CONSERVATION ISSUES

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Nontarget Feeding of Leaf-Beetles Introduced to Control Purple Loosestrife (*Lythrum salicaria* L.)

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ABSTRACT: Purple loosestrife (*Lythrum salicaria* L.) is an invasive nonindigenous plant that negatively affects North American wetlands. In 1992, four host-specific insect herbivores were introduced from the plant's native range as biological control agents and are now established in over 30 states and 10 Canadian provinces. Severe defoliation of purple loosestrife by *Galerucella calmariensis* L. and *G. pusilla* Duft. (Coleoptera: Chrysomelidae) selectively reduced purple loosestrife biomass by as much as 95% at many early release sites. At three sites, mass emergence of new generation *Galerucella* adults resulted in localized, short-term attack on *Rosa multiflora* Thunb., *Potentilla anserina* L., and *Decodon verticillatus* (L.) Elliott. Individuals of the same plant species away from the immediate emergence areas and at other release sites remained undamaged, and we observed neither feeding nor oviposition on the same plants by overwintered adults. Attack did not persist into the next growing season, and nontarget plants grew and appeared vigorous the following year, while purple loosestrife remained suppressed. Such "spillover" does not constitute a host shift; beetles are unable to complete development on these nontarget plants. Spillover effects have been observed in other biocontrol programs and do not affect distribution or abundance of nontarget species. We anticipate that occasional spillover with transient attack on nontarget species may occur at other release sites with high population densities of the *Galerucella* species. Careful monitoring is the best means to determine long-term impact.

Alimentación no Preferencial de Escarabajos Defoliadores Introducidos para Controlar la Loosestrife Púrpura (*Lythrum salicaria* L.)

RESUMEN: *Lythrum salicaria* L. Es una planta invasora alóctona que afecta negativamente los humedales de norte América. En 1992, se introdujeron cuatro insectos herbívoros huéspedes del rango nativo de *L. salicaria*, que ahora están establecidos en 30 estados y diez provincias canadienses. *Galerucella calmariensis* L. y *G. pusilla* Duft (Coleoptera: Chrysomelidae) causaron una severa defoliación de *L. salicaria* reduciendo su biomasa en casi el 95% en muchos de los lugares de liberación iniciales. En tres sitios, las nuevas generaciones de Galerucella adultos atacaron localmente a *Rosa multiflora* Thunb., *Potentilla anserina* L., y *Decodon verticillatus* (L.) Elliott. Individuos de la misma especie de planta, lejos de las áreas inmediatas de emergencia y en otros lugares de liberación permanecen sin ser dañados y no hemos observado alimentación ni oviposición en las mismas plantas por los adultos que pasaron el invierno. Los ataques no se mantuvieron en la siguiente estación, y las plantas que no fueron blanco de los ataques crecieron y parecían vigorosas al año siguiente, mientras que *L. salicaria* se mantuvo disminuida. Tal cambio momentáneo no constituye un cambio de huésped, los escarabajos no son capaces de completar su desarrollo fuera de sus plantas huéspedes. Efectos de cambios temporales han sido observados en otros programas de biocontrol y no afectan la distribución o abundancia de las plantas que no sean los blancos. Anticipamos que un cambio ocasional con ataques transitorios a las plantas que no eran los objetivos podía ocurrir en otros sitios de liberación con altas densidades de población de las especies de *Galerucella*. Un monitoreo cuidadoso es la mejor forma de determinar el impacto a largo término.

Index terms: biological control, *Decodon verticillatus*, nonindigenous invasive species, nontarget feeding, wetlands

INTRODUCTION

Invasive nonindigenous plants constitute a major threat to rare and endangered species (Wilcove et al. 1998) and the management of natural areas (MacDonald et al. 1989, Randall 1996). Purple loosestrife (*Lythrum salicaria* L.), a Eurasian perennial herb introduced to North America in the early 1800s (Thompson et al. 1987), can alter biogeochemical and hydrological processes in wetlands (Emery and Perry 1996, Grout et al. 1997) and threaten rare and endangered plant and animal species (Blossey 1999, Brown 1999, Blossey et al. 2001). Established *L. salicaria* populations persist for decades, are difficult to control using conventional techniques (chemical, physical, mechanical), and continue to spread into adjacent areas (Thompson et al. 1987). A classical biological weed control program was initiated in 1986 (Malecki et al. 1993), and four host-specific insect herbivores were introduced to North America (Malecki et al. 1993, Hight et al. 1995) in 1992. The selected species were a root-mining weevil, *Hylobius transversovittatus* Goeze; two leaf-feeding beetles, *Galerucella calmariensis* L. and *G. pusilla* Duft.; and a flower-feeding weevil, *Nanophyes marmoratus* Goeze.

Biological control, similar to chemical, mechanical, and physical control, may affect nontarget species. Benefits and risks associated with biological control have recently received much attention due to actual or suspected nontarget effects (Howarth 1991, Simberloff and Stiling 1996, Louda et al. 1997, McFadyen 1998, Follett and Duan 2000, Pemberton 2000, Wajnberg et al. 2001). Risks to nontarget species need to be weighed against the risks of allowing invasive species to remain unchecked. Recent reviews of nontarget effects in biological weed control (note: we did not consider the safety record and regulations for insect biological control) concluded that host-specificity tests are valuable and accurately predict potential nontarget effects (McFadyen 1998, Fowler et al. 2000, Pemberton 2000, Gassmann and Louda 2001). Nontarget impacts of *Rhinocyllus conicus* Fröhlich attacking native North American *Cirsium* species (Louda et al. 1997), and of *Cactoblastis cactorum* Berg. attacking native *Opuntia* species in Florida (Simberloff and Stiling 1996), are the result of poor decision-making processes before 1970 that allowed the release of nonspecific herbivores (Pemberton 2000, Gassmann and Louda 2001). Contemporary regulations (U.S. Department of Agriculture 1999) incorporate measures to avoid similar mistakes (Gassmann and Louda 2001).

Host-specificity tests are designed to prevent introducing species that may have negative impacts on nontarget species, yet these tests can not eliminate nontarget feeding entirely (Pemberton 2000). We must be concerned with introducing biological control agents if their impact on nontarget species reduces distribution and abundance of these nontarget species. Release of weed biocontrol agents is often permitted (after environmental assessment), even if the potential for nontarget attack exists, when potential harm caused by the herbivore is thought to be significantly less than harm caused by other control methods or by the failure to control the target invasive species. This assessment process is illustrated by the decision to introduce biological control agents for purple loosestrife (Blossey et al. 1994a, b; Blossey and Schroeder 1995). Herbicide treatments actually resulted in a further increase of purple loosestrife due to superior recruitment from the seed bank and accelerated suppression of native species (Skinner et al. 1994). Host-specificity tests identified two closely related native North American species, *Decodon verticillatus* (L.) Elliott (swamp loosestrife or waterwillow) and *Lythrum alatum* Pursh. (winged loosestrife), as potentially vulnerable to limited attack by newly emerged *Galerucella* beetles (Blossey et al. 1994a, b; Blossey and Schroeder 1995). However, the taller *L. salicaria* not only replaces *L. alatum* where ranges overlap; in areas where both species co-occur, the presence of *L. salicaria* reduces pollinator visitation and seed set of *L. alatum* (Brown 1999). Biocontrol agents were introduced based on risk assessments that concluded that benefits outweighed potential risks to *L. alatum* and *D. verticillatus* (Blossey et al. 1994a,b; Blossey and Schroeder 1995).

Successful weed biocontrol programs can reduce biomass of target plant species to very low levels (McEvoy et al. 1991), allowing other previously suppressed plant species to increase (which should benefit or allow recovery of native food webs). Long-term monitoring programs (incorporating target pest, control agent, and associated plant and animal communities) need to be designed to evaluate the full ecological impact (positive as well as negative) of biological weed control (Blossey 1999, Blossey and Skinner 2000). Biological control agents for purple loosestrife have now been released in over 30 states and 10 provinces in the United States and Canada, and a monitoring program was established (Blossey and Skinner 2000) to assess changes in abundance of insects and wetland plant communities. At many release sites, purple loosestrife is declining, but we also have recently observed nontarget feeding by *Galerucella* spp. The purpose of this paper is to discuss the implications of nontarget feeding detected at several field sites for the biological control program targeting purple loosestrife.

Status of *Galerucella calmariensis* and *G. pusilla*

Initial releases of the two leaf beetles *G. calmariensis* and *G. pusilla* occurred in seven states and six provinces (Hight et al. 1995). Demand for these species quickly exceeded their availability and mass-rear-

Table 1. Total number of release sites for biological control agents against purple loosestrife in 11 states, sites with quantitative monitoring using a standardized protocol, sites that are visited annually by state or university personnel ("Qualitative Monitoring"), release sites under control by collaborators ("Monitoring Uncertain" due to lack of information about local monitoring efforts), and year of first release.

States	Release Sites	Quantitative Monitoring	Qualitative Monitoring	Monitoring Uncertain	Year of 1st Release
Rhode Island	5	1	3	0	1994
Connecticut	21	20	1	0	1996
New York	166	27	9	130	1992
New Jersey	42	8	34	0	1994
Indiana	45	4	41	0	1994
Michigan	50	28	20	0	1994
Illinois	212	10	120	82	1994
Wisconsin	480	51	300	139	1994
Minnesota	560	20	290	250	1992
Colorado	3	3	0	0	1994
Oregon	100	23	50	27	1992
Total	1684	195	868	628	

ing procedures are now widely used by state and federal agencies, universities, schools, and private citizens (Blossey and Hunt 1999, Klepinger 1999). As a result of improved rearing abilities, over 5 million adults of both *Galerucella* species were released in more than 30 states and over 1600 wetlands nationwide. Although both species have very similar life histories (Blossey 1995c), *G. calmariensis* was easier to mass-produce (Blossey and Hunt 1999) and is most likely the dominant species in many releases.

We developed a standardized monitoring protocol, using permanent quadrats, to assess the impact of these biocontrol agents on purple loosestrife and the associated plant communities (instructions and forms are available at: *www.invasiveplants.net*). Monitoring is conducted in early summer during peak insect abundance and at the end of the growing season. In addition to insect abundance (using time-constrained counts), impact on the host plant (leaf area removed), percent cover, height, number of stems of purple loosestrife, and presence and abundance of other associated plants are recorded. Table 1 summarizes information on the number of release sites in 11 states. Biocontrol agents were released in 1684 wetlands invaded by purple loosestrife. Of these, 195 (11.6%) are monitored using quantitative data collections, and 868 (51.5%) are visited at regular intervals (mostly annually) to collect qualitative data (observations on presence/absence of biocontrol agents, assessment of population status and impact on purple loosestrife, and potential nontarget effects). All states with active rearing programs rely on cooperation by local collaborators. We have included these sites in the number of total release sites but due to uncertainty about monitoring efforts they are placed into the "uncertain" category.

The introduction of *G. calmariensis* and *G. pusilla* has increased the number of North American *Galerucella* species to five (Manguin et al. 1993). All species feed on wetland plants that may co-occur with purple loosestrife and are easily confused. *Galerucella calmariensis* and *G. pusilla* look alike, share similar life histories, and occupy the same ecological niche (Blossey 1995a-d). Adults overwinter in the leaf litter; they emerge in early spring, and their feeding causes a characteristic "shot-hole" pattern. Oviposition peaks in late May/early June; first instar larvae feed within leaf or flower buds; later instars feed on all aboveground plant parts. Larval feeding strips the photosynthetic tissue off individual leaves creating a "window-pane" (generally leaving the upper epidermis intact). Mature larvae pupate in the litter or soil beneath the host plant. At this time (mid- to late June in upstate New York) the damage to purple loosestrife becomes most conspicuous. Both *Galerucella* species are usually univoltine (one generation a year) although a partial second generation sometimes occurs. Peak dispersal of overwintered beetles occurs in spring; new generation beetles have dispersal flights shortly after emergence, are able to locate host plant patches as far away as 1 km within a few days, and are attracted to conspecifics (Grevstad and Herzig 1997).

Increasingly, observations and quantitative data from field releases show that the *Galerucella* species are able to build up large populations with dramatic impacts on purple loosestrife growth and abundance (Blossey and Skinner 2000, Lindgren 2000). Densities of over 8000 eggs m^{-2} were observed in Manitoba (Lindgren 2000). In Europe, larval densities of over 400/stem were common, resulting in complete defoliation of purple loosestrife (Blossey 1995b). In North America, areas dominated by purple loosestrife can have densities >50 stems m^{-2} (Blossey and Skinner 2000). A conservative estimate of 20 purple loosestrife stems m^{-2}, with 200 larvae/shoot, results in populations of 4000 larvae m^{-2}; and allowing for 50% mortality from larva to adult, an emergence of 2000 adults m^{-2} can be expected. Using these figures, we can assume that in extensive purple loosestrife populations, a single hectare can produce as many as 20 million new adults. The results of these population explosions are widespread defoliations of purple loosestrife, causing declines to less than 5% of its original abundance (Cornell University 1996, Blossey and Skinner 2000). Such impacts can extend well over 100 ha in a 5-year period (E. Holroyd, Bureau of Reclamation, Denver, pers. com.; B. Blossey, pers. obs.).

OBSERVATIONS

Observations in summer 1999 in Rhode Island, Michigan, and Connecticut at several of the permanent monitoring sites found that severe food limitation for newly emerging adults of *Galerucella* spp. resulted in heavy, albeit localized, attack of *Rosa multiflora*, *Potentilla anserina*, and *Decodon verticillatus* (plant nomenclature follows Gleason and Cronquist 1991).

Rhode Island

The Rhode Island site is located along the wetland walk at the Roger Williams Park Zoo in Providence. The entire wetland area is approximately 5.4 ha, half of which is covered by purple loosestrife. Zoo records indicate attempts to eradicate *L. salicaria* as early as 1984. Other associated wetland plants at the site include pussy willow (*Salix discolor*), black willow (*Salix nigra*) black tupelo (*Nyssa sylvatica*), bayberry (*Myrica pensylvanica*), pokeberry (*Phytolacca americana*), winterberry (*Ilex verticillata*), elderberry (*Sambucus* sp.), goldenrod (*Solidago* sp.), *Viburnum* sp., silky dogwood (*Cornus amomum*), arrow arum (*Peltandra virginica*), maple (*Acer* sp.), swamp azalea (*Rhododendron viscosum*), steeplebush (*Spiraea tomentosa*), swamp willow (*Decodon verticillatus*), and Joe-Pye-weed (*Eupatorium* sp.).

A mix of *G. calmariensis* and *G. pusilla* adults (500 in 1994, 600 in 1995, and 3000 in 1996) from Guelph University (Ontario, Canada), Cornell University, and Mission, Texas, were released at the zoo. In 1994 the first adults were released into a cage that was removed the following spring, before adult emergence. Subsequent open releases were made in June. The site has been regularly monitored at least twice per year for insects and plant growth. Establishment of a *Galerucella* population was confirmed in 1996 and 1997, and feeding caused some visible damage to purple loosestrife, with the first extensive defoliation occurring in June 1998. A limited amount of adult feeding was observed on *D. verticillatus*, but no larval development. As part of routine wetland management, park staff mowed all *D. verticillatus* plants in spring 1999. Purple loosestrife plants were damaged but not defoliated in July 1999, at the time when F_1 generation adults emerged from the soil. However, many of these adults laid eggs, producing a very large second generation that defoliated the entire purple loosestrife population in the 5.4-ha wetland. Emerging F_2 generation adults skeletonized *R. multiflora* bushes growing along the wetland boardwalk in the vicinity of the mass emergence. In addition, we noticed a single skeletonized new shoot of *S. discolor* and one leaf of *M. pensylvanica* with *Galerucella* feeding. An assessment of the extent of nontarget feeding on 20 September 1999 found feeding damage on multiflora rose bushes growing as far away as 50 m, but no damage on those 100 m away. Other wetland plants in the vicinity did not show any signs of attack. All reference specimens collected from *R. multiflora*, *S. discolor*, and *M. pensylvanica* were identified as *G. calmariensis*.

Michigan

The Michigan release site was the Nayanquing Point Wildlife Area, Bay County, an impounded Saginaw Bay coastal wetland managed as a wildlife refuge and hunting area, where purple loosestrife infests 40.5 ha and dominates 4.5 ha. Associated wetland plants include bluejoint (*Calamagrostis canadensis*), rush (*Juncus* sp.), heartsease (*Polygonum lapathifolium*), spike-rush (*Eleocharis* sp.), and rice-cut grass (*Leersia oryzoides*). A mixture of approximately 500 *G. calmariensis* and *G. pusilla* originating from Cornell University were released in sleeve cages in July 1994. Monitoring was conducted weekly from 19 June–2 August 1995 to evaluate establishment (Dalgarn and Kantak 1995). The site was visited in 1997 and 1998 to confirm continued insect activity. Moderate defoliation of *L. salicaria* was observed in 1998 in a limited area near the release site. The site was surveyed on 29 June 1999 using procedures of the standardized monitoring protocol. Teneral (newly emerged) adults were present, but no eggs or larvae were found in sample quadrats. All *L. salicaria* plants in the permanent quadrats were heavily defoliated and 100% desiccated. Insects had spread approximately 800 m from the original release site, and an estimated 4–6 ha of *L. salicaria* were 80–100% defoliated in 1999.

No live purple loosestrife foliage remained in the emergence area, and beetles were seen resting and dispersing from the site. Silverweed (*Potentilla anserina*) plants growing in the middle of a dike-top gravel road running through the site were ca. 60% defoliated by *Galerucella* feeding over a distance of about 10 m. Individuals of *P. anserina* growing a few meters away among other plants on the sides of the dike were untouched. Reference specimens collected from *P. anserina* were unfortunately lost prior to identification. The native leaf-beetle *G. quebecensis* Brown is known to feed on *Potentilla* spp., therefore there is the possibility that the insects attacking *P. anserina* were actually *G. quebecensis*. However, the similarity to the situation in Rhode Island and Connecticut leads us to interpret these observations as a likely case of nontarget feeding.

Connecticut

At the Connecticut site, purple loosestrife grows in a narrow fringe around a 2-ha lake located in the center of the University of Connecticut campus in Storrs. Associated wetland plants include *D. verticillatus*, sedges (*Carex* spp.), jewelweed (*Impatiens capensis*), rice cut-grass, yellow iris (*Iris pseudacorus*), goldenrod, Northern bugleweed (*Lycopus uniflorus*), arrow-leaved tearthumb (*Polygonum sagittatum*) asters (*Aster* spp.), and dodder (*Cuscuta* sp.). A mix of 1000 adults of *G. calmariensis* and *G. pusilla* obtained from Cornell University were released on 2 July 1996. Beetle establishment and impact were monitored using the standardized monitoring protocol and permanent quadrats along a 45-m linear transect. Leaf-beetles became established and extensive damage to purple loosestrife was obvious in the summer of 1998. In spring 1999, *Galerucella* adults and eggs were abundant around the entire lake perimeter; larval feeding completely defoliated purple loosestrife plants throughout the entire study area by late May. Emergence of the new generation began in mid-June with many *L. salicaria* plants around the lake showing an abundance of adults and extensive feeding damage.

University facilities personnel periodically mow all vegetation, including *L. salicaria*, along the lake perimeter outside the *Galerucella* biological control study area. Although the study area was marked off and was not affected, after vegetation was cut on 25 June 1999 few *L. salicaria* plants with green tissue remained at the lake. New generation adults that emerged in June had virtually no *L. salicaria* to feed on, and there were no other wetlands with purple loosestrife in the vicinity. Many of the F_1 adults moved onto two small patches of *D. verticillatus* growing near the study site. Before plants were cut, *Galerucella* adults were not observed feeding on *Decodon*. Within several days, the *D. verticillatus* plants were completely defoliated. Small groups of *L. salicaria* seedlings regrew during the remainder of the summer, and *Galerucella* feeding and recruitment were observed on these plants, whereas *D. verticillatus* did not regrow in 1999. At a second release site in Connecticut with a mix of *L. salicaria* and *D. verticillatus*, *Galerucella* spp. are established and the population is increasing, but feeding and oviposition is restricted to purple loosestrife.

Other Sites and Summary

At the Amwell Lake Wildlife Management Area in Hunterdon County, New Jersey, newly emerged *Galerucella* spp. adults fed on *R. multiflora* during a population explosion in summer 2000 (M. Mayer and R. Chianese, New Jersey Department of Agriculture, Trenton, pers. com.). Adult feeding was restricted to foliage of *R. multiflora* within a 1-m area adjacent to defoliated purple loosestrife, and no larvae or eggs were observed. At all other monitoring sites across North America (Table 1), despite similar population explosions of the *Galerucella* spp., no nontarget feeding was ever observed. It is critical to confirm species identification of *Galerucella* spp. Several initially suspected nontarget attacks in Minnesota were found to be the feeding by other native chrysomelid species such as the waterlily leaf beetle *Galerucella nymphaeae* (L.), (L. Skinner, Minnesota Department of Natural Resources, St. Paul, pers. com.).

At the three sites with nontarget feeding in 1999, attacked or defoliated plant individuals re-grew in 2000 and appeared healthy. Leaf beetle populations were much lower, but purple loosestrife growth was greatly suppressed. At Nayanquing in Michigan, cover of purple loosestrife dropped from over 39.8% to 3.2%, and native wetland plants have greatly expanded in frequency and cover (D. Landis, unpubl. data). Continued observations of *P. anserina* plants attacked in 1999 showed that no individual received more than a trace of feeding (<1% leaf area removed) in 2000. However, at an adjacent area with complete defoliation of purple loosestrife in 2000, *G. calmariensis* teneral adults attacked several branches of *Cornus stolonifera* L. At the sites in Connecticut and Rhode Island, no nontarget feeding was observed on plants that adults had fed on in 1999 (note that these beetles are the same individuals that fed on nontarget plants as teneral adults!). This supports data from host-specificity screening indicating that overwintered adults are more selective than inexperienced, newly emerged beetles (Blossey et al. 1994b). Feeding declined sharply with increasing distance from the emergence area, consistent with the expectations that inexperienced newly emerged adults learn to avoid unsuitable host plants (Bernays 1998). Pheromones of the *Galerucella* species may contribute to the very localized (a branch or a leaf) attack reported: adults are attracted to each other (Grevstad and Herzig 1997) and show highly aggregated distributions (Blossey 1995c). Such "spillover" nontarget effects are localized, temporary, and restricted to population outbreaks of biological control agents.

DISCUSSION

Release of insect herbivores from the home range of a nonindigenous plant is often met with concerns that (1) biocontrol agents may attack nontarget plants and (2) biocontrol agents may, over evolutionary time, become less host-specific and attack nontarget species (Secord and Kareiva 1996, Simberloff and Stiling 1996, Louda et al. 1997). Worldwide, more than 1200 programs have released 350 species of insects and pathogens targeting 133 plant species (Julien and Griffiths 1998). Several recent analyses (McFadyen 1998, Fowler et al. 2000, Pemberton 2000) concluded that host ranges of herbivorous biological control agents appear stable, and that nontarget use (defined as the ability to complete larval development) is largely restricted to close relatives (usually within the same genus) of the target weed species (often predicted by host-specificity tests). Although 24 (6.8 %) of all insect biocontrol agents are reported feeding on nontarget plants (Table 2), 10 of these instances can be classified as "spillover" and do not constitute host shifts. These herbivores are unable to complete development on the nontarget species and feeding instances are associated with population outbreaks. Interestingly, which plant species will be attacked during spillover events seems to be unpredictable (Table 2). Of larger concern are weed biocontrol agents that establish and sustain populations on nontarget plants. In many instances survival and recruitment is low (Turner 1985, Willis and Ash 1996) and attack of the nontarget is reduced as distance to the original host increases (A. Willis, CSIRO, Canberra, Australia, pers. com.; S. Schooler, Oregon State University, Corvallis, Oregon, pers. com.). Only 4 (1.7%) species are known to have established self-sustaining populations on nontarget species in the absence of the original host (Table 2), and this potential was known at the time of introduction. Host-specificity screening consistently has provided the best assurance for the safety of nontarget species (McFadyen 1998, Pemberton 2000, Gassmann and Louda 2001).

Spillover events, as described here for the *Galerucella* species and other biocontrol agents (Table 2), are associated with high population densities of control agents, often newly emerging adults, and food shortage. These individuals have to learn to recognize suitable host plants while rejecting suboptimal plants that often elicit deleterious postingestive effects (Bernays 1998). Under severe food limitation newly emerged adults appear to make "mistakes" in their food choice. That such feeding is spatially limited to plants (or branches) close to mass emergence sites suggests that adults quickly learn to recognize unsuitable species and leave the area in search of suitable host plants.

Host-specificity screening results for the two *Galerucella* species in Europe (Blossey et al. 1994a, b) led to predictions that temporary attack on *D. verticillatus* and *L. alatum* was likely, particularly at high densities of the control agents. These predictions were confirmed and, as predicted, attack was temporary and of no lasting consequence to *D. verticillatus* and *L. alatum* in Ontario (Corrigan et al. 1998). Our observations in Connecticut and Rhode Island further confirm these results. Additional host-specificity testing of *G. calmariensis* using 40 previously untested species supported the pre-introduction host-specificity results (Kaufman and Landis 2000). Although in no-choice feeding trials adult *G. calmariensis* nibbled on other species, particularly rosaceous plants, normal feeding, oviposition, and larval development was restricted to *L. salicaria* (Kaufman and Landis 2000). Over 1600 release sites are now established throughout North America (many with sharply increasing *Galerucella* populations 4–5 years after the initial release). Nontarget feeding is restricted to observations in Ontario (Corrigan et al. 1998) and those reported in this paper. The limited duration and extent of this attack does not affect distribution or abundance of the nontarget species.

The benefits of biological control must continue to be weighed against the risks of nontarget attack, risks of allowing invasive species to remain unchecked, and risks associated with other control measures (Blossey et al. 2001). We believe that despite the very limited incidence of nontarget feeding reported in this paper, the release of biocontrol agents against purple loosestrife will have a very positive effect on North American wetland ecosystems. At many biocontrol release sites, once-monotypic stands of *L. salicaria* are being

Table 2. Biological weed control agents and their attack on and damage to nontarget plants. "Spillover" species are those that attack nontarget plants at high population densities but do not develop on these species; "sustained attack" species are those that are able to sustain populations on the nontarget plant in the absence of the original host; and "unclassified" species are those for which there is insufficient information to place them in either category.

Agent	Target Weed	Released	Nontargets Attacked	Expected/ Predicted	Reference
SPILLOVER					
Neochetina eichhorniae (Warner)	*Eichornia crassipes* (Martius) Solms-Laubach water hyacinth	USA 1972	*Canna* spp.	No	Center 1982
			Pontederia spp., pickerel weed	No	Harris 1988
Cactoblastus cactorum (Berg)	*Opuntia ficus-indica* (L.) prickly pear	Australia 1922	Melons, tomatoes	No	
Chelnidae tabulata (Burmeister)	*Opuntia ficus-indica* (L.) prickly pear	Australia 1922	melons, tomatoes, nectarines, dates, peaches, and grapes	No	Harris 1988
Trichilogaster acaciaelongifoliae (Froggatt)	*Acacia longifolia* (Andrews) Willdenow, long leaved wattle	South Africa 1982	*Acacia melanoxylon*		Dennill et al. 1993
			Paraserianthes lophanta	No	Dennill et al. 1999
Teleonemia scrupulosa (Stal)	*Lantana camara* L. lantana	Uganda 1960	*Sesamum indicum* L.	No	Davies and Greathead 1967
		Hawaii 1902	*Myoporum sandwichense* (DC) Gray	No	Pemberton 2000
Uroplata girardi Pic	*Lantana camara*	Hawaii 1961 Australia 1966	Basil and other herbs	No	McFadyen 1998
Croesia zimmermannii Clarke	*Rubus argutus* Link prickly Florida blackberry	Hawaii 1964	*Rubus hawaiiensis*	Yes	McFadyen 1998
Zygogramma bicolorata Pallister	*Parthenium hysterophorus* L. parthenium	India 1984	*Helianthus annuus*	No	McFadyen 1998
Galerucella calmariensis L.	*Lythrum salicaria* L.	USA, Canada 1992	*Decodon verticillatus*	Yes	Blossey et al. 1994a
Galerucella pusilla Duft.	purple loosestrife		*Lythrum alatum*		Yes Corrigan et al. 1998
			Rosa multiflora		No this paper
			Salix discolor		No
			Potentilla anserina		No
			Cornus stolinifera		No
SUSTAINED ATTACK					
Tyria jacobaeae L.	*Senecio jacobaea* L. ragwort	New Zealand 1929	*Senecio triangularis*	Yes	Diehl and McEvoy 1990
		USA 1959	*Senecio integerrimus*		McEvoy and Coombs 2000
			Senecio pseudaureus		Pemberton 2000
Rhinocyllus conicus (Froehlich)	*Carduus nutans* L. nodding thistle	USA 1969	22 native *Cirsium* spp.	Yes	Turner et al. 1987
					Louda et al. 1997
					Pemberton 2000
Cactoblastus cactorum	*Opuntia ficus-indica* (L.) prickly pear	Caribbean 1957	Native *Opuntia* species in Florida	Yes	Simberloff and Stiling 1996
					Pemberton 1995

Table 2, *continued*

Agent	Target Weed	Released	Nontargets Attacked	Expected/ Predicted	Reference
Chrysolina quadrigemina (Suffr.)	*Hypericum perforatum* L. St. John's wort, Klamath weed	USA 1946	*Hypericum calycinum* L. *Hypericum concinnum* Benth.	Yes	Ehler 1991 Andres 1985
UNCLASSIFIED					
Bruchidius villosus Fabricius	*Cytisus scoparius* (L) Link broom	New Zealand 1987	*Chamaecytisus palmensis*	No	P. Syrett, Landcare Research, Lincoln, New Zealand, pers.com.
Priophorus morio (Lepeletier)	*Rubus argutus* Link prickly Florida blackberry	Hawaii 1966	*Rubus hawaiiensis* *Rubus macraei*	?	Pemberton 2000
Schreckensteinia festaliella Hübner	*Rubus argutus* Link prickly Florida blackberry	Hawaii 1963	*Rubus hawaiiensis* *Rubus macraei*	?	Pemberton 2000
Arcola (Vogtia) malloi Pastrana	*Alternanthera phylloxeroides* (Mart.) Griseb. alligatorweed	USA 1971	*Philoxerus vermicularis* (L.) R.Br.	?	Turner 1985 Cullen 1990
			Alternanthera flavescens	?	Pemberton 2000
Agrilus hyperici (Creutzer)	*Hypericum perforatum* L.	USA 1950	*Hypericum concinnum* Benth.	?	Turner 1985 Cullen 1990
Zeuxidiplosis giardi Kieffer	*Hypericum perforatum* L.	USA 1950	*Hypericum concinnum* Benth.	?	Turner 1985
Aculus hyperici Liro	*Hypericum perforatum* L.	Australia 1991	*Hypericum gramineum*	Yes	Willis and Ash 1996; A. Willis, CSIRO, Canberra, Australia, pers.com.
Microlarinus lareynii (Jacquelin du Val)	*Tribulus terrestris* L. puncturevine	USA 1961	*Kallstroemia grandiflora* Torr.	?	Turner 1985
M. lypriformis (Wollaston)	*Tribulus terrestris* L.	USA 1961	*K. grandiflora* and 2 other *Kallstroemia* spp.	?	Turner 1985 Pemberton 2000
Tmolus echion (Druce)	*Lantana. camara*	Hawaii 1902	*Clidemia hirta*	?	Julien and Griffiths 1998
Athesapeuta cyperi Marshall	*Cyperus rotundus* purple nut-sedge	Hawaii 1925	*Cyperus polystachyos*	?	Pemberton 2000

replaced by more diverse wetland plant communities (D. Landis, R. Wiedenmann, unpubl. data). At the Tonawanda Wildlife Management Area in western New York State, an area once dominated by purple loosestrife and abandoned by black terns (*Chlidonias niger* [L.]) has developed into an emergent marsh and is now again used as a breeding and foraging area for terns (D. Carroll, New York Department of Environmental Conservation, Alabama, N.Y., pers. com.; B. Blossey, pers. obs.). In a near-monotypic stand of purple loosestrife in a highly disturbed wetland in northwestern Illinois, 17 native plant species not previously observed were recorded in 1999 after extensive defoliation by the *Galerucella* species (R. Wiedenmann, unpubl. data). Similar results are expected to occur throughout the country, and we will continue our long-term monitoring program to assess changes associated with the release of biological control agents for purple loosestrife.

The history of biological weed control and current information suggest that nontarget feeding events are transient, only occur in years of extremely high *Galerucella* populations, and are spatially limited to plants close to high emergence areas. Short-term, transient, nontarget effects of biological control agents are acceptable if the net effect is a benefit to native taxa and ecosystems.

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