

INVASIVENESS IN WETLAND PLANTS IN TEMPERATE NORTH AMERICA

Susan M. Galatowitsch, Neil O. Anderson, and Peter D. Ascher

University of Minnesota
Department of Horticultural Science
305 Alderman Hall
St. Paul, Minnesota, USA 55108

Abstract: The spread of invasive taxa, including *Lythrum salicaria*, *Typha* × *glauca*, *Myriophyllum spicatum*, *Phalaris arundinacea*, and *Phragmites australis*, has dramatically changed the vegetation of many wetlands of North America. Three theories have been advanced to explain the nature of plant invasiveness. Aggressive growth during geographic expansion could result because 1) growth is more favorable under new environmental conditions than those of resident locales (environmental constraints hypothesis); 2) herbivores may be absent in the new locale, resulting in selection of genotypes with improved competitive ability and reduced allocation to herbivore defenses (evolution of increased competitive ability hypothesis); and 3) interspecific hybridization occurred between a new taxon and one existing in an area, resulting in novel phenotypes with selective advantages in disturbed sites or phenotypes that can grow under conditions not favorable for either parent (introgression/hybrid speciation hypothesis). A review of published literature found few studies that compare the growth and dynamics of invasive populations in their new range versus those in historic ranges. However, there is evidence that hydrologic alterations could facilitate invasions by *Typha* × *glauca* and *Phalaris arundinacea* and that increased salinity promoted spread of *Typha angustifolia* (parental taxon) and *Phragmites australis*. The potential for reduced herbivory causing aggressive growth is greatest for *Lythrum salicaria*. Introgressive hybridization is potentially a cause of invasiveness for all five species but has been established only for *Typha* × *glauca* and *Lythrum salicaria*.

Key Words: *Lythrum salicaria*, *Typha* × *glauca*, *Myriophyllum spicatum*, *Phalaris arundinacea*, *Phragmites australis*, exotic species, invasion, hybridization, herbivory, environmental constraints, introgression

INTRODUCTION

A substantial portion of the inland wetlands of North America have been impacted by perturbations, including vegetation removal, nutrient inputs, introduction of toxins, filling, surface and subsurface drainage, flooding, and excavation. These physical and chemical responses are accompanied by the replacement of the indigenous vegetation by one to a few invasive species. Invasive species are those that spontaneously (and aggressively) spread after deliberate or inadvertent introduction to a new locale (Rejmanek and Richardson 1996, in part). In the last century, several aggressive taxa, including *Typha* × *glauca* Godr., *Lythrum salicaria* L., *Myriophyllum spicatum* L., *Phalaris arundinacea* L., and *Phalaris australis* (Cav.) Trin. have invaded inland temperate wetlands in North America. Large-scale disruptions of intact wetland ecosystems seem to open up new ecological niches well-suited to the invaders (Barrett 1989). Invaders often readily exploit these new circumstances because they are both good colonizers and good competitors (e.g., Harper 1965). Once established, invaders are dif-

icult to remove, lowering the quality of existing wetlands and reducing the effectiveness of restoration efforts (Cutright 1978, Teale 1982, Mack 1985, Barrett 1989, Rendall 1989, Mack 1991).

Studies of the characteristics that relate to the invasive potential of species and those that relate to the invasion of the community may provide information that helps curtail further spread (Johnstone 1986). Considering species and community aspects separately does not effectively characterize the invasion process, however (Johnstone 1986, Gilpin 1990). Since plants require "safe sites" to establish (Harper 1977), an invasion can be viewed as the removal of barriers that previously excluded site occupation (Johnstone 1986). The barriers removed can be botanical (e.g., reduced competition) or non-botanical (e.g., changes in water chemistry), and the response to barrier removal can affect all species or selected species. Removal of barriers creates invasion windows. Johnstone's invasion windows effectively generalize aspects of a community that change invasion potential. However, the invasion window model does not explain why plants tend to be more vigorous and taller in alien environ-

ments and often produce more seed than in their native distribution (Crawley 1987). So, while establishment of some species may be predictable by the removal of barriers, spread to dominance within a site requires additional information.

Gilpin (1990) attributed the problem of predicting invasion succession to the misconception that a given taxa has intrinsic properties independent of its resident ecological context. For example, allocation of resources to vegetative vs. reproductive effort, growth form, and even tolerance to environmental conditions all could potentially differ as a plant species migrates from one continent to another. Developing sound hypotheses about potential impacts from invaders requires knowledge of the coupling parameters between the taxa and the new habitat. A plant may become invasive because of differences between the resident and new ecological context or because the new ecological context causes changes in the intrinsic properties of the species.

Three hypotheses have been advanced to explain plant invasiveness; they differ in their assumptions about coupling between taxa and new habitats. First, the environmental constraint hypothesis predicts that plants in a new ecological context spread aggressively when they occupy environments that are more favorable to their growth than found in their resident locale (Crawley 1987, Bryant et al. 1988). This hypothesis does not assume any intrinsic change in the properties of the species in regions where it is invasive, only differences in environmental conditions that increase resource availability. The other two hypotheses assume intrinsic changes to species explain the spread that occurs after initial establishment. The second hypothesis, evolution of increased competitive ability, predicts that if herbivores are absent in the new context, selection will favor genotypes with improved competitive abilities and reduced allocation of resources to herbivore defenses (Crawley 1987, Blossey and Notzold 1995). Finally, the introgression hypothesis predicts that when repeated, interspecific hybridization occurs between a taxa new to a region and one existing in an area, followed by backcrossing to either or both parental species, the influx of new genetic information results in novel phenotypes that have selective advantages in disturbed sites or that use resources unexploited by either parent species (Anderson 1949, Lewontin and Birch 1966, Nagle and Mettler 1969, Barber 1970, Levin and Bulinska-Radomska 1988). The primary importance of introgression in evolution is one of greatly enriching variation in the participating species (Anderson 1949, Stebbins 1959, 1969).

Response to different control strategies for a given species should vary depending on the nature of invasiveness. If a species has become invasive because en-

vironmental constraints have been eased, then wetland manipulations altering hydrology, nutrient levels, or water chemistry may be effective control strategies. The absence of predation potentially creates both invasion windows and intrinsic species changes. If North American populations have evolved to allocate less resources to defenses than to growing larger, re-introducing insect herbivores may be an effective long-term strategy for reducing invasiveness within a region. Opportunities to control invasive spread will be most limited for taxa that are products of introgression. The loss of geographic and reproductive barriers between the two parental species cannot be reasonably re-established. Knowing when introgression has been important would allow managers to minimize human alterations and actions that favor introgressive hybridization between natives and exotics.

This paper reviews information available from the published literature on the nature of invasiveness for five plant taxa that have aggressively spread in wetlands of temperate North America: *Myriophyllum spicatum*, *Phalaris arundinacea*, *Phragmites australis*, *Lythrum salicaria*, and *Typha* × *glauca*. These species have become the dominant vegetation in wetlands throughout the Great Lakes basin and elsewhere on the continent. The objectives of the review are to document the biogeography and biology of each species in North America in order to evaluate the relative importance of three hypotheses of plant invasiveness.

EVIDENCE FOR THE THREE HYPOTHESES OF PLANT INVASION

For most species, understanding the causes of invasiveness is attempted long after significant geographic expansion has occurred. Consequently, much of the relevant information is historical and circumstantial rather than directly observed. For populations that are invasive because environmental constraints have been minimized, resources used by the invader increased relative to other members of the community. If a commonly used resource (such as nutrients) increased in a wetland, the invasive species is the one that outcompeted others for use of this resource (e.g., Tilman 1990). Additional resources (e.g., light, space) enabling rapid population growth of a species also result if changes in environmental conditions cannot be tolerated by other species. The environmental constraints hypothesis may explain invasiveness for those species whose increased vigor and spread consistently has been coincidental with changes to environmental conditions.

On average, herbivores consume more than ten percent of plant production in natural communities (Coley et al. 1985). Some species suffer high levels of her-

bivory, yet have not evolved defensive mechanisms; whereas others allocate resources, presumably because protection has resulted in higher fitness (Coley *et al.* 1985). Both kinds of plants, those with and without defenses, can potentially experience gains in individual growth rates and population expansion if arrival in a new geographic area is a release from herbivore pressure. Species lacking defenses would be expected to show immediate increases in standing crop compared to plants in their historic range. If a species has evolved to allocate substantial resources to defense, a lag may be expected before growth increases. Defensive mechanisms may be lost over time as selection favors individuals with increased competitive ability rather than herbivore defense (Blossey and Notzold 1995). In either case, knowing the relative extent of herbivory in historic and newly invaded ranges is necessary for understanding if invasiveness can potentially be explained by release from herbivory. Whether evolutionary changes have occurred in the new range favoring resource allocation to competitive ability over herbivore defense can be demonstrated experimentally in common garden or reciprocal garden experiments (Blossey and Notzold 1995).

For introgression to be invoked as a cause of invasiveness, changes to both wetland conditions and to genetics of the taxa must have occurred. Alterations to wetland condition, however, only needed to be present at the time when hybrid populations initially established. In the first major treatise on introgression, Anderson (1949) showed that mutual introgression of *Iris hexagona* Walt. and *I. fulva* Ker-Gawl. resulted in hybrid populations with novel characteristics. These hybrids were found only in highly disturbed (i.e., overgrazed) floodplain areas (Anderson and Hubricht 1938, Anderson 1949). While the F_1 generation is usually intermediate to both parents for most traits, the F_2 and successive backcross generations segregate widely. Thus, if both parents differ by only twenty distinctive traits for habitat adaptation, the F_2 generation may segregate with as many as one million different individuals or genotypes (Anderson 1949). Over time, selection favors certain genotypes so that populations in late successional communities have reduced genotypic diversity. Thus, "hybrid habitats" (such as those created by natural or cultural disturbances) are essential for survival of introgressive individuals. So, introgression is most likely for formerly allopatric populations that have become sympatric in disturbed landscapes.

Incongruity can slow the rate of introgression or hybrid speciation such that a lag time of fifty or more years may be necessary before hybrid populations become invasive. When previously isolated taxa become sympatric, interspecific crossing frequently ends in failure. Observed aberrations and dysfunctions in such

crosses (i.e., incongruity) are from a lack or mismatch of genetic information (genomic or cytoplasmic) in one partner about the critical factors of the other (Bowley and Taylor 1987, Haghghi and Ascher 1988). While incongruity poses a barrier to gene exchange, it evolves passively and is not selected.

Few suspected introgressed taxa have been the subject of either morphological or molecular characterization. Historic and current observations that one or more population(s) exist that deviate for diagnostic characters of the parental species or that recombine traits from two or more different species, often trigger further consideration. Besides repeating the suspected cross and backcrosses (with controlled pollinations) and artificially creating the variation observed in natural populations, biochemical and molecular evidence is considered to be most reliable for establishing the introgressive history of a taxa (Heiser 1973). Modern molecular techniques have been used to detect introgressive hybridization events (Arnold *et al.* 1987, Hamrick 1989, Keim *et al.* 1989, Bousquet *et al.* 1990, Chechowitz *et al.* 1990). Comparison between cytoplasmic and nuclear genetic markers has produced the most reliable evidence for introgression in natural populations (Rieseberg *et al.* 1988, 1990). Measurements of variation from these biochemical methods include the number of alleles per locus and the percent polymorphic loci, allele frequency, and the average number of heterozygous loci for each individual (Hamrick 1989).

Morphological evidence can be used to accurately establish introgression if traits are selected carefully and enough traits are available (Anderson and Hubricht 1938). Reliable traits are those that are diagnostic for the parental species, whose expression is constant through all possible growing environments. Such traits are known as species genes (i.e., they characterize a species and lack genotype \times environment ($G \times E$) variation) (Lamprecht 1948). Traits controlled by species genes are the same for all members of the species (Lamprecht 1948, 1964). Species-specific traits reliable for introgression studies are those such as phyllotaxy and germination type (epigeal/hypogeal). Quantitative traits (e.g., lengths of corolla, leaves, and internodes) are usually not species-specific and subject to considerable $G \times E$ (Anderson 1949). Since these traits are not controlled by species genes, they are variable across environments, not diagnostic, and cannot be used to establish the presence of introgression. Once species gene traits have been identified, characterization of the naturally occurring hybrid swarms for morphological intermediacy or deviations can be performed. Since the diagnostic traits of a species are often strongly linked, many generations of introgressive hybridization are required before segregation (Ander-

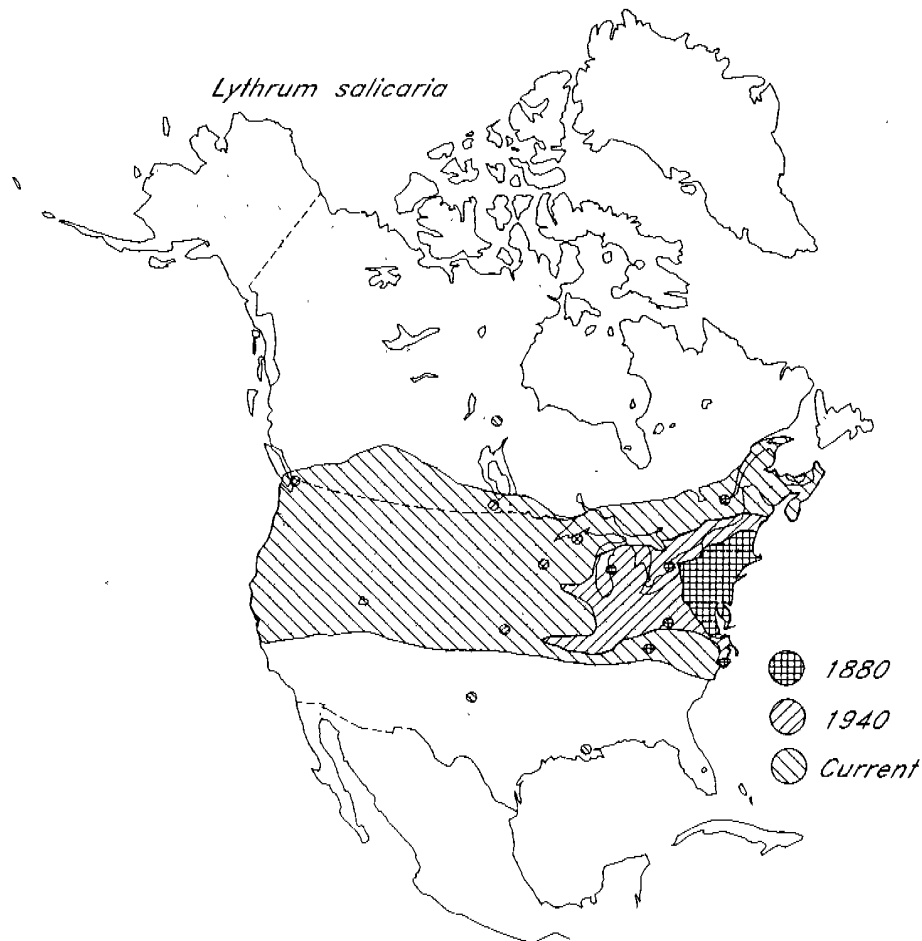


Figure 1. Changes in the distribution of *Lythrum salicaria* in North America (White and et al. 1993, Haber 1996).

son 1949). Thus, early hybrids of introgression may be intermediate for all characters, whereas advanced generations show recombinants or transgressive segregants for any or all parental traits.

BIOGEOGRAPHY OF INVASIVE TAXA

Lythrum salicaria

Lythrum salicaria was first documented to be present on the North American continent in 1814 by Pursh. Nearly half (14 of 30) of the *L. salicaria* populations reported before 1900 were located in the vicinity of estuarine waste grounds in New England, from Massachusetts to New Jersey (Thompson et al. 1987). Ship ballast from tidal flats in Europe deposited on these estuaries likely contained *L. salicaria* seed (Thompson et al. 1987, Wilcox 1989). In addition, *L. salicaria* is known to have arrived in North America in imported raw wood and on sheep, as well as having been purposefully introduced by immigrants prior to 1900 (Thompson et al. 1987). *Lythrum salicaria* was cultivated for its ornamental, medicinal, and bee-keep-

ing qualities (e.g. Pellett 1966, 1977). Opportunities for initial introductions, whether from ballast, livestock, or immigrants, were greatest in the early to mid 1800s (Thompson et al. 1987). Because these populations did not appear to spread, the species was considered to be indigenous to North America until 1889 (Gray et al. 1889).

Lythrum salicaria migrated inland along canals and other shipping waterways in the late 1800s (Figure 1). Also at this time, *L. salicaria* escapes from cultivation were widely reported (Stuckey 1980a). By 1900, inland populations were known from New Hampshire, Quebec, Ontario, Manitoba, Pennsylvania, Michigan, Ohio, West Virginia, and Tennessee (Stuckey 1980b). These populations initially were not considered invasive. Then, around 1930, *L. salicaria* began to rapidly spread across pastures and wetlands in Quebec (Louis-Marie 1944, Barabe 1951, Cutright 1986). Stuckey (1980a) found that *L. salicaria* remained localized after introduction or escape for 20 to 40 years. After this lag, aggressive spread from the source population has been the norm.

In spite of the history of *L. salicaria* in Quebec and elsewhere in the region, horticultural interest continued into the 1980s. The Morden Research Station in Manitoba developed *Lythrum* cultivars originating from crosses of *Lythrum virgatum* L. and *Lythrum alatum* Pursh from 1937 through the 1950s. Other growers introduced varieties of *L. salicaria*, as well (Rendall 1989). Since *L. virgatum* and *L. salicaria* are not morphologically distinct and can interbreed, *L. salicaria* continued spread via garden escapes. Some states (e.g., Minnesota, Indiana, Ohio, Washington, and Wisconsin) list both *L. virgatum* and *L. salicaria* as noxious weeds, thereby preventing their commercial sale. Currently, within North America, *L. salicaria* occurs primarily between the 40th and 50th parallels, west of the 100th meridian (Cutright 1986, Ithaca Journal 1989, Rendall 1989, Stuckey 1980a).

Typha × *glauca*

Typha angustifolia L. was not documented in the first floristic surveys of the Boston, New York, or Philadelphia areas (prior to 1820). This species may have arrived on the continent with European settlement (Stuckey and Salamon 1987). *Typha angustifolia* was apparently restricted to salt marshes of the Atlantic coast of North America until sometime within the past two hundred years (Smith 1987). As early as 1886, both *T. latifolia* L. and *T. angustifolia*, along with a possible hybrid of the two parents (*T. angustifolia* var. *elongata*, later recognized *T. × glauca*), were described for wetlands in the Cayuga Lake basin of New York State (Dudley 1886).

Migration of *T. angustifolia* to inland wetlands initially was reported from Michigan in 1900 (Stuckey and Salamon 1987), Massachusetts (Roscoe 1927), Iowa (Hayden 1939), and Utah (Wetmore 1921). Utah populations, assumed by Harris (1927) to be recent introductions, were restricted to a few saline wetlands near Great Salt Lake. Before the 1920s, *T. latifolia* was the only cattail species collected or reported from inland freshwater wetlands of the upper midwest despite extensive collections by early naturalists (Fassett and Calhoun 1952, Stuckey 1960). However, by 1949, Hotchkiss and Dozier mapped the expansion of *T. angustifolia* from the eastern seaboard to include Quebec, Ontario, and 19 states from Maine to North Dakota, Missouri to Pennsylvania (and isolated records in four western states). Hybrid cattails (*T. × glauca*) were documented from inland wetlands (including Great Lakes) in Ontario, Maine, New York, Pennsylvania, Michigan, Wisconsin, Minnesota, Iowa, and South Dakota (Figure 2) (Hotchkiss and Dozier 1949). From 1949 to 1967, the continuous range of *T. angustifolia* expanded westward to southeastern Manitoba, Mon-

tana, and northeastern Colorado (Smith 1967). Similarly, hybrid populations reported from this enlarged range include Quebec (Louis-Marie 1960), Manitoba (Love and Bernard 1959), and Nebraska (McMillan 1959). *Typha angustifolia* continues to expand, as evidenced by recent expansion into Saskatchewan (Harms and Ledingham 1986).

Myriophyllum spicatum

The early history of *Myriophyllum spicatum* in North America is confusing, owing to the existence of herbarium samples of *M. exalbescens* (Fern.) incorrectly labeled as *M. spicatum* (Faegri 1982). *Myriophyllum sibiricum* (Komarov) is considered a North American endemic or circumboreal (Aiken and McNeill 1980). While *M. spicatum* is generally thought to have been introduced to North America, the precise location(s) and timing of these events are disputed (Reed 1977, Couch and Nelson 1988, Smith and Barko 1990). Presumably, *M. spicatum* was introduced into North America in the late 1880s from the emptying of ship ballasts (Rawls 1978, Aiken et al. 1979, Orth and Moore 1984). Its presence was first documented in 1902 in Chesapeake Bay (Nichols and Mori 1971, Steenis and Stotts 1961). Evidence from sediment cores substantiated its recent arrival to Chesapeake Bay (Orth and Moore 1984). Submersed aquatic vegetation was present before 1770, whereas *M. spicatum* dated to approximately 1935. *Myriophyllum spicatum* remained an obscure component in the ecosystem until the 1950s (Springer and Stewart 1959, Coffey and McNabb 1974, Reed 1977). By 1963, *M. spicatum* had increased to a monospecific stand covering approximately 80,000 ha in Chesapeake Bay (Steenis and King 1964). Before 1950, *M. spicatum* existed in few other widely separated populations, including sites in Ohio, Arizona, and California (Couch and Nelson 1985). The species quickly spread from the Chesapeake Bay area to the south and north (Figure 3) (Coffey and McNabb 1974). Northward, *M. spicatum* spread through the Hudson River Valley to the St. Lawrence River Valley and west along the Great Lakes to southern Michigan (Coffey and McNabb 1974). During the 1960s, collections were first made in Vermont, New York, Pennsylvania, New Jersey, Delaware, Ontario, Quebec, Michigan, and Wisconsin (Nichols and Mori 1971, Nichols 1975, Aiken et al., 1979, Keast 1984). First recorded from the St. Clair-Detroit River system in 1974, *M. spicatum* became one of the dominant species within four years (Schloesser and Manny 1984). *Myriophyllum spicatum* was not known to occur in Minnesota until 1985 (Smith and Barko 1990). Transport of plant fragments on boats or trailers is commonly reported to be the major means

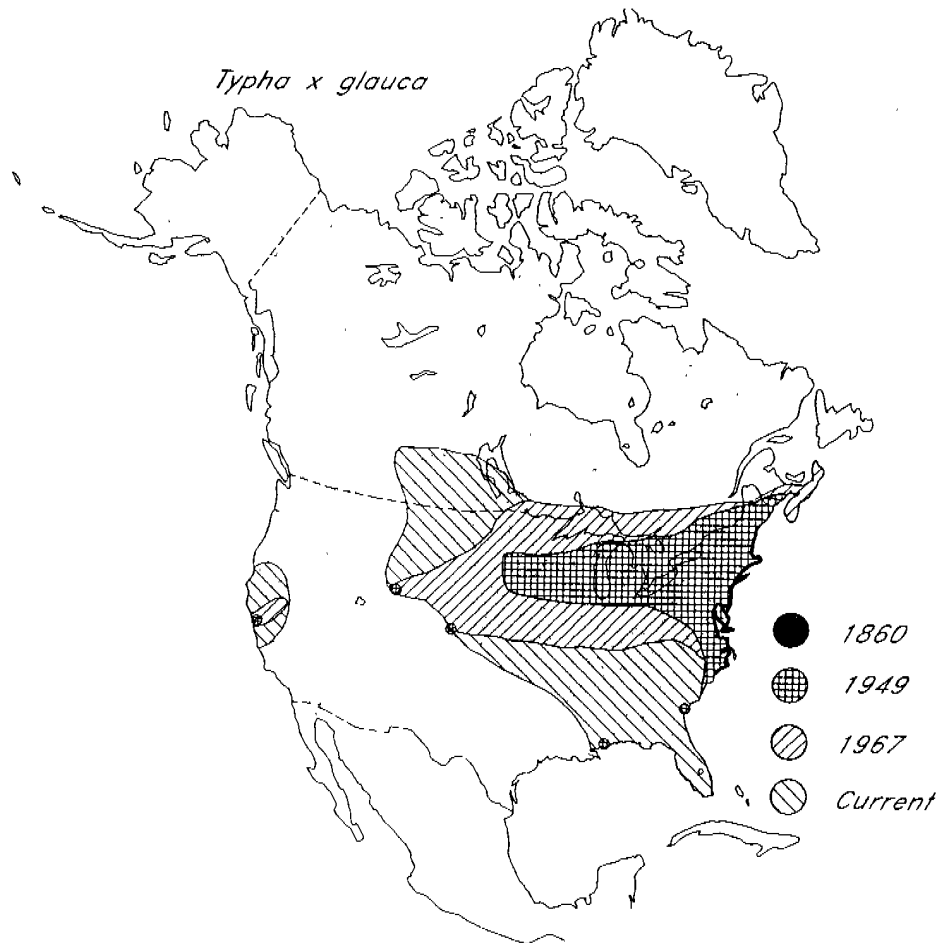


Figure 2. Changes in the distribution of *Typha* × *glauca* (and *Typha angustifolia*) in North America (Hotchkiss and Dozier 1949, Smith 1967, Lee 1975, Harms and Ledingham 1986).

of intra-lake and interlake dispersal (Aitkin et al. 1979, Kimbel 1982, Nichols and Shaw 1986, Madsen et al. 1988).

Spontaneous declines have been reported across the range of *M. spicatum* in a diverse range of wetlands, from coastal wetlands such as Chesapeake Bay and Rondeau Bay, Ontario to inland lakes in Wisconsin and Tennessee (Bayley et al. 1978, Aiken et al. 1979, Carpenter 1980, Hanna 1984, Orth and Moore 1984, Nichols and Shaw 1986, Painter and McCabe 1988, Madsen 1994, Nichols 1994, Shearer 1994, Sheldon 1994, Titus 1994). These declines generally occurred 15 to 20 years after the rapid growth and were not accompanied by rapid recolonization of other submersed aquatic vegetation.

Phalaris arundinacea

Reed canary grass, *Phalaris arundinacea*, has been an important cultivated forage grass in northern temperate regions of the world for nearly two centuries.

In Sweden, interest in cultivating *P. arundinacea* began in 1749 by Hesselgren (advised by Linnaeus) with a study reporting its high palatability to livestock (Alway 1931). Subsequently, *P. arundinacea* was found to have high yields and forage quality compared to other hay grasses in Lapland (Alway 1931, Ostrem 1987). In contrast, most wild populations of *P. arundinacea* found in England were presumed to have limited forage value; a variegated variety, however, was cultivated for ornamental purposes by 1812 (Alway 1931). Norwegian populations had low germination and long dormancy (Junttila et al. 1978, Berg 1982), whereas populations from other locales (i.e., France) had high germination, with no dormancy (Conchou and Patou 1987). Sown forage varieties of *P. arundinacea* were available across northern Europe by 1835 (Alway 1931).

Cultivation of *P. arundinacea* occurred around the same time in North America, along the Northern Atlantic coast and in the Pacific Northwest, as in Europe (Marten and Heath 1985). Field trials of *P. arundi-*

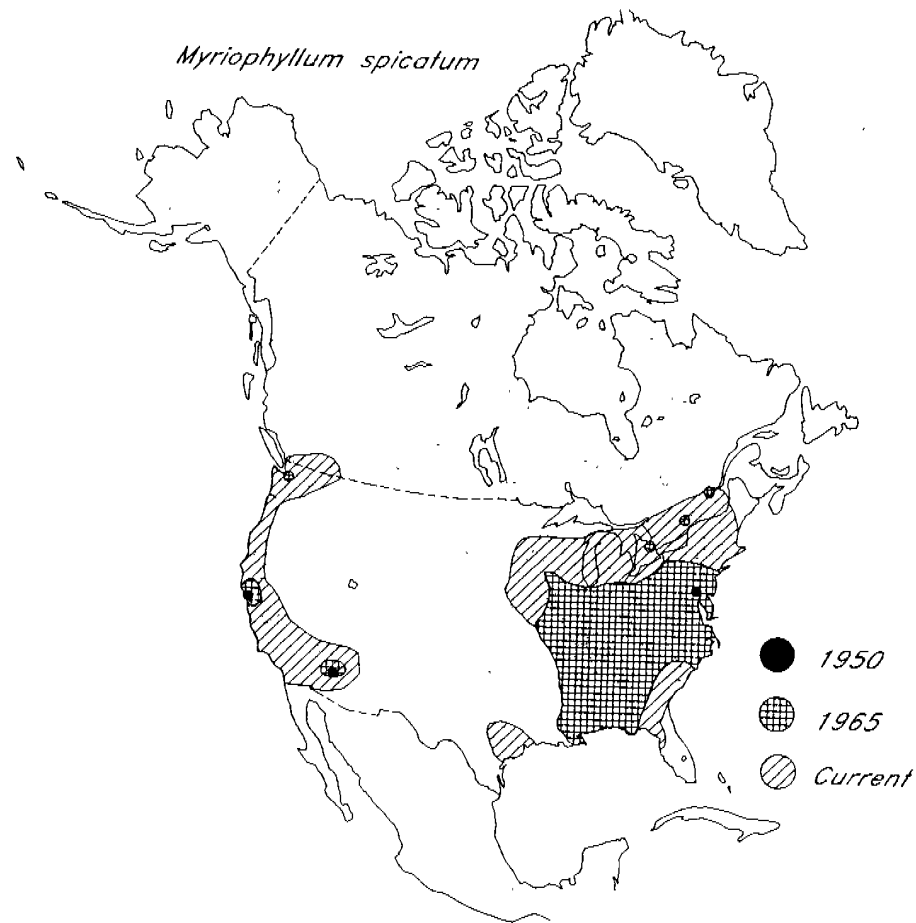


Figure 3. Changes in the distribution of *Myriophyllum spicatum* in North America (Reed 1977, Aiken, Newroth and Wile 1979, White *et al.* 1993).

nacea by rhizome transplants occurred in 1834 and 1835 in Connecticut and New Hampshire; a cultivated stand was reported from Oregon in 1885 (Anonymous 1834, Harris 1835, Marten and Heath 1985). Because they are adapted to wide extremes in soil moisture, *Phalaris* cultivars are widely grown in irrigated and non-irrigated forage systems and for land disposal of wastewater (Zeiders and Sherwood 1985).

Phalaris arundinacea is considered indigenous to the temperate regions of all five continents (Marten and Heath 1985), although its early cultivation makes its pre-agricultural distribution uncertain. *Phalaris arundinacea* appears to be a cryptogenic species: a species whose origin cannot be positively determined (Carlton 1996). Within North America, *P. arundinacea* is most abundant in the humid regions of the northern half of the U.S. and the southern third of Canada (Figure 4). In Ontario, Dore and McNeill (1980) consider *P. arundinacea* populations along the shores of the northern Great Lakes and possibly the upper Ottawa and French Rivers to be native genotypes, whereas inland stands in the southern part of the province are

European cultivars. However, native and introduced genotypes are not morphologically distinct (Dore and McNeill 1980).

Phragmites australis

Phragmites australis (syn. *Phragmites communis* Trin.) was named from an Australian specimen in 1799 but is most abundant in the northern hemisphere, especially in Europe (Clayton 1968, Haslam 1973). *Phragmites australis* is usually considered a circumboreal species that has not increased in range across North America since European settlement (e.g., Fernald 1950). There has been suspicion in recent decades that *P. australis*, like *Phalaris arundinacea*, is a cryptogenic species (Marks *et al.* 1993). *Phragmites australis* was described by Lindroth (1957) from ballast sources in southwestern England used by sailing ships in Newfoundland trade. However, remains of *Phragmites* were present in 3,000-year-old peat samples from tidal marshes in Connecticut (Niering and Warren 1977) and from 1,000-year-old artifacts (e.g., mats,

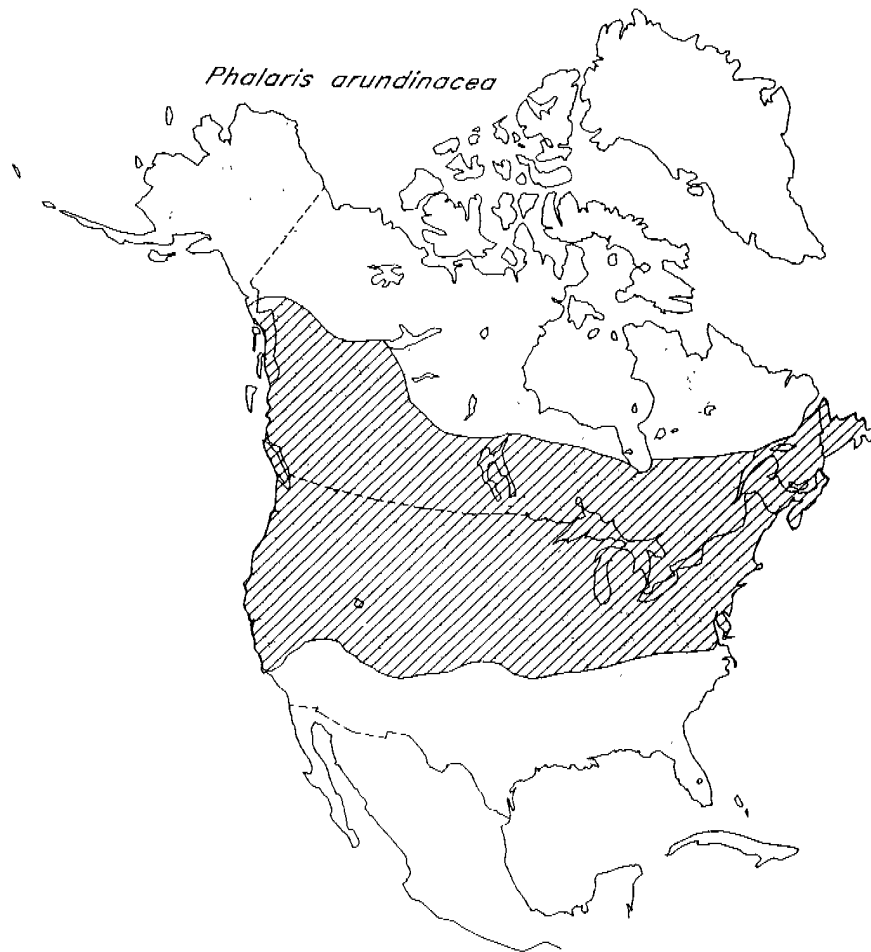


Figure 4. The distribution of *Phalaris arundinacea* in North America (Marten and Heath 1985, White et al. 1993).

woven objects) from Anasazi sites in southwestern Colorado (Breternitz et al. 1986, Kane and Gross 1986.).

Within North America, *P. australis* occurs from the Atlantic eastward to the prairie provinces (Figure 5). While populations of *P. australis* have decreased in Europe (Ostendorp 1989), dramatic increases in North American populations in the Great Lakes basin, north-eastern United States, Atlantic coastal marshes, and Mississippi River delta have been reported within the past forty years (Hauber et al. 1991, McNabb and Batterson 1991, Marks et al. 1993, Wijte and Gallagher 1996). In Europe, stressors such as recreational use, water-level changes, and eutrophication are considered potentially responsible for regression of reed beds (Ostendorp 1989).

CAUSES OF ESTABLISHMENT AND SPREAD

Release from Environmental Constraints

Four possible changes in environmental conditions have been linked to spread of these five invasive spe-

cies following intercontinental and continental transport: increased nutrient loading, vegetation removal, altered hydrology and increased salinity. Of these, only increased nutrient loading represents a direct increase in resource availability. The remaining factors result in potential increases in resources as other vegetation is removed or can no longer tolerate prevailing conditions.

Increased Nutrient Loads. Eutrophication is often mentioned as a potential cause to explain shifts towards invasive species. However, evidence is surprisingly scant in support of this hypothesis. All five species show increases in productivity with nutrient additions (particularly nitrogen) or appear to spread more rapidly in nutrient rich situations (Haslam 1965, Aiken et al. 1979, Marten and Heath 1985). In *P. australis*, wetland fertility appears to alter water depth tolerance. *Phragmites australis* does not extend beyond 0.75 m in small, oligotrophic lakes in England, whereas it extends into deeper water in eutrophic lakes (Haslam 1972).

High nutrient levels may actually impede spread of

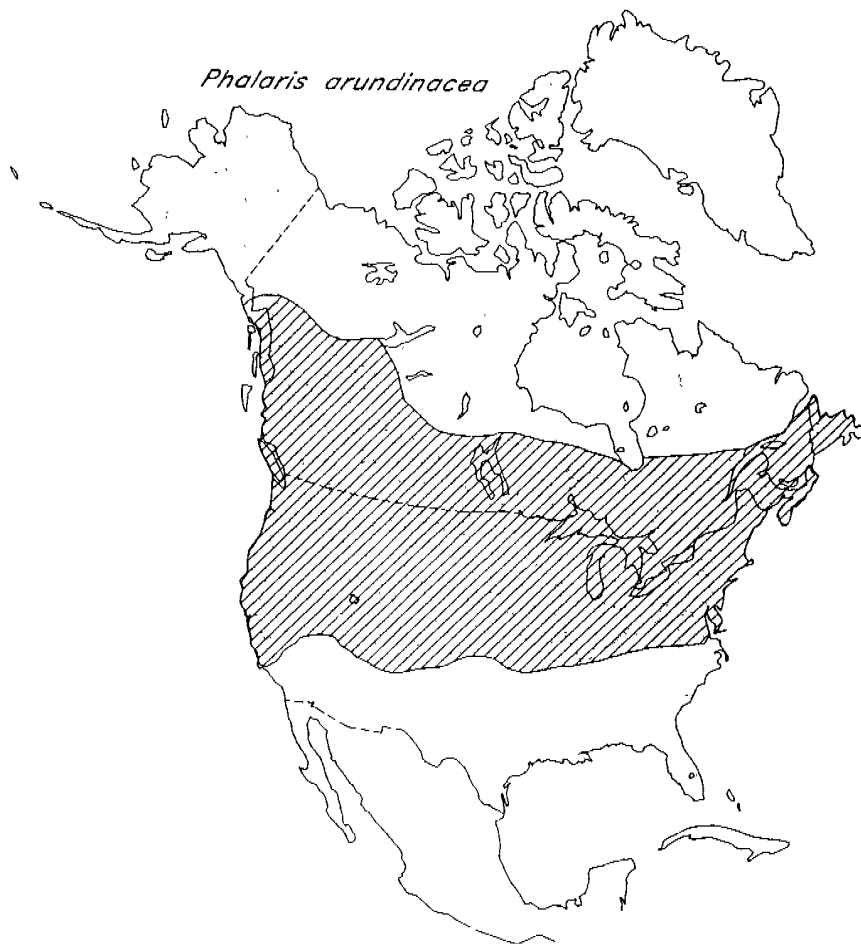


Figure 4. The distribution of *Phalaris arundinacea* in North America (Marten and Heath 1985, White et al. 1993).

woven objects) from Anasazi sites in southwestern Colorado (Breternitz et al. 1986, Kane and Gross 1986).

Within North America, *P. australis* occurs from the Atlantic eastward to the prairie provinces (Figure 5). While populations of *P. australis* have decreased in Europe (Ostendorp 1989), dramatic increases in North American populations in the Great Lakes basin, northeastern United States, Atlantic coastal marshes, and Mississippi River delta have been reported within the past forty years (Hauber et al. 1991, McNabb and Batterson 1991, Marks et al. 1993, Wijte and Gallagher 1996). In Europe, stressors such as recreational use, water-level changes, and eutrophication are considered potentially responsible for regression of reed beds (Ostendorp 1989).

CAUSES OF ESTABLISHMENT AND SPREAD

Release from Environmental Constraints

Four possible changes in environmental conditions have been linked to spread of these five invasive spe-

cies following intercontinental and continental transport: increased nutrient loading, vegetation removal, altered hydrology and increased salinity. Of these, only increased nutrient loading represents a direct increase in resource availability. The remaining factors result in potential increases in resources as other vegetation is removed or can no longer tolerate prevailing conditions.

Increased Nutrient Loads. Eutrophication is often mentioned as a potential cause to explain shifts towards invasive species. However, evidence is surprisingly scant in support of this hypothesis. All five species show increases in productivity with nutrient additions (particularly nitrogen) or appear to spread more rapidly in nutrient rich situations (Haslam 1965, Aiken et al. 1979, Marten and Heath 1985). In *P. australis*, wetland fertility appears to alter water depth tolerance. *Phragmites australis* does not extend beyond 0.75 m in small, oligotrophic lakes in England, whereas it extends into deeper water in eutrophic lakes (Haslam 1972).

High nutrient levels may actually impede spread of



Figure 5. The distribution of *Phragmites australis* in North America (Hitchcock 1935, Hocking *et al.* 1983).

the five species under consideration. For example, Shamsi and Whitehead (1977) found *L. salicaria* to be a better competitor against *Epilobium hirsutum* L. at low nutrient levels but not consistently at high levels. In Europe, eutrophication has been implicated in the decline of *P. australis* (Ostendorp 1989). Smith and Barko (1990) considered that invasion of *M. spicatum* may be caused by lowered nutrient inputs in eutrophic lakes. Nutrient and sediment loads to lakes decrease during droughts because of lower rates of surface runoff, reducing phytoplankton growth, and sediment-generated turbidity. Increased water clarity may promote growth and spread of *M. spicatum* in these areas.

Vegetation removal. Waste sites from industrial land use and construction activities are often documented as sites for wetland plant invasions. The earliest records of *L. salicaria* indicate a habitat preference for dumps and waste ground (Stuckey 1980a). Wilcox (1989) noted that construction associated with highway maintenance exposes barren, moist soil with land

clearing and water-level reduction, conditions favorable for *L. salicaria* establishment.

Reestablishment of many wetland species (i.e., annuals, emergent aquatics, trees, and shrubs), including invasive species, occurs on bare soils exposed after water levels recede (Harris and Marshall 1963, Stuckey 1980b). For example, in Great Lakes coastal wetlands, drought conditions of the mid-1930s were followed by an approximate 1 m rise in water levels by the mid-1940s (McDonald 1955). Emergent vegetation died en masse, presumably due to winter submergence. As water levels receded, the aerial extent of colonization and spread of *T. × glauca* was estimated to be nine times greater than that of *T. angustifolia*. Similarly, Shay and Shay (1986) report that *T. × glauca* became dominant following drawdown conditions at Delta Marsh, Manitoba in the 1960s. Unlike other emergent aquatics, stands of *Typha × glauca* did not decline with prolonged (four years) deep water (0.6 m) (Harris and Marshall 1963). Harris and Marshall (1963) noted that *T. × glauca* threatened to become a

problem species at Agassiz National Wildlife Refuge, Minnesota at high water by encroaching into openings created with the decline of other emergents or into areas that had not been previously vegetated. *Typha* × *glauca* seedlings are more tolerant of both prolonged flooding and partial drainage than is *T. angustifolia* (Steenis et al. 1958, McMillan 1959).

Seedling establishment of *L. salicaria*, *T. × glauca*, *P. australis*, and *P. arundinacea* is greatest on moist soil exposed to sunlight (Sifton 1959, Haslam 1971, Thompson et al. 1987, Conchou and Patou 1987, Blossy et al. 1994). How long these condition need to prevail is variable: *Lythrum salicaria* requires about fifty days for successful seedling establishment (Thompson et al. 1987), whereas *P. australis* requires 1–2 years (Haslam 1971). Shoot production of both *L. salicaria* and *P. australis* is poor in closed-canopy vegetation (Haslam 1971, Thompson et al. 1987). Litter removal by fire increases *P. australis* shoot density (Thompson and Shay 1985).

Some invasions of *M. spicatum* appear to have been triggered by drastic reductions in submersed aquatic vegetation. In Cayuga Lake, New York, the standing crop of *M. spicatum* dramatically increased while all other submersed vegetation declined following Tropical Storm Agnes in 1972 (Oglesby and Vogel 1976). The tropical storm prolonged the period of low water transparency by increasing suspended sediments during early summer. In other inland lakes, *M. spicatum* colonized areas that had been previously unvegetated (Keast 1984).

Altered Hydrology. All five species show a high degree of morphological plasticity in response to hydrologic changes. For example, *L. salicaria* develops aerenchyma on submersed stems (Thompson et al. 1987). *Myriophyllum spicatum* forms land-phase individuals during drawdown, unlike *M. sibiricum* that lacks this response (Menzie 1979).

Typha × *glauca* shows both individual and population plasticity to increased water depth (Waters and Shay 1990, 1992). Total shoot biomass production is greater in high water versus low water levels (van der Valk and Davis 1980). At Delta Marsh, Manitoba, *T. × glauca* had a maximum shoot height and density at 100 cm (Waters and Shay 1990, 1992). A second shoot density maximum also occurred at 25 cm. Except in deepest areas (100 cm), reduced density was coupled with increased shoot height. Luxuriant growth, in part, may be an edge effect or due to a juvenile growth form (Waters and Shay 1990). Waters and Shay (1990) consider the plasticity shown by *T. × glauca* to be a buffer against environmental variability.

Phragmites australis can grow at water depths of 2 m or more (Bjork 1967), although in some locales it

has been incapable of vegetative spread at water depths greater than 0.5 m (Shay and Shay 1986) or 1 m (Haslam 1970). Compared to other flood-tolerant plants, *P. australis* roots consume very little O₂ (Gries et al. 1990). Because it is phraetophytic, *P. australis* can persist in areas where summer water levels are a meter below ground surface (Shay and Shay 1986). Sudden changes in water level, however, are deleterious to *P. australis* (Haslam 1970).

Phalaris arundinacea thrives in wetlands with high annual or periodic fluctuations in water levels. Although recognized for high biomass production in flooded areas, *P. arundinacea* is more drought resistant than many grass species from upland areas (Wilkins and Hughs 1932, Ostrem 1987, Rice and Pinkerton 1993). Sheaffer et al. (1992) found reductions in above-ground standing crop of *P. arundinacea* to be comparable to *Bromus inermis* Leyss., *Dactylis glomerata* L., and *Phleum pratense* L.. They considered *P. arundinacea* to be among the most productive cool-season grasses during drought.

Phalaris arundinacea populations along the Garonne River, France, show two distinctly different growth strategies depending on prevailing water regime (Conchou and Pautou 1987). Individuals in aerated soils have a unimodal growth pattern and allocate more resources to seed production than do those in flooded areas. In persistently flooded areas, *P. arundinacea* plants are bimodal, with the first generation having low seed production and the second typically sterile. Two generations of shoots within a growing season were observed on the Garonne River in areas that are flooded in spring but aerated later in the season (Conchou and Fustec 1988). The first generation of shoots emerges when soil is submerged. Waterlogged conditions prevent growth of rhizomes and tillers, so nutrients are translocated to shoots (Klimesova 1994). Adventitious roots are common on shoots produced in submersed conditions (Conchou and Patou 1987). These shoots senesce in summer, as the water table falls below the soil surface. A second generation of shoots emerges during late summer drawdown. Uptake of nutrients from soil by roots and downward translocation of carbon from shoots replenishes rhizomes in fall before resubmergence. It is not known if these plastic growth strategies afford *P. arundinacea* an advantage over other wetland species that are artificially drained or receive stormwater inputs.

Increased Salinity. Increases in distribution of *Phragmites australis* and *Typha angustifolia* (and consequently *T. × glauca*) have been linked to salt contamination of wetlands because both taxa are known to be more tolerant of saline conditions than many other freshwater emergents, such as *T. latifolia* (Stuck-

ey 1969, McNaughton 1970, McNaughton and Wolf 1970, Smith 1987). Road de-icing salts increase pH and conductivity in inland wetlands in the vicinity of roads (Wilcox 1986a). Wilcox (1986b) observed that portions of Pinhook Bog (Indiana) contaminated by road salt were being invaded by *T. angustifolia*, whereas only *T. latifolia* was found in unimpacted areas of the same wetland. This study is consistent with others that have found *T. angustifolia* to grow in both brackish (including naturally basic or saline) wetlands and *T. latifolia* to be restricted to freshwater habitats (Fassett and Calhoun 1952, McMillan 1959). In contrast, Isabelle *et al.* (1987) found that *T. latifolia* and *L. salicaria* germinated in pure roadside snowmelt, whereas three other wetland species did not.

Recent increases of *P. australis* in mid-Atlantic and Mississippi River deltaic coastal wetlands are often attributed to saltwater intrusion associated with sequential tropical storms (Haslam 1979, Berstein 1981, Hauber *et al.* 1991). Wijte and Gallagher (1996) found germination in *P. australis* to be promoted under hypoxic conditions at moderate salinity (5–10 g/L NaCl). They suggest that neglected coastal impoundments become salinized beyond the limits of freshwater species and are then invaded by *Phragmites australis*. McNabb and Batterson (1991) have speculated that road salt runoff has promoted population expansions of *P. australis* in roadside ditches in Michigan. Hocking *et al.* (1983) found, however, *Phragmites australis* to be intolerant of high salinity, with growth reduced at 1.2%.

Although increased salinity has not been explicitly linked to outbreaks of *M. spicatum*, this species is known to tolerate saline conditions (0–12%), unlike many other submersed aquatic species, including *M. sibiricum* (Menzie 1979, Reed 1980, Twilley and Barako 1990). *Myriophyllum spicatum* was a minor component of Chesapeake Bay until major tropical storms changed salinity and turbidity and submersed beds declined (Bayley *et al.* 1978). Three tropical storms in 1954–55 pushed saline water further into the estuary than typical tidal flows.

Reduced Herbivory and the Evolution of Competitive Ability

In spite of significant interest in biocontrol as a management tool, plant-insect data are scant for wetland species, with some reports on *Phragmites australis* and more detailed studies of *Typha* spp., *Myriophyllum spicatum*, and *Lythrum salicaria*. In Europe, *P. australis* is a host (primary or secondary) to more than twenty species of herbivores, saprovores, and parasitoids (Haslam 1972, Tschardtke 1992). Insects infest approximately one-third of the shoots in Czecho-

slovakian *P. australis* beds (Skuhravy 1978). For example, larvae of the stem-boring moth *Archanara geminipuncta* Haworth infests and kills three growing shoots before pupating and overwintering inside thick stems (van der Toorn and Mook 1982, Vogel 1984, Mook and van der Toorn 1985, Tschardtke 1992). Thick-stemmed shoots are typical of wet habitats, whereas thin shoots are found in dry areas (Tschardtke 1990). Other important herbivores include *Lasioptera arundinis* Schiner (stem-borer), a gall-inducing midge—*Giraudiella inclusa* Fr., four gall-forming *Lipara* spp., and a leaf-feeding aphid, *Hyalopterus pruni* Geoffroy (Dill 1937, Skuhrava and Skuhravy 1981). However, gall infestation causes shoot elongation, not mortality, in affected *P. australis* ramets (Tschardtke 1989). Differences in herbivory between European and North American populations have not been reported.

Penko (1985) encountered *Bellura obliqua* Walker (a stem borer) egg masses and larvae more frequently on *Typha latifolia* than on *T. angustifolia* in Minnesota. He also noted that *T. × glauca* stands can be heavily infested by *B. obliqua*. *Bellura obliqua* can reduce standing crop of *T. latifolia* by up to 15% in managed stands (Penko and Pratt, 1986a). Penko and Pratt (1986b) found that larvae reared on *T. latifolia* had a higher survival rate and were somewhat larger than those reared on *T. angustifolia*. Several factors could potentially make *T. angustifolia* an inferior host. First, the stem structure of *T. angustifolia*, narrow and containing a tough central core, may be less inhabitable by growing *Bellura* larvae. Second, dispersal by early instars and overwintering larvae may be less successful in deeper water, where *T. angustifolia* is more abundant. Finally, *T. angustifolia* contains unidentified alkaloids and cyanogens not found in *T. latifolia*. Since *T. × glauca* is also heavily infested, it seems most likely that stem structure or chemical composition is a likely explanation for differential herbivory.

Spencer and Lekic (1974) found 15 insects associated with *Myriophyllum spicatum* in Yugoslavia, ten in Pakistan, and only one in the United States. They found that most herbivory occurs from polyphagous lepidopteran and coleopteran larvae. However, their review was not based on comprehensive information for North America, so it is not clear that *M. spicatum* populations in Eurasia experience greater herbivory than do those in North America. Creed and Sheldon (1994) found that growth declines in Vermont *M. spicatum* populations were caused by herbivory from a lepidopteran larvae, *Acentria ephemerella* Den. & Sch., and a weevil, *Euhrychiopsis lecontei* Dietz. Besides direct losses from herbivory, both insects seem to increase stem fragmentation and decrease buoyancy. Decreased buoyancy could result in population declines, whereas stem fragmentation may actually facilitate dispersal.

More than 120 phytophagous insects are associated with European populations of *L. salicaria*, including fourteen that may be host specific (Batra et al. 1986). A weevil, *Nanophyes marmoratus* Goeze is one of the most common insects associated with *L. salicaria*, destroying up to 69% of the ovules of some plants. Species of chrysomelids (e.g., *Pyrrhalta* sp.) have caused 50% defoliation of some populations in Italy, Austria, and Yugoslavia. In Northern Europe, the gall-forming *Dasineura salicariae* Kiefer prevents flowering and branching, reducing foliage production by 75% and seed production by 80%. Recent studies (Blossey 1993) found the root-boring weevil, *Hylobius transversovittatus* Goeze, to be present in two-thirds of the populations in northern and central Europe, with an attack rate of more than 75%. Intense herbivory by a diverse host-specific insect assemblage is absent from North America (Blossey and Notzold 1995).

Blossey and Notzold (1995) compared growth (in a common garden) of *Lythrum salicaria* plants from two locations (with and without herbivory in New York and Lucelle, Switzerland) and compared the growth of common herbivores (*Galerucella pusilla* Duff., *Hylobius transversovittatus*) when fed plants from each location. They predicted that if competitive ability has been selected over herbivore defenses in North American *Lythrum* populations, they produce more biomass than European populations. In addition, specialized herbivores should have greater performance when grown on North American *Lythrum*. New York populations grew taller and had significantly greater biomass than Swiss populations. Root-feeding larval survivorship and growth was also greater for insects raised on New York plants. Leaf feeders did not have improved performance. Blossey and Notzold conclude that, although they cannot exclude other possibilities, such as plasticity and maternal effects, plant growth patterns likely support the idea that North American populations have greater competitive ability since release from herbivore pressure.

Introgression and Hybrid Speciation

Typha glauca. In the case of *Typha* × *glauca*, the historic record of sympatry between putative parental species and rapid expansion of hybrid populations provides provocative and controversial insights into introgression. The taxonomic literature has indicated that hybrid populations are suspected on both the European and North American continents—a rather rare event (Hotchkiss and Dozier 1949, Smith, 1987). These putative hybrids have been described in a number of different ways: first as a varietal (*T. angustifolia* var. *elongata* (Dudley) Wieg.), then as interspecific hybrids (*T. × glauca* Gordon), and finally as a separate species

(*T. glauca*). Since 1888, *T. × glauca* has been recognized as an interspecific hybrid in Europe, a product of the cross *T. angustifolia* × *T. latifolia* (Smith 1987). In North America, however, its hybridity is controversial (Hotchkiss and Dozier 1949, Smith 1987). Interspecific hybridization within *Typha* is not uncommon; many other hybrids have been reported: *T. angustifolia* × *T. domingensis* (Smith 1961), *T. angustifolia* × *T. shuttleworthii* (Krattinger 1978), *T. domingensis* × *T. latifolia* (Rothmaler 1940), *T. domingensis* × *T. subulata* (Crespo and Perez-Moreau 1967), *T. latifolia* × *T. shuttleworthii* (Krattinger 1978), and *T. latifolia* × *T. subulata* (Crespo and Perez-Moreau 1967).

An examination of the geographical distribution of the putative parents and the hybrid populations provides several critical pieces of circumstantial evidence why the hybridity of *T. × glauca* has been accepted in Europe more than in North America. Both *T. angustifolia* and *T. latifolia* are old species (pollen deposits found in the Mesozoic period) and endemic to Eurasia; the former is found only in temperate regions while the latter is distributed from boreal to subtropical areas (Lee 1975, Smith 1987). While both species currently share distributions similar to Europe in North America, *T. angustifolia* may not be endemic to North America. Spreading *T. angustifolia* throughout the continent since the mid-1800s has created many areas of recent sympatry with *T. latifolia*. Since both species are wind pollinated, introgressive hybridization could have occurred simultaneously in different areas of sympatry during the late nineteenth and throughout the twentieth centuries (Smith 1967, Stuckey 1980). This would explain why European recognition of *T. × glauca* as an interspecific hybrid occurred as early as 1888 while North American recognition came much later.

Early studies of introgression in *Typha* documented that different kinds of colonies existed in North America, ranging from nearly pure stands of *T. angustifolia* (New York), pure or nearly pure stands of *T. latifolia* (Michigan), to stands that were pure *T. × glauca* (Hotchkiss and Dozier 1949, Fassett and Calhoun 1952). Mixed populations of both *T. angustifolia* and *T. latifolia* without *T. × glauca* were rarely reported. The distribution of *T. × glauca* most closely paralleled that of *T. angustifolia* throughout North America. Field studies of natural hybrids showed that *T. × glauca* occurred wherever the parental species were sympatric, particularly in disturbed habitats with altered water and soil conditions (Smith 1967).

The body of circumstantial evidence regarding the putative parents and *T. × glauca* led many researchers to study introgression in North American populations. The majority of research reports have supported introgressive hybridization (Calhoun 1952, Louis-Marie 1960, Smith 1961, 1967, Bayly and O'Neill 1971, Fas-

Table 1. Potential species and nonspecies gene traits of *Typha angustifolia* and *T. latifolia* (Gleason and Cronquist 1991).

Diagnostic Traits	<i>T. angustifolia</i> (L.)	<i>T. latifolia</i> (L.)
Stems	1-1.5 m	1-3 m
Leaf width	5-11 mm	(8-)10-23 mm
Compound pedicels	short, stout	long, slender
Pollen	monads	tetrads
Pistillate bracteoles	distally rounded	not present
Pistillate color	deep brown	brown
Pistillate length/width	10-20 cm/1-2 cm	10-15 cm/2-3 cm
Stigma	linear, thick	spatulate, broad
Sterile pistillate flower-shape of tip	dilated into cuneate, truncate tip	expanded into spatulate tip
Staminate bracteoles	brown, scale-like	white, capillary
Staminate/pistillate portions of spike	normally separated	contiguous or separated by <4 mm
Fruit	5-8 mm, copious hairs with brown tip	1 cm, copious white hairs arising near base (linear, not expanded upwards)
Achene	usually distinctly above middle of whole fruit	above middle of whole fruit
Habitat	marshes, more tolerant of salt & alkali	freshwater marshes, less tolerant of high conductivity waters

sett and, Lee 1975, Esnault and Larher 1982), but one has not (Sharitz *et al.* 1980). Early morphological studies by Fassett and Calhoun (1952) caused the most controversy regarding introgression. Failure to find pure stands of both parental species, failure to account for intraspecific environmental variation, and problematic identification of species vs. non-species genes were major issues with their work (Smith 1967, Lee 1975). They chose six traits: gap between pistillate/staminate parts of the spike, pistillate coloration, pistillate bracteoles, stigma shape, sterile pistillate flower shape, and hair shape in the sterile pistillate flowers. A comparison of these traits with the major diagnostic traits for the two putative parents (Table 1) shows that only three of the traits examined are diagnostic, species genes (pistillate bracteoles, stigma, shape of the tip in sterile pistillate flowers). However, the three traits selected by Fassett and Calhoun (1952) provide evidence of introgression into the hybrid populations (*T. × glauca*). Bayly and O'Neill (1971) found evidence of introgression using an eighteen point hybrid index for leaf width and four floral characteristics (gap between staminate/pistillate portions of spike, pistillate bracteoles, pistillate flowers, stigmas), of which two traits were non-species genes.

Biochemical markers such as esterase (EST), malate dehydrogenase (MDH), glutamate dehydrogenase (GDH), aspartate aminotransferase (AAT or GOT), isocitrate dehydrogenase (IDH), and alcohol dehydrogenase (ADH) indicated that *T. × glauca* were hybrid populations, although not all were necessarily F_1 hybrids (Lee and Fairbrothers 1973, Sharitz *et al.* 1980). *Typha × glauca* had lowered specific activities but

more isozymes than either parent. Lee (1975) found more isozyme variation within hybrid populations than with morphological markers. The differences in isozymes between the two parents correlated strongly with the diagnostic morphology that distinguishes *T. angustifolia* from *T. latifolia*. Backcrosses probably involve primarily *T. angustifolia*, since many of the hybrids that were not intermediates overlapped only with this parent.

Experimental hybridization between the putative parents produced F_1 interspecific hybrids that resembled natural hybrids with intermediate traits and depressed fertility (Marsh 1962, Smith 1967). The similarities between experimental and natural hybrids removed doubts that the putative hybrids (*T. × glauca*) were actually F_1 interspecific hybrids (Smith 1961, 1967). Later hybrid generations were rare and primarily backcrosses (BC_1 , BC_2) or recurrent backcrosses that resembled the recurrent parent. Clearly, hybridization between *T. angustifolia* and *T. latifolia* is unusually commonplace in North America (as it is in Europe) and occurs virtually everywhere the parents are sympatric and hybrid habitats exist (Smith 1967). Lee (1975) detected little morphological variation in the hybrids, concluding that diagnostic characters are tightly linked in *Typha*. Observations of *T. × glauca* support the prediction that competitive ability is due, in part, to the heterogeneity in habitat preferences: hybrid populations outcompete their parents (*T. angustifolia*, *T. latifolia*) in a variety of ecological conditions and tolerate water-level fluctuations better than either parent (McDonald 1955, Grace and Wetzel 1981, 1982a, b, Smith 1987, Waters and Shay 1990, 1992).

Table 2. Potential **species** and **nonspecies** gene traits of *Lythrum alatum* and *L. salicaria* (Anderson and Ascher 1994a,b, 1995, Anderson et al. 1995).

Character	<i>L. alatum</i> (Pursh)	<i>L. salicaria</i> (L.)
Styly	Distylous	Tristyous
Axillary flowers	Solitary	Whorled (>4) densely cymose
Calyx	Glabrous, oblong	Pubescent, urceolate
Phyllotaxy	Alternate, lowermost opposite	Opposite to whorled
Leaf shape	Linear-lanceolate to oblong-ovate	Lanceolate
Leaf base	Rounded to subcordate	Rounded or cordate
Leaf texture	Glabrous	Hirsute
Seed dormancy	Yes (20–80%)	None
Plant height	1.5–3'	3–15'
Stem appendages	Winged	None

Lythrum salicaria. Due to the myriad of dispersal mechanisms, *Lythrum salicaria* has had many separate, independent opportunities to form colonizing populations in North America since the mid 1800s (Anderson and Ascher 1995, Anderson et al. 1995). *Lythrum salicaria* L. is a polyploid ($4x$, $6x$), native to Eurasia, and currently grows both in natural habitats and in cultivated settings (Shamsi and Whitehead 1974). No other related species exist in its native range with which to cross-pollinate. *Lythrum salicaria* possesses heterostyly, macroscopic floral differences in pistil (stigma, style, ovary) and filament (anther) lengths such that three forms (tristyly) exist within a population (Darwin 1865). Eleven *Lythrum* species, primarily diploid ($2x$) and distylous (short and long pistils/filaments), are native to North America (Green 1889, Koehne 1885, 1903, Blackwell 1970, Graham 1975, Cody 1978). *Lythrum alatum* Pursh, winged loosestrife, is the most cosmopolitan of the North American species, being widespread throughout the United States and eastern Canada (Cody 1978). *Lythrum alatum* and *L. salicaria* can be distinguished by diagnostic, morphological characters (Table 2). While *L. alatum* is more mesophytic than *L. salicaria*, they both occur in overlapping ecotopes (Levin 1970).

Lythrum alatum has been the genetic source of dwarf, interspecific horticultural cultivars because of its short stature (Anderson and Ascher 1993a). Despite ploidy differences, *L. salicaria* ($4x$, $6x$) and *L. alatum* ($2x$) intercross freely in natural settings (Levin 1970). The presence of $2n$ gametes in the pollen and eggs allows for the production of fertile, tetraploid ($4x$) hybrids (Schoch-Bodmer 1938). This, coupled with the extensive cultivation of domesticated plants by gardeners produced from interspecific hybridization between *L. salicaria* \times *L. alatum* ('Morden Gleam', 'Morden Rose', and dwarf forms of 'Robert'), provide the opportunities for introgression between the two species. *Lythrum salicaria*'s popularity as a colorful garden perennial, widespread—but incorrect—belief

that cultivars are sterile, and occasional escapes into nearby wetlands increased the opportunity for establishment in disturbed habitats (Anderson and Ascher 1993a). Interspecific hybridization in *Lythrum*, however, is not as easily accomplished as in *Typha* which is wind pollinated. Pollen vectors (e.g., *Apis mellifera* L., *Bombus vagans* Smith, and *B. terricola* Grene) that frequent native *Lythrum* species also visit *L. salicaria* (Levin and Kerster 1973). Thus, all of the necessary components exist for introgression to occur between *L. salicaria* and *L. alatum*.

Unlike the case of *Typha* \times *glauca*, the taxonomic literature is silent regarding the occurrence of hybrid populations of *Lythrum* in North America. The lack of such reports in Europe is understandable, since no species are sympatric. In North America, the possibility of hybridization is extremely high. Anderson and Ascher (1993b, 1994a, 1995, Anderson et al. 1995) characterized native *L. alatum* and naturalized *L. salicaria* populations in Minnesota for morphological evidence of introgressive hybridization. Deviations from the diagnostic characters of the putative parental species were found with regularity in these populations. *Lythrum salicaria* individuals were found with *L. alatum* traits: alternate leaves (1.2% of all individuals), seed dormancy (>95%), solitary axillary flowers (3.8%), and glabrous calyx or leaf texture (54.8%). The most common *L. alatum* trait was seed dormancy; open-pollinated seed collected from natural populations showed significant seed dormancy for five established populations (Anderson and Ascher 1994b). For *L. salicaria*, the only requirement for germination is exposure to light (Lehmann 1918, Lehmann and Lakshmana 1924, Keddy 1986, Nicholls 1987). *Lythrum alatum* populations contained individuals with *L. salicaria* traits: opposite leaves throughout the entire stem and whorled, multiple (≥ 4) axillary flowers.

Tristyous *L. alatum* is nonexistent in Minnesota, although one has been found in neighboring Iowa (Anderson and Ascher, unpublished data). Distylous indi-

viduals of *L. salicaria* have also not been found in any Minnesota population (Anderson and Ascher, unpublished data). However, the integrity of tristylous and its linkage with self incompatibility is being dramatically eroded (Anderson and Ascher 1994a), causing a disruption of normal outcrossing. Seed set was rare among all possible intraspecific, compatible crosses. The average lengths of pistil and filaments are gradually being reduced such that the distance between shorts, mids, and longs is decreasing. Introgressive populations have an increased tendency to self pollinate (Anderson and Ascher 1993a, b, 1994a, b, O'Neill 1994), enabling small, isolated founder populations to generate progeny without outside pollen sources. Several new traits, not found in either *L. alatum* or *L. salicaria*, also frequently surfaced in the purple loosestrife populations: red or purple seed coat coloration, serrate leaf margins, white flowers, striations in the flower petals, and apetalous flowers (Anderson *et al.* 1995). Both *L. salicaria* and *L. alatum* were the parents responsible for the traits observed in introgressive populations.

Biochemical analysis of horticultural cultivars and the same weedy *L. salicaria* populations have not been significantly different (Strefeler *et al.* 1996). Enzymes with the greatest polymorphisms were PGI, PGM, and MDH, indicating a tendency for most allozymes to be shared between *Lythrum* species. *Lythrum alatum* isozymes are genetically distinct from weedy *L. salicaria* and cultivars, suggesting that most isozymes in the weedy form have been transmitted from *L. salicaria*. This is not surprising since the direction of the cross is always with *L. salicaria* as female: *L. salicaria* × *L. alatum* (Anderson and Ascher 1994a, b, 1995, Anderson *et al.* 1995).

Experimental hybrids have been easily created as the commercially grown 'Morden Rose', 'Morden Gleam', and 'Robert', from the cross *L. salicaria* × *L. alatum* (Harp 1957). Attempts to recreate this cross have failed, although the reciprocal cross produced as many as 114 seeds/capsule (Anderson and Ascher 1994a, b, 1995, Anderson, *et al.* 1995). These hybrids are intermediate to the parents for most species genes (Table 2) with the exception of styly (all are tristylous). Backcrosses to *L. alatum*, *L. salicaria*, or F₁ hybrid cultivars also produced seed. Experimental hybridization has not advanced far enough yet to elicit recombination of the genes controlling heterostyly.

The continuous cultivation of interspecific hybrids in gardens has meant they have been able to continually backcross with sympatric *L. salicaria* populations. Since both habitats occupied by the F₁ and *L. salicaria* are disturbed sites, introgressive hybrids could have established future generations in either location. The 126+ year period, from *L. salicaria*'s introduction and

establishment in 1814 (Pursh 1814) to the 1930s, when the first invasion of Quebec pastures and wetlands was noted (Louis-Marie 1944, Barabe 1951), was sufficient time for introgressive hybridization to begin and transgressive segregants to surface. Either these initial introgressives in Quebec served as the forerunners in the creation of *L. salicaria* as a noxious weed throughout North America or other introgressive events, occurring in areas of sympatry, simultaneously produced transgressive segregants that responded in a similar manner.

Myriophyllum spicatum. The case of *M. spicatum* shares many similarities with the introgressive histories of *Typha* × *glauca* and *Lythrum salicaria*, especially their introduction via ship ballasts, confusing taxonomic history and common misidentifications, a lag time between introduction/establishment and the sudden occurrence of invasive forms, and rapid spread via asexual propagation. However, introgression in *M. spicatum* is based primarily on circumstantial evidence that raises sufficient questions regarding interspecific hybridization.

Two common *Myriophyllum* species are widely distributed in North America: *M. sibiricum* and *M. spicatum*. Since the late 1950s, *M. spicatum* has become a noxious weed in North America, while *M. sibiricum* (considered a NA endemic) frequently remains an innocuous member of aquatic plant communities. The two taxa differ in floral bract and bracteole characteristics, the presence of distinct black scales or hydathodes, stem apex morphology, leaf and internode length, phytochemistry, propagation by turions (only *M. sibiricum* has turions), and number of leaf divisions (5–12 in *M. sibiricum*, 12–20 in *M. spicatum*) (Patten 1954, Nichols 1975, 1984). Significant differences in cold temperature requirements for these two species also exist. While their ranges overlap in Europe and North America, *M. sibiricum* does not grow south of the mean January isotherm of 0°C on either continent (Aiken and McNeill 1980, Aiken 1981, Faegri 1982). In contrast, *M. spicatum* grows successfully in Florida without a winter cold requirement but has been found only as far north as 60°N latitude.

Both species are easily confused when using morphological characters since there are few species genes (Aiken 1979, Nichols 1984, Kane and Albert 1989a, b). *Myriophyllum sibiricum* was first discovered and independently named by two taxonomists: as *M. sibiricum* by Komarov (1914) and *M. exalbescens* by Fernald (1919). The name *M. exalbescens* Fernald was used until 1986 when Komarov's work was discovered (Ceska and Ceska 1986). Patten (1954) considered *M. sibiricum* to be an interbreeding race of *M. spicatum*, thereby being reduced to a subspecies by himself and Hulten (1968). Nichols (1975) used 25 traits to distin-

guish the species and agreed with Jepson (1925) that it was a varietas, *M. spicatum* var. *exalbescens* (Fernald) Jepson. In Europe, it was also distinguished as a subspecies or varietas of *M. spicatum* using the epithet *squamosum*.

Experimental crosses between *M. spicatum* and *M. sibiricum* have produced almost 100% seed set, many of which produced viable progeny (Patten 1956, Aiken 1979, Aiken et al. 1979). *Myriophyllum spicatum* is extremely fertile; pistillate flowers are receptive prior to pollen-shed on the same plant, thereby encouraging outcrossing and maintaining genetic diversity (Aiken et al. 1979). Seeds vary in their dormancy requirements, with prolonged dormancy and erratic germination (necessitating scarification treatments) while others germinated immediately following harvest (Patten 1955, Sculthorpe 1967). *Myriophyllum spicatum* seedlings have rarely been reported in North America; neither have seedlings of other *Myriophyllum* species possessing high levels of genetic variability been reported. Although interspecific crosses between *M. spicatum* and *M. sibiricum* did not occur in the Chesapeake area (origin of many ballast species) during 1880 to 1950 (because *M. sibiricum* does not extend this far south), such a cross was documented in New Jersey (Patten 1954). It is highly probable that interspecific hybridizations have continued in other locations where the species are sympatric. Recent reports from Lake Mary and surrounding areas in Arizona suggest that this interspecific cross is occurring and collected specimens of "uncertain identity" are suspected to be hybrids (Ricketson 1989).

Whether *M. spicatum* will also cross with the other *Myriophyllum* species found in North America is unknown. Interspecific crosses between other *Myriophyllum* species could have occurred in the Chesapeake Bay, since *M. heterophyllum* Michx., *M. verticillatum* L., and *M. pinnatum* (Walt.) B.S.P. occur in this region. The differences in ploidy level between such species in an interspecific cross can be overcome by the natural production of $2n$ gametes and by successive backcrosses to either parent. This could explain why the explosive growth of *M. spicatum* and eventual predominance in Chesapeake Bay occurred several decades after its introduction.

Biochemical analysis of isozyme variation has been conducted in six Minnesota populations of *Myriophyllum spicatum* and one individual from Wisconsin (Furnier and Mustaphi 1992). Eleven enzyme systems, controlled by nineteen putative loci were analyzed. Three polymorphic loci existed and only two distinct multilocus genotypes were found in all lakes. Such isozyme information indicates that no more than two genotypes of *M. spicatum* were introduced into these lakes. While considerable seed production occurred in

these lakes, no segregation was found for any heterozygous bands. RAPD (Random Amplification of Polymorphic DNA) analysis of these populations has been conducted on these same populations (G. Furnier, personal communication). Due to the paucity of morphological, biochemical, and molecular genetic information, it is not yet possible to determine if introgression is an event giving rise to invasive *M. spicatum* populations in North America.

Phalaris arundinacea. While scientific data regarding introgression in *Phalaris* is lacking, circumstantial data suggest potential future studies. Three species of *Phalaris* occur in northeastern North America (Gleason and Cronquist 1991). *Phalaris arundinacea* is cross-pollinated, highly self-incompatible, and asexually propagated which lends itself readily to commercial F₁ hybrid seed production (Casler and Hovin 1980). Several forage cultivars of reed canary grass have been released from breeding programs, and considerable effort has recently been devoted to determining heritability of forage yield, protein content, and disease resistance (Casler and Hovin 1984, 1985, Frank et al. 1985, Zeiders and Sherwood 1985, Suprenant et al. 1988). The circumstantial evidence available for *P. arundinacea* would suggest that introgression may be a causative factor in its tolerance of different soil conditions and yield. However, no definitive research has been conducted to provide further data on this possibility.

Phragmites australis. *Phragmites australis* possesses many characteristics typical of introgressed taxa: aneuploidy, perenniality, asexual propagation, and rapid colonization of disturbed habitats (Hauber et al. 1991, Gervais et al. 1993). However, *P. australis* has been considered an extremely polymorphic species (Dykjova 1978), with few genotypic differences among populations within a region (Clayton 1967, van der Toorn 1972). Recent speculation that new, more invasive genotypes may have been introduced from the Old World (Metzler and Rosza 1987) is supported by recent studies in the Mississippi River delta region (Hauber et al. 1991). Infrared aerial photographs of the Garden Island Bay subdelta revealed the existence of clone-like circular patches and adjacent background morphological types. Two isozyme genotypes were found that correlated with the patch and background morphology. Of the forty isozyme loci that were scored, 20% were fixed for alternate alleles. The remarkable genetic uniformity of the two phenotypes provides evidence that *P. australis* is primarily vegetatively propagated. The invasive biotype differed genetically from more stable populations; stable populations along the Gulf Coast are genetically similar (Hauber 1992 in Marks et al. 1993). These data sug-

Table 3. Summary of evidence supporting the three hypotheses of increased invasiveness: environmental constraints, increased competitive ability, and introgression for the five North American taxa. Complete explanations provided in text. Strength of evidence is indicated by: E = experimental study (for controlled comparative study), O = field observations, C = circumstantial evidence, S = speculation.

Evidence supporting the hypothesis:	<i>Typha</i> × <i>glauca</i>	<i>Lythrum</i> <i>salicaria</i>	<i>Myrio-</i> <i>phyllum</i> <i>spicatum</i>	<i>Phalaris</i> <i>arundi-</i> <i>nacea</i>	<i>Phragmite</i> <i>australis</i>
Release from Environmental Constraints					
Preference for devegetated areas	O	O	O	O	O
Relatively high tolerance to water level fluctuations	O		C	E	O
Relatively high tolerance to eutrophication	E	C		E	
Relatively high tolerance to salinity	E		S		E
Increased Competitive Ability					
Diverse herbivore fauna associated with species	E	E	E		E
Paucity of herbivores in North America		O	C		
Long lags prior to expansion	O	O	O		
Decreased allocation to herbivore defense		E			
Introgression					
Recent sympatry of species or varieties	O	O	O	S	S
Cultivated varieties exist		E		E	
Preference for devegetated areas	O	O	O	O	O
Long lag prior to expansion	O	O	O		
Presence of introgressive populations	E	E	C		
Hybrid populations possess non-parental traits		E			
Hybrid populations have broader environmental range than parents	E				

gest that invasive biotypes have been recently introduced to the Mississippi delta region.

CONCLUSIONS

The preponderance of available information related to invasive plants in North American wetlands is descriptive accounts of range expansions and general habitat descriptions. Although understanding why certain plants are invasive is a logical prerequisite for developing prevention and control strategies, explicit studies to understand the factors promoting invasiveness have largely been limited to *Typha* × *glauca* and *Lythrum salicaria* (Table 3). For all five species, though, there has been surprisingly little experimentation on the responses of North American populations relative to European populations and to parental taxa (i.e., *T. angustifolia*, *T. latifolia*).

The strongest evidence of environmental stressors facilitating invasive expansion comes from the studies by Waters and Shay (1990, 1992) showing the plasticity of *T. × glauca* to grow vigorously over a great range of water conditions compared with other *Typha* spp. and from Conchou and Pautou (1987) and Conchou and Fustec (1988) who showed how *Phalaris arundinacea* modifies growth form and reproductive strategy in submersed and drawdown conditions. Com-

parable *Phalaris* research has not been conducted on North American ecotypes, however.

The potential for reduced herbivory to allow aggressive growth is greatest for *Lythrum salicaria*. The diverse and abundant insect community associated with *L. salicaria* in Europe is absent in North America. Blossey and Notzold (1995) showed that decreased herbivory has resulted in increased allocation to growth in North American populations. Both *Phragmites australis* and *Myriophyllum spicatum* are known to have diverse insect communities associated with European populations, but comparative North American data are lacking. Since *Typha latifolia* experiences greater herbivory (for at least one important stem border) than does the *T. angustifolia* (Penko and Pratt (1986a, b), aggressiveness in *T. × glauca* is unlikely to be caused by a release from herbivores.

Introgressive hybridization is potentially a cause of invasiveness for all five species but has been established only for *Typha × glauca* and *Lythrum salicaria* (Table 3). While the introgressive research conducted on *T. × glauca* confirms it to be a hybrid, future work is needed to clarify several confusing issues. Molecular analyses would help dispute or support introgression in those populations whose morphology does not differ markedly from parents (i.e., they do not appear to be intermediate, primary F₁ hybrids). Comparative

molecular analysis of F_1 and later cross and backcross generations of experimental hybrids with natural hybrids could clarify what generations of hybrids are established across North America. Such work could be done concomitantly with morphological analysis, using species genes. Additional ecological studies are needed to compare the competitive relationships between *T. × glauca*, *T. angustifolia*, *T. latifolia*, and other wetland plants. Future studies of introgression in *L. salicaria* should concern the use of molecular markers to provide additional data on gene flow between the two parental species. A comparative analysis between European and introgressive North American *L. salicaria* populations is needed to show the genetic differences between the two forms. The consequences of introgression to *L. salicaria* growth and environmental tolerances also have not been investigated to find out whether North American populations have broader environmental tolerance than parental species, as expected.

The genetic relationships between invasive populations and related taxa need to be established for *M. spicatum*, *P. arundinacea*, and *P. australis* populations in North America. For example, this information is needed for *P. arundinacea* to determine whether cultivars planted for soil erosion control and livestock forage are contributing to invasive spread. If so, curtailing its use needs to be considered. If the presence of introgression or hybrid speciation is established for any of these five species, the logical control strategy for uninvaded landscapes is to prevent any populations from becoming established within a locale. Moody and Mack (1988) considered the control of these "nascent foci" to be an effective way to limit the expansion of exotic species.

Management strategies designed to mimic natural disturbances (e.g., flooding, drawdown, fire) will not likely be effective for any of the five species considered in this review. All five species are known to preferentially colonize devegetated areas that routinely occur in wetlands from natural or cultural disturbances. Hobbs and Huenneke (1992) note that mimicking natural disturbances is increasingly impractical because altered landscape settings of remnant natural ecosystems favor undesirable invasions. Species that have newly evolved traits for aggressive growth (because of reduced herbivory or introgression), will not likely form co-dominant stands with native wetland vegetation over time.

For *Lythrum salicaria*, the introduction of biological control agents is expected to reduce populations (Hight et al. 1995). Three insects, two leaf-feeding beetles (*Galerucella californiensis* L., *Galerucella pusilla*) and one root-feeding weevil (*Hylobius transversovittatus*), have been released and produced successive genera-

tions. Because of abundant and persistent seed banks of *L. salicaria*, there may be considerable lag time until species control is achieved (Welling and Becker 1993). After herbivore communities have diminished *L. salicaria* stands, community dynamics may still be unpredictable because introgressant populations possess novel traits.

This review suggests that causes of invasiveness in North American wetlands species are related to long-term, large scale changes that cannot be reversed. Intercontinental transport of propagules with ship ballast and increasing connectivity between regions with ditches and canals (often with increased pollutant and nutrient loads) were likely the most important catalysts for profound evolutionary changes in wetland taxa. How these invasive species are altering community dynamics in North American wetlands awaits further study.

ACKNOWLEDGMENTS

This is Minnesota Agricultural Experiment Station Publication 981210013.

LITERATURE CITED

- Aiken, S. G. 1979. North American species of *Myriophyllum* (Haloragaceae). Ph.D. Dissertation. University of Minnesota, St. Paul, MN, USA.
- Aiken, S. G. 1981. A conspectus of *Myriophyllum* (Haloragaceae) in North America. *Brittonia* 33:57-69.
- Aiken, S. G. and J. McNeill. 1980. The discovery of *Myriophyllum exalbescens* Fernald (Haloragaceae) in Europe and the typification of *Myriophyllum spicatum* and *Myriophyllum verticillatum*. *Botanical Journal of the Linnean Society* 80:213-222.
- Aiken, S. G., P. R. Newroth, and I. Wile. 1979. The biology of Canadian weeds—*Myriophyllum spicatum*. *Canadian Journal of Plant Sciences* 59:201-215.
- Alway, F. J. 1931. Early trials and use of reed canary grass as a forage plant. *Journal of the American Society of Agronomy* 23: 64-66.
- Anderson, E. 1949. *Introgressive Hybridization*. John Wiley and Sons, Inc. New York, NY, USA.
- Anderson, E. and L. Hubricht. 1938. The evidence for introgressive hybridization. *American Journal of Botany* 25:396-402.
- Anderson, N. O. and P. D. Ascher. 1993a. Male and female fertility of loosestrife (*Lythrum*) cultivars. *Journal of the American Society of Horticultural Science* 118:851-858.
- Anderson, N. O. and P. D. Ascher. 1993b. Style morph frequencies in Minnesota populations of *Lythrum* (Lythraceae). I. Distylous *L. alatum* Pursh. *Plant Cell Incompatibility Newsletter* 25: 4-9.
- Anderson, N. O. and P. D. Ascher. 1994a. Erosion of style/anther length integrity in introgressive *Lythrum* hybrids. p. 269-272. In A. G. Stephenson and T-h Kao (eds.) *Pollen-Pistil Interactions and Pollen Tube Growth*. American Society of Plant Physiologists, Rockville, MD, USA.
- Anderson, N. O. and P. D. Ascher. 1994b. Self incompatibility (S1) in distylous *Lythrum alatum*, winged loosestrife. *HortScience* 29: 497 (Abstr.).
- Anderson, N. O. and P. D. Ascher. 1995. Style morph frequencies in Minnesota populations of *Lythrum* (Lythraceae). II. Tristylous *L. salicaria* L. *Sexual Plant Reproduction* 8:105-112.
- Anderson, N. O., P. D. Ascher, and B. E. Liedl. 1995. Importance

- of introgressive hybridization in the development of invasive *Lythrum salicaria*. HortScience 30:819. (Abstr.)
- Anonymous. 1932. Find 'Long Purples' in Interstate Park. Visitors to Harriman Preserve along Hudson River are attracted by the plant. Flower is an 'immigrant'. *Lythrum salicaria* in full blossom now in marshes and streams through the valley. New York Times, New York, NY, USA. Sunday, 21 August, p. 19.
- Anonymous. 1834. Ribbon grass. New England Farmer 13:41, 129.
- Arnold, M. L., P. Wilkinson, D. D. Shaw, A. D. Marchant, and N. Contreras. 1987. Highly repeated DNA and allozyme variation between sibling species: evidence for introgression. Genome 29: 272-279.
- Balough, G. R. and T. A. Bookhout. 1989. Purple loosestrife, *Lythrum salicaria*, in Ohio's Lake Erie marshes, USA. Ohio Journal of Science 89:62-64.
- Barabe, R. 1951. Progress report on the eradication of purple loosestrife (*Lythrum salicaria* L.) in Quebec. p. 83-90. In Proceedings of the 4th Meeting, Eastern Section, National Weed Committee, Ottawa, Canada.
- Barber, H. N. 1970. Hybridization and the evolution of plants. Taxon 19:154-160.
- Barrett, S. C. H. 1989. Waterweed invasions. Scientific American 260:90-97.
- Batra, S. W. T., D. Schroeder, P. E. Boldt, and W. Mendl. 1986. Insects associated with purple loosestrife (*Lythrum salicaria* L.) in Europe. Entomological Society Proceedings 88:748-759.
- Bayley, S., V. D. Stotts, P. F. Springer, and J. Steenis. 1978. Changes in submerged aquatic macrophyte populations at the head of Chesapeake Bay, 1958-1975. Estuaries 1:73-84.
- Bayly I. L. and T. A. O'Neill. 1971. A study of introgression in *Typha* at Point Pelee Marsh, Ontario. Canadian Field Naturalist 85:309-314.
- Berg, T. 1982. Seed dormancy in local populations of *Phalaris arundinacea*, reed canarygrass, western Norway. Acta Agriculturae Scandinavica 32:405-409.
- Berstein, N. P. 1981. Vegetational history of Mentor Marsh. Ohio Journal of Science 81:105-108.
- Bjork, S. 1967. Ecological investigations of *Phragmites communis*: studies in theoretical and applied limnology. Folia Limnologica Scandinavica 14:1-248.
- Blackwell, W. H. 1970. The Lythraceae of Ohio. Ohio Journal of Science 70:346-352.
- Blossey, B. and R. Notzold. 1995. Evolution of increased competitive ability in invasive non indigenous plants: a hypothesis. Journal of Ecology 83:887-889.
- Blossey, B. D. Schroeder, S. D. Hight, and R. A. Malecki. 1994. Host specificity and environmental impact of two leaf beetles (*Galerucella californiensis* and *G. pusilla*) for biological control of purple loosestrife, *Lythrum salicaria*. Weed Science 42:134-140.
- Blossey, B. 1993. Herbivory below ground and biological weed control: life history of a root-boring weevil on purple loosestrife. Oecologia 94:380-387.
- Bousquet, J., W. M. Cheliak, J. Wang, and M. Lalonde. 1990. Genetic divergence and introgressive hybridization between *Alnus sinuata* and *A. crispa* (Betulaceae). Plant Systematics and Evolution 170:107-124.
- Bowley, S. and N. L. Taylor. 1987. Introgressive hybridization. p. 23-59. In: B. R. Christie (ed.) CRC Handbook of Plant Science in Agriculture. Volume 1. Boca Raton, FL, USA.
- Breternitz, D. A., C. K. Robinson, and G. T. Gross. 1986. Dolores archeological program: final synthetic report. U.S. Department of the Interior, Bureau of Reclamation, Denver, CO, USA.
- Bryant, J. P., J. Tuomi, and P. Niemala. 1988. Environmental constraint of constitutive and long-term inducible defenses in woody plants. p. 367-389. In K. C. Spencer (ed.) Chemical Mediation of Coevolution. Academic Press, San Diego, CA, USA.
- Carlton, J. T. 1996. Biological invasions and cryptogenic species. Ecology 77:1653-1654.
- Carpenter, S. R. 1980. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. Canadian Journal of Botany 58:527-535.
- Casler, M. D. and A. W. Hovin. 1980. Genetics of vegetative stand establishment characters in reed canarygrass clones. Crop Science 20:511-515.
- Casler, M. D. and A. W. Hovin. 1984. Genotype \times environment interaction for reed canarygrass forage yield (*Phalaris arundinacea*, stability analysis). Crop Science 24:633-636.
- Casler, M. D. and A. W. Hovin. 1985. Predicting forage yield from morphological traits in reed canarygrass. Crop Science 25:783-787.
- Ceska, A. and O. Ceska. 1986. Notes on *Myriophyllum* (Haloragaceae) in the Far East: the identity of *Myriophyllum sibiricum* Komarov. Taxon 35:95-100.
- Chechowitz, N., D. M. Chappell, S. I. Guttman, and L. A. Weigt. 1990. Morphological, electrophoretic, and ecological analysis of *Quercus macrocarpa* populations in the Black Hills of South Dakota and Wyoming. Canadian Journal of Botany 68:2185-2194.
- Clayton, W. D. 1967. Studies in the Graminae: XIV. Kew Bulletin 21:111-117.
- Clayton, W. D. 1968. The correct name of the common reed. Taxon 17:168-169.
- Cody, W. J. 1978. The status of *Lythrum alatum* (Lythraceae) in Canada. The Canadian Field Naturalist 92:74-75.
- Coffey, B. T. and C. D. McNabb. 1974. Eurasian water-milfoil in Michigan. The Michigan Botanist 13:159-165.
- Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant herbivore defense. Science 230:895-899.
- Conchou, O. and E. Fustec. 1988. Influence of hydrological fluctuations on the growth and nutrient dynamics of *Phalaris arundinacea* L. in a riparian environment. Plant and Soil 112:53-60.
- Conchou, O. and G. Pautou. 1987. Modes of colonization of an heterogeneous alluvial area on the edge of the Garonne River by *Phalaris arundinacea*. Regulated Rivers 1:37-48.
- Couch, R. and E. Nelson. 1985. *Myriophyllum spicatum* in North America. p. 8-18. In L. W. J. Anderson (ed.) Proceedings of the First International Symposium on Watermilfoil (*Myriophyllum spicatum*) and Related Haloragaceae Species. Aquatic Plant Management Society, Washington, DC, USA.
- Couch, R. and E. Nelson. 1988. *Myriophyllum quitense* (Haloragaceae) in the United States. Brittonia 40:85-88.
- Crawley, M. J. 1987. What makes a community invasible? p. 429-453. In A. J. Gray, M. J. Crawley, and P. J. Edwards (eds.) Colonization, Succession and Stability. Blackwell, Oxford, England.
- Creed, R. P., Jr. and S. P. Sheldon. 1994. The effect of two herbivorous insect larvae on Eurasian watermilfoil. Journal of Aquatic Plant Management 32:21-26.
- Crespo, S. and R. Perez-Moreau. 1967. Revision del genero *Typha* en la Argentina. Darwiniana 14:413-429.
- Cutright, N. J. 1986. Regulation of purple loosestrife by states in the midwest. Proceedings of the North Central Weed Control Conference 41:123-125.
- Cutright, N. J. 1978. Purple loosestrife: beautiful exotic or unwanted weed? Wisconsin Natural Resources 2:26-27.
- Darwin, C. R. 1865. On the sexual relations of the three forms of *Lythrum salicaria*. Journal of the Linnean Society of Botany 8: 169-196.
- Dill, W. 1937. Der entwicklungsgang der Mehligigen Pflaumenblattlaus *Hyalopterus arundinis* Fabr. Im schweizerischen Mittelland. Dissertation. Entomologisches Institut, ETH Zurich, Switzerland.
- Dore, W. G. and J. McNeill. 1980. Grasses of Ontario. Research Branch, Agriculture Canada. Ottawa, ON, Canada. Monograph No. 26.
- Dudley, W. R. 1886. The Cayuga flora. Part I. A catalogue of the Phaenogamia growing without cultivation in the Cayuga Lake basin. Bulletin of Cornell University 2:1-132.
- Dykyjova, D. 1978. Plant growth and estimates of production: intraspecific and clonal variability and its importance for production estimates. p. 159-163. In D. Dykyjova and J. Kvet (eds.) Pond Littoral Ecosystems, Structure and Functioning., Springer Verlag, Berlin BHeidelberg, Germany.
- Esnault, M. A. and F. Lahrer. 1982. Interpretation des populations de *Typha* par l'analyse numerique des donnees morphologiques et par l'etude des formes isofonctionnelles de diverse enzymes. Candolea 37:633-648.

- Faegri, K. 1982. The *Myriophyllum spicatum* group in North Europe. *Taxon* 31:467-471.
- Fassett, N. C. and B. C. Calhoun. 1952. Introgression between *Typha latifolia* and *Typha angustifolia*. *Evolution* 6:367-379.
- Fernald, M. L. 1919. Two new *Myriophyllums* and a species new to the United States. *Rhodora* 21:120-124.
- Frank, A. B., J. D. Berdahl, and R. E. Barker. 1985. Morphological development and water use in clonal lines of four forage grasses. *Crop Science* 25:339-344.
- Furnier, G. R. and M. M. Mustaphi. 1992. Isozyme variation in Minnesota populations of Eurasian watermilfoil. *Aquatic Botany* 43:305-309.
- Gervais, C., R. Trahan, D. Moreno, A. M. Drolet. 1993. *Phragmites australis* in Quebec: geographical distribution, chromosome number, and reproduction. *Canadian Journal of Botany* 71:1386-1393.
- Gilpin, H. 1990. Ecological prediction. *Science* 248:88-89.
- Gleason, H. A. and A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. 2d ed. NY Botanical Garden, Bronx, NY, USA.
- Grace, J. B. and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*). *American Midland Naturalist* 118:463-474.
- Grace, J. B. and R. G. Wetzel. 1982a. Niche differentiation between two rhizomatous species: *Typha latifolia* and *Typha angustifolia*. *Canadian Journal of Botany* 60:46-57.
- Grace, J. N. and R. G. Wetzel. 1982b. Phenotypic and genotypic components of growth and reproduction in *Typha latifolia*: experimental studies in marshes of differing successional maturity. *Ecology* 62:789-801.
- Graham, S. A. 1975. Taxonomy of the Lythraceae in the southeastern United States. *SIDA* 6:80-103.
- Gray, A., S. Watson, and J. Coulter. 1889. *Manual of the Botany of the Northern United States, Including the District East of the Mississippi and North of North Carolina and Tennessee*. Sixth Edition, Ivison, Blakeman, Taylor and Company, New York, NY, USA.
- Green, E. L. 1889. The genus *Lythrum* in California. *Pittonia* 2:11-13.
- Gries, C., L. Kappen, and R. Losch. 1990. Mechanisms of flood tolerance in reed, *Phragmites australis* Trin. ex. Steud. *New Phytologist* 114:589-593.
- Habet, E. 1996. Invasive plants of Canada project. Report to the Ontario Ministry of Natural Resources, Ottawa, ON, Canada.
- Haghighi, K. and P. D. Ascher. 1988. Fertile, intermediate hybrids between *Phaseolus vulgaris* and *P. acutifolius* from congruity backcrossing. *Sexual Plant Reproduction* 1:51-58.
- Hamrick, J. L. 1989. Isozymes and the analysis of genetic structure in plant populations. p. 87-105. In D. E. Soltis and P. S. Soltis (eds.). *Isozymes in Plant Biology*. Discorides, Portland, OR, USA.
- Hanna, E. 1984. Restoration of aquatic vegetation in Rondeau Bay, Lake Erie. *The Plant Press* 2:99-101.
- Harms, V. L. and G. F. Ledingham. 1986. The narrow-leaved cattail, *Typha angustifolia* and hybrid cattail, newly reported from Saskatchewan. *Canadian Field Naturalist* 100:107-110.
- Harp, H. F. 1957. The Morden Lythrums. *Weekly Note*, n.p. Morden Research Station, Morden, Manitoba, Canada.
- Harper, J. L. 1965. Establishment, aggression and cohabitation in weedy species. p. 243-265. In H. G. Baker and G. L. Stebbins (eds.). *The Genetics of Colonizing Species*. Academic Press, New York, NY, USA.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press, London, England.
- Harris, S. W. and W. H. Marshall. 1963. Ecology of water level manipulation on a northern marsh. *Ecology* 44:331-343.
- Harris, A. 1835. Ribbon grass. *New England Farmer* 14:125.
- Harris, J. A. 1927. The cat tail, *Typha angustifolia*, in Utah. *Torreya* 27:9-11.
- Haslam, S. M. 1965. Ecological studies in the Breck fens. I. Vegetation in relation to habitat. *Journal of Ecology* 53:599-619.
- Haslam, S. M. 1970. The performance of *Phragmites communis* Trin. in relation to water-supply. *Annals of Botany* 34:867-877.
- Haslam, S. M. 1971. Community regulation in *Phragmites communis*. I. Monodominant stands. *Journal of Ecology* 59:65-73.
- Haslam, S. M. 1972. *Phragmites communis*. *Journal of Ecology* 60:585-610.
- Haslam, S. M. 1973. Some aspects of the life history and autecology of *Phragmites communis* - a review. *Polskii Archiwun Hydrobiologii* 20:79-100.
- Haslam, S. M. 1979. Infrared color photograph and *Phragmites communis*. *Polskie Archiwun Hydrobiologii* 26:65-72.
- Hauber, D. P., D. A. White, S. P. Powers, and F. R. DeFrancesch. 1991. Isozyme variation and correspondence with unusual infrared reflectance patterns in *Phragmites australis*. *Plant Systematics and Evolution* 178:1-8.
- Hayden, A. 1939. Notes on *Typha angustifolia* L. in Iowa. *Iowa State College Journal of Science* 13:341-351.
- Heiser, C. 1973. Introgression re-examined. *Botanical Review* 39:347-366.
- Hesselgren, N. L. 1787. *Pan Suecus*. p. 225-262. In C. von Linne (ed.). *Amoenitates Academicae*. Vol. 2. Third Edition. Erlangen, Sweden.
- Hight, S. D., B. Blossey, and R. Declerck-Floate. 1995. Establishment of insect biological control agents from Europe against *Lythrum salicaria* in North America. *Environmental Entomology* 24:967.
- Hobbs, R. J. and L. F. Huenneke, L. F. 1992. Disturbance, diversity and invasion: implications for conservation. *Conservation Biology* 6:324-337.
- Hocking, P. J., C. M. Finlayson, and A. J. Chick. 1983. The biology of Australian weeds. 12. *Phragmites australis* (Cav.) Trin. ex Steud. *The Journal of the Australian Institute of Agricultural Science* 49:123-132.
- Hotchkiss, N. and H. L. Dozier. 1949. Taxonomy and distribution of North American cattails. *The American Midland Naturalist* 41:237-254.
- Hulten, E. 1968. *Flora of Alaska and Neighboring Territories*. A Manual of Vascular Plants. Stanford University Press, Stanford, CA, USA.
- Isabelle, P. S., L. J. Fooks, P. A. Keddy, and S. D. Wilson. 1987. Effects of roadside snowmelt on wetland vegetation: an experimental study. *Journal of Environmental Management* 25:57-60.
- Ithaca Journal. 1989. Flower is pretty and also a problem: Plant is damaging delicate wetlands. *The Ithaca Journal*, Ithaca, NY, USA. August 18:7A.
- Jepson, W. L. 1925. *A Manual of the Flowering Plants of California*. University of California Press, Berkeley, CA, USA.
- Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. *Biological Review* 61:369-394.
- Junttila, O., L. Landgraff, and A. J. Nilson. 1978. Germination of *Phalaris* seeds. Seed problems. *Acta Horticulturae* 82:163-166.
- Kane, A. E. and G. T. Gross. 1986. Anasazi communities of Dolores: early Anasazi sites in the Sagenhen Flats area. Report to the U.S. Department of Interior, Denver, CO, USA.
- Kane, M. E. and L. S. Albert. 1989a. Abscisic acid induction of aerial leaf development in *Myriophyllum* and *Proserpinaca* species cultured *in vitro*. *Journal of Aquatic Plant Management* 27:102-111.
- Kane, M. E. and L. S. Albert. 1989b. Comparative shoot and root regeneration from juvenile and adult aerial leaf explants of variable-leaf milfoil. *Journal of Aquatic Plant Management* 27:1-10.
- Keast, A. 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. *Canadian Journal of Zoology* 62:1289-1303.
- Keddy, P. A. 1986. Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. *Journal of Ecology* 74:133-141.
- Keim, P., K. N. Page, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* 123:557-565.
- Kimbel, J. C. 1982. Factors influencing the potential intralake colonization by *Myriophyllum spicatum*. *Aquatic Botany* 14:295-307.
- Klimesova, J. 1994. The effects of timing and duration of floods on growth of young plants of *Phalaris arundinacea* L. and *Urtica dioica*: an experimental study. *Aquatic Botany* 48:21-29.
- Klopatek, J. M. and F. W. Stearns. 1978. Primary productivity of

- emergent macrophytes in a Wisconsin freshwater marsh ecosystem. *The American Midland Naturalist* 100:320-332.
- Kochne, E. 1885. The Lythraceae of the United States. *Botanical Gazette* 10:268-277.
- Koehne, E. 1903. Lythraceae. p. 1-78. In A. Engler (ed.) *Das Pflanzenreich*. Vol. 4. W. Engelmann, Leipzig, Germany.
- Komarov, V. L. 1914. Ex herbario Horti Botanici Petropolitani: Novitates Asiae orientalis. Decase II-VII. *Repertorium Specierum Novarum Regni Vegetabilis* ("Fedde Repert") 13:84-87, 161-169, 225-237.
- Krattinger, K. 1978. Biosystematische Untersuchungen innerhalb der Gattung *Typha*. Ph.D. Dissertation, Universitaet Zuerich, Zurich, Switzerland.
- Lamprecht, H. von. 1948. The genic basis of evolution. *Agri Hortique Genetica* 6:83-86.
- Lamprecht, H. von. 1964. Species concept and the origin of species. The two categories of genes: intra- and interspecific ones. *Agri Hortique Genetica* 23:272-280.
- Lee, D. W. 1975. Population variation and introgression in American *Typha*. *Taxon* 24:633-641. Lee, D. W. and D. E. Fairbrothers. 1973. Enzyme differences between adjacent hybrid and parent populations of *Typha*. *Bulletin of the Torrey Botanical Club* 100:3-11.
- Lehmann, E. 1918. Ueber die minimale Belichtungszeit, welche die Keimung der Samen von *Lythrum salicaria* ausloest. *Der Deutsche Botanische Gesellschaft* 36:157-163.
- Lehmann, E. and R. Lakshmana. 1924. Ueber die Gueltigkeit des Produktgesetzes bei der Lichtleimung von *Lythrum salicaria*. *Der Deutsche Botanische Gesellschaft* 42:5-54.
- Levin, D. A. 1970. Assortative pollination in *Lythrum*. *American Journal of Botany* 57:1-5.
- Levin, D. A. and Z. Bulinska-Radomska. 1988. Effects of hybridization and inbreeding on fitness in *Phlox*. *American Journal of Botany* 75:1632-1639.
- Levin, D. A. and H. W. Kerster. 1973. Assortative pollination for stature in *Lythrum salicaria*. *Evolution* 27:144-152.
- Lewontin, R. C. and L. C. Birch. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20:315-336.
- Lindroth, C. H. 1957. *The Faunal Connections Between Europe and North America*. John Wiley and Sons, Inc., New York, NY, USA.
- Louis-Marie, P. 1944. La salicaria dans le Quebec. *Inst. Ag d'Oka, Province de Quebec, Canada*.
- Louis-Marie, P. 1960. Cas d'introgression dans la flore du Quebec. *La Revue d'Oka* 34:1-11.
- Love, D. and J. B. Bernard. 1959. Flora and vegetation of the Otterburne area, Manitoba, Canada. *Svensk Botanisk Tidskrift* 53:335-461.
- Mack, R. N. 1985. Invading plants: their potential contribution to population biology. p. 127-142. In J. White (ed.) *Studies on Plant Demography*: John L. Harper Festschrift. Academic Press, London, UK.
- Mack, R. N. 1991. The commercial seed trade: an early disperser of weeds in the United States. *Economic Botany* 45:257-273.
- Madsen, J. D., L. W. Eichler, and C. W. Boylen. 1988. Vegetative spread of Eurasian watermilfoil in Lake George, New York. *Journal of Aquatic Plant Management* 26:47-50.
- Madsen, J. D. 1994. Invasions and declines of submersed macrophytes in Lake George and other Adirondack lakes. *Lake and Reservoir Management* 10:19-28.
- Marks, M., B. Lapin., and J. Randall. 1993. Element stewardship abstract: *Phragmites australis*. The Nature Conservancy, Arlington, VA. 32 p. Internet document (<http://www.tnc.org/science/src/weeds/phraust.htm>).
- Marsh, L. C. 1962. Studies in the genus *Typha*. Ph.D. Thesis. Syracuse University, Syracuse, NY, USA.
- Marten, G. C. and M. E. Heath. 1985. Reed canarygrass. p. 207-216. In M. E. Heath, R. F. Barnes, D. S. Metcalfe (eds.) *Forages: The Science of Grassland Agriculture*. Iowa State University Press, Ames, IA, USA.
- McDonald, M. E. 1955. Cause and effects of a die-off of emergent vegetation. *Journal of Wildlife Management* 19:24-35.
- McMillan, C. 1959. Salt tolerance within a *Typha* population. *American Journal of Botany* 46:521-526.
- McNabb, C. D. and T. R. Batterson. 1991. Occurrence of the common reed, *Phragmites australis* along roadsides in lower Michigan. *Michigan Academy of Science, Arts, and Letters* 23:211-220.
- McNaughton, S. J. 1970. Fitness sets for *Typha*. *American Naturalist* 104:337-341.
- McNaughton, S. J. and L. L. Wolf. 1970. Dominance and niche in ecological systems. *Science* 16:131-139.
- Menzie, C. A. 1979. Growth of the aquatic plant *Myriophyllum spicatum* in a littoral area of the Hudson River estuary. *Aquatic Botany* 6:365-375.
- Metzler, K. and R. Rozsa. 1987. Additional notes on the tidal wetlands of the Connecticut River. *Connecticut Botanical Society Newsletter* 15:1-6.
- Moody, M. E. and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25:1009-1021.
- Mook, J. H. and J. van der Toorn. 1985. Delayed response of the common reed *Phragmites australis* to herbivory as a cause of cyclic fluctuations in the density of the moth *Archanara geminipuncta*. *Oikos* 44:142-148.
- Mori. 1971. The littoral macrophyte vegetation of Lake Wingra. *Transactions of the Wisconsin Academy of Science* 59:107-119.
- Nagle, J. J. and L. E. Mettler. 1969. Relative fitness of introgressed and parental populations of *Drosophila maojavensis* and *D. arizonensis*. *Evolution* 23:519-524.
- Nicholls, M. S. 1987. Pollen flow, self pollination and gene specialization: factors affecting seed set in the tristylous species *Lythrum salicaria* (Lythraceae). *Plant Systematics and Evolution* 156:151-157.
- Nichols, S. A. 1975. Identification and management of Eurasian water milfoil in Wisconsin. *Wisconsin Academy of Science, Arts and Letters* 63:116-128.
- Nichols, S. A. 1984. Phytochemical and morphological differentiation between *Myriophyllum spicatum* and *Myriophyllum exalbescens* in two Wisconsin lakes. *Transactions of the Wisconsin Academy of Science, Arts, and Letters* 72:153-156.
- Nichols, S. A. 1994a. Evaluation of invasions and declines of submersed macrophytes for the Upper Great Lakes region. *Lake and Reservoir Management* 10:29-33.
- Nichols, S. A. 1994b. Factors affecting the distribution of Eurasian watermilfoil (*Myriophyllum spicatum*) biomass in Lake Wingra, Wisconsin. *Journal of Freshwater Ecology* 9:145-151.
- Nichols, S. A. and B. H. Shaw. 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus*, and *Elodea canadensis*. *Hydrobiologia* 131:3-21.
- Niering, W. A. and R. S. Warren. 1977. Our dynamic tidal marshes: vegetation as revealed by peat analysis. *Connecticut Arboretum Bulletin* 12:1-22.
- O'Neill, P. 1994. Genetic incompatibility and offspring quality in the tristylous plant *Lythrum salicaria*. *American Journal of Botany* 81:76-84.
- Oglesby, R. T. and A. Vogel. 1976. Changes in submerged plants at the south end of Cayuga Lake following Tropical Storm Agnes. *Hydrobiologia* 48:251-255.
- Orth, R. J. and K. A. Moore. 1984. Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: an historical perspective. *Estuaries* 7:531-540.
- Ostendorp, W. 1989. "Die-back" of reeds in Europe—a critical review of literature. *Aquatic Botany* 35:5-26.
- Ostrom, L. 1987. Studies on genetic variation in reed canarygrass, *Phalaris arundinacea*. II. Alkaloid type and concentration. *Hereditas* 107:235-248.
- Painter, D. S. and K. J. McCabe. 1988. Investigation into the disappearance of Eurasian watermilfoil from Kawartha Lakes. *Journal of Aquatic Plant Management* 26:3-12.
- Patten, B. C. 1954. The status of some American species of *Myriophyllum* as revealed by the discovery of intergrade material between *M. exalbescens* Fern. and *Myriophyllum spicatum* L. in New Jersey. *Rhodora* 56:213-225.

- Patten, B. C. 1955. Germination of the seed of *Myriophyllum spicatum* K. Bulletin of the Torrey Botanical Club 82:50-56.
- Patten, B. C. 1956. Notes on the biology of *Myriophyllum spicatum* L. in a New Jersey lake. Bulletin of the Torrey Botanical Club 83:5-18.
- Pellett, M. 1966. Purple loosestrife, colorful honey plant. American Bee Journal 106:134-135.
- Pellett, M. 1977. Purple loosestrife spreads down river. American Bee Journal 117:214-215.
- Penko, J. M. 1985. Ecological studies of *Typha* in Minnesota: *Typha*-insect interactions and the productivity of floating stands. M.S. Thesis. University of Minnesota, Minneapolis, MN, USA.
- Penko, J. M. and D. C. Pratt. 1986a. Effects of *Bellura obliqua* on *Typha latifolia* productivity. Journal of Aquatic Plant Management 24:24-28.
- Penko, J. M. and D. C. Pratt. 1986b. The growth and survival of early instars of *Bellura obliqua* (Lepidoptera: Noctuidae) in *Typha latifolia* and *T. angustifolia*. Great Lakes Entomologist 19:35-42.
- Pursh, F. 1814. Flora Americae Septentrionalis: or, A Systematic Arrangement and Description of the Plants of North America. White, Cochran and Co., London, England.
- Rawls, C. K. 1978. *Myriophyllum spicatum* p. 14-31. In J. C. Stevenson and N. Confer (eds.) Summary of available information on Chesapeake Bay submersed vegetation. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-78/66.
- Reed, C. F. 1977. History and distribution of Eurasian watermilfoil in United States and Canada. Phytologia 36:417-436.
- Reed, C. F. 1980. *Myriophyllum spicatum* L. along shores of Gulf of Mexico. Phytologia 45:383-384.
- Rejmanek, M. and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77: 1655-1660.
- Rendall, J. 1989. The *Lythrum* story: a new chapter. Minnesota Horticulturalist 117:22-24.
- Rice, J. S. and B. W. Pinkerton. 1993. Reed canarygrass survival under cyclic inundation. Journal of Soil and Water Conservation 48:132-135.
- Ricketson, J. M. 1989. Additions to the aquatic flora of Arizona. J. Arizona-Nevada Academy of Science 23:33-34.
- Ridley, H. N. 1930. The Dispersal of Plants Throughout the World. L. Reeve and Co. Ltd., Ashford, Kent, England.
- Rieseberg, L. H., D. E. Soltis, and J. D. Palmer. 1988. A molecular reexamination of introgression between *Helianthus annuus* and *H. bolanderi* (Compositae). Evolution 42:227-238.
- Rieseberg, L. H., R. Carter, and S. Zona. 1990. Molecular tests of the hypothesized hybrid origin of two diploid *Helianthus* species (Asteraceae). Evolution 44:1498-1511.
- Roscoe, M. V. 1927. Cytological studies in the genus *Typha*. Botanical Gazette 84:392-406.
- Rothmaler, W. 1940. De flora occidentali. I. *Typha*. Repertorium Specierum Novarum Regni Vegetabilis ("Fedde Repert") 49:169-171.
- Schloesser, D. W. and B. A. Manny. 1989. Distribution of Eurasian watermilfoil, *Myriophyllum spicatum* in the St. Clair Detroit River system in 1978. Journal of Great Lakes Research 10:322-326.
- Schoch-Bodmer, H. 1938. The proportion of long-, mid-, and short-styled plants in natural populations of *Lythrum salicaria* L. Journal of Genetics 36:39-43.
- Sculthorpe, C. D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London, England.
- Shamsi, S. R. A. and F. H. Whitehead. 1974. Comparative ecophysiology of *Epilobium hirsutum* and *Lythrum salicaria* L. I. General biology, distribution, and germination. Journal of Ecology 62: 279-290.
- Shamsi, S. R. A. and F. H. Whitehead. 1977. Comparative ecophysiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. IV. Effects of temperature and interspecific competition and concluding discussion. Journal of Ecology 65:71-84.
- Sharitz, R. R., Wincirter, S. A., M. H. Smith, and E. H. Liu. 1980. Comparisons of isozymes among *Typha* spp. in the Eastern USA. American Journal of Botany 67:1297-1303.
- Shay, J. M. and C. T. Shay. 1986. Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. Canadian Journal of Botany 64:443-454.
- Sheaffer, C. C., P. R. Peterson, M. H. Hall, and J. B. Stordahl. 1992. Drought effects on yield and quality of perennial grasses in the north central United States. Journal of Production Agriculture 5: 556-561.
- Shearer, J. 1994. Potential role of plant pathogens in declines of submersed macrophytes. Lake and Reservoir Management 10:9-12.
- Sheldon, S. P. 1994. Invasions and declines of submersed macrophytes in New England, with particular reference to Vermont lakes and herbivorous invertebrates in New England. Lake and Reservoir Management 10:13-17.
- Sifton, H. B. 1959. The germination of light sensitive seeds of *Typha latifolia*. Canadian Journal of Botany 37:719-739.
- Skuhrava, M. and V. Skuhravy. 1981. Die Gallmücken (Cecidomyiidae, Diptera) des Schilfs (*Phragmites communis* Trin.) Studie CSAV, Prag 3:1-150.
- Skuhravy, V. 1978. Invertebrates: destroyers of common reed. p. 376-388. In D. Dykova and J. Kvet (eds.) Pond Littoral Ecosystems, Springer-Verlag, Berlin, Germany.
- Smith, C. S. and J. W. Barko. 1990. Ecology of Eurasian watermilfoil. Journal of Aquatic Plant Management 28:55-64.
- Smith, G. E., T. F. Hall, and R. A. Stanley. 1967. Eurasian watermilfoil in the Tennessee Valley. Weeds 15:95-98.
- Smith, S. G. 1961. Natural hybridization and taxonomy in the genus *Typha*, with particular reference to California populations. Ph.D. Dissertation. University of California-Berkeley, Berkeley, CA, USA.
- Smith, S. G. 1967. Experimental and natural hybrids in North American *Typha* (Typhaceae). American Midland Naturalist 78:257-287.
- Smith, S. G. 1987. *Typha*: its taxonomy and the ecological significance of hybrids. Archiv fur Hydrobiologie 27:129-138.
- Spencer, N. R. and M. Lekic. 1974. Prospects for biological control of Eurasian watermilfoil. Weed Science 22:401-404.
- Springer, P. F. and R. E. Stewart. 1959. Condition of waterfowl feeding grounds on the Susquehanna Flats during the fall of 1959 with notes on the invasion of a serious pest plant. Bureau of Sport Fisheries and Wildlife, Washington, DC, USA. Administration Report.
- Stebbins, G. L. 1959. The role of hybridization in evolution. Proceedings of the American Philosophical Society 103:231-251.
- Stebbins, G. L. 1969. The significance of hybridization for plant taxonomy and evolution. Taxon 18:26-35.
- Stebbins, G. L. 1974. Evolution of morphogenic patterns. Brookhaven Symposium on Biology 25:27-243.
- Steenis, J. H., L. P. Smith, and H. P. Cofer. 1958. Studies on cattail management in the northeast. p. 149-155 In Transactions of the First North American Wildlife Conference. Montreal, ON, Canada.
- Steenis, J. H. and V. D. Stotts. 1961. Progress report on control of Eurasian watermilfoil in Chesapeake Bay. Proceedings of Northeast Weed Control Conference 15:566-570.
- Steenis, J. H. and G. M. King. 1964. Report of interagency meeting on watermilfoil. Maryland Game and Inland Fish Commission. Annapolis, MD, USA.
- Strefeler, M. S., E. Darro, R. L. Becker, and E. J. Katovich. 1996. Isozyme characterization of genetic diversity in Minnesota populations of purple loosestrife, *Lythrum salicaria* (Lythraceae). American Journal of Botany 83:265-273.
- Stuckey, R. L. 1969. The introduction and spread of *Lycopus asper* (Western water horsetail) in the western Lake Erie and Lake St. Clair region. The Michigan Botanist 8:111-120.
- Stuckey, R. L. 1980a. Distributional history of *Lythrum salicaria* (purple loosestrife) in North America. Bartonia 47:3-20.
- Stuckey, R. L. 1980b. Range expansion of native North American aquatic and wetland species. Ohio Journal of Science 80:22.
- Stuckey, R. L. and D. P. Salamon. 1987. *Typha angustifolia* in North America: a foreigner masquerading as a native. (Abstract). p. 4. In Proceedings of the Ohio Academy of Science, Columbus, OH, USA.
- Suprenant, J., D. K. Barnes, R. H. Busch, and G. G. Marten. 1988.

- Bidirectional selection for neutral detergent fiber and yield in reed canarygrass. *Canadian Journal of Plant Science* 68:705-712.
- Teale, E. W. 1982. Stems beyond counting, flowers unnumbered. *Audubon* 84:38-43.
- ter Heerd, G. N. J. and H. J. Drost. 1994. Potential for the development of marsh vegetation from the seed bank after a drawdown. *Biological Conservation* 67:1-11.
- Thompson, D. J. and J. M. Shay. 1985. The effects of fire on *Phragmites australis* in the Delta Marsh, Manitoba. *Canadian Journal of Botany* 63:1864-1869.
- Thompson, D. Q., R. L. Stuckey, and E. B. Thompson. 1987. Spread, impact and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. Fisheries and Wildlife Research 2. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA.
- Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3-15.
- Titus, J. E. 1994. Submersed plant invasions and declines in New York. *Lake and Reservoir Management* 10:25-28.
- Tscharntke, T. 1989. Changes in shoot growth of *Phragmites australis* caused by the gall maker *Giraudiella inclusa* (Diptera: Cecidomyiidae). *Oikos* 54: 370-377.
- Tscharntke, T. 1990. Fluctuations in abundance of a stem-boring moth damaging shoots of *Phragmites australis*: causes and effects of overexploitation of food in a late-successional grass monoculture. *Journal of Applied Ecology* 27:679-692.
- Tscharntke, T. 1992. Fragmentation of *Phragmites* habitats, minimal viable population sizes, habitat suitability and local extinctions of moths, midges, flies, aphids, and birds. *Conservation Biology* 6: 530-536.
- Twilley, R. R. and J. W. Barko. 1990. The growth of submersed macrophytes under experimental salinity and light conditions. *Estuaries* 13:311-321.
- Van der Toorn, J. 1972. Variability of *Phragmites australis* (Cav.) Trin. ex Steudel in relation to the environment. *Van Zee tot Land* 48:1-22.
- Van der Toorn, J. and J. H. Mook. 1982. The influence of environmental factors and management on stands of *Phragmites australis*. I. Effects of burning, frost, and insect damage on shoot density and shoot size. *Journal of Applied Ecology* 19:477-499.
- van der Valk, A. G. and C. B. Davis. 1980. The impact of a natural drawdown on the growth of four emergent species in a prairie glacial marsh. *Aquatic Botany* 9:301-322.
- Vogel, M. 1984. Okologische unteruchungen in einem *Phragmites* Bestand. *Berichte der Akademie für Naturschutz und Landschaftspflege Laufen* 8:130-166.
- Waters, I. and J. M. Shay. 1990. A field study of the morphometric response of *Typha glauca* shoots to a water depth gradient. *Canadian Journal of Botany* 68:2339-2343.
- Waters, I. and J. M. Shay. 1992. Effect of water depth on population parameters of a *Typha glauca* stand. *Canadian Journal of Botany* 70:349-351.
- Welling, C. H. and R. L. Becker. 1993. Reduction of purple loosestrife establishment in Minnesota wetlands. *Wildlife Society Bulletin* 21:56-64.
- Wetmore, A. 1921. Wild ducks and duck foods of the Bear River Marshes, Utah. *Bulletin of the U.S. Department of Agriculture* 936:1-20.
- White, D., E. Haber, and C. Keddy. 1993. Invasive plants of natural habitats in Canada. Environment Canada, Ottawa, ON, Canada.
- Wijte, A. H. and J. L. Gallagher. 1996. Effect of oxygen availability and salinity on early life history stages of salt marsh plants. I. Different germination strategies of *Spartina alterniflora* and *Phragmites australis* (Poaceae). *American Journal of Botany* 83: 1337-1342.
- Wilcox, D. A. 1986a. The effects of deicing salts on water chemistry in Pinhook Bog, Indiana. *Water Resources Bulletin* 22:57-65.
- Wilcox, D. A. 1986b. The effects of deicing salts on vegetation in Pinhook Bog, Indiana. *Canadian Journal of Botany* 64:865-874.
- Wilcox, D. A. 1989. Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. *Environmental Management* 13:365-370.
- Wilkins, F. S. and H. D. Hughs. 1932. Agronomic trials with reed canarygrass. *Journal of American Society of Agronomy* 24:18-28.
- Zeiders, K. E. and R. T. Sherwood. 1985. Environmental interactions among reed canarygrass genotypes for nutritive value, height and disease severity. *Agronomy Journal* 77:94-98.

Manuscript received 23 December 1996; revision received 16 September 1997; accepted 24 November 1997.