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FIELD OBSERVATIONS OF NON-TARGET FEEDING BY *GALERUCELLA CALMARIENSIS* [COLEOPTERA: CHRYSOMELIDAE], AN INTRODUCED BIOLOGICAL CONTROL AGENT OF PURPLE LOOSESTRIFE, *LYTHRUM SALICARIA* [LYTHRACEAE]

J.E. CORRIGAN[1], D.L. MACKENZIE[1] and L. SIMSER[2]

Abstract *Proc. ent. Soc. Ont.* 129: 99-106

Purple loosestrife, *Lythrum salicaria* L., is a herbaceous wetland perennial native to Eurasia. It is an invasive species of temperate wetland ecosystems in North America. In 1992, three species of insect herbivores from Europe, including *Galerucella calmariensis* L. and *G. pusilla* Duftschmidt were released as classical biological control agents against purple loosestrife. Host range testing had shown that these species might attack native North American species, such as *Lythrum alatum* Pursh., and *Decodon verticillatus* (L.) Ell., but review panels from the USDA and Agriculture Canada concluded that the benefits of controlling purple loosestrife outweighed potential risks to non-target plant species. The Royal Botanical Garden (RBG) properties are the site of 1993 releases of both imported *Galerucella* species. Extremely large populations of beetles (>500 egg masses/m^2) can now be found near the release areas. In late May 1998, feeding by adult *G. calmariensis* was observed on *D. verticillatus* cuttings growing outdoors at a RBG nursery. As well, egg masses of *G. calmariensis* were taken from *L. alatum* at RBG and were reared to adults on this host plant. Following these observations, all three plant species were monitored for attack through the first and second generation of the *Galerucella* beetles. Purple loosestrife plants sustained moderate to total defoliation in all areas monitored at RBG. *L. alatum* and *D. verticillatus* were only slightly affected by feeding activities of *Galerucella* beetles. Several plants of each non-target species sustained slight adult feeding damage and about 15 egg masses were found on the several hundred plants observed through the summer. No late-instar larvae were observed to develop on these plants in the field. We believe that non-target feeding by *G. calmariensis* represented a short-term "spill-over" effect, but further studies are required to evaluate this phenomenon more rigorously.

Introduction

Purple loosestrife, *Lythrum salicaria* L., is a herbaceous, wetland perennial that is native to Eurasia. It was introduced to the east coast of North America early in the nineteenth century (Stuckey 1980). Large populations now occur in wetlands across eastern North America and the plant has become established in temperate wetland habitats across the continent (White et al. 1993). In North America, dominant, persistent stands of purple loosestrife can displace resident plant species (Thompson et al. 1987; White et al. 1993; Mal et al. 1997). Large-scale displacement

[1] Department of Environmental Biology, University of Guelph, Guelph ON Canada N1G 2W1
[2] Royal Botanical Gardens, PO Box 399, Hamilton ON Canada L8N 3H8

of native plants by exotic species can result in permanent, deleterious changes to natural areas (Schmitz and Simberloff 1997). Based on its history on this continent, purple loosestrife is thought to be a harmful invader of Nearctic wetland ecosystems (Thompson et al. 1987; White et al. 1993).

A classical biological control program was initiated against this plant in the mid 1980's, and, in 1992, three species of insect herbivores from Europe, *Hylobius transversovittatus* Goeze [Coleoptera: Curculionidae], *Galerucella calmariensis* L. and its congener, *G. pusilla* Duftschmidt [Coleoptera: Chrysomelidae] were approved for release in North America (Hight et al. 1995). Host range testing showed that, in the absence of purple loosestrife, all three species could feed and oviposit on several related, native North American species, including, *Lythrum alatum* Pursh., winged loosestrife, and *Decodon verticillatus* (L.) Ell., swamp loosestrife, [both Lythraceae] (Kok et al. 1992; Blossey et al. 1994a,b). Review panels from the USDA and Agriculture Canada concluded that the potential benefits of controlling purple loosestrife outweighed risks to non-target plant species (Blossey et al. 1994a,b). They believed that non-target species were unlikely to be threatened by the *Galerucella* species in the field, as these beetles had strongly preferred *L. salicaria* in "choice" tests between this plant and non-target species (Blossey et al. 1994b). Despite approval to release the biological control agents, concerns remained as to the actual host choices that would be made by the agents after being released in North America (Kok et al. 1992; Blossey et al. 1994b; Dale 1998).

From 1992 to 1997, the Ontario Biological Control Program against purple loosestrife (Ontario Program) released approximately 320,000 beetles (*G. calmariensis* and *G. pusilla*) at over 200 sites around the province. By 1997, beetle populations at 15–18 of these sites had increased over 1000-fold (Ontario Program, unpublished data). Purple loosestrife plants at these sites sustained reductions in flowering and biomass of over 95%, with populations being replaced by species such as cattails, *Typha* spp., and reed canary grass, *Phalaris arundinacea* L. (Ontario Program, unpublished data).

In 1993, 1600 adult *Galerucella* (800 of each imported species; 1:1 sex ratio) were released at the Royal Botanical Gardens (RBG) in Burlington, Ontario. Large beetle populations have spread from the initial release sites and now occur on purple loosestrife throughout the RBG properties (Bowen 1998). On 19 May 1998, feeding by adult beetles resembling the released *Galerucella* species was observed on small cuttings of *D. verticillatus* growing outdoors at a RBG nursery (Lyall Rudderham, pers. comm.).

Evidence of non-target feeding by *Galerucella* species could be of great concern to the (over 25) North American biocontrol programs that have released the imported *Galerucella* against purple loosestrife. Moreover, observations of non-target feeding by biological control agents in field situations may support recent assertions of the unpredictability of the classical biological control of exotic weeds (Simberloff and Stiling 1996; Louda et al. 1997; Strong 1997). The following paper presents one season's data on the incidence of non-target feeding by *G. calmariensis*. The data reported here should not be taken as the "final word", and more investigations of this phenomena will be needed. However, with so many North American programs using *Galerucella* beetles, and with the current challenges to the practice of biological control, it is important that practitioner and critic alike be made aware of this phenomena in a timely manner.

Materials and Methods

The RBG Sites

The choice of sites was determined by the availability of each of the actual or potential host plant species inside a "zone of occupation" by the beetles on the RBG properties.

Mercer's Glen is a small, shallow pond located about 1 km from Lake Ontario near Cootes Paradise and Hamilton Harbour. In the early 1990's, this area supported a large population of mature *L. salicaria*, growing in large clumps (Bowen, 1998). The site does not contain *D. verticillatus* or *L. alatum*. Two releases of *Galerucella* beetles were made in Mercer's Glen in 1993 and, by 1997, extremely large beetle populations (estimated over 500 egg masses/m^2, Ontario Program) had caused large reductions in the biomass of *L. salicaria* in this area (Bowen 1998). At the RBG nursery, approximately 1 km from Mercer's Glen, about 200, two-year-old cuttings of *D. verticillatus* were being grown outdoors in small pots in standing water. There were no *L. salicaria* or *L. alatum* plants at this site. The Berry Tract is about 8 km from the nearest *Galerucella* release sites. This site contained a population of several hundred *L. alatum* located in a wet meadow. No *D. verticillatus* and only two plants of *L. salicaria* have been found there. The Double Marsh is located along the southern shore of Cootes Paradise, about 2 km from beetle release sites at Mercer's Glen. At this site, both *L. salicaria* and. *D verticillatus* were found, but there was no *L. alatum* at this site. Populations of *G. calmariensis* could be found on *L. salicaria* all around the shore of Cootes Paradise, but these populations were smaller than those observed at Mercer's Glen (Bowen 1998). Populations of *Galerucella nymphaea* (L.) a native of North America, can also be found in association with purple loosestrife at this site. At the Sunfish Ponds, an area about 0.75 km from two 1993 release sites on Grindstone Creek, *L. salicaria* grew in large clumps around the ponds, but there was no *L. alatum* or *D. verticillatus* growing at this site. Beetle populations had been observed here in 1996, but they were smaller than those found at the release sites (Ontario Program, unpublished data).

Observations of Beetle Activity at the RBG Sites

Observations were made at Mercer's Glen, the Berry Tract and Double Marsh during a site visit on 26 May 1998. On 1 June 1998, estimates of *Galerucella* egg mass density were taken from three, randomly selected 1 m^2 sample plots at Mercer's Glen. On 8 June 1998, five randomly selected 1 m^2 plots containing *L. alatum* plants were sampled for egg masses of *Galerucella* spp. at the Berry Tract. On a weekly basis through June, observations were made during walkabouts at each site to determine the size and distribution of the first generation populations of *Galerucella* at Mercer's Glen, Double Marsh and the Berry Tract.

For the second generation of the beetles, five randomly selected 1 m^2 plots were established on each of: i) *L. salicaria* at Double Marsh; ii) *D. verticillatus* at Double Marsh; iii) *L. alatum* at Berry Tract, and iv) *L. salicaria* at Sunfish Ponds. The number of egg masses of *Galerucella* per plot was counted, and the presence of larval or adult *Galerucella* was noted on a weekly basis from 29 June to 10 August 1998.

Results

Mercer's Glen

On 26 May 1998, the plants of *L. salicaria* were small (under 1 m), but the foliage already had been damaged heavily by feeding adult *Galerucella*. Very few adults were observed in the area, however every plant had a large number of egg masses and most plants had first- to second-instar larvae systematically defoliating the leaves at the top of the shoots.

The mean number of egg masses, 643.0 ± 332.4 (SD) per m^2, counted in three randomly sampled 1 m^2 plots on 1 June 1998, was the highest value recorded at a release site in Ontario (Ontario Program, unpublished data). There were many larvae feeding on the plants, and a number of these larvae appeared to be large enough to pupate.

By the middle of June, all of the purple loosestrife plants in Mercer's Glen were totally defoliated — even the outer layers of the stalks had been chewed away by the beetle larvae. Because no *L. salicaria* was available for oviposition after early to mid-June at Mercer's Glen, monitoring of egg mass abundance of the second beetle generation on *L. salicaria* was moved to the Sunfish Ponds site.

The RBG Nursery

There were approximately 200 plants of *D. verticillatus* at the nursery when observations were made on 26 May 1998. The two-year-old cuttings were under 20 cm in height and had 3–10 leaves per plant. Feeding damage was observed on fewer than 10% of the cuttings, but these plants were heavily damaged, and the foliar shot-hole feeding was consistent with that inflicted by adult *Galerucella*. A few plants had hosted rather large numbers of beetles (>20 per plant, Lyall Rudderham, pers. comm.). Twenty adult insects, collected while feeding on these plants on 19 May, were identified as *G. calmariensis* (Catherine Salole, pers. comm.; specimens in the University of Guelph collection). Several egg masses, thought to be of *G. calmariensis*, were found on the stalks of two of the cuttings that had been fed upon by the beetles.

After feeding had been detected on 19 May, the plants were treated with a mixture of diatomaceous earth and permethrin (Lyall Rudderham, pers. comm.). As of 26 May, there was no evidence of beetle activity on the plants following this treatment.

Through the month of June, two adult *G. calmariensis* were removed from *D. verticillatus* at the nursery. No *Galerucella* egg masses or feeding were observed on the plants through this time period.

The Berry Tract

This site contained the nearest population of *L. alatum* to the established populations of imported *Galerucella*, and it was monitored on 26 May 1998. Several hundred plants of *L. alatum*, approximately 30–50 cm in height, grew in clumps of about 2–8 shoots per clump. Approximately 50 clumps of *L. alatum* were inspected, and on three or four of the plants, shot-hole feeding damage, characteristic of *Galerucella* adults, was observed. On two plants, we found egg masses, believed to be those of *G. calmariensis*.

A shoot of *L. alatum* containing three small egg masses was brought back to the laboratory for rearing. Fourteen eggs were counted in the egg masses. The shoot was held in a closed plastic container, suspended over water on a platform of chicken wire, with the cut stem placed in the water to prevent desiccation. After the eggs hatched and larvae began to grow, fresh shoots of *L. alatum* were placed in the box to nourish them. When eight, full-grown larvae were ready to pupate, a 9 cm petri dish containing a small amount of potting soil was placed on the frame under the shoots. An unknown number of larvae entered the soil to pupate, and four adult beetles, later identified as *G. calmariensis*, were reared successfully from the shoots of *L. alatum* (Catherine Salole, pers. comm.; specimens in the University of Guelph collection).

In sampling done on *L. alatum* at the Berry Tract (10 June), two of the five, 1 m^2 plots contained egg masses of *G. calmariensis* and a total of seven egg masses were counted (1.4 ± 2.2 [SD] masses per m^2). One larval *Galerucella* was seen and there was evidence of slight adult (shot-hole) and larval feeding (shoot-tip damage, windowing of leaves) on a few plants. In two further visits to this site (17, 24 June) no beetle life stage or new feeding damage was observed on *L. alatum*, including the plants on which activity had been recorded on 8 June.

Double Marsh

At this site, the plants of *L. salicaria* and *D. verticillatus* grew relatively close to each other (0.5 to 20 m apart) as emergent shoots in about 0.5–1 m of water. *L. salicaria* grew in clumps of about 20–40 shoots, with foliage standing up to 0.5 m above the water. Clumps of *D. verticillatus* were smaller, consisting of 1–5 shoots and standing about 0.3 m out of the water.

About 20 specimens of each of *D. verticillatus* and *L. salicaria* were examined on 26 May, and adult *G. calmariensis* were found sitting on both plant species. Feeding damage by adult *Galerucella* and egg masses were found on plants of *L. salicaria*; however, neither larval or adult feeding damage was observed on *D. verticillatus*.

During weekly monitoring of the same plants done through June, *L. salicaria* showed moderate to heavy feeding damage by adults and larvae of *G. calmariensis*. Some plants were starting to bloom, but many were too damaged to do so. Plants of *D. verticillatus* were completely free of adult and larval feeding damage throughout the month of June, although four adult *G. calmariensis* and a single egg mass were observed on them.

Monitoring of Second Generation *G. calmariensis* Populations — July–August, 1998

Only *L. salicaria* was attacked by the second generation of *Galerucella*, with no ovipositions being recorded on *L. alatum* at the Berry Tract or on *D. verticillatus* at Double Marsh (Table I). At the Sunfish Ponds site, an average of about 882 egg masses per m^2 were recorded on *L. salicaria* in the first week of monitoring (Table I). These plants were quickly defoliated and became unsuitable for oviposition for the rest of the monitoring period.

The plots of *L. salicaria* at Double Marsh harbored moderate numbers of egg masses throughout the sampling period, yet no egg masses, larvae or adult *Galerucella* were found on *D. verticillatus* at any time (Table I). Incidentally, no individuals of *G. pusilla* were found on either non-target species at any point in our investigations in 1998.

TABLE I. Mean numbers ($\pm$ SD, n = 5) of egg masses per m^2 found for the second-generation, imported *Galerucella* spp. on *Lythrum salicaria*, *D. verticillatus* and *L. alatum* at several locations around the Royal Botanical Gardens, Burlington, Ontario. *Lythrum alatum* was not present at Double Marsh or Sunfish Ponds, *D. verticillatus* was absent from Sunfish Ponds and the Berry Tract, and only two plants of *L. salicaria* were detected at the Berry Tract.

Date (1998)	Double Marsh *L. salicaria*	Double Marsh *D. verticillatus*	Sunfish Ponds *L. salicaria*	Berry Tract *L. alatum*
June 29	8.6 ± 11.6	0	882.4 ± 489.8	0
July 6	35.4 ± 66.4	0	nd *	0
July 13	42.4 ± 79.3	0	nd	0
July 20	57.2 ± 101.1	0	nd	0
July 27	57.8 ± 47.2	0	nd	0
August 3	54.8 ± 100.6	0	nd	0
August 10	21.5 ± 32.6	0	nd	0

* nd = no data collected; plants unsuitable for oviposition

Discussion

In pre-release laboratory feeding trials in which the insects did not have access to *L. salicaria* (no choice tests), adult *G. calmariensis* were found to feed and oviposit on both *D. verticillatus* and *L. alatum* (Kok et al. 1992; Blossey et al. 1994b). *Lythrum alatum*, and two species of *Ammania* (*A. auriculata* Willd. and *A. latifolia* L.) were the only plants, other than *L. salicaria*, on which *G.*

calmariensis could complete larval development (Kok et al. 1992; Blossey et al. 1994b). Few adults were produced on these species, relative to the numbers reared from *L. salicaria* (Kok et al. 1992; Blossey et al. 1994b). Referring to *Galerucella*, Kok et al. (1992) concluded that: "both species of beetles are highly host specific and should not be a threat to non-target plants with the exception of *L. alatum*.". However, Blossey et al. (1994b) cautioned that it was unclear whether laboratory tests would have predictive power for field releases.

Our observations of activity by *Galerucella* in actual field releases closely parallel those recorded during host-specificity testing of the beetles prior to their release in North America (Kok et al. 1992; Blossey et al. 1994b). Adults of *G. calmariensis* fed and oviposited upon both *D. verticillatus* and *L. alatum* at RBG, although the populations of beetles found on these plants were several orders of magnitude smaller than those observed on *L. salicaria*. Four individuals of *G. calmariensis* completed development on *L. alatum* in the laboratory, but no late-instar larvae were ever observed on either non-target plant species in the field. Both plant species were located inside an area where populations of *Galerucella* could be found attacking virtually every purple loosestrife plant. We believe that the testing procedures used to determine the host range of *G. calmariensis* (Kok et al. 1992; Blossey et al. 1994b), provided accurate predictions of their performance in field releases.

We speculate that the situation that promoted non-target feeding by *G. calmariensis* on *D. verticillatus* at the nursery was, in essence, a "no-choice trial" for these insects. The Mercer's Glen release sites harbored extremely large populations of *Galerucella* in 1997 (estimated 500 egg masses/m^2). In July 1997, we observed mass emigrations of newly emerged, second generation adults, believed to be due to a scarcity of available foliage of purple loosestrife there (Ontario Program, unpublished data). In a number of successful biological control programs, "waves" of populations of biocontrol agents have been observed to move from their release sites to exploit their host species elsewhere (Kovalev 1989). The rapid rate with which *Galerucella* invaded all purple loosestrife populations around the RBG properties is thought to have resulted from waves of hungry beetles that migrated from areas where the purple loosestrife had been totally utilized.

Based on samples taken at Mercer's Glen on 1 June 1998 (over 600 egg masses/m^2), we concluded that many beetle adults had over-wintered at this site. We speculate that, in several areas where they over-wintered (such as Mercer's Glen), large populations of emerging adult beetles quickly utilized all available *L. salicaria*. Dispersing from these areas to find undamaged host plants, some adults encountered *D. verticillatus* in the nursery. For the beetles, these plants were their only (short-term) choice for feeding, and some adult *G. calmariensis* did attack a few of them.

At Double Marsh, *Galerucella* populations were much lower than those observed at Mercer's Glen. Plants of *L. salicaria* were less damaged and were healthy enough that adult *G. calmariensis* had a choice of these plants or of *D. verticillatus* on which to feed and oviposit throughout the season. Faced with this choice, *G. calmariensis* did not utilize the *D. verticillatus* plants at Double Marsh.

Use of *L. alatum* at Berry Tract was minimal, compared with that observed on *L. salicaria* plants around the RBG properties. The scarcity of purple loosestrife plants around the Berry Tract did not allow for estimates of the size of the populations of *G. calmariensis* in the immediate area. Nonetheless, the numbers of damaged plants and egg masses found on *L. alatum*, relative to those found on *L. salicaria* growing elsewhere at RBG, support the assertion (from host range testing) that *L. alatum* is not a favoured host for *G. calmariensis*.

We believe that non-target feeding by *G. calmariensis* represents a short-term "spill-over" effect. Once populations of *L. salicaria* are reduced by *Galerucella* species, beetle populations would collapse in response to the new carrying capacity of their principal host species, *L. salicaria*. We feel that the smaller beetle populations would pose no long-term threat to non-target species.

Other weed biological control programs have experienced similar short-term incidences of attack with no long-term effects on the non-target species (McFadyen 1998). Despite this history, two different outcomes have been suggested for the interactions between a relatively rare plant species and a herbivore that is found in high densities on its usual host.

Wan and Harris (1997) suggest that the probability of a host shift can be calculated by conducting several comparisons of relative feeding, oviposition and larval development between the intended host species and a non-target species. If the non-target host species is less acceptable or suitable than the intended host across several behavioral and physiological tests, then each "disadvantage" would serve to prevent the host shift. The multiplicative product of the test results would represent the relative probability of the natural enemy establishing a population on the non-target plant, compared to the target species (Wan and Harris 1997). For the *Galerucella* beetles, for which all parameters of relative suitability strongly favoured purple loosestrife (Kok et al. 1992; Blossey et al. 1994b), the relative utilization rates suggest that the probability of a host shift to either *L. alatum* or *D. verticillatus* is very low.

Unfortunately, another less desirable outcome of these interactions has been postulated (Howarth 1991; Strong 1997). In outbreak situations, a proportion of a large population of natural enemies attacking a targeted plant species can "spill over" onto a non-target species. The non-target species may or may not be "favoured" by the herbivores; in fact, it may not even be a suitable species for a long-term host shift. However, it is possible that a relatively small population of the non-target species may not be able to withstand even "incidental" feeding by a large number of herbivores. The authors concluded that local extinctions of rare, non-target species could occur as a side effect of a successful biological control program against another species (Howarth 1991; Strong 1997).

Critics of classical biological control have lamented the lack of follow-up ecological studies of the long-term impacts of these programs (Simberloff and Stiling 1996). We believe that *Galerucella* introductions at RBG afford an excellent opportunity to conduct such studies. In future research, we hope to provide data to help examine the divergent hypotheses about host shifts and impact of weed biological control agents on non-target species.

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J.E. CORRIGAN [1] , D.L. MACKENZIE [1] and L. SIMSER [2]

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Introduction

Purple loosestrife, Lythrum salicaria L., is a herbaceous, wetland perennial that is native to Eurasia. It was introduced to the east coast of North America early in the nineteenth century (Stuckey 1980). Large populations now occur in wetlands across eastern North America and the plant has become established in temperate wetland habitats across the continent (White et al. 1993). In North America, dominant, persistent stands of purple loosestrife can displace resident plant species (Thompson et al. 1987; White et al. 1993; Mai et al. 1997). Large-scale displacement

Department of Environmental Biology, University of Guelph, Guelph ON Canada N 1 G 2 W 1

Royal Botanical Gardens, PO Box 399, Hamilton ON Canada L8N 3H8

of native plants by exotic species can result in permanent, deleterious changes to natural areas (Schmitz and Simberloff 1997). Based on its history on this continent, purple loosestrife is thought to be a harmful invader of Nearctic wetland ecosystems (Thompson et al. 1987; White et al. 1993).

A classical biological control program was initiated against this plant in the mid 1980's, and, in 1992, three species of insect herbivores from Europe, Hylobius transversovittatus Goeze [Coleoptera: Curculionidae], Galerucella calmariensis L. and its congener, G. pusilla Duftschmidt [Coleoptera: Chrysomelidae] were approved for release in North America (Hight et al. 1995). Host range testing showed that, in the absence of purple loosestrife, all three species could feed and oviposit on several related, native North American species, including, Ly thrum alatum Pursh., winged loosestrife, and Decodon verticillatus (L.) Ell., swamp loosestrife, [both Lythraceae] (Kok et al. 1992; Blossey et al. 1994a,b). Review panels from the USDA and Agriculture Canada concluded that the potential benefits of controlling purple loosestrife outweighed risks to non-target plant species (Blossey et al. 1994a,b). They believed that non-target species were unlikely to be threatened by the Galerucella species in the field, as these beetles had strongly preferred!,, salicaria in "choice" tests between this plant and non-target species (Blossey et al. 1994b). Despite approval to release the biological control agents, concerns remained as to the actual host choices that would be made by the agents after being released in North America (Kok et al. 1992; Blossey et al. 1994b; Dale 1998).

From 1992 to 1997, the Ontario Biological Control Program against purple loosestrife (Ontario Program) released approximately 320,000 beetles (G. calmariensis and G. pusilla) at over 200 sites around the province. By 1997, beetle populations at 15-18 of these sites had increased over

1000-fold (Ontario Program, unpublished data). Purple loosestrife plants at these sites sustained reductions in flowering and biomass of over 95%, with populations being replaced by species such as cattails, Typha spp., and reed canary grass, Phalaris arundinacea L. (Ontario Program, unpublished data).

In 1993, 1600 adult Galerucella (800 of each imported species; 1:1 sex ratio) were released at the Royal Botanical Gardens (RBG) in Burlington, Ontario. Large beetle populations have spread from the initial release sites and now occur on purple loosestrife throughout the RBG properties (Bowen 1998). On 19 May 1998, feeding by adult beetles resembling the released Galerucella species was observed on small cuttings of D. verticillatus growing outdoors at a RBG nursery (Lyall Rudderham, pers. comm.).

Evidence of non-target feeding by Galerucella species could be of great concern to the (over 25) North American biocontrol programs that have released the imported Galerucella against purple loosestrife. Moreover, observations of non-target feeding by biological control agents in field situations may support recent assertions of the unpredictability of the classical biological control of exotic weeds (Simberloff and Stiling 1996; Louda et al. 1997; Strong 1997). The following paper presents one season's data on the incidence of non-target feeding by G. calmariensis. The data reported here should not be taken as the "final word", and more investigations of this phenomena will be needed. However, with so many North American programs using Galerucella beetles, and with the current challenges to the practice of biological control, it is important that practitioner and critic alike be made aware of this phenomena in a timely manner.

Materials and Methods

The RBG Sites

The choice of sites was determined by the availability of each of the actual or potential host plant species inside a "zone of occupation" by the beetles on the RBG properties.

Mercer's Glen is a small, shallow pond located about 1 km from Lake Ontario near Cootes Paradise and Hamilton Harbour. In the early 1990's, this area supported a large population of

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mature L. salicaria, growing in large clumps (Bowen, 1998). The site does not contain D. verticillatus or L. alatum. Two releases of Galerucella beetles were made in Mercer's Glen in 1993 and, by 1997, extremely large beetle populations (estimated over 500 egg masses/m 2 , Ontario Program) had caused large reductions in the biomass ofZ,. salicaria in this area (Bowen 1998). At the RBG nursery, approximately 1 km from Mercer's Glen, about 200, two-year-old cuttings ofD. verticillatus were being grown outdoors in small pots in standing water. There were no L. salicaria or L. alatum plants at this site. The Berry Tract is about 8 km from the nearest Galerucella release sites. This site contained a population of several hundred L. alatum located in a wet meadow. No D. verticillatus and only two plants of L. salicaria have been found there. The Double Marsh is located along the southern shore of Cootes Paradise, about 2 km from beetle release sites at Mer-cer's Glen. At this site, both L. salicaria and. D verticillatus were found, but there was no L. alatum at this site. Populations of G. calmariensis could be found on L. salicaria all around the shore of Cootes Paradise, but these populations were smaller than those observed at Mercer's Glen (Bowen 1998). Populations of Galerucella nymphaea (L.) a native of North America, can also be found in association with purple loosestrife at this site. At the Sunfish Ponds, an area about

0.75 km from two 1993 release sites on Grindstone Creek, L. salicaria grew in large clumps around the ponds, but there was no L. alatum or D. verticillatus growing at this site. Beetle populations had been observed here in 1996, but they were smaller than those found at the release sites (Ontario Program, unpublished data).

Observations of Beetle Activity at the RBG Sites

Observations were made at Mercer's Glen, the Berry Tract and Double Marsh during a site visit on 26 May 1998. On 1 June 1998, estimates of Galerucella egg mass density were taken from three, randomly selected 1 m 2 sample plots at Mercer's Glen. On 8 June 1998, five randomly selected 1 m 2 plots containing L. alatum plants were sampled for egg masses of Galerucella spp. at the Berry Tract. On a weekly basis through June, observations were made during walkabouts at each site to determine the size and distribution of the first generation populations of Galerucella at Mercer's Glen, Double Marsh and the Berry Tract.

For the second generation of the beetles, five randomly selected 1 m 2 plots were established on each of: i) L. salicaria at Double Marsh; ii) D. verticillatus at Double Marsh; iii) L. alatum at Berry Tract, and iv) L. salicaria at Sunfish Ponds. The number of egg masses of Galerucella per plot was counted, and the presence of larval or adult Galerucella was noted on a weekly basis from 29 June to 10 August 1998.

Results

Mercer's Glen

On 26 May 1998, the plants of L. salicaria were small (under 1 m), but the foliage already had been damaged heavily by feeding adult Galerucella. Very few adults were observed in the area, however every plant had a large number of egg masses and most plants had first- to second-instar larvae systematically defoliating the leaves at the top of the shoots.

The mean number of egg masses, 643.0 ± 332.4 (SD) per m^2, counted in three randomly sampled 1 m^2 plots on 1 June 1998, was the highest value recorded at a release site in Ontario (Ontario Program, unpublished data). There were many larvae feeding on the plants, and a number of these larvae appeared to be large enough to pupate.

By the middle of June, all of the purple loosestrife plants in Mercer's Glen were totally defoliated — even the outer layers of the stalks had been chewed away by the beetle larvae. Because no L. salicaria was available for oviposition after early to mid- June at Mercer's Glen,

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monitoring of egg mass abundance of the second beetle generation on L. salicaria was moved to the Sunfish Ponds site.

The RBG Nursery

There were approximately 200 plants of D. verticillatus at the nursery when observations were made on 26 May 1998. The two-year-old cuttings were under 20 cm in height and had 3-10 leaves per plant. Feeding damage was observed on fewer than 10% of the cuttings, but these plants were heavily damaged, and the foliar shot-hole feeding was consistent with that inflicted by adult Galerucella. A few plants had hosted rather large numbers of beetles (>20 per plant, Lyall

Rudderham, pers. comm.). Twenty adult insects, collected while feeding on these plants on 19 May, were identified as G. calmariensis (Catherine Salole, pers. comm.; specimens in the University of Guelph collection). Several egg masses, thought to be of G. calmariensis, were found on the stalks of two of the cuttings that had been fed upon by the beetles.

After feeding had been detected on 19 May, the plants were treated with a mixture of diatomaceous earth and permethrin (Lyall Rudderham, pers. comm.). As of 26 May, there was no evidence of beetle activity on the plants following this treatment.

Through the month of June, two adult G. calmariensis were removed from D. verticillatus at the nursery. No Galerucella egg masses or feeding were observed on the plants through this time period.

The Berry Tract

This site contained the nearest population of L. alatum to the established populations of imported Galerucella, and it was monitored on 26 May 1998. Several hundred plants ofL. alatum, approximately 30-50 cm in height, grew in clumps of about 2-8 shoots per clump. Approximately 50 clumps of L. alatum were inspected, and on three or four of the plants, shot-hole feeding damage, characteristic of Galerucella adults, was observed. On two plants, we found egg masses, believed to be those of G. calmariensis.

A shoot of L. alatum containing three small egg masses was brought back to the laboratory for rearing. Fourteen eggs were counted in the egg masses. The shoot was held in a closed plastic container, suspended over water on a platform of chicken wire, with the cut stem placed in the water to prevent desiccation. After the eggs hatched and larvae began to grow, fresh shoots of L. alatum were placed in the box to nourish them. When eight, full-grown larvae were ready to pupate, a 9 cm petri dish containing a small amount of potting soil was placed on the frame under the shoots. An unknown number of larvae entered the soil to pupate, and four adult beetles, later identified as G. calmariensis, were reared successfully from the shoots of L. alatum (Catherine Salole, pers. comm.; specimens in the University of Guelph collection).

In sampling done on L. alatum at the Berry Tract (10 June), two of the five, 1 m^2 plots contained egg masses of G. calmariensis and a total of seven egg masses were counted (1.4 ± 2.2 [SD] masses per m^2). One larval Galerucella was seen and there was evidence of slight adult (shot-hole) and larval feeding (shoot-tip damage, windowing of leaves) on a few plants. In two further visits to this site (17, 24 June) no beetle life stage or new feeding damage was observed on L. alatum, including the plants on which activity had been recorded on 8 June.

Double Marsh

At this site, the plants of L. salicaria and D. verticillatus grew relatively close to each other (0.5 to 20 m apart) as emergent shoots in about 0.5-1 m of water. L. salicaria grew in clumps of about 20-40 shoots, with foliage standing up to 0.5 m above the water. Clumps of D. verticillatus were smaller, consisting of 1-5 shoots and standing about 0.3 m out of the water.

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About 20 specimens of each of D. verticillatus and L. salicaria were examined on 26 May, and adult G. calmariensis were found sitting on both plant species. Feeding damage by adult

Galerucella and egg masses were found on plants of L. salicaria; however, neither larval or adult feeding damage was observed on D. verticillatus.

During weekly monitoring of the same plants done through June, L. salicaria showed moderate to heavy feeding damage by adults and larvae of G. calmariensis. Some plants were starting to bloom, but many were too damaged to do so. Plants of D. verticillatus were completely free of adult and larval feeding damage throughout the month of June, although four adult G. calmariensis and a single egg mass were observed on them.

Monitoring of Second Generation G. calmariensis Populations — July-August, 1998

Only L. salicaria was attacked by the second generation of Galerucella, with no ovipositions being recorded on L. alatum at the Berry Tract or on D. verticillatus at Double Marsh (Table I). At the Sunfish Ponds site, an average of about 882 egg masses per m 2 were recorded on L. salicaria in the first week of monitoring (Table I). These plants were quickly defoliated and became unsuitable for oviposition for the rest of the monitoring period.

The plots of L. salicaria at Double Marsh harbored moderate numbers of egg masses throughout the sampling period, yet no egg masses, larvae or adult Galerucella were found onD. verticillatus at any time (Table I). Incidentally, no individuals of G. pusilla were found on either non-target species at any point in our investigations in 1998.

TABLE I. Mean numbers (± SD, n = 5) of egg masses per m 2 found for the second-generation, imported Galerucella spp. on Lythrum salicaria, D. verticillatus and L. alatum at several locations around the Royal Botanical Gardens, Burlington, Ontario. Lythrum alatum was not present at Double Marsh or Sunfish Ponds, D. verticillatus was absent from Sunfish Ponds and the Berry Tract, and only two plants of L. salicaria were detected at the Berry Tract.

Double Marsh Double Marsh Sunfish Ponds Berry Tract

Date (1998) L. salicaria D. verticillatus L. salicaria L. alatum

June 29 8.6 ± 11.6 882.4 ± 489.8

July 6 35.4 ± 66.4 nd *

July 13 42.4 ± 79.3 nd

July 20 57.2 ±101.1 nd

July 27 57.8 ±47.2 nd

August 3 54.8 ± 100.6 nd

August 10 21.5 ± 32.6 nd

* nd = no data collected; plants unsuitable for oviposition

Discussion

In pre-release laboratory feeding trials in which the insects did not have access to L. salicaria (no choice tests), adult G. calmariensis were found to feed and oviposit on both D. verticillatus andL. alatum (Kok et al. 1992; Blossey et al. 1 994b). Lythrum alatum, and two species of Ammania (A. auriculata Willd. and A. latifolia L.) were the only plants, other than L. salicaria, on which G.

calmariensis could complete larval development (Kok et al. 1992; Blossey et al. 1994b). Few adults were produced on these species, relative to the numbers reared from L. salicaria (Kok et al. 1992; Blossey et al. 1994b). Referring to Galerucella, Kok et al. (1992) concluded that: "both species of beetles are highly host specific and should not be a threat to non-target plants with the exception of L. alatum." '. However, Blossey et al. (1994b) cautioned that it was unclear whether laboratory tests would have predictive power for field releases.

Our observations of activity by Galerucella in actual field releases closely parallel those recorded during host-specificity testing of the beetles prior to their release in North America (Kok et al. 1992; Blossey et al. 1994b). Adults of G. calmariensis fed and oviposited upon both D. verticillatus and L. alatum at RBG, although the populations of beetles found on these plants were several orders of magnitude smaller than those observed on L. salicaria. Four individuals of G. calmariensis completed development on L. alatum in the laboratory, but no late-instar larvae were ever observed on either non-target plant species in the field. Both plant species were located inside an area where populations of Galerucella could be found attacking virtually every purple loosestrife plant. We believe that the testing procedures used to determine the host range of G. calmariensis (Kok et al. 1992; Blossey et al. 1994b), provided accurate predictions of their performance in field releases.

We speculate that the situation that promoted non-target feeding by G calmariensis on D. verticillatus at the nursery was, in essence, a "no-choice trial" for these insects. The Mercer's Glen release sites harbored extremely large populations of Galerucella in 1997 (estimated 500 egg masses/m 2). In July 1997, we observed mass emigrations of newly emerged, second generation adults, believed to be due to a scarcity of available foliage of purple loosestrife there (Ontario Program, unpublished data). In a number of successful biological control programs, "waves" of populations of biocontrol agents have been observed to move from their release sites to exploit their host species elsewhere (Kovalev 1989). The rapid rate with which Galerucella invaded all purple loosestrife populations around the RBG properties is thought to have resulted from waves of hungry beetles that migrated from areas where the purple loosestrife had been totally utilized.

Based on samples taken at Mercer's Glen on 1 June 1998 (over 600 egg masses/m 2), we concluded that many beetle adults had over-wintered at this site. We speculate that, in several areas where they over-wintered (such as Mercer's Glen), large populations of emerging adult beetles quickly utilized all available L. salicaria. Dispersing from these areas to find undamaged host plants, some adults encountered D. verticillatus in the nursery. For the beetles, these plants were their only (short-term) choice for feeding, and some adult G. calmariensis did attack a few of them.

At Double Marsh, Galerucella populations were much lower than those observed at Mercer's Glen. Plants ofZ. salicaria were less damaged and were healthy enough that adult G. calmariensis had a choice of these plants or of D. verticillatus on which to feed and oviposit throughout the season. Faced with this choice, G. calmariensis did not utilize the D. verticillatus plants at Double Marsh.

Use of L. alatum at Berry Tract was minimal, compared with that observed on L. salicaria plants around the RBG properties. The scarcity of purple loosestrife plants around the Berry Tract did not allow for estimates of the size of the populations of G. calmariensis in the immediate area. Nonetheless, the numbers of damaged plants and egg masses found on L. alatum, relative to those found on L. salicaria growing elsewhere at RBG, support the assertion (from host range testing) that L. alatum is not a favoured host for G. calmariensis.

We believe that non-target feeding by G. calmariensis represents a short-term "spill-over" effect. Once populations of L. salicaria are reduced by Galerucella species, beetle populations would collapse in response to the new carrying capacity of their principal host species, L. salicaria. We feel that the smaller beetle populations would pose no long-term threat to non-target species.

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Other weed biological control programs have experienced similar short-term incidences of attack with no long-term effects on the non-target species (McFadyen 1998). Despite this history, two different outcomes have been suggested for the interactions between a relatively rare plant species and a herbivore that is found in high densities on its usual host.

Wan and Harris (1997) suggest that the probability of a host shift can be calculated by conducting several comparisons of relative feeding, oviposition and larval development between the intended host species and a non-target species. If the non-target host species is less acceptable or suitable than the intended host across several behavioral and physiological tests, then each "disadvantage" would serve to prevent the host shift. The multiplicative product of the test results would represent the relative probability of the natural enemy establishing a population on the non-target plant, compared to the target species (Wan and Harris 1997). For the Galerucella beetles, for which all parameters of relative suitability strongly favoured purple loosestrife (Kok et al. 1992; Blossey et al. 1994b), the relative utilization rates suggest that the probability of a host shift to either L. alatum or D. verticillatus is very low.

Unfortunately, another less desirable outcome of these interactions has been postulated (Howarth 1991; Strong 1997). In outbreak situations, a proportion of a large population of natural enemies attacking a targeted plant species can "spill over" onto a non-target species. The non-target species may or may not be "favoured" by the herbivores; in fact, it may not even be a suitable species for a long-term host shift. However, it is possible that a relatively small population of the non-target species may not be able to withstand even "incidental" feeding by a large number of herbivores. The authors concluded that local extinctions of rare, non-target species could occur as a side effect of a successful biological control program against another species (Howarth 1991; Strong 1997).

Critics of classical biological control have lamented the lack of follow-up ecological studies of the long-term impacts of these programs (Simberloff and Stiling 1996). We believe that Galerucella introductions at RBG afford an excellent opportunity to conduct such studies. In future research, we hope to provide data to help examine the divergent hypotheses about host shifts and impact of weed biological control agents on non-target species.

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