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LIFE HISTORY AND TAXONOMIC STATUS OF PURPLE LOOSESTRIFE IN MINNESOTA: IMPLICATIONS FOR MANAGEMENT AND REGULATION OF THIS EXOTIC PLANT[1]

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Abstract.--Purple loosestrife *Lythrum salicaria* is a plant native to Eurasia and established in North American wetlands where it is considered a problem because it can displace native vegetation and consequently reduce the value of infested areas as wildlife habitat. In this report we review research conducted primarily in Minnesota on the seed bank and recruitment dynamics, taxonomy, and phosphorus cycling of this species. A limited amount of research done in Manitoba and elsewhere also is reviewed in this report.

Any reduction in the number of established purple loosestrife plants in a wetland, whether it is the result of artificial manipulation or natural factors, is often short-lived due to recruitment from the seed bank. The ability to prevent recruitment of purple loosestrife or deplete the seed bank of this species would be a valuable tool for wetland managers interested in limiting the spread of this species. The development of these approaches to management must be based on an understanding of seed germination characteristics, seedling recruitment processes, seed bank size, and seed bank longevity in loosestrife. Seeds of purple loosestrife from Minnesota were found to germinate at rates generally greater than 65% in the presence of water, light and temperatures of at least 15°-20° C. In 10-20% of a population of purple loosestrife seeds, germination under appropriate environmental conditions may be prevented by the physiological status of the seeds. These results are consistent with those from previous studies which showed that seeds of purple loosestrife germinate at high rates over a broad range of environmental conditions. Attempts to prevent recruitment of purple loosestrife from wetland seed banks were made using a selective herbicide and plant competitors. In these studies, it was possible to reduce but not prevent the recruitment of loosestrife. Seed banks were studied at four sites in Minnesota where populations of as many as 410,000 purple loosestrife seeds per square meter were present at these sites. Further, many loosestrife seeds

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were present in the soil below depths of 1-2 cm which can prevent seed germination and seedling emergence. These results indicate that purple loosestrife has the ability to produce a large and persistent seed bank in Minnesota wetlands. Once such a seed bank has developed in a wetland, it is probably not possible to eliminate loosestrife from that site. For this reason, the current policy of the Minnesota Department of Natural Resources is to attempt to eliminate recently established, small populations before attempting to control long-established, large populations of loosestrife.

From the perspective of managers interested in limiting the spread of purple loosestrife, there are two important taxonomic questions. First, can cultivars or other variants of loosestrife sold in the horticultural trade be distinguished from purple loosestrife? Second, are cultivars incapable of sexual reproduction, as has been argued by some who believe these plants should be sold in the horticultural trade? The taxonomic relationships among purple loosestrife and cultivars are complex. Many cultivars are indistinguishable from many purple loosestrife populations. Five specimens labeled and sold as a single cultivar of purple loosestrife were subjected to electrophoretic analysis of isozymes which demonstrated that three of the five plants were genetically different from one another, i.e., the cultivar was not a true clone. More importantly, cultivars were found to possess high levels of male and female fertility, and to produce seeds which germinated at high rates. Cultivars produced viable seeds even when self-pollinated, a type of mating which in purple loosestrife produces seeds that germinate at rates much lower than those of seeds produced by cross-pollination. Consequently, the distribution of loosestrife cultivars through the horticultural trade can be expected to contribute to the spread of this species. Since the Minnesota Legislature resolved to limit the spread of purple loosestrife in the State, this body acted appropriately in passing legislation prohibiting the sale of purple loosestrife. The Minnesota Department of Agriculture made purple loosestrife a primary noxious weed and subsequently prohibit the sale of this species and wand loosestrife *L. virgatum* and any cultivar derived from either of these species.

One possible consequence of the establishment of purple loosestrife in a wetland is an alteration in nutrient cycling patterns, which in turn could affect the functional value of the wetland. Current research demonstrated no large differences in levels of phosphorus between stands of loosestrife and cattail *Typha latifolia* in Minnesota wetlands. Additional research would be necessary to determine how displacement of cattail by loosestrife might alter phosphorus cycling in these wetlands.

Introduction

Purple loosestrife *Lythrum salicaria* is a plant native to Eurasia and established in the United States and Canada. This perennial emergent is considered a problem in North American wetlands because it can displace native vegetation and consequently reduce the value of infested areas as wildlife habitat (Thompson et al. 1987). Also, concern has been expressed that establishment of purple loosestrife in a wetland may reduce the number of native plant species present (Moore and Keddy 1989). Effects such as these may reduce the overall biodiversity of Minnesota wetlands.

A variety of methods have been employed in attempts to eliminate purple loosestrife from wetlands in North America (Thompson et al. 1987). The method most commonly used in Minnesota and elsewhere is the application of herbicides. Reduction in the number of established loosestrife plants resulting from the application of herbicides is often short-lived due to reestablishment of this species through recruitment from the seed bank. The seed bank is the population of seeds either lying on or buried in the soil. Recruitment includes seed germination, emergence of new seedlings, and subsequent establishment of these seedlings. Wetland managers need an understanding of the recruitment dynamics of purple loosestrife and the potential for disruption of this process as a basis for management of this species in Minnesota.

During the 1980s, concern arose about the spread of purple loosestrife in Minnesota. In 1987, the Minnesota Legislature passed a bill which designated the Department of Natural Resources (DNR) as the lead agency in the effort to limit the spread of purple loosestrife in the state (Rendall 1989). Legislation was also passed making the sale of purple loosestrife a misdemeanor. The Minnesota Department of Agriculture concurrently added purple loosestrife to the state list of primary noxious weeds, which also resulted in the prohibition of sale of this species in the horticultural trade. Addition of purple loosestrife to the list of primary noxious weeds also gave authority to the State to mandate control of this species on all public and private lands in the state. It subsequently became apparent that these actions were inadequate since variants of purple loosestrife, including wand loosestrife *L. virgatum* and a number of cultivars, were still commercially available, even though morphologically they cannot be consistently and reliably distinguished from purple loosestrife. Consequently, the definition of loosestrife in the Minnesota noxious weed law was revised to include wand loosestrife and any combination thereof with purple loosestrife.

Nevertheless, a number of questions about the taxonomy of this species remained unresolved. Generally, it was unclear how wand loosestrife and the various cultivars are related to purple loosestrife and what role, if any, these other taxa might play in the spread of that species. There was controversy over whether or not cultivars or horticultural varieties of purple loosestrife are capable of sexual reproduction, but no research had been done to answer this question.

In 1989, the Purple Loosestrife Program of the DNR requested support from the Legislative Commission on Minnesota Resources (LCMR) to initiate research on purple loosestrife. The Minnesota Legislature subsequently approved funding for research on purple loosestrife as recommended by the LCMR. The purpose of this research was to provide information on this species in Minnesota necessary for the development of longterm integrated pest management (IPM) strategies to limit the spread of purple loosestrife. IPM utilizes appropriate biological, cultural and chemical control methods when and where needed. Research funded by the Minnesota Legislature included studies in each of three areas: seed bank and recruitment dynamics, taxonomy and genetics, and phosphorus cycling. Results from studies in each of these areas are reviewed in separate sections of this report. Copies of the reports on purple loosestrife research done in Minnesota and Manitoba with funding from the Minnesota Legislature and reviewed here are on file at the DNR offices in St. Paul.

Important plant attributes such as rate of seed germination can vary among populations with different flower morphologies (Nicholls 1987; Anderson and Ascher 1991; Charvat and Stenlund 1991). Nevertheless, in this review we present results for populations which include individuals with different floral morphologies, the proportions of which were not always constant among populations. The rationale for this approach is that populations of purple loosestrife, not subpopulations distinguished by flower morphology, are the management focus.

Seed Bank and Recruitment

Any reduction in the number of established purple loosestrife plants in a wetland, whether it is the result of artificial manipulation or natural factors, is often short-lived due to recruitment from the seed bank. The ability to prevent recruitment of loosestrife or deplete the seed bank of this species would be a valuable tool for wetland managers interested in limiting the spread of this species. The development of these approaches to management must be based on an understanding of the seed bank and recruitment dynamics of this species. Specifically, managers must be familiar with seed germination characteristics, seedling recruitment processes, seed bank size, and seed bank longevity in purple loosestrife.

Seed Germination and Dormancy

Relationships between germination rates of purple loosestrife seeds and environmental conditions are often studied because seeds can easily be exposed to a range of laboratory conditions. Loosestrife seeds germinated at rates up to 95% if given water and light at a temperature of 20°C (Table 1). Under these environmental conditions, 50% germination was reached within 3-6 days. Exposure to diurnally fluctuating temperatures did not increase germination in purple loosestrife (Grime et al. 1981; Thompson and Grime 1983; Shipley et al. 1989). The requirement for light is minimal as a 98% reduction in light levels from 4,000 to 100 μW cm^{-2} due to experimental shading, did not reduce germination rates of loosestrife seeds which were 65 and 68%, respectively (Grime et al. 1981). Germination in the dark was much lower than in the light (Table 1). When seeds maintained in the dark were exposed to 30°C, they had a germination rate of 25% (Shamsi and Whitehead 1974; Charvat and Stenlund 1991).

Seed dormancy is important in the life history of purple loosestrife because it can delay germination and thereby allow dispersal of the plant in time and space. For example, seeds may lie dormant in wetland soil for years and germinate after the plant, which produced it, is dead. Seeds may be carried by water and spread loosestrife throughout a river basin. Three types of dormancy are distinguished by Harper (1977). A viable seed may not germinate when it matures even under environmental conditions known to meet the requirements of the species; this is innate dormancy. Alternatively, a seed may be able to germinate when it matures, but is prevented from doing so because it is not exposed to the appropriate environmental conditions; this is enforced dormancy. Lastly, a seed may be able to germinate when it matures, but is prevented from doing so because environmental conditions are not appropriate, and subsequently will not germinate even under appropriate environmental conditions; this is induced dormancy.

Evidence of innate dormancy in seeds of purple loosestrife comes from research done in Great Britain and Minnesota. An increase germination rate over time, such as that observed between zero and three months in seed collected in Great Britain (Table 2), suggests that some seeds were innately dormant at zero months. Similarly, Charvat and Stenlund (1991) reported that seeds collected in Minnesota showed an increase in rate of germination after two weeks storage under a temperature regime of 15°C and 6°C but not 20°C and 10°C (Table 2). In addition, Anderson and Ascher (1991) found that treatment of loosestrife seed with 500 ppm gibberellic acid, a substitute for cold stratification, resulted in a germination rate of 80%, which was higher ($p=0.02$) than the 71% observed in the absence of gibberellic acid.

Evidence of induced dormancy in seeds of purple loosestrife comes from research done in Minnesota on the longevity of seeds experimentally buried in wetland soil. Seeds collected from live plants in September germinated at a rate of 100% immediately after collection (Welling and Becker 1991). After 5 months burial over winter, the rate of germination in populations of experimentally buried seeds had decreased to 83%. One year later, after burial for two winters, the rate of germination in experimentally buried seeds had increased to 96%. These results suggest that exposure to the environment of wetland soil during the first winter of burial induced dormancy in 13-17% of the seed population. This effect did not persist through the second winter of burial. In another study of longevity of purple loosestrife seeds collected in Minnesota, there was no evidence of induced dormancy. The germination rate of these seeds was 81% immediately after collection and 85%

Table 1. Germination characteristics of seeds of purple loosestrife collected from populations in different locations.

			Dark at 20°C	14-15 hours light at 20°C	
Study	Location	Seed age (months)	Germination (%)	Germination (%)	Days to 50% germination
Shamsi and Whitehead (1974)	United Kingdom	Unknown	3[a]	95[a,b]	3
Grime et al. (1981)	Sheffield, United Kingdom	Unknown	0[c]	65[c]	6
Shipley et al. (1989)	Ontario, Canada	9	13[a]	80[a]	4
Charvat and Stenlund (1991)	Minnesota, USA	9	5[d]	67[d]	4[a]

[a] Experiments conducted under temperature regime of constant 20°C.
[b] Assumed to be constant light.
[c] Experiments conducted under temperature regime of 20°C during the day and 15°C during the night.
[d] Experiments under temperature regime of 20°C during the day and 10°C during the night.

Table 2. Germination rates of seeds of purple loosestrife after storage for varying lengths of time at 5°C under laboratory conditions.

Study	Light regime	Duration of storage at 5°C (months)					
		0	0.5	2.5	3	9	12
Grime et al. (1981)	20/15[a]	60	--	--	89[b]	66	76
Charvat and Stenlund (1991)[c]	20/10[d]	94	95	100	--	--	--
Charvat and Stenlund (1991)[c]	15/6[d]	76	97	98	--	--	--

[a] Experiments were conducted under conditions of a 15 hour day and 9 hour night.
[b] This rate is higher ($P < 0.01$) than those observed at other times.
[c] Seeds collected from plants with mid-length styles only.
[d] Experiments were conducted under conditions of a 12 hour day and 12 hour night.

after 6 months storage under laboratory conditions at 5°C (Charvat and Stenlund 1991). Fourteen months after collection and 8 months after burial in wetland soil, these seeds germinated at a rate of 55%. The results from these two studies are not directly comparable since there were differences in experimental conditions.

Evidence of enforced dormancy in seeds of purple loosestrife comes from further studies, also done in Minnesota. Welling and Becker (1990) reported that nearly all of the seeds found in samples of wetland soil examined with a dissecting microscope germinated when environmental requirements were met. Of the limited numbers of seeds recovered from this soil which contained embryos that did not germinate, most were dead. In addition, recruitment under conditions chosen to encourage high rates of germination did not exhaust the seed bank in a 1 cm deep layer of wetland soil in experimental flats. Emergence of seedlings from experimentally buried seeds decreased linearly (Figure 1) from 90% at the soil surface to 0% at 2 cm. The evidence reviewed here indicates that enforced dormancy is more important than either innate or induced dormancy in determining the behavior of purple loosestrife seeds in wetlands as opposed to laboratory environments.

Recruitment from the Seed Bank

Recruitment in purple loosestrife has not been studied as much as seed germination. Recruitment begins with seed germination and requires that seedlings emerge from the soil and become established, i.e., capable of survival independent of seed reserves. This process is important because it is the primary means by which loosestrife becomes established in wetlands. Recruitment also is a complicated process that can be affected by not only the physical environment, but also by other plant species as well as herbivorous animals.

In studies of recruitment from the seed banks of two Minnesota wetlands where purple loosestrife was present, loosestrife was the species most frequently encountered in seedling communities (Welling and Becker 1991). This result is not surprising given the high rate of seed production (Thompson et al. 1987), the broad range in environmen-

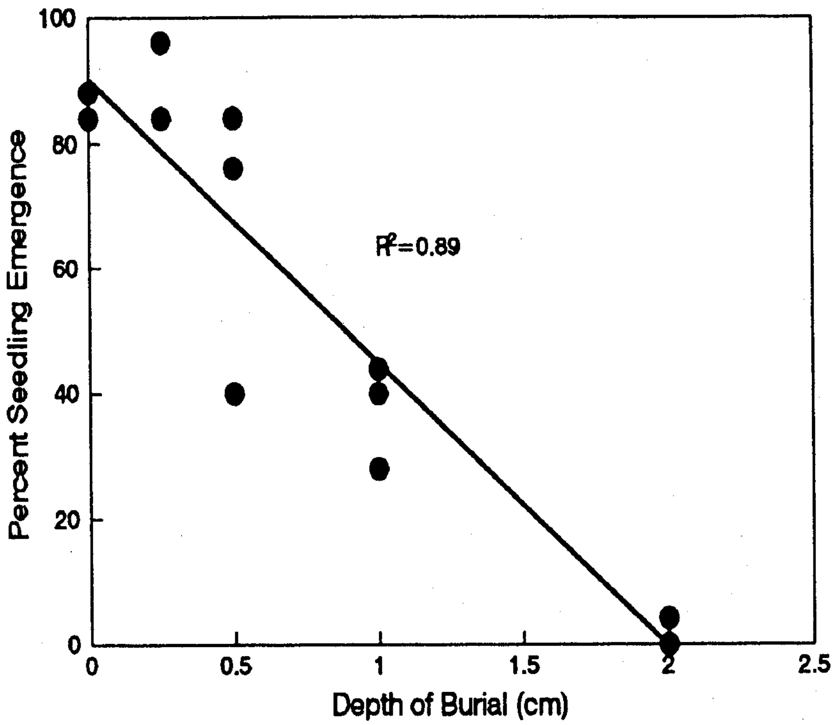

Figure 1. Relationship between emergence of seedlings and depth of seed burial in purple loosestrife. Emergence was strongly related to depth of burial ($P=0.001$, $R^2=0.89$; from Welling and Becker 1990).

tal conditions which will allow seed germination, and the minimal innate dormancy present in this species.

Several attempts have been made to determine whether recruitment of loosestrife in the field can be prevented by the introduction of other plant species as competitors (Malecki and Rawinski 1985; Balogh 1986; Skinner and Hollenhorst 1989). In addition, the application of herbicides to seedlings would likely prevent recruitment, but most studies of purple loosestrife and herbicides have dealt primarily with established plants (Thompson et al. 1987). Inconsistencies in the results from previous studies, as well as a lack of information on the effects of efforts to manage loosestrife on recruitment of other wetland plants, led to further research.

Welling and Becker (1991) evaluated three approaches to the prevention of recruitment of purple loosestrife from the seed banks of two Minnesota wetlands under conditions created to promote recruitment both in controlled and uncontrolled environments. The first treatment was the application to seedling communities of 2,4-D, an herbicide to which dicots are susceptible but monocots are tolerant. Two potential competitors, Japanese millet *Echinochloa crus-galli* var. *frumentacea* and annual rye grass *Lolium multiflorum* were introduced into the seedling communities. The greatest reduction in recruitment resulted from the application of 2,4-D in the controlled environment where the herbicide reduced loosestrife seedling frequency of occurrence, population density, and biomass by 60, 85, and 80%, respectively. The introduced competitors had the potential to reduce the growth, but could not consistently reduce the number of purple loosestrife seedlings recruited in the controlled environment. The competitors failed to establish and consequently had no effect on recruitment in the uncontrolled environment (the field). The greatest changes in overall recruitment resulted from the application of 2,4-D which reduced the number of dicot species present in the controlled environment. This treatment also had the potential to allow increased growth of cattail seedlings *Typha latifolia*.

A fourth approach to disrupting recruitment of purple loosestrife was evaluated in Minnesota. Since cattail, *Typha latifolia*, litter has been reported to have allelopathic potential on development of its own seedlings (McNaughton 1968), Charvat and Stenlund (1991) investigated the impact of cattail litter on recruitment of loosestrife. Three percent extract of cattail leaves, either sterilized or unsterilized, had no effect on the rate of germination of loosestrife seeds maintained on filter paper in petri dishes. Neither form of this extract affected shoot growth, but both the sterilized and unsterilized forms prevented root development in seedlings under laboratory conditions. It is unclear what implications these results may have for recruitment of purple loosestrife from wetland seed banks under field conditions. In an attempt to reproduce the allelopathic effects of cattail observed under laboratory conditions, Grace (1983) found little evidence of such effects under conditions similar to those in a wetland. Germination of cattail seeds was unaffected by treatment with senesced leaves or soil surface water from pots containing growing cattail plants. In addition, germination in seeds sown on the soil surface in tubs was unaffected by the presence of established cattail plants. Further, purple loosestrife appears to establish readily in the presence of cattail, the plant species most frequently found growing with loosestrife (Thompson et al. 1987).

Seed Bank Size and Longevity

Knowledge of the size and longevity of populations of purple loosestrife seeds in the soil (the seed bank) will enable wetland mangers to determine the potential for re-infestation of an area following control of established plants. In Great Britain, where purple loosestrife is native, the species has been classified as having a persistent bank of buried seeds in the soil throughout the year (Grime et al. 1988). In three Minnesota wetlands, there were 410,000 purple loosestrife seeds/m^2 in the top 5 cm of soil in stands of emergent vegetation (Welling and Becker 1990). This seed bank is at least 10 times larger than the size of any other wetland seed bank, all species included, listed by Leck (1989). Charvat and Stenlund (1991) examined the distribution of loosestrife seeds in the soils along a gradient perpendicular to the shoreline of a Minnesota lake. Densities of seeds per gram of dried soil were greatest at the water's edge and decreased with distance from the lakeshore. This distribution of seeds was likely due to the pattern of establishment of loosestrife where the plant became established first at the lakeshore and later at some distance back from the water. In addition, seeds of purple loosestrife were much more numerous than those of other dicots or monocots in the seed bank of the Minnesota lake sampled (Charvat and Stenlund 1991).

There are no published studies of loosestrife seed longevity in wetland soils where this plant is considered a problem. Consequently, two studies of the longevity of purple loosestrife seed in marsh soils have been undertaken in Minnesota. Welling and Becker (1991) buried experimental populations of loosestrife seeds in nylon bags in wetland soil. These bags are to be collected and assayed at intervals over the next 20 years. Changes in the rate of germination of loosestrife seeds during the first 17 months of this study have been described in the previous dormancy discussion. For overall seed longevity, no significant reduction in the size of the experimental seed bank occurred during this period. Charvat and Stenlund (1991) also buried experimental populations of loosestrife seeds in nylon bags in the soil of a Minnesota wetland. These bags are to be collected and assayed at intervals over the next nine years. They found a 36% reduction in the rate of germination of loosestrife seeds during the first eight months of burial in wetland soil after six months storage under laboratory conditions. The results from these two studies are not directly comparable since there were differences between experimental conditions.

The oldest loosestrife seeds for which germination rates are known is material stored dry at 3-4°C in a laboratory by Shamsi and Whitehead (1974) who reported a germination rate of 80% after 3 years. The rates of germination in seeds experimentally buried in Minnesota do not differ noticeably from those observed in New York (Rawinski 1982) where loosestrife seeds germinated at a rate of 80% after 2 years submersion in pond water. More generally, seeds of wetland plants have been found to germinate after submersion for five years in a canal in Washington (Comes et al. 1978). Considering the results from previous studies, it is unlikely that a large reduction in the survival of purple loosestrife seeds will be observed in Minnesota after three years burial or perhaps at any time. It will be important to continue these studies of seed longevity of purple loosestrife experimentally buried in Minnesota wetlands.

Taxonomy and Genetics

From the perspective of managers interested in limiting the spread of purple loosestrife, there are two important taxonomic questions. First, can cultivars or other variants of loosestrife sold in the horticultural trade be distinguished from purple loosestrife? Second, are any of these cultivars capable of sexual reproduction? It has been argued by some that these plants are incapable of sexual reproduction and consequently should be allowed to be sold in the horticultural trade. In this review we treat purple loosestrife and wand loosestrife as the same species and refer to it as loosestrife. This is the approach taken by Anderson and Ascher (1991) and S. Graham (1989 personal communication to Anderson and Ascher 1991:165). Winged loosestrife *L. alatum* is a native species that is reliably distinguishable from purple loosestrife.

Differentiation of Purple Loosestrife and Cultivars

It is possible to distinguish limited numbers of cultivars from limited numbers of purple loosestrife populations on the basis of morphology. Ottenbreit (1991) examined wand loosestrife cv. Morden Pink, winged loosestrife x Morden Pink cv. Morden Gleam, and purple loosestrife x wand loosestrife cv. Dropmore Purple, and three populations of purple loosestrife in Manitoba. The cultivars were found to be morphologically distinct from one another and from the loosestrife populations as a group. The pubescence of the calyxhypanthium was greater and the calyx lobes shorter in purple loosestrife than in the cultivars. The three cultivars studied by Ottenbreit (1991) were distinguished from one another on the basis of flower morphology and petal color. This author observed high levels of variability in vegetative characteristics of different populations, and cautioned that the amount of tomentosum in purple loosestrife can vary among environments. She noted that it is impossible to determine whether morphological dissimilarities among populations of loosestrife in the field are due to genotypic differences resulting from hybridization or phenotypic plasticity. It is not known how many of the 18 different cultivars studied by Ottenbreit (1991) or the 21 different populations of cultivars studied by Anderson and Ascher (1991) might reliably be differentiated from purple loosestrife on the basis of morphology, but it seems unlikely if not impossible that all these taxa can be distinguished from one another.

In addition, Ottenbreit (1991) subjected measurements of flowers from 18 to 20 individual plants of each of 3 cultivars and 3 purple loosestrife populations in Manitoba to canonical discriminant analysis which assigns individuals to similar groups. All cultivars were assigned to the groups from which they originally came, but several purple loosestrife plants were reclassified with plants from a population other than the one from which they came. Subsequently, 37 crosses were performed among the 6 studied populations, and the 295 progeny were examined and the measurements subjected to discriminant analysis. Only 50% of the progeny were classified with one or the other of their parents, and 37% of the offspring were classified with one loosestrife population. This suggests that this one population has hybridized with cultivars and generally reflects the genetic similarity between the cultivars and purple loosestrife.

In Minnesota, Darmo et al. (1991) used gel electrophoresis of isozymes to characterize genetic variation in 12 populations of purple loosestrife, 3 winged loosestrife, 1 of wand loosestrife, and 16 cultivars. Three of the 22 examined isozyme systems were utilized as they had excellent resolution and high activity. Most loosestrife, other than winged loosestrife, had high proportions of polymorphic loci. Genetic variation was high both within and among populations of purple loosestrife, and was not correlated with geographical location. These observations are consistent with the perennial, out-crossing nature of purple loosestrife, and is indicative of plants with widespread geographic distribution.

Darmo et al. (1991) used principal component analysis of isozyme frequencies to examine the genetic similarities among loosestrife taxa. Three populations of winged loosestrife, a native species, were genetically different from all examined populations of purple loosestrife and cultivars. The cultivars as a group could be genetically distinguished from most but not all of the 12 populations of purple loosestrife included in this analysis. As a group, 11 cultivars of putative purple loosestrife origin were not genetically distinguishable from a group of 9 cultivars of putative wand loosestrife origin. For the cultivars, more than one plant was assayed for only the 'Robert' cultivar. Of five different plants labeled and sold as the 'Robert' cultivar, three could be differentiated from one another on the basis of isozyme banding patterns. This indicates that the plants labeled and sold as the cultivar 'Robert' do not constitute a true clone, i.e., a population produced by asexual reproduction.

Sexual Reproduction by Cultivars

The sexual reproductive system in the loosestrife genus is complex and has been the subject of much research (Darwin 1865; Mulcahy and Caporello 1970; Nicholls 1987, among others). Flowers of the loosestrife species studied are heterostylous. In purple loosestrife and wand loosestrife, there are three style lengths, and in winged loosestrife there are two style lengths. In the tristylous case, a flower of one style length has two sets of stamens of different lengths; long-styled plants have short and mid-length stamens, mid-styled plants have short and long stamens, and short-styled plants have mid-length and long stamens. This is a heteromorphic, sporophytic self-incompatibility system in that only matings between styles and stamens of the same length can produce offspring. Such matings are referred to as compatible crosses. This system is effective but not strict since some incompatible matings, which include self-pollinations, produce progeny (Mulcahy and Caporello 1970).

Cultivars have been found to be both male as well as female fertile, and to produce viable seeds from incompatible as well as compatible crosses. Anderson and Ascher (1991) studied 6 cultivars of purple loosestrife parentage, 8 cultivars of wand loosestrife parentage, 17 populations of purple loosestrife, and 5 populations of winged loosestrife. For these populations, they determined rates of male and female fertility as well as seed viability. Male fertility is inferred if pollen grains stain when treated with aniline blue. Pollen stainability in the cultivars averaged 86%, ranging from 15 to 100%. Pollen stainability in purple loosestrife and winged loosestrife averaged 90%, ranging from 33 to 100%. All taxa possessed high levels of male fertility.

Female fertility is the number of seeds set or produced per capsule in compatible crosses. Average numbers of seeds set were nearly equal in open-pollinated cultivars and purple loosestrife, 47 vs. 48 seeds per capsule, respectively (Anderson and Ascher 1991). Ranges in the numbers of seeds set also were similar in cultivars and purple loosestrife, 0 to 236 vs. 0 to 156, respectively. Seeds set in winged loosestrife were similar to those observed in purple loosestrife and the cultivars. Generally, the number of seeds produced was highly variable with variances often exceeding the means.

The cultivars, purple loosestrife, and winged loosestrife all produced seeds when self-pollinated, i.e., from incompatible matings, though the numbers of seeds set were lower than those produced by comparable cross-pollinations (Anderson and Ascher 1991). Some loosestrife plants pollinated themselves and produced seeds in the absence of either insect vectors or interventions by researchers. These results indicate that an incomplete self incompatibility system is present in all studied taxa.

Ottenbreit (1991) found that seed germination rates in open-pollinated populations were lower in cultivars than in purple loosestrife, but the cultivars were far from sterile (Table 3). In addition, Ottenbreit (1991) found that cultivars produce less seeds than purple loosestrife, 3 to 50 vs 10 to 85 seeds per capsule, respectively. Anderson and Ascher (1991) reported a germination rate of 66% for open-pollinated loosestrife seeds (Table 3), a rate they considered low, possibly due to dormancy in these seed populations (see *Seed Germination and Dormancy*). Experimental crosses produced seeds from compatible cultivar x cultivar matings which germinated at a rate one-half that observed for compatible loosestrife x loosestrife matings. Self-pollination reduced seed germination by one-half in loosestrife, and by 80% in the cultivars, as compared to compatible crosses.

Phosphorus Cycling

One possible consequence of the establishment of purple loosestrife in a wetland is an alteration in nutrient cycling patterns, which in turn could affect the functional value of the wetland. In many lakes and streams in Minnesota, phosphorus is the limiting nutrient for plant growth. Consequently, Emery et al. (1991) examined standing crops and concentrations of phosphorus in tissue of purple loosestrife and cattail, which is the plant most often displaced by loosestrife.

In 11 Minnesota wetlands, the aboveground biomass during late August and early September in monodominant stands of purple loosestrife was less ($P = 0.004$) than that of cattail, 440 vs 660 grams dry weight (DW)/m^2, respectively (S. Emery, personal communication, University of Minnesota). The concentration of phosphorus in plant tissue was greater ($P < 0.001$) in loosestrife than in cattail, 2.5 vs 1.7 g of phosphorus/g of plant DW, respectively. Conversion of these values to concentrations per unit area indicates that there was no difference between stands of loosestrife and cattail in levels of phosphorus which averaged 1.1 grams of phosphorus/m^2.

In decomposition studies of loosestrife and cattail, ash-free dry weight (AFDW) decreased most rapidly in purple loosestrife leaves during fall (Emery et al. 1991). The rate of decrease in AFDW of cattail shoots was intermediate between that of loosestrife

Table 3. Rates of germination of seeds produced by different matings among purple loosestrife and cultivars.

Study	Type of mating	Number of populations or crosses	Experimental conditions	Percent germination
Ottenbreit (1991)	open-pollinated purple loosestrife	11	A[a]	98
	open-pollinated cultivars	17	A	88
Anderson and Ascher (1991)	open-pollinated purple loosestrife[b]	4	B	66
	compatible purple loosestrife x purple loosestrife[c]	24	C	83
	self-pollinated purple loosestrife	49	C	39
	compatible purple loosestrife x cultivar	24	C	85
	compatible cultivar x purple loosestrife	46	C	73
	compatible cultivar x cultivar	19	C	40
	self-pollinated cultivars	8	C	8

[a] Explanations of experimental conditions:
A Seeds maintained in petri dishes on filter paper moistened with distilled water in light for hours at 25°C and in the dark for 10 hours at 10°C.
B Seeds maintained in petri dishes on moistened filter paper in the light for 8 to 24 hours per day at 20°C.
C Seeds maintained on soil in plug trays on a greenhouse mist-bench in the light for 10 hours at 21°C.

[b] Data for "bulk seed collections."

[c] Crosses are given as female plant x male plant.

leaves and stems, which decreased at the lowest rate. Little change was observed in the phosphorus concentrations in decomposing plant tissue, except in over-wintered cattail shoots which showed an increase in the fall phosphorus concentration.

In dormant plants growing in artificial wetlands, there were no differences in either above- or below-ground biomass between wetlands containing loosestrife and those containing cattail (Troelstrup 1991). Although the concentration of phosphorus in below-ground tissue was higher ($P = 0.005$) in loosestrife than in cattail, 2.86 vs 2.18 mg phosphorus/g DW, respectively, the levels of phosphorus in plant tissue per square meter were not different between loosestrife and cattail. The levels of phosphorus per gram DW of soil also did not differ between artificial wetlands containing loosestrife and those containing cattail.

No large differences were found in levels of phosphorus per square meter between loosestrife and cattail either in the field or in artificial wetlands. Additional research would be needed to determine how displacement of cattail by loosestrife might alter phosphorus cycling in Minnesota wetlands.

Implications for Management and Regulation

Seed bank and recruitment

Purple loosestrife has the ability to produce a large and persistent seed bank in Minnesota wetlands. Once such a seed bank has developed, which may occur within 5 to 10 years after the plant is first observed in a wetland, it is probably not practical to eliminate loosestrife from that wetland. For this reason, the current policy of the Minnesota Department of Natural Resources is to attempt to eliminate recently established, small populations before attempting to control large, long established populations of loosestrife. This is the general approach to plant invasions recommended by Moody and Mack (1988).

In wetlands with large, long established populations of loosestrife, which indicates the presence of a persistent seed bank, established plants may be eliminated by the use of herbicide or other methods. Nevertheless, it is likely that purple loosestrife will be reestablished in such a wetland through recruitment from the seed bank. Such recruitment can be reduced, but not prevented by the use of herbicides or perhaps by competitor introductions. Though purple loosestrife may constitute a large part of the seedling community in a wetland due to a high recruitment rate, this does not appear to significantly reduce the size of the purple loosestrife seed bank. The presence of a large and persistent seed bank in a wetland can lead to recruitment of additional loosestrife seedlings following minor soil surface disturbance. The possibility that purple loosestrife may be reestablished in a wetland through recruitment from the seed bank exists as long as the seeds can remain viable while buried in wetland soil, assuming that environmental conditions are suitable, at least periodically, for recruitment. These seeds can probably remain viable for considerably more than three years. The future results from studies of longevity of purple loosestrife seeds buried in Minnesota wetlands will be valuable to wetland managers.

Current approaches to managing purple loosestrife include the use of herbicides, manipulation of water levels, and pulling by hand. These approaches all require participation of managers, presumably over an extended period of time. An alternative to these manipulations is biocontrol, which in this case means the introduction of insects native to Eurasia that appear to keep loosestrife abundance low by feeding on plants (Thompson et al. 1987). Biocontrol, if successful, has an advantage over the manipulations described above in that insects, once established, will control loosestrife without requiring further action by managers. Nevertheless, objections to the introduction of biocontrol agents may arise due to concern that these insects may consume and damage desirable plants.

Taxonomy and genetics

The taxonomic relationships among purple loosestrife and cultivars are complex. It may be possible to distinguish among limited numbers of cultivars and populations of purple loosestrife, either on the basis of differences in morphology or isozymes present in plant tissue. Nevertheless, many cultivars are indistinguishable from many purple loosestrife populations. In addition, different plants labelled and sold as a single cultivar may not constitute a true clone. More importantly, cultivars were found to possess high levels of male and female fertility, and to produce seed which germinated at high rates. Even when self-pollinated, cultivars produced seed which germinated at a rate of 8%, which is significant given the high rate of seed production in this species. Consequently, the distribution of loosestrife cultivars through sale in the horticultural trade can be expected to contribute to the spread this species. Since the Minnesota Legislature resolved to limit the spread of purple loosestrife in the State, this body acted appropriately in authorizing the Minnesota Department of Agriculture to make purple loosestrife a primary noxious weed and subsequently prohibit the sale of this species and wand loosestrife and any cultivar derived from either of these species.

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