

# Why Some Wetland Plants Are Invasive and How They Affect Restoration

*The author follows up on previous research on the causes of invasive plant species, highlighting subsequent findings on four common invasive species and how these invasions affect wetland restoration projects. This article will also appear as a Research Brief on the Society of Wetland Scientists website.*

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The proportion of wetland restoration projects affected by invasive species is likely very high. Either invasive species are present at the start of a project and their removal is attempted during site preparation or they arrive soon after, as the site adjusts to its new hydrology and vegetative cover is minimal. If the goals of a restoration project are narrowly focused on flood abatement or water quality improvement, the presence of invasive species is a minor concern. If, however, the desire is to achieve multiple benefits, including the restoration of plant biodiversity, then invasive species control is a priority. Plant communities influence nutrient cycling and food webs, provide food and habitat structure to animals, and contribute to a wetland ecosystem's aesthetic appeal. Consequently, the restoration of a wetland's plant communities is often considered crucial to project success.

Unfortunately, invasive species removal is often an expensive, protracted process, which in some situations is futile. Invasive species are not only good at spreading, they are highly persistent, especially in degraded wetlands where conditions are typically more favorable for them than other plant species. Understanding why a particular wetland plant is invasive can help frame practical restoration decisions, such as selecting effective control strategies and evaluating the commitment needed to accomplish control. For this reason, in 1999, my colleagues and I reviewed the published literature on five wetland species that were invasive in North American freshwater wetlands: *Phalaris arundinacea*, *Lythrum salicaria*, *Typha x glauca*, *Myriophyllum spicatum*, and *Phragmites australis* (Galatowitsch et al. 1999). We looked for evidence that could explain why each of these species was invasive and considered how the underlying reasons for its invasiveness could affect control effectiveness.

Our 1999 article focused on three theories that had been proposed to explain why these species had become invasive: (1) the environmental conditions in these new geographic areas are more favorable than in their resident locales; (2) free of the herbivore community with which they were long associated in

the resident locale, natural selection in their new locale favors increased growth over herbivore defense; and (3) interspecific hybridization occurred between the newly arriving species (or subspecies) and a closely related resident species that produced hybrid strains with high-growth potential under a wide range of conditions. Since this paper was published, the invasiveness of these species and consequences of their spread has received considerable research attention. In this research brief, I will highlight the progress that has been made over the past 13 years to understand why four of these species (excluding *Myriophyllum*, which mostly occurs in lakes) invade North American wetlands, and how these invasions affect restoration efforts.

## **PHALARIS ARUNDINACEA (REED CANARY GRASS)**

*Phalaris arundinacea* has been cultivated as a forage crop in North America for two centuries and in Europe for at least three centuries. In North America, the species has also been widely used for soil-erosion control. Domesticated varieties have been developed for forage and ornamental use; most of the world's commercial seed is produced in Minnesota, near the Canadian border. In 1999, we characterized *Phalaris arundinacea* as potentially indigenous to both North America and Europe, but a cryptogenic species, one whose origin could not be positively determined. Hybridization between North American and European strains of the species was considered a possible explanation for the invasiveness of *Phalaris*, but research had not yet been conducted on genetic differences across its range. Studies had shown that *Phalaris* was strongly competitive in wetlands enriched with nutrients or that experience high amplitude changes in water levels. However, whether some genotypes, such as cultivated varieties, had a greater capacity to capitalize on conditions found in degraded wetlands was unknown. Likewise, there was no evidence that competitive ability of some genotypes had become more competitive because they were freed from herbivore pressure.

Scientists recently evaluated genetic patterns among cultivars and wild populations in Europe and North America using molecular approaches. They found evidence of genotypes dis-



tinctive to both continents, indicating *Phalaris* has long been circumboreal. Multiple introductions across the Atlantic (in both directions), subsequent spread, and incorporation into early cultivars have resulted in a high level of genetic mixing. Wild populations of recent cultivars and native genotypes are uncommon in North America (e.g., Casler et al. 2009). These recent cultivars, bred primarily for low alkaloid content, grow more vigorously than wild-source plants in upland sites, but apparently not in wetlands (Jakubowski et al. 2011).

There is strong experimental evidence of the competitive superiority of *Phalaris* from wild populations in response to eutrophication (both nitrogen and phosphorus), as well as hydrologic alterations (Figure 1). Nutrient-rich or hydrologically altered wetlands invaded by *Phalaris* invariably become dominated by the species, which suppresses the abundance and richness of the native plant community. *Phalaris* is very persistent and difficult to eradicate, even with multiple treatments of herbicide. Remnant native vegetation does not typically respond as desired to treatments with selective herbicides, or prescribed fire or mowing; if rhizomes are killed, *Phalaris* reinvasion from seed is very rapid. Native species, such as sedges, can outcompete *Phalaris* at low levels of soil fertility, but restoration methods to reduce soil nutrient availability are either infeasible to implement at the ecosystem scale, i.e., carbon amendments, or cause a high level of damage, i.e., scraping.

#### ***PHRAGMITES AUSTRALIS* (COMMON REED)**

*Phragmites australis* has been widely distributed in North America for thousands of years, based on peat samples and domestic artifacts. At the time of our *Wetlands* article, concern was growing about dramatic increases in *Phragmites* populations in Atlantic Coast, Gulf Coast, and Great Lake wetlands. Eutrophication and water level fluctuations were implicated in the decline of *Phragmites* in Europe,

Figure 1 (left): Although both of these “mesocosms” were seeded with the same mix of 11 native species and provided with the same amount of nutrients, the one on the left was also seeded with reed canarygrass (1/12 of the mix). After only one year, the reed canarygrass comprised one-half the aboveground and belowground biomass, demonstrating the ability of the species to rapidly outcompete its neighbors (Green & Galatowitsch 2002).

Figure 2 (right): In North America, one strain of *Phragmites australis* (“Haplotype M”), is highly invasive. It is more strongly clonal than indigenous strains, forming rhizomes and stolons of 10 meters or more in a single growing season, as shown here on a river sand bar.

so other causes of invasiveness seemed more likely. Reduced investment in herbivore defense was considered potentially responsible, since, in Europe, a diverse insect community regulates *Phragmites* populations. Spreading, morphologically distinct populations in the Mississippi Gulf Coast in the early 1990s were thought to be recently introduced strains, or as we speculated, introgressed hybrids between new and resident genotypes.

Molecular approaches to genetics, combined with ecological experiments, have greatly advanced our understanding of the underlying causes of invasiveness in *Phragmites* in recent years. There are three genetically and ecologically distinct lineages, i.e., haplotypes, of *Phragmites* in North America (Saltonstall 2010). “Haplotype M,” likely a relatively recent introduction to North America, is invasive (Figure 2). Populations of this haplotype are genetically variable,

Intact Coastal Wetlands

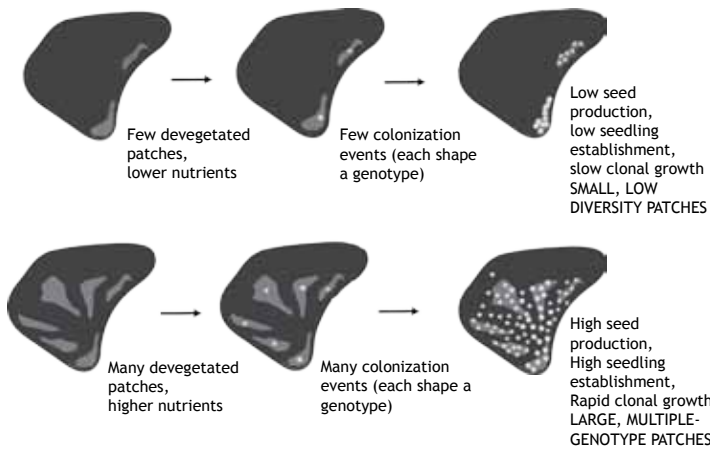


Figure 3: The invasiveness of *Phragmites australis* in U.S. coastal marshes is strongly influenced by stressors tied to land use, such as increased nutrient and sediment runoff. These stressors cause more bare, nutrient rich patches to form within a stand of emergent vegetation, which increase the incidence of colonization by seed. Sexual reproduction is promoted with the availability of multiple genotypes within the wetland, because selfing is minimized. Seed production and clonal spread is also stimulated by increased nutrient availability in the soils (adapted from McCormick et al. 2010).

indicating there were multiple introductions. There have been no reports of hybridization in the wild between native and introduced *Phragmites*, although they can interbreed.

Invasiveness in *Phragmites* is most likely linked to genetic and ecological factors that promote reproduction by seed (McCormick et al. 2010; Kettenring et al. 2011). In a new locale, colonized by one to a few individuals and spreading clonally, the production of viable seed is limited by partial self-incompatibility and limited mate availability. These barriers are alleviated as new seeds arrive; genetically variable populations can produce substantially more viable seed. In degraded wetlands, there are more unvegetated patches from sediment deposition and other stressors; these present greater opportunities for successful colonization by dispersing seeds. Increased nutrient levels also stimulate seed production. Multiple stressors (disturbance, eutrophication) can interact to cause a self-reinforcing increase in *Phragmites* propagule pressure, which likely accelerates invasion in a locale (Figure 3). The practical implications of these findings are clear: small populations should not be allowed to persist and accumulate genetic variation, and reducing nutrient inputs to wetlands may help reduce the overall rate of spread of *Phragmites* in the landscape.

Where *Phragmites* has invaded, the abundance and richness of native species are often reduced. *Phragmites* produces dense standing and collapsed litter that suppress the growth of its neighbors. Control using herbicide, fire, and even tillage typically only results in short-term population reductions. Results of field experiments in invaded wetlands suggest prescribed litter removal may allow for the recovery of some native wetland plant species, even if *Phragmites* populations cannot be effectively controlled.

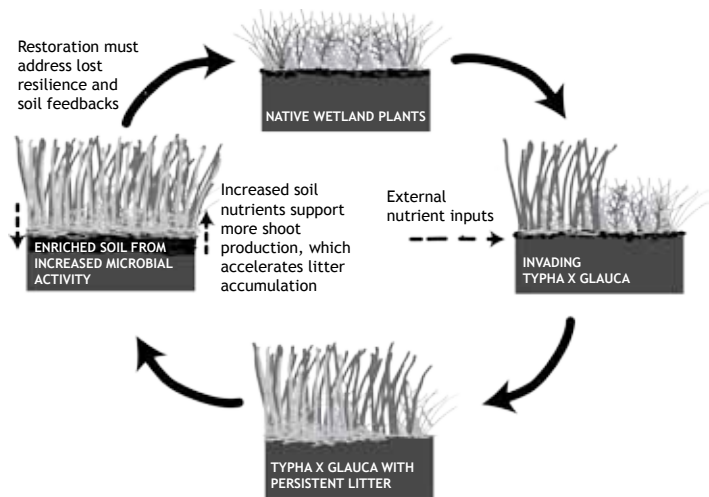


Figure 4: *Typha x glauca* suppresses resident native plant species after it invades a wetland by producing persistent litter, as well as from resources captured by its live biomass. Standing and collapsed dead shoots block light, restricting the growth of neighboring vegetation. The thick litter layer may also serve as a carbon source for microbes that increase soil nutrient levels, thereby creating a feedback to shoot production, which responds positively (Tuchman et al. 2009).

**LYTHRUM SALICARIA (PURPLE LOOSESTRIFE)**

*Lythrum salicaria* probably arrived in North America in the early 1800s in the ballast of European ships crossing the Atlantic Ocean. Later, it was inadvertently introduced on imported wool and sheep and deliberately introduced for beekeeping and ornamental uses. The species began to spread rapidly into central North America around 1930. Our 1999 article reviewed evidence suggesting *Lythrum salicaria* could have formed introgressive hybrids with the native North American species *Lythrum alatum*. These studies, however, did not clearly show that the putative hybrids were larger or produced more seed, i.e., traits linked to invasiveness. Recent studies of *Lythrum salicaria* populations in North America found a surprisingly high level of genetic diversity, likely attributable to multiple introductions and subsequent genetic mixing (Chun et al. 2009). Whether invasiveness has been enhanced by this mixing has not been reported.

Bernd Blossey and Rolf Notzold (1995) showed that *Lythrum salicaria* plants from North America grew larger than those from Europe in a common garden and that some insect herbivores hosted by the species in Europe grew more rapidly when fed North American plants. A loss of herbivore defenses was considered the most likely reason for *Lythrum*'s spread in North America. Based on this assumption, biocontrol agents were selected (*Galerucella californiensis* and *G. pusilla*), tested, and released in multiple locations of the United States in the late 1990s. These insects usually dramatically reduced *Lythrum* abundance in the wetlands where they were released.

There is growing evidence that *Lythrum salicaria* may not be as invasive as once presumed, based on spread into wetlands with existing vegetation and suppression of native species (Lavoie 2010). Apparently, *Lythrum* is not a strong invader unless disturbances re-

move existing vegetation (Hager 2004). Once established, though, it is very persistent. In some situations *Lythrum salicaria* diminishes native plant species richness where it has invaded, perhaps where *Lythrum* is most dense (Schooler et al. 2006).

#### ***TYPHA X GLAUCA* (HYBRID CATTAIL)**

Of the four species we investigated in our 1999 article, the research record on invasiveness was most extensive for *Typha x glauca*. Numerous studies since the 1960s showed that hybridization between *Typha latifolia* and *T. angustifolia* occurred wherever the two species were sympatric, resulting in *Typha x glauca*. *Typha angustifolia* apparently was restricted to Atlantic coastal marshes until the beginning of the 20th century. As *Typha angustifolia* migrated westward, reaching the Great Plains by mid-century, it hybridized with *Typha latifolia*. Both *Typha angustifolia* and *T. x glauca* were known to be salt tolerant, leading researchers to suspect this migration could have been enabled, especially in recent decades, by the runoff of road de-icing salts and other contaminants into freshwater wetlands. Many studies have shown that *Typha x glauca* tolerates a greater range of environmental conditions, such as water-level fluctuations, than either parent. Invasiveness seemed unlikely to be caused by reductions in herbivore defenses, because it had not originated from a cross-continental introduction.

Using molecular markers, researchers recently confirmed that in mixed stands *Typha angustifolia* and *T. latifolia* can readily hybridize (Travis et al. 2010). These hybrid plants are generally larger than those of either species, providing evidence that hybridization plays a major role in the invasiveness of *Typha x glauca* in North America. Most of the individuals in the population are, however, first generation hybrids (up to 90%) rather than backcrosses, i.e., introgressed hybrids.

Several studies in the past decade detail the effects of *Typha x glauca* on plant communities. As the abundance of *Typha x glauca* increases, the species' richness and floristic quality declines. Native species diminish because they are under "sustained, multi-generational attack" (Larkin 2012). While a current year's *Typha* crop competes with native species for light and nutrients, standing, dead *Typha* shoots and collapsed litter, which accumulate for several years, have a much greater effect. This dead material intercepts light, smothers new growth, and modifies the environment. Ecologists suspect that the increasing stores of carbon on the marsh surface stimulate microbial activity, including those that fix nitrogen and enrich the soil (Tuchman et al. 2009). It is well-established that *Typha* plants more readily exploit increases in soil nutrients than do native vegetation. If there is a positive feedback between *Typha* litter and soil nutrients, nutrient inputs from the surrounding landscape are less likely to determine where invasions occur.

These research advances have several important implications for wetland restoration. First, removing external sources of nutrients may alone be insufficient to create conditions favorable for restoration of the native plant community. Likewise, using herbicide to reduce the size of the current population

does not address the legacy effects of litter accumulation and internal soil enrichment. Prescribed fire or soil scraping may be suitable if part of a more comprehensive transition strategy to reassemble the native plant community.

#### **CONCLUSIONS**

Since 1999, molecular techniques have clarified the genetic mechanisms promoting invasiveness in these taxa. Only *Typha x glauca* may be more invasive because of hybridization (though not introgressive hybridization); the other three species are more successful because genotypes from multiple introductions have mixed. Land use stressors, especially increased nutrient inputs, stimulate growth and, in at least one species, seed production. Controlled experiments on several of these species highlight the importance of positive feedbacks for promoting invasiveness. If the feedbacks between soils and invasive wetland plant populations are not addressed as part of restoration, these species will persist or rapidly reinvade. Feedbacks also reinforce the rationale for focusing more efforts on scouting and rapid response. ■

#### **REFERENCES**

In addition to cited sources, this list includes articles that review key advances in invasion biology or ecological restoration for the four species considered here.

- Blossey, Bernd & Rolf Notzold, *Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants: A Hypothesis*, 83 J. ECOLOGY 887-89 (1995).
- Casler, Michael D. et al., *DNA Polymorphisms Reveal Geographic Races of Reed Canarygrass*, 49 CROP SCI. 2139-48 (2009).
- Chun, Young Jim et al., *Comparison of Quantitative and Molecular Genetic Variation of Native vs. Invasive Populations of Purple Loosestrife (Lythrum salicaria L., Lythraceae)*, 18 MOLECULAR ECOLOGY 3020-35 (2009).
- Galatowitsch, Susan M. et al., *Invasiveness in Wetland Plants in Temperate North America*, 19 WETLANDS 733-55 (1999).
- Green, Emily K. & Susan M. Galatowitsch, *Effects of Phalaris arundinacea and Nitrate-N Addition on the Establishment of Wetland Plant Communities*, J. APPLIED ECOLOGY, 134-44 (2002).
- Hager, Heather A., *Competitive Effect Versus Competitive Response of Invasive and Native Wetland Species*, 139 OECOLOGIA 140-49 (2004).
- Jakubowski, Andrew R. et al., *Has Selection for Improved Agronomic Traits Made Reed Canarygrass Invasive?*, 6 PLoS ONE e25757 (Oct. 2011).
- Kercher Suzanne M. & Joy B. Zedler, *Multiple Disturbances Accelerate Invasion of Reed Canary Grass (Phalaris arundinacea L.) in a Mesocosm Study*, 138 OECOLOGIA 455-64 (2004).
- Kettenring, Karin M. et al., *Mechanisms of Phragmites australis Invasion: Feedbacks Among Genetic Diversity, Nutrients, and Sexual Reproduction*, 48 J. APPLIED ECOLOGY 1305-13 (2011).
- Larkin, Daniel J. et al., *Mechanisms of Dominance by the Invasive Hybrid Cattail Typha x glauca*, 14 BIO. INVASIONS 65-77 (2012).
- McCormick, Melissa K. et al., *Spread of Invasive Phragmites australis in Estuaries With Differing Degrees of Development: Genetic Patterns, Allele Effects and Interpretation*, 98 J. ECOLOGY 1369-78 (2010).
- Saltonstall, Kristin et al., *Genetics and Reproduction of Common Reed (Phragmites australis) and Giant Reed (Arundo donax)*, 3 INVASIVE PLANT SCI. MGMT. 495-505 (2010).
- Schooler, Shon et al., *Negative Per Capita Effects of Purple Loosestrife and Reed Canarygrass on Plant Diversity in Wetland Communities*, 12 DIVERSITY & DISTRIBUTIONS 351-63 (2006).
- Travis, Stephen E. et al., *Hybridization Dynamics of Invasive Cattail (Typhaceae) Stands in the Western Great Lakes Region of North America: A Molecular Analysis*, 98 J. ECOLOGY 7-16 (2010).
- Tuchman, Nancy C. et al., *Patterns of Environmental Change Associated With Typha x glauca Invasion in a Great Lakes Coastal Wetland*, 29 WETLANDS 964-75 (2009).