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Impact and management of purple loosestrife (*Lythrum salicaria*) in North America

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Abstract. The invasion of non-indigenous plants is considered a primary threat to integrity and function of ecosystems. However, there is little quantitative or experimental evidence for ecosystem impacts of invasive species. Justifications for control are often based on potential, but not presently realized, recognized or quantified, negative impacts. Should lack of scientific certainty about impacts of non-indigenous species result in postponing measures to prevent degradation? Recently, management of purple loosestrife (*Lythrum salicaria*), has been criticized for (1) lack of evidence demonstrating negative impacts of *L. salicaria*, and (2) management using biocontrol for lack of evidence documenting the failure of conventional control methods. Although little quantitative evidence on negative impacts on native wetland biota and wetland function was available at the onset of the control program in 1985, recent work has demonstrated that the invasion of purple loosestrife into North American freshwater wetlands alters decomposition rates and nutrient cycling, leads to reductions in wetland plant diversity, reduces pollination and seed output of the native *Lythrum alatum*, and reduces habitat suitability for specialized wetland bird species such as black terns, least bitterns, pied-billed grebes, and marsh wrens. Conventional methods (physical, mechanical or chemical), have continuously failed to curb the spread of purple loosestrife or to provide satisfactory control. Although a number of generalist insect and bird species utilize purple loosestrife, wetland habitat specialists are excluded by encroachment of *L. salicaria*. We conclude that (1) negative ecosystem impacts of purple loosestrife in North America justify control of the species and that (2) detrimental effects of purple loosestrife on wetland systems and biota and the potential benefits of control outweigh potential risks associated with the introduction of biocontrol agents. Long-term experiments and monitoring programs that are in place will evaluate the impact of these insects on purple loosestrife, on wetland plant succession and other wetland biota.

Key words: biological control, invasions, invasive plant management, *Lythrum salicaria*, purple loosestrife

Introduction

The invasion of non-indigenous plants is considered one of the primary threats to rare and endangered species (Usher 1988; Macdonald 1989; Wilcove et al. 1998) and to the integrity and function of ecosystems (Drake et al. 1989; Randall 1996; Williamson 1996). National parks, nature preserves and other protected areas are managed for the preservation of their native fauna and flora and natural processes (Usher 1988;

Randall 1996). Management practices should favor the long-term sustainability and health of these areas which may be dramatically altered by the invasion of non-indigenous species. In fact, invasive species were identified as a threat for almost 50% of 1880 species listed as imperiled under the Endangered Species Act by the US Fish and Wildlife Service (Wilcove et al. 1998). While we have accumulating evidence for negative impacts of non-indigenous species as a group (US Congress 1993; Randall 1996), the full extent of changes in ecosystem processes and floral and faunal composition as a result of the increased abundance of a single non-indigenous species is often anecdotal. Considering the worldwide increasing number of invasive species, the limited availability of quantitative data regarding their ecosystem impacts is not surprising. In the absence of quantitative evidence the important question for natural resource managers is how much evidence for negative impacts is sufficient or necessary before beginning control programs and whether preventive management, including eradication of newly arrived species and of small populations, can be justified.

Common sense, experience, and theory predict that control of invasive species is most economical and successful when these species occur in small populations (Moody and Mack 1988; Welling and Becker 1990, 1993; Williamson 1996). At low abundance, non-indigenous plants may have no or only minor undetectable ecosystem impacts. Justification of control of small populations can then only be based on principles of economy, feasibility, and concerns over potential (but not presently realized, recognized or quantified) negative impacts of species. This approach has been strongly criticized when applied to purple loosestrife (*Lythrum salicaria* L.), an Eurasian wetland plant introduced to North America (Anderson 1995; Hager and McCoy 1998; Treberg and Husband 1999). According to these authors, reliable scientific evidence of detrimental effects of purple loosestrife on North American wetlands is insufficient to warrant control, particularly biocontrol (Hager and McCoy 1998). We recognize the considerable need to collect and publish quantitative evidence for ecosystem impacts of non-indigenous species to guide management decisions (Blossey 1999). In this paper we (1) present evidence for negative ecosystem impacts of purple loosestrife in North America and (2) describe the current research and monitoring focus of the biological control programme targeting purple loosestrife.

Purple loosestrife in North America

Initially introduced to North America in the early 1800s, *L. salicaria* has since spread throughout the continent with considerable help from beekeepers and horticulturists (Thompson et al. 1987). Wetland managers have for decades attempted to halt the spread of purple loosestrife or to control existing populations using flooding, mowing, disking, burning and herbicide – with little or no effect (Thompson et al. 1987; Skinner et al. 1994). *L. salicaria* now occurs in all lower 48 states (except Florida) of the US and in 9 Canadian provinces and it has been declared a noxious weed in at least 19 states. Abundance of *L. salicaria* varies throughout this range with populations at the fringes in the South, North and West still expanding, while a significant portion of the potentially available habitat in the Northeast and Midwest has been invaded. Only areas that undergo frequent treatment with herbicides can occasionally be kept free of *L. salicaria* (Balogh and Bookhout 1989).

Thompson et al. (1987) justified the initiation of a national program to control purple loosestrife as follows: "Although we need quantitative measurements of the effects of various stages of *L. salicaria* invasion on the structure, function, and productivity of North American wetland habitats, the replacement of a native wetland plant community by a monospecific stand of an exotic weed does not need a refined assessment to demonstrate that a local ecological disaster has occurred". Negative impacts of purple loosestrife on many wetland biota (plants, birds, reptiles, mammals etc.) were suspected by wetland managers throughout the country and a grassroots effort culminated in the initiation of a biological control program in the 1980's (Thompson 1991; Malecki et al. 1993; Hight et al. 1995; Blossey et al. 1996). Over the past 2 decades, and particularly in the last few years, a number of studies have confirmed the suspicions of negative ecosystem impacts of purple loosestrife voiced by wetland managers over 30 years ago (Table 1).

Thompson et al. (1987) suspected negative impacts of purple loosestrife on many waterfowl and marsh bird species in addition to negative impacts on a number of mammals and the bog turtle. Recent studies (Hickey 1997; Hickey and Malecki 1997; Lor 2000) investigated nest site selection, habitat use and ecology of black terns, rails, grebes, and the least bittern (*Ixobrychus exilis*), all with declining populations and therefore listed as species of management concern in the Northeast by the US Fish and Wildlife Service (Schneider and Pence 1992). At an 8000 ha wetland complex in western New York, black terns used only 4.2% of the potentially available habitat (emergent marsh) and none of >100 recorded nests was found in purple loosestrife (Hickey 1997; Hickey and Malecki 1997; J. Hickey, pers. comm., 1998). Black terns were considered a common species at the Montezuma National Wildlife Refuge in upstate New York with an estimated 1000 breeding pairs in the late 1950's (Hickey and Malecki 1997). The population at Montezuma became extinct by 1987 (Hess 1989). The local extinction of black terns coincided with a population explosion of purple loosestrife (Thompson et al. 1987) from few individuals in 1956 to a coverage of over 19% of the total area (600 ha), representing 40% of the emergent marsh habitat in 1983, (T. Gingrich, Refuge biologist, Montezuma National Wildlife Refuge, pers. comm., 1999, based on Refuge Narrative Reports). Although no cause and effect relationship can be established, the habitat preferences reported by Hickey and Malecki (1997) demonstrate that emergent marsh colonized by purple loosestrife does not constitute suitable nesting habitat for black terns.

Lor (2000) documented the avoidance of purple loosestrife for foraging and nesting by Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Least Bittern

Table 1. Ecosystem impacts of purple loosestrife (*Lythrum salicaria*).

Reason	Field	Laboratory, micro- and mesocosms	Reference
Reduction of high quality bird habitat			
Black Tern (*Chlidonias niger*)	X		Hickey 1997
			Hickey and Malecki 1997
Least Bittern (*lxobrychus exilis*)	X		Lor 2000
Pied-billed Grebe (*Podilymbus podiceps*)	X		Lor 2000
Virginia Rail (*Rallus limicola*)	X		Lor 2000
Sora (*Porzana carolina*)	X		Lor 2000
Long billed marsh-wren (*Cistothorus palustris*)	X		Rawinski and Malecki 1984
			Whitt et al. 1999
Reduction in plant biodiversity			
Reduction in native plant species	X		Gabor et al. 1996
Domination of seed bank	X		Welling and Becker 1990
Superior competitive ability of purple loosestrife		X	Weiher et al. 1996
			Mal et al. 1997
Replacement of cattail (*Typha* spp.)		X	Weihe and Neely 1997
	X		Mal et al. 1996
			Weiher et al. 1996
Reduction in pollination and seed set of native rare plant *Lythrum alatum*	X		Brown 1999
Alternation of wetland function			
Changes in decomposition rates and timing	X		Emery and Perry 1996
	X		Barlocher and Biddiscombe 1996
	X		Grout et al. 1997
Changes in porewater chemistry (reduced P)	X		Templer et al. 1998
Increased evapotranspiration rates	X		Yavitt (unpublished data)

(*I. exilis*), American Bittern (*Botaurus lentiginosus*) and Pied-billed Grebe (*Podilymbus podiceps*). Although pied-billed grebe nests were found at the water edge of flooded 1–2 year-old-purple loosestrife stands, older stands and the interior of younger stands are avoided. Adjacent areas dominated by native plants, particularly cattails, constituted high quality nesting and foraging habitat (Lor 2000). Another wetland specialist, the marsh wren (*Cistothorus palustris*) was conspicuously absent in purple loosestrife dominated wetlands but used adjacent cattail marshes (Rawinski and Malecki 1984; Whitt et al. 1999).

In a series of laboratory, mesocosm, and field experiments, the competitive superiority of purple loosestrife over native wetland plant species has been demonstrated (Table 1). Seedbanks, particularly in areas with established purple loosestrife populations, can be dominated (>400 000 seeds per m^2) by *L. salicaria* (Welling and Becker 1990, 1993). Water level fluctuations exposing open moist soils are required to trigger germination of many emergent aquatic plant species, including purple loosestrife (Shamsi and Whitehead 1974; van der Valk and Davies 1978; Shipley and Parent 1991). Not only does purple loosestrife outnumber native species in seedbanks (Welling and Becker 1993), seeds germinate faster (3–4 days) and reached higher germination rates than most native species (Shipley and Parent 1991). Seedling relative growth rate is among the fastest of all wetland plants tested (Shipley and Parent 1991) resulting in superior competitive ability (Gaudet and Keddy 1988). Long-term mesocosm experiments established that *L. salicaria* will replace *Typha latifolia* under shaded and unshaded conditions regardless of initial densities (Weihe and Neely 1997). Similar results were obtained using over 20 other wetland plant species and manipulating nutrient levels and seasonal flooding (Weiher et al. 1996). However, *L. salicaria* establishment and dominance was lowest when soil fertility was low and mesocosms were seasonally flooded. In all other treatments purple loosestrife eliminated all dicot species within five years (Weiher et al. 1996). A temporal component in the outcome of competition between *T. latifolia* and *L. salicaria* was found in a replacement series study in the field (Mal et al. 1997). *L. salicaria* needed four years to establish competitive superiority (*T. latifolia* was dominant in year one). The studies by Mal et al. (1997) and Weiher et al. (1996) demonstrate that careful interpretation of short-term data is warranted, particularly if such data are used to predict long-term outcome of competition in the field (Mal et al. 1997).

That expanding purple loosestrife populations cause local reductions in native plant species richness has been demonstrated by the temporary return of native species following the use of herbicide (Gabor et al. 1996). However, without the continued use of herbicides, purple loosestrife re-invades and re-establishes dominance within a few years (Gabor et al. 1996).

Winged loosestrife, *L. alatum*, is the most widespread native species of *Lythrum* in the US (Graham 1975). The taller, non-indigenous *L. salicaria* was suspected to replace the native *L. alatum* where ranges overlap (Blossey et al. 1994b). Recent work by Brown (1999) has demonstrated that in areas where both species co-occur, the presence of *L. salicaria* reduced pollinator visitation to *L. alatum* resulting in significantly reduced seed set of *L. alatum*. Pollinators preferred *L. salicaria* over *L. alatum* flowers and once on purple loosestrife were unlikely to visit *L. alatum* (Brown 1999). Moreover, presence of foreign (*L. salicaria*) pollen further reduced seed set of *L. alatum* and a small, albeit low, percentage of viable seeds indicated the potential for hybridization (Brown 1999). Clearly, the impact of *L. salicaria* on *L. alatum* involves direct interspecific competition and competition for pollination. The impact of the invasive *L. salicaria* on native plants may be much greater than previously anticipated (Brown 1999).

Hypotheses that wetland function would be affected by purple loosestrife encroachment have now been confirmed (Table 1). Areas dominated by purple loosestrife show significantly lower porewater pools of phosphate in the summer compared to areas dominated by *T. latifolia* (Templer et al. 1998). Purple loosestrife leaves (which have twice the phosphorous concentration of *Typha* leaves) decompose more rapidly than cattail (Emery and Perry 1996) or *Carex lyngbyei* (Grout et al. 1997) leaves resulting in a nutrient flush in the fall (Emery and Perry 1996; Grout et al. 1997). At the end of the growing season (end of September) 73% of *T. latifolia* and 82% of *L. salicaria* leaves produced the same year were still attached to the stems (Barlocher and Biddiscombe 1996). By December 13th, *L. salicaria* had dropped 92.2% of its leaves, whereas *T. latifolia* did not lose any leaf biomass during this period (Barlocher and Biddiscombe 1996). Decomposition of cattail and sedge leaves occurs in the winter and particularly in spring. This change in timing of nutrient release by decomposing purple loosestrife results in significant alterations of wetland function and may effectively accelerate eutrophication downstream (Emery and Perry 1996). The rapid decay of purple loosestrife tissue at a time of little primary production that could take advantage of a nutrient flush, could also jeopardize detritivore consumer communities adapted to decomposition of plant tissues in spring (Grout et al. 1997). In the Pacific Northwest, where purple loosestrife has only recently invaded, detrital-based foodwebs including endangered salmon species may be negatively affected by further encroachment of purple loosestrife (Grout et al. 1997).

We know of a number of additional studies that are in progress including several evaluating the impact of purple loosestrife on soil biogeochemistry (Yavitt, pers. comm., 1999) and on amphibian communities. We welcome additional work and encourage studies of specialized phytophagous insect herbivores and their natural enemies. Population increases of purple loosestrife may not immediately endanger native wetland plant species, however, insect herbivores specialized on native plant species and their natural enemies may be particularly vulnerable to population reductions of their hosts and habitat fragmentation (Kruess and Tscharntke 1994). In summary, our review demonstrates that the invasion of purple loosestrife into North American temperate wetlands results in undesirable ecosystem impacts. As suspected by wetland managers decades ago, prevention of establishment and control of *L. salicaria* was and is warranted. In the following section we will examine the effectiveness of traditional (mechanical, physical and chemical) control measures and discuss the rationale for the development of biological control.

Conventional purple loosestrife management

Management goals such as the protection of native fauna and flora and natural processes in National Parks and other natural areas promoted attempts to control purple loosestrife by cutting as early as 60 years ago, and later treatments included flooding, disking, fire and herbicides (see Thompson et al. 1987 for a review). Assessments of chemical and physical control for purple loosestrife management has continued (Malecki and Rawinski 1985; Balogh and Bookhout 1989; Haworth-Brockman et al. 1993; Welling and Becker 1993; Gabor et al. 1995, 1996; Gardner and Grue 1996;

Katovitch et al. 1996; Nelson et al. 1996). Long known by wetland managers (but not quantified or published in the peer reviewed literature), experiments confirm that flooding of less than 30 cm does not kill purple loosestrife seedlings (Haworth-Brockman et al. 1993) and adult plants thrive under flooded conditions. Moreover, raising water-levels and preventing draw-downs (where possible) prevents the germination of many native wetland species that rely on exposed mud-flats for regeneration from the seedbank (van der Valk and Davis 1978). Consistently, herbicides are able to kill purple loosestrife seedlings and established plants (Malecki and Rawinski 1985; Welling and Becker 1993; Gabor et al. 1995, 1996; Katovitch et al. 1996); however, without repeated, often annual (Balogh and Bookhout 1989) treatments, purple loosestrife regenerates from the seedbank within a few years (Malecki and Rawinski 1985; Gabor et al. 1995, 1996). In Canada not a single herbicide is registered for use over water, treatments conducted so far have been on experimental use permits only (C. Lindgren, purple loosestrife coordinator, Canada, pers. comm., 1999). Mowing and disking are non-selective and disruptive treatments, and require the removal of all cut plant parts because purple loosestrife is able to regenerate from stem fragments (Brown and Wickstrom 1997).

The most comprehensive program to prevent the expansion of purple loosestrife was attempted by the Minnesota Department of Natural Resources (DNR). The first purple loosestrife plant in a garden in the town of Duluth was reported in 1907; the first documented occurrence outside cultivation dates to 1929 (herbarium record, University of Minnesota). Expanding *L. salicaria* populations resulted in legislation declaring purple loosestrife a noxious weed in the state in 1987. The Purple Loosestrife Program within DNR (see Skinner et al. 1994 for details) focuses on inventory, monitoring, control, and research, and maintains a computerized annually updated database of locations, habitat types, and area of purple loosestrife infested wetlands, (all published in annual reports available from the MN DNR, St Paul). In Minnesota, purple loosestrife was known to occur at two sites in 1938, at seven sites in 1954, 11 sites in 1963, 22 sites in 1980 (1938–1981 are based on herbarium records) and 67 sites in 1986 (Figure 1). With the increased emphasis on inventory, known occurrences of purple loosestrife skyrocketed to 1340 by 1990, representing over 20 000 ha of affected wetland habitat (Figure 1). In 1999 almost 2000 wetlands representing over 23 000 ha were infested by purple loosestrife (Figure 1). The expansion of *L. salicaria* occurred despite the efforts by the purple loosestrife program to stop the spread. Between 1987 and 1999 the DNR spent over $2.2 million on purple loosestrife management (Figure 1). These expenditures were about equally allocated to salaries, herbicide treatments and research but did not include control costs covered by private citizens or other land management agencies in the state.

The Minnesota program initially relied on use of 2,4-D (Welling and Becker 1993; Skinner et al. 1994), switched to glyphosate and has lately experimented with triclopyr under an experimental use permit. Between 1990 and 1999, herbicides were applied to an average of 150–160 sites per year. While purple loosestrife populations

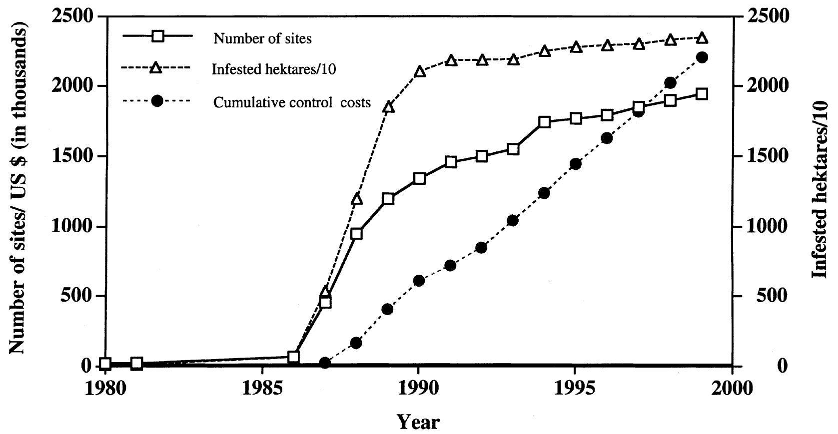

Figure 1. Number and total area of wetlands infested with purple loosestrife in Minnesota and cumulative control costs.

could be temporarily reduced, no permanent reductions were achieved, re-treatments were necessary, and the non-selective nature of these herbicides resulted in reductions of desirable plant species such as cattails, sedges, grasses, *Sagitaria* spp. and others (Skinner et al. 1994). Wetlands with large purple loosestrife seedbanks sometimes responded to herbicide treatments with an increase of cover of purple loosestrife due to simultaneous loss of native species and massive recruitment of seedlings. In some of these wetlands, purple loosestrife was more abundant after herbicide treatment than before (Skinner et al. 1994). Concerns over lack of control success and worker safety due to potential harmful effects of exposure to herbicides has resulted in a systematic reduction of the statewide spraying program.

In 1992, the Minnesota DNR began supporting research to develop and implement biological control for purple loosestrife, although spot application of herbicides continues (Skinner et al. 1994). At present, chemical control programs target individual watersheds (giving priority to those that do not have other purple loosestrife infestations), small populations, and populations furthest upstream (small populations have the smallest seed bank and seeds are mainly dispersed downstream). These treatments are occasionally successful in eradicating newly established and small populations that lack a seedbank. Similar negative experiences are reported by personnel in many different land management agencies, however, little or none of this work has been published in peer reviewed journals. Instead, annual reports and internal monitoring programs have guided adaptive management decisions on US Fish and Wildlife Service National Wildlife Refuges and in other natural areas. The results are similar; a consistent pattern of failure to achieve the desired population reductions of purple loosestrife.

In summary, traditional control methods have been tried for decades but continue to produce the same predictable results: short term positive effects – reduced abundance and biomass of *L. salicaria* with temporary return of native plant species – but they are not affording desirable long-term suppression of purple loosestrife. Repeated treatments are expensive, and the use of non-selective herbicides or changes in hydrologic regimes can have significant negative impacts on non-target species. The available evidence (published and unpublished) was reviewed by panels established by the US Department of Agriculture and Agriculture Canada and during the National Environmental Assessment prepared by the US Fish and Wildlife Service. Biological control was approved because (1) conventional control methods have consistently failed to provide economically and ecologically sound control and (2) the release of control agents is expected to have a positive effect on native biodiversity and will effectively reduce pesticide use in wetlands.

Invasive species in natural areas, biological control and the Precautionary Principle

The management of non-indigenous plants requires multiple decisions at various local, regional, and national levels and involves regulatory agencies and land managers. At present, introductions of non-indigenous plant material into the United States follow an 'innocent until proven guilty' approach; i.e. plants are allowed to be introduced unless they have been identified as having harmful effects. We believe that the 'Precautionary Principle' (O'Riordan and Cameron 1994; Underwood 1997) should be applied to non-indigenous species management. The principle could be phrased in two parts: (a) the introduction of non-indigenous plants has the potential to result in negative ecological impacts on native species or ecosystem processes, (b) introduction and spread of non-indigenous species has resulted in severe negative ecological impacts warranting changes in management philosophies and policies. In fact, land management agencies such as the National Park Service, the US Fish and Wildlife Service and The Nature Conservancy have now adopted policies of preventing establishment of non-indigenous species and controlling those that have established (US Department of Interior 1996; Stein and Flack 1996). These policies are not based on quantitative evidence for negative ecological impacts for each single non-indigenous species in each natural area but rather a response to impacts of non-indigenous species as a group. The common goal is to prevent any negative impacts before they have occurred. At an early stage, the control or eradication of a non-native species poses no threat to native ecosystems, however the continued presence or spread of such species may. This policy accepts that species that may be perfectly benign and never would become seriously invasive would be controlled or eradicated upon arrival. Control of invasive species is most economical and successful when these species occur in small populations (Moody and Mack 1988; Welling and Becker 1990, 1993; Williamson 1996). Waiting for recognition and quantification of impacts may jeopardize any chances for successful control. We consider it particularly dangerous to assume that there are no impacts based on absence of investigations or published data. It is ill advised to wait for population declines or extinctions of native species to occur; even on a local level since particular genotypes or subspecies may be lost. Lack of scientific certainty should not be a reason to postpone measures to prevent degradation (Dovers and Handmer 1995).

Such indiscriminate treatment of species as a group based on their origin is a direct result of the inability to predict species distributions, invasiveness and impact (Williamson 1996). Statistical regularities, such as the tens-rule (Williamson and Fitter 1996) just allow us to make the crude prediction that one out of every ten species that naturalize will become a pest. The recent surge in the interest in ecosystem impacts of invasive species may well lead to better predictions and better tools for assessing impacts. This, in turn, could lead to the a prioritization of control attempts focusing on the most damaging species. We recognize the need to assure that control measures themselves do not jeopardize management goals. Mechanical, physical and chemical control as well as biological control can have unanticipated non-target effects and a balance has to be achieved and careful consideration has to be given to all alternatives, including 'no action' scenarios (Simberloff and Stiling 1996).

Earlier in this paper we summarized evidence for negative ecosystem impacts and for the failure of conventional techniques to provide satisfactory and long-term control of purple loosestrife. The release of host specific insects from the native range of purple loosestrife was approved in an attempt to prevent further environmental degradation of North American wetlands. As with any other control technique, risks are associated with the use of biological control agents. The introduction of biological control agents from the home range of a non-indigenous plant is often met with concerns that (1) biocontrol agents may attack non-target plants and (2) that biocontrol agents may, over evolutionary time, become less host specific and then potentially attack non-target species. What sets biological weed control apart from any other treatment is the fact that it cannot be discontinued after control agents have been released. Any biocontrol introduction should require extensive research to reduce the probability of non-target impacts (Simberloff and Stiling 1996) and the precautionary principle should be applied to biological weed control (McEvoy and Coombs 2000). The principle as worded by McEvoy and Coombs (2000) has four parts: "(a) potential harm to non-target organisms can arise from the release of biological control organisms, (b) actual harm to non-target organisms of sufficient magnitude and severity has occurred to warrant new principles for conducting biological control introductions, (c) burden of proof for showing that new control organisms are necessary, safe, and effective rests with those proposing the activity, and (d) the process of applying the precautionary principle must be open, informed, and democratic and must include potentially affected parties. It must also involve an examination of the full range of alternatives, including no action" (McEvoy and Coombs 2000). We will examine how the principle has been applied to classical biological weed control and to control of purple loosestrife.

This discussion is limited to classical biological weed control, the introduction of host-specific insects or pathogens from the native range of a non-indigenous plant.

We are not considering or discussing the use of biocontrol organisms to control insect pests, snails, mammals or species other than plants and acknowledge the existence of ecological disasters associated with the introduction of generalist predators (Howarth 1991; Simberloff and Stiling 1996). We will use the four parts of the precautionary principle as applied to weed biocontrol (McEvoy and Coombs 2000) to guide our discussion. Biological weed control assumes all potential control agents to be guilty until proven innocent and thus already conforms to the shift in modus operandi outlined by Simberloff and Stiling (1996) and applies the first part of the precautionary principle (McEvoy and Coombs 2000; USDA 1999). Any proposed introduction of a weed biocontrol agent into the US or Canada requires extensive documentation of the experimentally determined host specificity. The list of test plant species includes species that are close relatives to the target weed, species with similar morphology, similar secondary chemisty, species that occur in the same habitats, rare and endangered species, and crop species. Safety evaluations occur in the native range or in quarantine. In the case of the US, this evidence is submitted to and reviewed by the Technical Advisory Group for the introduction of biological weed control agents (USDA 1999).

Assessing the potential for evolution of decreased specificity is far more difficult, if not impossible. A review of weed biocontrol introductions (McFadyen 1998) and a recent symposium on non-target effects of biological control (International Organization of Biological Control, Montpellier, France, October 1999) did not find any evidence for evolution of weed control agents regarding their host specificity. We acknowledge that the absence of evidence cannot 'prove' the non-existence of such evolution. The data are insufficient and we encourage detailed follow-up investigations, however, the claims that weed biological control agents have evolved the ability to complete development on unpredicted host plants can not be substantiated by available evidence. Examples for evolution of control organisms (Secord and Kareiva 1996; Simberloff and Stiling 1996) include a single weed biocontrol agent, the gall wasp *Trichilogaster acaciaelongifoliae*. This wasp was introduced from Australia to South Africa and has reached extremely high populations on its target host, *Acacia longifolia*, (Dennill and Donnelly 1991). Trees of two other introduced and invasive species, *A. melanoxylon* and *Paraserianthes lophantha* (which was not tested during host specificity screening) growing in the vicinity of large *T. acaciaelongifoliae* populations are now being attacked (Dennill and Donnolly 1991). However, this does not constitute an evolution of the host range as initially suspected (Dennill et al. 1993) since *T. acaciaelongifoliae* is unable to sustain populations on *A. melanoxylon* or *P. lophantha* in the absence of *A. longifolia* (Dennill et al. 1999). This constitutes a 'spill-over' effect which have been observed in other weed biocontrol programs, and which are usually temporary (McFadyen 1998).

Worldwide, in more than 1200 programs over 350 species of insects and pathogens were released against 133 plant species (Julien and Griffiths 1998). A comprehensive review incorporating both published and unpublished reports and communications reported damage to non-target plants for eight insect species (McFadyen 1998). For three of these species the host specificity screening did not predict attack of non-target plants (McFadyen 1998), however, in all cases the damage inflicted was temporary or minor (spill-over effects, see above). For five of these species, the attack of non-target hosts was known and predicted by host specificity screening before initial releases were approved (McFadyen 1998). Two controversial examples of non-target impacts of weed biological control agents in North America involve species with a broad host range. The first species is a thistle head feeding weevil, *Rhinocyllus conicus*. The species was introduced from Europe in the 1960s as a control agent for nodding thistle (*Carduus nutans*) and now attacks native North American thistles (Turner et al. 1987; Louda et al. 1997). The weevil was introduced despite field data showing attack of four different thistle genera in Europe and attack of various species in the subtribe Carduinae during host specificity testing (Zwölfer and Harris 1984). Economic considerations and the (in retrospect) erroneous assumption that preference for *C. nutans* would greatly reduce or eliminate the risk to native North American thistles (Zwölfer and Harris 1984), overrode any concerns over attack on non-target species. The second species is *Cactoblastis cactorum*, a moth used to control *Opuntia* cacti around the world (Julien and Griffiths 1998), now attacking endangered *Opuntia* species in southern Florida (Simberloff and Stiling 1996). The moth was introduced as a biological control agent into the Caribbean, and its introduction to Florida may be a result of importation of infested plants from the Caribbean by the horticultural industry (Pemberton 1995). Regardless of the mode of introduction, it remains questionable whether the species should have been purposefully introduced to the Caribbean. However, better screening protocols or pesticide applications by the horticultural industry could have likely prevented the introduction of *C. cactorum* (Pemberton 1995).

For us, these examples and others referenced by McFadyen (1998) illustrate that it is not the data on host specificity or safety features associated with the particular organisms that cause the controversies. Host specificity screening consistently has provided the best assurance for the safety of non-target species. What caused the current debate on the safety of biological weed control are decisions in the past to release species with a broad host range (neither *R. conicus* nor *C. cactorum* are species specific) or the release locations (like the Caribbean in close vicinity to the continental US).

Introducing biological control agents is not risk free, weighing all alternatives and making a democratic decision is the challenge facing biological control. Application of the precautionary principle to weed biocontrol (McEvoy and Coombs 2000) is realized for the first two parts of the principle. Whether we can restrict the number of control agents necessary for success will require more follow-up work and experimental approaches. What needs to be discussed are (1) who is involved in making the decisions and are all stakeholders currently represented (USDA 1999), (2) how can we guarantee an open and informed decision making process based on the best available evidence, and (3) what are the 'rules of the game' i.e. do all decisions require consensus, can the majority override minority opinions or can minority opinions block the release of control agents and how can conflicts be resolved. This is not the place to discuss procedures but it is essential that a societal consensus can be reached. Any such decisions will involve considering the best available evidence from data represented in peer-reviewed scientific publications in addition to unpublished reports, other non-refered publications, and expert opinions. It is prudent to consider this 'gray literature' for the wealth of information, knowledge and expertise that it represents (for example long-time observations of biologists and managers at National Wildlife Refuges, in National Parks or other natural areas). Similar observations at multiple locations, for example for the inability to control purple loosestrife using herbicide, lends credence to otherwise anecdotal evidence. As for peer reviewed information, careful evaluation of the information will reveal differences in quality and applicability but we should make an effort to incorporate valuable information obtained by those that are charged with daily management of our natural resources.

The biological control program targeting purple loosestrife in North America

Much of the emphasis in biological weed control programmes has been on finding, screening, releasing and distributing control organisms, while little emphasis has been placed on post-release monitoring (McEvoy and Coombs 1999). Excellent large scale experimental opportunities associated with these programmes have been passed up by practitioners and scientists alike, and rarely were data gathered on plant–insect interactions, insect establishment or plant succession in any rigorous fashion (Crawley 1989; McClay 1995; McFadyen 1998). The program targeting *L. salicaria* was intended first and foremost to reverse the extensive degradation of wetland habitats attributed to purple loosestrife encroachment. A second emphasis was the improvement of the scientific basis of biological weed control through research on plant–insect interactions, the ecology and genetics of invasions, factors controlling re-establishment of native vegetation, and rigorous post-release monitoring of target weed and non-target species (Malecki et al. 1993). Such investigations should increase the visibility and credibility of biological weed control as a predictive science with proven implementation procedures based on rigorous experimental tests (Malecki et al. 1993).

The use of non-indigenous plants by indigenous herbivores is well documented and may actually contribute to the control of introduced plants (Amrine and Stasny 1992; Mack 1996). It is therefore essential to assess the potential of these native (or accidentally introduced) herbivores as control agents prior to the introduction of non-indigenous species. Hight (1990) examined the phytophagous insect community on purple loosestrife in the northeastern United States and concluded that although over 90 species were collected on *L. salicaria* and 60 actually completed their development on the plant, none of these arthropods was able to stop the population and range expansion of purple loosestrife. Additional surveys and studies on the potential of insects (Halbert and Voegtlin 1994; Voegtlin 1995; Nechols et al. 1996; Diehl et al. 1997) and fungi (Nyvall 1995; Nyvall and Hu 1997) came to the same conclusion, although some species showed promise in the lab and even at some field sites but ultimately have little use as biocontrol agents in the field.

The purple loosestrife biocontrol programme was initiated by a grassroots movement of natural areas managers and is independent of agricultural or economic interests. The purple loosestrife program has certainly applied the precautionary principle before considering species with a demonstrated restricted host range for introduction (Blossey et al. 1994a, b; Blossey and Schroeder 1995). Control agents were only introduced after conventional techniques failed to provide satisfactory control and only a subset of the available species was introduced (Malecki et al. 1993). A questionnaire summarizing research findings and potential risks associated with the release of control agents, was sent to land managers in over 30 states affected by purple loosestrife. This provided an opportunity for input in decision making (Blossey et al. 1994a) before any introductions occurred. Ultimately, after years of research in Europe, it was determined that potential benefits outweigh risks and biocontrol agents were introduced in 1992 and 1994 (Malecki et al. 1993; Blossey et al. 1994a, b; Hight et al. 1995). The selected species were a root-mining weevil, *Hylobius transversovittatus* Goeze, two leaf-beetles, *Galerucella calmariensis* L. and *G. pusilla* Duft., and a flower feeding weevil *Nanophyes marmoratus* Goeze. Combining species attacking flowers, leaves, and roots was predicted to enhance control (Malecki et al. 1993).

All species have established throughout the range of purple loosestrife. The most abundant and widespread species are the two leaf beetles where easy mass production techniques were developed (Blossey and Hunt 1999). State and federal agencies as well as private citizens and schools now participate in rearing, release and monitoring and the *Galerucella* species have been released in 33 states and >1500 wetlands nationwide. The nocturnal root-feeder has been difficult to mass produce and field populations are low. The development of an artificial diet (Blossey et al. 2000), will accelerate redistribution programs and make the species more widely available. The flower feeding weevil is established in the US and Canada but the species is the least widespread.

Purple loosestrife and its associated herbivores were used to test selection (Blossey 1995a) and host specificity screening procedures (Blossey et al. 1994a, b; Blossey and Schroeder 1995) for weed biocontrol agents. Experiments were designed to assess release methods for successful establishment (Hight et al. 1995) and models were developed to explore factors underlying success and failure of establishment in biocontrol introductions (Grevstad 1996, 1999) and dispersal (Grevstad and Herzig 1996).

With the introduction of two leaf-beetles, an early paper (Manguin et al. 1993), provided a new key for identification of all North American *Galerucella* species. Nechols et al. (1996) assessed the likelihood for interference of potential native natural enemies of the two leaf beetles on establishment and control potential. Further work evaluated competition between the two *Galerucella* species which share the same ecological niche on their host plant (Blossey 1995b; Rawlinson and Blossey, unpublished manuscript) and their impact on plant performance (Blossey 1995c; Blossey and Schat 1997; Stamm-Katovitch et al. 1998, 1999) and plant architecture (Schat and Blossey, unpublished manuscript). Similar information on life history, ecology and impact is available for the root-feeding weevil (Blossey 1993; Nötzold et al. 1998; McAvoy and Kok 1999).

Purple loosestrife was also used as a model to explain the increased competitive ability of invasive plants that may result from shifts in resource allocation patterns from defence to vegetative growth (Blossey and Nötzold 1995; Blossey and Kamil 1996; Willis et al. 1999; Willis and Blossey 1999). This hypothesis (Blossey and Nötzold 1995) may provide a useful screening tool to assess the invasive potential of non-indigenous plants before their introduction (Blossey and Kamil 1996).

Although it can often take 10–20 years before the success or failure of a weed biocontrol program can be assessed, the first post-release evaluations have been published for purple loosestrife (Piper 1996; Lindgren 1997; McAvoy and Kok 1997; Blossey and Skinner 2000) and the potential for integration of biological and chemical control was evaluated (Lindgren et al. 1998). A particular emphasis has been the monitoring of two native plant species, *Decodon verticillatus* (swamp loosestrife or waterwillow) and *L. alatum* (winged loosestrife). Host specificity screening results (Blossey et al. 1994a, b) led to predictions that the potential for temporary attack of *D. verticillatus* and *L. alatum* does exist, particularly at high densities of the control agents. Predictions that beetles may nibble at *D. verticillatus* and *L. alatum* (Blossey et al. 1994a, b) were confirmed as temporary and of no lasting consequence to the native species (Corrigan et al. 1998), however, evaluations continue.

An important cornerstone of our post-release monitoring has been the development of a standardized monitoring protocol to encourage participation and facilitate comparison of data obtained across North America (Blossey 1999). This protocol incorporates measures of target weed populations, control agent abundance, and wetland plant communities in permanent 1 m^2 quadrats. To allow widespread adoption of protocols for such long-term investigations (5–20 years) and participation by non-academic personnel, the monitoring protocol was designed to balance scientific sophistication with ease of application. National and local workshops introduced personnel in the use of the protocol, and instructions and forms are available at: http://www.dnr.cornell.edu/bcontrol/weeds.htm. This has allowed widespread adoption and participation by natural resource managers and students. Data generated by these studies will provide valuable information on ecological interactions and principles underlying biological weed control.

Vegetation succession is a slow process and for many results and evaluations we need to continue our investigations long-term. We are able to provide ‘snapshots’ but all our field sites are changing. At some of the early release sites, the attack by host specific insects has resulted in dramatic declines of purple loosestrife (Blossey

2000; Blossey and Skinner 2000; E. Coombs, D. Eberts, D. Ellis, R. Casagrande, J. Corrigan, C. Lindgren, R. Wiedenmann, pers. comm., 1999). At many sites, the once monotypic stands of *L. salicaria* are replaced by a diverse wetland plant community. At the Tonawanda Wildlife Management Area in western New York State, an area once dominated by purple loosestrife and abandoned by black terns, has developed into a emergent marsh and is, now again used as breeding and foraging area for the terns (D. Carroll, pers. comm., 1999; B. Blossey, pers. obs., 1999).

At several sites, other invasive species such as *Phragmites australis* (common reed) or *Phalaris arundinacea* (reed canary grass) expand as purple loosestrife is controlled, clearly not a desired result. At yet other sites, dense purple loosestrife litter limits growth or recruitment of native species. In cooperation with wetland managers, we have started experiments to assess whether management of vegetation succession after successful suppression of purple loosestrife using fire, flooding, disking, or mowing is able to achieve desired plant communities and whether these management techniques are compatible with sustained suppression of purple loosestrife by biocontrol agents. Long-term monitoring will determine local trends and help in assessing the need and feasibility of additional restoration work to obtain a diverse wetland flora and prevent the expansion of other invasive species. Together with scientists at the Bureau of Reclamation we are also evaluating the prospects of aerial photography and remote sensing to monitor landscape level changes in wetland plant communities as a result of insect feeding on purple loosestrife. A multitude of scientists and students is engaged in many other projects that will make valuable contributions to ecology and management of invasive plants.

We believe that the purple loosestrife biocontrol programme, initiated by a grassroots movement of natural areas managers and, thus, independent of agricultural or economic interests, has made and will continue to make a valuable contributions to weed biocontrol and ecology. A retrospective analysis can conclude that although quantitative data on the ecosystem impacts of *L. salicaria* were scarce, recent evidence is growing and confirming large negative impacts of the species on native North American species and ecosystem processes. The inability to prevent this degradation by conventional means clearly justifies the potential risks associated with the introduction of additional non-indigenous biological control agents. Merging an applied program with basic ecological research has resulted in the development of purple loosestrife as a model system for similar investigations and will benefit ecology and weed biocontrol theory and practice.

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