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Host Specificity and Environmental Impact of Two Leaf Beetles (*Galerucella calmariensis* and *G. pusilla*) for Biological Control of Purple Loosestrife (*Lythrum salicaria*)[1]

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Abstract. **Many prime wetlands in North America have been degraded following encroachment by the exotic plant purple loosestrife. Conventional methods are unsuccessful in providing long-term control. Host specificity studies demonstrated the suitability of two leaf beetles, *Galerucella calmariensis* and *G. pusilla*, as biological weed control agents. Adults oviposited only on plants within the genus *Lythrum*. The only species other than purple loosestrife where adult feeding and oviposition occurred and that supported successful larval development was winged lythrum. Swamp loosestrife and winged lythrum may be vulnerable to limited attack by newly emerged teneral adults. Evaluation of the potential environmental impact of the two leaf beetles showed that benefits of an introduction outweigh potential risks to winged lythrum or swamp loosestrife. Their field release was approved in 1992. Nomenclature: Purple loosestrife, *Lythrum salicaria* L. #[3] LYTSA; winged lythrum, *Lythrum alatum* Pursh # LYTAL; *Galerucella calmariensis* L.; *Galerucella pusilla* Duftschmid.**

Additional index words. **Leaf beetles, wetlands, *Decodon verticillatus* (L.) Ell # DEOVE, LYTSA, LYTAL.**

INTRODUCTION

Purple loosestrife is a herbaceous perennial of Eurasian origin that has become naturalized in North America. It arrived as a contaminant of ship ballast and was purposefully introduced as a medicinal herb and ornamental. The plant has become a serious weed in marshes and alluvial wetlands (24, 25). By the 1830s, purple loosestrife was well established along the New England seaboard. During the 1880s the plant spread westward throughout New York and the St. Lawrence Valley via river systems and canals (25). Recently, expansion in the range of purple loosestrife had coincided with increased land development, construction of road systems, commercial distribution of the plant for horticultural purposes, and regional propagation for bee forage (19, 25). The plant now occurs throughout the Northeastern U.S. and adjacent Canada. In the western states, purple loosestrife occurs in scattered locations and impedes the flow of water in irrigation systems.

Invasion of wetlands by purple loosestrife replaced native plant species and degraded the habitat for wildlife. Large monotypic stands of purple loosestrife threaten various endangered species, such as a local bulrush (*Scirpus longii* Fern.) in Massachusetts (10), dwarf spikerush [*Eleocharis parvula* (Roemer and J. A. Schultes) Link ex Buff. and Fingerh.] in New York (20), and the bog turtle (*Clemmys muhlenbergi* Schoepf) in the Northeastern U.S. (25). No effective method is available to control purple loosestrife, except where it occurs in small localized stands. Chemical control is costly and requires long-term application (23). Glyphosate [N-(phosphonomethyl)glycine], 2,4-D [(2,4-dichlorophenoxy)acetic acid], and, on an experimental basis, triclopyr {[(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid} commonly are used to control purple loosestrife. Use of these nonspecific herbicides has had detrimental effects on nontarget wetland plants (23).

Importation of specialized phytophagous insects from Europe, which severely damage purple loosestrife (3, 4), represents a classical biological weed control program that offers the best means to control this invasive exotic (12, 13, 16).

In the hierarchical selection of weed management techniques, biological weed control is often considered as a last resort. This was the case for spotted knapweed (*Centaurea maculosa* Lam.) (7) and purple loosestrife (25). Biological weed control has been conducted over a century with no undesirable effects or host shifts severely damaging a nontarget plant (7). Successful biological control is highly cost effective, long term, nonpolluting, and self-sustaining. Function of the invaded environments is often restored.

Galerucella calmariensis and *G. pusilla* severely damage purple loosestrife in Europe (3). The biology and host specificity of these two leaf beetles were studied to evaluate their suitability as biological control agents. In addition, the suitability of a third species, the root-boring weevil *Hylobius transversovittatus* Goeze, was investigated simultaneously (5).

The numerous small purple to red flowers of purple loosestrife are trimorphic. Plants bloom from late June into September. Mature plants with 30 to 50 annual shoots grow over 2 m high and produce more than two million seeds a year. Germination is restricted to open wet soils and requires high temperatures. The laterally branching rootstock serves as a storage organ from which shoots emerge after overwintering or burndown from herbicide control attempts. Monospecific stands of purple loosestrife are found in North America, but only small scattered populations occur in its native range (2, 25).

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[3]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 1508 West University Ave., Champaign, IL 61821-3133.

Table 1. Test plant species for host specificity screening with biological control agents against purple loosestrife.

A.	Taxonomically associated plants:		
	Lythraceae	1. *Lythrum salicaria*[ab]	2. *L. lineare* L.
		3. *L. alatum* Pursh.[b]	4. *L. californicum* Torr. & Gray
		5. *L. hyssopifolia* L.[a]	6. *Decodon verticillatus* (L.) Ell[b]
		7. *Rotala ramosior* (L.) Koehne[b]	8. *Ammania auriculata* Willd
		9. *A. coccinea* Rottb	10. *A. robusta* Heer & Regel
		11. *A. latifolia* L.	12. *Cuphea viscosissima* Jacq
		13. *C. wrightii* Gray	14. *C. laminuligera* Koehne
		15. *C. lanceolata* Alton	16. *C. lutea* Rose
		17. *Lagerstroemia indica* L.[a,b]	
	Punicaceae	18. *Punica granatum* L.[a]	
	Melastromataceae	19. *Rhexia mariana* L.[b]	
	Onagraceae	20. *Ludwigia alternifolia* L.	21. *Epilobium angustifolium* L.
		22. *Oenothera biennis* L.	23. *Gaura parviflora* Dougl.
		24. *G. biennis* L.[c]	25. *Circaea quadrisulcata* (L.) Hara[b]
	Thymelaceae	26. *Dirca palustris* L.[c]	
B.	Associated wetland plants of wildlife importance:		
	Typhaceae	27. *Typha latifolia* L.	
	Sparganiaceae	28. *Sparganium eurycarpum* Engelm.	
	Alismataceae	29. *Sagittaria latifolia* Willd.	
	Poaceae	30. *Zizania aquatica* L.[b]	
	Cyperaceae	31. *Scirpus americanus* Pers.	32. *S. acutus* Muhl.
		33. *Carex comosa* Bostt.	
	Salicaceae	34. *Salix interior* Rowlee[b]	
	Polygonaceae	35. *Rumex verticillatus* L.[c]	36. *R. crispus* L.[a]
		37. *Polygonum coccineum* Muhl.	
	Chenopodiaceae	38. *Chenopodium hybridum* L.[c]	39. *C. album* L.[a]
	Ranunculaceae	40. *Ranunculus sceleratus* L.	41. *R. bulbosus* L.[a]
C.	Important agricultural plants:		
	Poaceae	42. *Triticum aestivum* L. 'Blue Boy'[a]	
		43. *Oryza sativa* L. 'Bluebonnet'[a]	
		44. *Zea mays* L. 'Pioneer 37-44'	
	Chenopodiaceae	45. *Beta vulgaris* L. 'Golden Tankard'[a]	
	Fabaceae	46. *Glycine max* L. 'Pella'[a]	
	Malvaceae	47. *Gossypium hirsutum* L. Tameot CD3H'	
	Asteraceae	48. *Helianthus annuus* L. 'Mingren'	

[a]Species not native to North America.
[b]Species also tested in quarantine (14).
[c]Species tested in quarantine only (14).

The two *Galerucella* species live sympatrically in the same ecological niche on their host plant (2, 15). The beetles' distributions overlap widely and adults can be separated without difficulty (18, 22). Chromosome analysis (17), electrophoresis data (15), and behavioral studies[4] have demonstrated their reproductive separation.

The following life history description applies to both *Galerucella* species. Adults appear on their host plant at the early stage of shoot development in April or May and start feeding on the meristematic tissues of young tips before the leaves unfold. Oviposition commences after about 1 wk of feeding, peaks during May and June, and continues at a reduced rate until the end of July. Egg masses are laid on leaves and stems. Eggs are circular, opaque in color, and have a reticulate chorion. Young larvae feed preferably on developing leaf- and flowerbuds and older larvae feed on any part of the plant. Mature larvae leave the plant and pupate in the litter or soil beneath the host. New generation beetles occur mainly during July and some have a minor oviposition period prior to overwintering.

Adult feeding and larval development occur almost throughout the growing season of purple loosestrife. Shoot development can be retarded or eliminated, and at high beetle densities whole populations can be defoliated, preventing flowering and seed production (3). The aim of this research was to investigate host specificity of *G. calmariensis* and *G. pusilla* and to discuss the potential environmental impact of releasing the leaf beetles into North American wetlands.

MATERIALS AND METHODS

Forty-eight plant species (Table 1) were approved for host specificity screening tests by the Technical Advisory Group for

[4]Personal communication, G. Petersen, Grad. Stud., Zool. Inst., Christian-Albrechts Univ., Kiel, Germany.

the Introduction of Biological Control Agents of Weeds (TAG)[5], U.S. Department of Agriculture, Animal and Plant Health Inspection Service. The plants selected belonged to one of three groupings: taxonomically associated plants, associated wetland plants of wildlife importance, and important agricultural plants (Table 1). The phylogenetically related plants of the first group are based on the system of Cronquist (8). The order Myrtales has 12 families, and four of these families (Lythraceae, Thymelaceae, Onagraceae, and Melastomataceae) are native to much of North America. Of the remaining eight families, five are strictly tropical in their distribution and lack important introductions into North America. Three families (Trapaceae, Myrtaceae, and Punicaceae), while primarily tropical in distribution, have members introduced and established in North America. Only the Punicaceae are included in the test list because of pomegranate (*Punica granatum* L.), an introduced semitropical agricultural fruit that is grown in the U.S., although outside the range of purple loosestrife. Plants that make up the second group are not taxonomically related to purple loosestrife but occur in the same habitat and are therefore likely to be exposed to any introduced biological control agent. The third group contains a selection of crop plants that were tested as an additional safety factor.

The host specificity testing was split between the International Institute of Biological Control in Europe and the quarantine facility at Virginia Polytechnic Institute & State University, Blacksburg, Virginia (14). The majority of plant species were tested in Europe. Screening tests were conducted in a greenhouse at Christian-Albrechts University (CAU), Kiel, northern Germany, under a natural photoperiod and fluctuating temperatures (10 to 30 C) during 1989 and 1990. Test plant species were grown in commercial potting soil in 10-cm-diameter clay pots from seeds, roots, or tubers, either shipped from the U.S. or obtained from European field populations. Most plants were grown outdoors to insure healthy specimens. Those with a southern distribution were grown in the greenhouse. Plants that were difficult to grow in northern Germany or where additional information was desired were tested in quarantine at VPI and SU (14).

Adult feeding and oviposition tests. In May 1989 and 1990 the adults used in feeding and oviposition tests were collected with an aspirator from purple loosestrife plants at several sites in northern Germany. Experiments were conducted in May and June throughout the oviposition period of the beetles. Beetles were allowed to feed on purple loosestrife for 1 wk following their use in the tests to insure oviposition capacity.

Several weeks-old well-developed potted test plants were offered in a multiple-choice design (without purple loosestrife) in screened cages of 40 by 40 by 60 cm. Pomegranate and crepe myrtle (*Lagerstroemia indica* L.) were offered as cut shoots obtained from the Botanical Gardens at CAU. Depending on the size of the plants, four to seven pots were used per test. Test plant species were arranged in random combinations and exposed to five pairs of adults in each test. For each plant species, tests were replicated five times. A control consisting of beetles caged exclusively on purple loosestrife was run simultaneously.

After 5 d, test plants were removed from the cages. Number of eggs laid and feeding intensity (no feeding, nibbling, slight to moderate feeding, regular feeding) were recorded. Nibbling was the presence of a few feeding marks on test plants, slight to moderate feeding was the removal of an obvious amount of leaf tissue, and regular feeding was the removal of the same amount of leaf tissue as occurred on the purple loosestrife controls during the same time.

No-choice adult feeding and oviposition tests. In an additional no-choice experiment, three pairs of adult *G. calmariensis* or *G. pusilla* were caged in clear plastic cylinders (20 cm high and 15 cm in diameter) on cut shoots of winged lythrum and purple loosestrife. The experiment was started with newly emerged, overwintered adults. The beetles originated from a laboratory colony and were not allowed to feed on purple loosestrife prior to the experiment. Each *Galerucella* species was replicated five times on each plant species. Adult survival and number of eggs laid were recorded and food was replaced at weekly or biweekly intervals.

No-choice larval transfer tests. Experiments were conducted in a no-choice design with leaves in petri dishes. New leaves were placed on a moistened cotton sheet to keep them fresh. Five newly hatched first instar larvae were transferred with a fine hair brush to a leaf. Experiments for each test plant species were replicated five times. Survival and feeding was recorded every 2 d and leaves were replaced.

Field tests. At two sites in northern Germany (Gammendorf and Meggerdorf) five well-developed potted plants of purple loosestrife, winged lythrum, and swamp loosestrife (15 potted plants per site) were dug into the ground. At both sites densities of the leaf beetles were high enough to cause considerable damage to naturally growing purple loosestrife plants. Potted plants at Gammendorf were exposed to beetles that had overwintered and started ovipositing. Plants were exposed during the entire oviposition period from June 1 to July 15, 1991. Plants at Meggerdorf were placed in close proximity to purple loosestrife plants that had been defoliated by *Galerucella* larvae. They were exposed from July 15 to August 15, 1991 to evaluate feeding behavior of the emerging new generation beetles under food shortage.

RESULTS AND DISCUSSION

Adult feeding and oviposition tests. Outside the genus *Lythrum*, adults of both species occasionally nibbled but never oviposited on test plants (Tables 2, 3). Normal feeding of both species was restricted to purple loosestrife. Slight to moderate feeding occurred on winged lythrum, California loosestrife (*L. californicum* Torr. and Gray), and hyssop lythrum (*L. hyssopifolia* L., #LYTHY) (Tables 2, 3). Occasional nibbling was observed on another seven plant species for *G. calmariensis* (Table 2), and three species for *G. pusilla* (Table 3). Normal oviposition of both species was restricted to purple loosestrife, moderate oviposition

[5]Abbreviations: TAG, Technical Advisory Group for the Introduction of Biol. Control Agents of Weeds; CAU, Christian-Albrechts Univ., Kiel, 2300 Kiel, Germany; VPI&SU, Virginia Polytechnic Inst. and State Univ., Blacksburg, VA.

Table 2. Results of adult feeding, oviposition, and larval transfer tests with *Galerucella calmariensis.*

Test plant species	Adult feeding[a]	Larval feeding[a]	Eggs laid	Larvae alive after day			Adults emerged
				5	10	15	
			no.				
Lythrum salicaria	++	++	180	20	19	19	8
L. lineare	(+)	(+)	—	6	—	—	—
L. alatum	+	+	45	6	4	1	1
L. californicum	+	(+)	2	—	—	—	—
L. hyssopifolia	+	(+)	2	—	—	—	—
Decodon verticillatus	(+)	(+)	—	—	—	—	—
Ammania auriculata	(+)	(+)	—	4	1	1	1
A. coccinea	(+)	(+)	—	3	3	2	—
A. robusta	—	(+)	—	—	—	—	—
A. latifolia	—	(+)	—	4	3	2	2
Cuphea lutea	(+)	(+)	—	2	2	2	—
Epilobium angustifolium	(+)	—	—	—	—	—	—
Glycine max 'Pella'	(+)	—	—	—	—	—	—

[a]++ indicates normal feeding, + indicates slight to moderate feeding, (+) indicates occasional nibbling, and dashes indicate that no feeding, oviposition, nor larval development occurred.

occurred on winged lythrum, and a few eggs were laid on California loosestrife and hyssop lythrum.

No-choice adult feeding and oviposition tests. Adults caged exclusively on winged lythrum showed a drastically reduced oviposition capacity (Figures 1, 2) and most eggs were infertile. Moreover, adults had a reduced life span and by the beginning of June all adults had died. Adults on purple loosestrife continued oviposition for an additional 2 mo (Figures 1, 2).

No-choice larval transfer tests. Normal larval feeding was restricted to purple loosestrife, and slight to moderate feeding was observed on winged lythrum (Tables 2, 3). Some larvae of *G. calmariensis* survived up to 15 d on five other test plant species in the family Lythraceae. A single *G. calmariensis* larva reached the adult stage on winged lythrum and *Ammannia auriculata* Willd. and two on pink ammannia (*A. latifolia* L., #AMMTE). No *G. pusilla* larvae completed development on any plant species other than purple loosestrife and winged lythrum (Table 3). Larvae that successfully completed development of plants other than purple loosestrife were much smaller than those developing on the regular host plant. The normal pupal weight of *G. calmariensis* on purple loosestrife is about 5 mg; those developing on other plants reached 2 to 2.5 mg. Winged lythrum was the only species accepted for oviposition and allowing larval development. All other test plant species were either unsuitable for larval development or not chosen for oviposition.

Field tests. At Gammendorf, no winged lythrum or swamp loosestrife plants were attacked, but the purple loosestrife control plants showed identical damage to that observed on the naturally growing purple loosestrife (estimated 50 to 70% defoliation). The overwintered ovipositing beetles neither fed nor oviposited

Table 3. Results of adult feeding, oviposition, and larval transfer tests with *Galerucella pusilla.*

Test plant species	Adult feeding[a]	Larval feeding[a]	Eggs laid	Larvae alive after day			Adults emerged
				5	10	15	
			no.				
Lythrum salicaria	++	++	190	20	19	18	8
L. lineare	(+)	(+)	—	—	—	—	—
L. alatum	+	+	43	13	9	8	4
L. californicum	+	(+)	12	—	—	—	—
L. hyssopifolia	+	(+)	3	5	—	—	—
Decodon verticillatus	(+)	—	—	—	—	—	—
Ammania auriculata	—	(+)	—	2	—	—	—
A. coccinea	—	(+)	—	—	—	—	—
A. robusta	—	(+)	—	2	2	—	—
A. latifolia	—	(+)	—	1	1	—	—
Cuphea lutea	—	(+)	—	2	1	1	—
Lagerstroemia indica	—	(+)	—	2	—	—	—
Epilobium angustifolium	(+)	—	—	—	—	—	—
Sparganium eurycarpum	—	(+)	—	—	—	—	—

[a]++ indicates normal feeding, + indicates slight to moderate feeding, (+) indicates occasional nibbling, and dashes indicate that no feeding, oviposition, nor larval development occurred.

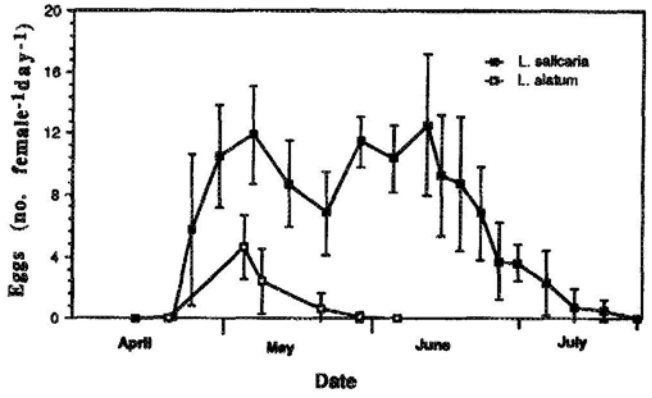

Figure 1. Oviposition of *Galerucella calmariensis* on *Lythrum salicaria* and *Lythrum alatum* during 1990. Values are means of 5 replicates ± SD.

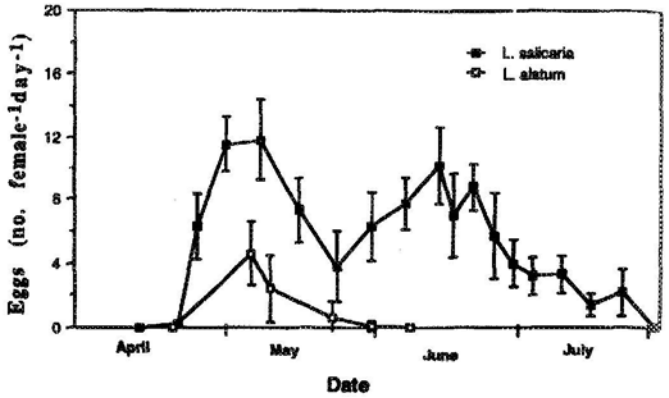

Figure 2. Oviposition of *Galerucella pusilla* on *Lythrum salicaria* and *Lythrum alatum* during 1990. Values are means of 5 replicates ± SD.

on the two test plant species, and no larvae moved onto these plants from adjacent attacked purple loosestrife plants.

When the potted plants were re-collected at Meggerdorf, all purple loosestrife control plants had been completely defoliated and an estimated 30 to 40% of the leaf surface of the two test plant species, winged lythrum and swamp loosestrife, had been consumed. All naturally growing purple loosestrife plants remained defoliated at the site. Any new growth was consumed. Feeding damage was from newly emerged adults only because no oviposition nor larval feeding was noted.

Swamp loosestrife and winged lythrum are native members of North American wetlands and at risk of being replaced by purple loosestrife in areas where they co-occur[6]. The European host plant specificity tests clearly demonstrated that swamp loosestrife is not at risk of becoming a field host of *G. calmariensis* or *G. pusilla*. Field tests at Meggerdorf showed that limited feeding by newly emerging teneral adults of both species occurred at the end of the growing season, but such feeding will likely be of little significance. Risk assessment relative to other biological control agents for purple loosestrife is discussed by Blossey et al. (5).

Reduced oviposition and larval development was observed on winged lythrum in confinement but never on exposed plants at Gammendorf. In addition, potted plants of winged lythrum and swamp loosestrife kept in the CAU garden together with purple loosestrife from 1986 to 1991 were never colonized by migrating beetles. During the same period hundreds of feral endemic beetles of both *Galerucella* species colonized purple loosestrife plants in the garden plot every spring. Thus, there is strong indication that under field conditions winged lythrum is safe from attack by the two *Galerucella* species. However, as with swamp loosestrife at Meggerdorf, limited pre-overwintering feeding by F_1 beetles occurred when regular host plants had been devastated.

During host specificity screening tests under quarantine (14), both *Galerucella* species showed a broader host range than under conditions in northern Germany. Adults used in Europe and at VPI & SU belonged to the same populations. Some concerns were raised by the quarantine studies regarding attack of winged lythrum, swamp loosestrife, and crepe myrtle (14). However, plants grown under artificial conditions (as is necessary in quarantine) develop different cell structures as well as physiological anomalies (i.e., changes in water content and secondary plant metabolites) which are important in host selection and acceptance by insect herbivores (1, 6). The experimental host range of insects tested under artificial conditions, and especially under no-choice conditions, is generally larger than in the field (9, 21).

The broadest host range for *G. pusilla* in the field and laboratory in Europe and at VPI & SU under quarantine conditions was found when plant parts were offered in no-choice tests (Table 4). Feeding and oviposition were reduced (sometimes nonexisting) in multiple-choice tests or when potted plants were offered in the tests. Under open field conditions using potted plants, the least amount of feeding and oviposition occurred on the test plants. However, feeding of newly emerged F_1 beetles on winged lythrum and swamp loosestrife at Meggerdorf demonstrated the difficulties in interpretation of test results.

The host range of a species under investigation can be quite different, depending on the type of tests performed and the stages and age of specimens used in the experiments. Given these differences in test results, we recommend that host specificity tests be as similar to open field conditions as possible, at least for "critical" test plants. In cases where different tests produce contradictory results, the more natural test should be given greater weight.

Unfortunately, follow-up studies on the host specificity of released biological control agents in their new home have rarely been executed. Therefore it is unclear whether any of the laboratory no-choice tests have predictive power or are purely arti-

[6]Personal communication, N. A. Anderson, Grad. Asst., Dep. Hortic. Sci., Univ. Minnesota, St. Paul, MN; and personal communication, C. Eckert, Asst. Prof., Dep. Biol., Queen's Univ., Kingston, Ontario, Canada.

Table 4. Comparison of host specificity screening results with *Galerucella pusilla.*

Test[a]	Plant parts	*Lythrum salicaria*	*Lythrum alatum*	*Decodon verticillatus*	*Lagerstroemia indica*
Laboratory:					
No-choice:					
Larval feeding	Leaves	+++	+	—	(+)
Larval development	Leaves	+++	++	—	—
Multiple choice:					
Adult feeding	Potted plants	+++	+	(+)	—
Oviposition	Potted plants	+++	++	—	—
Field:					
Garden:					
Adult feeding/oviposition/larval development	Potted plants	+++	—	—	—
Fehmarn:					
Adult feeding/oviposition/larval development	Potted plants	+++	—	—	Test not performed
Meggerdorf (F_1 adults):					
Adult feeding/oviposition/larval development	Potted plants	+++	++	+	Test not performed
Quarantine (adopted from (15)):					
No-choice:					
Larval development	Leaves	+++	+	—	—
Adult feeding	Cut shoots	+++	++	++	—
Adult feeding	Potted plants	+++	—	+	+
Oviposition	Cut shoots	+++	++++	+	+
Multiple choice:					
Adult feeding	Cut shoots	+++	++	+	—
Oviposition	Cut shoots	+++	+	—	—

[a]+++ indicates normal feeding, oviposition, or larval development; ++ indicates moderate feeding, oviposition, or larval development; + indicates slight feeding, oviposition, or larval development; (+) indicates occasional nibbling by larvae or adults; ++++ indicates that more eggs were laid on a test plant than on the control purple loosestrife, and dashes indicate that no feeding, oviposition, nor larval development occurred.

facts due to the artificial test conditions. Researchers lack enthusiasm to do these studies, because reviewers still rely on results of no-choice starvation tests at the exclusion of meaningful field studies (11).

Lacking rigorous follow-up studies on specific cases, a historical perspective of weed biocontrol has shown that host shifts of released agents never severely damaged nontarget plant species (7). However, a large number of promising candidates have not been released, because they failed in screening tests of questionable predictive power (10). To increase the success rate of weed biocontrol it is often necessary to introduce several control agent species per target weed (8). To exclude potential candidates because of questionable host specificity results might exclude the most promising agents. Predictive power of screening tests can be increased by comparing the realized host range in the field after release with those obtained in the experiments. This analysis should improve knowledge about the quality of the tests being used now and ways to improve them.

Results of the host specificity screening of both *G. calmariensis* and *G. pusilla* demonstrate that both species are highly host specific. Release of both agents in North America was approved by TAG in 1992. In summer 1992, both insect species were introduced into field nurseries in North America.

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