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Invasive Plant Species in Diked vs. Undiked Great Lakes Wetlands

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ABSTRACT. *We compared the standing vegetation, seed banks, and substrate conditions in seven pairs of diked and undiked wetlands near the shores of Lake Michigan and Lake Huron, North America. Our analysis tested the null hypothesis that construction of artificial dikes has no effect on the vulnerability of Great Lakes coastal wetlands to non-native and native invasive species. Both the standing vegetation and seed banks in diked wetlands contained significantly more species and individuals of invasive plants. In addition, diked wetlands exhibited significantly higher levels of organic matter and nutrient levels, and significantly higher average pH. Two pervasive non-native invasive species in the Great Lakes region,* Lythrum salicaria *(purple loosestrife) and* Phalaris arundinacea *(reed canary grass) were significantly more abundant in diked wetlands.* Typha *spp. (cattail) also formed a much higher percent vegetation cover in the diked wetlands. Our results support the view that diking of shoreline wetlands modifies natural hydrologic regimes, leading to nutrient-rich aquatic environments that are vulnerable to invasion. The shallower, more variable water levels in non-diked wetlands, on the other hand, appear to favor another undesirable invasive species,* Phragmites australis *(common reed grass).*

INDEX WORDS: *Great Lakes, invasive species, coastal wetlands, diked wetlands.*

INTRODUCTION

The key factor distinguishing North American Great Lakes coastal wetlands from freshwater inland wetlands is the connection with a larger water body, which affects hydrologic circulation patterns, nutrient dynamics, climate variation, and disturbance regimes (Keough *et al.* 1999). These coastal wetlands span an array of geomorphic settings, including open and protected embayments, sand-spit embayments, shallow sloping beaches, dune and swale complexes, barrier beaches, drowned-river-mouths, and river delta wetlands (Albert 2003, Wilcox and Whillans 1999).

Fluctuation in water levels is the dominant factor in controlling the composition of coastal wetland vegetation in the Great Lakes (Keddy and Reznicek 1986, Farney and Bookhout 1982). Seed bank dynamics can play an important role in the response of wetlands to natural hydrologic disturbances such as periods of drawdown and flooding (Baldwin *et al.* 2001, Keddy and Reznicek 1986, Schneider and Sharitz 1986, Smith and Kadlec 1983). Indeed, wetland plant species in general often have large persistent seed banks (van der Valk and Davis 1976, 1978; Thompson and Grime 1979) which are important in the re-colonization of recently disturbed habitat (Moore and Keddy 1988).

Many wetlands along the shores of the Great Lakes have been diked to address issues caused by water-level changes and wave action (Maynard and Wilcox 1997). Dikes allow artificial manipulation of water levels to effectively manage vegetation for wildlife, particularly waterfowl (Mitsch 1992, Mitsch and Gosselink 2000). However, creation of dikes typically isolates wetlands from the lake, thereby removing the natural hydrological and nutrient exchange processes that shape the coastal environment (Mitsch 1992, Sherman *et al.* 1996, Maynard and Wilcox 1997, Hill *et al.* 1998, Wilcox and Whillans 1999).

Increasingly, non-native plant species have become part of today's wetland vegetation, particularly in areas that have been disturbed (Mitsch and Gosselink 2000). For example, *Lythrum salicaria* (L.) (purple loosestrife), *Phragmites australis*

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(Cav.) Trin. ex Steud (common reed grass), and *Typha* spp. (L.) (cattail) have aggressively colonized wetlands in the Great Lakes region (Mitsch and Gosselink 2000). Many of these invasive plants have limited value for waterfowl and other native wetland animals (Odum 1987, Thiet 2002). Changes in hydrologic regimes, soil conditions, and nutrient levels collectively coincide with a shift in plant community composition and may enhance the susceptibility of wetland habitats to invasion (Burke and Grime 1996, Flack and Benton 1998, Mack *et al.* 2000, Svengsouk and Mitsch 2001, Woo and Zedler 2002).

In this paper, we examine the composition of wetland plant assemblages and seed banks in seven diked wetlands along the Great Lakes shoreline and seven nearby wetlands that are still connected to the lake. Our objective is to test the hypothesis that diking significantly affects the vulnerability of coastal wetlands to invasive species. A more complete description of the vegetation in these wetlands and a discussion of the broader floristic implications of dike construction are provided elsewhere (Herrick 2003, Herrick *et al. in prep*).

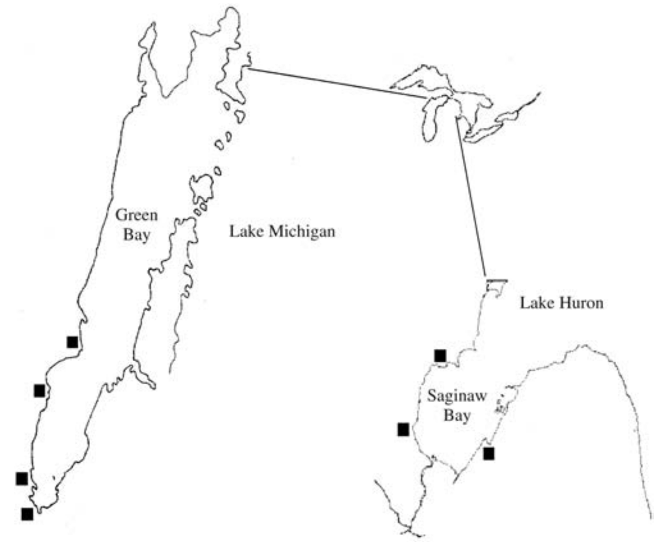

FIG. 1. Locations (black squares) of the seven diked and seven undiked pairs of coastal wetlands on Green Bay (Lake Michigan) and Saginaw Bay (Lake Huron), USA. Each square corresponds to one diked and one undiked wetland.

STUDY SITES AND METHODS

In 2002, seven pairs of diked and undiked Great Lake wetlands were selected for this study (Fig. 1), four near the west shore of Green Bay, Lake Michigan (44°33′–44°58′ N, 87°43′–88°02′ W) and three on Saginaw Bay, Lake Huron (43°43′–43°59′ N, 83°31′–83°56′W). The undiked wetlands were exposed to large expanses of open water, although all were associated with embayments (including Saginaw Bay and Green Bay themselves), providing some degree of protection from high energy wave action of the Great Lakes (Appendix A). Shale, as well as limestone and dolomite characterize the underlying bedrock type in these bays (Minc and Albert 2002).

Wet meadows commonly occur along the gentle-sloping shores of Lakes Michigan and Huron (Keddy and Reznicek 1986) and usually support more plant species than other vegetation types such as marshes (Keddy 2000). Previously, Herrick (2003) recorded a total of 15 wet meadow species and 13 marsh/emergent species in the undiked wetlands. Although species richness of wet meadow and marsh/emergent plants differed only slightly, the marsh/emergent species were characterized by a much denser cover. Wet meadows are produced and sustained by cycles of flooding and drawdown (Keddy 2000), thus, the increased protection from direct wave action in the bays, as well as the embayments at most of the undiked sites, may be reasons why the marsh vegetation dominates the cover at our study sites.

Coastal wetlands on Green Bay are situated near the floristic tension zone (Curtis 1959) on a relatively flat topography (Harris *et al.* 1977) and display both northern and southern vegetation characteristics. Emergent zone dominants include *Ceratophyllum demersum* (L.) (coontail), *Elodea canadensis* (Michx.) (Canadian waterweed), *Lemna minor* (L.) (common duckweed), *Spirodela polyrhiza* (L.) Schleiden (giant duckweed), *Sagittaria latifolia* (Willd.) (broadleaf arrowhead), *Typha* spp., and the non-native invasives *L. salicaria*, *Phalaris arundinacea* L. (reed canary grass), and *P. australis*. Common wet meadow species include *Calamagrostis canadensis* (Michx.) Beauv. (bluejoint), *Carex stricta* (Lam.) (upright sedge), *Carex lacustris* (Willd.) (hairy sedge), and *Impatiens* spp. (L.) (touch-me-not) (Minc and Albert 2002).

Similar to Green Bay, Saginaw Bay consists of gently sloping wetlands with a mix of northern and southern species, probably also associated with a climatic tension zone across the bay (Minc and Albert 2002). Common emergent marsh species include *Schoenoplectus acutus* Muhl. ex Bigelow (A.

& D.) (hardstem bulrush), *Schoenoplectus pungens* (Vahl) Palla (common threesquare), *Typha* spp., *Najas flexilis* (Willd.) Rostk. & Schmidt (nodding waternymph), and the non-native invasive *P. australis*. Common wetland plants in wet meadows are *Impatiens* spp., *Rorippa* spp. (Scop.) (yellowcress), *Schoenoplectus tabernaemontani* (C.C. Gmelin) Palla (softstem bulrush), *S. pungens*, *Polygonum lapathifolium* (L.) (curlytop knotweed), and the non-native invasives *L. salicaria*, and *P. arundinacea* (Minc and Albert 2002).

The year 2002 was the fourth consecutive low-water year in the Lake Michigan-Huron basin. In the undiked wetlands, *S. tabernaemontani*, *S. pungens*, and *S. latifolia* exhibited the highest percent cover after *Typha* spp. (Herrick 2003). Presumably the drawdown of the marsh zone initiated dense regeneration of these species. Similarly, *Schoenoplectus* and *Sagittaria* species regenerated in Metzger Marsh, Lake Erie during a low-water year (Keddy 2000).

At each site, we compared undiked wetlands with adjacent or nearby diked wetlands. Most of the diked and undiked wetlands were considerably longer (parallel to the shoreline) than they were wide. All dikes were constructed from dredged sediments and rip-rap between 1933 and 1960 (personal communication with site managers). Most of the earthen dikes were vegetated and accessible by vehicle. The distance from the inner edge of the dike to the waterline, where aquatic vegetation began, varied from approximately 3 m to 10 m. We chose to sample at two distances from the waterline (toward the center of the wetland) in order to represent a portion of the shoreline gradient. Five points at least 50 m apart were selected randomly along the waterline of each wetland. Two 10 m sampling transects were established parallel to the waterline, at 1 m and at 10 m from the shoreline point. Five 1-m^2 quadrats were placed evenly along each 10 m transect.

Seed bank and sediment samples were collected from 19 April to 10 May 2002. At the time of sampling, the water level of the Lake Michigan-Huron basin was approximately 176.06 m. which was below the long-term mean of 176.42 m. The seed bank and sediment were sampled within 1 m^2 quadrats by taking a single, 10 cm diameter soil core to a depth of 5 cm.

In the laboratory, we removed litter, roots, and tubers from the pooled field samples. These samples were then moved to a greenhouse where the soil was spread as a 1-cm thick layer over a 1–1.5 cm. layer of sterilized sand in 29×29×5 cm plastic flats. Half of each pooled sample was maintained at moist (non-flooded treatment) conditions, while the other half was kept under 4–5 cm of water (flooded treatment). The two treatments applied to the soil samples are commonly used to obtain a representative sample of all seed species present in the soil. The number of seeds that germinated under both treatment conditions were combined for use in statistical analysis. Flats were placed in a random block design in a greenhouse. Six flats with only sterile sand were placed randomly in the greenhouse to test for contamination. No germination occurred in these flats.

Non-flooded treatment samples were watered at least once daily and flooded samples were watered as needed to maintain a constant water depth. Seedlings were counted and removed when they were identifiable. The experiment commenced during the second week of June 2002 and was terminated at the end of November 2002. Any unidentifiable seedlings at this time were transferred to pots and grown to an identifiable stage. Although most viable seeds germinate within a 4-month assay period (Galatowitsch and van der Valk 1996), we found that several species did not begin to germinate until mid-October. Thus the experiment was extended for approximately 6 weeks beyond the standard 4-month period. Seedling counts were used to estimate the number of viable seeds of a species per square meter, in a layer of soil 5 cm thick.

At the same time as the seed banks samples were collected, an additional soil core was taken at the mid-point of each transect. These samples were analyzed for pH, organic matter content, total nitrogen, available phosphorus, available potassium, and soil texture. Soil samples were given a texture code of 1 = sandy, 2 = silty, 3 = organic, and 4 = red calcareous based solely on sight and touch.

At each quadrat, percent cover of all plant species was estimated in early August 2002 according to a standard cover-abundance scale modified from Daubenmire (1959): (1) 0–1%, (2) 2–5%, (3) 6–25%, (4) 26–50%, (5) 51–75%, (6) 76–95%, and (7) 96–100%. The midpoint of each class was used to quantify cover. At the time of vegetation sampling the water-levels had risen to 176.32 m, still below the long-term mean of 176.59 m for the Lake Michigan-Huron basin.

For the purpose of this study, invasive species are defined as all non-native species and *Typha* spp. Because of the difficulty identifying non-flowering

Typha seedlings in the greenhouse (Sharitz *et al.* 1980), we did not separate the native species (*Typha latifolia* L. (broadleaf cattail)) from the invasive *Typha* species or races. Species of adult *Typha* include the native species *T. latifolia*, the introduced *Typha angustifolia* (L.) (narrowleaf cattail) (Stucky and Salamon 1987), and their highly aggressive hybrid *Typha* × *glauca* (Godr.) (e.g., McNaughton 1966, Smith 1967, Lee and Fairbrothers 1973, Galatowitsch *et al.* 1999). Because all species of *Typha* are highly aggressive and are capable of forming dense, monotypic stands (Boyd 1971, Svengsouk and Mitsch 2001, Woo and Zedler 2002) all *Typha* spp. have been included in the invasive species category.

Percent cover and seed densities of invasive species were used in separate, paired, three-way General Linear Models (GLM) to detect the influence of wetland type (diked vs. undiked), site (seven localities), distance from the waterline (1 m and 10 m), and the interaction components. Mann-Whitney U tests were used to compare soil variables and species richness in the standing vegetation and seed bank samples. All statistical analyses were performed using SAS statistical package (Statistical Analysis Systems, Version 8.0, Cary, NC).

RESULTS

The seven diked and seven undiked wetlands were similar in mean area ($\bar{X}_{diked}$ = 123 ha, range 7.8–367 ha; $\bar{X}_{undiked}$ = 93 ha, range 13–223 ha, $p > 0.05$, Mann-Whitney test), although the areas of diked wetlands showed a greater range. The soils of diked wetlands were significantly more acidic than those of undiked wetlands ($\bar{X}_{diked\ pH} = 6.71$, $\bar{X}_{undiked\ pH} = 7.87$, $P < 0.001$). In addition, diked wetlands had significantly higher percent organic matter ($\bar{X}_{diked} = 36.24$, $\bar{X}_{undiked} = 1.94$, $P < 0.001$), total N (mg/L) ($\bar{X}_{diked} = 42.29$, $\bar{X}_{undiked} = 19.71$, $P \leq 0.0001$), available P (mg/L) ($\bar{X}_{diked} = 110.14$, $\bar{X}_{undiked} = 37.14$, $P < 0.001$) and available K (mg/L) ($\bar{X}_{diked} = 14{,}405.0$, $\bar{X}_{undiked} = 1{,}181.0$, $P < 0.05$) measurements than soils in undiked wetlands. Water depths at the 1 m and 10 m distance from the waterline did not differ significantly in diked or undiked wetlands ($P > 0.05$).

Sandy soil characterized all but one of the undiked wetlands (which had silty soil). Soil samples from all seven of the diked wetlands, on the other hand, were identified as organic soil type (Herrick 2003). The standing vegetation in diked wetlands yielded a mean of 21 species per wetland compared with a mean of 16 species per wetland for the undiked wetlands, a difference that was not statistically significant (Mann-Whitney test, P = 0.2694). Both wetland types had similar numbers of native species, although cover of these species was significantly different (P < 0.05; Fig. 2). Common

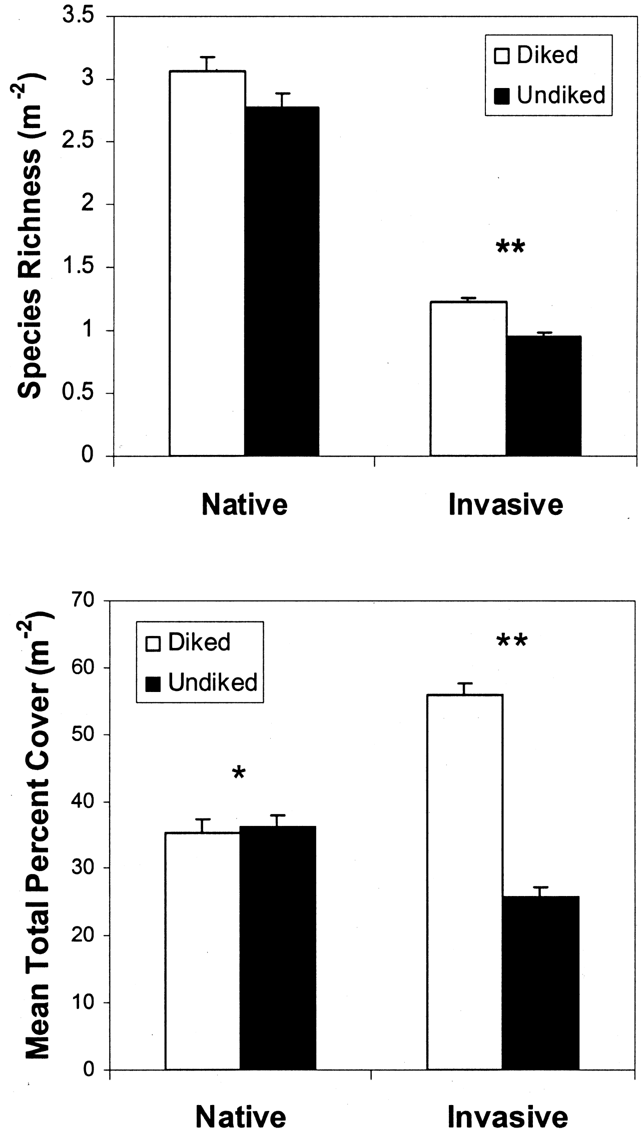

***FIG. 2.** (top) Mean richness of native and invasive/Typha spp. species in the vegetation of diked and undiked wetlands. (bottom) Mean total percent cover of native and invasive/Typha spp. species in the vegetation of diked and undiked wetlands. Data are means (+ 1 se) of 350 plots. Asterisks indicate significant (* P < 0.05, ** P < 0.0001) differences between wetland types.*

TABLE 1. Occurrence of invasive species and* Typha *spp. in the standing vegetation of coastal wetlands. Mean percent cover was estimated from wetlands where each species was detected.

	Diked coastal wetlands		Undiked coastal wetlands	
Species	No. of wetlands	Mean % cover	No. of wetlands	Mean % cover
Phragmites australis (Cav.) Trin.	3	2.00	4	6.27
Lythrum salicaria (L.)	3	6.12	3	0.37
Phalaris arundinacea (L.)	3	4.15	0	—
Solanum dulcamara (L.)	4	0.14	0	—
Salix fragilis (L.)	1	0.31	2	1.03
Polygonum convolvulus (L.)	1	0.63	0	—
Cirsium arvense (L.) Scop.	4	0.09	1	0.03
Chenopodium rubrum (L.)	1	0.32	0	—
Myriophyllum spicatum (L.)	0	—	1	0.28
Cuscuta gronovii (Willd.)	1	0.1	0	—
Epilobium hirsutum (L.)	0	—	1	0.01
Typha spp. (L.)	6	58.54	7	21.68

native species in diked wetlands included *C. canadensis*, *C. lacustris*, *Carex* spp., and *Leersia oryzoides* (L.) Sw. (rice cutgrass). Common native species found in undiked wetlands were *Eleocharis erythropoda* (Steud.) (bald spikerush), *S. latifolia*, *L. minor*, *S. pungens*, and *S. tabernaemontani*.

The standing vegetation of diked and undiked wetlands differed significantly in richness and cover of invasive species ($P < 0.0001$, Fig. 2). Twelve invasive species including *Typha* spp. were found in the diked wetlands, undiked wetlands or both (Table 1). *Typha* spp. comprised significantly greater mean percent cover in diked wetlands than in undiked wetlands (Table 1).

P. australis, *L. salicaria*, and *P. arundinacea* are common invasive species found throughout North America (Galatowitsch *et al.* 1999), including our study sites. *P. australis* was found in both diked and undiked wetlands, but at a significantly greater percent cover in undiked wetlands ($\bar{X}_{\text{diked}} = 2.00$, n = 150; $\bar{X}_{\text{undiked}} = 6.27$, n = 200; $P < 0.0001$). *L. salicaria* also was found in both diked and undiked wetlands but at a significantly greater percent cover in diked wetlands ($\bar{X}_{\text{diked}} = 6.12$, n = 150; $\bar{X}_{\text{undiked}} = 0.37$, n = 150; $P < 0.0001$). *P. arundinacea* was found only in diked wetlands.

The seed banks of diked wetlands contained a mean of 25 species per wetland compared to 20 species in undiked wetlands (Mann-Whitney U test, $P < 0.0286$; Herrick 2003). Diked wetlands yielded significantly greater numbers and higher seed densities of native species compared to undiked wetlands (Fig. 3). Native species found frequently in diked wetland seed banks included *S. pungens*, *S. latifolia*, *Carex* sp., *L. oryzoides*, *P. lapathifolium,* and *Rorippa islandica* (Oeder) Borbas (northern marsh yellowcress). Native species found frequently in undiked wetlands were *Carex* sp., *L. oryzoides*, *Juncus* sp. (L.) (rush), *Cyperus rivularis* (Kunth) (slender flatsedge), *E. erythropoda*, and *E. acicularis* (L.) R & S (needle spikerush). Herrick (2003) provides a complete description of the seed bank community at these sites, including species lists.

Invasive species in the seed banks of diked vs undiked wetlands differed significantly ($P < 0.0001$) in richness and seed density (Fig. 3). Nine invasive species including *Typha* spp. were found in the seed banks of diked and/or undiked wetlands (Table 2). Thirty percent of the 13,990 seeds that germinated from the diked wetland seed banks were invasive species or *Typha* spp. In contrast, only 8 % of the 5,093 seeds that germinated from the undiked wetland seed banks were invasive or *Typha* spp. *Chenopodium rubrum* (L.) (red goosefoot) exhibited the highest seed density among invasive species, but it was found only at one diked wetland. *L. salicaria* had the second greatest seed density among invasive species, appearing in six of seven diked wetland seed banks and in three undiked wetland seed banks. *L. salicaria* also had a significantly greater mean number of seeds per m^2 in the diked wetlands than in the undiked wetlands ($\bar{X}_{\text{diked}} = 369$ (n = 300), $\bar{X}_{\text{undiked}} = 3$ (n = 150); $P < 0.0001$). *P. australis* and *P. arundinacea* were not found in either the diked or undiked wetland seed banks.

Seven of eight invasive species and *Typha* spp. germinated in the non-flooded soil treatment from diked wetlands, while four invasive species and

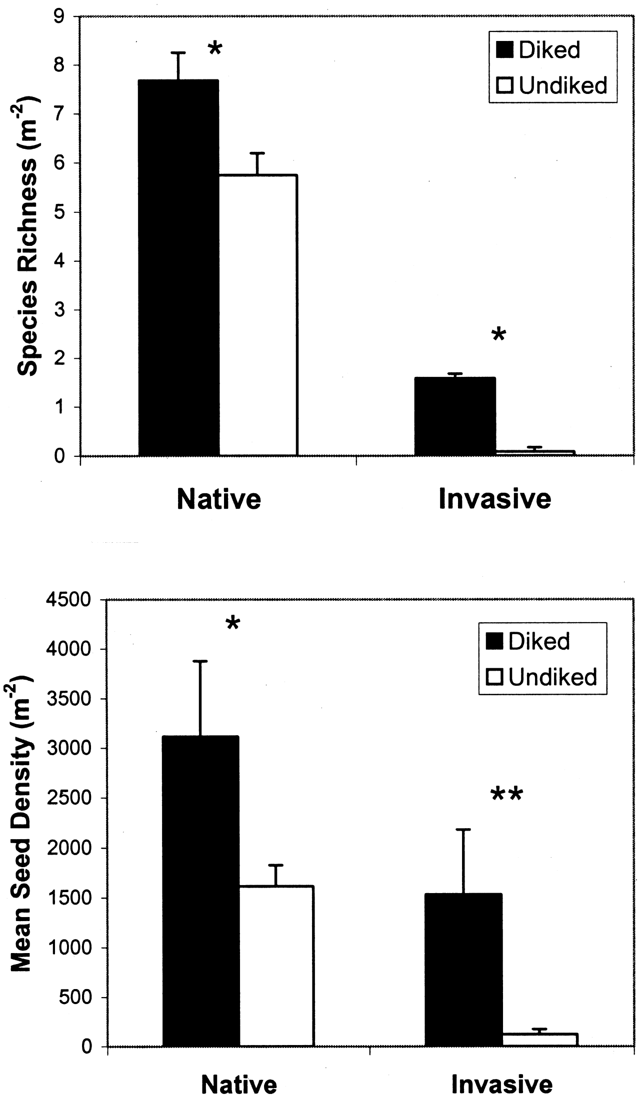

FIG. 3. (top) Mean richness of native and invasive/Typha spp. species in the seed banks of diked and undiked wetlands. (bottom) Mean seed density of native and invasive/Typha spp. species in the seed banks of diked and undiked wetlands. Data are means (+ 1 se) of 70 plots. Asterisks indicate significant (* $P < 0.05$, ** $P < 0.0001$) differences between wetland types.

Typha spp. germinated in the non-flooded treatment from undiked wetlands (Table 3). Eighty-six percent of all germinated seeds from invasive species or *Typha* spp. were from the diked wetlands.

Only four of the twelve invasive species found in the standing vegetation were also found in the seed bank. Likewise, four of the nine invasive species found in the seed bank were also found in the standing vegetation. Of the five seed bank species not found in the standing vegetation, four of these germinated in high percentages under non-flooded (drawdown) conditions in the diked wetland soils (Table 3).

DISCUSSION

Our data indicate that diked wetlands in the Great Lakes coastal zone are highly invasible by non-indigenous or aggressive plant species. The data also suggest that the seed banks of diked wetlands harbor larger numbers of seeds from invasive/aggressive species compared to seed banks in undiked wetlands.

An increase in nutrient availability is known to increase productivity of invasive species (Aerts and Berendse 1988, Huenneke *et al.* 1990, Svengsouk and Mitsch 2001). This same effect was apparent in our study. Diked wetland soils contained significantly higher levels of soil organic matter, N, P, and K and, correspondingly, a greater richness and cover of invasive species. This finding is consistent with a study by Wilson and Keddy (1986) which showed that competitive performance of plant species varies predictably with a soil organic matter gradient. Guadet and Keddy (1995) showed that standing crop plant species with high competitive abilities, such as *L. salicaria*, *P. arundinacea*, and *T.* x *glauca* occur in nutrient rich areas whereas species with low competitive abilities such as *E. erythropoda* and several *Juncus* spp. are more prominent in low–nutrient areas. Similarly in our study, the non-native invasive species, *L. salicaria*, *P. arundinacea*, and *Typha* spp. exhibited relatively high percent coverages in the nutrient-rich diked wetlands. *E. erythropoda*, *Juncus balticus* (Willd.) (Baltic rush), *Juncus brachycephalus* (Engelm.) Buch. (smallhead rush), and *Juncus brevicaudatus* (Engelm.) Fern. (narrowpanicle rush) were better represented in the sandy, nutrient poor undiked wetlands (Herrick 2003). In particular, more than half of the total cover in diked wetlands consisted of dense stands of *Typha* spp., which is known to form monotypic stands in fertile wetland systems (Hutchinson 1975, Grace and Wetzel 1981). Although plant biomass was not measured in this study, the cover values of the standing vegetation suggest that diked wetlands are more productive areas for invasive species.

Wave action characteristic of natural coastal wetlands promotes a high rate of nutrient exchange between the wetland and the lake. Because diked

TABLE 2. Occurrence of invasive species and* Typha *spp. in the seed banks of diked and undiked coastal wetlands. Seed density was estimated from wetlands where each species was detected.

Species	Diked coastal wetlands: No. of wetlands	Diked coastal wetlands: Mean seed density (no. seeds m^{-2})	Undiked coastal wetlands: No. of wetlands	Undiked coastal wetlands: Mean seed density (no. seeds m^{-2})
Lythrum salicaria (L.)	6	369	3	3
Echinochloa crus-galli (L.) Beauv.	3	26	4	8
Panicum dichotomum (L.)	2	20	0	0
Rumex spp. (L.)	2	22	1	10
Cirsium arvense (L.) Scop.	2	3	0	0
Chenopodium rubrum (L.)	1	6,939	0	0
Plantago major (L.)	1	3	0	0
Digitaria sanguinalis (L.) Scop.	0	0	1	20
Typha spp. (L.)	7	204	5	155

wetlands are isolated from the lake, they do not experience frequent water level fluctuations and undergo relatively little nutrient exchange with the lake (Mitsch 1992). Diked wetlands that receive agricultural and other urban runoff may become nutrient sinks, in which species with high competitive abilities such as *Typha* spp. and other invasive plants are prone to displace native vegetation (Svengsouk and Mitsch 2001, Wilson and Keddy 1986). Woo and Zedler (2002) found that nutrient additions alone were enough to stimulate the expansion of *T*. x *glauca* across a remnant sedge meadow.

As noted previously, differences exist between the observed vegetation types of coastal wetlands in bays of the Great Lakes (marsh/emergent species) and the coastal areas of the larger lakes (wet meadow species). This phenomenon may be due to the "sheltering effect" of the bays that provide a relative decrease in wave action on the coastal vegetation. Interestingly, diked wetlands had an even greater percent cover of marsh/emergent species, dominated by *Typha* spp, than undiked wetlands (Herrick 2003), presumably due to the increased protection provided by the dikes.

Decreased hydrological exchange between large lakes and diked wetlands likely stabilizes water levels compared with the natural fluctuations in undiked wetlands. Because *Typha* spp. is highly tolerant of deeper, standing water (Thiet 2002), it is not surprising that several diked wetlands are dominated by cattail. Non-native, invasive species *L. salicaria* and *P. arundinacea* also were found in a higher percent cover in diked wetlands. Consistent with the findings of Wilson and Keddy (1986), our results imply that species like *Typha* spp. are inhibited by natural hydrologic disturbance. Wilcox *et al.* (1993) suggested that *L. salicaria* would likely in-

TABLE 3. The percentage of samples where invasive species and* Typha *spp. seeds were germinated in the greenhouse. Results are derived from growth trays where the soil was not flooded vs trays where the soil was kept flooded.

Species	Diked: Non-Flooded	Diked: Flooded	Undiked: Non-Flooded	Undiked: Flooded
Cirsium arvense (L.) Scop.	100	0	0	0
Chenopodium rubrum (L.)	100	0	0	0
Digitaria sanguinalis (L.) Scop	0	0	100	0
Echinochloa crus-galli (L.) Beauv.	67	5	16	12
Lythrum salicaria (L.)	92	7	1	0
Panicum dichotomum (L.)	100	0	0	0
Plantago major (L.)	100	0	0	0
Rumex spp. (L.)	76	5	19	0
Typha spp. (L.)	35	29	14	22

crease its dominance in wetlands with stable water levels.

Unlike other invasive species, *P. australis* was more extensive in the undiked wetlands. Although *P. australis* has been shown to survive inundation at depths greater than 2 m. (Bjork 1967), it is more commonly found in shallower water or areas not permanently inundated compared to flood tolerant species like *Typha* spp. (Squires and van der Valk 1992). Shay and Shay (1986) found that *P. australis* was incapable of vegetative spread at water depths greater than 0.5 m. *P. australis* was observed as small patches in the diked wetlands, although outside of our sampling plots.

Undiked wetlands appear to be subjected to intense wave action, leading to relatively sandy soils, lower cover of invasive species, and the presence of *Eleocharis* spp., *Cyperus* spp., and *Juncus* spp. in the seed banks (Keddy and Reznicek 1985). Undiked wetlands also had a lower seed density (1,250 to 2,943 seeds m^{-2}) than was found in other studies of lakeshore marshes (Nicholson and Keddy 1983, Keddy and Reznicek 1982) possibly due to several years of low water levels that depleted the seed banks (Herrick 2003, Herrick *et al.*, in prep.). Our observation and that of Squires and van der Valk (1992) also suggest that *P. australis* is favored by wide-ranging water-level fluctuations and may not be as successful under the relatively stable water level conditions found in diked wetlands.

Drawdowns have been shown to be an effective wetland management tool for maintaining productivity in diked waterfowl marshes (Kadlec 1962, Harris and Marshall 1963). However, receding water levels caused by late summer drawdowns can create exposed mudflats which provide excellent substrates for germination of *L. salicaria* (Smith 1959, 1964; Rawinski and Malecki 1984). Inspection of the seed banks of diked wetlands in our study reveals that these wetlands are highly susceptible to invasion by *L. salicaria* after drawdown. This is reinforced by the fact that 92 % of *L. salicaria* seeds germinated under the saturated (drawdown) soil treatment.

A greater number of seedlings germinated under non-flooded soil conditions than in the flooded treatment, as has been shown in other marsh seed bank studies (van der Valk and Davis 1978, Smith and Kadlec 1985). In addition, because four invasive seed bank species in the diked wetland soils that were not found in the vegetation germinated well under non-flooded conditions, the use of drawdowns as a management tool for diked wetlands may increase the potential for invasive species to be expressed in the vegetation. However, seeds of *Typha* spp. were found in relatively equal distributions and densities in the seed banks of both wetland types. Smith and Kadlec (1985) found that seeds of *Typha* spp. germinated more effectively in a flooded treatment. Bedish (1967) also found that *T.* × *glauca* required flooded conditions for germination.

This investigation suggests that diked wetlands and undiked wetlands experience very different ecological dynamics, clearly reflected in the composition of emergent vegetation and seed banks. These differences have implications for the conservation, management, and restoration of Great Lakes coastal wetlands. Due to the higher numbers of seeds from invasive species in diked wetland soils and the greater percentage of germination by these species under non-flooded conditions, management strategies that are designed to mimic natural disturbances (e.g., periodic drawdowns) will likely promote germination and propagation of invasive species at our diked wetland study sites.

Attempts to restore coastal wetlands by creating additional dikes between the lake and the wetland might eliminate or reduce important ecological attributes of the coastal ecosystem. Diked wetlands may become fertile sites for invasive species, which might in turn spread into surrounding natural wetlands and perhaps other coastal habitats. Restoration of coastal wetlands by removing dikes from existing wetland complexes will re-introduce the natural hydrologic regime and could promote a more natural plant community that will be less vulnerable to invasive plant species, with the notable exception of *P. australis*.

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APPENDIX A

Study site name, location, surface area, geomorphic type, year diked, and potential nutrient sources for seven pairs of diked and undiked Green Bay, Lake Michigan and Saginaw Bay, Lake Huron coastal wetlands. Data were gathered from the Wisconsin Department of Natural Resources, Michigan Department of Natural Resources and United States Environmental Protection Agency.

Site	Name	Location	Surface area (diked/undiked)	Geomorphic Type	Year Diked	Potential Nutrient Sources
1	Ken Euers Wildlife Area	Lower Green Bay, Lake Michigan, just west of the mouth of the Fox River	8/36 ha.	open wetland complex; highly affected by seiche activity	~1960	Nutrients from Fox River and Green Bay; agricultural/ residential presures
2	Sensiba Wildlife Area	Western shore of Green Bay, Lake Michigan in northern Brown Counrty, WI	182/38 ha.	protected embayment	1960	Nutrients from Fox River and Green Bay; agricultural/ residential presures
3	Oconto Marsh	Western shore of Green Bay, Lake Michigan, north of Sensiba Wildlife Area	90/223 ha.	Delta and open embayment; low beach ridges and swales	1967	Discharge from the Oconto River; nutrients from Fox River and and Green Bay; other agricul-tural/residential pressures
4	Peshtigo Harbor	Western shore of Green Bay, Lake Michigan, approximately three miles southeast of the city of Peshtigo, WI	115/13 ha.	Delta and open embayment	NA	Peshtigo River; polluted or adverly affected by pollution from upstream discharges of sudge deposits;agricultural/ residential pressures
5	Fish Point Wildlife Area	Northeast Tuscola County in east central Lower Michigan adjacent to Saginaw Bay, Lake Huron	178/129 ha.	Sand-spit embayment and open embayment	mid 1950s	Runoff from agricultural fields, other residential pressures
6	Nayanquing Point Wildlife Area	Western shore of Saginaw Bay, Lake Huron, in Bay County Lower Michigan	37/110 ha.	Sand-spit embayment	early 1950s	Runoff from agricultural fields, other residential pressures
7	Wigwam Bay Wildlife Area	Arenac County in east central lower Michigan adjacent to Saginaw Bay, Lake Huron	367/103 ha.	Delta and open embayment	1933	Runoff from agricultural fields, other residential pressures