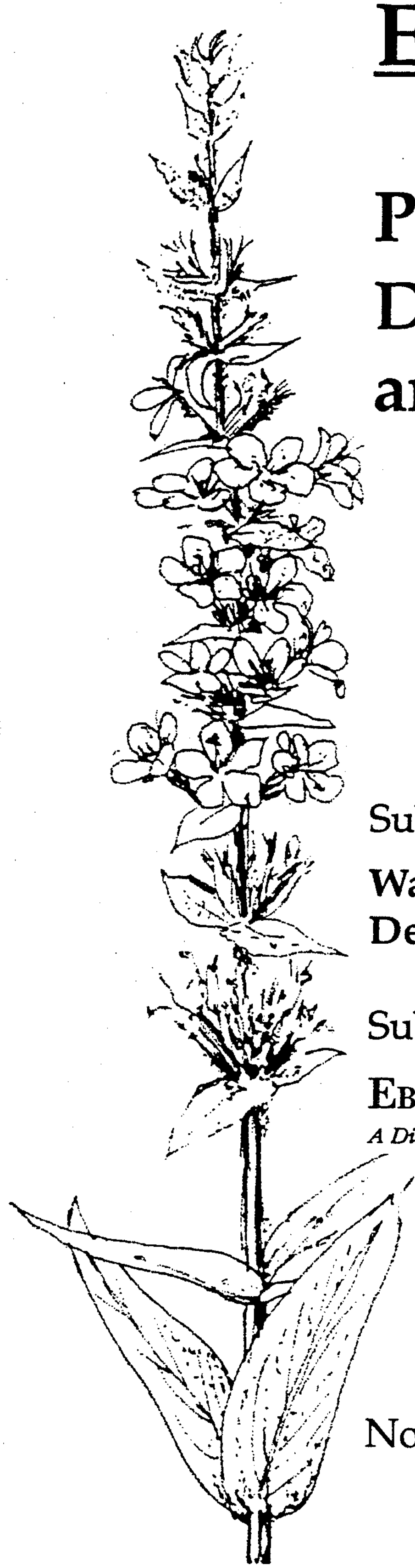
FINAL REPORT

Element B

Purple Loosestrife: Distribution, Biology, and Ecology



Submitted to

Washington State
Department of Ecology

Submitted by

EBASCO ENVIRONMENTAL
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ABSTRACT

Purple loosestrife (*Lythrum salicaria* and *L. virgatum*) is an emergent Eurasian wetland plant that is rapidly invading wetlands in the Pacific Northwest. Difficult to control once established, this invasive perennial forms monospecific stands that displace native vegetation. Development of an effective management plan for this noxious emergent plant species requires thorough knowledge of its biological characteristics and ecological requirements. To assist in plan development, this report provides information on the biology, ecology, and distribution of purple loosestrife in Washington. Suggestions for further research are also included.

Loosestrife is a non-rhizomatous, tap-rooted perennial that inhabits a wide range of soil, hydrological, light, and competitive conditions in wetland habitats in Washington. Slow-moving watercourses with broad alluvial deposits provide optimal sites for purple loosestrife colonization, whereas fast-flowing streams and rivers often do not. The plant thrives in habitats where surface water flow rate is reduced.

Reproduction is primarily by seed. The small seed may be easily transported by water, wind, and animal and human vectors. Seedlings are produced in such great quantities as to frequently preclude the germination and growth of competing native species. Mature plants possess a dense, woody, fibrous root system comprised of an abbreviated taproot and lateral roots with numerous shoot buds. The root systems of adjacent plants may intertwine to form a dense mat that excludes native vegetation.

A complex of stenophagous arthropod herbivores limits the development and spread of purple loosestrife throughout its native range. This situation does not occur in North America, where the species experiences a low level of herbivory by unspecialized phytophages. Many of the European arthropods inflict significant injury to the leaves, stems, and roots of seedlings. The plant's observed rapid rate of spread is due in large part to the absence of damaging natural enemies in North America.

FINAL REPORT

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PURPLE LOOSESTRIFE: DISTRIBUTION, BIOLOGY, AND ECOLOGY

Submitted to:

Washington State Department of Ecology

Submitted By:

Ebasco Environmental

Project Manager
Jay Brueggeman

Technical Lead
Gary Piper, Ph.D.

Contributors
Stacy Giles Emory, M.S.
Clayton Antieau, M.S.

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1.0 INTRODUCTION

1.1 PURPOSE

The Washington State Departments of Agriculture, Ecology, Fisheries, Natural Resources, and Wildlife, and the Washington State Noxious Weed Control Board, acting as lead agencies, have proposed to develop and implement a management plant for noxious emergent plant species occurring in the state of Washington. Species of concern include three species of cordgrass or *Spartina* (*S. patens*, *S. alterniflora*, and *S. anglica*), purple loosestrife (*Lythrum salicaria*, *L. virgatum*), garden loosestrife (*Lysimachia vulgaris*), giant hogweed (*Heracleum mantegazzianum*), and indigo bush (*Amorpha fruticosa*). The lead agencies want to determine which management alternative or combination of alternatives would provide the most effective management of noxious emergent plant species with the least environmental impacts. The ultimate goal of the proposal is to develop criteria and approaches for managing infestations of existing noxious species and new invaders.

Through a public scoping process, the lead agencies have determined that a management program could have significant adverse environmental impacts. Thus, an environmental impact statement (EIS) is required under RCW 43.21C.030(2)(c). Topics to be discussed in the EIS have been identified by the lead agencies, including biology and ecology of problem species, management alternatives, and mitigation strategies. Ebasco Environmental was contracted by the nominal lead agency, the Washington State Department of Ecology, to assemble and synthesize available information on these topics of interest for inclusion in the EIS.

Development of an effective management plan for noxious emergent weed species requires thorough knowledge of the biological characteristics and ecological requirements of that species. To assist in plan development, this report provides information on the biology, ecology, and distribution of *Lythrum salicaria* (and *L. virgatum*, when available), purple loosestrife, in Washington. Separate reports detail the biology and ecology of the other species of concern occurring in Washington.

1.2 OBJECTIVES

The objectives of this report are to:

(1) summarize information on the distribution of purple loosestrife, including locations of infestations in Washington; and,

(2) characterize the biology and ecology of purple loosestrife. Topics discussed include taxonomy, physiology, preferred habitat, life history, modes of dispersal, and factors affecting growth, spread, and dieback.

Discussion of biological and ecological characteristics focuses on those attributes that contribute to the invasive nature of purple loosestrife and that have implications for its control. Primary sources of information for this report were published journal articles and published and unpublished studies and local and regional authorities. Information was obtained from both national and international sources.

2.0 DISTRIBUTION

2.1 HISTORICAL DISTRIBUTION

Lythrum salicaria is an emergent aquatic plant of Eurasian origin (Stuckey 1980). The distribution of purple loosestrife in the Northern Hemisphere is shown in Figure 1. This species was first noted in North America in the early 1800's in estuaries in the northeast. This infestation and the species' subsequent spread throughout North America is discussed in detail by Stuckey (1980). In general, the timing of this range extension is closely associated with exploration and emigration from northern Europe and the development of inland canals and maritime commerce (Thompson *et al.* 1987). Introduction of purple loosestrife into North America appears to be a repeated event through the first half of the 19th century. Purple loosestrife is present in most of the marine estuaries of northern Europe that were export centers to North America and was probably introduced into North American estuaries in shipping ballast (Stuckey 1980). There is also evidence that seeds of this species arrived inadvertently on imported raw wool or sheep brought over from Europe.

Purposeful introduction of the plant may also be responsible for its extended distribution in North America. Purple loosestrife was valued as an herb in northern Europe and seeds may have been imported and cultivated by immigrants. Although *L. salicaria* is rarely used now, it was recommended in early herbals (Grieve 1959). Powders made from dried leaves and extracts from the roots were used to treat gastro-intestinal disorders. Fresh or dry leaves were also used to heal wounds, ulcer, and sores (see Thompson *et al.* 1987 and references therein for a discussion of purple loosestrife's other herbal properties). In addition, Thompson *et al.* (1987) cite horticultural escapes and attempts by beekeepers to naturalize this species as a honey plant as possible contributing factors to its early spread. The distribution of *L. salicaria* in North America as of 1900 is illustrated in Figure 2.

2.2 PRESENT-DAY DISTRIBUTION

Although established in North America since the early 1800's, purple loosestrife was not interpreted as a noxious weed problem until the 1930's, when it became aggressive in the floodplain pastures of the St. Lawrence River (Stuckey 1980). Subsequently, this species has spread extensively and become common in other river floodplain areas and in the previously glaciated regions of the northern United States. It has also infested streams, irrigation ditches, riparian areas, and pastures. The known distribution of purple loosestrife in North America prior to 1940 is illustrated in Figure 3. By 1985, the species had been reported in all major river basins except the Arkansas, Colorado, and Rio Grande (Thompson *et al.*

1987, Figure 4). This species has also become a serious problem in wetlands and irrigation systems in the Great Plains and far West. The initial multiple infestations in widely scattered habitats in north, south, and central Europe suggest a robust and varied genetic stock. A large gene pool may be responsible for its successful and rapid infestation across North America (Thompson *et al.* 1987).

2.3 PACIFIC NORTHWEST DISTRIBUTION

Purple loosestrife was first identified and documented in Washington in 1929 from the boggy margins of Lake Washington near the University of Washington campus and along the shores of Lake Sammamish (Brookreson 1991). First reports of its establishment in the Pacific Northwest were from marine estuaries, suggesting again that marine commerce was a primary factor in its spread (Thompson *et al.* 1987). In the last 20 years, however, purple loosestrife has become well-established in wetland reclamation projects and riparian wetlands in the Northwest (Thompson 1989). Serious recent infestations in Washington have been in irrigation areas (Thompson *et al.* 1987).

Based on a tentative inventory, purple loosestrife occurs in at least 30 of Washington's 39 counties (Hovanic 1992, pers. comm.). It appears to be colonizing more slowly in western Washington than in eastern Washington. This differential rate of spread may be the result of more competitive wetland species in western Washington, climatic differences, fertility of waters, or intraspecific variation (Brookreson 1991). The extensive irrigation canal system in eastern Washington (Winchester and Frenchman Hill Wasteways) has also facilitated its rapid spread. Wetlands of the Columbia Basin were created in the 1950s by the Bureau of Reclamation irrigation project. These wetlands formed as water was supplied to and then flowed off the land. Wetland species, therefore, were probably barely established when purple loosestrife was first introduced to the Winchester Wasteway area in the 1960s, providing the opportunity for relatively rapid invasion of purple loosestrife (Hovanic 1992, pers. comm.) At present, the Washington State Departments of Wildlife and Agriculture are compiling a purple loosestrife inventory database, and this information will be used to more accurately map the distribution of purple loosestrife in Washington. Site-specific information is being compiled and a current distribution map will be available upon completion of that study.

3.0 BIOLOGY AND ECOLOGY

3.1 TAXONOMY AND PHYSIOLOGY

3.1.1 Taxonomic Status of Species Present in Washington

Lythrum is one of the largest genera in the loosestrife family (Lythraceae). The family is mainly distributed in the tropics, but also in temperate regions. There are approximately 22 genera and 450 species (Heywood 1978). Many species in the Lythraceae are known chiefly

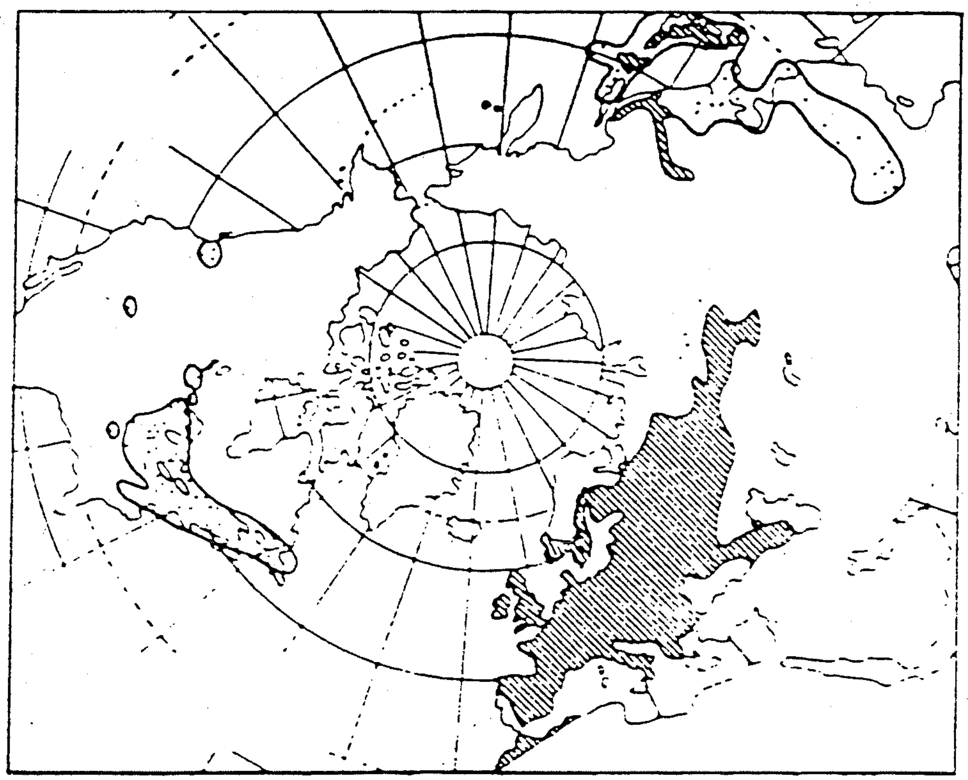

Figure 1. Distribution of *Lythrum salicaria* in the Northern Hemisphere (after Hultén 1964, 1971). Shaded areas indicate zones of more or less continuous distribution; dots represent collection sites; solid lines indicate probable outer distribution boundary; dashed lines are tentative outer limits.
Source: Thompson, Daniel Q. et al. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands. 1987. Courtesy of U.S. Fish and Wildlife Service Research 2.

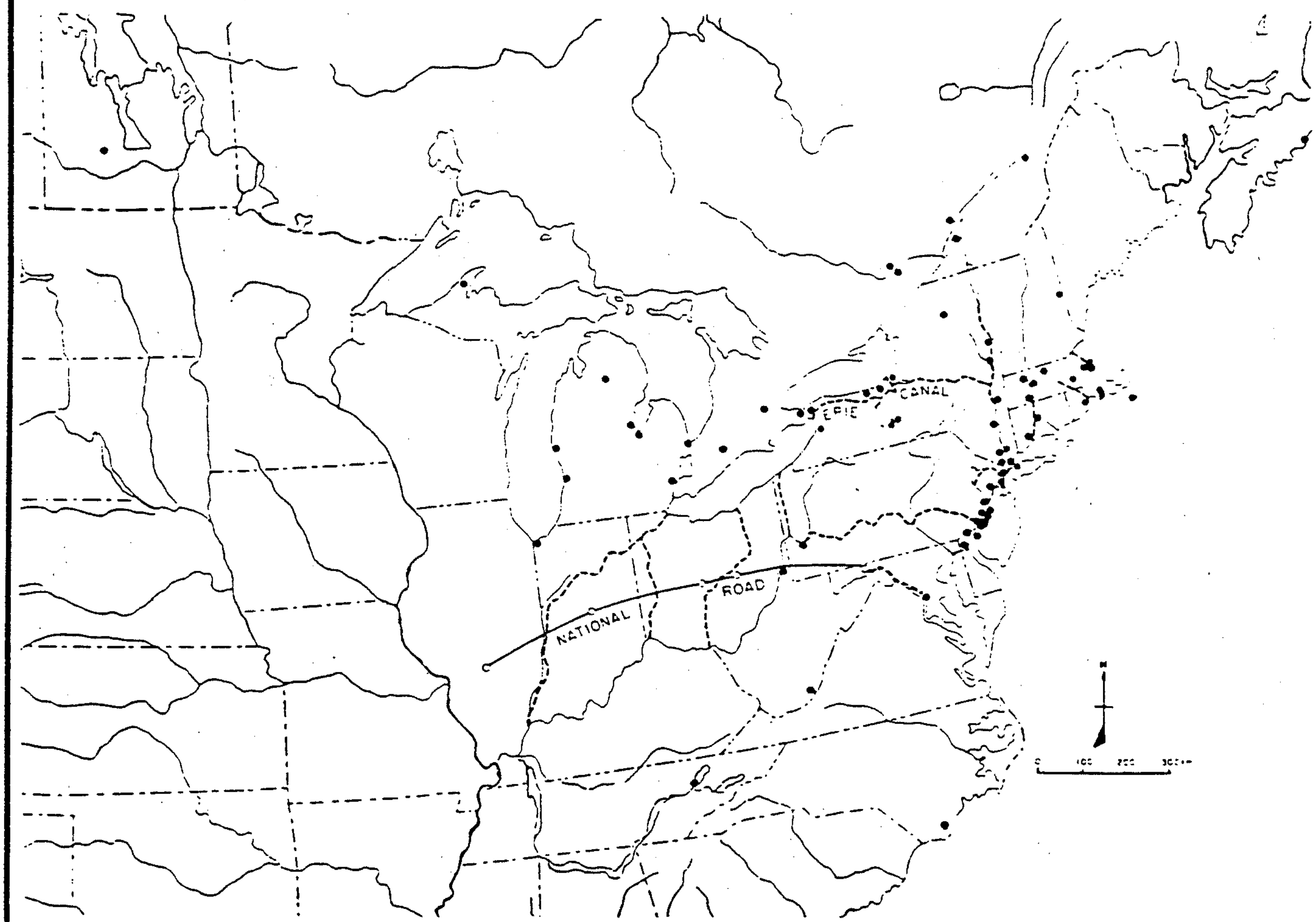

Figure 2. Spread of *Lythrum salicaria* as of 1900 (after Stuckey 1980).
Source: Thompson, Daniel Q. et al. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands. 1987. Courtesy of U.S. Fish and Wildlife Service Research 2.

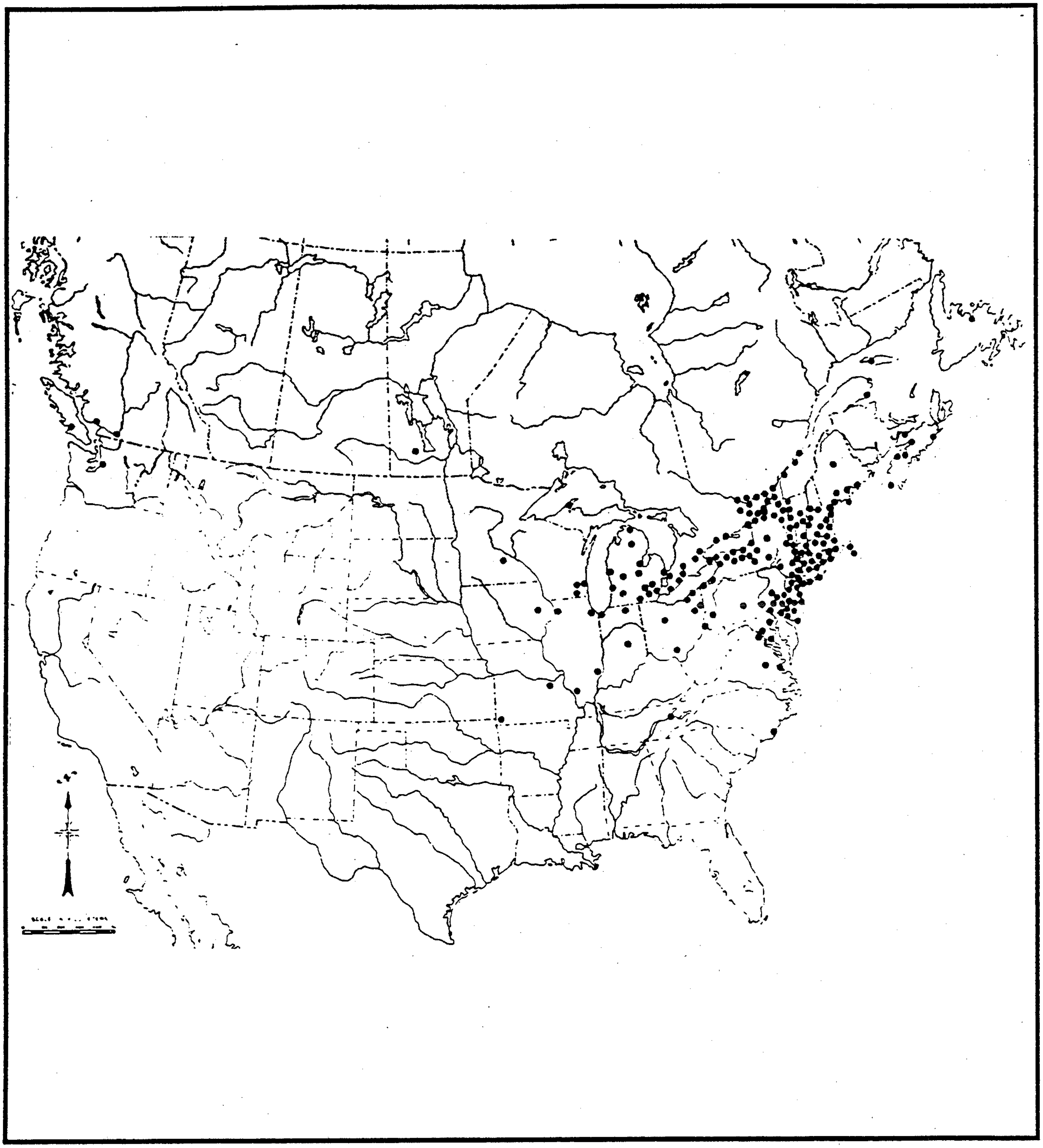

Figure 3. Distribution of *Lythrum salicaria* as of 1940 (after Stuckey 1980).

Source: Thompson, Daniel Q. et al. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands. 1987. Courtesy of U.S. Fish and Wildlife Service Research 2.

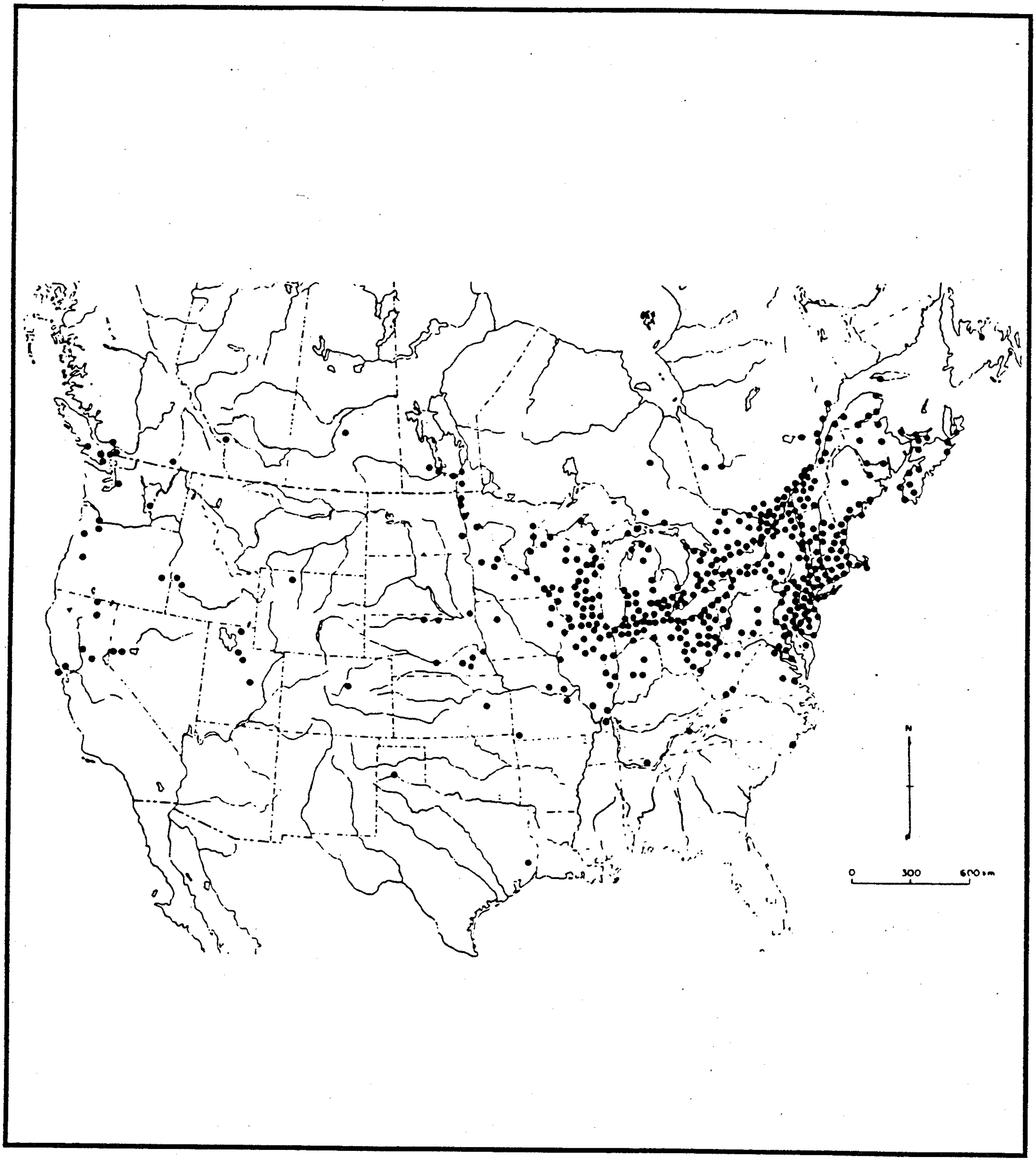

Figure 4. Distribution of *Lythrum salicaria* as of 1985.
Source: Thompson, Daniel Q. et al. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands. 1987. Courtesy of U.S. Fish and Wildlife Service Research 2.

as sources of certain dyes (henna, for example), but are also cultivated as ornamental trees and shrubs (warmer climates), and perennials (temperate regions).

In his synopsis of *Lythrum* in the United States, Shinners (1953) recognized 12 species. *L. salicaria* is one of three *Lythrum* species thought to be introduced to North America. Although morphologically similar to another non-indigenous species, *L. virgatum,* Thompson *et al.* (1987) contend that *L. salicaria* is taxonomically well-defined. Both species are purple-flowered (and have both been referred to as purple loosestrife), but can be distinguished, in general, by leaf shape and degree of pubescence. Thompson *et al.* (1987) noted intraspecific variability in the amount of leaf pubescence in herbarium specimens of *L. salicaria*. Shamsi and Whitehead (1974b) indicate this variability could be in response to differing levels of light intensity. The glabrous-leaved forms of *L. salicaria* are difficult to distinguish from *L. virgatum*. However, other characteristics can be used to distinguish between these two species (for example, leaf base shape and relative length of calyx lobes and appendages).

L. salicaria is well-documented as occurring in at least 30 of Washington's 39 counties (Hovanic 1992, pers. comm.). It is uncertain if *L. virgatum* has naturalized in Washington (there are no records of this species in the University of Washington herbarium), and is not recognized by Hitchcock and Cronquist in the Flora of the Pacific Northwest (1973). However, these closely related species are both listed as noxious weeds in Washington because of their similar habitat requirements, and because they are not easily distinguished from each other in the field. It is also of note that two additional non-native species of *Lythrum* have been introduced into Washington and are invading disturbed wetland habitats: *L. hyssopifolia* and *L. peplus* (*Peplis portula* L.). Neither of these species is listed as a noxious weed in Washington.

3.1.2 Hybridization with Native and Non-native Species

The three species of loosestrife documented in Washington (*L. salicaria*, *L. hyssopifolia* and *L. peplus*) are not native to the United States. A fourth species native to the United States, *L. alatum*, is listed in Hitchcock and Cronquist (1973) but apparently has not been reported in Washington, although it does occur in British Columbia (Taylor and MacBride 1977). As mentioned in Section 3.1.1, it is uncertain if *L. virgatum* occurs in Washington, but there is evidence that this species hybridizes with *L. alatum* (see below). In his pollination studies of *L. salicaria* and *L. alatum*, Levin (1970) found that despite frequent pollinator flights between these two species there was no evidence of hybridization. Hybridization of purple loosestrife with native species, therefore, does not seem to be a major concern.

Information on hybridization of purple loosestrife with non-native species is scant and seems to be limited to cultivars of this and related species. One cultivar ['Morning Gleam' - 1953 (Morden)] appears to be the product of interspecific hybridization between *L. virgatum* and *L. alatum*. Research at the University of Minnesota is being conducted to determine if natural populations of purple loosestrife hybridize with sterile horticultural cultivars of either

L. salicaria or *L. virgatum*. All *L. salicaria* cultivars examined to date have been shown to be fertile and thus capable of producing viable seeds when crossed (Brungardt 1992).

Little literature is available regarding ploidy levels of purple loosestrife and their relationship to interspecific hybridization, adaptation, and speciation. Research to establish the fertility levels in *L. salicaria* and its cultivars, *L. virgatum*, and *L. alatum* has revealed primarily tetraploid population of purple loosestrife, although diploid and hexaploid populations have been noted (Anderson and Ascher 1990).

3.1.3 Physiological Processes

Purple loosestrife is a dicotyledonous plant and photosynthesizes using the C_3 photosynthetic pathway. During its seasonal growth period, *L. salicaria* possesses the ability to quickly respond to changes in its localized environment by initiating morphological adjustments. For example, inundation of stems and roots by an elevated water level leads to the formation of aerenchyma, specialized tissue that increases the plant's buoyancy and enhances its ability to survive prolonged submergence. This trait gives the species a competitive advantage over other wetland plant species (Thompson *et al.* 1987).

No unusual physiological processes are known for this species that would benefit development of an effective management plan. In addition, there are no published research data available to indicate whether *L. salicaria* seedlings or established plants are allelopathic.

3.2 HABITAT REQUIREMENTS OF PURPLE LOOSESTRIFE

3.2.1 Plant community types

Lythrum salicaria was first reported from the northeastern coast of North America in 1814 (Stuckey 1980). Although the species presently occurs across most of the northern United States and southern Canada, heaviest infestations occur in the previously glaciated regions of the northeastern United States and southeastern Canada. It also occurs in locations in the Midwest, Pacific Northwest, and California (Thompson *et al.* 1987).

The plant is found in wetlands such as cattail marshes, sedge meadows, and open bogs. It can also be found along stream and river banks, lake shores, and on alluvial floodplains. Populations may develop in drainage or irrigation ditches and other disturbed wet soil areas such as cranberry bogs and wild-rice beds. Habitat vulnerability to invasion by *L. salicaria* can be judged by determining existing plant associates. Typical plant associates resident in susceptible habitats (depending on region) include common cattail (*Typha latifolia* L.), blue cattail (*T. glauca* Godr.), reed canarygrass (*Phalaris arundinacea*), common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), bulrushes (*Scirpus* spp.), sedges (*Carex* spp.), water horsetail (*Equisetum fluviatile* L.), and willows (*Salix* spp.) (Piper 1992, per. comm.).

3.2.2 Substrate

Soil type appears to be relatively unimportant and is not usually a factor in restricting the distribution of *L. salicaria* (Thompson *et al.* 1987). Soil moisture is of greatest significance in the plant's ability to invade and successfully establish (Thompson *et al.* 1987). However, recent observations on the lower Columbia River in Washington indicate infestations may occur first on silty soils, rather than on sandy soils, and in areas that do not receive wave action (Dolstad 1992, pers. comm.).

3.2.3 Climate

The worldwide distribution of *L. salicaria* clearly identifies it as a plant of temperate climates (Thompson *et al.* 1987, Figure 1). Temperature may be a limiting factor in the northern distribution of the plant in North America. Prolonged winter temperatures below -29°C (5°F) reduce its survivability (Thompson *et al.* 1987). It successfully endures periods of subzero winter temperatures often experienced in Washington. However, the species has also invaded subtropical areas and is now known from Africa (Ethiopia), Australia, New Zealand, and Tasmania (Thompson *et al.* 1987).

3.2.4 Soil Moisture/Surface Hydrology

Purple loosestrife has a strong affinity for moist or saturated soils. It occasionally may be found in drier sites but the plants are not as vigorous as those occurring in wetter soils, although plants still flower and produce seeds. Watershed type strongly influences the plant's ability to become established. Slow-moving watercourses with broad alluvial deposits provide many colonization sites for purple loosestrife (Parker and Burrill 1992), whereas fast-flowing streams and rivers usually do not. The plant thrives in habitats where surface water flow rate is reduced.

Periodic shallow flooding does not appear to jeopardize plant survival (Malecki and Rawinski 1985). Smith (1964) noted older plants were able to survive for many years even when submerged to depths of 60 to 90 cm (24 to 35 in). Thompson *et al.* (1987) indicated prolonged flooding with at least 70 cm (28 in) of water killed most first-year plants.

3.3 REPRODUCTION

3.3.1 Sexual reproduction

3.3.1.1 Phenology

Lythrum salicaria is an emergent, 0.5 to 3.0 m (1.6 to 9.8 ft) tall, herbaceous perennial hydrophyte with an abbreviated taproot. Seed germination occurs in late spring and early summer. Seedling growth is rapid and first-year plants may produce a flowering shoot up to 30 cm (11.8 in) in height. The production of distinctive reddish-purple flowers on terminal spire-shaped panicles begins in late June and continues until September or October. Seeds are produced in capsules that dehisce when mature, releasing the seeds. Seeds from early flowers begin to ripen in mid-July and continue to mature as flower development progresses into the late summer. The semi-woody stems die in the fall but remain attached to the root crown for several years. Purple loosestrife overwinters as a root crown or in the seed stage. New stems develop from buds 2 cm (.8 in) under the soil surface on the perennial rootstock during spring. As the rootstock ages, the number of aerial shoots produced increases. Plants with 30 to 50 stems are commonly observed (Thompson *et al.* 1987). Variation in leaf arrangement patterns and morphology have been recorded (Shamsi and Whitehead 1974b).

3.3.1.2 Pollination

The bisexual flowers of purple loosestrife are insect-pollinated (Graham 1964). Self-pollination is possible (Stout 1923), but cross-pollination is more prevalent because of the heterostylous condition of the flowers (Darwin 1865, Stout 1925, Levin 1970, Mulcahy and Caporello 1970, Halkka and Halkka 1974). In Europe and North America, pollination is effected by different species of bees from the subfamilies Anthophorinae, Apinae, Bombinae, Megachilinae, Melittinae, and Xylocopinae (Levin 1970; Batra *et al.* 1986). The plant has often been promoted by apiarists as an acceptable pollen and nectar source for the honey bee, *Apis mellifera* (Pellett 1966). The butterflies *Pieris rapae*, *Colias philodice*, and *Cercyonis pegala* have also been reported to be agents of pollen transfer (Levin 1970). Many other species of predaceous, parasitic, phytophagous, and saprophagous insects visit *L. salicaria* flowers for pollen and nectar (Batra *et al.* 1986).

3.3.1.3 Seed Production/Dispersal

Reproduction in purple loosestrife is primarily accomplished through seed production. Seed crop size is dependent on a plant's age, size, and vigor. Up to 900 seed capsules may be produced on an averaged-sized one-year old plant, each capsule yielding about 120 seeds (Rawinski 1982). Older multi-stemmed plants reportedly may produce between two and three million seeds (Thompson *et al.* 1987). A monospecific stand of the plant may yield up to 59 billion seeds per hectare (Teale 1982). Each seed weighs about 0.06 mg (Shamsi and Whitehead 1974a).

Seed dispersal by water is common (Ridley 1930), with the minute seeds often floating or drifting with the current for a number of days before sinking or germinating (Thompson *et al.* 1987). Wind is of little consequence in the long distance transport of *L. salicaria* seeds (Thompson *et al.* 1987). Seeds also may be readily disseminated in mud adhering to the feet or body surfaces of livestock, waterfowl and other wetland animals. Red-winged blackbirds (*Agelaius phoeniceus*) have been observed eating the seeds (Rawinski 1982) and some of the hard seeds probably pass through the digestive system unharmed and are deposited in feces at sites distant from the initial point of ingestion. Additional information on dispersal is found in Section 4.1.2.

Seed bank potential for purple loosestrife is enhanced by the high viability of its seeds. Viability decreased from 99 to 80% after two years of submersion in a natural body of water (Rawinski 1982). Information on propagule longevity in the soil or water is not conclusive, but longevity may be at least two years or longer according to Shamsi and Whitehead (1974a) and Rawinski (1982). In a recent study conducted in Minnesota, researchers found over 400,000 *L. salicaria* seeds per m^2 in the upper 5 cm (2 in) of wetlands soils they sampled (Welling and Becker 1990). They also reported that most seeds located in the top 2 cm (.8 in) of soil successfully germinated; seeds buried below this depth remained dormant possibly because seed requires a certain amount of light (see Section 3.3.1.4) to germinate.

3.3.1.4 Seed Germination and Seedling Survival

Temperature and Weather

Germination of overwintered seeds occurs in late spring or early summer. The critical temperature for germination of *L. salicaria* seeds lies between 15 and 20°C (59 and 68°F), with no germination observed below 14°C (57°F) (Shamsi and Whitehead 1974a). Purple loosestrife seed germination occurs in the presence or absence of light, with germination being more pronounced in lighted or open situations (Shamsi and Whitehead 1974a). These authors also found that lengthening the photoperiod to which the seeds were exposed did not accelerate the rate or percentage of germination. In laboratory experiments, approximately 90% of the seeds tested germinated within a week after initial exposure to light and optimal temperatures.

Substrate and Moisture Requirements

Seeds germinate in acidic or alkaline soils. Shamsi and Whitehead (1974a) reported germination down to pH 4.0 and Thompson *et al.* (1987) recorded germination at a pH of 9.1. The latter authors indicated that optimum soils for the growth of *L. salicaria* are those that are slightly acid or neutral. Germination rates appear to be similar in nutrient-rich and nutrient-deficient soils (Shamsi and Whitehead 1974a).

Floating seeds or seedlings require a moist soil substrate to facilitate successful establishment. Seedlings develop best in high organic matter content soils but will tolerate various soil types, including clay, sand, muck, and silt, as long as there is sufficient moisture (Thompson *et al.* 1987). The plant is particularly invasive in alluvial floodplains, wetlands, irrigation wasteways and canals, roadside or railroad ditches, wet pastures, and also along stream or river banks and pond and lake shores (Stuckey 1980).

Seedling growth is rapid, with much of the plant's photosynthate being utilized for root development (Bodmer 1928, Thompson *et al.* 1987). A seedling's growth rate may exceed 1 cm/day under favorable conditions (Rawinski 1982). Seedlings emerging in the spring grow rapidly, and in eight to ten weeks are capable of producing a floral shoot during the first year. Those developing in the summer produce only five to six pairs of leaves before growth ceases (Shamsi and Whitehead 1974a). Spring-produced seedlings exhibit a higher survival rate than do summer-produced seedlings. Established seedlings can survive inundation by waters of low turbidity up to depths of 45 cm (Hayes 1979).

Competition

The ability of purple loosestrife to compete successfully with other wetland plant species for light, water, and nutrients depends on several interrelated factors. These include the timing of *L. salicaria* emergence in relation to that of other plant species, its site density, and its growth form. *Lythrum* seedlings appear during the spring and quickly develop an extensive root system to facilitate the acquisition of water and nutrients. Seeds usually occur in such large numbers and germinate simultaneously in such high densities (10,000 to 20,000 per m^2 or 10.8 ft^2) that growth of competing plant seedlings is effectively suppressed (Rawinski 1982). Rapid shoot and leaf development further contribute to the shade blanket above the understory vegetation. Extremely high densities of *L. salicaria* seedlings often appear at a site following the application of an herbicide used to kill mature plants. The herbicide eliminates intraspecific competition offered by older plants and renders the treatment site vulnerable to reinfestation.

Watercourses and wetlands having shade-covered areas are less susceptible to invasion and colonization by purple loosestrife (Thompson *et al.* 1987). Seed germination and seedling growth are best in sites receiving full sun (Shamsi and Whitehead 1974b, 1977b). Malecki and Rawinski (1985) found that certain early-germinating plant species can out-compete *L. salicaria* seedlings by monopolizing available sunlight.

Herbivory

A complex of stenophagous arthropod herbivores limit the development and spread of purple loosestrife throughout its native range (Blossey and Schroeder 1986). This situation does not occur in North America where the plant experiences a low level of herbivory by unspecialized phytophages (Hight 1990; Piper, unpublished data). Many of the European arthropods inflict significant injury to the leaves, stems and roots of seedlings (Batra *et al.* 1986). The importance of avian and mammalian feeding on *L. salicaria* seedlings has not been determined.

3.3.2 Vegetative Reproduction

The rootstock is the main organ of perenniation; vegetative spread is therefore limited (Shamsi and Whitehead 1974a). Mature plants possess a dense, woody, fibrous root system comprised of an abbreviated taproot and lateral roots with numerous shoot buds. Root systems of adjacent plants may intertwine to form a dense mat that makes it difficult, if not impossible, to successfully completely uproot individual plants older than one year. The taproot normally only penetrates to a depth of up to 30 cm (12 in) (Parker and Burrill 1992).

However, some infestations have been noted to be shallowly rooted and easily uprooted by hand (Dolstad 1992, pers. comm.).

Purple loosestrife is a simple perennial; it does not spread by rhizomes (Thompson *et al.* 1987). The plant can spread vegetatively by resprouting from cut stems and regenerating from fragmented rootstock sections (Rawinski 1982). Although lateral root crown growth offers new sites of origin for peripheral stems, purple loosestrife individuals do not spread far by their roots (Parker and Burrill 1992). This species can be vegetatively spread during local perturbations (adventitious roots and shoots from crippled, trampled, or buried stems) (Thompson 1987, WDNR 1990). The distances that purple loosestrife can potentially be spread vegetatively have not been investigated.

3.3.3 Plant Growth and Competition

3.3.3.1 Nutrient and Moisture Requirements

Substrate and moisture requirements for post-seedling stage plants are comparable to those for seedlings (Thompson *et al.* 1987). Shamsi and Whitehead (1977a) determined the response of purple loosestrife to deficiencies in nitrogen, phosphorous, and potassium in laboratory experiments (plant growth in response to increased levels of these nutrients was not examined). Plant growth was more adversely affected by a lowered nitrogen level than by reductions in phosphorous and potassium. The plant responded to diminished levels of nitrogen and phosphorous with an increase in root area.

3.3.3.2 Temperature and Weather

Lythrum growth rate is strongly influenced by temperature, with the most rapid development occurring at temperatures above 20°C (68°F) (Shamsi and Whitehead 1977b). Cool spring and early summer weather may retard aerial stem development from established rootstocks or seedling growth, which may impact plants' abilities to compete effectively against other species (Shamsi and Whitehead 1977b). The extent to which this is true in the Pacific Northwest has not been investigated.

Purple loosestrife growth potential is maximized in open, fully sunlit situations. Thompson *et al.* (1987) observed that the plant can survive in partial shade, but noted less vigor and a diminished reproductive capacity. Shamsi and Whitehead (1974b) showed that as the light intensity level decreased from 100 to 70 to 40%, reductions in capsule and seed production intensified with each reduction, with significant reductions in flower, capsule, and seed number and weight (but not viability) being recorded at the 40% illumination level. In response to lowered light levels, *L. salicaria* grew leaves that were larger, thinner, and less tomentose.

3.3.3.3 Competition

Purple loosestrife rapidly develops an efficient root system that ensures plant survival. Plants that are several years old usually possess well developed rootstocks with ample carbohydrate storage reserves. This energy is utilized for new shoot growth in the spring and for regrowth should the initial shoots be cut, burned, or killed by foliar herbicides or should the roots be damaged. The dense, shallow mat of roots that forms during an infestation provides a physical barrier that discourages establishment of other species at the site.

This tall, multi-stemmed, leafy plant denies other plants access to sunlight. Shade-intolerant species are soon out-competed. Accumulation of sediments and detritus around the plant's roots enables purple loosestrife to invade deeper water and to form dense stands that shadeout desirable emergent plants and exclude floating plants by preempting open water spaces.

During its seasonal growth period, *L. salicaria* possesses the ability to quickly respond to changes in its localized environment by initiating morphological adjustments. For example, inundation of stems and roots by an elevated water level leads to the formation of aerenchyma, specialized tissue that increases the plant's buoyancy and enhances its ability to survive prolonged submergence. This trait gives the species a competitive advantage over other wetland plant species (Thompson *et al.* 1987).

The use of competing vegetation to manage purple loosestrife has been attempted in several wildlife refuges. Rawinski (1982) planted the weed with Japanese millet (*Echinochloa crus-galli* var. *frumentacea* (Roxb.) W.F. Wright), a desirable wildlife food plant. He found the millet seedlings out-competed those of *L. salicaria*. He also observed that the millet had to be planted immediately after marsh drawdown in order to be effective. Rapid germination and growth of millet enables it to establish quickly and dominate available space. Balough (1986) found that *Echinochloa* does not regenerate well and would have to be replanted annually. He seeded pale smartweed (*Polygonum lapathifolium* L.), a European native, at a purple loosestrife-infested site and found it out-competed the weed. The effect was only of short-term duration as loosestrife shoots produced the following year from rootstocks of established plants negated the effect of the competitive planting. Malecki and Rawinski (1985) suggested that reed canarygrass (*Phalaris arundinacea* L.), a Eurasian grass, may also show promise as a competitive species.

3.3.3.4 Herbivory

Livestock and wildlife graze the early foliage but tend to avoid maturing plants (Parker and Burrill 1992). Rawinski and Malecki (1984) indicated that white-tailed deer (*Odocoileus virginianus*) may use the plant as a browse plant. However, their feeding did not seriously impair the plant's growth rate. Browsing leads to the development of shorter but more highly branched plants. The use of purple loosestrife as a food source by other mammalian herbivores is not well documented. Its seeds are inedible to most wetlands bird species (Rawinski 1982).

In the plant's native homeland of Europe, *L. salicaria* usually occurs as a minor component (1-4% of cover) of mixed wetlands vegetation, rarely being found in monospecific stands (Bodrogkozy and Horvath 1977). Plants are typically less than 1 m (3.2 ft) in height and only produce a maximum of 5 to 10 flowering shoots (Blossey and Schroeder 1991) in contrast to those plants found in North America. The explanation for this phenomenon may be based in part on poorly known or documented genetic differences among European and North American *L. salicaria* biotypes, but plant scarcity in the native homeland is primarily due to occurrence of an extensive guild of injurious, phytophagous insects (Batra *et al.* 1986). In contrast, entomofauna associated with the weed in North America is thought to be depauperate (Hight 1989; Piper, unpublished data).

4.0 BIOLOGY OF INFESTATION

4.1 DISPERSAL AND ESTABLISHMENT

4.1.1 Natural Modes of Dispersal

The annual seed crop produced by an infestation of purple loosestrife is prodigious. Spread of the plant to new sites readily occurs when seeds or seedlings (Ridley 1930) are moved by water currents. Seeds are thought to also be dispersed by aquatic birds and mammals, and to a lesser extent by wind. Animals may contribute to the long distance spread of seeds that survive passage through the animals' digestive tracts and are scattered in the droppings. Additionally, seeds may adhere to plumage, pelage, and muddy feet of animals and be distributed to new areas. With the exception of Kerner (1902, as cited in Thompson *et al.* 1987) there is no evidence of these modes of animal dispersal. Purple loosestrife was one of 21 species included in Kerner's list of seeds found in mud obtained from beaks, feet, and feathers of various water birds. Migratory waterfowl may transport the seeds long distances by this method (Thompson *et al.* 1987).

Stem sections severed by animals such as the muskrat (*Ondatra zibethica*) or broken by strong winds may fall into the water. These floating stem fragments may produce roots, and upon contact with soil, may generate new plants (Thompson *et al.* 1987).

4.1.2 Human-mediated Modes of Dispersal

Humans are the primary dispersers of Lythrum *salicaria* seeds over long distances and were responsible for initially introducing the plant to North America from its native European range in the early 19th century in contaminated soils used for ship ballast, livestock bedding and forage, and on imported sheep or raw wool (Thompson *et al.* 1987). The sale of *L. salicaria* and *L. virgatum* seed and rootstock by some horticultural concerns has also contributed to the spread of these species. Purple loosestrife seeds frequently appear in wildflower seed mixes sold by native plant seed companies (Thompson *et al.* 1987). Nurseries throughout the United States previously sold the plant to Washington gardeners for its ornamental value. The enactment of a quarantine (Chapter 16-752 WAC) in Washington in 1990 now effectively prohibits such transactions and diminishes the spread of this plant as well as the closely related *L. virgatum* and any hybrids via commercial avenues. Plants grown as ornamentals have sometimes accidentally escaped from cultivation and initiated local and regional infestations. Beekeepers have often grown the plant along waterways to provide summer forage for honey bees, thus contributing to the plant's spread (Hayes 1979).

People may also unknowingly transport propagules on their apparel and footwear after having frequented purple loosestrife-infested areas. Mud-coated seeds can adhere to boats, boat trailers, and all-terrain or passenger vehicles utilized in such sites and easily be moved long distances. Wind currents formed by the high-speed passage of vehicles along infested highway corridors may also facilitate short distance seed dispersal (Wilcox 1989).

Although purple loosestrife is capable of invading undisturbed habitats, the spread and dominance of this plant is most pronounced in aquatic habitats subjected to human perturbation. In sites where the plant is currently or has been present, any minor disturbance of the soil surface will usually result in the plant's rapid appearance through recruitment from the seed bank (Welling and Becker 1990).

Disturbance of shoreline and wetland soils resulting from construction activities may contribute to the plant's establishment and/or spread. These might include utility line and irrigation canal installations, highway rights-of-way maintenance (Wilcox 1989), and ditching operations. Heavy machinery and service vehicles used in such activities may also contribute to the dissemination of seeds and stem or root sections. Soils transported away from ditching operations may be contaminated with purple loosestrife propagules. Roadside ditches are frequently colonized by the plant. Waterborne seed moving in the ditches may contribute to its localized spread.

4.2 PERSISTENCE AND SPREAD

4.2.1 Growth and Rate of Spread

A detailed chronology of this hydrophyte's range expansion within the United States was presented by Thompson *et al.* (1987). *L. salicaria* is an opportunistic plant and can readily invade virtually any native wetland habitat. Although the plant can enter relatively undisturbed habitats, its rate of spread is slower than that experienced when disturbed sites are invaded. Most wetland perturbations result from some human-based activity.

Infestations of purple loosestrife appear to follow a pattern of establishment, maintenance at low numbers, and then rapid population increase under optimal conditions (Stuckey 1980; Thompson *et al.* 1987). The species flourishes in wetland habitats that have been disturbed or degraded from draining, drawdowns, bulldozing, siltation, shore manipulation, dredging, and livestock and wildlife trampling. Mudflats exposed following drawdowns are rapidly colonized if *L. salicaria* seeds are present (Cutright 1978). As the level of human traffic in an infested wetland intensifies, the plant's rate of spread within or from the site is accelerated. Any of the previously described seed or plant dispersal methods may be important in facilitating spread of the plant to new areas. Isolated wetlands are more protected from invasion by seed, whereas wetland sites linked by a common waterway are extremely vulnerable (Thompson *et al.* 1987).

The plant's observed rapid rate of spread is due in large part to the absence of damaging natural enemies in North America. Introduction and eventual establishment of European root, stem, bud, leaf, flower, and seed destroying insects show promise of eventually curtailing the plant's invasive nature (Hight and Drea 1991).

Purple loosestrife is spreading much more rapidly in eastern than in western Washington (Brookreson 1991). This may be attributable in part to the occurrence of more competitive plant species in wetlands west of the Cascades, climatic differences, soil nutrient level variations, lower population densities, or presence of less aggressive *L. salicaria* biotypes.

4.2.2 Factors Affecting Recessions and Senescence

Purple loosestrife invasiveness is dependent upon disturbance of wetlands habitats. If the resident emergent vegetation around invader plants is not disturbed, seedling spread will be minimized due to competition for space and sunlight.

Cool summer weather may reduce plant growth rate and seed crop size and thereby inhibit the plant's rate of spread. Drought conditions are likely to benefit the plant. As the water level gradually drops due to evaporation, new areas become available for colonization by seedlings (Thompson *et al.* 1987). The same scenario is frequently repeated in wildlife refuges or impoundments when water levels are purposely manipulated by resource managers.

Although *L. salicaria* can withstand temporary flooding with few adverse effects, prolonged (three or more years) elevations in water level leading to submergence of plants may reduce vigor and density (Malecki and Rawinski 1985).

There are several documented cases of dieback of purple loosestrife stands in Europe (Shamsi and Whitehead 1974a), the ultimate causes of which unfortunately were not elucidated. Therefore, it is unknown whether plant competition, herbivory, or both factors were responsible for the observed declines. A number of host-specific consumer arthropods have been identified as being important regulators of *L. salicaria* populations in Europe.

5.0 INFORMATION AND RESEARCH NEEDS

There is much that still remains unknown about aspects of purple loosestrife biology, ecology, and impact on native wetland communities in Washington. Research must be undertaken to address the following questions:

1. Can natural populations of purple loosestrife hybridize with "sterile" horticultural cultivars of *Lythrum salicaria* or with *L. virgatum*?

   Research in progress: University of Minnesota researchers are attempting to answer this question. All *L. salicaria* cultivars examined to date have been shown to be fertile and thus capable of producing viable seed when crossed (Brungardt 1992). It is virtually impossible to distinguish wild purple loosestrife from marketed cultivars (Anon. 1990). Studies are being continued.

2. What is the longevity of purple loosestrife seed?

   Research in progress: A botanist at the University of Minnesota is presently studying seed longevity (Anon. 1990). Research findings are unavailable.

3. Can seed bank longevity be determined?

   Research in progress: None.

4. Is it possible to force seed germination to deplete the seed bank? What time interval would be required to effect this procedure?

   Research in progress: None.

5. How extensive is the seed bank in comparison to the visible *L. salicaria* infestation?

   Research in progress: None.

6. How is seed viability affected by selective and non-selective herbicides applied to flowering plants?

   Research in progress: Washington Department of Wildlife personnel are determining the effect of glyphosate on seed germination success when plants are sprayed in late July and early August. November-December germination trials showed that 25% of the seeds from the sprayed plots and 50% of the seeds from an unsprayed control plot germinated. Seeds from these same lots were overwintered outdoors and subjected to another germination trial in the spring. In all seed lots (treatments and control), 90+% of the seeds germinated. An early-season glyphosate application to blooming plants apparently does not prevent them from producing viable seed. Further replicated experimentation is required to evaluate spray impacts on seed viability.

7. What is the survival rate of seedling, second-year, and older plants subjected to fluctuating water levels?

   Research in progress: None.

8. Does purple loosestrife possess allelopathic properties that contribute to its aggressiveness?

   Research in progress: None.

9. How significant are livestock and wildlife as herbivores of purple loosestrife? Can livestock (sheep, goats, cattle, etc.) be managed in an infested site to reduce seed production and stand density?

   Research in progress: None.

10. How will the impact of exotic arthropod herbivores released against purple loosestrife populations be assessed?

    Research in progress: Washington State University, through its Department of Entomology, in collaboration with the U.S. Fish and Wildlife Service, the U. S. Bureau of Reclamation, and Oregon State University, will evaluate impacts resulting from natural enemy releases according to pre-established protocols. Three European insect species were received in Washington in 1991, two of which were initially released at a field site in Grant County. All three bioagents are currently in culture at Washington State University in order to increase stocks available for planned 1993 releases (Piper 1992, pers. comm.).

11. What plant species could be used to out-compete purple loosestrife? How would these replacement species be managed?

    Research in progress: The Washington Department of Wildlife is conducting research on the ability of several phreatophytes (cottonwood and willow species) to shade out or suppress purple loosestrife. It is still to early to assess the competitive values of the plantings (Beckstead *et al.* 1991). University of Minnesota weed scientists are also exploring competitive planting utilization (Anon. 1990).

12. What are the quantifiable impacts of purple loosestrife on native wetland plant species?

Research in progress: A study proposed by researchers at the University of Washington, Cooperative Fish and Wildlife Research Unit, will address this question. Field investigations will commence in 1993.

13. What are the quantifiable impacts of purple loosestrife on waterfowl, marsh bird, shorebird, songbird, raptor, furbearer, reptile, amphibian, and fish populations?

Research in progress: This aspect will be pursued by the University of Washington research team and by Washington Department of Wildlife personnel. Preliminary findings from an on-going Department of Wildlife study indicate a lower utilization of *L. salicaria*-infested wetlands by waterfowl and other wildlife (Beckstead *et al.* 1991). Department staff will also determine if the weed has any effect on fish use of affected waters.

14. What are the comparative rates of spread of *L. salicaria* in western and eastern Washington? These rates might be useful in testing various hypotheses currently offered to explain the differences in their infestations between eastern and western Washington (for example, more competitive wetland species in western Washington, climatic differences, fertility of the waters, or more aggressive purple loosestrife biotypes).

Research in progress: None

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