

SWS Research Brief

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Why invasive species stymie wetland restoration

Introduction

The proportion of wetland restoration projects affected by invasive species is likely very high. Invasive species may be 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 when vegetative cover is minimal. 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 wetland species that were invasive in North American wetlands: *Phalaris arundinacea*, *Lythrum salicaria*, *Typha x glauca*, 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.

Since this paper was published, the invasiveness of these species and consequences of their spread have 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 these species 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. Domesticated varieties have been developed for forage, ornamental use, and soil erosion control. In 1999, we characterized *Phalaris* 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 genetic differences across its range had not been studied. *Phalaris* was found to be strongly competitive in wetlands enriched with nutrients or that experienced high-amplitude changes in water levels. However, it was unknown if some genotypes, such as cultivated varieties, had a greater capacity to capitalize on conditions found in degraded wetlands.

Genetic patterns among cultivars and wild populations were recently evaluated



Figure 1. After one year, *Phalaris* comprised one half of the biomass of the mesocosm on the left, even though it was only 1/12 of the seed mix, demonstrating the ability of the species to outcompete its neighbors (Green and Galatowitsch 2002).

in Europe and North America using molecular approaches. Evidence of genotypes distinctive to both continents indicated that *Phalaris* has long been circumboreal. Multiple introductions in both directions across the Atlantic, subsequent spread, and incorporation into early cultivars have resulted in a high level of genetic mixing (e.g., Casler et al. 2009). 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).

The competitive superiority of *Phalaris* from wild populations has been experimentally demonstrated in response to eutrophication as well as to hydrologic alterations. Nutrient-rich or hydrologically-altered wetlands invaded by *Phalaris* invariably become dominated by the species, which suppresses the abundance and richness of the native community. *Phalaris* is difficult to eradicate, even with multiple treatments of herbicide. Native species, such as sedges, can outcompete *Phalaris* at low levels of soil fertility, but restoration methods to reduce soil nutrient availability are infeasible to implement at the ecosystem scale (carbon amendments) or cause additional damage (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 several US locations. Eutrophication and water level fluctuations were implicated in the decline of *Phragmites* in Europe, so other causes of invasiveness seemed more likely.

“UNDERSTANDING WHY A PARTICULAR WETLAND PLANT IS INVASIVE CAN HELP FRAME PRACTICAL RESTORATION DECISIONS”

Reduced investment in herbivore defense was potentially responsible since a diverse insect community regulates *Phragmites* populations in Europe. Morphologically distinct populations spreading in the Mississippi Gulf Coast in the 1990s may be recently introduced strains or were, as we speculated, introgressed hybrids between new and resident genotypes.



Figure 2. In North America, one strain of *Phragmites australis* (“Haplotype M”) is highly invasive and more strongly clonal than indigenous strains, forming rhizomes and stolons 10 m or more in a single growing season.

Molecular approaches to genetics, combined with ecological experiments, have greatly advanced our understanding of the underlying causes of invasiveness in *Phragmites*. There are three genetically and ecologically distinct lineages (haplotypes) of *Phragmites* in North America (Saltonstall 2010). “Haplotype M”, likely a recent introduction to North America, is invasive. Populations of this haplotype are genetically variable, indicating multiple introductions. Hybridization in the wild between native and introduced *Phragmites* has not been reported, 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 clonal individuals, 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 seeds. In degraded wetlands, there are more devegetated 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 propagule pressure, which likely accelerates invasion in a locale. The practical implications of these findings are clear:

- 1) small populations should not be allowed to persist and accumulate genetic variation and 2) reducing nutrient inputs to wetlands may help limit *Phragmites* spread.

Where *Phragmites* has invaded, the abundance and richness of species are often reduced, *Phragmites* produces dense litter that suppresses the growth of its neighbors. Control using herbicide, fire, and tillage typically only results in short-term population reductions.

Field experiments in invaded wetlands suggest prescribed litter removal may allow for the recovery of some native species, even if *Phragmites* populations cannot be controlled.

Lythrum salicaria
Purple loosestrife

Lythrum salicaria probably arrived in North America in the early 1800s in the ballast of European ships. 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 *L. salicaria* could have formed introgressive hybrids with the native North American species *Lythrum alatum*. Recent studies of *L. salicaria* 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 is unknown.

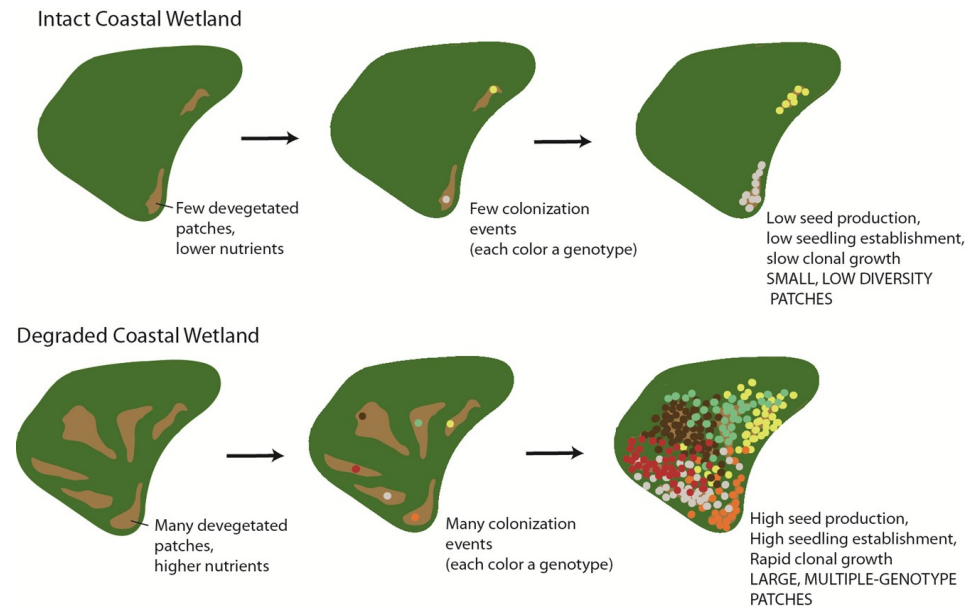


Figure 3. *Phragmites australis* invasiveness in coastal marshes is influenced by stressors that cause more bare, nutrient-rich patches to form. Bare patches increase the incidence of colonization by seed. Sexual reproduction is promoted with the availability of multiple genotypes because selfing is minimized. Seed production and clonal spread is also stimulated by increased nutrient availability in the soils (adapted from McCormick et al. 2010).

Some of the most invasive wetland species are successful because of genetic changes and a high capacity to capture resources. Persistence is often the result of reinforcing feedbacks.

Lythrum salicaria plants from North America grow larger than those from Europe in a common garden, and some insect herbivores hosted by the species in Europe grow more rapidly when fed North American plants. A loss of herbivore defenses has been considered the most likely reason for *Lythrum*'s spread in North America. Based on this assumption, biocontrol agents were selected, 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.

Typha x glauca Hybrid cattail

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*.

T. angustifolia apparently was restricted to Atlantic coastal marshes until the beginning of the 20th century. Both *T. angustifolia* and *T. x glauca* are somewhat salt tolerant, leading researchers to suspect that migration could have been enabled, especially in recent decades, by the runoff of road de-icing salts and other contaminants into freshwater wetlands. *Typha x glauca* tolerates a greater range of environmental conditions, such as water level fluctuations, than either parent.

Analysis of molecular markers indicates that *T. angustifolia* and *T. latifolia* in mixed stands can readily hybridize (Travis et al. 2010). As the abundance of *T. x glauca* increases, the species richness and floristic quality decline because they are under "sustained multi-generational attack" (Larkin 2012). While a current year's 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 abundant soil nutrients than do native vegetation.

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 invasive plant population does not address the legacy effects of litter accumulation and internal soil enrichment.

Conclusions

Only *Typha x glauca* may be more invasive because of hybridization; the other three species (*Phalaris arundinacea*, *Phragmites australis*, *Lythrum salicaria*) 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 with some 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.

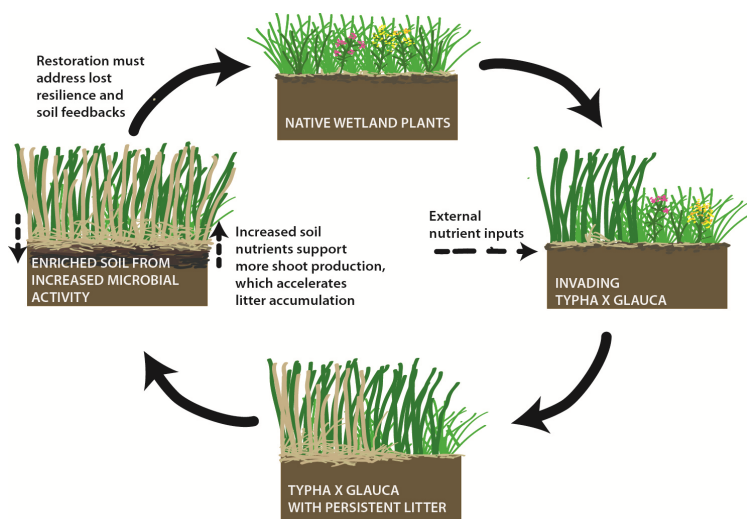


Figure 4. *Typha x glauca* suppresses its neighbors by capturing resources as it grows and by producing persistent litter. Dead shoots block light, restricting the growth of other plants. The thick litter layer likely increases the carbon available to microbes, and consequently soil nutrient levels. This creates a positive feedback to shoot production (Tuchman et al. 2009).

For more information:

The Wetlands (1999) paper and citations therein present early information on invasiveness of wetland plants:
Galatowitsch, Susan M. et al., *Invasiveness in Wetland Plants in Temperate North America*, 19 WETLANDS 733-55 (1999).

A selection of more recent papers include those cited in this research report:

- 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).
- 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).
- Jakubowski, Andrew R. et al., *Has Selection for Improved Agronomic Traits Made Reed Canarygrass Invasive?*, 6 PLOS ONE e25757 (Oct. 2011).
- 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, Allee 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).
- 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).

About the Author:

Susan M. Galatowitsch is a Professor at the University of Minnesota. Her research focuses on revegetation, management of invasive species, and climate change adaptation for wetland and riparian ecosystems. In addition to many research publications, she has written two books, *Ecological Restoration* (2012) and *Restoring Prairie Wetlands: An Ecological Approach* (1994, with Arnold van der Valk). Dr. Galatowitsch has taught courses in restoration ecology, landscape ecology, horticultural science, and conservation biology. She is a fellow of the Society of Wetland Scientists.

Contact Information: email: galat001@umn.edu



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Karen L. McKee

karenmckee@cox.net