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Rapid Invasion of a Great Lakes Coastal Wetland by Non-native *Phragmites australis* and *Typha*

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ABSTRACT. *Great Lakes coastal wetlands are subject to water level fluctuations that promote the maintenance of coastal wetlands. Point au Sauble, a Green Bay coastal wetland, was an open water lagoon as of 1999, but became entirely vegetated as Lake Michigan experienced a prolonged period of below-average water levels. Repeat visits in 2001 and 2004 documented a dramatic change in emergent wetland vegetation communities. In 2001 non-native* Phragmites *and* Typha *were present but their cover was sparse; in 2004 half of the transect was covered by a 3 m tall, invasive* Phragmites *and non-native* Typha *community. Percent similarity between plant species present in 2001 versus 2004 was approximately 19% (Jaccard's coefficient), indicating dramatic changes in species composition that took place in only 3 years. The height of the dominant herbaceous plants and coverage by invasive species were significantly higher in 2004 than they were in 2001. However, floristic quality index and coefficient of conservatism were greater in 2004 than 2001. Cover by plant litter did not differ between 2001 and 2004. The prolonged period of below-average water levels between 1999 and early 2004 exposed unvegetated lagoon bottoms as mud flats, which provided substrate for new plant colonization and created conditions conducive to colonization by invasive taxa. PCR/RFLP analysis revealed that* Phragmites *from Point au Sauble belongs to the more aggressive, introduced genotype. It displaces native vegetation and is tolerant of a wide range of water depth. Therefore it may disrupt the natural cycles of vegetation replacement that occur under native plant communities in healthy Great Lakes coastal wetlands.*

INDEX WORDS: Phragmites australis*, Great Lakes coastal wetlands, invasion, vegetation replacement.*

INTRODUCTION

Phragmites australis (Cav.) Trin. ex Steud. (hereafter *Phragmites*) was historically infrequent in U.S. wetlands, but has expanded tremendously with the introduction of Eurasian genotypes (Blossey 2002). *Phragmites* is a cryptic invasive species (*sensu* Richardson *et al*. 2000) in the U.S., with both native and non-native genotypes that differ in their aggressiveness (Galatowitsch *et al*. 1999, Saltonstall 2002). *Phragmites* occurs throughout the entire U. S. and southern Canada in freshwater and brackish to saline wetlands (Chambers *et al.* 1999), prevailing especially in tidal wetlands along the Atlantic coast. However, recent expansion of *Phragmites* occurrence in the Great Lakes region has been observed (McNabb and Batterson 1991, Lynch and Saltonstall 2002, Wilcox *et al*. 2003). *Phragmites* is considered an indicator of wetland disturbance because it forms monospecific stands that displace native species, reducing plant biodiversity and the habitat available for associated fauna (Marks *et al*. 1994, Chambers *et al*. 1999, Meyerson *et al.* 2000). Variations in climatic conditions (Minchinton 2002), alteration of the hydrologic regime (Bart and Hartman 2000, 2003), changes in land use (Lynch and Saltonstall 2002), and nutrient increase (Bertness *et al*. 2002, Minchinton and Bertness 2003) may be responsible for *Phragmites* expansion. Saltonstall's (2002) genetic study suggested that the invasive haplotype M, introduced from Eurasia, is responsible for the observed expansion. However, in areas where native and non-native populations are sympatric, care should be taken to identify the origins of populations subject to management. This is particularly important in the Midwest, where native populations still thrive at many sites (Salton-

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stall 2003). For example, Lynch and Saltonstall (2002) documented the expansion of the native *Phragmites* genotype at a Lake Superior wetland.

Coastal wetlands along Lake Michigan's Green Bay are known to be dynamic, experiencing vast changes in the extent of emergent vegetation as water levels fluctuate over decadal cycles (Epstein *et al.* 2002). Emergent plants germinate on lakebed exposed during low-water years, persist during average water level conditions, and decline after a series of high-water years, the marshes reverting to open water (Harris *et al.* 1977, Bosley 1978). *Typha* is commonly mentioned as a key genus involved in these vegetation cycles, but *Phragmites* is not.

Data about plant species in wetlands of Green Bay on Lake Michigan were collected by the Great Lakes Environmental Indicators project (GLEI) during mid-June 2001, when the water level of Lake Michigan was 54 cm below average (USCOE 2006). During a repeat visit to wetlands of the Green Bay area three years later, large stands of *Phragmites* were observed in the Point au Sauble lagoon where little or no *Phragmites* had occurred in 2001. During the interim between the two sample dates, Lake Michigan experienced a prolonged period of below-average water levels.

The goal of this paper is to document the rapid change in wetland vegetation of a Green Bay lagoon over a 3-year period associated with the rapid invasion of *Phragmites*. Specific objectives were to compare vegetation structure and community composition before and after *Phragmites* invasion, evaluate edaphic conditions within areas that were and were not colonized by *Phragmites*, and determine if the expanding areas of *Phragmites* are of the invasive genotype.

METHODS

Study Area

The 81 ha Point Au Sauble lagoon is located on the eastern shore of Green Bay, 10 km northeast of the city of Green Bay in Brown County, Wisconsin. It is currently owned by the University of Wisconsin-Green Bay and has been preserved in a natural state by The Nature Conservancy and duck hunting groups for many decades (UWGB Cofrin Center for Biodiversity 2004). Point au Sauble is covered by a variety of plant communities such as floodplain forest, shrub-carr, sedge meadow, emergent aquatic, and Great Lakes beach, but the area sampled was described by earlier accounts as an open-water lagoon (Epstein *et al*. 2002). Although wetlands are common along the western shore of Green Bay, Point au Sauble is one of only a few coastal wetlands on the eastern shore of Green Bay.

Abiotic Data Collection

The soils at each plot were examined to a depth of 30 cm below the litter layer using a soil probe, and assigned to one of the following broad categories: organic, sand, silt, or clay. "Organic" soils were those composed of organic soil material (peat or muck) in a histic epipedon (Soil Survey Staff 1999); undecomposed plant litter overlying the soil surface was excluded when making this determination. Only the surface 30 cm was considered. We did not attempt to discern if soils in the organic category were true histosols. The texture of mineral soils (i.e., sand, silt, clay) was determined by feel using standard field methods (Soil Survey Staff 1951). The hand texturing was done by co-author Johnston, who is a professional soil scientist certified by the American Society of Agronomy and experienced at wetland soil characterization using both field and laboratory methods. Soil texture by plot in 2004 varied from silty to organic soils (Table 1).

Lake level data recorded every 6 minutes at Green Bay, Wisconsin (Station ID 9087079) were obtained from the National Oceanic and Atmospheric Administration (NOAA 2006), and were averaged over the time period from 0800 hours to 1800 hours local standard time to determine average water levels on the days sampled. Monthly average and monthly minimum lake levels, based on data collected from 1918-2005, were obtained from the U.S. Army Corps of Engineers (USCOE 2006).

Vegetation Sampling

The Point au Sauble lagoon was initially sampled on 19 Jun 01 as part of GLEI, a large, multi-investigator project designed to identify biotic indicators of human disturbance (Danz *et al*. 2005). The GLEI vegetation sampling protocol (Bourdaghs *et al*. 2006, Johnston *et al*. 2007 this issue) was used in both 2001 and 2004, when a repeat visit to the lagoon was made on 7 Jul 04. A north-south trending transect was placed across the lagoon at Point au Sauble, and 11 sampling locations (plots) were established at approximately 20 m intervals along the transect (Fig. 1). At each sampling location, a 1 m^2 plot was established and its geographic coordinates

TABLE 1. Point au Sauble wetland conditions by plot.

Variable/ Plot number	Water depth (cm) 2001	2004	Substrate type In 2004
Plot 1 (at the North end of the peninsula)	10	26	Silt
Plot 2	14	26	Silt
Plot 3	15	27	Silt
Plot 4	9	27	Silt
Plot 5	8	20	Silt
Plot 6	4	20	Organic
Plot 7	11	18	Organic
Plot 8	8	37	Organic
Plot 9	9	33	Organic
Plot 10	0	5	Sand
Plot 11 (at the South end of the peninsula)	0	0	Organic

recorded using a hand held Garmin GPSMAP 76 unit (Garmin International Inc., Olathe, KS). All vascular plant species observed within the plot were identified to the species or genus level; there were no unidentified plants present. All GLEI project field crews met every summer and conducted field work together to ensure that species identification and the visual cover estimates were consistent between field crews. The non-native cattail *Typha angustifolia* and its hybrid *Typha* × *glauca* could not be reliably distinguished because of the paucity of fruiting heads, and were combined into a single class called "invasive *Typha*." *Sagittaria latifolia* Willd. was identified as *Sagittaria* sp. by the GLEI field crew in 2001, but because we found *Sagittaria latifolia* in 2004 at the same plots, we felt confident to call *Sagittaria latifolia* the one identified in 2001. Cover class was estimated visually for each taxon using modified Braun-Blanquet cover class ranges: < 1%, 1 to < 5%, 5 to < 25%, 25 to < 50%, 50 to < 75%, and 75 to 100% (ASTM 1997). Summed individual taxa percent cover in a quadrat could exceed 100% because canopies of different species overlap one another. Cover estimates were also recorded for herbaceous litter, open water (defined as water open to the sun in patches 10 cm × 10 cm or greater), and standing water (defined as any water above the soil surface, including water below thatch and green vegetation). Water depth and canopy height were recorded at each sampling location. The height of the dominant herbaceous plant was determined as the average height of the dominant herbaceous plant per plot, measured to

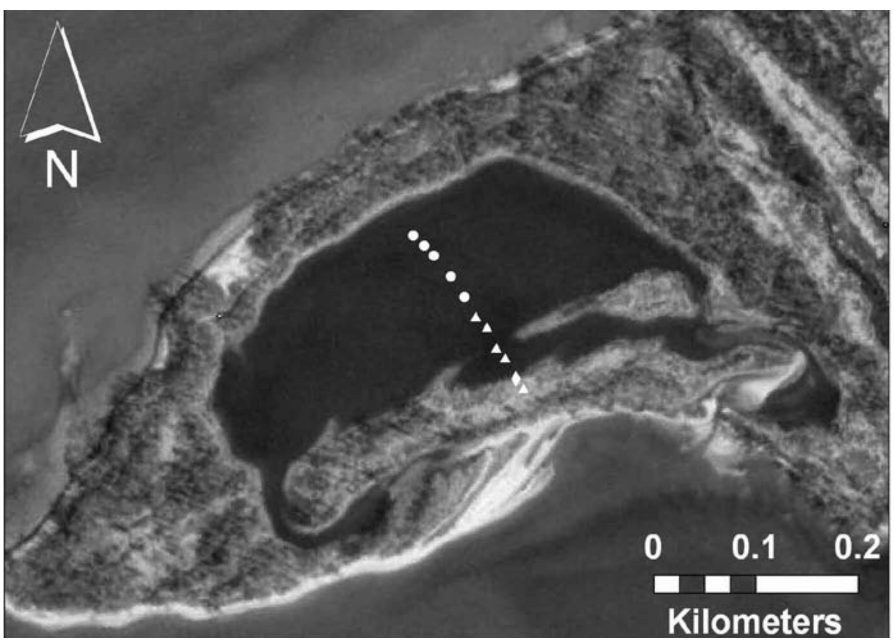

FIG. 1. Aerial photo of the Point au Sauble peninsula (Brown County, Wisconsin) taken on 4 Oct 99. Circles indicate silty substrates, triangles and diamond indicate organic and sand substrates, respectively. Image courtesy of the U.S. Geological Survey.

the nearest 5 cm. If a plant species could not be identified in the field, it was collected, pressed, and identified in the lab. Plant nomenclature conventions in this study follow the Interagency Taxonomic Information System (ITIS, http://www.itis.usda.gov), a national standardized plant nomenclature source. Prior to data analyses, cover classes were converted to the midpoint percent cover of each class (e.g., 37.5% for the 50 to < 75% class). The average of midpoint percent cover was computed for each plant species based on all plots in the transect. Geographic coordinates of the initial 11 sampling locations were uploaded into a Garmin GPS unit, and used to return to the same locations on 7 Jul 04.

Genetic Analysis of *Phragmites*

DNA was extracted from dried leaf tissues of one ramet (located in the center of the stand) of the *Phragmites* stand using Extract-N-Amp (Sigma-Aldrich, St. Louis, MO) according to manufacturer's directions. DNA from one ramet was judged sufficient because all the *Phragmites* plants appeared to belong to the same clone, and shared morphological characteristics typical of the non-native genotype (Blossey 2002). Generally, in polyclonal reed stands, different clones are morphologically distinguishable (Koppitz 1999). Two non-coding chloroplast regions were amplified using the polymerase chain reaction (PCR). Amplification primer pairs used were *trn* and *rbc* (Saltonstall 2003). Two 20 µL PCR reactions were made from each sample, generally according to the manufacturer's directions. Instead of 4 µL of template, as recommended by the manufacturer, it was determined that better results were obtained using 1 µL of template. The difference was made up by adding 3 µL of a 1:1 mixture of the Extract-N-Amp extraction and dilution reagents. Either 50 ng each of forward and reverse *trn* primers or 12.5 ng each of *rbc* primers were used.

The two PCR products were subjected to restriction enzyme digests to detect restriction fragments length polymorphisms (RFLP). Each PCR product was divided into two 10 µL portions; one was subjected to restriction digest and the other held as a control. From each plant, the *rbc* PCR product was digested using the restriction enzyme *Hha*I, which cuts only the non-native genotype, and the *trn* PCR product was digested with *Rsa*I, which cuts only the native genotype (Saltonstall 2003). Restriction fragments were electrophoresed in 2% TAE gel and visualized with ethidium bromide using a ChemiDoc XRS Imaging Station (BioRAD, Hercules, CA).

Data Analysis

Species composition similarity was calculated for 2001 and 2004 using Jaccard's similarity index (Greig-Smith 1964). Mean coefficient of conservatism (a numerical score that ranges from 0 to 10, assigned to each plant species in a local flora that reflects the likelihood that a species is found in natural habitats) and floristic quality index (FQI) values were also compared in 2001 versus 2004. FQI is computed by multiplying the mean coefficient of conservatism of the species in a community ($\bar{C}$) by the square root of the total number of native species: FQI = $\bar{C} * \sqrt{N}$, C-values used were those assigned for the state of Wisconsin (Bernthal 2003).

Species diversity and evenness were compared in 2001 versus 2004. We used Shannon-Weiner species diversity index:

$$H' = -\sum_{i-1}^{S} p_i \ln p_i$$

and Pielou's J index for evenness: **H´ / lnS**, where: S is species richness and p_i is the relative abundance of the ith species (Magurran 1988).

Water depth and height of the dominant herbaceous plant in 2001 versus 2004 were compared using *t*-tests. Kruskal-Wallis nonparametric tests were used to compare the coverage by open water (defined as water open to the sun in patches 10 cm × 10 cm or greater), coverage by herbaceous litter, coverage by invasive species, and mean *Phragmites* cover per plot in 2001 versus 2004 (none of the data sets were normally distributed). A one-way ANOVA followed by Tukey's HSD comparison test was used to compare 2004 *Phragmites* cover on three different types of soil (*i.e.*, silt, organic, and sand). Simple regression was used to test if there was an effect of 2004 water depth on *Phragmites* cover. All tests were conducted at an alpha level of 0.05 using the SAS ® 9.1 (SAS Institute 2001).

RESULTS

Digital orthophotography acquired on 10 Apr 99, when the lake level was 176.3 m (18 cm below average), showed an open water lagoon at Point au Sauble (Fig. 1). The lake level dropped precipitously later in 1999, and was 27 to 54 cm below average throughout Jan 00 to Apr 04 (Fig. 2). The lake level during the first field data collection on 16

Jun 01 was 176.1 m, ~0.5 m below average. Lake level had rebounded to 176.5 m by the second field data collection date on 9 Jul 04 (Table 2).

During initial vegetation sampling on 19 Jun 01, all 11 sample plots contained emergent wetland vegetation. By 7 Jul 04 the water levels had rebounded to 176.5 m, mean water depth per plot was significantly greater, and mean coverage of open water patches was lower. Despite the deeper water, all sample plots remained vegetated (Table 2).

As of 2001, *Sagittaria latifolia* Willd. (arrowhead) was the predominant plant (Table 3). *Sagittaria* occurred on both silty and sandy substrates. Two annual species, *Bidens cernua* L. (nodding beggartick) and *Impatiens capensis* Meerb. (jewelweed) were also abundant. *Bidens* occurred towards the north edge of the transect, on silty substrates, with standing water as deep as 9 cm, while *Impatiens* grew mainly on sandy substrates. *Schoenoplectus tabernaemontani* (Torr.) M.T. Strong (softstem bulrush) was the fourth most abundant species with an average cover of 10.2%. Invasive *Typha* was present but sparse (2.7% cover). It occurred in plots with sandy substrate, without standing water. A few stems of *Phragmites* (cover class of 1 to 5%) were present in only a single plot.

In 2004, the wetland was dominated by invasive *Typha* and *Phragmites* (Table 2). *Phragmites* was present in four plots with a cover of 100%. These four plots were located towards the north edge of the transect and the substrate was silty. *Phragmites* was also present with lower cover in two other plots with silty (3% cover) and sandy substrate (37.5% cover). Invasive *Typha* was present in six plots, with a cover ranging from 60 to 100%. Invasive *Typha* did not occur in the plots where *Phragmites* occurred except for the plot where *Phragmites* had low cover of 3%, and *Typha* generally grew on organic soil substrates (five out of the six plots were covered by organic substrate). *Ricciocarpus natans*, a free-floating liverwort, covered the water surface beneath the *Phragmites*, although it had not been observed in 2001. The species with the second greatest plant cover in 2001, *Bidens cernua*, was completely absent in 2004. Several other species

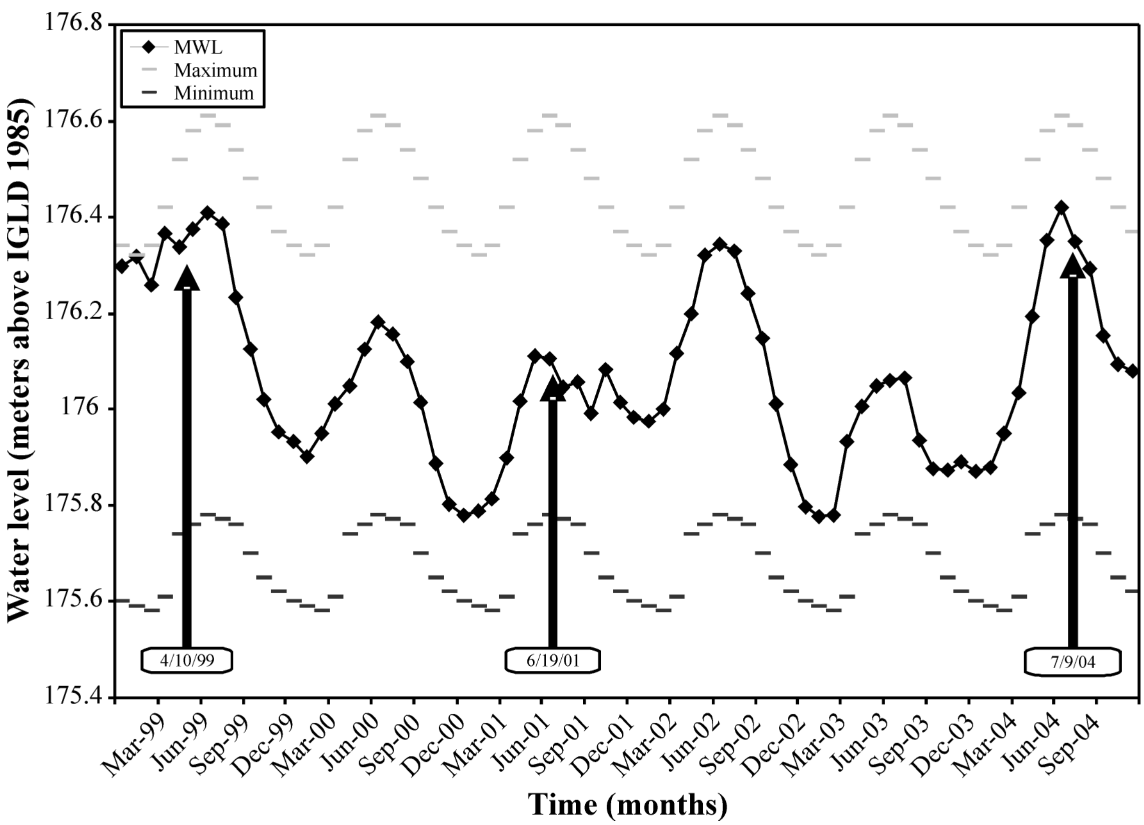

FIG. 2. Monthly mean water levels (MWL) at Green Bay, Lake Michigan, WI from 1999 to 2004 (USCOE 2006). Arrows denote dates of aerial photo acquisition and field sampling.

*TABLE 2. Comparison of Point au Sauble wetland conditions between 2001 and 2004. (** significant at P ≤ 0.05)*

Variable	Value in 2001	Value in 2004	P-value	Statistics	Degrees of freedom
Species richness	15	29	—	—	—
Mean water depth (cm)	8	22	0.0003**	$t = 5.5$	1, 10
Mean canopy height (cm)	112	234	0.0002*	$t = 5.7$	1, 10
Mean coverage by herbaceous litter (%)	79	81	0.9611	$\chi^2 < 0.1$	1
Mean coverage by open water (%)	16	8	0.0413*	$\chi^2 = 4.2$	1
Mean coverage by invasive species per plot (%)	3	84	<.0001*	$\chi^2 = 16.4$	1
Mean *Phragmites* cover per plot (%)	0.3	35.5	0.0167	$\chi^2 = 5.7$	1
Mean coefficient of conservatism	3	4	—	—	—
Floristic Quality Index	9	17	—	—	—
Shannon-Wiener	1.8	2.1	—	—	—
Evenness	0.65	0.64	—	—	—
Mean annual lake levels (m above IGLD 1985)	175.9	176.1	—	—	—
Lake level on the sampling days (m above IGLD 1985)	176.1	176.5	—	—	—

that were abundant in 2001 had greatly reduced cover in 2004: *Sagittaria latifolia*, *Impatiens capensis,* and *Schoenoplectus tabernaemontani*. PCR/RFLP genetic analysis revealed that *Phragmites* sampled from Point au Sauble belongs to the introduced genotype (Fig. 3).

Eighteen of the species found in 2004 were not observed in 2001 (Table 3). Species richness almost doubled between 2001 and 2004 (Table 2). Shannon-Wiener diversity index was higher in 2004 than 2001 (2.1 compared to 1.8), while evenness was 0.64 in 2004 compared to 0.65 in 2001. A total of seven species out of 33 occurred in the wetland during both 2001 and 2004, resulting in a Jaccard similarity index of only 18.9%. Given the rapid and significant increase in coverage by invasive species (Table 2), we expected a decline in species richness and therefore a decline in the FQI of the wetland. Contrary to expectations, both FQI and $\bar{C}$ were greater in 2004 than 2001.

Average canopy height doubled over the three year time period (Table 2). A 3 m tall *Phragmites* stand dominated the community in 2004, followed by two other invasive species, *Typha* × *glauca* and *Typha angustifolia* (all have tall stature).

Mean 2004 *Phragmites* cover was significantly less in organic soils than in the silty bottom soils of the lagoon ($n = 11$, $P < 0.01$). The plot water depth did not significantly affect *Phragmites* cover in 2004 ($R^2 = 0.05$, $P = 0.52$). Cover by herbaceous plant litter was not significantly different between 2001 and 2004. In 2004, species richness was significantly lower in plots where *Phragmites* had a 100% cover as opposed to the plots where *Phragmites* had a low cover (3% and 37.5% respectively) or was absent (mean species richness of 1 as opposed to 6; $\chi^2 = 21.8$, $P < 0.001$). In 2001, we did not observe a difference in species richness between plots with and without *Phragmites*, as *Phragmites* was present in only one plot with a cover of 3% in 2001.

DISCUSSION

The conversion of the Point au Sauble wetland from an open-water lagoon in 1999 to an invasive-dominated lagoon in 2004 was surprisingly rapid. Changes in species composition and increases in vegetation height were dramatic over the three year time period between initial and repeated GLEI sampling in 2001 and 2004.

Changes in plant communities of Great Lakes wetlands are driven by fluctuations in water levels. Daily, seasonal, and annual lake-level changes are important, but decadal changes play the major role in shaping Great Lakes wetland plant communities (Wilcox 2004). Wetland plant communities are not only adapted to these fluctuations, but this natural cycle is beneficial to plant biodiversity and essential to maintaining wetland condition (Keddy and Reznicek 1986).

As water level increases, emergent communities are reduced in area or eliminated and the open-water complex develops (Wilcox 2004). Deeper water is often associated with a decrease in emergent cover, as plants intolerant of flooding are killed by insufficient root aeration. For example, Gathman *et al.* (2005) documented the quick re-

TABLE 3. Species present at Point au Sauble wetland in 2001 and 2004 and their C-values (Bernthal 2003).

Scientific name	C-value	Cover in 2001	Cover in 2004
Bidens cernua L.	4	23.9	—
Calamagrostis canadensis (Michx.) Beauv.	5	—	1.4
Carex bebbii Olney ex Fern.	4	—	< 0.1
Carex hystericina Muhl. ex Willd.	3	—	< 0.1
Carex lacustris Willd.	6	—	< 0.1
Cirsium arvense (L.) Scop.	*	—	0.3
Calystegia sepium ssp. *sepium* (L.) R. Br	2	—	< 0.1
Cynoglossum officinale L.	*	—	3.4
Eleocharis erythropoda Steud.	3	0.2	< 0.1
Epilobium ciliatum Raf.	3	0.2	—
Eupatorium perfoliatum L.	6	< 0.1	< 0.1
Impatiens capensis Meerb.	2	13.7	1.4
Juncus balticus Willd.	5	—	< 0.1
Leersia oryzoides (L.) Sw.	3	0.3	0.3
Lemna minor L.	4	4.8	—
Lycopus americanus Muhl. ex W. Bart	4	—	< 0.1
Lysimachia thyrsiflora L.	7	—	4.8
Lythrum salicaria L.	*	< 0.1	—
Phalaris arundinacea L.	*	0.3	1.4
Phragmites australis (Cav.) Trin. ex Steud.	*	0.3	35.5
Ranunculus sp.		1.6	—
Ricciocarpus natans L.		—	16.0
Sagittaria latifolia Willd.	3	24.5	4.6
Schoenoplectus fluviatilis (Torr.) M.T. Strong	6	—	1.4
Schoenoplectus tabernaemontani (K.C. Gmel.) Palla	4	10.2	1.7
Solanum dulcamara L.	*	—	< 0.1
Sparganium eurycarpum Engelm. ex Gray	5	—	< 0.1
Taraxacum officinale G.H. Weber ex Wiggers	*	—	< 0.1
Typha latifolia L.	1	0.8	—
Invasive *Typha*	*	2.7	45.7
Urtica dioica L.	1	—	3.4
Verbena hastata L.	3	—	1.4
Veronica anagallis-aquatica L.	4	—	< 0.1

* indicates an introduced species that was not assigned a C-value; species identified at genus level were not assigned any C-values.

sponse of wetland plant species to a three-year (1996-1998) water level change in coastal Lake Huron wetlands. In their study, stem density, per-plot species richness, and Shannon diversity in the wet meadow and transition zones decreased as water depth increased from 1996 to 1997. An increase in these same measures was noted in 1998 with the decrease in water level (Gathman *et al.* 2005).

Periods of extremely low water expose unvegetated lagoon bottoms as mud flats, providing a substrate for new plant colonization. Annuals and other opportunistic species such as *Schoenoplectus tabernamontani* rapidly increase in abundance, and are typically replaced by cattail as the plant community matures (Harris *et al.* 1977, Bosley 1978). From 1997 to 2001, the water level dropped 1.25 m in Lake Michigan, the largest drop since data records were kept (NOAA 2003).

Some of the observed species changes at Point au Sauble were predictable outcomes of succession as plants colonized the exposed lagoon bottom. The annual species *Bidens cernua* and *Impatiens capensis* do not grow vigorously and are usually found on exposed sandy or muddy shores (Chadde 1998). Their loss was expected as the site evolved from a newly established community dominated by annuals to a more mature community dominated by

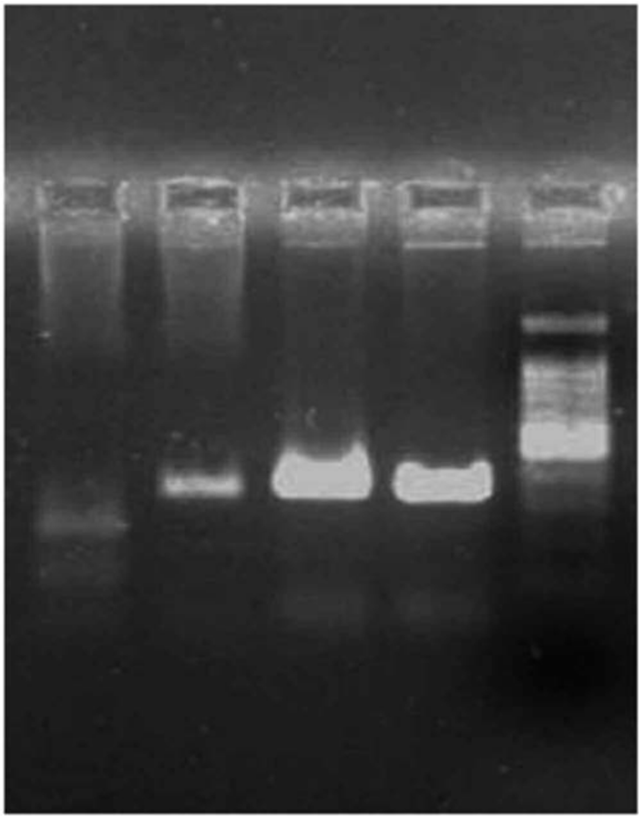

FIG. 3. PCR/RFLP analysis of non-native **Phragmites** *population from Point au Sauble wetland. Lanes 1 and 2 contain the* **rbc** *primer with the HhaI digested DNA and undigested DNA, respectively. Lanes 3 and 4 contain the* **trn** *primer with the RsaI digested DNA and undigested DNA, respectively. Lane 5 contains a 100 bp ladder (Promega, Madison, WI). The* **rbc** *product digested and the* **trn** *product did not, indicating the source DNA was from the invasive genotype.*

perennials. The decreased cover of *Schoenoplectus tabernaemontani* and *Sagittaria latifolia* was presumably due to shading by taller successional plants.

Prior authors have identified the dynamic nature of Point au Sauble and other Green Bay wetlands in response to such water level fluctuations (Epstein *et al.* 2002, UWGB 2004). The difference between our observed changes at Point au Sauble and previous reports, which point out the dominance of *Typha* spp. as the water level increases (UWGB 2004), is the dominance of *Phragmites*. The fact that *Phragmites* expanded so rapidly in only 3 years is a cause of concern. Moreover, *Phragmites* from Point au Sauble was found to belong to the more aggressive, introduced genotype. Therefore it may disrupt the natural cycles of vegetation replacement that occur under native plant communities in healthy coastal wetlands.

Although there was an increase in species richness between 2001 and 2004, we believe that this is transient based on our data collected at this site. We expect to see a decrease in species richness in plots with the continued expansion and densification of *Phragmites*, similar to what we have seen at the four plots where *Phragmites* had a 100% cover.

Phragmites is an invasive taxon (*sensu* Richardson *et al.* 2000) that is a clonal dominant (*sensu* Boutin and Keddy 1993). Under the predictions of the hump-backed model (Grime 2000, Moore and Keddy 1989), the large standing crop of this clonal dominant species would be expected to reduce species richness because the greatest species richness is usually reached at moderate standing crops. *Phragmites* forms monospecific stands with a consequent reduction in species diversity (Marks *et al.* 1994). Such a reduction did occur in the four plots where *Phragmites* had a 100% cover in 2004, species richness being significantly lower in these four plots than in the plots where *Phragmites* was not present or had a low cover.

"Mean coverage by invasive species" was an indicator that suggested a degradation of the lagoon. Species richness and other metrics commonly used as wetland indicators (i.e., FQI and mean coefficient of conservatism) did not point out a degradation of this wetland. However, greater values of all these three metrics are expected as the site evolved from a newly established community dominated by annuals to a more mature community dominated by perennials. The greater height of the dominant herbaceous plants in 2004 can be explained by the dominance of *Phragmites* or *Typha* in almost all of the plots. These are invasive species in the U.S. and grow taller than native species (Galatowitsch *et al.* 1999). Plant size larger than that of associate species is a key trait that allows plant species to dominate, such that tall stature is a characteristic of competitive species (Grime 1973, Grime 2000). Monoculture is achieved by larger species through their ability to compete for light (tall shoots), for water and nutrients (high below ground biomass), and through the presence of a high density of herbaceous litter throughout the year (Grime 2000). Both *Typha* and *Phragmites* form mono-dominant stands, and both are well adapted to sustained inundation (Haslam 1971, Shay and Shay 1986). These features promote *Phragmites* as a good competitor in the stands where it occurs (Haslam 1971).

While predicting invasion of a community is difficult because there is no unique theory to successfully explain plant invasions (Williamson 1999, Grime 2000, Zedler and Kercher 2004), fluctuation of resource availability may be one of the key factors that control invasibility (Davis *et al.* 2000). New substrate availability makes an area susceptible to invasion (Grime 2000) and is one of the factors that make riparian areas more prone to invasion (Tickner *et al.* 2001).

Establishment of *Phragmites* typically occurs on bare, unvegetated moist soils after water levels recede (Chambers *et al.* 1999, Galatowitsch *et al.* 1999, Ailstock *et al.* 2001, Pengra *et al.* 2007). This species typically invades starting from the upland fringe of the wetland via stolons and rhizomes. Alternatively, it may start on a high point within the wetland, such as a dike remnant, and then spread into the wetland plain. Unlike rhizomes, stolons are located aboveground and usually elongate more rapidly than rhizomes. *Phragmites* propagation by seeds is limited (Haslam 1970, 1971). Vegetative propagation is efficient through rhizome portions transported by water, man, or stolons from nearby colonies (Haslam 1971). We observed long *Phragmites* stolons on beach areas north of the lagoon, and believe that stolon growth was the primary mechanism of *Phragmites* expansion within the lagoon.

The rapid invasion of Point au Sauble by *Phragmites* cannot and should not be considered representative of all Great Lakes coastal wetlands. Although the extremely low water levels between 1999 and early 2004 occurred throughout lakes Michigan and Huron, *Phragmites* stands observed elsewhere in Green Bay by co-author Tulbure as a 2004 field assistant to Pengra (2005) were much less extensive than those found at Point au Sable. In that study, Pengra and co-workers visited 82 Green Bay wetland locations with emergent vegetation and found that 34 of them had *Phragmites* present in 2004. We believe that this could be because the Au Sauble wetland is a lagoon protected in the interior of a hook-shaped peninsula, whereas other sites are sandy peninsulas and associated embayments that are more open to wave action (e.g., Little Tail Point, and Long Tail Point, Wisconsin DNR 2006). Also, other sites had organic substrates (e.g., Sensiba Wildlife Area) rather than silty substrate as Point au Sauble, which might have been less prone to *Phragmites* invasion. We believe that the exposure of unvegetated silty mineral soils at Point au Sauble, which suggests the presence of a depositional environment, created conditions conducive to *Phragmites* colonization and may be atypical for the region. Based on these results, we predict that sites with exposed mineral soils are most susceptible to *Phragmites* invasion, and future studies should further test this hypothesis.

The GLEI project was designed to be conducted as single-sampling event, not an analysis of change over time. However, these results illustrate the benefits of the sampling and documentation protocol established by GLEI. Without the careful records kept by the GLEI sampling crew in 2001, documentation of this rapid *Phragmites* expansion would not have been possible.

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