



Figure 1. (Left) native broadleaf cattail, *T. latifolia*, and (right) nonnative narrowleaf cattail, *T. angustifolia*, in the field.

Cattail hybridization in national parks: An example of cryptic plant invasions

By Joy Marburger and Steve Travis

NPS/JOY MARBURGER

HYBRIDIZATION IS A GENETIC PROCESS IN WHICH individual organisms from two genetically distinct populations mate and produce offspring. It can occur between distinct populations of the same species or between two different species. Plant hybrids of different species in the same genus are called *interspecific* hybrids or crosses. Hybridization between two closely related species is actually a common occurrence in nature with regard to plants, but is also being greatly influenced by human activities (Allendorf et al. 2001). Hybrids can produce either sterile (not viable) or fertile (viable) seed. They can also exhibit “hybrid vigor” or heterosis, which results in more robust growth than exhibited by the parent species. This phenomenon determines the kind of effect that a hybrid will have on its own population and others with which it interacts. Hybrid zones occur where the ranges of two species meet; hybrids are continually produced in great numbers in these zones. Hybrid zones are useful as biological model systems for studying the mechanisms of speciation confirmed by DNA analysis.

The main harmful genetic effect of hybrids on native species is the loss of both genetic diversity and locally adapted populations, such as rare and threatened species (Rieseberg 1991; Ellstrand and Elam 1993). From a conservation perspective, hybrids can

Abstract

Hybridization of plants occurs when two species from the same or different genera mate and can successfully produce viable seeds. Hybridization of plants can increase genetic diversity, but it can also result in aggressive taxa that can displace native species and decrease wetland plant biodiversity. Here we identify two cattail species, *Typha latifolia* L. and *T. angustifolia* L., and hybrids of these two species referred to as *T. x glauca* Godr. using molecular markers called microsatellites, since morphological characteristics are not reliable indicators for identifying cattail taxa. The importance of cattail hybridization is that it has facilitated cattail spread in various wetlands of North America. From 2004 to 2012 we evaluated whether hybridization of cattails was occurring in seven Great Lakes national parks and two other national parks. We present results for Apostle Islands National Lakeshore, Cuyahoga Valley National Park, Indiana Dunes National Lakeshore, Pictured Rocks National Lakeshore, St. Croix National Scenic Riverway, Sleeping Bear Dunes National Lakeshore, and Voyageurs National Park. All parks except Pictured Rocks included hybrid taxa. The technique holds promise for cattail taxonomic identification for wetland managers. Cattail management methods are also described.

Key words

cattails, hybrids, microsatellites, *Typha* species

negatively affect biodiversity if they spread aggressively in a community. The spread of aggressive hybrid groups can reduce the growth of, or replace, native species (Vilà et al. 2000). The main anthropogenic factors promoting hybridization of species are increased species dispersal by humans, landscape fragmentation, and land disturbance. Enhanced cross-pollination of two species and increased range expansion of an exotic species into native ranges are the result primarily of human activity.

Certain differences in flowering times, pollination, and seed dispersal patterns differentiate parental species from hybrids (Vilà et al. 2000); however, the barriers to crossing can break down if life history traits overlap. For example, production of fertile hybrids can result when the pollen cells of one species can fertilize ovules (immature seeds) in the other species and the chromosomal barriers (such as pairing during meiosis) are overcome by similarity of the chromosomes or through polyploidy (multiple sets of paired chromosomes).

Introgressive hybridization (transfer of traits between species) can also increase genetic biodiversity of a taxon (Vilà et al. 2000) and can be the source of new adaptations. However, in many cases the genetic integrity of a common native species can be threatened. This is the case with the hybridization of the California cordgrass *Spartina foliosa* with the introduced *S. alterniflora* (Daehler and Strong 1997) in San Francisco salt marshes.

Hybridization of cattails and their recent expansion in national parks

Three species of cattails (*Typha* spp.) occur in the United States—*Typha latifolia* L. (broad-leaf cattail), *T. angustifolia* L. (narrow-leaf cattail), and *T. domingensis* Pers. (southern cattail)—and an interspecific hybrid taxon referred to as *T. × glauca* (fig. 1). The three species are primarily cross-pollinated by wind. The three distinct species have the same chromosome number ($2N=30$; Smith 2000), which may facilitate successful hybridization. They also reproduce by asexual cloning through rhizome growth. The taxonomic relationships of *Typha* spp. was extensively described in the 1960s–1980s by Galen Smith, who also conducted experimental crossing of the species (Smith 1967, 1986, 1987). Smith obtained fertile seeds from some of these experimental crosses. Others have described the expansion of whole *Typha* stands or discrete patches of hybrids within stands based on hydrological alterations (Wilcox et al. 1985; Wilcox 2011) without any reference to genetic structure. Unfortunately, such morphological and environmental analyses are hindered by the complex blending of characters that typically occurs in cases of continuous hybridization (e.g., Rieseberg and Ellstrand 1993).

North American expansion of cattails over the past 100 years (Grace and Harrison 1986; Galatowitsch et al. 1999) has been driven by a combination of environmental (e.g., Wilcox et al. 1985; Woo and Zedler 2002) and evolutionary forces (Travis et al. 2010; Ball and Freeland 2013). *Typha × glauca* is considered the most invasive North American *Typha* species (Smith 1987; Galatowitsch et al. 1999), although some consider *T. angustifolia* equally invasive (Tulbure et al. 2007). *Typha × glauca* is reportedly more effective at supplanting native vegetation (Galatowitsch et al. 1999; Woo and Zedler 2002; Boers et al. 2007) and inhibits germination of native species once established (Frieswyk and Zedler 2006). In addition, *T. × glauca* competitively dominates both *T. angustifolia* and *T. latifolia* (Waters and Shay 1992; Kuehn et al. 1999), with the latter generally considered the least aggressive of the three. In spite of a general recognition of *T. × glauca* as the most invasive cattail species, explicit tests of the role of hybridization in the rapid spread of cattails are lacking (Frieswyk and Zedler 2006).

Managers in the Great Lakes national parks have observed that cattail populations have been expanding in wetland habitats. In 2003, biologists at Indiana Dunes National Lakeshore (Indiana), St. Croix National Scenic Riverway (Wisconsin), and Voyageurs National Park (Minnesota) noted that there were no taxonomic plant keys that could accurately identify the cattails. The question was raised about how to identify and manage cattail populations in the national parks in order to reduce or prevent the negative impacts of hybrid and nonnative species expansion that reduce wetland plant biodiversity.

Evaluation of cattail populations in national parks

Microsatellite DNA analysis is a relatively new tool used to evaluate plant species and their evolutionary relationships. Microsatellite DNA refers to repeating sequences of 1–6 unique base pairs (base pairs = adenine [A] with thiamine [T] and cytosine [C] with guanine [G]). The number of repeats varies among species and between members of a species, which determines relationships and genetic diversity. The analysis includes several markers (DNA sequences), and each is copied using polymerase chain reaction (PCR) technology to improve their detection in a gene analyzer. Over time, as a plant or animal population interbreeds, the microsatellites will recombine during sexual reproduction and the population will maintain a variety of microsatellites that is characteristic of that population and distinct from other populations that do not interbreed. Thus pure parental types can be detected from their hybrid offspring.

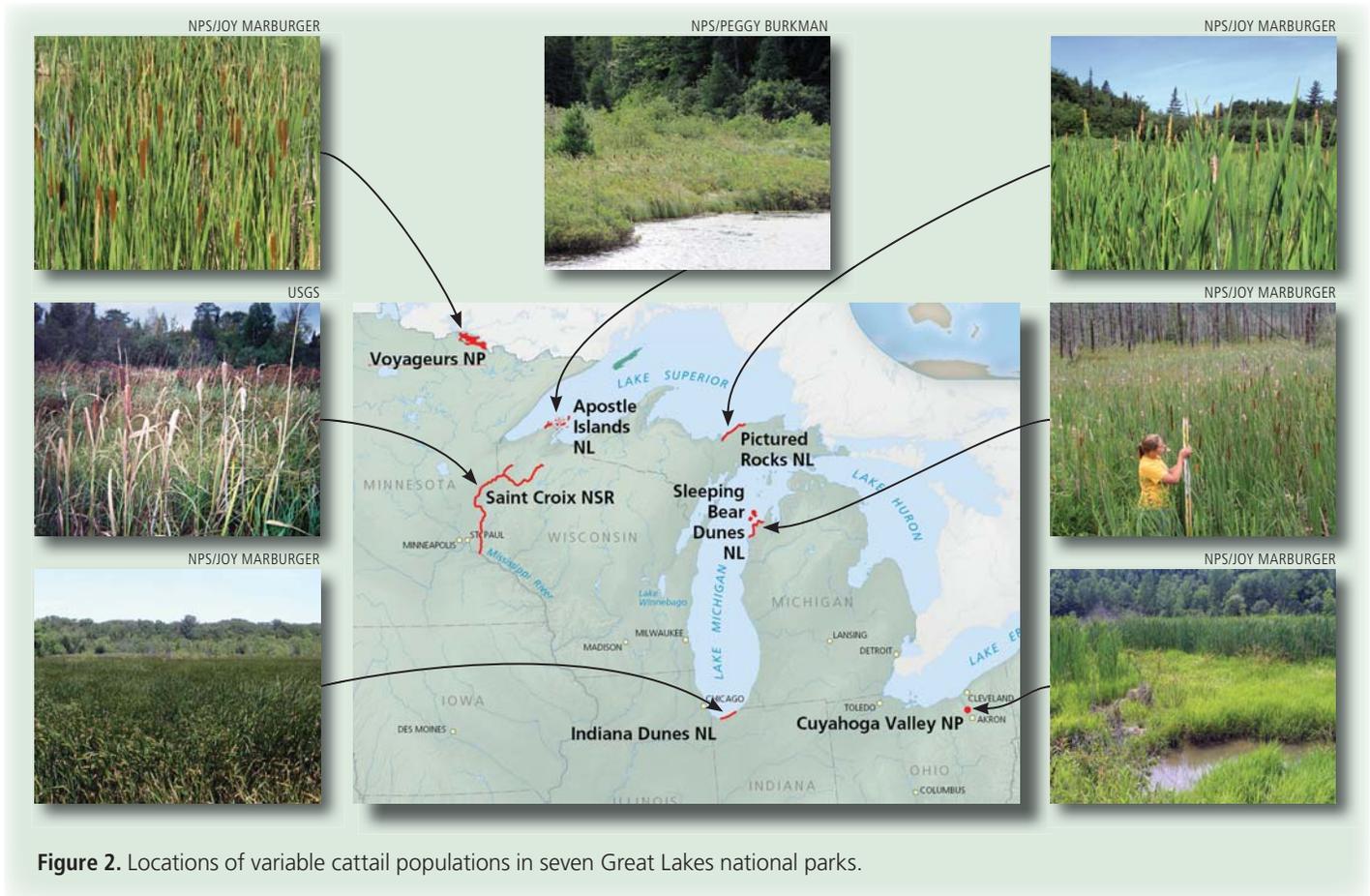


Figure 2. Locations of variable cattail populations in seven Great Lakes national parks.

From 2004 to 2012, park managers and the authors of this article surveyed nine national parks for morphological (form and structure) characteristics of cattails and to collect leaf material for microsatellite DNA marker analysis to determine the presence of *T. latifolia*, *T. angustifolia*, and hybrids. In 2004 we conducted surveys at Indiana Dunes National Lakeshore (Indiana Dunes), St. Croix National Scenic Riverway (St. Croix), and Voyageurs National Park (Voyageurs). From 2006 to 2010 we surveyed Cuyahoga Valley National Park (Cuyahoga Valley) in Ohio, Pictured Rocks National Lakeshore (Pictured Rocks) in Michigan, and Sleeping Bear Dunes National Lakeshore (Sleeping Bear Dunes) in Michigan. Point Reyes National Seashore (Point Reyes) in California and Everglades National Park (Everglades) in Florida were surveyed in 2011 as requested by park managers, and Apostle Islands National Lakeshore (Apostle Islands) in Wisconsin was added in 2012. In addition to the genetic surveys, we conducted a seed bank survey at Cuyahoga Valley, Pictured Rocks, and Sleeping Bear Dunes to determine if native wetland plant species were dormant in the seed bank. In this article we present molecular and seed bank results for these parks in the Great Lakes Inventory and Monitoring Network (fig. 2).

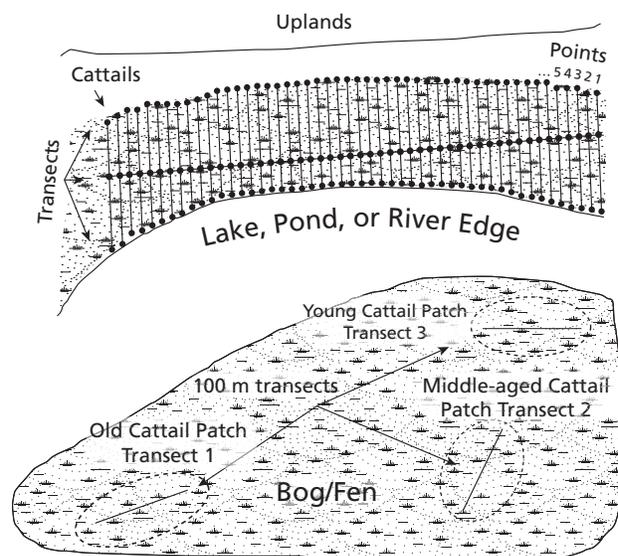


Figure 3. Cattail collection method was based on habitat classification as lake, pond, river (Apostle Islands, Cuyahoga Valley, Pictured Rocks, St. Croix, Sleeping Bear Dunes, Voyageurs), or bog/fen (Indiana Dunes). We sampled 25–50 plants per transect in all cases except for Pictured Rocks (14 plants per transect).

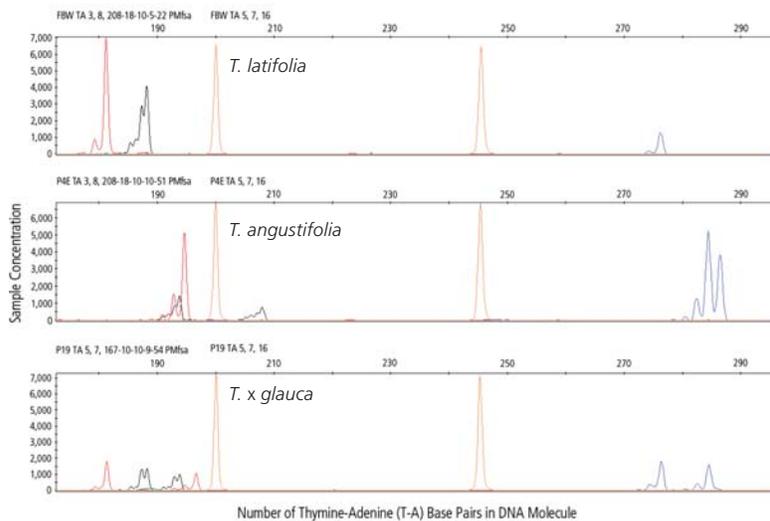


Figure 4. Standard DNA microsatellite graph showing detection of *Typha latifolia*, *T. angustifolia*, and hybrid *T. x glauca*. Note that the number of peaks for the hybrid includes peaks for both species with one peak of *T. angustifolia* absent. Orange peaks are size standards for DNA base pairs of thymine-adenine. The horizontal axis shows DNA fragment size.

Methods

Adult plant sampling

All sampling sites were located in areas where managers had a question about the identification of cattails. We marked the specific locations using a GPS unit with submeter accuracy. The methods differed somewhat at each site because of logistics, based on whether or not the wetland was near a lake or river or was contained in a bog/fen habitat (fig. 3). For seven Great Lakes parks (Apostle Islands, Cuyahoga Valley, Indiana Dunes, Pictured Rocks, St. Croix, Sleeping Bear Dunes, and Voyageurs) we surveyed one to three 100-meter (328 ft) transects at a particular location in the park. At Voyageurs additional sampling was conducted in isolated lakes. Plants were individually measured every 2 or 4 meters (6.6 or 13.1 ft) along each transect, and a leaf sample was collected from each plant for DNA analysis. We measured more than 1,200 plants, including those from isolated lakes in Voyageurs, and collected leaf samples at all sites for DNA analysis.

Data collection

Adult plants—morphology

We measured each plant collected along the transects in centimeters for plant height, leaf width at the widest point, female inflorescence length and width, and gap length (the length of these

three features for plants in flower). We collected 15 centimeters (6 in) of a mature healthy leaf from each plant for genetic analysis. We cut leaf material with scissors and placed it in a sealed plastic bag labeled with park name, date, location, transect, and point. The leaves were kept inside a soft-sided lunch cooler with a frozen ice pack to prevent heat damage. After completing data and plant collections at a site, we shipped leaf materials via overnight carrier for molecular analysis. In the lab, the leaves were frozen at -80°C (-112°F) until genetic analysis could be conducted.

Genetic analysis to determine identity of plants

We used molecular techniques employing microsatellite DNA based on previously developed methods to identify each plant's relatedness via clones of the same plant, since cattails spread by underground rhizomes, and the plant's genetic parentage, whether or not it was hybrid, *T. latifolia*, or *T. angustifolia* (Tsyusko-Omel'tchenko et al. 2003; Ball and Freeland 2013). The majority of plants were genotyped using six species-diagnostic DNA microsatellite loci based on techniques previously described (Travis et al. 2010; Travis et al. 2011; Tsyusko-Omel'tchenko et al. 2003). Figure 4 shows typical results of microsatellites for *Typha* taxa.

Seed bank samples

Seed bank samples were obtained at Cuyahoga Valley, Pictured Rocks, and Sleeping Bear Dunes to determine the proportion of cattail seeds in the soil where adult plants had been surveyed and to determine the biodiversity of native plants in the soil seed bank that could provide information relevant to management strategies. Soils were classified by type at each site for each park and sampled to determine the nature of plant biodiversity at the sites. Each soil core was about 10 cm (4 in) in diameter and 20 cm (8 in) in depth and was collected using a golf turf auger (see sidebar, next page). Soil samples were collected in sealed plastic bags along the middle transect every 4 meters (13 ft) at each site. Twenty-five sample cores were taken in Cuyahoga Valley and Sleeping Bear Dunes, and 14 were taken at Pictured Rocks. We used the auger because it causes less compression of soils and has the capacity to cut through highly fibrous material (recommended by D. Mason, botanist, Indiana Dunes National Lakeshore). Soils were stored in a portable cooler during transport and kept in a refrigerator at Indiana Dunes until prepared for the seed bank study on 11 June 2009.

The genetic nature of germinated cattail seedlings was also determined using the same techniques as for adult plants. We removed cattail seedlings and individuals from each bucket and placed them in plastic bags labeled with park, date, location, transect, and bucket number. We shipped them in an insulated cooler with a frozen ice pack by overnight mail to the principal investigator at the University of New England for genetic analysis. Plant

Soil seed bank analysis methods



We analyzed the seed bank at three parks (Cuyahoga Valley, Pictured Rocks, and Sleeping Bear Dunes) using the following methods adapted from van der Valk and Davis (1978) and Egan and Ungar (2000). (A) Soil was collected with a golf course soil auger. (B) Commercial plastic buckets measuring 25 cm in diameter × 25 cm in depth (10 × 10 in) were filled 75% with commercial sand. Four holes were drilled in each bucket about 2.5 cm (1 in) above the bottom. Each container was labeled with a permanent marker indicating the soil core sample and where it was taken along the transect. After removing debris (twigs, stones), we homogenized the soil sample and placed it on top of the sand. We washed the tools with well water between making sample additions to the buckets. (C) We then randomly placed the buckets with the seed bank soil samples in plastic-lined tanks (2 sq m or 22 sq ft) in a greenhouse at Indiana Dunes and maintained the samples with well water sufficient to saturate the soil, but with no standing water. We evaluated the samples for the number of seedlings and identified each to species as the plants matured.



NPS/JOY MARBURGER (3)

seedlings of all species in the seed bank were identified from both vegetative and flowering structures using standard plant taxonomic keys.

Results and discussion

Midwestern national parks

Morphological characteristics and water depth proved to be unreliable indicators for species identification in most populations. A number of natural and anthropogenic factors can cause mor-

phological variation and hinder identification: (1) two genetically variable, outcrossing (cross-pollinating) cattail species produce various kinds of hybrids because of random mating; (2) proximity of a site to all seed sources; (3) site soil conditions; (4) hydroperiod (water depth and fluctuation); (5) land use characteristics such as proximity to roads and waterways, and (6) geographic location of a site. Human-related disturbance allows translocation of species, and habitat modifications accelerate rates of hybridization or transfer of genes to related species (Allendorf et al. 2001).

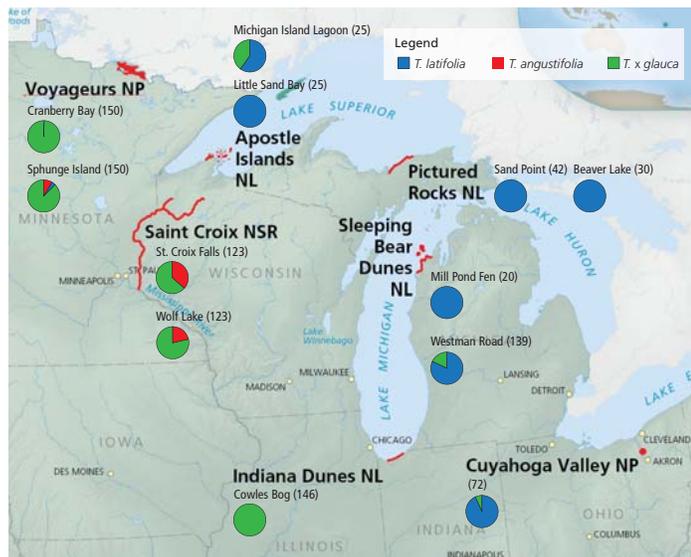


Figure 5. Based on eight nuclear and chloroplast microsatellite markers used in genetic analysis, all parks except Pictured Rocks showed some degree of cattail hybrids present. Pictured Rocks plants were identified as *Typha latifolia*. Numbers in parentheses represent the total stems genotyped at each study site.

The results of genetic analysis of adult and seed bank cattail populations in the seven Great Lakes national parks (fig. 5) provided important insight into the extent and amount of variation among the hybrids, particularly the variation found in the first set of three parks (Indiana Dunes, St. Croix, and Voyageurs). St. Croix and Voyageurs had backcrossed and advanced-generation hybrids in addition to first generation hybrids (F₁); Indiana Dunes Cowles Bog had only F₁ hybrids. Apostle Islands, Cuyahoga Valley, Sleeping Bear Dunes, Pictured Rocks, and Voyageurs had small populations of the native cattail species occupying small isolated lakes and ponds or island lagoons (Travis et al. 2010, 2011; unpublished data). *T. angustifolia*, the nonnative species, was found in St. Croix and Voyageurs. The results for Sleeping Bear Dunes showed the presence of *T. latifolia* (the native species) in both the adult and seed bank populations, with a few hybrids; one nonnative *T. angustifolia* was present in the seed bank. The populations at Cuyahoga Valley were re-analyzed with two additional microsatellite markers (total 8) and one chloroplast (photosynthetic structures in plant cells) DNA marker (Ball and Freeland 2013) that confirmed the presence of hybrids, although most of the plants were identified as *T. latifolia*. The results presented here reflect the genetic makeup of only the sampled populations, not all the cattail populations in a park. Random mating of species and hybrids could produce different genetic results for other populations. Using morphological and molecular markers, Snow et al. (2010) found a trend of morphological traits that suggested that hybrids and backcrossed generations favored nonnative *T. angustifolia*.

Because of the high cattail genetic variability among parks in the NPS Midwest Region, molecular identification techniques are currently the only reliable method to identify cattail taxa, although use of pollen morphology has been suggested as another identification method (Dugle and Coppins 1972; Smith 1987).

Seed bank studies revealed the nature of plant biodiversity in each park site that was evaluated. The cattail taxa and seed bank response were unique to each site. Cattail seedlings were grouped as *Typha* spp. and seedlings from each park were randomly subsampled for genetic analysis. Seed bank results are summarized in fig. 6 (next page). Native wetland plant species, such as dicot herbs, grasses, sedges, and rushes, were represented in the soils of all the parks, but percentages varied widely. Number of cattail seedlings germinating from the seed bank also varied considerably, with the greatest number occurring in Cuyahoga Valley (59%), followed by Pictured Rocks (25%) and Sleeping Bear Dunes (3%).

Cuyahoga Valley National Park

Here, the most common species in the seed bank was cattail (*Typha* spp.), which comprised nearly 60% of all species observed. The most common wetland species other than cattail was rice cut-grass, *Leersia oryzoides*, which comprised about 33% of the seed bank.

Pictured Rocks National Lakeshore

In this park the most common species was *Symphytotrichum lanceolatum*, an aster, which comprised almost 58% of the seed bank. This was surprising since the aboveground plant population was dominated by sweet gale, *Myrica gale*. A rush, *Juncus acuminatus*, was fairly common, representing about 11% of the seed bank. Cattails (*Typha* spp.) comprised 25% of the seed bank.

Sleeping Bear Dunes National Lakeshore

The most common species were sedges, *Carex* sp., and rushes, *Juncus* sp., which comprised almost 81% of the total number of species and individuals. Late boneset (an aster), *Eupatorium serotinum*, was fairly common, representing about 9% of the seed bank. Only about 3% of the species in the seed bank were cattail seedlings. The fact that *Carex lurida* occurred in 57% of the seed bank recruits at Sleeping Bear Dunes indicated that some *Carex* species do persist in wetland soils until favorable conditions allow them to germinate (van der Valk and Davis 1978).

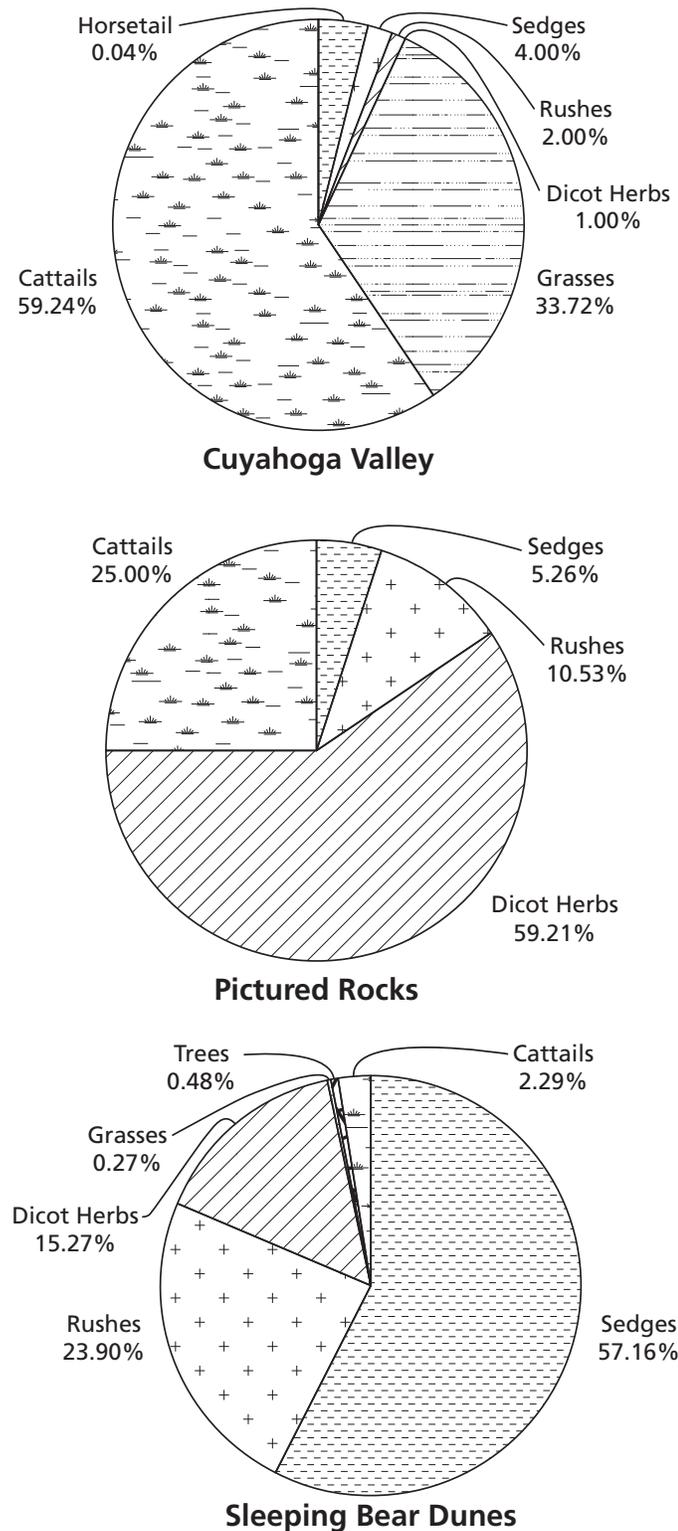


Figure 6. The pie charts show the percentages of plant species groups developing from the seed bank in three parks. The unique character of the seed bank at each park reflects the influence of environmental factors such as hydrology, proximity to source plants, and soil conditions.

Implications of restoring wetlands in national parks

Is native *Typha latifolia* being eliminated as a distinct species through hybridization and introgression of genes from the introduced *T. angustifolia*? The harmful effects of hybridization have led to the extinction of many populations of plant and animal species (Allendorf et al. 2001). In this case interspecific hybridization appears to be driven more by human-influenced than by natural evolutionary mechanisms. Landscape changes that result from urbanization and agricultural development have brought about wetland disturbances that promote plant invasions. The movement of plants across the landscape via human-made canals and waterways through the Laurentian Great Lakes states has promoted expansion of *T. angustifolia* westward from the North American coastline (Gallatowitsch et al. 1999). Hybridization of cattail species and clonal spread may thus be a considerable force in their expansion in wetlands of Great Lakes national parks (Travis et al. 2011).

More extensive investigations are needed of the occurrence and rate of hybridization at other locations within and outside of the national parks. Limitations of the previous studies include insufficient number of diagnostic markers to detect all the various hybrid types in a park and to detect parental differences. Since cattails are primarily a cross-pollinated genus, random mating within a population with both the native and nonnative species present can result in hybrids carrying any percentage of the non-native genes. Can the native *T. latifolia* be “rescued” from introgressive genes from *T. angustifolia*? This approach may be possible where populations consist primarily of parental individuals and first-generation (F₁) hybrids, as long as sufficient large numbers of diagnostic markers are examined to ensure that the species is pure (Allendorf et al. 2001). This is possibly the case for Voyageurs, where we identified cattail populations of native *T. latifolia* in isolated lakes. At Indiana Dunes, on the other hand, all the plants surveyed in Cowles Bog appeared to be primarily F₁ hybrids and no native *T. latifolia* could be rescued. Before restoration of a site, cattail genotypes should be evaluated and the seed bank assessed to determine management strategies.

Research reveals that many sedge species (*Carex* spp.) do not persist in the seed bank over time under unfavorable germination conditions (van der Valk et al. 1999). In this pilot study of the seed bank in three parks, we detected *Carex* spp. only in Sleeping Bear Dunes. Other native forbs and grasses were evident, especially in the Sleeping Bear Dunes seed bank. This indicates that even in highly invaded sites, such as Indiana Dunes and Cuyahoga Valley, the seed bank can be a source of native plants once the

cattails have been removed (discussed in next section). However, the array of native species varies widely and wetland managers often supplement the seed bank by planting both locally harvested seeds and container-grown plants, especially the sedges. Container-grown plants have better establishment success when transferred to field conditions. Planting of native material from nursery stock is also applied to enhance biodiversity.

Even with the presence of *Typha* taxa, the seed bank in the sampled sites reflected a diversity of native wetland plant species. Thus, removal of cattails, even those of questionable parentage, could result in a fairly diverse native wetland population. However, several cycles of cattail removal would likely be required, since seeds germinate at various time periods because of variation in seed dormancy and environmental conditions.

One of the critical questions that remains is to what degree the spread of *T. × glauca* or hybrids is dependent on human-related disturbance such as altered hydrology and elevated nutrient levels (Wilcox 2011; Woo and Zedler 2002), or whether or not hybrid vigor alone would be sufficient for the evolution of cattail invasiveness. A controlled, scaled-down approach to the elucidation of the relative roles of constant vs. variable water levels, high vs. low nutrient levels, and low vs. high levels of competition with native wetland taxa in the spread of *T. latifolia*, *T. angustifolia*, and *T. × glauca* and its respective backcrosses would greatly elucidate the roles of environment and genetics in cattail invasions.

Management of cattails in Great Lakes national parks

All *Typha* species can reproduce sexually by wind-dispersed seeds (achenes) and by growth of underground stems called rhizomes. The hybrids often have fertile seeds, but much of their aggressive spread is by clonal growth of rhizomes from the parent plant. Various methods have been used to control cattails in wetlands to preserve wildlife habitat and plant diversity. Controversy has surrounded the setting of appropriate conservation policies to deal with hybridization and introgression (Allendorf et al. 2001). Any policy that deals with hybrids must be flexible and must recognize that nearly every situation that involves hybridization is different enough that general rules are not likely to be effective. Each park with cattail populations could develop a vegetation management plan based on cost-benefit analysis of cattail removal.

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Management questions

1. Is there an acceptable proportion of mixtures of cattail taxa? Should a certain proportion of exotic and hybrid cattails be allowed to persist in wetlands managed by the National Park Service?
2. Can parental individuals of native *T. latifolia* be “rescued” from hybrid and exotic populations?
3. What management strategies are used to control cattail populations?
4. What is the trade-off between cost to remove large monotypic stands of cattails and cost of prevention of small hybrid populations from expanding?

Items 1, 2, and 4 require more applied research that can guide management decisions. To address the third question, several methods are currently in use to control cattails. The list in table 1, next page, provides a summary of these methods obtained from several sources (Buele 1979; Comes and Kelly 1989; USACE ERDC n.d.a; Wisconsin Department of Natural Resources 2013).

Summary and future research

The recent research on cattail hybridization in North America shows the pattern of a supposedly introduced species, *T. angustifolia*, spreading over the landscape (Galatowitsch 1999) and hybridizing with a native species, *T. latifolia*, resulting in hybrid swarms of mixed genotypes with morphological characteristics of both species or resembling one or the other species. The hybrids also exhibit more robust growth than both parental species, which reduces plant biodiversity (Farrer and Goldberg 2009; Snow et al. 2010; Travis et al. 2010, 2011; Tuchman et al. 2009; Woo and Zedler 2002). Although this body of work explores the nature of cattail populations from genetic and ecological perspectives, there are no models that predict the mechanisms and

Table 1. Cattail management methods

Method	Description
Animal grazing	Muskrats mostly on stems and rhizomes, and geese on young plants. This approach does not control cattail expansion because of the variable number and activity of the animals feeding on rhizomes and seedlings.
Hand pulling	This method works in very small sites on young plants with no extensive rhizomes. It also works for controlling seedling establishment in small areas newly invaded by cattails. It is labor-intensive and requires frequent visits to a site because the seedlings germinate at various times and begin producing rhizomes shortly after germination.
Mechanical-physical methods	
Crushing, cutting, shearing, disking	This works temporarily to create openings, but both native and nonnative species, including cattails, may become established in these openings. Rhizomes must be damaged to an extent that they do not regenerate, which is difficult since they are below the ground surface. Cutting or disking can create more propagules that can resprout during wetter conditions. This method is often combined with water-level management (drowning sprouts) and herbicide treatment.
Water-level management	Water-level management is highly effective where water-level control technology exists in a managed wetland, such as pumps, canals, and levees in a restoration site. Drawdown of water accompanied by herbicide treatment greatly reduces standing live material. Drawdown can occur naturally during the dry season when herbicides can be applied to large areas using an amphibious or all-terrain vehicle. Flooding cattail plants may also be effective if the entire plant is covered with water. In order for this to be effective, cattail stems must be cut or removed and flooded to at least 0.3 m (1 ft) above the cut stems for at least a few weeks to kill the plant.
Chemical control	National Park Service–approved herbicides (applied mid- to late-summer at plant maturity, but before seed dispersal) must be used according to product label and NPS guidelines for protected areas and sensitive organisms. Herbicides should not be stored in steel containers, since they may chemically react with the metal to produce explosive hydrogen gas.
Glyphosate	Glyphosate is a systemic herbicide that is transported through the plant and preferred for cattail treatment. It is approved for use by the National Park Service. It kills plants by interfering with photosynthesis, and therefore must be applied with great caution. A “sticking” agent is required in the formulation for application to cattails in aquatic environments to prevent water pollution. Formulations depend on the extent of cattail invasion. For single plants, a “glove of death” can be used to apply the herbicide. A manager wears an outer glove made of cloth, preferably cotton, that is saturated with herbicide, along with an inner glove of rubber or other impenetrable material to prevent skin contact. Herbicide is applied directly to the stems and leaves. For large populations, spraying (backpack, overland vehicle, air boat, helicopter, plane) is preferred, as it is effective, but there is risk of over spraying nontarget plants.
Diquat	Diquat is a contact herbicide that does not travel through the plant and is therefore not as effective as glyphosate. It also requires the addition of a “sticking” agent in aquatic environments to prevent water pollution. There are more restrictions for its use on public lands.
Prescribed burning	Use of prescribed fire to control cattails has mixed results. It burns off the top growth during a drawdown, but the rhizomes generally survive and can resprout, leading to recolonization of a site unless herbicides are applied to the aboveground stems. Under drier conditions, burning can cause subsurface peat fires that can result in extensive damage to soil structure and cause soil subsidence.
Combination of treatments	Depending on the particular circumstance, combination treatments are often very effective, such as combining crushing with herbicide application. Cutting stems below the water surface and flooding to at least 0.3 m (1 ft) above the cut surface for one month or more is effective. Removal of aboveground plant material by cutting or herbiciding before flooding is also effective. Repeated spot treatment with herbicides is often necessary after initial treatment because of resprouting of rhizomes and seedling germination.

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(Photos) Change in wetland vegetation communities after major removal of hybrid cattails in Cowles Bog, Indiana Dunes National Lakeshore: (A) before and (B) after herbicide and mechanical treatment and native plant growth from the seed bank. Restoration practices included cattail treatment with glyphosate herbicide supplemented with planting native plant species and volunteer growth of native plant species from the seed bank.

consequences of invasions caused by cattail hybridization (as well as for other taxa). Managers and scientists need extensive data on hybrid ecology and biology as well as carefully designed field experiments in order to compare parent and hybrid responses to various environmental conditions and to identify potential sites for hybrid zone formation and expansion in wetlands. The following avenues for research exist:

1. Development of additional molecular markers from both nuclear and chloroplast DNA.
2. Determination of the extent of cattail hybridization regionally and nationally, including more detailed summaries of the number of hybrid taxa.
3. Comparison of life history traits, flowering patterns of the species and hybrids, pollen flow, seed fertility, clonal growth, and viable seed production in the taxa.
4. Establishment of seedlings and their growth response to various environments and habitat alterations.
5. Comparison of the ecological effects of cattail hybrids with parental species on biodiversity at various levels of complexity.
6. Management that includes development of rapid hybrid and parental identification as well as various control strategies.
7. Barriers and promoters of hybridization at the molecular, cellular, and landscape levels.
8. Models to predict the mechanisms and routes of hybridization.
9. Climate change impacts on 1–8.

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About the authors

Joy Marburger (joy_marburger@nps.gov) is research coordinator with the Great Lakes Research and Education Center, Indiana Dunes National Lakeshore, Porter, Indiana. **Steve Travis** is an ecological geneticist with the Department of Biological Sciences, University of New England, Biddeford, Maine.