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Performance of a Biological Control Agent, *Galerucella calmariensis* L. (Coleoptera: Chrysomelidae) on Purple Loosestrife *Lythrum salicaria* L. in Southern Manitoba (1993-1998)

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Abstract

In an effort to control the exotic perennial purple loosestrife (*Lythrum salicaria* L.) the leaf-defoliating beetle *Galerucella calmariensis* L. was released in Manitoba, Canada. To monitor the performance of the biocontrol agent, fixed monitoring stations (FMS) were established in the Netley-Libau Marsh (Libau 2 FMS, Libau 3 FMS and a Control FMS) and in the Delta Marsh (Delta FMS). Data were collected in 10-day intervals from 30 randomly tagged stems in each FMS beginning in the late spring and ending in early fall. In the Libau 3 FMS, a significant increase in the *G. calmariensis* population occurred between 3-YRPR (years post release) and 4-YRPR, herbivory resulted in the total elimination of purple loosestrife sexual reproduction and significantly smaller stem heights by 4-YRPR. In the Libau 2 FMS, there were significant increases in the number of larvae and adults observed between 4-YRPR and 5-YRPR, herbivory resulted in a significant reduction in the mean number of seed capsules produced per tagged stem. In the Delta Marsh FMS, *G. calmariensis* herbivory resulted in all purple loosestrife stems being destroyed by mid-July of each year of this study. In the Delta Marsh FMS, peak population numbers were observed 3-YRPR with subsequent declines in the mean number of beetles, larvae and egg masses in each successive year. Results from the Delta Marsh FMS indicated that once the purple loosestrife population was suppressed, *G. calmariensis* experienced a negative population growth. The data indicated a general *L. salicaria*-*G. calmariensis* interaction model where we may expect the following sequence: significant increases in the *G. calmarienis* population as early as 3-YRPR or 4-YRPR; followed by the suppression or elimination of purple loosestrife sexual reproduction; a decline in overall stem heights followed by a reduction in the number of purple loosestrife stems; followed by a change in *G. calmariensis* population growth curve from positive to negative. It is evident that the biological control agent *G. calmariensis* is capable of providing successful control of target weed purple loosestrife within a period as short as 3-YRPR.

Keywords: Purple Loosestrife; *Lythrum salicaria*; *Galerucella calmariensis*; leaf-eating beetle; classical biological control; monitoring impacts

Introduction

Purple loosestrife (*Lythrum salicaria* L., Lythraceae) is an exotic perennial weed introduced into North America in the early 1800s (Thompson *et al.* 1987) and has since spread across Canada. Purple loosestrife degrades natural habitats such as wetlands and

riparian areas reducing biological diversity by out-competing native vegetation. White *et al.* (1993) reported purple loosestrife as an alien species that presents a serious threat to native plant communities of natural habitats. The aggressive nature of purple loosestrife has also been documented by Mal *et al.* (1997) who demonstrated the ability of purple loosestrife to replace the native perennial wetland species *Typha angustifolia* and by Johansson and Keddy (1991) who placed purple loosestrife at the top of a competitive plant hierarchy. Mal *et al.* (1992) concluded that where purple loosestrife populations are on the increase, wildlife species are in decline.

The classical biological control of non-native weeds is the deliberate use of exotic herbivorous organisms to reduce the population density of an alien target weed below its economic injury level (Gassmann and Schroeder 1995). McEvoy and Cox (1991) reported the goal of biological weed control is to achieve and maintain low population levels of a target weed while allowing for the return of desirable native vegetation. A classical biological weed control program has the potential to provide sustainable long-term control of a target weed. Current purple loosestrife management efforts are focused on the introduction and establishment of several biological control agents (Hight *et al.* 1995, Malecki *et al.* 1993). *Galerucella calmariensis* L. (Coleoptera: Chrysomelidae) and *G. pusilla* Duftschmid are leaf-eating beetles that have been approved for introduction and release by the Canadian and United States governments in 1992 (Blossey *et al.* 1994, Hight *et al.* 1995). *Hylobius transversovittatus* Goeze (Coleoptera: Curculionidae) is a root-mining weevil that attacks the main storage tissues of purple loosestrife. The flower-feeding weevil *Nanophyes marmoratus* Goeze, capable of reducing seed production (Blossey and Schroeder 1995, Hight *et al.* 1995, Malecki *et al.* 1993) has also been released in North America against purple loosestrife.

Blossey *et al.* (1994) described the life history of *G. calmariensis*. Adult beetles emerge from winter diapause in late spring feeding on young leaves and meristematic tissues of purple loosestrife. Females begin oviposition 7 to 10 days after emergence/feeding. Young instar larvae are found in the host plant shoots while older instars feed on all plant tissue. Mature larvae pupate in the soil and emerge as teneral adults in 7 to 10 days. New generation beetles may have a short oviposition period prior to entering the soil to overwinter.

Purple Loosestrife Invasion into Manitoba

The first documented report of purple loosestrife in Manitoba was from the Neepawa area in 1896 (Fletcher 1900). Ottenbreit (1991) reported that the next collection was not until 1944 from the Lockport/Red River region of Manitoba and that by the end of the 1950's purple loosestrife had colonized the Delta Marsh, Otterburne, Fannystelle, and the Cypress River. By the mid-1980's purple loosestrife had formed contiguous populations along the Red River and Assiniboine Rivers (Ottenbreit 1994) and by the mid-1990's purple loosestrife had established itself in every major river system in southern Manitoba. A conservative estimate has 12,250 acres of Manitoba habitat impacted by purple loosestrife (this does not include large continuous populations in the Netley-Libau Marsh). As a result, purple loosestrife and all cultivated varieties of purple loosestrife were designated noxious weeds in 1996 under the Manitoba Noxious Weed Act.

The horticultural industry provided an additional vector for the spread of purple loosestrife with the introduction of *Lythrum* cultivars. *Lythrum* cultivars, developed in

Manitoba as early as 1937, were promoted as ideal perennials for the home garden as they tolerated dry soils and were winter-hardy (Harp and Collicutt 1983). Subsequent research (Ottenbreit 1994, Anderson and Ascher 1993, Lindgren and Clay 1993) indicated that *Lythrum* cultivars were not sterile and contributed to the spread of purple loosestrife. In Manitoba, purple loosestrife infestations along the Assiniboine River, Red River, Winnipeg River, Delta Marsh, Netley Libau Marsh, Red Rock Lake, Portage la Prairie, Tobacco Creek, and the Northumberland drain are most likely the result of garden cultivar escapes.

To control purple loosestrife in Manitoba, the Manitoba Purple Loosestrife Project (MPLP) was formed in 1992. The MPLP is a non-profit coalition comprised of 10 environmental and agricultural organizations. The MPLP initiated a classical biological weed control program against purple loosestrife in 1992 with the release of *H. transversovattitus* (eggs in potted plants) followed by multiple releases of *G. calmariensis* (adult beetles) and *G. pusilla* (adult beetles) in 1993, and releases of *N. marmoratus* in 1997. Funding from the MPLP, Ducks Unlimited Canada, and Ontario Ministry of Natural Resources allowed for the initial introduction of biological control agents for purple loosestrife into Canada in 1992.

While the leaf-defoliating beetle *G. calmariensis* has been released and established at a number of sites across North America (Hight *et al.* 1995, McAvoy *et al.* 1997) there has been little published data describing its impact or performance. It is important that we monitor the initial and long-term performance of *G. calmariensis* by providing the quantitative data required to justify further deployment of the agent and the continuance of a biological weed control program against purple loosestrife. The objective of this paper is to describe the initial impacts and performance of *G. calmariensis* on three purple loosestrife populations in southern Manitoba from 1993 through 1998.

Study Areas

Netley-Libau Marsh.

The Netley-Libau Marsh is an area of 136,000-ha of land and water with 848-km of shoreline located at the southern end of Lake Winnipeg, approximately 65-km north of Winnipeg, Manitoba. The marsh is a complex of lakes and streams whose water levels are influenced by Lake Winnipeg and is an important waterfowl nesting and staging habitat. The marsh is recognized as a Manitoba Heritage Marsh and an Important Bird Area (IBA). The Libau Marsh is the portion of the Netley-Libau Marsh which extends east of the Red River and west of the Brokenhead River. Mean monthly temperatures range from -19.8 °C in January to +19.1 °C in July while mean annual precipitation is 507.2 mm (Environment Canada 1981). Based upon reports of purple loosestrife populations located on the Red River near Lockport in 1944 (Ottenbreit, 1991), purple loosestrife most likely was established down river in the Netley-Libau Marsh in the late 1940s to early 1950s. A vegetation survey carried out by D. Hinks (1936) under the authority of the Winnipeg Game and Fish Association examined thirteen waterbodies with the Netley-Libau Marsh and did not identify any purple loosestrife infestations. A survey conducted in 1992 by the author revealed purple loosestrife could be found throughout the Netley-Libau Marsh complex. *Galerucella calmariensis* were released into two purple loosestrife populations in the Netley-Libau Marsh, hereafter referred to as Libau 2 FMS (50° 20”N; 96° 39”W) and Libau 3 FMS (50° 18”N; 96° 44”W). A control FMS (50° 21”N; 96° 42”W) was also established within the Netley-Libau Marsh.

Delta Marsh.

The Delta Marsh is a lacustrine marsh (21,870-ha) on the south shore of Lake Manitoba separated from Lake Manitoba by a forested barrier-beach ridge and approximately 100-km north-west of Winnipeg, Manitoba. The dominant macrophyte species include *Scirpus* spp., *Typha* spp., *Carex atherodes, Scolochoa festucacea* and *Phagmites australis*. The marsh is recognized as a Manitoba Heritage Marsh, an Important Bird Area (IBA) and a RAMSAR site. Mean monthly temperatures range from -19.8 °C in January to +19.1 °C in July while mean annual precipitation is 498.6 mm (Environment Canada 1981). The Delta Marsh release site is approximately 40-m^2 and bounded by a gravel road on all sides. *Galerucella calmariensis* were released into a purple loosestrife population within the Delta Marsh (50°11" N; 98°18" W) northeast of the Delta Waterfowl and Wetlands Station.

Walker (1965) studied the Delta Marsh vegetation from 1959 to 1961 making no mention of the presence of *L. salicaria* within her vegetation sampling transects. However, while purple loosestrife was being introduced into the Delta Marsh in the early 1960's by local residents as a landscape ornamental, others already recognized it as an invasive plant and were advising against its introduction (J. Shay (previously J. Walker) personal communication 1999). It was not long after that purple loosestrife was described as a weed problem in the Delta Marsh by Friesen (1966), who reported the weed replacing native plant species important for waterfowl.

Monitoring Methods

Fixed monitoring stations (FMS) were established in the Netley-Libau Marsh in 1993 (Libau 2 FMS) and 1994 (Libau 3 FMS and a Control FMS), and in the Delta Marsh (Delta Marsh FMS) in 1996. Fixed monitoring stations allowed for unobtrusive data collection, as *G. calmariensis* will readily drop off host plants if disturbed by placing down a temporary meter square. Each FMS was 10-m long by 5-m wide and divided into 1-m^2 sampling quadrats. From each of the 10 strata that represented the long axis of the FMS, a 1-m^2 sampling quadrat was randomly selected and permanently marked with steel rebar (stratified random sample design). Within each 1-m^2 quadrat, 3 purple loosestrife stems were randomly selected in each year, tagged with orange flagging tape and numbered for identification. Data were not collected on the same stems through consecutive sampling years. Stems were selected as the sampling unit as it is very difficult to define an individual purple loosestrife plant without digging up the root system.

Beginning in late May/early June (depending on spring conditions), data were collected every 10 days from each FMS. Purple loosestrife performance was measured by data collected from tagged stems that included: stem height, the number of seed capsules produced per stem, number of seeds produced per seed capsule, and the portion of the main terminal spike comprised of bud length, inflorescence length, and seed length. Tagged purple loosestrife stems completely defoliated were recorded as 0-cm and considered dead. Stem heights were recorded using a PVC pipe (1.25-cm) demarcated to 200-cm. Performance of *G. calmariensis* were measured through data on the number of egg masses per stem, the number of larvae per stem, and the number of adult beetles per stem. The number of eggs per egg mass were recorded in 1997 and 1998. Native flora and fauna were identified and recorded within each sampling quadrant.

During the last week in August and the first week in September of each year, all individual stems in each sampling quadrant were counted and measured. Seed capsules from

tagged stems were removed, counted, and placed into plastic zip-lock bags. To determine the mean number of seeds per seed capsule, three seed capsules were randomly selected from each zip-lock bag and the number of seeds per capsule were counted under a dissecting microscope.

Insect and Field Release Material

Biological control agents were released throughout the summer months of 1993, 1994 and 1995 (Table 1). Adult beetles were obtained from the Agriculture Canada Research Station located in Lethbridge, Alberta. Beetles were received on an "as available" basis, hence no attempt was made to release identical numbers of beetles into each site. Beetles were initially released into screened release cages (1.2 x 1.2 x 1.2 m) dug 3-cm into the ground to prevent insect escape. Cage frames were constructed of wood and covered with a small mesh material that prevented beetles from escaping. Cages were removed 7 to 10 days after initial release allowing beetles to naturally disperse.

Table 1
***Galerucella calmariensis* liberations 1993-1995. Adult beetles were released inside field cages which were removed after 7 to 10 days. Release year (RY) represents initial year beetles were liberated into each FMS.**

Release Site	Month Released	No. Released
Delta Marsh	August 1993 (RY)	250
Libau #2	August 1993 (RY)	605
	June 1994	140
Libau #3	August 1994 (RY)	378
	July 1995	200

Statistical Analysis

General linear modeling techniques were used to analysis the *G. calmariensis* and purple loosestrife performance data collected on 10-day intervals from 1996 to 1998. To avoid concerns of pseudo-replication the data were summarized by averaging to obtain one observation per site, quadrant, year and sampling period combination. Data represented counts hence were subjected to a log-transformation. Contrasts were performed on statistically significant main effects. Where possible results are discussed by early, mid, or late month categories in an effort to describe seasonal phenology. Each FMS was treated individually and there was no attempt to statistically analysis means between FMS's.

Results and Discussion

Estimating Sampling Effort. Monitoring the performance of a biological control agent requires a number of resources of which the most important is the human resource. Sampling effort is directly related to the availability of human resources. An estimation of the sampling effort expended in this study was calculated as follows: 1-h per sampling period x 4-FMS x 8 sampling periods x 2 observers or 64-h annually. Time expended counting seed capsules and the number of seeds per capsule was approximately 8-

hrs/FMS x 4-FMS x 2 observers or 64-h annually. Time spent counting and measuring final stem heights was 8-hrs/FMS x 4 FMS x 2 observers or 64-h annually. In this study approximately 200-h of sampling effort was expended annually towards the collection of monitoring data. Resources allocated towards traveling, data entry and data analysis would greatly increase the annual sampling estimate.

Galerucella calmariensis Phenology and Performance

Oviposition. Oviposition began in early June. Data analysis revealed significant differences between sampling period means. Contrasts identified oviposition peaks occurred in mid-June through late-June. For example, the peak of oviposition occurred in the Libau 2 FMS on 16 June 4-YRPR with a mean of 1.5 egg masses per purple loosestrife stem (mean stem height was 48.5-cm); while in the Delta Marsh FMS the peak of oviposition was on 27 June 4-YRPR with a mean of 2.8 egg masses per purple loosestrife stem (mean stem height was 41.4-cm) (Table 2). Oviposition in the Libau 2 FMS (5-YRPR) provided the one exception in this study where oviposition followed a bimodal curve with oviposition peaks in both late June and then again in early July. An earlier spring occurred in 1998 and oviposition begun on 20 May in the Libau 2 FMS (5-YRPR) when the mean purple loosestrife stem height was 24.3-cm and in the Libau 3 FMS (4-YRPR) when the mean purple loosestrife stem height was 24.6-cm. Oviposition generally began later in Manitoba when compared to the oviposition period reported by McAvoy *et al.* (1997) that began in May and ended in early June for beetles in Virginia. Within each FMS *G. calmariensis* were found to oviposite egg masses in all quadrats.

Table 2
Monitoring *G. calmariensis* population growth from 1996 to 1998. Means were calculated every 10 days from data collected off 30 tagged purple loosestrife stems in each FMS. Data represents the highest mean recorded in each year, the maximum value found on any one tagged stem follows in brackets.

		Mean ± Standard Error / per stem (Maximum)			
FMS Site	**YRPR (Year)**	**Adults**	**Egg Masses**	**No. Eggs**	**Larvae**
Libau 2	3-YRPR (1996)	$0.2^{a} \pm 0.1$ (2)	$3.4^{a} \pm 0.8$ (18)	n/a	$2.2^{a} \pm 0.8$ (17)
	4-YRPR (1997)	$0.3^{a} \pm 0.1$ (3)	$1.5^{b} \pm 0.4$ (8)	8.5 ± 2.2 (49)	$1.8^{b} \pm 0.7$ (18)
	5-YRPR (1998)	$4.9^{b} \pm 1.3$ (29)	$2.6^{a} \pm 0.7$ (23)	12.4 ± 3.9 (108)	$2.9^{c} \pm 0.9$ (20)
Libau 3	2-YRPR (1996)	$0.1^{a} \pm 0.1$ (2)	$0.3^{a} \pm 0.1$ (3)	n/a	$0.4^{a} \pm 0.2$ (8)
	3-YRPR (1997)	$0.1^{a} \pm 0.1$ (3)	$0.1^{b} \pm 0.05$ (2)	0.7 ± 0.7 (23)	$0.4^{a} \pm 0.3$ (9)
	4-YRPR (1998)	$3.7^{b} \pm 1.0$ (24)	$4.6^{c} \pm 0.7$ (17)	20.8 ± 3.7 (71)	$13.2^{c} \pm 3.8$(105)
Delta	2-YRPR (1995)	n/a	6.5 JD	3.7 JD	n/a
	3-YRPR (1996)	$1.0^{a} \pm 0.2$ (6)	$21.1^{a} \pm 1.7$ (39)	63.2^{JD}	$23.3^{a} \pm 3.1$(109)
	4-YRPR (1997)	$2.8^{b} \pm 1.1$ (26)	$2.8^{b} \pm 0.7$ (19)	12.7 ± 4.1 (112)	$3.0^{b} \pm 0.6$ (13)
	5-YRPR (1998)	$0.4^{c} \pm 0.2$ (6)	$1.8^{c} \pm 0.5$ (10)	7.6 ± 2.2 (42)	$0.3^{c} \pm 1.2$ (33)

Note: Superscripted JD: Data extrapolated from J.K. Diehl (1999).

Note: Means followed by the same superscripted letter within columns are not significantly different. For statistical purposes data were subjected to a log-transformation. Above data are actual means prior to log-transformation.

Data analysis revealed significant differences existed between years in the mean number of egg masses recorded within the Libau 3 ($F = 93.10$; df = 2,18; $P < 0.0001$), Libau 2 ($F = 25.55$; df = 2, 8.27; $P < 0.0003$), and Delta Marsh FMS ($F = 79.34$; df = 2, 21.96; $P < 0.0001$). Libau 3 FMS contrasts revealed a significant increase in the mean number of egg masses oviposited 4-YRPR as compared to previous years. In the Delta Marsh FMS, significant declines were observed in the mean number of egg masses oviposited in each successive year of this study indicating a negative population growth. Peak oviposition occurred in the Delta FMS 3-YRPR as the number of eggs per stem increased from 3.7 eggs/stem (2-YRPR) to 63.2 eggs/stem (3-YRPR). Diehl (1999) reported egg densities increased from 202 eggs/m^2 (2-YRPR) to 8,297 eggs/m^2 (3-YRPR). In the Libau 2 FMS there were no significant differences between the mean number of egg masses oviposited 3-YRPR and 5-YRPR, however significantly fewer egg masses were observed 4-YRPR.

The number of eggs per egg mass were recorded in the last two years (1997 & 1998) of this study. For the Libau 2 FMS, mean egg mass size was 5.7 (74 egg masses with 423 eggs) 4-YRPR and 4.2 (279 egg masses with 1173 eggs) 5-YRPR. Between 4-YPPR and 5-YRPR a 3.7-fold increase in the number of egg masses oviposited and a small decrease in the size of the egg masses were observed. For the Libau 3 FMS, mean egg mass size was 4.3 (6 egg masses with 26 eggs) 3-YRPR and 3.6 (316 egg masses with 1137 eggs) 4-YRPR, a dramatic 52-fold increase in the number of egg masses was observed and a small decrease in the mean egg mass size was noted. At the Delta Marsh FMS, mean egg mass size was 5.0 (164 egg masses with 826 eggs) 4-YRPR and 4.0 (117 egg masses with 478 eggs) 5-YRPR, a slight decrease in the number of egg masses oviposited and in the mean egg mass size was observed. Mean egg mass sizes were similar to those reported by Blossey (1995) (mean=5.3) for beetles in Germany and by Lindgren (1997) (mean=5.8).

Larvae. Peak numbers of larvae were recorded in sampling periods extending from late June through early July annually. For example, peak numbers of larvae were observed on 22 June 1998 in the Libau 3 FMS (4-YRPR) where a mean of 13.2 larvae per stem were observed on purple loosestrife stems (mean stem height 72.9-cm) while the highest number of larvae found on any one stem was 105 (Table 2). First and second instar larvae were found on/in purple loosestrife shoot apex, in many cases the larvae were not visible until the apex of the stem was slightly opened. Third instar larvae were observed on leaf tissue and were most commonly found on the underside of the leaves. Identical larvae feeding niches were also reported by McAvoy *et al.* (1997) for larvae in southwest Virginia and by Blossey (1995) for beetles in Germany. When compared to adult beetle herbivory, it was the larvae stages that appeared to cause the most damage to purple loosestrife. Complete defoliation by larvae stages led to the elimination of purple loosestrife sexual reproduction in the Delta Marsh and in the Libau 3 FMS. This is supported by Crawley (1983) who reported cumulative herbivory damage by larvae stages removed young leaf tissues and the associated photosynthate production.

Data analysis revealed significant differences between years for the mean number of larvae recorded for the Libau 3 FMS ($F = 74.93$; df = 2, 18; $P < 0.0001$), Libau 2 FMS ($F = 8.48$; df = 2, 92; $P < 0.0001$), and Delta Marsh FMS ($F = 61.17$; df = 2, 20.99; $P < 0.0001$). In the Libau 3 FMS significantly more larvae (mean = 13.2 larvae per stem) were recorded 4-YRPR (mean stem height 72.9-cm) (Table 2). At the Delta Marsh FMS a decline in the mean number of larvae observed in each successive year of this study indicated a negative population growth. In the Libau 2 FMS significantly more larvae were

observed 4-YRPR as compared to 3-YRPR and 5-YRPR respectively suggesting little change in the beetle population.

Adults. Adult beetles emerged from winter diapause in late May through early June depending on the climatic conditions of the particular year. In southern Manitoba, the perennial marsh-marigold *Caltha palustris* L. can be used as emergence-barometer as *G. calmariensis* adults were commonly observed emerging from winter diapause when *C. palustris* was in bloom. Post-diapause beetles were commonly found aggregated on purple loosestrife in the spring, likely as part of a reproductive strategy. Post-diapause adults were not observed in early July and were assumed dead. Significant differences between sampling periods and between year contrasts identified peak numbers of post-diapause beetles in early June and mid-June. Contrasts further indicated peak numbers of new generation adults (F_1 adults) were found in late-July and early August. New generation adults were observed to be active through August and in some years well into October.

The mean number of adults observed were significantly different between years for the Libau 3 FMS ($F = 24.36$; df = 2,18; $P < 0.0001$), Libau 2 FMS ($F = 16.36$; df = 2, 8.22; $P < 0.0014$), and Delta Marsh FMS ($F = 6.02$; df = 2,42; $P < 0.0001$). Data analysis for Libau 3 FMS revealed significant differences for the year effect where significantly more adults were recorded 4-YRPR (Table 2). Contrasts for Libau 2 FMS revealed significantly more adults (overwintered and new generation) were observed 5-YRPR, which may indicate the beginning of an exponential population growth similar to that observed in the Libau 3 FMS (4-YRPR). Delta Marsh FMS year to year contrasts indicated declines in the mean number of post-diapause adults observed (peak numbers were observed in the early-June sampling periods) as well as declines in the mean number of new generation adults (peak numbers were observed in mid-July sampling periods).

G. calmariensis impact on purple loosestrife

Terminal Spike Data. Analysis of variance for the Libau 3 FMS and Libau 2 FMS revealed significant differences between years for the portion of the main terminal spike comprised of bud length, inflorescence length and seed length (Table 3). Libau 3 FMS contrasts indicated significant decreases occurred in each successive year for bud length, inflorescence length, and seed length until 4-YRPR when *G. calmariensis* herbivory resulted in total elimination of terminal spike and sexual reproduction (Table 3). Libau 2 contrasts revealed bud length, inflorescence length and seed length were significantly smaller 5-YRPR as compared to 4-YRPR. In the Delta Marsh *G. calmariensis* herbivory eliminated reproduction by 3-YRPR.

Stem Heights and Number of Stems. Analysis of variance for the Libau 3 FMS and Libau 2 FMS revealed significant differences between years for mean stem height mean while there was little change in stem height means in the Control FMS (Table 3). Libau 2 FMS contrasts revealed no significant change in stem heights between 5-YRPR and 4-YRPR, while stem heights 3-YRPR were significantly smaller. Contrasts for the Libau 3 FMS indicated mean stem heights 4-YRPR were significantly smaller than stem heights in each of the previous years.

The penultimate of a biological weed control program is the suppression of the target weed population to "tolerable" levels, perhaps best achieved by a reduction in the number of target weed stems. Data analysis revealed statistically significant differences in the

Table 3
Impact of *G. calmariensis* herbivory on purple loosestrife.
The total number of stems per 1-m² were counted in late August or early September of each year. Terminal spike means and stem heights were calculated from 30 tagged stems every 10 days from each FMS.
Means were chosen from sampling periods most representative of appropriate purple loosestrife phenological stage.

FMS Site		Mean ± Standard Error				
		1994	1995	1996	1997	1998
Control	No. Stems	63.0^{a} ± 11.6	61.2^{a} ± 9.3	62.7^{a} ± 10.8	41.5^{a} ± 4.8	75.3^{a} ± 13.0
	Stem Hght.	n/a	n/a	99.6^{a} ± 3.8	103.4^{a} ± 5.7	102.2^{a} ± 5.5
	Blm. Stems	23.5 ± 5.6	42.6 ± 7.3	42.8 ± 6.8	26.9 ± 3.7	48.1 ± 8.4
	Veg. Stems	39.5 ± 7.4	18.6 ± 2.9	29.6 ± 6.6	14.6 ± 2.8	27.0 ± 5.3
	Bud Length	n/a	n/a	6.3^{a} ± 0.2	5.0^{a} ± 0.5	3.1^{a} ± 0.6
	Inflor. Length	n/a	n/a	8.7^{a} ± 0.6	5.2^{b} ± 0.9	5.5^{b} ± 1.1
	Seed Length	n/a	n/a	25.6^{a} ± 1.7	18.2^{b} ± 2.2	7.8^{c} ± 1.9
		1-YRPR	2-YRPR	3-YRPR	4-YRPR	5-YRPR
Libau 2	No. of Stems	14.6^{a} ± 7.8	15.2^{a} ± 5.3	15.2^{a} ± 6.2	16.8^{a} ± 5.2	19.2^{a} ± 5.4
	Stem Hght	n/a	n/a	103.1^{a} ± 4.7	122.1^{b} ± 4.5	124.3^{b} ± 5.3
	Blm. Stems	4.4b^{c} ± 1.7	10.2^{c} ± 3.3	6.4^{b} ± 2.1	12.4^{a} ± 3.7	8.6 ± 3.5
	Veg. Stems	10.2^{a} ± 6.2	4.2^{a} ± 2.1	8.8^{a} ± 4.4	4.4^{a} ± 1.5	10.4^{a} ± 1.9
	Bud Length	n/a	n/a	1.4^{a} ± 0.4	3.8^{b} ± 0.5	2.2^{a} ± 0.5
	Inflor. Length	n/a	n/a	2.0^{a} ± 0.6	6.5^{b} ± 1.0	3.2^{a} ± 1.1
	Seed Length	n/a	n/a	3.5^{a} ± 1.2	17.4^{b} ± 3.1	5.6^{a} ± 1.6
		RY	1-YRPR	2-YRPR	3-YRPR	4-YRPR
Libau 3	No. of Stems	13.0^{a} ± 4.8	144.6^{ab} ± 52.2	54.3^{ab} ± 8.5	48.7^{ab} ±13.5	35.4$^{ab, c}$ ± 5.0
	Stem Hght	n/a	n/a	104.7^{a} ± 8.1	110.8^{a} ± 4.1	76.3^{b} ± 4.7
	Blm. Stems	9.1^{b} ± 3.7	25.4^{b} ± 8.5	25.5^{b} ± 6.0	60.4^{a} ±18.9	0.0^{b} ± 0.0
	Veg. Stems	3.9^{ab} ± 1.5	119.3^{ac} ± 55.7	28.8^{a} ± 5.7	12.6^{abd} ± 1.6	35.4^{ac} ± 5.0
	Bud Length	n/a	n/a	5.7^{a} ± 0.6	2.7^{a} ± 0.3	0.0^{b} ± 0.0
	Inflor. Length	n/a	n/a	8.3^{a} ± 1.0	5.7^{a} ± 1.0	0.0^{b} ± 0.0
	Seed Length	n/a	n/a	23.7^{a} ± 3.0	23.8^{a} ± 3.3	0.0^{b} ± 0.0
		2-YRPR	3-YRPR	4-YRPR	5-YRPR	
Delta	No. of Stems	31.8 ± 2.5^{JD}	0.0^{a} ± 0.0	25.6^{b} ± 4.7	19.6^{b} ± 4.1	
	Stem Hght.	n/a	0.0^{a} ± 0.0	30.7^{b} ± 2.2	22.8^{c} ± 2.5	
	Blm. Stems	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	
	Veg. Stems	0.0^{a} ± 0.0	25.6^{b} ± 4.7	19.6^{b} ± 4.1	0.0 ± 0.0	
	Bud Length	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	
	Inflor. Length	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		
	Seed Length	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		

Note. Means followed by the same letter within rows are not significantly different.
For statistical purposes data were subjected to a log-transformation during analysis.
Above means represent actual means prior to log-transformation.

Note: Superscripted JD indicates data source J.K. Diehl (1999).

number of stems between years for the Libau 3 and Delta FMS while no significant changes were recorded in the Control or Libau 2 FMS (Table 3). In the Libau 3 FMS no change in the mean number of stems was noted 2-YRPR or 3-YRPR, however *G. calmariensis* herbivory resulted in a significant reduction in the number of stems 4-YRPR. At the Delta Marsh FMS, *G. calmariensis* significantly reduced the number of purple loosestrife stems, contrasts indicated significantly more stems 4-YPPR and 5-YRPR as compared to the mean number of stems 3-YRPR (when all stems were destroyed and no additional growth occurred after 16 July). By 4-YRPR and 5-YRPR the Delta purple loosestrife population was comprised of new stems which had emerged from the seed bank in late summer, and final stem height means were 23.9-cm and 12.0-cm respectively.

In the Libau 3 FMS (1-YRPR) hundreds of seedlings (all under 12-cm in height) were recorded in two quadrats in September of 1995. These two sampling quadrats contained 438 and 462 stems, as compared to the remaining 8 sampling quadrats where the mean was 68.2 stems per quadrant. These seedlings resulted in the mean number of stems and standard error per quadrat being much higher 1-YRPR as compared to other years (Table 3). These seedlings failed to establish and survive through to 2-YRPR. An emergence of seedlings was not observed in any of the other FMS. For statistical purposes, these data were removed from the data analysis. Significantly fewer stems were recorded 4-YRPR as compared to 1-YRPR, fewer stems were also found 3-YRPR and 2-YRPR but contrasts were not significant indicating that *G. calmariensis* has yet to impact the number of stems in the Libau 3 FMS.

No tagged stems produced flowers, buds or seeds in the Delta Marsh FMS over the duration of this study. In each year of this study *G. calmariensis* herbivory resulted in the total destruction (dead standing stems devoid of foliage) of all spring emerged stems at the Delta Marsh FMS. For example, all tagged stems were dead by 4 August 5-YRPR, 21 July 4-YRPR, and by 16 July 3-YRPR. All purple loosestrife in the area surrounding the FMS were also destroyed by 8 August 4-YRPR. Mean stem heights for 4-YRPR and 5-YRPR (Table 3) were derived from stem emerging in late summer as *G. calmariensis* larvae totally defoliated stems that had emerged in the spring.

Seed and Seed Capsule Production. The first quantitative evidence that *G. calmariensis* herbivory was negatively impacting purple loosestrife was evident in a reduction in purple loosestrife sexual reproduction (*G. calmariensis* impact was consisting of defoliation was not a monitoring parameter in this study). Sexual reproduction is the main mechanism responsible for the propagation and spread of purple loosestrife. In the Libau 3 FMS there were significant differences between years ($F = 38.34$; $df = 4,35$; $P < 0.0001$) in the mean number of seed capsules produced per tagged stem and year to year contrasts revealed a significant decline occurred 4-YRPR. Herbivory resulted in no purple loosestrife sexual reproduction 4-YRPR (Figure 1). In both the Libau 2 FMS and Libau 3 FMS, the mean number of seed capsules per tagged stem increased after beetle release. The increase in seed capsule production may have been a compensatory response of purple loosestrife to *G. calmariensis* herbivory. Benner (1988) reported that when *Thlaspi arvense* L. (Brassicaceae) was subjected to apex removal plants produced more fruits. Once *G. calmariensis* herbivory reaches a threshold level (i.e. Libau 3 FMS 4-YRPR) purple loosestrife may not be able to compensate through increased seed capsule production. For example, in the Libau 3 FMS a 80% reduction in the number of seed capsules produced followed and eventually total seed capsule suppression resulted.

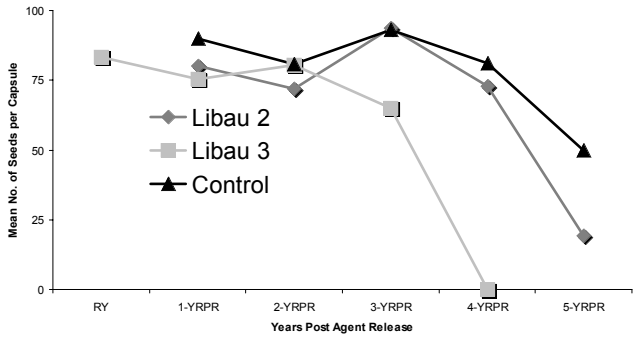
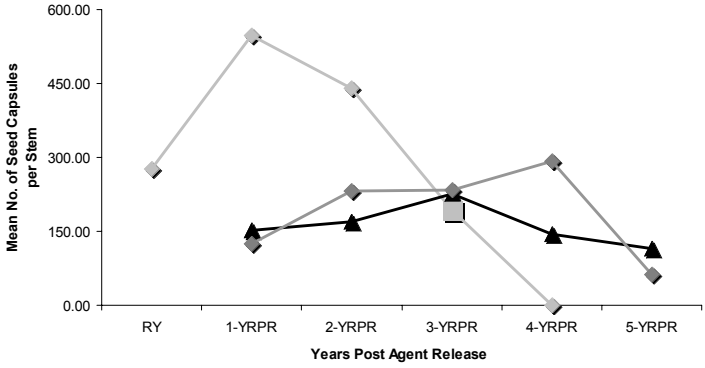


Fig. 1. Relationships between *G. calmariensis* and purple loosestrife sexual reproduction as measured by seed capsule and seed production in initial release year (RY) and years post release (YRPR). The mean number of seed capsules per tagged stem were calculated from the N=30 randomly tagged purple loosestrife stems from each FMS. The mean number of seeds per seed capsule were calculated by counting the number of seeds from three randomly selected seed capsules from each of the thirty tagged stems (N=90). At the Libau 3 FMS *G. calmariensis* were able to eliminate all sexual reproduction 4-YRPR.



Libau 2 FMS there were significant differences ($F = 13.59$; $df = 4,16$; $P < 0.0001$) between years in the mean number of seed capsules produced per tagged stem with significantly less seed capsules produced 5-YRPR as compared to prior years. The mean number of seed capsules per stem and the mean number of seeds per seed capsule remained similar until 5-YRPR when reductions close to 80% were recorded. Based upon the Libau 3 FMS data, it is projected that seed capsule and seed production may be eliminated by 6-YRPR at the Libau 2 FMS.

Shamsi and Whitehead (1974) reported that purple loosestrife seed capsules yielded 120 seeds per capsule while Thompson *et al.* (1987) reported a mean of 90 seeds per capsule. Data collected between 1994 and 1998 from the Control FMS located in the Netley-Libau Marsh revealed a mean of 76.3 seeds per seed capsule (N=387 seed capsules were sampled).

In the Libau 3 FMS, the mean number of seeds per capsule did not show a gradual decline while under *G. calmariensis* attack but remained constant until herbivory led to

the total elimination of seed capsules. Purple loosestrife sexual reproduction was eliminated in the Libau 3 FMS (4-YRPR) when *G. calmariensis* means reached 3.7 adults, 4.6 egg masses and 13.2 larvae per tagged stem. In comparison, studies conducted in northern Germany (Megerdorf and Ponitz) Blossey (1995) reported reductions in flowering and seed output to less than 1% when the average number of *G. calmariensis* larvae per cm of shoot reached 1.9 (Ponitz) and 3.1 (Meggerdorf). Seed production was eliminated in the Libau 3 FMS (4-YRPR) with a lower number of larvae per cm of stem (mean = 0.18) as compared to the sites in Germany studied by Blossey (1995).

G. calmariensis Population Growth

Notable *G. calmariensis* population growth was observed in the Libau 3 FMS (4-YRPR) as the number of adults increased 3-fold, the number of egg masses increased 4-fold, and the number of larvae increased 13-fold in comparison to the population 3-YRPR (Table 2). In the Libau 2 FMS a smaller population growth was also observed between 4-YRPR and 5-YRPR, similar to the *G. calmariensis* population growth that occurred in the Libau 3 FMS between 3-YRPR and 4-YRPR.

Delta Marsh yearly contrasts revealed significant declines occurred in the *G. calmariensis* population in each successive year from 3-YRPR to 5-YRPR indicating a negative population growth occurred during this study (Table 2). While biological control agents were released in the Delta Marsh in 1993, a FMS was not established until 1996 (3-YRPR). Visual observations indicated that a large increase in the *G. calmariensis* population occurred between 2-YRPR and 3-YRPR. This is further supported by data collected by Diehl (1999), who reported a 2537% increase in the number of eggs/m^2 between 2-YRPR and 3-YRPR which resulted in a reduction in overall number of stems from 32 m^2 (2-YRPR) to 0 m^2 (3-YRPR) around the immediate release site. Observations prior to the establishment of the FMS coupled with the data from this study suggest that the *G. calmariensis* population peaked 3-YRPR, dramatically suppressed the purple loosestrife population, then entered a period of negative population growth.

McAvoy *et al.* (1997) initially released 544 *G. calmariensis* and 1056 *G. pusilla* into 0.4 ha of purple loosestrife in 1992 (further releases followed in 1993) in Virginia. McAvoy *et al.* (1997) monitored the beetle population between 1993 and 1995 and reported no change in the *G. calmariensis* population and minimal beetle impact on the purple loosestrife population. In Virginia, the highest number of eggs found per stem to be 11.67 in 1995. In comparison, the highest number of eggs found on one stem in the Libau 3 FMS (4-YRPR) was 71 eggs and 42 eggs for at the Delta FMS (5-YRPR), both sites were subjected to severe defoliation. It is evident that *G. calmariensis* performance, colonization, and impact will vary both locally and regionally.

While the Delta FMS received the least number of *G. calmariensis* (N=250), the beetles achieved purple loosestrife suppression within the shortest time period. Purple loosestrife control may have been exacerbated in the Delta Marsh FMS due to cumulative stresses resulting from *G. calmariensis* herbivory coupled with flooding. The Delta FMS held 20-35 cm of standing water through to the fall 3-YRPR. Harris (1980) suggested more effective weed control maybe achieved through stress loading where the introduction of a biological control agent is supplemented with additional environmental stresses. Harris (1980) reported that many successes in weed biocontrol were the result of a combination of several stresses. White (1984) suggested that physiologically stressed plants become a better source of food for herbivores because of an increase an the amount of available

nitrogen. Young herbivores feeding on the stressed foliage may then benefit with an increased chance of survival. Prolonged flooding 3-YRPR may have disrupted purple loosestrife metabolism increasing host plant quality, subsequently increasing the overall fitness of *G. calmariensis,* leading to destruction of purple loosestrife stems. Releasing *G. calmariensis* into flooded habitats has been generally avoided due to the presumed absence of suitable pupation areas. Data from the Delta FMS suggests that *G. calmariensis* has the ability to survive under flooded situations, this is also supported by Diehl (1999). Larvae may have migrated off-site finding suitable pupation areas.

The Delta Marsh FMS also benefited from *G. calmarienis* completing two generations both 2-YRPR and 3-YRPR (Diehl 1999). Second generations were not observed in any of the Libau FMS. Physiologically stressed host plants producing higher levels of nitrogen may have contributed to *G. calmariensis* second generations. Second generations are not uncommon, for example, at a release site (not part of this monitoring study) in the Libau Marsh hundreds of thousands adult beetles were observed well into October of 1998. In the following spring not one purple loosestrife stem could be found over the approximately 4 acre site. The mechanisms which drive second generations requires further research.

Insects and Plants Associated with FMS's

In monitoring the performance of a non-indigenous biological control agent it is paramount that we monitor for changes that may occur in the associated flora community as a result of target plant control and be vigilant of potential host-plant switches. This is of particular importance if the plant species present at the release habitat were not included in the initial screening tests. For example, in the original feeding and oviposition screening tests a total of 44 plants were utilized of which 13 were characterized as wetland plants of wildlife importance (Blossey *et al.* 1994). When compared to the original screening tests, only four plants in the same genus (*Typha, Carex, Salix, Polygonum*) were found at FMS's employed in this study (Table 4). Over the duration of this study no *G. calmariensis* feeding or oviposition was observed on non-target plants within the FMS's.

A number of insect herbivores, mostly generalists, were found to feed on purple loosestrife during the course of this study. The most common insect was the four-lined plant bug *Poecilocapsus lineatus* (Fabricius). The stink bug *Apoecilus bracteatus* (Fitch) was observed as a common predator of *G. calmariensis* larvae at the Libau FMS sites but did not appear to be an impediment to *G. calmariensis* population growth. For example, on 14 June 1996, eight adult stinkbugs were counted inside on 1-m^2 sampling quadrant at the Libau 2 FMS. Native insects did not impact *G. calmariensis* establishment within the FMS's studied. An intensive survey of insects associated with purple loosestrife in Manitoba (Diehl *et al.* 1997) also found no native herbivores were capable of impacting purple loosestrife populations.

***L. salicoria* - *G. calmariensis* Interaction Model**

It is evident that the biological control agent *G. calmariensis* is capable of providing successful control of target weed purple loosestrife within a period as short as 3-YRPR. The data collected in this study allow for the construction of a simplistic *L. salicaria* - *G. calmariensis* interaction model. The data depict a pattern where we can expect significant increases in the *G. calmarienis* population 3-YRPR or 4-YRPR. The increased herbivory load will suppress (Libau 2 FMS) or eliminate seed production (Libau 3 and Delta FMS)

Table 4
Plant species associated with purple loosestrife in the Delta Marsh, Libau 2, Libau 3 and Control FMS. *Galerucella calmariensis* were not found to feed on or oviposit on any of the below non-target flora.

Common Name	Scientific Name	FMS Site
Swamp Smartweed	*Polygonum persicaria*	Control, Libau 2, Libau 3
Sedges	*Carex spp.*	Control, Libau 2, Libau 3
Willow	*Salix petiolaris*	Control
Horsetail	*Equisetum spp.*	Control, Libau 2
Silverweed	*Potentilla anserina*	Control, Libau 2,
Water Horehound	*Lycopus americanus*	Control, Libau 2,
Cattail	*Typha latifolia*	Libau 2
Canada Thistle	*Cirsium arvense*	Libau 2
Canada Anemone	*Anemone canadensis*	Libau 2
Wild Vetch	*Vicia americana*	Libau 2
Tuffed Loosestrife	*Lysimachia thyrsiflora*	Libau 2
Reed Grass	*Phragmites australis*	Delta Marsh
Wild Mint	*Mentha arvensis*	Delta Marsh, Libau 3
Smooth Aster	*Aster laevis*	Delta Marsh
Halberdleaf Tear-thumb	*Polygonum arifolium*	Delta Marsh
Whitetop	*Scolochloa festucacea*	Delta Marsh
Hemp Nettle	*Galeopsis tetrahit*	Libau 3

depending upon the magnitude of the population growth and contributions from other abiotic variables that may further stress the target weed. Attacked stems experiencing severe herbivory are significantly smaller by the end of the growing period (Libau 2 FMS) and may be destroyed as was the case in the Delta FMS 3-YRPR. In the following year a reduction in the number of purple loosestrife stems may be observed and again all stems may be subject to complete defoliation. Once the number of stems is significantly reduced, the *G. calmariensis* population experiences a negative population growth (or a population crash), as was the case in the Delta FMS. Further monitoring will provide data necessary to further develop a *L. salicaria* - *G. calmariensis* interaction model and identify controlling variables.

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