33 ± 31.22 a	240.33 ± 55.73 a	—	—	—	—
Sessile joyweed	40 ± 26.69 a	106.33 ± 31.06 a	53.33 ± 9.21 a	170.67 ± 33.82 a	—	—
Callaloo	0	0	0 b	0.33 ± 0.33 b	0	0
Sugar beet	0	0	0 b	1.33 ± 0.88 b	10.67 ± 3.38 a	14.33 ± 4.67 a
Chard	0	0	0 b	1.67 ± 0.88 b	11.67 ± 5.36 a	39.67 ± 10.04 a

Means in the same column followed by the same letters are not significantly different, $P > 0.05$.

weed and sessile joyweed (Figure 1). Two of three tested plant species were attacked by alligatorweed flea beetle. There was no significant difference in feeding areas (Table 3) when alligatorweed flea beetle was on these two species at 12 h ($F_{(1,4)} = 0.025$; $P = 0.88$) and at 24 h ($F_{(1,4)} = 5.24$; $P = 0.08$).

Choice behavior responses of alligatorweed flea beetle adults to the four test plants

The choice behavior responses of alligatorweed flea beetle adults to the host plant alligatorweed and nontarget species sessile joyweed, sugar beet and chard with a Y-tube olfactometer results showed that alligatorweed flea beetle adults had a strong preference to the host plant alligatorweed , and the preference rate of alligatorweed flea beetle to the host plant could reach up to 72 to 100% (Figure 2).

Field adult choice tests

In field studies, *A. hygrophila* adults showed a significant preference for alligatorweed over the other three tested species (Figure 3). The feeding areas of alligatorweed flea beetle on alligatorweed (271.7 ± 22.3 mm^2) were higher than on sessile joyweed (117 ± 51.7 mm^2) but the difference was not significant ($F_{(1,4)} = 7.54$; $P > 0.05$). Alligatorweed flea beetle also preferred ovipositing on the host plant alligatorweed Twelve and four egg masses were found on alligatorweed and sessile joyweed respectively; besides this, only one egg mass was found on chard.

Alligatorweed flea beetle had a significant difference in host selection to 20 representative plant species. In this study, nontarget feeding was observed on sugar beet and chard in the choice tests with the presence of the host plant species alligatorweed. Therefore, alligatorweed flea beetle adults may have nontarget effects sugar beet and chard. However, based on the no choice tests alligatorweed flea beetle adult could not produce progeny to establish a stable population. Choice behavior responses showed that the flea beetles had a small chance to choose sugar beet and chard and additional field studies also showed that the flea beetles did no damage to sugar beet and chard. In conclusion, alligatorweed flea beetle could not complete their development on these test plant species. The damage on the other plants was considered to be occasional, producing minimal risk in the field, thus this species would have limited nontarget effects on native plants and ecosystems.

Beyond doubt, the alligatorweed flea beetle appeared to have a strong preference for the host plant alligatorweed. However, alligatorweed flea beetle did not just feed slightly on the congeneric species sessile joyweed, but adult feeding and oviposition did occur under the same laboratory conditions. Sessile joyweed is a native weed of rice crops throughout tropical lands, and of other cereal crops,

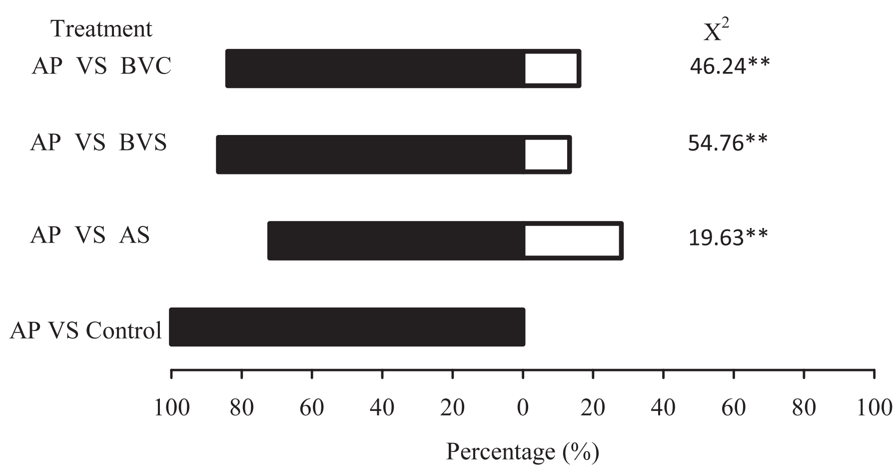

Figure 2. Preference rate of alligatorweed flea beetle adults on four test species. AP refers to alligatorweed flea beetle adult made a choice to alligatorweed, AS refers to alligatorweed flea beetle adult made a choice to sessile joyweed, BVS refers to alligatorweed flea beetle adult made a choice to sugar beet, BVC refers to alligatorweed flea beetle adult made a choice to chard Control refers to alligatorweed flea beetle adult made a choice to the no plant. χ^2 test for significant differences between numbers of flea beetles in each arm. The black portion refers to alligatorweed flea beetle adult made a choice to alligatorweed, the white portion refers to *A. hygrophila* adult made a choice to the other three test species and the control. ** $P < 0.01$.

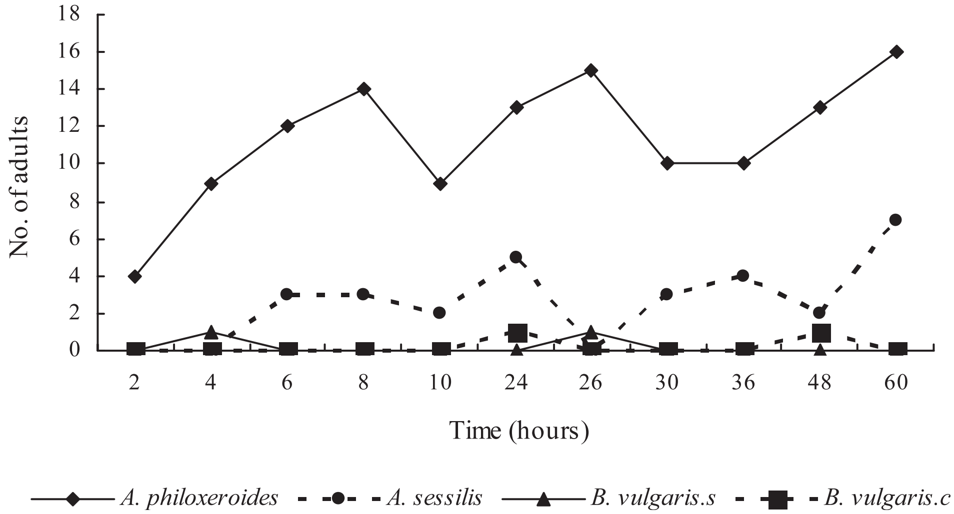

Figure 3. Preference of alligatorweed flea beetle adults on four test plant species in the field studies

sugarcane, and banana. Lu et al. (2010) reported that alligatorweed flea beetle cannot pupate on sessile joyweed, thus there would be no risk of nontarget damage on *A. sessilis* in ecosystems where there are no congeneric hosts. However, in natural ecosystems, indigenous sessile joyweed and invasive alligatorweed always grow intermingled; sessile joyweed could provide a marginally suitable host for the flea beetle. As a result, it is possible that sessile joyweed could facilitate the biological control of alligatorweed. Additionally, limiting the growth and density of sessile joyweed potentially threatens the native ecological balance and biological diversity. Callaway et al. (1999) suggested that host-specific biological control agents can produce strong non-target effects through indirect interactions associated with ecological replacement, compensatory responses and food-web subsidies (Pearson and Callaway 2003). Burger and Louda (1994) reported that the spread of cactus moth disrupts interactions between native prickly pear and their associated insects. Therefore, the field populations of alligatorweed flea beetle on sessile joyweed and the indirect nontarget effects arising from such subsidies should be monitored for any potential adverse effects to the native systems in the future.

Alligatorweed flea beetle presents some risk to the congeneric plant, sessile joyweed, which has a close phylogenetic relationship to the target weed alligatorweed. We suspect that the congeneric species had the same secondary plant metabolites to attract the flea beetle to feed and oviposit. Another view suggested that specialist insects using the same plant taxon had evolved different detoxification or excretion mechanisms to avoid the impact of the same secondary plant metabolites (Saikkonen et al. 1996). Avoiding competition and reducing mortality from natural enemies has also been proposed as the main factors of agents of selection in the evolution of the specialistic feeding habit of herbivorous insects (Schoonhoven et al. 2005).

In addition, according to our no-choice host specificity tests, the survival rates of adults which were confined to some nonhost species were lower than the control without any plants. We speculate that some nonhost plants may produce defenses such as secondary metabolites that have negative effects on the development of alligatorweed flea beetle.

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