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Predictable risk to native plants in weed biological control

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Abstract Data on field host use of 112 insects, 3 fungi, 1 mite, and 1 nematode established for biological control of weeds in Hawaii, the continental United States, and the Caribbean indicate that the risk to native flora can be judged reliably before introduction. Virtually all risk is borne by native plant species that are closely related to target weeds. Fifteen species of insects introduced for biological control use 41 native plant species; 36 of which are congeneric with target weeds, while 4 others belong to two closely allied genera. Only 1 of 117 established biological organisms uses a native plant unrelated to the target weed. Thus the elements of protection for the native flora are the selection of weed targets that have few or no native congeners and the introduction of biological control organisms with suitably narrow diets.

Keywords Biological control of weeds · Non-target use · Insect/plant interactions

Introduction

Environmental safety is an important issue for biological control (Andres 1985; Turner 1985; Pemberton 1985a, 1985b, 1995, 1996; Funasaki et al. 1988; Howarth 1991; Miller and Applet 1993; Lockwood 1993a, 1993b; Carruthers and Onsager 1993; Center 1995; McEvoy 1996; Simberloff and Stiling 1996; Morohasy 1996; Onstad and McManus 1996; Hawkins and Marino 1997; Louda et al. 1997; Strong 1997; Thomas and Willis 1998; Strong and Pemberton 2000). There is now evidence of harm to a few non-target, native species caused by insects and other organisms imported to suppress pests, but a general assessment of the kinds and degrees of risk to native organisms owing to biological control is lacking. As a step towards risk management, I offer herein an analysis of the patterns of host use by insects imported to control weeds. One of the primary concerns regarding the safety of biological control is the stability of the host ranges of the organisms introduced. Biological control can be viewed as a grand experiment in which the stability of the host ranges of insects and other organisms employed can be examined. The present analysis is based upon 117 natural enemies (112 insects, 3 fungi, 1 mite and 1 nematode) introduced and established for biological control of 55 weed species in Hawaii, the continental United States and the Caribbean since 1902 (Julien and Griffiths 1998). This is the first comprehensive assessment of the risk to non-target, native plants posed by insects introduced for biological control.

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Materials and methods

The principal source of information is specialized entomological literature, which is supplemented by unpublished reports and personal communications from researchers familiar with the projects. "Use" is defined as completed life cycle of the introduced agent upon the non-target plant species. Use does imply harm to either individuals or populations of the non-target plants; harm is largely unstudied for non-target species in biological control. Except for cacti (*Opuntia* spp.) used by the moth *Cactoblastis cactorum* (Bergroth) in Florida, the data on non-target use are for within the country where the agents were released. *Cactoblastis cactorum* was included in the analysis because its presence in Florida is a result of biological control in the Caribbean biogeographic region (Simmons and Bennett 1966), a region to which southern Florida belongs. Introductions after 1994 were excluded because I judged that insufficient time had passed for agent population growth and dispersal to potential non-target plant species. Data from Hawaii were analyzed separately from the continental United States and Caribbean data because both the weeds and native floras are taxonomically distinct.

This analysis concentrates upon the distinction between weeds with closely-related native relatives and those lacking close relatives in the area of introduction. Close relatives are defined as congeneric species of plants and species in closely related genera that previously have been classified as in the same genus (i.e. *Cirsium* and *Carduus* thistles). Agents established on weeds with close relatives and on weeds without close relatives have been released for similar lengths of time; 21.4 versus 23.8 years in the continental United States and the Caribbean and 47.2 versus 50.4 years in Hawaii (calculated from Julien and Griffiths 1998).

Table 1 Known non-target native host plants of introduced biological control agents of weeds in the continental United States, the-Caribbean and Hawaii

Target weed	Nontarget plant host	Biological control agent	Location	Reference
Alternanthera philoxeroides (alligatorweed-Amaranthaceae)	*Alternanthera flavescens* (yellow joyweed-Amaranthaceae)	*Arcola* (=Vogtia) *malloi* (Lepidoptera:Pyralidae)	FL	Pemberton unpublished data
	Blataparon (= *Philoxerus*) *vermiculare* (samphire-Amaranthacae)	Same	LA, TX	Vogt et al. 1992
Carduus acanthoides, Carduus nutans, Carduus pycnocephalus, Carduus tenuiflorus, Cirsium arvense, Cirsium vulgare, Silybum marianun (introduced thistles-Asteraceae)	*Cirsium andersonii* (rose thistle-Asteraceae)	*Rhinocyllus conicus* (Coleoptera: Curculionidae)	CA	Turner et al. 1987
	Cirsium brevistylum (clustered thistle)	Same	CA	Turner et al. 1987
	Cirsium calcareum (=*C. pulchellus*) (Cainville thistle)	Same	CO	Louda et al. 1997
	Cirsium californicum (California thistle)	Same	CA	Goeden 1986, Turner et al. 1987
	Cirsium callilepis (fringebract thistle)	Same	CA	Turner et al. 1987
	Cirsium canescens (prairie thistle)	Same	NE WY	Louda et al. 1997 Littlefield personal communication
	Cirsium ciliolatum (Ashland thistle)	Same	CA	Turner et al. 1987
	Cirsium cymosum (peregrine thistle)	Same	CA	Turner et al. 1987
	Cirsium douglasii (Douglas' thistle)	Same	CA	Turner et al. 1987
	Cirsium eatonii (=*C.tweedyi*) (Eaton's thistle)	Same	CO	Louda et al. 1997
	Cirsium edule (edible thistle)	Same	OR	Coombs personal communication
	Cirsium flodmanii (Flodman's thistle)	Same	WY	Littlefield personal communication
	Cirsium fontinale (fountain thistle)	Same	CA	Turner et al. 1987
	Cirsium hydrophilum (Suisun thistle)	Same	CA	Turner et al. 1987
	Cirsium occidentale (cobwebby thistle)	Same	CA	Goeden 1986, Turner et al. 1987
	Cirsium ownbeyi (Ownbey's thistle)	Same	CO	Dawson and Grant personal communication
	Cirsium pastoris (snowy thistle)	Same	CA	Turner et al. 1987
	Cirsium quercetorum (Alameda Co. thistle)	Same	CA	Herr personal communication
	Cirsium remotifolium (=*C. centaureae*) (thistle)	Same	CO	Louda et al. 1997
	Cirsium scariosum (meadow thistle)	Same	WY	Littlefield personal communication
	Cirsium tioganum (stemless thistle)	Same	CA WY	Turner et al. 1987 Littlefield personal communication
	Cirsium undulatum (wavyleaf thistle)	Same	MT WY NE	Reese 1977 Littlefield personal communication Louda et al. 1997
Carduus acanthoides, Carduus nutans, Cirsium vulgare (intrdouced thistles-Asteraceae)	*Cirsium discolor* (field thistle)	*Trichosirocalus* (=*Ceutorrhy- chidius*) *horridus* (Coleoptera: Curculionidae)	VA	McAvoy et al. 1987
Cyperus rotundus (purple nut sedge-Cyperaceae)	*Cyperus polystachyos* (manyspike flatsedge-Cyperaceae)	*Athesapeuta cyperi* (Coleoptera: Curculionidae)	HI	Poinar 1964, Funasaki et al. 1988
Hypericum perforatum (common St. Johnswort-Clusiaceae)	*Hypericum concinnum* (goldwire-Clusiaceae)	*Agrilus hyperici* (Coleoptera: Buprestidae)	CA	Andres 1985
		Chrysolina quadrigemina (Coleoptera: Chrysomelidae)	CA	Andres 1985
		Zeuxidiplosis giardi (Coleoptera: Chrysomelidae)	CA	Andres 1985

Table 1 (continued)

Target weed	Nontarget plant host	Biological control agent	Location	Reference
Lantana camara (lantana-Verbenaceae)	*Myoporuum sandwicense* (*naio*- Myoporaceae)	*Teleonemia scrupulosa* (Hemiptera: Tingidae)	HI	Maehler and Ford 1955, Bianchi 1961
Opuntia lindheimeri, Opuntia stricta, Opuntia triacantha (weedy native cacti in the Caribbean Antigua, Cayman Is., Montserrat and Nevis-Cactaceae)	*Opuntia cubensis* (bullsuckers-Cactaceae)	*Cactoblastis cactorum* (Lepidoptera: Pyralidae)	FL	Johnson and Stiling 1996
	Opuntia humfusa (pricklypear)	Same	FL	Johnson and Stiling 1996
	Opuntia spinosissima (semaphore pricklypear)	Same	FL	Johnson and Stiling 1996
	Opuntia stricta (erect pricklypear)	Same	FL	Johnson and Stiling 1996
	Opuntia triacantha (Spanish lady)	Same	FL	Johnson and Stiling 1996
Rubus argutus (prickly Florida blackberry-Rosaceae)	*Rubus hawaiensis* (Hawaii blackberry- Rosaceae)	*Croesia zimmermani* (Lepidoptera: Tortricidae)	HI	Markin personal communication
		Priophorus morio (Hymenoptera:Tenthredindae)	HI	Markin personal communication
		Schreckensteinia festaliella (Lepidoptera: Heliodinidae)	HI	Markin personal communication
	Rubus macraei ('akala)	*Croesia zimmermani* (Lepidoptera: Tortricidae)	HI	Markin personal communication
		Priophorus morio (Hymenoptera:Tenthredindae)	HI	Markin personal communication
		Schreckensteinia festaliella (Lepidoptera: Heliodinidae)	HI	Markin personal communication
Senecio jacobaeae (tansy ragwort-Asteraceae)	*Senecio integerrimus* (lambstongue groundsel-Asteraceae)	*Tyria jacobaeae* (Lepidoptera: Arctiidae)	OR	Coombs personal communication
	Senecio pseudaureus (falsegold groundsel)	Same	OR	Coombs personal communication
	Senecio triangularis (arrowleaf groundsel)	Same	OR	Diehl and McEvoy 1990
Tribulus terrestris (puncturevine-Zygopyhyllaceae)	*Kallstroemia californica* (California caltrop-Zygophyllaceae)	*Microlarinus lareynii* (Coleoptera: Curculionidae)	AZ	Turner unpublished data
		Microlarinus lypriformis (Coleoptera: Curculionidae)	AZ	Turner unpublished data
	Kallstroemia grandiflora (Arizona poppy)	*Microlarinus lareynii* (Coleoptera: Curculionidae)	AZ	Turner 1985
		Microlarinus lypriformis (Coleoptera: Curculionidae)	AZ	Turner 1985
		Microlarinus lypriformis (Coleoptera: Curculionidae)	TX	Boldt and Robbins personal communication

Results

Taxonomically isolated weeds provide much safer targets for biological control than do weeds with close relatives in the native flora (Table 2). Only 1 of 117 established agents has come to use a native, non-target plant unrelated to the target weeds. Virtually all of the non-target, native plant species (40/41) that have been attacked by biological control insects are closely related to the target weed species (Table 1); 36 plants belong to the same genus as the target weeds, while the other four species are in two closely allied genera. (*Kallstroemia*, with three species adopted by the two *Microlarinus* weevils introduced against puncturevines (*Tribulus* spp.), was previously included in the genus *Tribulus* (Zygophyllaceae). *Blutaparon* (= *Philoxerus*) *vermiculare* (L.) Mears, adopted by the moth *Acrola malloi* (Pastrana) introduced against alligatorweed [*Alternanthera philoxeroides* (Martius) Grisebach], is in the same tribe (Gomphreneae) as *Alternanthera* in the Amaranthaceae. Most of the native plants (37/41) that have become hosts of biocontrol insects belong to genera of plants used by these insects in their areas of origin. [Three exceptions are species of *Kallstroemia,* a genus limited to the Americas. Pre-release host specificity testing on weevils indicated that *Kallostroemia* spp. were acceptable hosts of the *Microlarinus* biocontrol weevils (Andres and Angalet 1963). The other exception is the alligatorweed moth *Acrola malloi* now using *Blutaparon* (= *Philoxerus*) *vermiculare* as a host, used *Philoxerus* species in its na-

Table 2 Comparison of non-target use of native plants by introduced agents in biological control projects on target weeds with close relatives with projects on target weeds which lack close relatives. Close relatives are defined to belong or previously to belong to the same genus as the weed

	Target weeds with relatives	Target weeds without relatives
US Mainland and Caribbean		
% projects with non-target use	48.5 (14/29)	None (0/6)
% agents adopting native hosts	17.9 (10/56)	None (0/12)
Number non-target plants used	37	None
Hawaii		
% projects with non-target use	100 (2/2)	5.6 (1/18)
% agents adopting native hosts	80 (4/5)	2 (1/49)
Number non-target plants used	3	1
Total (combined)		
% projects with non-target use	51.6 (16/31)	4.2 (1/24)
% agents adopting native hosts	23 (14/61)	1.6 (1/61)
Number non-target plants used	40	1
Total agents	117 (5 were released in both regions but counted only once)	
% agents using native plants	12.8 (15/117)	
% agents with unpredicted use of native plants	0.8 (1/117)	

tive South America (Vogt et al. 1963).] Overall, 12.8% (15/117) of the established agents attack native plants (Table 2). Almost a quarter (23%, 14/61) of the agents established on weeds with close relatives use non-target, native plant species, compared to 1 of 61 insects that have established on weeds without close relatives. Half (51.6%, 16/31) of the projects on target weeds with close relatives have resulted in the non-target use of native plants by biological control agents, compared to 4.2% (1/24) of projects on weeds without close relatives.

In the continental United States and the Caribbean, at least 37 native plants have become hosts to ten species of insects introduced for biological control (Tables 1, 2). More than half (22/37) of these are native *Cirsium* thistles used by *Rhinocyllis conicus* (Frolich), the European weevil introduced to the continental United States against exotic thistles. In mainland United States and the Caribbean, about a fifth (17.9%, 10/56) of the insects established on target weeds with close relatives have adopted non-target hosts, compared to none of the 12 agents established on weeds without close relatives.

In Hawaii, both projects conducted against weeds with close relatives resulted in non-target use of native species; four of the five insect species established now use native plant species as hosts (Tables 1, 2). The project to control an introduced blackberry (*Rubus argutus* Link) led to the establishment of three insect species in the 1960s; all three use the two native Hawaiian blackberry species. The other project in this category, to control purple nutsedge (*Cyperus rotundus* L.), established two insect species and one of these, a weevil (*Athesapeuta cyperi* Marshall) introduced in 1925, uses a native sedge (*Cyperus polystachyos* Rottb.). By comparison, only 1 of the 18 (5.6%) projects against Hawaiian weeds that lack close relatives has produced native plant use (Tables 1, 2). In these, only 1 of 49 (1.6%) established biological control agents now uses a native Hawaiian host. The lacebug *Teleonemia scrupulosa* Stal, introduced for control of *Lantana camara* L. (Verbenaceae), was reported to use *naio* [*Myoporum sandwicense* (DC) Gray] an endemic shrub in the Myoporaceae.

Discussion

Teleonemia scrupulosa, the single insect to be recorded to use a native plant that is not related to its host, was collected in Mexico and released in Hawaii in 1902 (Funasaki et al. 1988), without host specificity testing. It has been thought to be a lantana specialist (Winder and Harley 1983). The Myoporaceae and Verbenaceae are in the same order – the Lamiales (Angiosperm Phylogeny Group 1998), but lantana and *naio* are not closely related. The true host range of *T. scrupulosa* is unclear. When introduced to Uganda for lantana control, it fed on and damaged sesame (*Sesamum indicum* L. – Pedaliaceae, also in the order Lamiales), and reproduced on the plant to a limited extent (Davies and Greathead 1967). This record and unverified records on *Lippia alba* (Verbenaceae) in the Antilles, ebony (*Diospyros* sp., Ebenaceae) in the United States (Drake and Ruhoff 1965), and a *Xanthium* species (Asteraceae) in Hawaii (Funasaki et al. 1988) suggest that the insect may not be the specialist that it has been presumed to be. Recent searches in an area of the island of Hawaii, where both *naio* and lantana grow closely together, found much *T. scrupulosa* damage to lantana but none to *naio* (S. Hight and P. Conant, personal communication).

Risks to closely related plants of target weeds are amply illustrated by the cases of *Cirsium* thistles and *Opuntia* cacti in North America, each of these speciose genera are threatened by a biological control insect. The European weevil *Rhinocyllus conicus,* introduced in 1969, was first detected using a NorthAmerican native thistle 20 years ago (Reese 1977), and substantial harm to a native thistle was reported in 1997 (Louda et al. 1997).

Table 3 Proportion of congeneric native plant species of target weeds known to be hosts for introduced biological control agents

Genus	Number of species in the Continental United States	Co-occurring species with the target weed	Number used by biocontrol agents
Alternanthera (Amaranthaceae)	5	5	None
Centaurea (Asteraceae)	3	3	None
Cirsium (Asteraceae)	90	90	22 widespread
Convolvulus (Convulvulaceae)	2	2	None
Cuscuta (Cuscutaceae)	38	38	None
Cyperus (Cyperaceae)	10 in Hawaii	10	1 in Hawaii
Eurphorbia sensu *lato* (Euphoribiaceae)	117	42	None
Hypericum (Clusiaceae)	50	46	1 in California
Linaria = *Nuttallannthus* (Schrophulariaceae)	3	2	None
Lythrum (Lythraceae)	6	4	None
Opuntia (Cactaceae)	66	61	5 of 6 Florida spp.
Rubus (Rosaceae)	2 in Hawaii	2	2 in Hawaii
Salvia (Lamiaceae)	49	43	None
Senecio (Asteraceae)	102	63	3 in Oregon

Currently 22 of 90 *Cirsium* thistles are known hosts of the weevil and more use of and damage to native and rare *Cirsium* thistles will likely occur as the weevil spreads. Some thistles, such as *C. canescens* Nutt. in Nebraska, may be significantly harmed (Louda et al. 1997), but while others, such as *C. hydrophilum* (Green) Jepson in California, will experience use but not significant harm (Herr 1999). While all 90 native *Cirsium* spp. may be in the weevil's physiological host range, many will escape use and/or significant damage because they are not in the weevil's ecological host range. For instance, thistles that flower after the adult female weevils no longer lay eggs will escape use because the eggs are laid only within flower buds.

Cactoblastis cactorum, an Argentine moth, was introduced to the Caribbean in 1957 against native cactus weeds (Cock 1985). It was detected in south Florida in 1987 and has now spread northward at least to Georgia along the Atlantic coast. *C. cactorum* may have entered Florida as a contaminate of commercial nursery stocks of *Opuntia* imported from the Caribbean (in which it was repeatedly detected) (Pemberton 1996), and/or as a migrant from Cuba or other Caribbean islands (Johnson and Stiling 1996). If it spreads westward, up to 60 native species, including ca. 12 rare species, of *Opuntia* in the U.S. may be used and damaged. [*Opuntia* numbers estimated from the U.S. flora PLANTS database (USDA-NRCS 1999); rare *Opuntia* from the US Fish and Wildlife (Federal Register 1993).] *Opuntia* species thought to be at risk grow in the warmer areas of the United States, where *C. cactorum* can live. Mexico has large numbers of *Opuntia* species that the moth could use and possibly impact (Zimmermann 2000). The interception of *C. cactorum* in Laredo, Texas in 1995 in *Opuntia* plants from Mexico indicates that the moth is probably already in Mexico (USDA-APHIS 1999). Both the thistle weevil and the cactus moth effectively controlled their target weeds (Julien and Griffiths 1998; Simmons and Bennett 1966).

Overall, relatively few of the native plants congeneric with the adopted native plants and the target weeds are known to be used by insects introduced for biological control. For instance, only 1 of 46 *Hypericum*, 3 of 63 *Senecio*, and none of the 43 *Salvia* native species, that are broadly sympatric with the target weeds in these genera, are used by the insects (Table 3).

These patterns of non-target, native plant use by introduced biological control insects indicate that the risk to native flora can be judged reliably before introduction. The first element of protection for the native flora is the choice of weed targets that have few native congeners. Native plants in the same genus as target weeds have a predictable chance of being attacked, while more distantly-related plants have little risk. The second element of safety is employing insects and other natural enemies with diets narrow enough to avoid damaging native plants in the area of introduction. Careful determination of the candidate insect's field host range in its native area, coupled with rigorous host plant testing, will predict the potential host range in the intended area of introduction. The diet needs not just to be narrow, but suitably narrow. *Rhinocyllus conicus,* introduced to North America and Argentina (Enrique et al. 1983) to control weedy thistles, illustrates the point. In North America, the weevil threatens native *Cirsium* thistles because its host range is too broad, but in Argentina, where there are no native thistles, the weevil's host range is suitably narrow, enabling it to be used without risk to native plants.

These data also dispel some concern that the physiological, genetically-determined host ranges of herbivorous insects employed for biological control of weeds are unstable. The most obvious indication of the evolution of host ranges would be increased, or at least changed, taxonomic breadth after introduction, which is not indicated by these data.

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References

Andres LA (1985) Interaction of *Chrysolina quadrigemina* and *Hypericum* spp. in California. In: Delfosse ES (ed) Proceedings of the VI international symposium on biological control of weeds, Vancouver, Canada,1985. Agriculture Canada, pp 235–239

Andres LA, Angalet GA (1963) Notes on the ecology and host specificity of *Microlarinus lareynii* and *M. lypriformis* (Coleoptera: Curculionidae) and biological control of puncture vine, *Tribulus terrestris*. J Econ Entomol 56:333–340

Angiosperm Phylogeny Group (1998) An ordinal classification for the families of flowering plants. Ann Mo Bot Garden 85:531–553

Bianchi F (1961) *Teleonemia scrupulosa*. Proc Hawaii Entomol Soc 17:313

Carruthers RI, Onsager JA (1993) Perspective on the use of exotic natural enemies for biological control of pest grasshoppers (Orthroptera: Acrididae). Environ Entomol 22:885–903

Center T (1995) Selection criteria and ecological consequences of importing natural enemies (book review). Biodivers Conserv 4:524–526

Cock M (1985) A review of biological control of pests in the Commonwealth Caribbean and Bermuda up to 1982. Tech Commun 9, CIBC, CAB, Farnham Royal, UK

Davies JC, Greathead DJ (1967) Occurrence of *Teleonemia scrupulosa* on *Sesamum indicum* Linn. in Uganda. Nature 230: 102–103

Diehl J, McEvoy P (1990) Impact of the cinnabar moth (*Tyria jacobaeae*) on *Senecio triangularis,* a non-target native plant in Oregon. In: Delfosse ES (ed) Proceedings of the VII international symposium on biological control of weeds. Rome, Italy, 1988. Ministry of Agriculture, Forestry, Rome, and CSIRO, Melbourne, pp 119–126

Drake CJ, Ruhoff FA (1965) Lacebugs of the world. Bull U S Nat Mus 243

Enrique AE, Cordo HA, de Crouzel IS, Gimenez Tanzi MR (1983) Importacion de *Rhinocyllus conicus* Froelich y *Trichosirocallus horridus* Panzer para el control biologico fr lod "Cardos" en la Argentina. Maleza (ASAM, Argentina) 11:232–241

Federal Register (1993) 58: No. 5114

Funasaki GY, Lai P-Y, Nakahara LM, Beardsley J, Ota AK (1988) A review of biological control introductions in Hawaii: 1890–1985. Proc Hawaii Entomol Soc 28:105–160

Goeden D, Ricker DW (1986) Phytophagous insect faunas of the two most common native *Cirsium* thistles, *C. californicum* and *C. proteanum*, in southern California. Ann Entomol Soc Am 79:953–962

Hawkins BA, Marino PC (1997) The colonization of native phytophagous insects in North America by exotic parasitoids. Oecologia 112:566–571

Herr J (1999) Non-target impact of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on rare native California *Cirsium* spp. thistles. Abstracts of the X International symposium on biological control of weeds, Bozeman, Montana, USA, p 43

Howarth FG (1991) Environmental impacts of classical biological control. Annu Rev Entomol 36:485–509

Johnson DM, Stiling PD (1996) Host specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia* – feeding moth, in Florida. Environ Entomol 25:743–748

Julien MH, Griffiths MW (eds) (1998) Biological control of weeds: A world catalogue of agents and their target weeds, edn 4. CAB International, Wallingford, UK

Lockwood JA (1993a) Environmental issues involved in biological control of rangeland grasshoppers (Orthroptera: Acrididae) with exotic agents. Environ Entomol 22:503–518

Lockwood JA (1993b) Benefits and costs of controlling rangeland grasshoppers (Orthroptera: Acrididae) with exotic organisms: search for the null hypothesis. Environ Entomol 22:904–914

Louda SM, Kendall D, Connor J, Simberloff D (1997) Ecological effects of an insect introduced for the biological control of weeds. Science 277:1088–1090

Maehler MR, Ford MR (1955) *Teleonemia scrupulosa.* Proc Hawaii Entomol Soc 15:377

McAvoy T, Kok L-T, Mays WT (1987) Dispersal of *Trichosirocalus horridus* (Panzer) (Coleoptera: Curculionidae) in southwest Virginia. J Entomol Sci 22:324–329

McEvoy P (1996) Host specificity and biological pest control. BioScience 46:401–405

Miller M, Applet G (1993) Biological control: a little knowledge is a dangerous thing. Rutgers Law Rev 45:285–334

Morohasy J (1996) Host shifts in biological weed control: real problems, semantic difficulties or poor science. Int J Pest Manage 42:71–75

Onstad DW, McManus ML (1996) Risk of host expansion by parasites of insects. BioScience 46:430–435

Pemberton RW (1985a) Native plant considerations in the biological control of leafy spurge. In: Delfosse ES (ed) Proceedings of the VI international symposium on biological control of weeds, Vancouver, Canada, 1984. Agriculture Canada, pp 365–390

Pemberton RW (1985b) Native weeds as candidates for biological control research. In: Delfosse ES (ed) Proceedings of the VI international symposium on biological control of weeds, Vancouver, Canada, 1984. Agriculture Canada, pp 869–877

Pemberton RW (1995) *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in the United States: an immigrant biological control agent or an introduction of the nursery industry. Am Entomol 41:230–232

Pemberton RW (1996) The potential of biological control for the suppression of invasive weeds in southern environments. Castanea 61:313–313

Poinar GO Jr (1964) Observations on nutgrass insects in Hawaii with notes on the host range of *Bactra truculenta* Meyrick and *Athesapeuta cyperi* Marshall. Proc Hawaii Entomol Soc 18:417–423

Reese NE (1977) Impact of *Rhinocyllus conicus* on thistles in southwestern Montana. Environ Entomol 6:839–842

Simberloff D, Stiling P (1996) How risky is biological control? Ecology 77:1965–1974

Simmons F, Bennett F, Biological control of *Opuntia* spp. by *Cactoblastis cactorum* in the Leeward Islands (West Indies) Entomophaga 11:183–189

Strong DR (1997) Fear no weevil. Science 277:1058–59

Strong DR, Pemberton RW (2000) Biological control of invading species: risk and reform. Science 288:1969–1970

Thomas MB, Willis AJ (1998) Biological control - risky but necessary? Trends Evol Ecol 13:325–328

Turner C E (1985) Conflicting interests and biological control of weeds. In: Delfosse ES (ed) Proceedings of the VI international symposium on biological control of weeds, Vancouver, Canada, 1984. Agriculture Canada, pp 203–225

Turner CE, Pemberton RW, Rosenthal SS (1987) Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) in California. Environ Entomol 16:111–115

USDA-APHIS (1999) Quarantine data base

USDA-NRCS (1999) The PLANTS database (http://plants.usda.gov/plants)

Vogt GB, Quimby PC Jr, Kay SH (1992) Effects of weather on the biological control of alligatorweed in the lower Mississippi River region, 1973–83. USDA, ARS Tech Bull 1766

Winder JA, Harley KS (1983) The phytophagous insects on lantana in Brazil and their potential for biological control in Australia. Trop Pest Manage 29:346–362

Zimmermann HG (2000) A new pest on Opuntiae in wait for Mexico. In: Aguirre Rivera JR, Reyes Aguero JA (eds) Proceedings of the VIII congress and the VI international congress on the understanding and utilization of cactus pear, University of San Potosi, Mexico, 1999. pp 333–341 (in press)