Biological Control of Purple Loosestrife (*Lythrum salicaria*) in Quebec

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A thesis

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Abstract

Two European leaf-eating beetles, *Galerucella calmariensis* L. and *G pusilla* (Duft.)(Chrysomelidae:Coleoptera) were released at four sites in Quebec to manage the semi-aquatic exotic weed, purple loosestrife (*Lythrum salicaria* L.). Protocols for monitoring the *Galerucella* populations and detecting changes in the plant communities were implemented. In addition, the effect of seeding with native plants species in conjunction with *Galerucella* herbivory was tested in an experiment at a purple loosestrife stand in Ontario. Releases of lab-reared beetles in Quebec in 1996 did not survive to 1997 at any of the 4 sites, but releases of field collected beetles in 1997 overwintered successfully at 3 of the 4 sites. The density of purple loosestrife in 1998 ranged from 28% (Cap Tourmente) to 84% (Hull). The density of *Galerucella* in 1998 ranged from 6 (Lac St François) to 50 (Hull) adults/m^2/min. In the Ontario experiment, herbivory and seeding together interacted to increase the biomass of other plant species significantly—and thereby reduced the dominance (proportion of the biomass) of purple loosestrife—but did not have a significant effect on the biomass of purple loosestrife in the first season.

Resumé

Deux espèces de coléoptères, *Galerucella calmariensis* et *Galerucella pusilla*, ont été introduites sur quatre sites au Québec pour contrôler la salicaire pourpre, un mauvais herbe des terres humides. Une étude de la végétation de ces sites a été faite afin de surveiller l'évolution de la situation pendant les prochaines années. Par ailleurs, l'effet de l'ensemencement de douze espèces de plantes indigènes en combinaison avec *Galerucella* a été examiné dans une experience en Ontario. Au Québec, les introductions (en 1996) de *Galerucella* élevées en laboratoire n'ont pas réussi; cependant, les insectes ramassés dans les champs et introduits en 1997 ont survécu à l'hiver dans trois des quatre sites. Pour l'année 1998, la densité de la salicaire a varié de 28% à 84%, tandis que la densité de la *Galerucella* a varié de 6 à 50 adultes/m^2/minute. L'expérience ontarienne a pour sa part permis d'observer une interaction entre l'insecte herbivore et les plantes indigènes ensemencées pour augmenter la biomasse des autres espèces de plantes (et ainsi réduire la domination relative de la salicaire pourpre); toutefois, cela n'a pas eu d'effet sur la biomasse totale de la salicaire après la première saison.

Literature Review

Invasion History and Ecology of Purple Loosestrife

Purple loosestrife is an aquatic perennial which likes wet, slightly acid ground, but which can tolerate a wide range of moisture and nutrient conditions and soil types. It is this adaptability, combined with effective means of both dispersal (seeds, via water) and spread (stem and root buds), which make purple loosestrife an opportunistic invader of disturbed habitats. In its native range of northern Europe, purple loosestrife is an early successional species—ie. it colonizes disturbed areas and can form monotypic stands for only a few years before it is displaced by more competitive plant species, and reduced to just a scattered presence. Similarly in North America, since its arrival via ship ballast in the late 17^{th}/early 18^{th} century, purple loosestrife has been colonizing disturbed habitats, dispersing mainly along shipping routes and newly built canal systems in the 19^{th} century, and facilitated by massive irrigation projects and general development in this century (Louis-Marie 1944, Thompson et al 1987). The difference here is that, several decades after the extensive takeover of purple loosestrife began causing concern, there is still no sign of succession by North American plants. Here, purple loosestrife is both opportunistic and competitive, and in fact there is some indication that it is able to invade not only disturbed habitats but intact plant communities as well, albeit at a slower rate (Balogh and Bookhout 1989).

The relatively greater competitive abilities of purple loosestrife in North America must be due either to an actual genetic difference in the purple loosestrife itself, to physical or biological differences in the environments here, or due to some combination thereof. There is some evidence that *Lythrum salicaria* has undergone introgressive hybridization with *Lythrum alatum* (winged loosestrife) in North America (Anderson and Ascher 1996), and some of the new genetic information may have been adaptive here, perhaps explaining the rapid expansion in this century after an initial lag in the 19^{th} century. North American purple loosestrife does grow taller than European purple loosestrife (Edwards et al 1995), which may indicate a greater proportion of resources allocated to growth at the expense of reproduction--an indication of a more competitive, less ruderal species (Harper 1977). It seems unlikely, however, that this cross alone can explain entirely the difference between the behavior of the two populations—and one would wonder why such an aggressive genotype in North America had never found its way overseas and staged a similar takeover of European wetlands.

Differences in the physical environment are also unlikely to be critical: it has been shown that temperate plants tend to be pre-adapted to regions of a similar latitude, due to the similar climates and glacial histories (Stukey 1980), and given the range of conditions in which purple loosestrife is dominant here, there are certainly comparable habitats in Europe. The most important factor is therefore likely to be a difference in the biotic environment. There could be differences in any of the organisms which interact with purple loosestrife: other plants, microorganisms in the rhizosphere, pathogens, herbivores, or competitors. While the two main competitors of purple loosestrife are the same in Europe and North America (*Typha* spp (cattails) and *Phalaris arundinacea* (canary reed-grass)), it is possible that a more complex interaction—such as higher levels of herbivory from muskrats on *Typha* (Thompson et al 1987)--is altering their relative competitiveness. While none of these biological factors have been investigated and therefore none can be dismissed, one of the most obvious explanations is the lack of predator pressure on purple loosestrife in its new continent. In North America, 64 insects have been found in or on purple loosestrife plants, few of which feed on it and none of which feed on it exclusively. By contrast, in Europe purple loosestrife is host to 184 species of insect (Malecki et al 1993), and 14 of these eat nothing else (Batra et al 1986). While there may well be other factors involved, the absence of this strong predator pressure is a likely candidate to explain at least partially the advantage purple loosestrife has over its competitors in North America.

Impact of Purple Loosestrife

There has been some concern on the effect of purple loosestrife on soil conditions, that it may impede water flow, increase siltation, and/or sequester high levels of nutrients (Balogh and Bookout 1989, Templer et al 1998). The loss of access to open water could also have implications for many terrestrial species which feed on fish and aquatic invertebrates, and the loss of mudflats could be important for foraging shorebirds (Rawinski 1982). However, Most of the concern surrounding the spread of purple loosestrife is due to speculation about its potential displacement of native vegetation, and the subsequent effects on the wildlife which depend on that vegetation. Harris (1988) reports that purple loosestrife has been partly implicated in the decline of both *Scirpus longii* (Fern) and *Eleocharis parvula* (Rom & J.A.Schultes) in Massachusetts. At least one-third of threatened and endangered species in the United States live in wetlands (Murdock 1994), and Thompson et al (1987) suggest several examples of vertebrate species which may be particularly threatened by the invasion of purple loosestrife—the Black Tern (*Clidonias niger)*, Canvasback duck (*Aythya valisineria*), and the Bog Turtle (*Clemmys muhlenbergi*). There have been some reports of native birds, insects, mammals, and fish beginning to make use of purple loosestrife (Anderson 1995, Rawinski 1982, Strong et al 1984, Barbour and Kiviat 1998) but the overwhelming consensus is that the plant is very little used compared with the species which it is thought to be displacing (Hight 1990, Thompson et al 1987, Smith 1959, Friesen 1966, Rawinski 1982).

In a critical review of the literature, Anderson (1995) points out that there is no quantitative evidence linking purple loosestrife with diminishing plant or animal species, and suggests that the former has simply been assumed based on increasing purple loosestrife cover, while the latter has been assumed based on the former. Andrews' point is well taken, in that there is currently no specific information as to which species (plant or animal) are most affected, the extent of the effects, or which areas are the most severely threatened. Such studies are needed in order to target management efforts in critical habitats, where that which is being displaced is most rare and/or valued—and also to ensure that the remedial action taken is not in fact more disruptive than the weed itself. However, the conversion of such vast tracts of ecologically critical wetlands into virtually monotypic stands of an exotic species is likely to have a substantial impact, and should not be ignored simply because this impact has not been adequately studied and cannot be precisely predicted. Thompson et al (1987) argue that, in the context of an already precarious wetland ecosystem, the conservative response would be to attempt to minimize what could be an irreversible impact. Ashton and Mitchell (1989) warn about the dangers of inaction, pointing out that a failure to limit the spread of an aquatic weed will only increase the size of the problem and the subsequent remedial action required.

Conventional Control Efforts

The problem with minimizing the impact of purple loosestrife is that most of the control methods which have been tried are potentially more disruptive to the ecosystem than the invader itself (Thompson et al 1987), sometimes ironically improving the conditions for a disturbance-adapted species like purple loosestrife.

All methods of physical removal have proven either ineffective or unfeasible. Pulling the entire plant out manually is the most effective of these, although it does not work as well for plants over 2 years old, and it would require an enormous investment of labour for many years to exhaust the seed bank and prevent re-establishment (Louis-Marie 1944, Thompson et al 1987). Plowing and seeding with replacement species such as Japanese Millet (*Echinchloa frumentacea*) or Reed Canarygrass (*Phalaris arundinacea* L.) is temporarily effective in reducing small and accessible loosestrife stands which can be treated manually, but for larger areas the methods needed to plow and seed would cause too great a disturbance (Rawinski 1982). Simply plowing the plants without reseeding is an even more temporary measure, both because of the massive seed bank, and because any small part of a stem or a root left behind will take root again (Louis-Marie 1944, Thompson et al 1987). Flooding has been shown to substantially shrink a stand of *L. salicaria,* but the degree to which the water levels must be raised (at least 60cm) would constitute a major disturbance to a wetland ecosystem (Louis-Marie 1944, McKeon 1959, Thompson et al 1987). Draining causes a similar disturbance, and is entirely ineffective in any case. Fire can be effective at eliminating a large stand temporarily, but because the growth points on the root crown are 2cm. below the surface, the plants always re-emerge the next season (Louis-Marie 1944, McKeon 1959).

Chemical treatments have not provided a feasible solution for the kinds of tracts which exist in North America. The chemicals currently used in managing Purple Loosestrife are glyphosate (Rodeo), 2,4-D, and triclopyr. While all are somewhat effective at clearing large stands of the weed, they are all non-specific among broadleaf plants and thus potentially damaging to the sensitive habitats in concern, particularly since the treatment will need to be reapplied indefinitely in order to prevent reestablishment (Christy et al 1981, Stamm-Katovich et al 1996, Blossey 1995, Blossey et al1994, Wahlers et al 1998). Mullin (1998) recommends using spot treatments of glyphosate or triclopyr on newly establishing stands of purple loosestrife, to completely eliminate all traces of the plant and prevent colonization altogether. However, even this kind of treatment will need to be continually reapplied if the source of the pioneer propagules is left unchecked.

Biological Control

The failure of conventional methods led researchers to turn to biological control. While biological control can be done without importing exotic agents, such cases usually require a great deal of maintenance, involving mass rearing and periodic concentrated releases. It would also be necessary to find natural enemies in the affected region, and in the case of purple loosestrife there is not much to choose from. Though there have been native North American agents suggested for purple loosestrife—three fungal species (Nyvall 1997) and one aphid (Voegtlin 1995)—none appear to be able to inflict substantial damage, and there have been no published reports on the use of any of these species.

In classical biological control, a natural predator is imported from the native range of the pest species and introduced to a problematic invading species in the hopes of re-establishing an equilibrium in which the two species are maintained at acceptably low levels. When proper screening procedures are used in selecting control agents, the method tends to have a low impact on the ecosystem under treatment (Harris 1988). For a perennial exotic weed of natural habitats which exists in vast tracts, biological control is likely to be both the safest and the most effective management strategy, provided a suitable agent can be found.

The concern with introducing a foreign species is that once released it may feed upon more than its target host, possibly multiplying to large numbers and having widespread unforeseen effects on the ecosystem. However, in a review of the over-300 cases of insects introduced to control weeds, Harris (1988) points out that there has never been a single instance of an agent exterminating a plant, targetted or otherwise. He suggests that concern about the impact on rare plants is unfounded—reasoning that so long as the insect prefers the targetted plant and the targetted plant is more abundant, it will not be advantageous for the insect to seek out the rare plant. In fact it is the common plants and crops which should cause the most concern, since an insect species may be subject to selection for preferential consumption of a non-target host which is more abundant than the target weed. For this reason, Harris (1988) stresses that insects which can complete development on a common desirable plant in the area being treated should not be released, even if the insect shows a marked preference for the host plant.

Approved Biological Control Agents for Purple Loosestrife

After screening procedures for host-specificity, five insects have been authorized for release in the United States and Canada for the purposes of controlling purple loosestrife.

Two of these species attack flowers and seeds: *Nanophyes marmoratus* and *N brevis* (Curculionidae: Coleoptera) (Blossey & Schroeder 1992). Feeding on reproductive parts is not likely to be an efficient means of stressing purple loosestrife, which tends to have a massive and long-lived seed bank wherever it has been present for more than a couple of years (Welling and Becker 1990), and which reproduces primarily vegetatively anyway (Thompson 1987). It has been suggested, however, that these agents might be useful in conjunction with other agents, reducing seed output and adding to the overall stress inflicted on the plant (Blossey & Schroeder 1992). There are no published reports of establishment results for either *Nanophyes* spp. in North America.

Another of the approved species, *Hylobius transversovittattus* (Goeze.) (Curculionidae, Coleoptera) is a root-boring weevil which has shown a high degree of host-specificity (Malecki et al. 1991). It is of particular interest in that it is the only one of the five with the potential to act directly on the persistent and seemingly indestructible rootstocks of purple loosestrife, rather than just on the shoots. There have been some positive results in experiments using *H transversovittatus* in conjunction with competitor plant species (Noetzold et al 1998), but it has not yet been widely released due to difficulties with rearing, establishment, and monitoring.

The two agents most widely released on *L.salicaria* are the leaf-feeders. *Galerucella calmariensis* L. and *G. pusilla* (Duft.) (Chrysomelidae, Coleoptera) (Hight et al 1995). Both of these beetles were able to complete development on only one other plant species: *Lythrum alatum* Pursh. (winged loosestrife). It was judged that *L.alatum* would not be in significant danger because the beetles clearly preferred *L. salicaria*, and while *L. alatum* can be found in small numbers in *L. salicaria* habitats, it is also broadly distributed outside *L. salicaria*'s range. Both species also fed on several other species (mostly Lythraceae sp.) under no-choice conditions, but *Decodon verticillatus* (L)Ell. is the only other species which was fed upon even in the presence of *L. salicaria.* Because *D verticillatus* does not support development and because it is sparsely distributed, it was judged that the danger posed by the encroaching purple loosestrife was greater than that posed by the beetles (Kok et al. 1992, Blossey et al. 1994).

Releases of both *Galerucella* species in North America began in 1992 and both have been widely released in northeastern United States and throughout Canada (Blossey and Schat 1997, Blossey 1995). The most extensive *Galerucella* release program is in Ontario, and the results have been promising: Of over 200 release areas treated since 1992, over 70% have shown successful establishment of reproducing populations by 1996, and of those, 30 % showed "strong" populations (over 10 egg masses/m^2), in which plants are extensively damaged and flowering is visibly suppressed. There are also several sites designated as "hotspots", with beetle egg mass densities of 200/m^2 and a complete suppression of purple loosestrife flowering (Corrigan 1996). Dispersal is minimal, however, so that hundreds of releases have been necessary to spread the agent to all the affected areas. Also, a concern which remains in Ontario is that even in areas where purple loosestrife has been killed off in sizable patches, there is still no significant replacement by other plant species—dead purple loosestrife plants are still replaced by adventitious purple loosestrife shoots throughout the season. The concern is that the dramatic removal of purple loosestrife may leave a void which invites colonization by disturbance-adapted species, which could be purple loosestrife or something else equally undesirable. Theoretically, purple loosestrife should eventually be replaced by more competitive species, but in certain critical areas this may not be soon enough.

Introduction

Biologically Controlling Purple Loosestrife in Quebec

The ability to inflict substantial damage on their target hosts makes *Galerucella* a rare success among insects introduced to control weeds (Harris 1988), and it is by far the most promising method of controlling purple loosestrife currently available. Towards the development of a management strategy for purple loosestrife in Quebec, pilot releases of *Galerucella* were made at four sites along the St Lawrence and Ottawa Rivers, to determine whether or not they could establish in Quebec and, if so, to provide a source population for future releases. Protocols were implemented to monitor future changes in the vegetation composition and in the *Galerucella* population.

To address the problem of slow succession, experiments in Ontario were designed to investigate the effects of seeding with native plant species in an area of heavy *Galerucella* damage, to see whether this combination of treatments would reduce purple loosestrife dominance more effectively than would beetles alone or seeding alone. There are two ways in which seeding may accomplish this result: 1) By increasing the biomass of non-purple loosestrife plants—if the seeds are able to establish, their presence alone is a step towards mitigating the disturbance caused by the invasion of purple loosestrife--restoring the displaced vegetation and impeding a re-invasion by this or any other invasive species; 2) by decreasing the biomass of purple loosestrife. If the planted species are able to compete for resources as well as space, they may provide an additional stress on purple loosestrife, which is susceptible to nutrient limitation (Edwards et al 1995). A lack of nutrients can interfere with a plant's ability to compensate for damage due to herbivory (Steinger and Muller-Shärer 1992), and so there may even be a synergistic effect between competition and herbivory.

The objectives of this study are: 1) to establish populations of *Galerucella* at targetted purple loosestrife stands in Quebec; and 2) to determine whether a combination of seeding treatments and beetle herbivory has a greater effect on purple loosestrife dominance than does beetle herbivory alone.

Methods and Species Used

Quebec Releases

Galerucella: The two species of control agents, *Galerucella pusilla* and *G calmariensis* are almost identical physiologically and ecologically. They overwinter as adults in the soil, emerge in mid to late May, feed on leaves and oviposit throughout June and July. Eggs hatch after about 1 week and larvae also feed on foliage, leaving "windowing" damage which is easily distunguishable from the adult "shothole" damage. Usually there is one generation per year, but dense populations may have two.

Both *Galerucella* species were introduced in Quebec in 1996, 1997 and 1998. All releases were done without cages.

1996: In July 1996, 300 mating pairs of *Galerucella* adults which had been reared in the Biological Control laboratory at Guelph University were released at each of four sites in Quebec: at Lac St François National Wildlife Reserve (45°10'N, 74°22'W), near Nicolet at the National Defense Proof and Experimental Test Establishment (46°10'N, 72°45'W), in Hull on National Capital Commission land near the Champlain bridge (45°26'N, 74°44'W), and at Cap Tourmente National Wildlife Reserve (47°04'N, 70°48'W) (see appendix 3 for site maps). *G. pusilla* was released at the first two sites, and *G calmariensis* at the last two. At each site, all 600 beetles were released in one marked quadrat of $1m^2$. All releases took approximately 48 hours from the laboratory to the field.

1997: Two releases of ~1000 individuals were made at each site (total of 8000 individuals released). The first releases (July 7^{th} and 8^{th})--a mixture of both larvae and adults—were released at the same quadrats marked in 1996, except at Cap Tourmente where the beetles were released at a new quadrat. The second releases, all adults, were done at newly established quadrats in nearby areas of the same sites. All 8000 *Galerucella* were collected from the field in Toronto Ontario. at a site on Dixie road where *Galerucella* have been established since 1993. Beetles were collected by shaking purple loosestrife shoots into breathable nylon mesh bags. They were transported in these bags, provided with fresh purple loosestrife shoots and wet paper towels for moisture. No distinction was made between the two *Galerucella* species.

At **Cap Tourmente**, the first release was approximately 1:1 adults:larvae, and they were released 30 hours after being collected, about 17 of which were spent in a car. The second release was almost 100% adult beetles, made 28 hours after collection.

In **Hull**, the first release was about 3:1 adults to larvae, and the second release was all adults. both releases occurred 5-6 hours after collection

At **Lac St François**, the first release was about 3:1 adults to larvae, and occurred 8-9 hours after collection. The second release was all adults and took 34 hours from the time they were collected.

At **Nicolet** the first release had an adult/larvae ratio of ~1:1, whereas the second was entirely adults. Both releases took about 24 hours.

1998: On July 29-30, 1000-2000 *Galerucella* larvae—again collected from the Dixie road site in Toronto without discriminating between species—were sent via overnight courier and were released at each of three new release areas established at Hull, Lac St François , and Cap Tourmente. In Hull, beetles were released 24 hours after collection; in Lac St François, 29 hours; and at Cap Tourmente it was 48 hours. Larvae were kept cool and moist and were provided with a continuous supply of fresh purple loosestrife shoots.

Vegetation surveillance: In 1996, 1997, and 1998, 5 quadrats of $1m^2$ were randomly selected and surveyed from $400m^2$ around the initial release area at each site. The survey involved counting the number of each species of plant within each quadrat, identifying the species, and weighing one representative specimen of every plant species present so that all the counts of plant numbers could be converted to estimates of biomass/m^2 . In the case of purple loosestrife, 10 specimens were randomly collected and the average mass was taken. From these data could be estimated the average mass/m^2 and the percent composition of the vegetation community at each site in each year. No control areas were established because of the difficulty of finding areas which were comparable and yet not within the dispersal range of the release areas—particularly in the anticipation of future wide-scale releases, in which case monitoring and keeping such areas

Galerucella-free would become difficult and counterproductive. Although unable to definitively establish a cause, this monitoring protocol will detect whether purple loosestrife dominance is increasing or decreasing progressively over the years, and also any changes in the diversity and biomass of other species.

Measurements and Statistical Analysis: Beetle densities were estimated the year following a release, in early June, once adults had emerged and begun oviposition. Numbers of adult beetles found in one minute of visual searching were recorded for each marked quadrat and averaged for the number of adults per m^{2}.

T-tests were used to detect changes in purple loosestrife biomass, non-purple loosestrife biomass, and the ratio of the two, between the years at each site. In 1998 the five quadrats selected were permanently marked at 3 of the release areas (Hull, Lac St François, and Cap Tourmente—a total of 15 permanently marked quadrats) so that a paired t-test can be used in future to detect changes over years at each site.

Ontario Beetle and Seeding Experiment

The experiment was intended to test the combined effect of plant competition (seeding with other plant species) and herbivory (by *Galerucella*) on the dominance of purple loosestrife in established stands.

The experimental design required 4 treatments (seeds and beetles, beetles alone, seeds alone, and no treatment), each with 5 replicates. The experimental unit was a $1m^2$ quadrat in a stand of purple loosestrife.

In 1997 10 quadrats of $1m^2$ were selected and marked at stands of purple loosestrife at the Royal Botanical Gardens in Burlington, and in the East Don Parklands in Toronto (for a total of 20 quadrats). The vegetation in each of these quadrats was surveyed following the same procedure as in Quebec (see above). The site in Burlington has had *Galerucella* established since 1994, and so these quadrats were used for the *beetles* and *beetles and seeds* treatments. Suitable control areas could not be found in the same area in Burlington, since the population growth and dispersal of beetles has been so successful that it was impossible to find an area nearby which was not either already infected or likely to become infected in the near future. The quadrats in Toronto were therefore used for the *seeds* and the *control* treatments.

In the spring of 1998, seeds of 12 competitor plants which had been collected, stored, and refridgerated at the RBG were mixed into 10 containers, each with the same composition of seeds of each species, along with 2 cups of peat soil (see appendix 1 for list of species and quantities). This mixture was spread on the soil surface in five randomly selected Toronto quadrats on May 7th, and in five of the Burlington quadrats on June 12th and June 26th. The delay in seeding the Burlington plots was due to unusually high flooding in early spring. The vegetation on all 20 plots was then surveyed (as in 1997) on August 15th-16th.

Measurements and Statistical Anaylsis: Changes in Purple Loosestrife density (both numbers of shoots and biomass), changes in the biomass of all other plants, and changes in the percent composition for each treatment were detected using paired t-tests. A one-way paired ANOVA was also performed on each of these measures to test for an interaction between the beetle and seeding treatments, and to test the effect of the treatments by comparing with the control. Results of these ANOVAs should be interpreted with caution, however, since the treatments were carried out at two different sites and were seeded at different times, and so the assumption of random assignment to treatment groups was violated.

Results

Quebec Releases

Galerucella : In the spring of 1997 no evidence of survivors from the 1996 *Galerucella* releases were found at any of the four release areas. At sites with open water within 200m, the water's edge was also checked for signs of *Galerucella* presence, as they are known sometimes to migrate to water.

In the spring of **1998** *Galerucella* adults were found to have successfully overwintered at both sites in Hull, and at one of the two sites at both Cap Tourmente and Lac St Francois. No signs of *Galerucella* presence were found at Nicolet. The highest densities of beetles were found in Hull (50 observed/min/m^2.), followed by Cap Tourmente (7/min/m^2) and Lac St François (6/min/m^2).

Vegetation: Vegetation changes from 1997 to 1998 showed no clear trend across sites (Table 1 and Figures 1, 2 and 3 summarize these results, and Appendix 2 gives a list of plant species found at each site).

At **Lac St François** The ratio of purple loosestrife to other plants decreased significantly ($p=.041$, data log transformed) due to a decrease in purple loosestrife ($p=.011$, data log-transformed), while the biomasss of other plants (combined) did not change significantly.

At **Cap Tourmente**, the biomass of purple loosestrife decreased but not significantly, and the biomass of other plants increased but not significantly, so that the change in their ratio was almost significant ($p=.064$).

In **Hull** there were significant increases in the biomass of both purple loosestrife ($p=.013$) and all other plants ($p=.019$, data log-transformed), so that the proportions did not change significantly. In Hull there was also a significant increase in the number of purple loosestrife flowering spikes per square metre ($p=.001$).

At **Nicolet**, no vegetation survey was done in 1998, as no beetles had been established.

TABLE 1 Summary of Quebec Releases of *Galerucella* on Purple Loosestrife

	Beetle density (#observed/ min)	**PL #shoots				PL biomass (g/m2)				PL %of biomass				non-PL biomass (g/m2)				#species		#PL flowers			
	1998	97	98	Δ	t/p*	97	98	Δ	t/p*	97	98	Δ	t/p*	97	98	Δ	t/p*	97	98	97	98	Δ	t/p*
Lac St Francois	6	38	42.2	4.2	Insig.	**593**	**186**	**-407**	**t=3.11, p=.01**	**73**	**50**	**-23**	**t=2.18, p=.04**	201	192	-9	Insig.	19	20	27	29	2	Insig.
Hull	50	47	51.6	4.6	Insig.	**335**	**705**	**371**	**t=3.16, p=.01**	85	84	-1	Insig.	**44**	**130**	**86**	**t=-2.53, p=.032**	3	6	**17**	**77**	**60**	**t=4.8, p=.002**
Cap Tourmente	7	13	15.6	3	Insig.	83	54	-29	t=1.5, p=.09	41	28	-13	t=1.7, p=.064	115	198	83	Insig.	12	20	15	21	6	Insig.

*t- and p-values (for 2-tailed t-tests) are given where results are significant or almost significant (ie where.p<.1) Results are given in boldface where significant (where p<.05)
Where variances were not equal between years, t-tests did not assume equal variances
** PL signifies purple loosestrife throughout the table

Fig. 1 Change in Purple Loosestrife Biomass after one year of Herbivory--Quebec

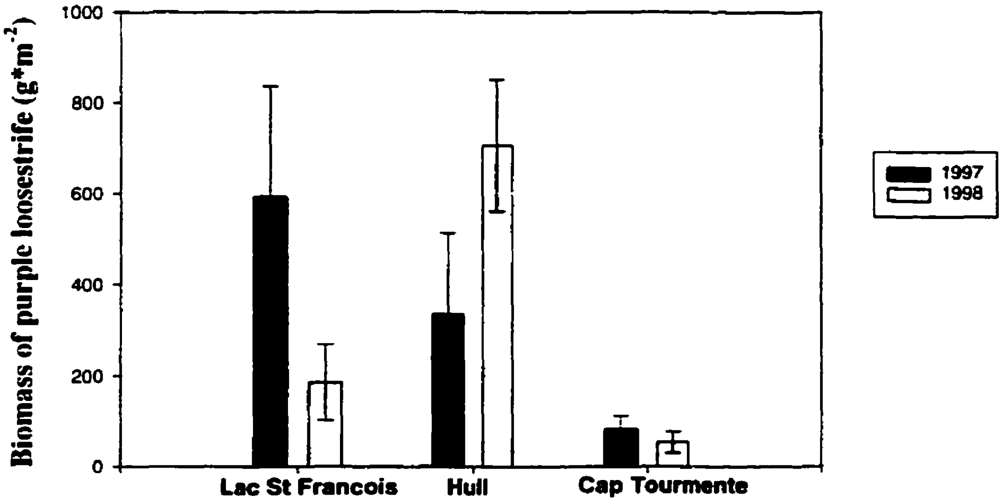


Fig. 2 Change in the Biomass of Non-Purple Loosestrife Plants after one year of Herbivory--Quebec

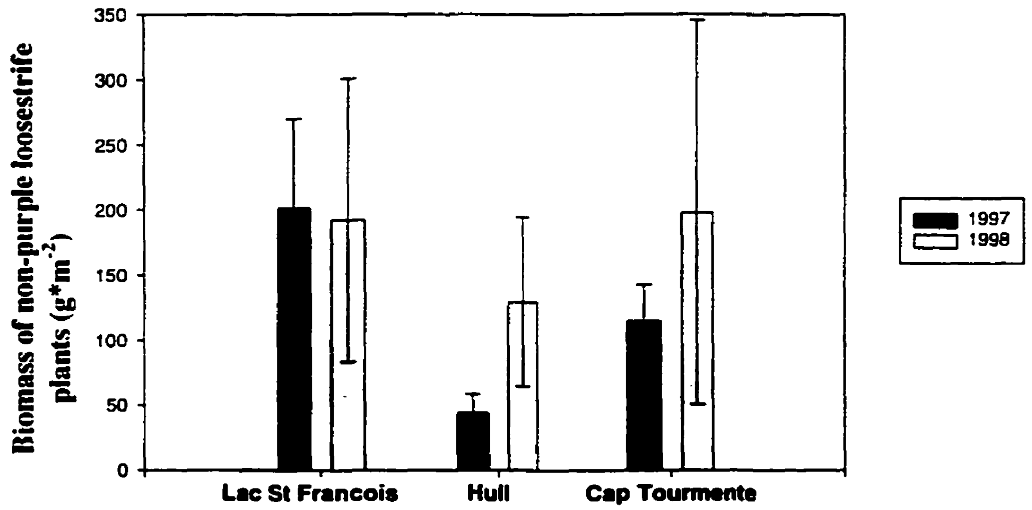
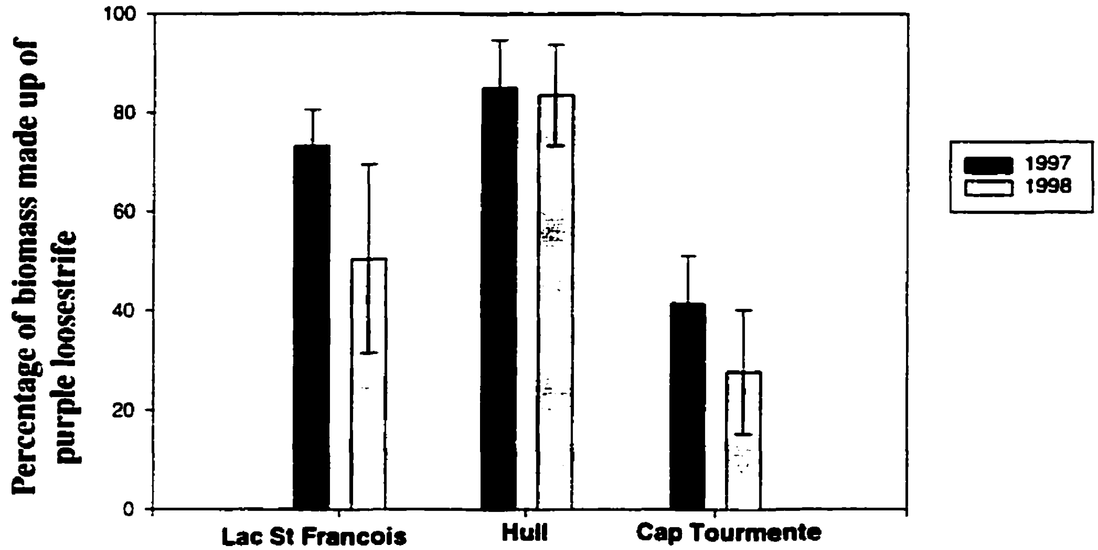


Fig. 3 Change in Dominance of Purple Loosestrife after one year of Herbivory--Quebec



Ontario Experiment

Results of the Ontario experiment are summarized in table 2 and figures 4, 5 and 6. The beetles-and-seeds treatment is the only one which showed a significant decrease in the purple loosestrife proportion of plant biomass (p=.015, data were transformed using an inverse sine function), due both to an insignificant decrease in purple loosestrife biomass, and to an increase in the biomass of all other plants combined, which was significant (p=.043) using the Wilcoxan signed-rank test for non-normal distributions. Plots with beetles alone showed a significant decrease in the biomass of Purple loosestrife (p=.01, data log transformed), and an insignificant increase in the biomass of other plants. Plots with only seeds and plots with no treatment both showed significant increases in the biomass of purple loosestrife (p=.006 and p=.01, respectively) and insignificant decreases in the biomass of other plants.

The one-way ANOVA contrasts showed a significant interaction effect between the seeding and beetle treatments on the number of purple loosestrife shoots (p=.010), but not for any of the other measures tested. When compared with the control, plots with beetles and seeds and plots with just beetles showed a significant effect in reducing purple loosestrife biomass when compared with the control (p=.000 and p=.001 respectively), and seeds alone showed no significant effect on any measure tested. Again, these ANOVA's are comparing areas which differ in more that just the treatments applied, and must be interpreted with caution.

Of the 11 competitor species planted, 2 were present when plots were surveyed in August: *Asclepias incarnata* (swamp milkweed), and *Eupatorium maculata* (joe pye-weed). *Convolvulus arvensis* (field bindweed) was also present in significant quantities in 1998 but not in 1997, although it was not one of the species planted.

TREATMENT	PURPLE LOOSESTRIFE BIOMASS g/m^2			ALL OTHER PLANTS—BIOMASS g/m^2			PERCENT PURPLE LOOSESTRIFE BY BIOMASS		
	97	98	t①/p	97	98	z②/p	97	98	t/①p
Beetles and Seeds	64	54.8	t=.402 p=.350	**0.8**	**377.6**	**z=-.2023 p=.043**	**98.3**	**47.3**	**t=3.27 p=.001**
Beetles	**161**	**119**	**t=3.83 p=.010**	36	241.4	z=-.0483 p=.138	81.1	62.5	t=-1.22 p=.088
Seeds	**418**	**1718**	**t=-4.24 p=.006**	47	18.1	z=-.730 p=.465	**88.5**	**98.5**	**t=1.42 p=.006**
Control (no treatment)	**294**	**1167**	**t=2.132 p=.097**	37	27.1	z=-.405 p=.686	**89**	**97.3**	**t=-1.31 p=.013**

① t-values are for two-tailed paired t-tests assuming unequal variances. Percentage-data were transformed with inverse sine function.

② z-values are for wilcoxon signed-rank non-parametric test, used where distributions were not normal.

Fig. 4 Change in biomass of purple loosestrife under different conditions-- Ontario

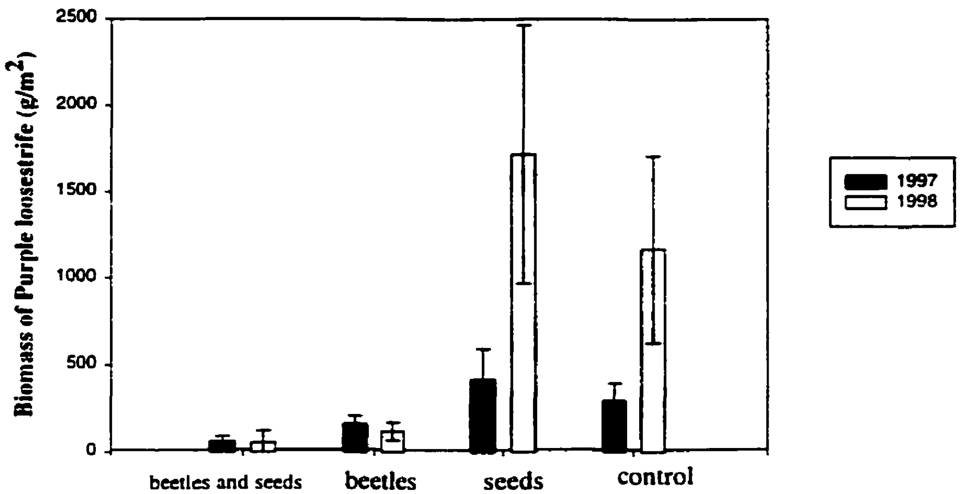


Fig. 5 Change in the dominance of purple loosestrife under different conditions-- Ontario

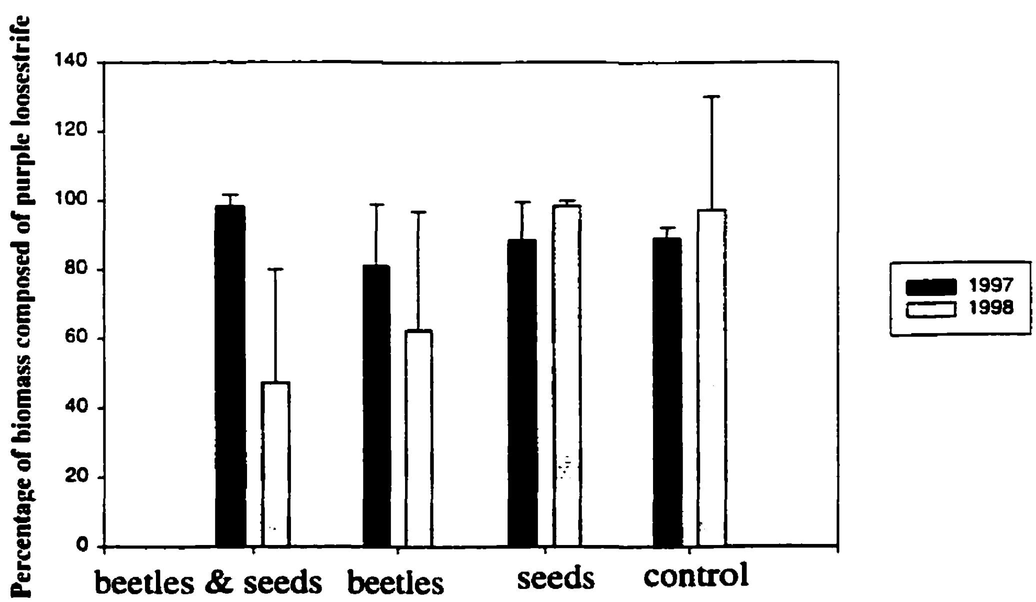
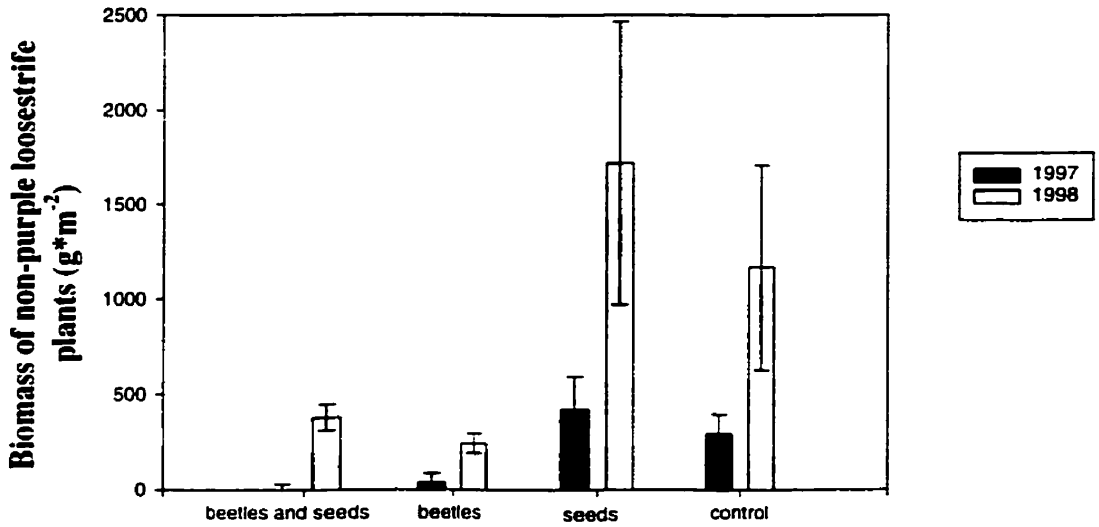


Fig. 6 Change in the Biomass of Non-Purple Loosestrife Plants under different treatments--Ontario



Discussion

Quebec Releases

Galerucella: In the Ontario program the success rate for uncaged *Galerucella* releases is 80% (Corrigan 1996). The failure of *Galerucella* to establish in Quebec sites in 1996 could have been due to environmental conditions, release protocol, or some combination of the two. Because *Galerucella* has been successfully established in Manitoba, Ontario, and Prince Edward Island, we know that they are capable of surviving climatic extremes similar to those experienced in Quebec. It is unlikely, therefore, that the harsh winter of 1996/97 would alone be a strong enough factor to preclude establishment, but it may have been one of many factors weakening the population. There were numerous changes made to the release protocol which may have contributed to the greater success rate in 1997 than in 1996: the time the beetles spent in transit was greatly reduced, the beetles were collected from the field instead of being laboratory-reared, and instead of releasing only adults, a certain proportion of the individuals released were larvae. Unquantified observations from the Ontario program suggest that larvae may establish more successfully than adults (Corrigan 1996), possibly because adults are capable of dispersing upon release, scattering themselves around before overwintering and making next season's mating a remote prospect. Adults which have pupated in the release area, on the other hand, may be more likely to stay put and remain close to their conspecifics.

The releases in 1997 showed a 75% success rate for sites, with two release areas per site. *G pusilla* and *G calmariensis* like water, and relative availability of water may account for differences between sites: Hull was the wettest site, being on the river and partially inundated, and showed the highest survival rate; whereas Nicolet was the driest site, and failed to recover beetles in both years.

While permanent establishment cannot be certain after only one year, a survey of intentional releases of exotic insects found that survival through one generation indicated an 80% chance of long-term establishment (Crawley 1989).

Vegetation: At Lac St François and Cap Tourmente the purple loosestrife was less dominant in 1998, after one year of beetle presence, than in 1997. Without control areas, it is impossible to determine the cause of these changes, but if such declines continue in the future under fluctuating environmental conditions, it will be reasonable to assume that *Galerucella* herbivory is the cause.

In Hull, despite a much higher beetle density, the dominance of purple loosestrife remained unchanged. In fact the biomass of both purple loosestrife and of other plants combined more than doubled, and the number of flowering spikes of purple loosestrife more than tripled. It seems likely that there was some other factor limiting or inhibiting production in all plants in the 1997 season, which did not apply in 1998. It is also possible that *Galerucella* herbivory stimulated compensatory growth in purple loosestrife in the 1998 season. This site had larger, denser infestations of purple loosetrife than did the other sites, and during the first year of herbivory rootstocks were likely strong enough to provide the biomass for new growth aboveground, possibly even over-compensating for the damage done (Blossey and Schat 1997, McAvoy et al 1997). In this case, the impact will become visible in the upcoming years, as the next season's growth must begin with depleted rootstocks (Schat and Blossey 1996) as well as the pressure of continued, probably even heavier, *Galerucella* herbivory.

Ontario Experiment

The only treatment which showed a significant decline in purple loosestrife dominance was seeding and beetle herbivory together. This significant change in the proportions of the plant composition was due to the combined effect of an insignificant decline in purple loosestrife biomass and a significant increase in the biomass of other plants.

Because the beetles and seeds treatment showed a significant increase in the biomass of other plants and the beetles alone did not, seeding appears to have augmented the effect, if any, of the beetles on the presence of other plants. Although the seeds-alone treatment is not strictly comparable with the treatments involving beetles—having taken place at different sites—the fact that seeded plots actually showed an insignificant *decline* in other-plant biomass, greater than that shown by the control, indicates that there was likely an interaction between the beetles and the seeds. That is, the seed treatment alone did not have any effect on the presence of other plants without the beetle activity to weaken the purple loosestrife and allow them to compete. Similarly, the beetles are able to weaken the purple loosestrife enough so that other plants can compete, but where the other plants are not opportunistic enough, seeding treatments can encourage their establishment. The result is promising both in that it implies that the replacement of *Galerucella*-treated purple loosestrife by other plant species is just a matter of time, and also in that it demonstrates a possible means of accelerating that process where *Galerucella* beetles have been established.

The beetles and seeds treatment did not show a significant change in the biomass of purple loosestrife plants, however, indicating that the increased presence of other plants did not deprive the purple loosestrife of resources to any measurable degree in the first season. It is possible that purple loosestrife, which is known to sequester large amounts of nutrients (Templer et al 1998), may have been able to rely on its stores, and that the effects would take longer than one season to become evident.

Interestingly, though there is no measurable interaction effect between beetles and seeds on the biomass of purple loosestrife in this season, the ANOVA suggests an interaction effect on the number of purple loosestrife shoots. Again, this result cannot be conclusively attributed to the interaction, since the beetle and seeding treatments took place in different purple loosestrife stands. However, if the two stands were in fact comparable in their responses to treatments, this interaction effect might indicate that the other plants were interfering with the growth of new purple loosestrife shoots by competing for available space. The lack of any effect on purple loosestrife *biomass* indicates that it was not a competition for resources which reduced the number of shoots--rather, the lack of space may have forced the purple loosestrife to channel its resources into fewer, larger shoots.

The effect of seeding in conjunction with beetle herbivory was thus to increase the presence of other plants, and perhaps to reallocate purple loosestrife resources to growing fewer, larger shoots, but not to decrease the aboveground biomass of purple loosestrife more than did beetles alone.

Beetle herbivory alone decreased purple loosestrife aboveground biomass significantly (and this decline continues after 4 years of heavy infestation and damage), but though the plants were visibly decimated, they still made up between 90 and 100% of the plant biomass. In Toronto plots, in the absence of *Galerucella*, purple loosestrife biomass increased significantly whether seeding treatments were applied or not, indicating that this purple loosestrife stand is continuing its growth. An ANOVA which contrasted the seeding treatment and the control suggested that the seeding alone had no significant effect on this growth. The biomass of other plants decreased insignificantly with seeds or without, and although the decrease was smaller in seeded plots, the effect was not found to be significant. These findings are not surprising since previous studies have not found any other species which are able to compete with even newly planted purple loosestrife seedlings, let alone with established stands (Rawinski 1982, Noezthold et al 1998).

Conclusions

While the most efficient control would in principle be achieved by inflicting a variety of additive stresses (Müller-Schärer and Frantzen 1996, Steinger and Müller-Schärer 1992), the context of a sensitive wetland habitat precludes the use of most non-specific management techniques which can be used to control weeds in agriculture, such as water and nutrient manipulations or chemical treatments. It would however be possible to incorporate a combination of biological agents which occupy different niches on the target weed. While *Galerucella* alone is often able to inflict devastating damage on purple loosestrife, there are sites in Ontario where results have been less dramatic (Dech and Nosko 1997), possibly because they are too dry, or due to other unknown variables. Other species may be useful in compensating for *Galerucella*'s inconsistency under different conditions, and for its poor dispersal.

The root borer *Hylobius tranversovittatus*, for example, does not live in even temporarily inundated stands, but may be effective in areas such as Nicolet, where *Galerucella* may have failed to establish because it was too dry. Species which are good dispersers, such as *Nanophyes marmoratus* and *N brevis*, may be useful in getting to the many smaller, lower priority areas where purple loosestrife has a scattered distribution. *Nanophyes* could probably not co-exist with *Galerucella* species in the same stands--since they feed on flowers and seeds, which are largely absent where there is a strong *Galerucella* population--but if the *Nanophyes* species can reach these smaller stands they may be able to contain the spread and to prevent further dispersal of seeds. They may also be useful in areas which are too wet even for *Galerucella*.

Research could also be done on the possibility of encouraging potential agents which are native to North America, such as the aphid *Myzus lythri*, which migrates from its primary host *Prunus* spp. to purple loosestrife stands in late spring. These aphids are able to do substantial damage to purple loosestrife when they arrive early enough in the season and in sufficient numbers, but may be generally limited by the availability of its primary host *Prunus* spp.(Voegtlin 1995). The presence and abundance of *M lythri* may be maximized by planting these primary host species close enough to target purple loosestrife stands such that both are within the aphid's migratory range. Similarly, conditions which would encourage the infection of purple loosestrife by North American fungus species might be further investigated (Nyvall 1997).

The use of multiple agents with a range of distributions, habitat preferences, and niches, could thus deprive purple loosestrife of what would otherwise be complete refuges from control efforts (Malecki et al 1993).

The use of competitor plant species, although they did not measurably affect purple loosestrife aboveground biomass in one season, may also be a low-impact stress in the long term, while at the same time hastening the succession of other plants and reducing the probability of invasion by another aggressive species. Of the 11 species whose seeds were spread, only two emerged and persisted until the end of the season. Some managers might be interested in identifying one or a few good waterfowl forage plants which can germinate and compete reliably, so that succession can be fast, predictable, and useful—eg. one could use Japanese Millet, which has demonstrated some ability to compete with purple loosestrife (Rawinski 1982), ***Juncus effusus*, *Epilobium ciliatum*, *E hirsutum*, *E roseum***, and/or *Calamagrostis canadensis*, which are all competitors of purple loosestrife in Europe (Edwards et al 1995). The problem with this approach is that it focuses on the needs of only one or a few elements of the ecosystem. Even selecting species from the species of the targeted stand which have demonstrated themselves better early successional competitors may be counter-productive, depending on the goals being sought. While it may be a more efficient way of restoring non-purple loosestrife ground cover, it also ignores a whole variety of plant species which may be ecologically important, and which may ironically be those in greatest need of intervention. Moreover, it is probable that many of the species which failed to establish in this experiment were limited by sub-optimal seed storage and treatment, and research investigating optimal germination conditions and treatment techniques for the seeds used might improve the success of this method considerably (Soh et al 1996, Leck 1996).

Summary

Results from this study suggest that *Galerucella pusilla* and *Galerucella calmariensis* are able to establish in Quebec, and results from previous releases in Ontario suggest that *Galerucella* ought to be a principle component in Quebec's purple loosestrife management strategy. This strategy could also involve seeding with other plant species, for more concentrated restoration efforts in areas designated more ecologically critical and/or threatened. Such efforts would hasten the succession of other plants and hopefully moderate the disturbance caused both by the invasion of purple loosestrife, and by its relatively sudden removal. It may also contribute to the weakening of the purple loosestrife. Research on germination and storage requirements would improve the efficacy of such restorative plantings--particularly for those species which are found to have poor germination. Research on the integration of other biological control agents with *Galerucella* and on their ability to establish/disperse under different conditions in Quebec would also contribute to the development of a more comprehensive management plan.

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Appendix 1

APPENDIX 1 COMPETITOR PLANT SPECIES USED IN ONTARIO EXPERIMENT

Species	***amount of seed/m²***
Scirpus atrivirens	*2tbs (wet)*
Verbena hastata	*1tsp (dry)*
Scirpus validus	*4tbs (wet)*
Typha latifolia	*4tbs (dry)*
Asclepias incarnata	*4tbs (dry)*
Eupatorium maculata	*4tbs (dry)*
Carex stipata	*4tbs (wet)*
Carex bebbii	*4tbs (wet)*
Rumex orbiculatus	*2tbs (wet)*
Juncus nodosus	*4tbs (wet)*
Carex vulpenoidea	*4tbs (dry)*

Appendix 2 Plant species found at Quebec sites

Lac St Francois

Amphicarpa bracteata (L) Fernald— hog peanut (Leguminosae)
Asclepias incarnata L.— swamp milkweed (Asclepiadaceae)
Aster lanceolatus (old name "simplex")—lanceolate aster (Compositae)
Carex Bebbii Olney.—Bebb's sedge (Cyperaceae)
Carex Muhlenbergii Schk.–Muhlenberg's sedge (Cyperaceae)
Carex scoparia Schk.–broom sedge (Cyperaceae)
Equisetum arvense L.—horsetail (Equisetaceae)
Eupatorium maculatum L.— joe pye weed (Compositae)
Eupatorium perfoliatum L—boneset (Compositae)
Galium palustre L— marsh bedstraw (Rubiaceae)
Iris versicolor L. – blue-flag (Iridaceae)
Juncus dudleyii Weigand– Dudley's rush (Juncaceae)
Lycopus uniflorus Michx.— northern bugleweed (Labiatae)
Lysmachia terrestris L.BSP.— terrestrial loosestrife (Primulaceae)
Mentha canadensis L– American mint (Labiatae)
Mimulus ringens L— monkeyflower (Scrofularaceae)
Oenothera sp. (Onagraceae)
Poa sp. (Graminae)
Scirpus atrovirens Willd.– blackish bulrush (Cyperaceae)
Solidago canadensis L. or *gigantea* Ait. — canadian goldenrod (Compositae)
Vicia cracca L.— cow vetch (Leguminoseae)

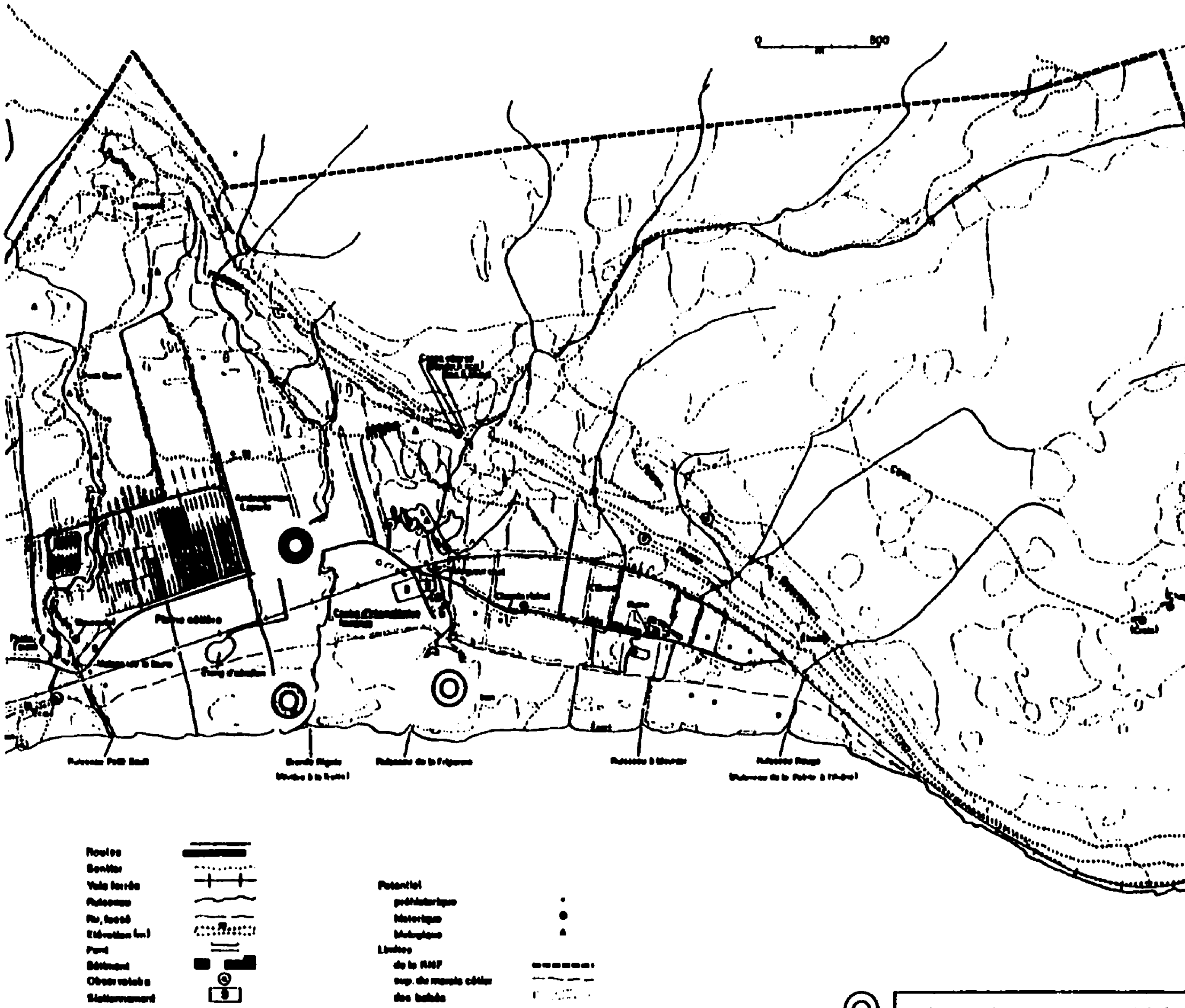
Hull

Acer saccharum Marsh. – sugar maple (Aceraceae)
Calamagrostis canadensis Michx. Beauv.– Canada reed-grass (Graminae)
Carex sp.(Cyperaceae)
Cornus stolonifera Michx.— red osier dogwood (Cornaceae)
Equisetum arvense L.— field horsetail (Equisetaceae)
Galium sp.(Rubiaceae)
Graminae (unidentified)
Hypericum mutilum L.–(Hyperaceae)
Lathyrus palustris L.— marsh wild pea (Leguminosae)
Leersia oryzoides— rice cut-grass (Graminae)
Mimulus ringens L—monkeyflower (Scrofularaceae)
Onoclea sensibilis L.–sensitive fern (Polypodaceae)
Phalaris arundinacea L– canary reed-grass (Graminae)
Polygonum persicaria L.–lady's thumb (Polygonaceae)
Polygonum sp.(Polygonaceae)
Scirpus caespitosus L.--(Cyperaceae)
Scirpus smithii L. (Cyperaceae)
Sium suave Walt.— water parsnip (Umbelliferae)
Asclepias incarnata L.—swamp milkweed (Asclepiadaceae)

Cap Tourmente

Agrostis sp. (Graminae)
Angelica atropururea L.–(Umbelliferae)
Bromus inermis Leyss.– awnless brome-grass (Graminae)
Cirsium arvenseL. Scop.— Canada thistle (Compositae)
Echinocystis lobata—wild cucumber
Eleocharis obtusa (Willd) Schultes.—blunt spike-rush (Cyperaceae)
Eupatorium maculatum L.— joe pye weed (Compositae)
Graminae (unidentified)
Impatiens capensis L.—jewelweed (Balsaminaceae)
Lathyrus palustris L— march wild pea (Leguminoseae)
Leersia oryzoides L.Sw.– rice cut-grass (Graminae)
Lolium perenne L.– ray grass (Graminae)
Lycopus americanus Muhl.– American bugleweed (Labiatae)
Lysmachia terrestris L. BSP.— terrestrial loosestrife (Primulaceae)
Myostis laxa Lehm.– small forget-me-not (Boraginaceae)
Onoclea sensibilis L.— sensitive fern (Polypodiaceae)
Phalaris arundinacea L– canary reed-grass (Graminae)
Poa palustris L– swamp meadow-grass (Graminae)
Polygonum aviculaire L.– knot grass (Polygonaceae)
Polygonum sagittatum— arrow leaved tearthumb (Polygonaceae)
Polygonum sp (Polygonaceae)
Potentilla norvegica L.—rough cinquefoil (Rosaceae)
Scirpus atrocinctus Fern.—black girded woolgrass (Cyperaceae)
Sium suave Walt.– water parsnip (Umbelliferae)
Vicia cracca— cow vetch (Leguminoseae)

Cap Tourmente National Wildlife Reserve 47°04'N, 70°48'W

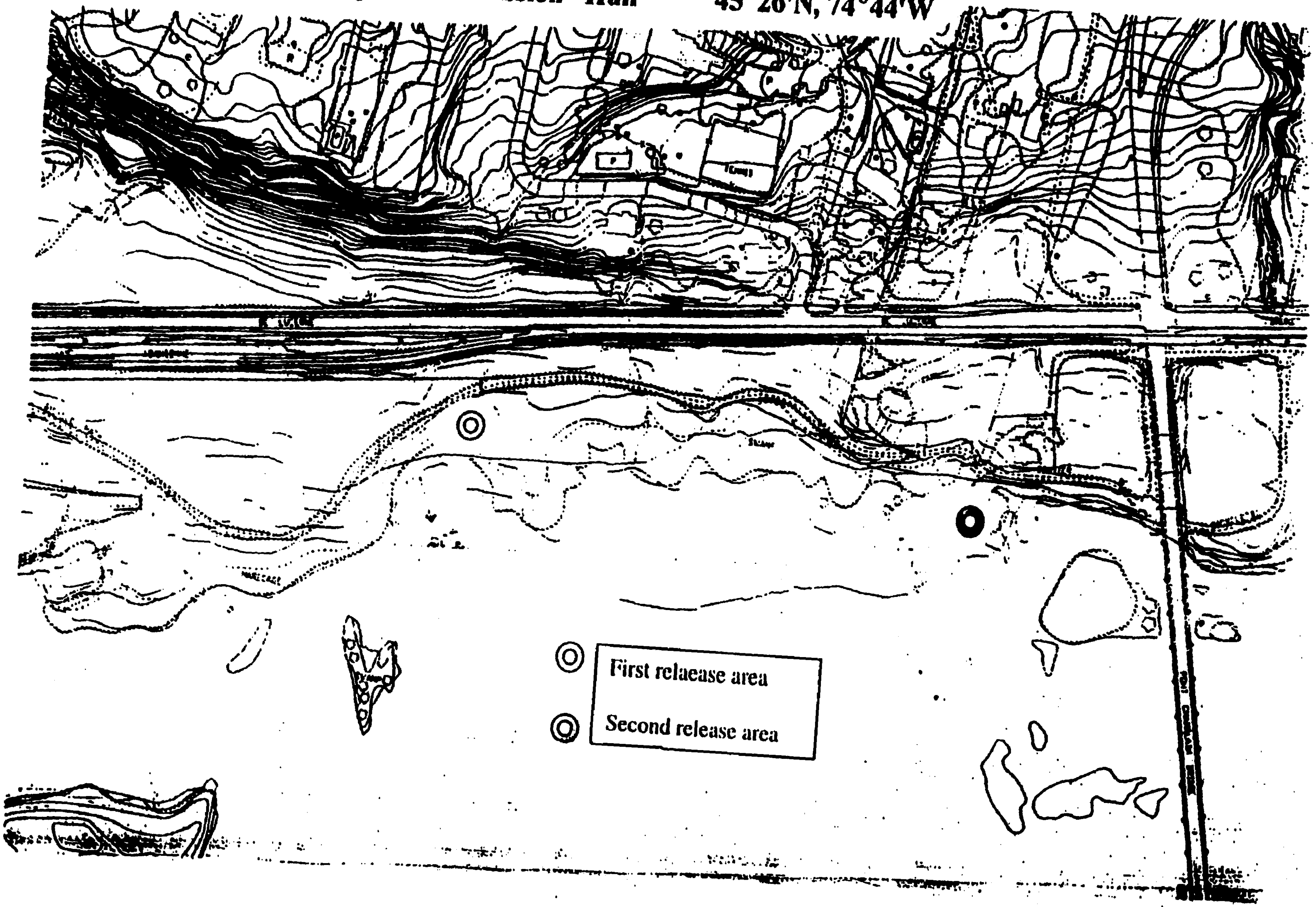


◎ First release area (1996 only)

◎ Second release area

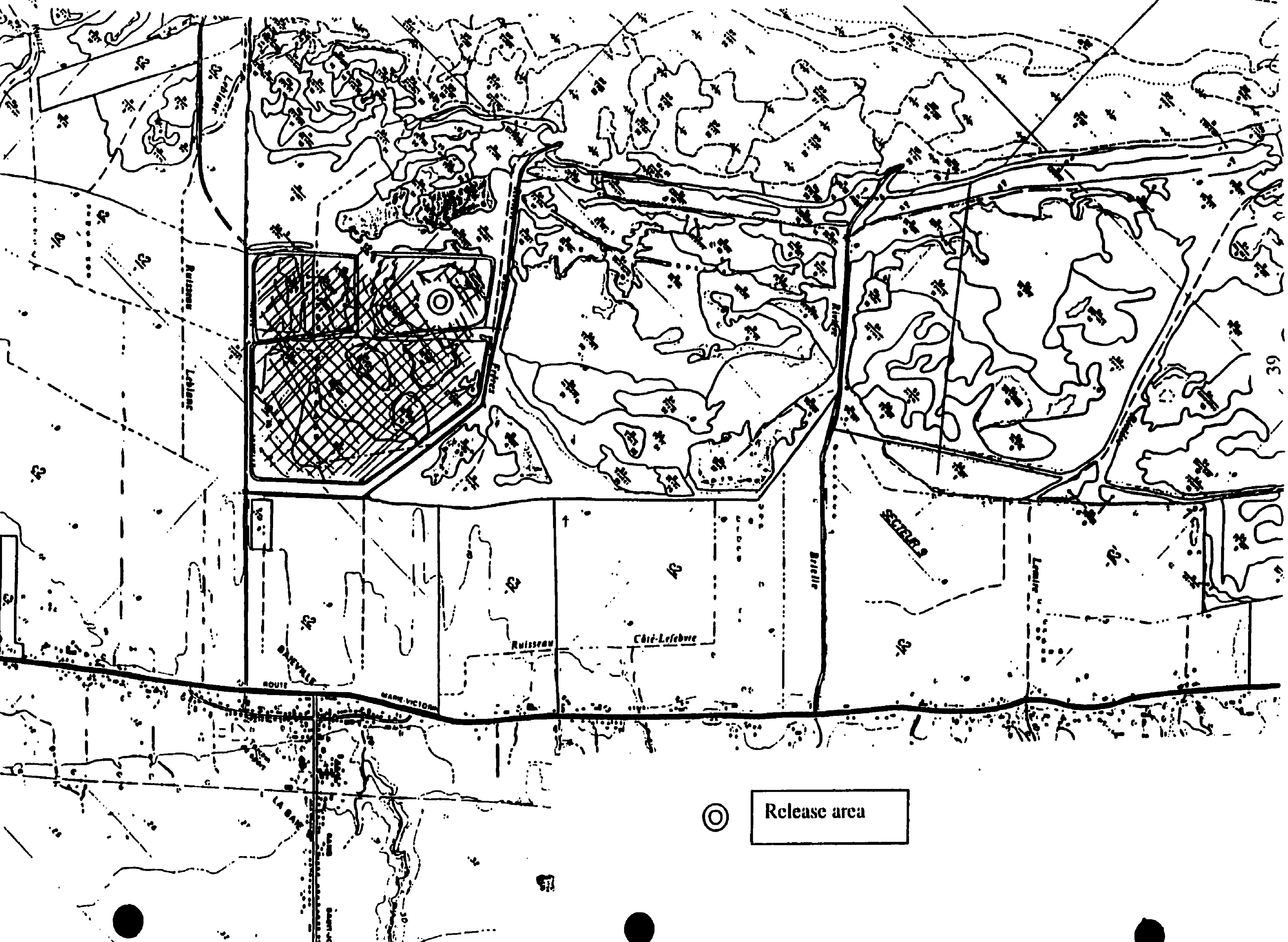
● Third release area

National Capital Commission– Hull 45°26'N, 74°44'W

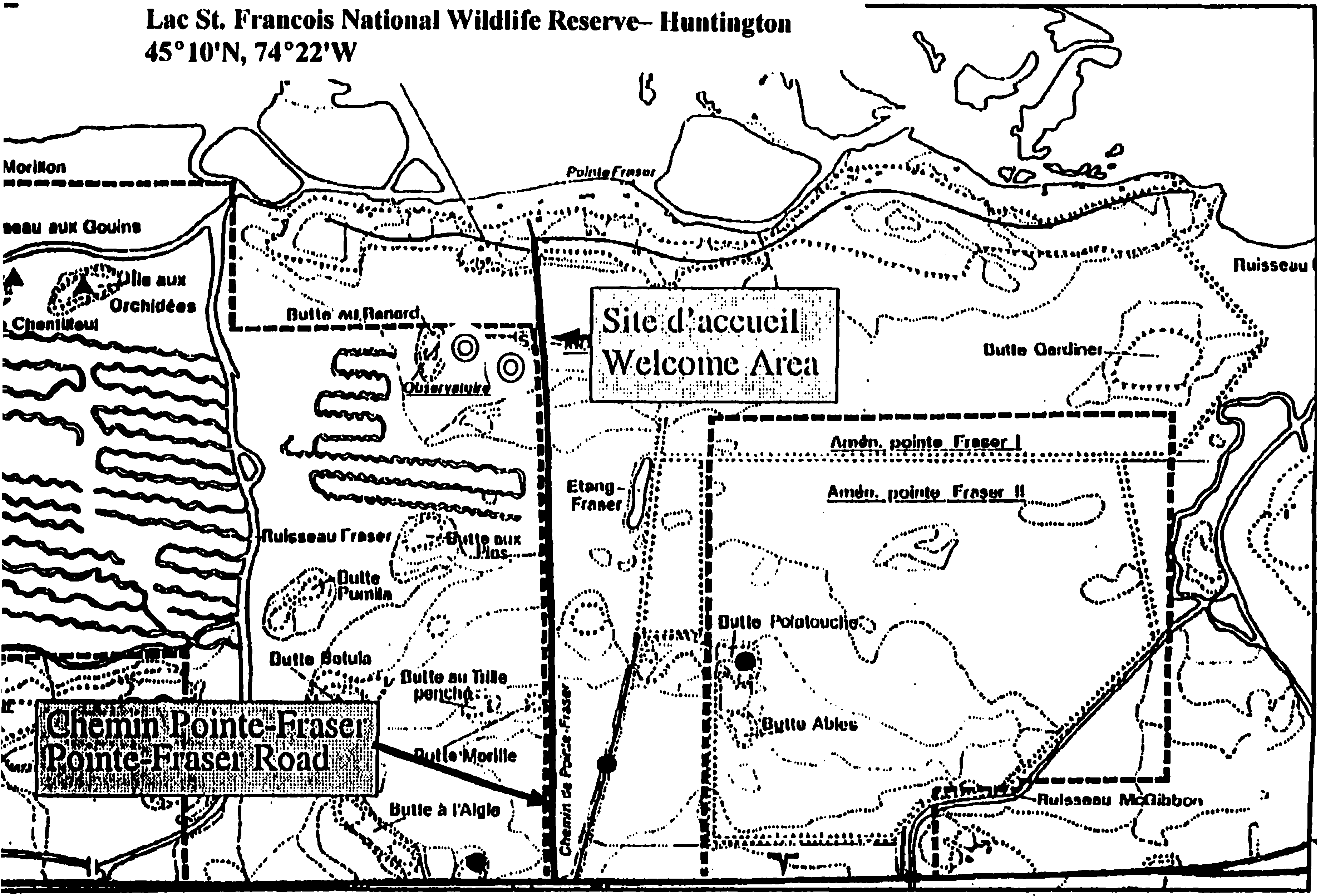


National Defense Proof and Experimental Test Establishment– Nicolet

46° 10'N, 72°45'W



Lac St. Francois National Wildlife Reserve– Huntington
45°10'N, 74°22'W



◎	First release area
◎	Second release area