

Host range of *Secusio extensa* (Lepidoptera: Arctiidae), and potential for biological control of *Senecio madagascariensis* (Asteraceae)

M. M. Ramadan¹, K. T. Murai¹ & T. Johnson²

¹ State of Hawaii Department of Agriculture, Plant Pest Control Branch, Honolulu, Hawaii, USA

² Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Volcano, Hawaii, USA

Keywords

Host range, *Secusio extensa*, *Senecio madagascariensis*

Correspondence

Mohsen M. Ramadan (corresponding author),
State of Hawaii Department of Agriculture,
Plant Pest Control Branch, 1428 South King
Street, Honolulu, Hawaii 96814, USA.
E-mail: Mohsen.M.Ramadan@hawaii.gov

Received: September 15, 2009; accepted:
April 6, 2010.

doi: 10.1111/j.1439-0418.2010.01536.x

Abstract

Secusio extensa (Lepidoptera: Arctiidae) was evaluated as a potential biological control agent for Madagascar fireweed, *Senecio madagascariensis* (Asteraceae), which has invaded over 400 000 acres of rangeland in the Hawaiian Islands and is toxic to cattle and horses. The moth was introduced from southeastern Madagascar into containment facilities in Hawaii, and host specificity tests were conducted on 71 endemic and naturalized species (52 genera) in 12 tribes of Asteraceae and 17 species of non-Asteraceae including six native shrubs and trees considered key components of Hawaiian ecosystems. No-choice feeding tests indicated that plant species of the tribe Senecioneae were suitable hosts with first instars completing development to adult stage on *S. madagascariensis* (78.3%), *Delairea odorata* (66.1%), *Senecio vulgaris* (57.1%), *Crassocephalum crepidioides* (41.2%), and at significantly lower rates on *Emilia fosbergii* (1.8%) and *Erechtites hieracifolia* (1.3%). A low rate of complete larval development also was observed on sunflower, *Helianthus annuus* (11.6%), in the tribe Heliantheae. However, sunflower was rejected as a potential host in larval-feeding and adult oviposition choice tests involving the primary host *S. madagascariensis* as control. Although larvae died as first instars on most test species, incomplete development and low levels of feeding were observed on nine species in the tribes Heliantheae, Cardueae and Lactuceae. Larvae did not feed on any non-Asteraceae tested, including species with similar pyrrolizidine alkaloid chemistry, crops, and six ecologically prominent native species. Because all species of Senecioneae are non-native and weedy in Hawaii, these results indicate that *S. extensa* is sufficiently host-specific for introduction for biological control. High levels of feeding damage observed on potted plants indicate that *S. extensa* can severely impact the target fireweed as well as *D. odorata*, a noxious weed in native Hawaiian forests.

Introduction

Madagascar fireweed, *Senecio madagascariensis* Poirlet (Asteraceae, Senecionae), is a daisy-like annual or biennial branching herb that grows upright to 50 cm in height with small (1.5 cm diam) yellow flowers.

The seed heads produce numerous plumed achenes (as many as 30 000 per plant) that disperse easily by wind, allowing rapid infestation of pastures (Motooka et al. 2004). All parts of fireweed contain pyrrolizidine alkaloids (PAs) which when consumed by animals are converted into toxic compounds that

cause liver damage (Dale Gardner et al. 2006). Young animals are particularly vulnerable to PAs since senecionine may accumulate in milk (Small et al. 1993). Although unpalatable, fireweed is consumed by livestock when other feed is not available (Sindel and Michael 1988; Scott et al. 1998) or when small plants are intermixed with desirable forage. Contaminated hay or silage from invaded fields may also cause poisoning since the toxins are unaffected by drying (Dickinson et al. 1976; Sindel 1986).

Fireweed is native to the southeastern region of Africa, where it is known to occur from coastal areas to 1500 m above sea level. It is distributed from Madagascar and the Mascarene Islands through coastal Mozambique to Kwazulu-Natal and the Eastern and Western Cape provinces of South Africa (Sindel et al. 1998). In Madagascar, fireweed occurs in small isolated populations in the low elevation southeast and the semi-arid southwest of the island (Marohasy 1989). In its native region, fireweed is not perceived as an invasive species and is only common on vacant lands, sand dunes, lands cleared for agriculture, and along roadsides (M. Ramadan, pers. obs.).

Fireweed has variable growth habits and leaf shapes dependant on the type of soil and habitat, (Le Roux et al. 2006). Genetic analyses of fireweed in Australia showed a close match with the *S. madagascariensis* complex from South Africa and a slight difference from *S. madagascariensis* from Madagascar (Scott et al. 1998). Molecular analysis of Hawaiian fireweed populations showed that they also match populations from South Africa more closely than populations from Madagascar and Swaziland (Le Roux et al. 2006). Hawaiian populations are thought to have arrived in carpet grass seed shipments from Australia (Motooka et al. 2004).

A significant weed of agricultural grasslands in Australia, fireweed has spread through many parts of coastal New South Wales and southeastern Queensland, as well as southeastern Buenos Aires province in Argentina (Sindel et al. 1998). It also has been recognized as a noxious weed in Colombia, Venezuela, Uruguay, and Japan (Satoru et al. 1999). Efforts to control fireweed by mechanical, chemical and biological means, using herbivores already present, failed against well-established populations in Australia, and a previous biological control project against fireweed was halted because of lack of funds (Marohasy 1989; MacFadyen and Sparks 1996).

Fireweed has been spreading widely in the Hawaiian Islands since its first appearance around 1980.

Infestations on Oahu and Kauai have been controlled mechanically, but on Maui and Hawaii, where more than 400 000 acres of rangelands have been invaded, chemical and mechanical control is not economically practical. Chemical control of fireweed on the island of Hawaii alone would cost over eleven million dollars per year, estimated as three treatments with the systemic herbicide MCPA @ \$11 per acre on 350 000 acres (P. Motooka, University of Hawaii, CTAHR, 2002 pers. comm.). Generalist herbivores (e.g. grasshoppers, weevils, thrips, aphids, scale insects, whiteflies, and mites) that currently feed on fireweed in Hawaii cause insignificant damage (M. Ramadan, pers. obs.). Classical biological control using host-specific natural enemies from the native range was selected as a method for reducing existing fireweed populations, curbing their spread and decreasing reliance on costly chemicals. The potential for classical biological control of fireweed in Hawaii appears good because, unlike in Australia, there are no native species in the same tribe as fireweed (Senecioneae) and none of the naturalized species is economically important.

The Hawaii Department of Agriculture (HDOA) initiated a survey for potential biological control agents in South Africa (Kwazulu-Natal province) and Madagascar (southeastern Toliara province) during August and September of 1999. During this survey, eleven insects and two pathogens were shipped to the HDOA Insect Containment Facility for evaluation and host range testing (M. Ramadan, unpublished data). A yellow rust fungus identified as *Puccinia lagenophorae* Cooke (Basidiomycetes: Uredinales) from fireweed in Australia, South Africa, and Madagascar was tested on 42 species in eight tribes of Asteraceae. The rust severely infected fireweed, but tests were discontinued when two Hawaiian endemic species were found to be susceptible (Killgore et al. 2001). The insect agents included five flower-head feeders, three stem borers, two root feeders, and a defoliating arctiid moth. Host testing on seven of these species and a white rust were terminated because of rearing problems or minimal impact on fireweed. One insect, the arctiid moth *Secusio extensa* (Lepidoptera: Arctiidae), showed potential as an agent and was therefore studied further.

This report summarizes results of detailed studies on the host range of the Madagascan fireweed moth, *S. extensa*. A cohort of this species was introduced in October 1999 to the HDOA Insect Containment Facility, where host-specificity tests were conducted to address its potential as a biological control agent and its possible impact on non-target species.

Materials and Methods

Origin and identity of agent population

Caterpillars of the fireweed moth, *S. extensa* (Butler), (Lepidoptera: Arctiidae) were collected from the southern region of Toliara Province, Madagascar. Young and mature larvae were collected from fireweed infested plants at three localities along the sand dunes of the Indian Ocean: Saint Luce (24°.46'S, 47°.10'E), Evatra (24°.58'S, 47°.05'E), and Fort Dauphin (25°.02'S, 46°.56'E). Larvae were reared to the pupal stage on field collected fireweed cuttings immersed in water. The initial cohort produced from this collection was 606 pupae, out of which 398 developed into adults (34% pupal mortality) with a sex ratio of approximately 1 : 1.

Adult moths were identified as *S. extensa* (Butler) by John Rawlins of the Carnegie Museum of Natural History. There is no published information on the life history of this mottled beige moth. The genus contains a number of other species of which *Secusio pustularia* Walker and *Secusio pulverata* from mainland Africa are closely related (Mlawula Nature Reserve Fauna 2005).

Voucher specimens were placed in the insect reference collection of the HDOA, the Bishop Museum, Honolulu, Hawaii, and the Department of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA.

Insect rearing and colony maintenance

Secusio extensa was reared continuously in the HDOA Insect Containment Facility at 22.0 ± 1.0°C at night and 34.0 ± 2°C during the day, 60–80%RH, and 13L: 11D photoperiod (under fluorescent light plus natural sunlight through window glass panels). To maintain the gene pool of the moth population during host range studies, a random sample of 50 first instars from egg batches of at least three females per generation were used in the rearing protocol. Newly hatched larvae were placed on a potted fireweed plant (≈50 cm in height, 2–3 months old) in a cage (80 × 50 × 50 cm). Newspaper was spread on the bottom of each cage for mature larvae to pupate. Host plants were added *ad libitum* until all larvae pupated. Pupae were removed and placed into emergence cages (65 × 45 × 45 cm) with water and honey.

After emergence, adult moths were paired in plastic rearing containers (1.9 l) for mating and egg

deposition. Moths were provided with honey on the lid netting and a water container with a cotton wick. Eggs were collected daily and placed in Petri dishes. Newly hatched larvae were used in host range tests and colony maintenance.

Colonies were continuously propagated on potted fireweed for about eight generations per year.

Fireweed was propagated on Oahu from field collected plants shipped from the island of Hawaii. In case of a shortage of fireweed, *Crassocephalum crepidioides* (Benth.) was added to the cages mainly during the intense feeding periods of the final instar. This plant has been shown in previous experiments to be a secondary host for *S. extensa*. However, larvae in control cages for host-specificity tests were reared exclusively on the primary host, *S. madagascariensis*.

Test plant species

Plants for host range testing were chosen following a protocol proposed by Wapshere (1974, 1989). Under this procedure, potential biological control agents were exposed to a sequence of plant species, from the most closely related to fireweed (tribe Senecioneae) to successively more distant relatives, until the host range was adequately circumscribed. *S. madagascariensis* belongs to the family Asteraceae and subfamily Asteroideae. In Hawaii, the Asteraceae are represented by 76 genera and 181 species distributed in 12 tribes. Half of the species are endemic. Ninety species are naturalized, and many are common weeds, but few have become serious problems (Wagner et al. 1999). Members of the tribe Senecioneae are represented by six genera (*Crassocephalum*, *Delairea*, *Emilia*, *Erechtites*, *Petasites*, and *Senecio*), all naturalized and non-native in the Hawaiian Islands (Wagner et al. 1999). *Delairea odorata*, *Senecio vulgaris*, and *S. madagascariensis* are invasive weeds on Hawaii and Maui and of no economic importance.

Seventy-one species of Asteraceae were tested, representing the two subfamilies and all 12 tribes, particularly members of the tribes of Helenieae and Heliantheae, which are closely related to Senecioneae (Judd et al. 2002) (table 1). Outside the Asteraceae, two species that, like fireweed, contain pyrrolizidine alkaloids and nine other common plant species were tested. In addition, six ecologically prominent native Hawaiian shrubs and trees were recommended for testing by the US-Fish and Wildlife Service (table 1). Plant species were identified by Hawaii Department of Agriculture staff and botanists

Table 1 Plant list of Asteraceae and non-Asteraceae used for host range experiments of *Secusio extensa*. Systematic arrangements of Asteraceae (sorted by species within subfamily and tribe) adopted from Judd et al. (2002) and Wagner et al. (1999)

Family/Subfamily	Tribe	Species	Common name	Status	
Asteraceae: Asteroideae	Anthemideae	<i>Artemisia mauiensis</i> (A. Gray) Skottsbo.	Ahinahina	endemic	
		<i>Achillea filipendulina</i> Lam.	Fern leaf yarrow	naturalized	
	Astereae	<i>Conyza bonariensis</i> (L.) Cronq.	Hairy horseweed	naturalized	
		<i>Conyza canadensis</i> (L.) Cronq.	Horseweed	naturalized	
		<i>Heterotheca grandiflora</i> Nutt.	Telegraph weed	naturalized	
		<i>Erigeron</i> sp.	Pink jewel, Fleabane	naturalized	
		<i>Erigeron karvinskianus</i> DC	Daisy fleabane	naturalized	
		<i>Remya kauaiensis</i> Hillebr.	Kauai remya	endemic	
		<i>Tetramolopium filiforme</i> Sherff	Ridgetop tetramolopium	endemic	
		<i>Tetramolopium rockii</i> Sherff	Dune tetramolopium	endemic	
		Calenduleae	<i>Calendula officinalis</i> L.	Pot marigold	naturalized
		Eupatorieae	<i>Ageratina adenophora</i> (Spreng.) R. King & H. Robinson	Maui pamakani	naturalized
	<i>Ageratina riparia</i> (Regel) R. King & H. Robinson		Hamakua pamakani	naturalized	
	<i>Ageratum conyzoides</i> L.		Maile honohono	naturalized	
	Gnaphalieae	<i>Ageratum houstonianum</i> Mill.	Maile honohono	naturalized	
		<i>Gnaphalium purpureum</i> L.	Purple cudweed	naturalized	
		<i>Helichrysum bracteatum</i> (Vent.) Andr.	Bracted strawflower	naturalized	
	Helenieae	<i>Argyroxiphium</i> sp.	Silversword	endemic	
		<i>Dubautia arborea</i> (A. Gray) D. Keck	Kupaoa	endemic	
		<i>Dubautia herbstobatae</i> G. Carr	Naenae	endemic	
		<i>Dubautia laevigata</i> A. Gray	Smooth dubautia	endemic	
		<i>Dubautia laxa</i> Hook. & Arnott	Naenae pua melemele	endemic	
		<i>Dubautia raillardoides</i> Hillebr.	Naenae ula	endemic	
		<i>Dubautia scabra</i> (DC) D. Keck	Rough dubautia	endemic	
		<i>Flaveria trinervia</i> (Spreng.) C. Mohr	Clustered yellowtops	naturalized	
		<i>Gaillardia grandiflora</i> Van Houtte	Blanket flower	naturalized	
		<i>Tagetes erecta</i> L.	Aztec marigold	Hybrid cultivar	
		<i>Wilkesia hobbdi</i> St. John	Dwarf iliau	endemic	
		Heliantheae	<i>Bidens alba</i> (L.) DC	Spanish needles	naturalized
			<i>Bidens amplexans</i> Sherff	Kokolau	endemic
			<i>Bidens bipinnata</i> L.	Spanish needles	endemic
			<i>Bidens campylotheca</i> Schultz-Bip.	Viper beggarticks	endemic
			<i>Bidens cosmoides</i> (A. Gray) Sherff	Poola nui	endemic
			<i>Bidens menziesii</i> (A. Gray) Sherff	Kookoolau	endemic
	<i>Bidens pilosa</i> L.		Ki, hairy beggarticks	naturalized	
	<i>Bidens</i> sp.			endemic	
	<i>Eclipta prostrata</i> (L.) L.		False daisy	naturalized	
	<i>Galinsoga quadriradiata</i> Ruiz & Pav.		Peruvian daisy	naturalized	
	<i>Helianthus annuus</i> L.		Common sunflower	naturalized	
	<i>Lipochaeta subcordata</i> A. Gray		Grassland nehe	endemic	
	<i>Lipochaeta connata</i> (Gaud.) DC		Nehe	endemic	
	<i>Montanoa hibiscifolia</i> Benth.		Tree daisy	naturalized	
	<i>Parthenium hysterophorus</i> L.		False ragweed	naturalized	
	<i>Sigesbeckia orientalis</i> L.		Small yellow crown-beard	naturalized	
	<i>Synedrella nodiflora</i> (L.) Gaertn.		Nodeweed	naturalized	
	<i>Tithonia diversifolia</i> (Hemsl.) A. Gray		Tree marigold	naturalized	
	<i>Tridax procumbens</i> L.		Coat buttons	naturalized	
	<i>Verbesina encelioides</i> (Cav.) Benth. & Hook.	Golden crown-beard	naturalized		
	<i>Wedelia trilobata</i> (L.) Hitchc.	Creeping daisy	naturalized		
	<i>Xanthium strumarium</i> L.	Kikania, cockleburr	naturalized		
	Inuleae	<i>Zinnia peruviana</i> (L.) L.	Peruvian zinnia, Pua pihi	naturalized	
		<i>Pluchea indica</i> (L.) Less.	Indian pluchea	naturalized	
		<i>Pluchea carolinensis</i> (Jacq.) G. Don	Sour bush	naturalized	

Table 1 Continued

Family/Subfamily	Tribe	Species	Common name	Status
	Senecioneae	<i>Crassocephalum crepidioides</i> (Benth.) S. Moore	Red flower rag-leaf	naturalized
		<i>Emilia fosbergii</i> Nicolson	Pualele, Florida tassel flower	naturalized
		<i>Erechtites hieracifolia</i> (L.) Raf. Ex DC	American burnweed	naturalized
		<i>Farfugium japonicum</i> (L.) Kitam ¹	Leopard plant	ground cover plant
		<i>Delairea odorata</i> Lem.	Cape ivy	naturalized
		<i>Senecio confuses</i> (DC.) Britten ¹	Mexican flame vine	escaped cultivation
		<i>Senecio madagascariensis</i> Poir.	Madagascar fireweed	naturalized
		<i>Senecio vulgaris</i> L.	Common groundsel	naturalized
Cichorioideae	Arctoteae	<i>Gazania rigens</i> (L.) Gaertner ¹	Gazania	naturalized
	Cynareae	<i>Arctium lappa</i> L.	Gobo	naturalized
		<i>Centaurea melitensis</i> L.	Napa thistle	naturalized
		<i>Cirsium vulgare</i> (Savi) Ten.	Bull thistle	naturalized
	Lactuceae	<i>Lactuca sativa</i> L.	Manoa lettuce	naturalized
		<i>Lactuca serriola</i> L.	Prickly lettuce	naturalized
		<i>Reichardia picroides</i>	Picridium	naturalized
		<i>Sonchus oleraceus</i> L.	Pualele	naturalized
		<i>Taraxacum officinale</i> W. W. Weber	Common dandelion	naturalized
		<i>Youngia japonica</i> (L.) DC	Oriental hawkbeard	naturalized
	Vernonieae	<i>Elephantopus mollis</i> Kunth	Elephant foot	naturalized
Non-Asteraceae				
Fabaceae		<i>Crotalaria mucronata</i> Desv. ¹	Smooth rattle pod	naturalized
		<i>Crotalaria spectabilis</i> Roth ¹	Common rattle pod	naturalized
Musaceae		<i>Musa acuminata</i> Colla	Common banana	cultivated
Caricaceae		<i>Carica papaya</i> L.	Papaya	cultivated
Urticaceae		<i>Pipturus albidus</i> (Hook. & Arn.) A. Gray	Mamaki	endemic
Arecaceae,		<i>Cocos nucifera</i> L.	Sprouted coconut palm	cultivated
Araceae		<i>Colocasia esculenta</i> (L.) Schott	Taro	naturalized
Cucurbitaceae		<i>Coccinia grandis</i> (L.) Voigt	Ivy gourd	naturalized
Poaceae		<i>Sorghum bicolor</i> (L.) Moench	Sorghum	naturalized
		<i>Saccharum officinarum</i> L.	Sugarcane	cultivated
Convolvulaceae		<i>Ipomoea batatas</i> (L.) Lam.	Sweetpotato	cultivated
Plants recommended by US-Fish and Wildlife Service ²				
Fabaceae		<i>Acacia koa</i> A. Gray	Koa	endemic
		<i>Sophora chrysophylla</i> (Salisb.) Seem.	Mamani	endemic
Myoporaceae		<i>Myoporum sandwicense</i> (A. DC.) A. Gray	Naio	endemic
Myrtaceae		<i>Metrosideros polymorpha</i> Gaudich.	Ohia lehua	endemic
Dicksoniaceae		<i>Cibotium glaucum</i> (Sm.) Hook. & Arn.	Hapuu	endemic
Sapindaceae		<i>Dodonaea viscosa</i> (L.) Jacq.	Aalii	endemic

¹Plant species tested as bouquets of cut foliage.

²Tests conducted at USFS-HVNPQF, island of Hawaii.

at the Bishop Museum, Honolulu, using keys and descriptions in Wagner et al. (1999).

Potted test plants, propagated from seeds or field collected as young plants, were held in outdoor cages and transferred into quarantine when needed for host range testing. Plants were usually 75 cm or smaller in height so as to fit in test cages. When ready for use, plants were checked for contaminants (i.e. aphids, mites, thrips, and lepidopteran larvae or eggs) and thoroughly cleaned with water or dipped in soapy water at least one week prior to testing. No insecticides were used on test plants.

No-choice larval-feeding tests

Most tests were conducted at the Hawaii Department of Agriculture Insect Containment Facility, Honolulu, island of Oahu, during 1999–2005. Tests with six non-Asteraceae plant species were conducted by the USDA Forest Service, at the Hawaii Volcanoes National Park Quarantine Facility on the island of Hawaii during 2001 (averaging 20.5°C, 80%RH).

Potential host range was estimated by measuring mortality and rates of development of newly hatched

larvae exposed to test plants versus the control, *S. madagascariensis*. Generally, potted plants were used in tests, but occasionally bouquets of cut foliage were used (for details see table 1). Each plant was placed in a 80 × 50 × 50 cm cage and 50 newly emerged, unfed first instars (<12 h old) were transferred onto the plant leaves using a soft camel hair brush. Observations on the numbers of larvae remaining on the plant, feeding marks, and larval development were recorded every 24 h. If feeding occurred, new plants were added, *ad libitum*. Surviving larvae were monitored and their development beyond the first instar was observed until they perished or successfully pupated. Numbers of pupae and enclosing adults were recorded. Tests were terminated when all larvae had died or completed development to adult moths. Tests were replicated at least three times for each plant species using new insect cohorts and new potted plants. Plants that supported larval development were tested further using more replicates and subjected to choice and oviposition tests.

Larval-feeding damage was scored from 0 to 5 as: (0) no damage, (1) probing and superficial feeding on less than 5% damage of leaf area, (2) light feeding on 5–20% of leaf area, (3) moderate feeding on >20–40% of leaf area, (4) severe damage on >40–60% of leaf area, and (5) intense feeding on >60% of leaf area and stems, eventually killing the plant.

Choice larval-feeding tests with sunflower

Further studies included choice tests with the only plant species outside the tribe Senecioneae that yielded live adults from no-choice trials, common sunflower, *Helianthus annuus*.

Potted plants of fireweed and sunflower were offered simultaneously in 80 × 50 × 50 cm cages. Twenty-five first instars (<12 h-old) were carefully transferred into a paper cone attached with tape to the upper cage wall, giving the wandering larvae a choice between the two plants. Plants were placed adjacent to each other with the leaves touching one another and the cage walls. Two hours after placement of larvae, the number of larvae on each plant was counted. Observations on their feeding damage and development were continued daily until all larvae reached the pupal stage. This test was replicated five times using fresh plants and separate cohorts of larvae. An additional five replicates of this experiment were conducted by placing the larvae directly on sunflower, instead of on the cage walls.

Oviposition choice tests

Representative species of Senecioneae (*C. crepidioides*, *S. vulgaris*) and Heliantheae (*H. annuus*, *Bidens pilosa*) that supported larval development were subsequently exposed in tests of adult host choice for oviposition. No-choice feeding tests on these species already showed some degree of larval development. Therefore, only choice oviposition tests were conducted to determine adult host recognition. Since oviposition behaviour can depend on mating status and age of females, tests were conducted during and beyond the peak mating and oviposition period of *S. extensa*. Female mating status was determined by dissection for the presence of sperm and observations on egg hatching (M. Ramadan, unpublished data; Renwick and Chew 1994). Because flowers may be an important factor for oviposition choice, flowering plants were used in all tests.

Five pairs of newly emerged (<12 h-old) *S. extensa* adults were confined for a day in a plastic container (1.9 l) with water and honey, for mating and ovarian maturation. On the second day, the moths were transferred to a large screen cage (1.0 × 1.0 × 1.7 m) containing one potted sunflower and one potted fireweed (control). Honey and water were provided for moth feeding. Plants were kept about 40 cm apart, and were watered and rotated daily. Plants were examined daily for 7 days. Leaves containing eggs were excised, and eggs counted. Eggs on cage walls were also recorded and removed daily. This test was replicated five times using fresh plants and separate moth cohorts. Relative acceptability of plants for oviposition was calculated as the total eggs laid on each plant as a percentage of the total eggs deposited in the cage.

Adult oviposition choice tests with *C. crepidioides*, *S. vulgaris* and *B. pilosa* were conducted in small cages (80 × 50 × 50 cm) with a single pair of newly emerged moths provided with a bouquet of test plant and a bouquet of fireweed control per replicate. Tests continued until the adult female died, with methods otherwise the same as described above. Each test was replicated 9–10 times using new cuttings and new insects.

Data analysis

Data from oviposition tests, number of leaves on which eggs were found, number of eggs laid on each leaf, and percentage of eggs laid on the plant were analyzed using Student's *t*-test at $P < 0.05$. Percentage data were analyzed using PROC ANOVA (SAS

Institute 1985) and were arcsine-square root transformed before statistical analysis to meet underlying assumption of ANOVA (Zar 1999). Untransformed mean values are reported in the text and tables. Survival data were analyzed by one way analysis of variance (ANOVA) and means were separated by the Tukey Kramer honestly significant difference (HSD) multiple comparison test.

Results

No-choice larval-feeding tests

Except for one species, all tested plants in the tribe Senecioneae supported development of *S. extensa* to the adult stage (table 2). *S. extensa* caused extensive damage on *D. odorata* and *S. vulgaris*, comparable to damage on fireweed (table 2). Survival to the adult stage was $66.1 \pm 2.0\%$ and $57.1 \pm 2.1\%$ for *D. odorata* and *S. vulgaris*, respectively, not significantly different from survival on control plants (78.3%). Survival to adult was significantly reduced to $41.2 \pm 7.4\%$ when larvae developed on *C. crepidioides* (d.f. = 6, 47; $F = 51.08$; $P = 0.0001$). Larvae also fed on the Mexican flame vine, *Senecio confusus* (DC) ($n = 1$). In contrast, on *Emilia fosbergii* and *Erechtites hieracifolia* less than 2% of the tested larvae developed to adult, indicating that these are inferior hosts (fig. 1). No larval development occurred on cuttings of the ground cover Japanese silver leaf, *Farfugium japonicum* (L.) Kitam (table 2).

Apart from plant species in the tribe Senecioneae, six plant species in the tribe Heliantheae supported development of *S. extensa* to some degree (table 2). Only *H. annuus* supported development to adult ($11.6 \pm 3.2\%$). Feeding damage to *H. annuus* was superficial to light (damage rating of 1–2). Survival rates of all immature stages and adults reared on *H. annuus* during no-choice trials were significantly reduced compared to those reared on fireweed (table 3). A mean of 4.9 ± 2.9 (9.1%) of larvae developed to the final fifth instar when fed on *B. pilosa*. However, larvae were smaller in size (57–83% of that on fireweed), caused minor damage (damage rating of 1–2), and took longer to reach the pupal stage. Only two out of 410 larvae on *B. pilosa* survived to pupate, and no adults emerged (table 2). On other Heliantheae, including a few endemic *Bidens* species, larvae did not survive beyond the third instar (damage ratings of 0–1) (table 2).

On non-Asteraceae, no larvae survived beyond the first instar, including tests with Hawaiian forest trees and shrubs conducted at the Hawaii Volcanoes

National Park Quarantine Facility, where a mean of 79.2% of larvae developed to adult on *S. madagascariensis* (table 2). No feeding or survival of first instars was observed on other non-asters, including the pyrrolizidine alkaloid producing *Crotalaria mucronata* and *Crotalaria spectabilis* (table 2).

Choice larval-feeding test with sunflower

Within two hours of release in a cage containing sunflower and fireweed, first instars moved to the natural host fireweed. No larvae remained on cage surfaces or sunflower and no back movement to the sunflower plant occurred. When larvae were placed directly on sunflower, they all moved quickly to adjacent fireweed branches, indicating a negative feeding response to sunflower. Larvae matured to the fifth instar with no feeding on sunflower except for probing and superficial damage of less than 2% of leaf area (table 3). In one replicate where all fireweed leaves had been consumed fifth instars remained on the fireweed plant devouring the stems but did not touch the sunflower. Larvae were seen on sunflower, occasionally molting, but no feeding was observed. New fireweed plants were added *ad libitum* when larvae reached the fifth instar. Results indicate that *H. annuus* is unlikely to be selected for feeding in the presence of its natural host, *S. madagascariensis*.

Oviposition choice tests

Oviposition choice tests were conducted with four plant species that had supported development to pupae and/or adults of *S. extensa*. No eggs were laid on *B. pilosa* and *H. annuus*. Oviposition of *S. extensa* on its natural host, *S. madagascariensis* was 5.4 times higher than on the test plant *C. crepidioides*. In contrast, oviposition on *S. vulgaris* and *S. madagascariensis* were not significantly different (table 4).

Discussion

Secusio extensa is the first insect proposed for release in Hawaii to suppress populations of fireweed. It is also the first arctiid proposed for biological control in the state. Successful use of arctiid moths for biological control of Asteraceae are well documented elsewhere. Siam weed, *Chromolaena odorata* (L.) R. M. King & H. Robinson (Asteraceae: Eupatoriaceae), one of the most serious weeds in pastures, forests, orchards and commercial plantations in Africa, Asia and the Pacific region (Desmier de Chenon et al. 2002,

Table 2 Results of no-choice larval-feeding tests with *Secusio extensa*

Family/Tribe	Species	N	Average no. larvae per replicate	No. larvae remain on plant within 48 h (Mean ± SEM)	Feeding rate ¹	No. larvae survived beyond first instar (Mean ± SEM)					No. pupae reared (Mean ± SEM)	No. adults eclosed (Mean ± SEM)	Suitability for Development ²
						II instar	III instar	IV instar	V instar				
Asteraceae:	<i>Artemisia mauiensis</i>	5	50	0.8 ± 0.6	0-1	0	0	0	0	0	0	0	-
Anthemideae	<i>Achillea filipendulina</i>	4	62	0.8 ± 0.8	0-1	0	0	0	0	0	0	0	-
Astereae	<i>Conyza bonariensis</i>	5	50	1.2 ± 0.7	0	0	0	0	0	0	0	0	-
	<i>Heterotheca grandiflora</i>	4	50	0	0	0	0	0	0	0	0	0	-
	<i>Conyza canadensis</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Erigeron</i> sp.	5	31	0.4 ± 0.4	0	0	0	0	0	0	0	0	-
	<i>Erigeron karvinskianus</i>	5	50	0.6 ± 0.6	0	0	0	0	0	0	0	0	-
	<i>Remya kauaiensis</i>	5	44	0	0-1	0	0	0	0	0	0	0	-
	<i>Tetramolopium filiforme</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Tetramolopium rockii</i>	5	50	0	0	0	0	0	0	0	0	0	-
Calenduleae	<i>Calendula officinalis</i>	5	50	0	0	0	0	0	0	0	0	0	-
Eupatorieae	<i>Ageratina adenophora</i>	5	50	0.4 ± 0.4	0	0	0	0	0	0	0	0	-
	<i>Ageratina riparia</i>	13	25	0	0	0	0	0	0	0	0	0	-
	<i>Ageratum conyzoides</i>	7	50	0.3 ± 0.2	0-1	0	0	0	0	0	0	0	-
	<i>Ageratum holustonianum</i>	5	35	0	0	0	0	0	0	0	0	0	-
Gnaphalieae	<i>Gnaphalium purpureum</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Helichrysum bracteatum</i>	3	4	0	0	0	0	0	0	0	0	0	-
Helenieae	<i>Argyroxiphium</i> sp.	5	50	0.2 ± 0.2	0	0	0	0	0	0	0	0	-
	<i>Dubautia herbstobatae</i>	6	37	1.0 ± 0.5	0-1	0	0	0	0	0	0	0	-
	<i>Dubautia laxa</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Dubautia laevigata</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Dubautia raillardioides</i>	5	20	0	0	0	0	0	0	0	0	0	-
	<i>Dubautia scabra</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Dubautia arborea</i>	5	30	0.2 ± 0.2	0	0	0	0	0	0	0	0	-
	<i>Flaveria trinervia</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Gaillardia grandiflora</i>	9	10	0	0	0	0	0	0	0	0	0	-
	<i>Tagetes erecta</i>	5	25	0	0	0	0	0	0	0	0	0	-
	<i>Wilkesia hобыi</i>	8	46	2.0 ± 1.3	0	0	0	0	0	0	0	0	-
Heliantheae	<i>Bidens alba</i>	5	50	1.4 ± 0.7	0-1	0	0	0	0	0	0	0	-
	<i>Bidens amplexans</i>	1	50	0	0	0	0	0	0	0	0	0	-
	<i>Bidens bipinnata</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Bidens campylothecha</i>	6	30	2.8 ± 1.4	0-1	0	0	0	0	0	0	0	-
	<i>Bidens cosmoides</i>	5	50	1.4 ± 0.7	0-1	0	0	0	0	0	0	0	-
	<i>Bidens menziesii</i>	4	62	9.5 ± 4.8	0-1	9.3 ± 2.8	8.0 ± 2.9	0	0	0	0	0	-
	<i>Bidens pilosa</i>	7	59	10.1 ± 4.3	1-2	10.1 ± 4.3	9.3 ± 4.5	7.4 ± 3.8	4.9 ± 2.9	0.3 ± 0.2	0	0	-
	<i>Bidens</i> sp.	6	50	3.5 ± 1.8	0-1	1.5 ± 1.0	0	0	0	0	0	0	-
	<i>Eclipta prostrata</i>	5	50	0	0	0	0	0	0	0	0	0	-

Table 2 (Continued)

Family/Tribe	Species	Average no. larvae per replicate	No. larvae remain on plant within 48 h (Mean ± SEM)	Feeding rate ¹	No. larvae survived beyond first instar (Mean ± SEM)					No. pupae reared (Mean ± SEM)	No. adults enclosed (Mean ± SEM)	Suitability for Development ²
					II instar	III instar	IV instar	V instar	V instar			
	<i>Galinisoga quadriradiata</i>	6 50	6.3 ± 3.0	0-1	3.0 ± 1.6	0.5 ± 0.5	0.3 ± 0.3	0.3 ± 0.3	0	0	-	
	<i>Helianthus annuus</i>	11 59	13.0 ± 3.1	1-2	12.5 ± 3.0	12.2 ± 3.0	11.6 ± 3.1	10.7 ± 3.2	8.3 ± 3.2	7.7 ± 2.7	+ inferior host	
	<i>Lipochaeta subcordata</i>	5 50	0	0	0	0	0	0	0	0	-	
	<i>Lipochaeta cornata</i>	4 50	0	0	0	0	0	0	0	0	-	
	<i>Montanoa hibiscifolia</i>	5 50	0	0	0	0	0	0	0	0	-	
	<i>Parthenium hysterophorus</i>	5 42	1.0 ± 0.8	0-1	0	0	0	0	0	0	-	
	<i>Sigesbeckia orientalis</i>	6 50	0.2 ± 0.2	0-1	0	0	0	0	0	0	-	
	<i>Synedrella nodiflora</i>	5 50	0.2 ± 0.2	0-1	0	0	0	0	0	0	-	
	<i>Tithonia diversifolia</i>	5 42	0	0	0	0	0	0	0	0	-	
	<i>Tridax procumbens</i>	5 38	0	0	0	0	0	0	0	0	-	
	<i>Verbesina encelioides</i>	5 50	0	0	0	0	0	0	0	0	-	
	<i>Wedelia trilobata</i>	11 20	0	0-1	0	0	0	0	0	0	-	
	<i>Xanthium strumarium</i>	5 50	6.8 ± 3.4	0-1	1.2 ± 0.6	0	0	0	0	0	-	
	<i>Zinnia peruviana</i>	5 47	0.4 ± 0.4	0-1	0	0	0	0	0	0	-	
Plucheae	<i>Pluchea indica</i>	5 50	0	0	0	0	0	0	0	0	-	
	<i>Pluchea carolinensis</i>	5 50	0	0	0	0	0	0	0	0	-	
Senecioneae	<i>Crassocephalum crepidioides</i>	8 54	38.0 ± 6.2	4-5	40.0 ± 3.9	38.0 ± 4.8	37.1 ± 4.6	36.5 ± 4.8	29.6 ± 6.0	22.6 ± 4.3	+ Potential host	
	<i>Emilia fosbergii</i>	8 40	14.1 ± 4.5	2	14.1 ± 4.5	12.1 ± 4.2	11.3 ± 4.2	9.1 ± 3.8	1.3 ± 0.8	0.9 ± 0.6	+ inferior host	
	<i>Erechtites hieracifolia</i>	6 50	19.8 ± 3.5	1	17.5 ± 3.5	16.5 ± 4.1	13.5 ± 4.2	11.7 ± 4.2	0.8 ± 0.3	0.7 ± 0.2	+ inferior host	
	<i>Farfugium japonicum</i>	5 25	4.4 ± 1.2	1	0	0	0	0	0	0	-	
	<i>Delairea odorata</i>	3 50	45.0 ± 24.5	5	39.3 ± 18.9	38.7 ± 19.3	38.7 ± 19.3	38.7 ± 19.3	35.3 ± 18.4	32.7 ± 16.2	+ Potential host	
	<i>Senecio madagascariensis</i>	16 67	66.6 ± 4.5	5	61.8 ± 1.1	61.5 ± 4.4	61.1 ± 4.5	60.3 ± 4.6	57.4 ± 4.4	52.3 ± 4.0	+ normal host	
	<i>Senecio vulgaris</i>	3 62	61.3 ± 4.7	5	55.7 ± 1.2	55.7 ± 1.2	48.7 ± 3.5	43.7 ± 3.3	40.3 ± 3.4	35.0 ± 1.2	+ Potential host	
Arctoteae	<i>Gazania rigens</i>	5 50	0.4 ± 0.4	0	0	0	0	0	0	0	-	
Cardueae	<i>Arctium lappa</i>	9 87	5.6 ± 2.5	0-1	4.2 ± 1.4	2.2 ± 1.0	0.1 ± 0.1	0	0	0	-	
	<i>Centaurea melitensis</i>	3 50	4.0 ± 4.0	0-1	0.7 ± 0.7	0	0	0	0	0	-	
	<i>Cirsium vulgare</i>	4 50	0	0	0	0	0	0	0	0	-	
Lactuceae	<i>Lactuca sativa</i>	7 50	3.9 ± 0.7	0-1	1.4 ± 0.5	0.6 ± 0.6	0.4 ± 0.4	0.3 ± 0.3	0	0	-	
	<i>Lactuca serriola</i>	6 46	0.8 ± 0.8	0-1	0	0	0	0	0	0	-	
	<i>Sonchus oleraceus</i>	5 50	1.0 ± 0.4	0-1	0	0	0	0	0	0	-	
	<i>Taraxacum officinale</i>	5 47	1.6 ± 0.9	0	0	0	0	0	0	0	-	
	<i>Youngia japonica</i>	6 29	0.2 ± 0.2	0	0	0	0	0	0	0	-	
	<i>Reichardia picroides</i>	5 50	0.2 ± 0.2	0	0	0	0	0	0	0	-	
	<i>Reichardia picroides</i>	5 50	0.2 ± 0.2	0	0	0	0	0	0	0	-	
Vernonieae	<i>Elephantopus mollis</i>	5 50	0.4 ± 0.2	0	0	0	0	0	0	0	-	

Table 2 (Continued)

Family/Tribe	Species	N	Average no. larvae per replicate	No. larvae remain on plant within 48 h (Mean ± SEM)	Feeding rate ¹	No. larvae survived beyond first instar (Mean ± SEM)					No. pupae reared (Mean ± SEM)	No. adults enclosed (Mean ± SEM)	Suitability for Development ²
						II instar	III instar	IV instar	V instar				
Non-Asteraceae													
Fabaceae	<i>Crotalaria mucronata</i>	5	50	0	0	0	0	0	0	0	0	0	-
	<i>Crotalaria spectabilis</i>	5	50	0	0	0	0	0	0	0	0	0	-
Musaceae	<i>Musa acuminata</i>	3	37	0	0	0	0	0	0	0	0	0	-
Caricaceae	<i>Carica papaya</i>	3	50	0	0	0	0	0	0	0	0	0	-
Urticaceae	<i>Pipturus albidus</i>	2	50	0	0	0	0	0	0	0	0	0	-
Araceae	<i>Colocasia esculenta</i>	1	25	0	0	0	0	0	0	0	0	0	-
Areaceae,	<i>Cocos nucifera</i>	1	50	0	0	0	0	0	0	0	0	0	-
Cucurbitaceae	<i>Coccinia grandis</i>	3	50	0	0	0	0	0	0	0	0	0	-
Poaceae	<i>Sorghum bicolor</i>	1	50	0	0	0	0	0	0	0	0	0	-
	<i>Saccharum officinarum</i>	1	50	0	0	0	0	0	0	0	0	0	-
Convolvulaceae	<i>Ipomoea batatas</i>	1	50	0	0	0	0	0	0	0	0	0	-
Plants recommended by US-Fish and Wildlife Service													
Dicksoniaceae	<i>Cibotium glaucum</i>	5	50	0.4 ± 0.2	0	0	0	0	0	0	0	0	-
Fabaceae	<i>Acacia koa</i>	5	50	0.4 ± 0.2	0	0	0	0	0	0	0	0	-
	<i>Sophora chrysophylla</i>	5	50	0.2 ± 0.2	0	0	0	0	0	0	0	0	-
Myoporaceae	<i>Myoporum sandwicense</i>	5	50	1.4 ± 0.5	0	0	0	0	0	0	0	0	-
Myrtaceae	<i>Metrosideros polymorpha</i>	5	50	1.2 ± 0.7	0	0	0	0	0	0	0	0	-
Sepindaceae	<i>Dodonaea viscosa</i>	5	50	0.4 ± 0.4	0	0	0	0	0	0	0	0	-
Asteraceae	<i>Senecio madagascariensis</i>	5	25	25 ± 0.0	5	22.2 ± 1.2	21.2 ± 0.6	21.2 ± 0.6	21.2 ± 0.6	20.4 ± 0.5	19.8 ± 0.4	0	+ normal host
	(control)												

¹Feeding rates: 0, no damage; 1, probing and superficial damage (<2% feeding on leaf area); 2, light damage (feeding on 5–20% of leaf area); 3, moderate damage (feeding on 21–40% of leaf area); 4, severe damage (feeding on 41–60% of leaf area); 5, intense damage (>60% of leaf area and stems that eventually kills the plant).

²Negative sign (–) indicates unsuitability for development, positive sign indicates some degree of suitability (inferior, potential, and normal hosts support <25%, <50 to <75%, and >75% of the larvae transferred to adult stage, respectively).
n, number of replicates.

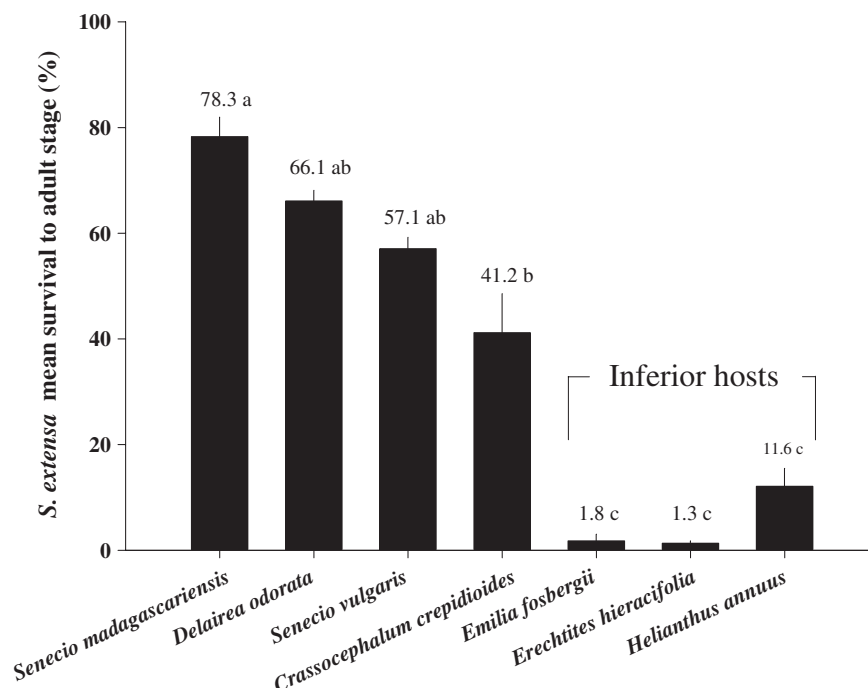


Fig. 1 Survival to adult stage of *Secusio extensa* reared on *Senecio madagascariensis* and six test plant species during no-choice larval-feeding trials. Bars (mean + SEM) topped by the same letters are not significantly different ($P > 0.05$; Tukey's HSD test).

Zachariades and Goodall 2002), has been suppressed in the Mariana Islands with the introduction of the arctiid moth, *Pareuchaetes pseudoinsulata* Rego Barros (Muniappan et al. 1989). Establishment of *P. pseudoinsulata* in Ghana led to reduction in *C. odorata* populations from 85% to 37% of total infested land. Biological control positively enhanced forest regeneration and biodiversity in an estimated 52 349 km²

within 7 years (Timbilla and Braimah 2000). Successful biological control programs with the cinna-bar moth, *Tyria jacobaeae* (L.), also an arctiid, contributed to the control of tansy ragwort, *Senecio jacobaea* L., in the continental United States and New Zealand (McEvoy et al. 1991; Coombs et al. 1996; McLaren et al. 2000). Within a span of 5 years, the average density of the weed in Oregon

Table 3 Survival and feeding of *Secusio extensa* exposed as first instar to *Helianthus annuus* (test plant) and *Senecio madagascariensis* (control) in starvation no-choice and choice tests

Developmental stage	Percentage survival on test plant and feeding rate				Percentage survival on control (n = 10)	
	No-choice test (n = 10)		Choice test (n = 5)		Mean ± SEM	Feeding damage ¹
	Mean ± SEM	Feeding damage ¹	Mean ± SEM	Feeding damage ¹		
Second instar	21.0 ± 5.1b	1	0c	0–1	100.0 ± 0a	1–2
Third instar	17.4 ± 4.8b	2	0c	0	100.0 ± 0a	2–3
Fourth instar	16.0 ± 4.9b	2	0c	0	100.0 ± 0a	4
Fifth instar	14.0 ± 4.9b	3	0c	0–1	96.2 ± 1.3a	5
Pupa	10.2 ± 3.7b	–	0b	–	92.4 ± 3.3a	–
Adult	9.0 ± 3.2b	–	0b	–	85.8 ± 3.9a	–

¹Feeding damage ratings: 0, no damage; 1, probing and superficial damage (<2% feeding on leaf area); 2, light damage (feeding on 5–20% of leaf area); 3, moderate damage (feeding on 21–40% of leaf area); 4, severe damage (feeding on 41–60% of leaf area); 5, intense damage (>60% of leaf area and stems that eventually kills the plant).

n = number of replicates.

Means on the same row followed by the same letter are not significantly different (Tukey HSD; $P = 0.05$). Survivorship data were arcsine transformed.

Table 4 Oviposition preference of *Secusio extensa* on *Senecio vulgaris*, *Crassocephalun crepidioides*, *Bidens pilosa*, *Helianthus annuus* (test plants) and the natural host, *Senecio madagascariensis* (control)

Parameter per replicate (mean ± SEM)	<i>S. vulgaris</i> (n = 10)	<i>C. crepidioides</i> (n = 10)	<i>B. pilosa</i> (n = 9)	<i>H. annuus</i> (n = 5)
No. plant leaves on which eggs found:				
<i>Test plant</i>	1.9 ± 0.6	1.1 ± 0.4	0	0
<i>control</i>	2.6 ± 0.7	3.2 ± 0.7	5.0 ± 1.4	5.6 ± 2.6
χ^2	(0.736)NS	(2.650)*	(3.638)**	(2.186)NS
Total eggs deposited on plant:				
<i>Test plant</i>	17.3 ± 6.5	6.7 ± 2.7	0	0
<i>control</i>	20.8 ± 5.4	35.9 ± 7.8	30.6 ± 8.4	75.2 ± 29.6
χ^2	(0.415)NS	(3.531)**	(3.633)**	(2.539)*
% eggs deposited on plant ¹ :				
<i>Test plant</i>	15.2 ± 6.4	4.6 ± 1.9	0	0
<i>control</i>	23.1 ± 5.1	21.0 ± 3.8	14.3 ± 3.3	18.0 ± 6.1
χ^2	(1.535)NS	(3.579)**	(7.350)***	(4.672)**

¹Calculated as the number of eggs deposited on plant divided by total eggs deposited on plant and cage walls multiplied by 100. Percentage data were arcsine transformed before analysis.

² χ^2 -test value in parenthesis; NS, not significant, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$, ***, $P < 0.001$. n = number of replicates.

was reduced to about 10% of the original coverage, and reported cases of tansy ragwort poisoning have declined more than 20 fold (Burrill et al. 1994).

Taxonomic relationships of the moth *S. extensa* are uncertain. Butler first described *S. extensa* under the genus *Sommeria* from specimens collected at Betsileo, Madagascar. This arctiid was subsequently placed in the genus *Diota* and later moved to *Galtara*, with *Galtara extensa* Butler as the only species in this genus from Madagascar. Pending revision of the closely related genera *Secusio* and *Galtara*, our taxonomist prefers to place this moth under the senior name *Secusio* (J. Rawlins, Carnegie Museum, personal communication). Since its description by Butler in 1880, there have been no records of this moth appearing as a crop pest anywhere in the world under possible synonyms. A narrow host range for *S. extensa* is consistent with its relation to the subfamily Nyctemerinae, many of which are obligate feeders on species of the tribe Senecioneae (*Emilia*, *Senecio*, and other genera) (DaCosta and Weller 2005). A similar arctiid species native to mainland Africa, *Diota rostrata*, also has been found only on Senecioneae, and was considered for biological control of *D. odorata* in California until it was found to accept a *Senecio* species that is native there (Balciunas et al. 2003).

While other species of the genus *Secusio* (*S. pulverata*, *S. pustularia*, *S. strigata*) are common on mainland Africa (Swaziland, Rwanda, South Africa), *S. extensa* has not been recorded in any survey. It is only found in Madagascar in habitats where populations of *S. madagascariensis* are present. During two field surveys

in Madagascar, in summer 1999 and in the rainy season in 2005, all plants near fireweed populations with *S. extensa* (sweet potato, cassava, cucurbits, rice fields, Rubiaceae, pineapple, tomato, and grasses) were carefully examined, and this insect was found only on *S. madagascariensis*. Examination of four common Asteraceae (*Emilia tranvaalensis*, *Tridax procumbens*, *Sonchus oleraceus*, and *B. pilosa*) present at the survey sites in Madagascar showed that the plants were not attacked by this arctiid (M. Ramadan unpublished data).

Our quarantine tests of larval feeding and oviposition preferences similarly indicate a narrow host range for *S. extensa* restricted to the tribe Senecioneae. Only *S. madagascariensis*, *S. vulgaris* and *D. odorata* (formerly placed in genus *Senecio*) were completely suitable hosts for *S. extensa*. Lower levels of oviposition and larval survival on *C. crepidioides* indicated that this species is an inferior host compared to fireweed. Other members of this tribe, *E. fosbergii* and *E. hieracifolia*, were only marginally suitable hosts. Responses of *S. extensa* to host plants may be mediated by chemical differences, given that different types of PAs are known from Asteraceae (restricted to 26 genera in the tribes Eupatorieae and Senecioneae). Members of *Crassocephalum*, *Emilia*, *Erechtites*, *Farfugium*, and *Senecio* are known to contain alkaloids that may differ from the senecionine chemotype of fireweed (Röder 1995).

A few plants in the tribe Heliantheae supported limited larval development of *S. extensa* during starvation tests, but are unlikely to serve as hosts in nature. On the naturalized weed *B. pilosa*, two larvae

survived to pupate, but no adults emerged. Low levels of feeding and inability to develop on *B. pilosa* and native *Bidens* species suggest that these plants lie outside the range of potential hosts. Limited feeding on non-hosts during cage trials is a common result in no-choice specificity tests, which tend to overestimate host ranges of phytophagous insects (Heard 2000; Zachariades et al. 2002). Low rates of complete development to adult stage on *H. annuus* indicated greater potential as a host, however sunflower was not selected for larval feeding or oviposition in choice trials. During oviposition experiments, moths deposited eggs on cage walls and on fireweed, but never on sunflower, indicating a lack of necessary visual and chemical cues and possibly a deterrent effect of this plant (Hanson 1983; Papaj and Rausher 1983; Relf Diane 1996, Ashfaq and Aslam 2001). These data support the conclusion that *S. extensa* will not choose sunflower as a host in the field. Sunflower in Hawaii is an exotic ornamental naturalized at high elevation on Hawaii Island (Wagner et al. 1999) and grown as a minor seed crop on Kauai (<http://pacific.bizjournals.com/pacific/stories/2009/08/03/story3.html>).

It appears that the host range of *S. extensa* in Hawaii would be restricted to a few weedy members of the tribe Senecioneae. Since there are no native or economically significant species in this tribe, this biological control agent is not likely to be a threat to agriculture or the environment in the state of Hawaii.

Several factors suggest that *S. extensa* is capable of having substantial impact on fireweed infestations in Hawaii. *S. extensa* was considered the most damaging insect to fireweed during the summer season in Madagascar, where heavy feeding caused rapid destruction of plants. Attributes that contribute to the ability of *S. extensa* to reproduce prolifically on fireweed include a short life cycle (41 days), high fecundity, and lack of diapause. Females distribute eggs effectively, laying a low number of eggs per day (21.8 eggs) in comparison with the total egg load in ovaries (227.1 eggs) (M. Ramadan, unpublished data). In Madagascar where adult moth populations were very high, only eight mature larvae were collected per plant on average. Larvae and adults are nocturnal, avoiding heat, desiccation, and daytime predators. It is also equipped with chemical protection against predators. All these qualities are indicators of a successful biological control agent (Harris 1973). In addition, the high reproductive output of this species and the ease of mass production under

laboratory conditions can enhance its success during field colonization.

While parasitoids and predators are suspected of frequent interference with lepidopteran biological control agents in Hawaii, quantitative demonstration of severe effects on these agents is lacking. To the contrary, the ivy gourd moth, *Melittia oedipus* (Lepidoptera: Sesiidae) was attacked by no larval or pupal parasitoids and only *Eupelmus* sp. (Hymenoptera: Eupelmidae), which emerged from <10% of field collected eggs (Chun and Marianne 2001, M. Chun unpublished data). Mean egg parasitism by *Trichogramma chelonis* Ishii of *Pyrausta perelegans* Hampton (Lepidoptera: Crambidae), introduced for biological control of banana poka, *Passiflora mollissima* (H.B.K.) and *Schreckensteinia festaliella* (Lepidoptera: Schreckensteiniidae) introduced for biological control of *Rubus* species, were 9.2% and 33%, respectively (Ramadan et al. 2008, M. Ramadan unpublished data). In Madagascar, *S. extensa* larvae were attacked by *Apanteles* sp. (Hymenoptera: Braconidae) and two unidentified tachinids (Diptera: Tachinidae), however overall parasitism by the three species was less than 10% during a high population season in 1999 (M. Ramadan, unpublished data).

Secusio extensa is likely to be well-defended against potential natural enemies in Hawaii. Pyrrolizidine alkaloids (PAs) often serve as chemical mediators of plant-herbivore-predator interactions (Von Rosenegk Nickisch and Wink 1993). Arctiid moths usually store PAs from plant sources and thereby become protected against antagonists. Behavioural response of the Puerto Rican tree frog, *Eleutherodactylus coqui* Thomas (Anura: Leptodactylidae), exposed to *S. extensa* showed that adult moths and larvae are unpalatable (M. Ramadan, unpublished data). A moth will emit alkaloid-laden hemolymph through membranes on thoracic segments when disturbed. There are some reports suggesting a chemical defense of arctiids against predation by spiders (Conner et al. 2001). Alkaloid-laden eggs were rejected and not pierced by larvae of the green lacewing, *Ceraeochrysa cubana* (Neuroptera: Chrysopidae) (Eisner et al. 2000). PAs are known to protect Arctiidae, Danainae, and Ithomiinae butterflies against the orb-weaving spider *Nephila clavipes* (Araneae: Araneidae) (Silva and Trigo 2002). Ingested PAs, which are toxic to unspecialized insects and vertebrates, are efficiently metabolized in the hemolymph of the cinnabar moth, *Tyria jacobaeae* for protection against predators (Nauermann et al. 2002).

In spite of its chemical defenses, *S. extensa* is not expected to cause any human health concerns if

released in Hawaii. While some arctiid larvae possess urticating hairs that can irritate human skin, *S. extensa* possesses only plumose setae which have no physical effect on humans. During the rearing and handling of thousands of *S. extensa* larvae and adults over several years, no health problems arose due to caterpillar exposure.

We examined a handful of potential biological control agents from the native region of fireweed and selected the Madagascan arctiid moth, *S. extensa*, believing it could reduce the vitality of the target weed. Based on evaluations of host range tests we anticipate this moth to be specific to *S. madagascariensis* when released in Hawaii and the risk of direct impacts on plants other than tribe Senecioneae, which does not contain any native or economically important plant species in Hawaii, is minimal. Currently, the HDOA has submitted a petition for permission to release this moth as the first biological control agent against fireweed. It is expected that infestation of *S. extensa* to spread gradually at each release site reaching damaging levels within a few years reducing fireweed's vigor, and capacity for reproduction.

Acknowledgements

We would like to thank Dr. Neil Reimer, Dr. Renato Bautista, Ken Teramoto (Hawaii Department of Agriculture, Honolulu) and two JEN anonymous reviewers for helpful comments that improved this manuscript. Dr. Stephen Hight, Ivan Horiuchi, and Wendell Sato (USDA Forest Service) assisted in host testing of forest plants and maintained a back up colony at the Hawaii Volcanoes National Park Quarantine Facility during 1999–2001. Marianne Chun, Walter Nagamine, and Harvey Lee (HDOA, Honolulu) assisted in rearing the insect and propagating test plants. Pat Conant and Clyde Hirayama (HDOA, Hilo) assisted in plant collections and foliage cuttings of fireweed during the course of this study. We also thank Bernarr Kumashiro (HDOA, Honolulu) and Dr. John Rawlins (Carnegie Museum, Pittsburg, PA, USA) for moth identification, and Becky Azama and Derek Arakaki (HDOA, Honolulu) for plant identification. Dr. George Markin (USDA-Forest Service) provided helpful suggestions on host range testing.

M. Ramadan is grateful for research and export permits of fireweed insects issued by the Madagascar Ministry of Agriculture at Antananarivo, Madagascar. The Maui County and the Hawaii Cattlemen's Association have granted funds to the HDOA Exploratory Entomologist to conduct surveys in Africa.

References

- Ashfaq M, Aslam M, 2001. Response of different pests to some sunflower (*Helianthus annuus* Linnaeus, Compositae) genotypes and their correlation with yield component under field conditions. *J. Biol. Sci.* 9, 835–839.
- Balciunas J, Mehelis C, Chau M, 2003. Biological control of Cape ivy project, Annual Research Report. http://www.ars.usda.gov/SP2UserFiles/Place/53254300/Reports/2003_Annual.pdf [accessed on January 2010].
- Burrill LC, Callihan RH, Parker R, Coombs E, Radtke H, 1994. Tansy ragwort (*Senecio jacobaea* L.). Pacific Northwest Cooperative Extension Publications, Oregon, Idaho, WA, Publication (PNW 175).
- Chun, Marianne Early, 2001. Biology and host specificity of *Melittia oedipus* (Lepidoptera: Sesiidae), a biological control agent of *Coccinia grandis* (Cucurbitaceae). *Proc. Hawaiian Entomol. Soc.* 35, 85–93.
- Conner WE, Boada R, Schroeder F, Gonzalez A, Meinwald J, Eisner T, 2001. Chemical defense: bestowal of a nuptial alkaloidal garment by male moth on its mate. *Proc. Natl Acad. Sci. USA.* 97, 14406–14411.
- Coombs EM, Radtke H, Isaacson DL, Snyder SP, 1996. Economic and regional benefits from the biological control of tansy ragwort, *Senecio jacobaea*, in Oregon. In: Proceedings of the IX International Symposium on Biological Control of Weeds. Ed. by Moran VC, Hoffmann JH, University of Cape Town, Stellenbosch, South Africa, 489–494.
- DaCosta MA, Weller SJ, 2005. Phylogeny and classification of Callimorphini (Lepidoptera: Arctiidae: Arctiinae). *Zootaxa.* 1025, 1–94.
- Dale Gardner R, Mark Thorne S, Russell Molyneux J, James Pfister A, Alan Seawright A, 2006. Pyrrolizidine alkaloids in *Senecio madagascariensis* from Australia and Hawaii and assessment of possible livestock poisoning. *Biochem. Syst. Ecol.* 34, 736–744.
- Desmier de Chenon R, Sipayung A, Sudharto P, 2002. A decade of biological control against *Chromolaena odorata* at the Indonesian oil palm research institute in Marihat. In: Proceedings of Fifth International Workshop on Biological Control and Management of *Chromolaena odorata*, Durban, South Africa, 23–25 October 2000. Ed. by Zachariades CR, Muniappan R, Strathie LW, ARC – PPRI (2002), Pretoria, South Africa, 46–52.
- Dickinson JO, Cooke MP, King RR, Mohamed PA, 1976. Milk transfer of pyrrolizidine alkaloids in cattle. *J. Am. Vet. Med. Assoc.* 169, 1192–1196.
- Eisner T, Eisner M, Rossini C, Iyenger V, Roach B, Benedikt E, Meinwald J, 2000. Chemical defense against predation in an insect egg. *Proc. Natl Acad. Sci. USA.* 97, 1634–1639.
- Hanson FE, 1983. The behavioral and neurophysiological basis of food plant selection by lepidopterous larvae. Chapter1: 3-23. In: Herbivorous insects: host seeking

- behavior and mechanisms. Ed. by Ahmad S, Academic Press, Inc., New York, 257.
- Harris P, 1973. The selection of effective agents for the biological control of weeds. *Can. Entomol.* 105, 1495–1503.
- Heard TA, 2000. Concepts in insect host-plant selection behavior and their application to host specificity testing. In: *Host-specificity testing of exotic arthropod biological control agents: the biological basis for improvement in safety*. Ed. by Van Driesche RG, Heard T, McClay AS, Reardon R, Vol. FHTET-99-1, USDA Forest Service Bulletin, Morgantown, WV, USA, 1–10.
- Judd WS, Campbell CS, Kellogg EA, Stevens PF, Donoghue MJ, 2002. *Plant systematics: a phylogenetic approach*, 2nd edn. Sinauer Associates, Inc., Sunderland, MA, USA, 576.
- Killgore EM, Ramadan MM, Gardner DE, 2001. Evaluation of *Puccinia lagenophorae* as a biological agent for *Senecio madagascariensis* in Hawaii. *Phytopathology*. 91(6 suppl.), S48.
- Le Roux JJ, Wieczorek AM, Ramadan MM, Tran CT, 2006. Resolving the native province of invasive fireweed (*Senecio madagascariensis* Poir.) in the Hawaiian Islands as inferred from phylogenetic analysis. *Divers. Distrib.* 12, 694–702.
- MacFadyen R, Sparks D, 1996. Biological control of fireweed. In: *Proceedings of the eleventh Australian weeds conference*. Ed. by Shepherd RCH, Weed Science Society of Victoria Inc., Melbourne, Vic., 305–308.
- Marohasy JJ, 1989. A survey of fireweed (*Senecio madagascariensis* Poir.) and its natural enemies in Madagascar with a review to biological control in Australia. *Plant Prot. Q.* 4, 139–140.
- McEvoy P, Cox C, Coombs E, 1991. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecol. Appl.* 14, 430–442.
- McLaren DA, Ireson J, Kwong RM 2000. Biological control of ragwort (*Senecio jacobaea* L.) in Australia. In: *Proceedings of the X International Symposium on Biological Control of Weeds*, 4–9 July 2000. Ed. by Spencer NR, Montana State University Bozeman, Montana, USA, 67–79.
- Mlawula Nature Reserve Fauna, 2005. Moths checklist. <http://www.sntc.org.sz/checklist/mlmotch.html> [accessed on December 2009].
- Motooka P, Nagai G, Onuma K, DuPonte M, Kawabata A, Fukumoto G, Powley J, 2004. Control of Madagascar Ragwort (aka Madagascar fireweed, *Senecio madagascariensis*). Alien Pest Alert, University of Hawaii at Manoa, and Hawaii Department of Agriculture, CTAHR publication WC-2.
- Muniappan R, Sundarramurthy VT, Viraktamath CA, 1989. Distribution of *Chromolina odorata* (L.) (Asteraceae) and bionomics and consumption and utilization of food by *Pareuchaetes pseudoinzulata* (Lepidoptera: Arctiidae) in India. In: *Proceedings of the VII International Symposium on Biological Control of Weed*, 1988, Rome, Italy. Ed. by Delfosse ES, Ministero Dell'Agricoltura E Delle Foreste, Rome/CSIRO, Melbourne, 401–409.
- Naumann C, Hartmann T, Ober D, 2002. Evolutionary recruitment of a flavin-dependent monooxygenase for the detoxification of host alkaloid-defended arctiid moth. *Proc. Natl Acad. Sci. USA.* 99, 6085–6090.
- Papaj DR, Rausher MD, 1983. Individual variation in host location by phytophagous insects. Chapter 3:77–124. In: *Herbivorous insects: host seeking behavior and mechanisms*. Ed. by Sami Ahmad S, Academic Press, Inc., New York, USA, 257.
- Ramadan MM, Markin GP, Johnson MW, 2008. Field biology of *Pyrausta perelegans* (Lepidoptera: Crambidae), a flower-bud feeder of the forest invasive vine *Passiflora mollissima* in Hawaiian forests. *Trop. Lepidoptera Res.* 18, 71–79.
- Relf Diane, 1996. Learning from poisonous plants. *Consumer Horticulture*, and Sheri Dorn, Horticulture Extension Technician, Virginia Tech, The Virginia Gardener Newsletter, vol.13, no. 8. Website: http://nasdonline.org/static_content/documents/1479/d001272.pdf [accessed on January 2010].
- Renwick JAA, Chew FS, 1994. Oviposition behavior in Lepidoptera. *Annu. Rev. Entomol.* 39, 377–400.
- Röder E, 1995. Medicinal plants in Europe containing pyrrolizidine alkaloids. *Die Pharmazie.* 50, 83–98.
- SAS Institute, 1985. *SAS User(s) Guide: Statistics*, Version 5. SAS Institute Inc., Cary, NC, USA, 956.
- Satoru K, Hiroshige K, Makato O, Ohta M, 1999. *Senecio madagascariensis*: a naturalized species in Japan. *Acta Phytotaxonomica et Geobotanica.* 50, 244–246.
- Scott LJ, Congdon BC, Playford J, 1998. Molecular evidence that fireweed (*Senecio madagascariensis*, Asteraceae) is of South African origin. *Plant Syst. Evol.* 213, 251–257.
- Silva KL, Trigo JR, 2002. Structure-activity relationships of pyrrolizidine alkaloids in insect chemical defense against the orb-weaving spider *Nephila clavipes*. *J. Chem. Ecol.* 28, 657–668.
- Sindel BM, 1986. The ecology and control of fireweed (*Senecio madagascariensis* Poir). *Plant Prot. Q.* 1, 163–172.
- Sindel BM, Michael PW, 1988. Survey of the impact and control of fireweed (*Senecio madagascariensis* Poir.) in New South Wales. *Plant Prot. Q.* 3, 22–28.
- Sindel BM, Radford IJ, Holtkamp RH, Michael PW, 1998. *Senecio madagascariensis* Poir. In: *The biology of Australian weeds*. Volume 2. Ed. by Panetta FD, Groves RH, Shepherd RCH, R.G. and F.J. Richardson, Melbourne, Vic., 247–267.
- Small AC, Kelly WR, Seawright AA, Mattocks AR, Jukes R, 1993. Pyrrolizidine alkaloids in a two month old foal. *J. Vet. Med. A.* 40, 213–218.

- Timbilla JA, Braimah H, 2000. Establishment, spread and impact of *Pareuchaetes pseudoinzulata* (Lepidoptera: Arctiidae) an exotic predator of the Siam weed, *Chromolaena odorata* (Asteraceae: Eupatoriae) in Ghana. In: Proceedings of the X International Symposium on Biological Control of Weeds. 4-14 July 1999. Ed. by Spencer NR, Montana State University, Bozeman, Montana, USA, 105–111.
- Von Rosenegk Nickisch E, Wink M, 1993. Sequestration of pyrrolizidine alkaloids in several arctiid moths (Lepidoptera: Arctiidae). *J. Chem. Ecol.* 19, 1889–1903.
- Wagner WL, Herbst DR, Sohmer SH, 1999. Manual of the flowering plants of Hawaii. Revised edition volume 1. . Bishop Museum special publication 97, University of Hawaii press, Honolulu, HAWAII, pp, 988.
- Wapshere AJ, 1974. A strategy for evaluating the safety of organisms for biological weed control. *Ann. Appl. Biol.* 777, 201–211.
- Wapshere AJ, 1989. A testing sequence for reducing rejection of potential biological control agents for weeds. *Ann. Appl. Biol.* 114, 515–526.
- Zachariades C, Goodall JM, 2002. Distribution, impact and management of *Chromolaena odorata* in Southern Africa. In: Proceedings of fifth international workshop on biological control and management of *Chromolaena odorata*, Durban, South Africa, 23-25 October 2000. Ed. by Zachariades CR, Muniappan R, Strathie LW, Pretoria, South Africa, ARC - PPRI, (2002), 34–39.
- Zachariades C, Strathie LW, Kluge RL, 2002. Biology, host specificity and effectiveness of insects for the biological control of *Chromolaena odorata* in South Africa. In: Proceedings of fifth international workshop on biological control and management of *Chromolaena odorata*, Durban, South Africa, 23-25 October 2000. Ed. by Zachariades CR, Muniappan R, Strathie LW, Pretoria, South Africa, ARC - PPRI (2002), 160–166.
- Zar JH, 1999. Biostatistical analysis, 4th edn. Prentice Hall, Inc., New Jersey, USA, pp. 929.