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ORIGINAL PAPER

Environmental Conditions Promoting Non-native *Phragmites australis* Expansion in Great Lakes Coastal Wetlands

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Abstract The invasion and expansion of the non-native *Phragmites australis* in Great Lakes coastal wetlands is of increasing concern, but quantitative studies of the extent, rate, and causes of invasion have been lacking. Here we revisited 307 plots in 14 wetlands along the Great Lakes coast in 2005 that had previously been sampled for vegetation in 2001–2003. During the 2–4 years between sample events, *Phragmites* occurred in 101 plots. Genetic analysis revealed that none of the *Phragmites* samples collected at the 14 wetlands belonged to the native genotype. Decreases in water depth and bare soil area were associated with the greatest increases in *Phragmites* cover. *Phragmites* invasion was greater on Lakes Michigan, Huron, and Erie than it was on Lake Ontario, and occurred predominantly on sandy substrates. Soil water concentrations of NO_3-N, NH_3-N, and soluble reactive P did not differ significantly between plots with and without *Phragmites*. Monitoring coastal wetlands where water level has dropped and controlling *Phragmites* at early stages of invasion are essential for maintaining healthy Great Lakes coastal wetlands of high species diversity and wildlife habitat. This becomes important as water levels in the Great Lakes have reached extreme lows and are expected to decline with future climate change.

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Introduction

Phragmites australis (Cav.) Trin. ex Steud. (hereafter *Phragmites*) has expanded tremendously in North America with the introduction of the M Eurasian genotype, and has become one of the most invasive plants in wetlands along the Atlantic coast (Ailstock et al. 2001; Minchinton 2002; Bart et al. 2006). The species has become a problem more recently along the Great Lakes coast, where rapid *Phragmites* expansion has been noted on Lake Erie (Wilcox et al. 2003; Ghioca-Robrecht et al. 2008) and Green Bay (Pengra et al. 2007; Tulbure et al. 2007). Lacking the salinity gradients that limit the seaward expansion of *Phragmites* on ocean coasts (Meyerson et al. 2000; Bart and Hartman 2003), wetlands of the Great Lakes coast may be particularly susceptible to future invasion by *Phragmites*. Research is needed to understand the mechanisms and factors that make coastal wetlands in this region susceptible to *Phragmites* invasion.

Great Lakes coastal wetlands are dynamic, with average annual water levels changing by a meter or more over decadal time scales (Wilcox et al. 2007). These water level fluctuations are a major factor controlling the composition of native vegetation in Great Lakes coastal wetlands, producing and maintaining plant species diversity by cycles of drawdown and flooding (Keddy and Reznicek 1986; Hudon 1997; Keddy 2000; Gathman et al. 2005). When non-native aggressive taxa such as *Phragmites* germinate, proliferate and form monotypic stands, the germination of native species dependent on fluctuating water levels is obstructed (Haslam 1972; Thiet 2002; Herrick and Wolf

2005). This reduces plant species diversity and wetland functionality (Chambers et al. 1999; Galatowitsch et al. 1999).

Average annual lake levels on Lakes Michigan and Huron were >0.5 m below the long-term average between 2000 and 2008 (http://www.glerl.noaa.gov/data/now/wlevels/levels.html), which may have contributed to the recent expansion of *Phragmites* on their coasts. Prolonged low Great Lakes levels exposed unvegetated lake bottom sediments, providing a substrate for colonization by new plants, such as invasive *Phragmites* (Pengra et al. 2007; Tulbure et al. 2007). Repeat visits to a Green Bay coastal wetland in 2001 and 2004 showed a 100-fold increase in *Phragmites* cover (Tulbure et al. 2007). Unlike the lake level of Lake Ontario, which has been partially regulated since 1958, lakes Erie, Michigan, and Huron are not regulated and their lake levels therefore respond more to climatic and other large scale changes (Sellinger et al. 2008). Wetland values such as diversity, primary productivity, and habitat for wildlife and waterfowl will be affected if an increase in frequency and duration of low water levels results from future climate change (Mortsch 1998).

A number of factors have been shown to facilitate *Phragmites* invasion, including land use changes in a wetland's watershed (King et al. 2007), increases in nitrate and the concentration of other nutrients (Marks et al. 1994; Bertness et al. 2002; Minchinton and Bertness 2003), the presence of exposed mineral soil (Tulbure et al. 2007), and alterations of the hydrologic regime by roads, dikes, and ditches (McNabb and Batterson 1991; Bart and Hartman 2000, 2003;Herrick and Wolf 2005; Maheu-Giroux and de Blois 2007; Johnston et al. 2008). The use of dikes is a prevalent feature in coastal wetlands on the southwestern shore of Lake Erie (Kroll and Gottgens 1997; Gottgens et al. 1998).

Once it invades, *Phragmites* expands rapidly via rhizomes and seeds (Haslam 1973; Bart and Hartman 2003) and becomes monodominant in a wetland, displacing the native flora (Marks et al. 1994; Chambers et al. 1999; Meyerson et al. 2000). *Phragmites* expands vegetatively by horizontal rhizome growth at a rate of 1–2 m/yr (Haslam 1972), grows taller and has higher biomass than other marsh species (Meyerson et al. 2000), outcompeting co-occurring plant species by shading and litter mat formation (Haslam 1973). The native subspecies *Phragmites australis* subsp. *americanus* Saltonstall, P.M. Peterson & Soreng, which is endemic to the Great Lakes, is considered to be less aggressive than the non-native M Eurasian genotype (Saltonstall et al. 2004).

Despite anecdotal accounts of recent *Phragmites* expansion on the Great Lakes, quantitative studies of the rate and extent of *Phragmites* invasion are lacking. The EPA-funded Great Lakes Environmental Indicators (GLEI) project collected data on plant species of Great Lakes coastal wetlands during 2001–2003 (Johnston et al. 2007a). This provided baseline vegetation data and a unique opportunity to assess *Phragmites* shifts in time. In the present study, we returned in 2005 to 14 Great Lakes coastal wetlands in the Eastern Broadleaf Forest ecoprovince (Keys et al. 1995) that had some *Phragmites* present when first sampled, and quantified short-term changes in the extent of *Phragmites* cover.

The overarching aim of this study was to determine what characteristics caused coastal wetlands in the southern Great Lakes region to be susceptible to *Phragmites* invasion. Specific objectives were to: (1) determine the nativity of *Phragmites,* (2) determine whether *Phragmites* expanded since first sampled at the 14 revisited wetlands; (3) identify natural and anthropogenic factors that influenced invasive *Phragmites* success at these wetlands; (4) assess whether short-term change in *Phragmites* cover differed on different soil types, and whether nutrient concentrations were different in *Phragmites* versus non-*Phragmites* stands, and (5) examine whether the increase in *Phragmites* cover was greater on Great Lakes wetlands in which there was a drop in water levels between 1999 and 2001 (i.e., Lakes Michigan, Huron, Erie) than on the lake where there was an increase in water levels between 1999 and 2001 (i.e., Lake Ontario).

Methods

Site Selection and Vegetation Sampling

The GLEI project sampled 35 Great Lakes coastal wetlands within the Eastern Broadleaf Forest (EBF) ecoprovince, which encompasses Lake Ontario, Lake Erie, and southern Lakes Huron and Michigan (GLEI sites listed in Johnston et al. 2007a). Of these wetlands, we revisited 14 of the 16 that contained *Phragmites* in 2001–2003 when they were first sampled as part of the GLEI project; time constraints prevented us from revisiting the other two (Fig. 1, Tables 1 and 2). We focused on the EBF region because the invasive genotype was documented to occur in numerous coastal wetlands of the southern Great Lakes but not the northern Great Lakes (Saltonstall 2002). A total of 307 1-m × 1-m plots were sampled at the 14 wetland sites and the number of plots sampled per wetland ranged from 8 to 96 proportional to wetland size (Table 1).

Geographic coordinates of each 1-m × 1-m plot within the wetland study sites had been recorded using a hand held Garmin GPSMAP 76 unit (Garmin International Inc., Olathe, KS) during initial sampling in 2001–2003, and were used to return to the same locations during the summer of 2005. Plot locations were the average of

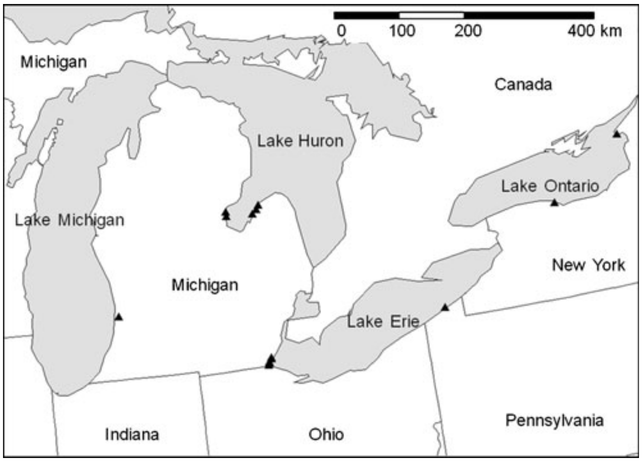

Fig. 1 Location of the 14 wetland sites (black triangles) re-sampled in 2005

hundreds of readings recorded by a tripod-mounted GPS set to continuously record as field researchers were collecting vegetation data at each plot (Johnston et al. 2009a). All the sites were herbaceous wetlands in level terrain, therefore errors introduced by blocked or multipath signals due to topography or canopy cover were minimal.

Plots were distributed along randomly placed transects within areas mapped as emergent vegetation (Cowardin et al. 1979) by national and state wetland inventories along the Great Lakes. Transects were established with a geographic information system (GIS) prior to field campaigns, using a program called Sample (http://www.quantdec.com/sample) to randomize transect placement. Each transect intersected a randomly selected point generated by the Sample program, and was oriented along the perceived water depth gradient, extending from open water to the upland boundary. Transect length and target number of plots were determined in proportion to the size of the wetland to be sampled (20 plots/60 ha, minimum transect length=40 m, minimum plots/site=8). Plot locations were established in the field by dividing each transect into 20 m segments and randomly locating a plot in each segment using a random number table (Bourdaghs et al. 2006). Within each plot percent cover of *Phragmites* was estimated visually according to modified Braun-Blanquet cover class ranges (ASTM 1997): < 1%, 1 to<5%, 5 to < 25%, 25 to<50%, 50 to<75%, 75 to 100%. Prior to data analyses, cover classes were converted to the midpoint percent cover of each class using the algebraic mid-points of the six cover class ranges (0.5, 3.0, 37.5, 62.5, 87.5).

Leaf samples were collected from *Phragmites* stands at each wetland revisited and identified as native or non-native genotype using the genetic analysis described in (Tulbure et al. 2007) and based on Saltonstall's (2002) protocol.

Table 1 Comparison of *Phragmites* cover at 14 Great Lakes wetland study sites between first and second sampling. Invaded = plots where *Phragmites* was not present in 2001, but expanded in 2005; Increased/ decreased = plots where *Phragmites* was present in 2001 but increased/ decreased in cover by 2005; Remained unchanged = plots where *Phragmites* cover did not change from 2001 to 2005

Site name	Lake	Mean *Phragmites* cover per plot (%) at each site		Number of samples (plots), *n*	Number of plots with *Phragmites*		Number of plots where *Phragmites*			
		2001–03	2005		2001–03	2005	Invaded	Increased	Decreased	Remained unchanged
Kalamazoo River	Michigan	0.03	0.65	96	1	1		1		
White Feather Creek	Huron	0.09	7.63	27	5	8	3	4		1
Neuman Road	Huron	0.04	0.08	13	1	2	1			1
Blind Pass	Huron	4.34	24.48	22	10	12	5	5	3	2
Wildfowl Bay	Huron	8.07	24.00	22	10	12	5	4	3	3
Caseville	Huron	35.63	78.44	8	8	8		6		2
Otter Creek	Erie	12.73	21.88	24	7	6	1	3	2	2
Toledo Beach	Erie	26.25	26.25	10	3	3				3
Bay Creek	Erie	17.50	32.15	13	4	8	5	1	2	1
Little Lake Creek	Erie	64.05	73.80	10	10	10		3		7
Kelly Doty Drain	Erie	52.50	39.14	11	10	7		2	4	4
Presque Isle	Erie	2.70	19.30	15	2	10	8	2		
Braddock Bay	Ontario	0.60	2.50	25	1	1		1		
Fox Creek	Ontario	0.27	0.05	11	1	1			1	
Total number of plots (*n*)				**307**	**73**	**89**	**28**	**32**	**15**	**26**

Table 2 Description of water level at 14 wetland sites. Lake level changes based on July average monthly levels (see Table 4) except where indicated. Negative numbers indicate declines in water levels

Site	Lake	Initial sample year	Lake level change, m	Diked?	Number of plots where water level		
					increased	decreased	same
Kalamazoo River	Michigan	2002	−0.14	N	4	18	74
White Feather Cr.	Huron	2003	0.15	N	21	1	5
Neuman Road	Huron	2003	0.15	N	9	0	4
Blind Pass	Huron	2003	0.15	N	8	6	8
Wildfowl Bay	Huron	2003	0.15	N	7	0	15
Caseville	Huron	2003	0.15	N	1	2	5
Otter Creek	Erie	2002	−0.02	N	4	9	11
Toledo Beach	Erie	2002	−0.02	Y	7	1	2
Bay Creek	Erie	2002	−0.02	N	0	4	9
Little Lake Creek	Erie	2003	0.04	Y	0	3	7
Kelly Doty Drain	Erie	2003	0.04	Y	3	2	6
Presque Isle[a]	Erie	2003	−0.04	N	0	8	7
Braddock Bay[ab]	Ontario	2002	−0.53	N	0	18	7
Fox Creek[a]	Ontario	2001	−0.17	N	0	5	6

[a] 2005 lake level from August used to correspond with final sampling date

[b] lake level from June used to correspond with initial sampling date

Abiotic Factors

Thirteen abiotic environmental factors were measured in the field or derived from mapped data for each of the 14 study sites (Table 3). At each plot, vegetation data were collected, water depth was measured, and bare soil area was estimated using the same six cover class ranges used for plants. Water depth was measured using a meter stick, which was inserted until we felt resistance from bottom sediments without applying pressure. The values obtained in 2005 were subtracted from comparable values for water depth and bare soil area measured initially by the GLEI project to compute change in water depth (WaterDepthDiff) and bare soil (BareSoilDiff). The substrate at each plot was 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, 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. The texture of mineral soils (i.e., sand, silt, clay) was determined by feel using standard field methods (Soil Survey Staff 1951).

In 2005 we measured nitrate (NO_3-N), ammonia (NH_3-N), and soluble reactive phosphorus (SRP) in soil water in *Phragmites* versus non-*Phragmites* stands at each wetland site. *Phragmites* stands were chosen that were 100% covered with *Phragmites* and along or close to the initial GLEI sample transect, but not necessarily coinciding with it. Non-*Phragmites* stands were chosen that had no *Phragmites* present and were at the same elevation and as close as possible to the *Phragmites* stands so as to minimize confounding differences due to edaphic conditions. We dug holes using an auger in the plant rooting zone, and water that accumulated in the holes was used for nutrient analysis. All nutrients were measured in the field using a Digital Hach PortableDR/890 Colorimeter (Hach Company, Loveland, CO). Nutrient measurements were taken at three locations in each stand type (*Phragmites* vs. non-*Phragmites*). Nitrate was measured using the Chromotropic Acid Method (estimated detection limit, EDL, of 0.3 mg/L NO_3-N); ammonia was measured using the Salicylate Method (EDL of 1 mg/L NH_3-N), and SRP using the Ascorbic Acid Method (EDL of 0.05 mg/L PO_4; Hach Company 2005).

We examined digital orthophotos taken 1–8 years prior to the initial field work (USGS 2007) to determine if sites were previously diked. The agriculture and urban indices were developed by the GLEI project using methods described by Danz et al. (2007), but were calculated for watersheds draining to the specific wetlands studied (Hollenhorst et al. 2007). The agricultural index was derived from 21 variables characteristic of the major types of stresses in a wetland's watershed associated with agricultural activities (e.g., nutrient runoff, fertilizers, pesticide application, and erosion), and the urban index was derived from 14 variables associated with human population, road density, and developed land in the

Table 3 Coefficients and *p*-values from the mixed model of difference in *Phragmites* cover as a function of explanatory variables

Variables	Description	Unit of measure	Type[a]	Scale	Reference	Mixed model with 13 variables			Mixed model with 8 variables		
						Estimate	*p*-value	VIF	Estimate	*p*-value	VIF
Intercept						−55.92			30.54		
Lake	Great Lakes (Michigan-Huron or Erie-Ontario)	unitless	C		see text		0.98			0.02	
Substrate	clay,organic, sand, silt	unitless	C	plot	see text		0.67			0.57	
WaterDepthDiff	difference in water depth between first and second sampling	cm	N	plot	see text	−0.96	0.19	1.33	1.31	0.05	1.07
BareSoilDiff	difference in bare soil area between second and first sampling	%	N	plot	see text	−0.26	0.12	1.26	−0.3	0.05	1.04
UrbanIndex	urban PC	unitless	N	watershed	Danz et al. 2007	82.58	0.12	7.69	4.65	0.36	1.46
AgIndex	agriculture PC	unitless	N	watershed	Danz et al. 2007	11.04	0.53	**10.25**			
Nitrogen	field-measured average inorganic nitrogen	mg/L	N	wetland	see text	33.96	0.18	9.34	12.06	0.13	1.76
Phosphorus	field-measured soluble reactive phosphorus	mg/L	N	wetland	see text	−3.67	0.87	2.61	1.39	0.89	1.27
Ratio	watershed to wetland area ratio	unitless	N	wetland	Brazner et al. 2007	0.21	0.13	**13.34**			
	watershed area	ha	N	watershed	Brazner et al. 2007	0.01	0.15	**13.78**			
WetlandArea	wetland area	ha	N	wetland	Brazner et al. 2007	0.01	0.53	1.62	0.01	0.19	1.26
RowWatershed	row crops	areal fraction	N	watershed	Brazner et al. 2007	76.45	0.56	**38.29**			
UrbanWatershed	development	areal fraction	N	watershed	Brazner et al. 2007	−82.93	0.37	**28.61**			

Variables with bolded VIF values were eliminated from the initial mixed model to reduce multicollinearity

[a] The type of variable is denoted by N = numerical, C = categorical

watershed (Danz et al. 2007). Principal component analysis was carried out for each category of variables, and the resulting principal components were standardized so that the mean equaled 0 and the standard deviation equaled 1. Index values for all GLEI EBF wetland study sites ranged from 0.11 (least stress) to 1.14 (most stress) for the agricultural index and from −2.09 to 1.82 for the urban index. The values of the agricultural index at our revisit sites ranged from 0.25 to 1.14, while the urban index ranged from −1.11 to 1.82. Areal proportions of row crop and development within watersheds around the National Wetlands Inventory boundary were computed to account for anthropogenic disturbance at different spatial scales (Brazner et al. 2007).

Data Analysis

To gain insight into the drivers of change in *Phragmites* cover between the two sampling events, we used mixed models incorporating both fixed and random effect variables with PROC MIXED, SAS Version 9.1 (SAS Institute Inc. 2001), with plots nested within wetland sites. We used 13 explanatory variables as fixed effects, which were hypothesized to influence *Phragmites* change (Table 3). We assessed the degree of multicollinearity among the continuous explanatory variables by computing variance inflation factors (VIF, Neter et al. 1990). Five variables (agriculture PC, watershed to wetland area, watershed area, row crops, and development in the watershed) with the highest VIFs were eliminated from the model to reduce collinearity, which resulted in VIFs <= 10 in the new mixed model.

A one-way ANOVA followed by Tukey's HSD comparison test was used to analyze: a) initial *Phragmites* cover on four different soil types (i.e., sand, silt, clay, and organic); b) change in *Phragmites* cover at wetland sites located on Great Lakes in which there was a drop in water levels between 1999 and 2001 (i.e., Lakes Michigan/Huron, and Erie) versus lakes where there was an increase in water levels between 1999 and 2001 (i.e., Lake Ontario). The years 1999–2001 were chosen as a surrogate for exposure of bare soil during the first year of sampling. We used Wilcoxon non-parametric two-sample tests to examine differences in nutrients between *Phragmites* versus non-*Phragmites* stands. All tests were conducted in SAS ® 9.1 (SAS Institute Inc. 2001). All data were arcsine transformed prior to data analysis (none of the data sets was normally distributed).

Results

Phragmites Nativity and Expansion

Phragmites occurred in about one-third of the 307 plots sampled at the 14 wetland sites. PCR/RFLP genetic analysis of leaf samples revealed that none of the *Phragmites* sampled at the 14 wetland sites belonged to the native genotype. Out of the 307 plots revisited at 14 wetlands along the Great Lakes, *Phragmites* occurred in 101 plots. At the other 206 plots, *Phragmites* was absent during the first and second sampling events. Out of the 101 plots that had *Phragmites, Phragmites* invaded 28 plots, increased cover in 32 plots, disappeared or decreased cover in 15 plots, and remained unchanged in 26 plots (Table 1).

Eight sites exhibited increases in *Phragmites* cover of 7.5 percentage points or more. This ranged from 7.54 percentage points at White Feather Creek wetland, which had 0.09% mean *Phragmites* cover (as mean plot value per site) in 2003 and increased to 7.63% by 2005. A high increase of 42.8 percentage points occurred at Caseville wetland, which started with a mean *Phragmites* cover of 35.63% in 2003 and reached 78.44% by 2005. The change is even more dramatic given that it took place only 2 or 3 years after the initial sample date (Table 1). One site (Kelly Doty Drain) first sampled in 2003 exhibited a 13.4% decrease in *Phragmites* cover. The remaining five sites (Kalamazoo River, Neuman Road, Toledo Beach, Braddock Bay, and Fox Creek) remained essentially unchanged between first and second sampling times (Table 1). Four out of the five Lake Huron sites experienced large increases in *Phragmites*, as did four sites on Lake Erie, but the Lake Michigan and Lake Ontario sites did not change substantially. The increase in *Phragmites* was due either to invasion of new plots or increase in cover at plots where it already occurred (Table 1). At two sites, Bay Creek and Presque Isle, the number of plots newly invaded by *Phragmites* was greater than the number of plots where it merely increased in cover (Table 1). *Phragmites* disappeared completely from most of the plots that exhibited a decrease in *Phragmites* cover between the initial and 2005 sampling (12 out of 15 plots).

Water depth changes in the plots sampled were generally consistent with the overall lake level trends from initial to 2005 sampling: increases occurred primarily at sites where the lake level was at least 10 cm higher in 2005 than during the initial sampling (e.g., Lake Huron), and decreases occurred primarily at sites where the lake level was at least 10 cm lower in 2005 (e.g., Lake Ontario, Table 2; USCOE, http://www.lre.usace.army.mil/greatlakes/). All plots that lacked water standing above the soil surface were assigned a water depth of 0, regardless of depth to the water table beneath the soil surface, which explains the predominance of "same" values recorded. Plot-scale water level decreases in Little Lake Creek despite lake level increases are probably due to artificial water level control by dikes. The relatively few undiked plots in which the plot-scale change in water depth is inconsistent with the lake level change may be due to changes in bottom configuration (e.g., dredging, siltation).

Natural and Anthropogenic Factors that Influenced *Phragmites* Success

The VIF-adjusted, 8-variable mixed model related change in *Phragmites* cover with difference in water depth, difference in bare soil area, urban PC, nitrogen, phosphorus, wetland area, lake, and substrate (Table 3). Three of these variables were individually statistically significant: difference in water depth, difference in bare soil area, and lake. An increase in *Phragmites* cover was associated with decreasing water depth and less bare soil, and *Phragmites* cover increased more on Lake Michigan-Huron than on Lake Erie-Ontario (t-value=2.35, df=74, p=0.02). Of these variables, the lake and decrease in water depth are environmental factors promoting *Phragmites* invasion, whereas the decrease in bare soil area is a consequence of that invasion. The greatest decrease in bare soil occurred at plots where *Phragmites* increased in cover (Fig. 2a), suggesting that the newly exposed substrate was colonized by *Phragmites*. Plots invaded by *Phragmites* experienced a decrease in measured water depth from first to second sampling, plots where *Phragmites* increased in cover had relatively stable water levels, plots exhibiting a decrease in *Phragmites* cover had water depth increases averaging 7 cm, whereas other plots experienced little change in water depth over the same time period (Fig. 2b). Even though Urban Index was not a significant predictor of change in *Phragmites* cover, *Phragmites* first appeared where the Urban Index was low, but it increased where it was dramatically higher (Fig. 2d). This might suggest that *Phragmites* expansion is facilitated by disturbance and urban land uses along wetland-terrestrial borders, as previous studies have found (Bertness et al. 2002; Minchinton and Bertness 2003; King et al. 2007).

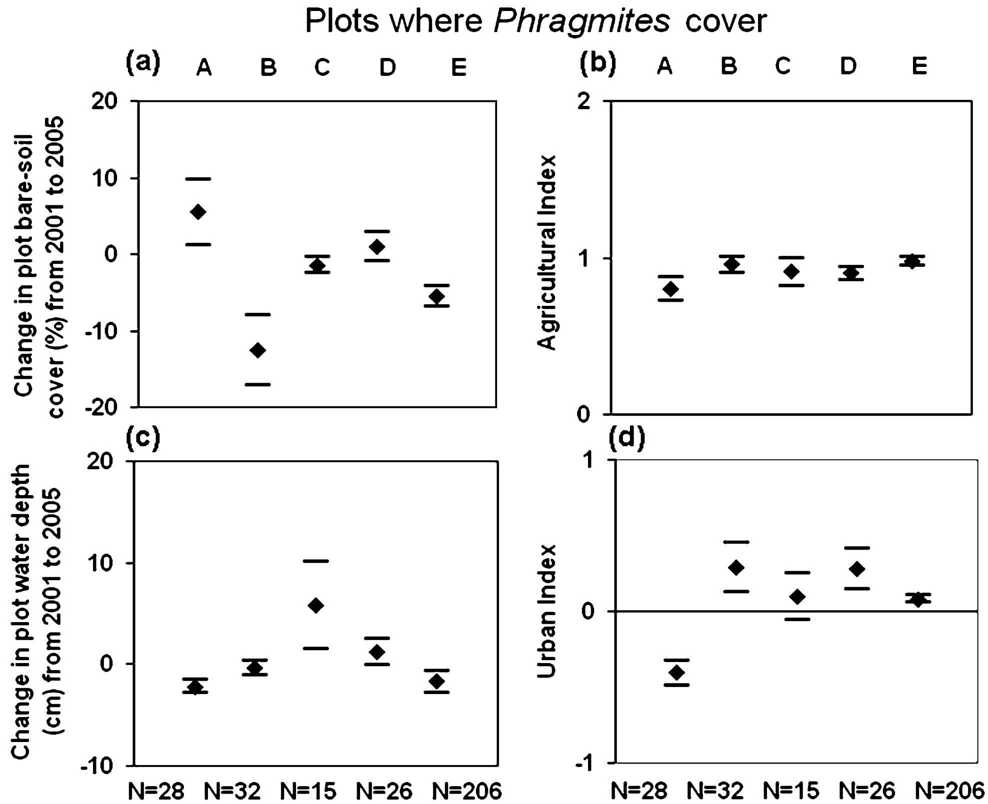

Fig. 2 Plot environmental conditions in relation to *Phragmites* cover change categories (A = invaded, B = increased, C = decreased, D = same, and E = was zero). Mean values and standard errors for (**a**) Change in bare soil area (%). Negative values indicate a decrease in bare soil area between first sampling date and 2005, (**b**) Agricultural index, (**c**) Change in water depth (cm). Negative values indicate a decrease in water levels between the first sampling date and 2005. (**d**) Urban index

Substrate and Nutrients

Phragmites cover was significantly greater on sand than on clay and organic soils (F=5.19, df=4, $p<0.01$), with the highest average cover of 13.5% on sand, 6.2% on silt, 2.2% on clay, and 1.7% on organic soil. Although initial substrate type was not a significant predictor of *Phragmites* cover change, 59% of the plots where *Phragmites* occurred had sandy substrate, whereas 52% of the plots where *Phragmites* did not occur had organic soils (Fig. 3).

Average NO_3-N concentration was 0.28 mg/L in *Phragmites* stands compared to 0.32 mg/L in non-*Phragmites* stands; both values were close to the detection limit, and their difference was not statistically significant (χ^2=0.65, df=1, p=0.42). Average NH_3-N concentrations were also close to the detection limit, and no statistically significant difference was noted between the two groups (χ^2=0.22, df=1, p=0.64) in *Phragmites* (1.05 mg/L) versus non-*Phragmites* (1.02 mg/L) stands. Average concentrations of SRP were well above detection limits, but no statistically significant difference was observed in SRP concentrations (χ^2=0.33, df=1, p=0.56) between *Phragmites* (0.3 mg/L) versus non-*Phragmites* stands (0.43 mg/L) when data were analyzed together for all fourteen sites.

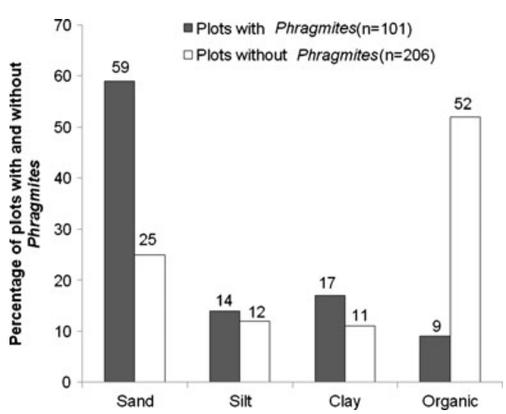

Fig. 3 Substrate type of *Phragmites* plots on the first sampling event

Antecedent Lake Levels

Between 1999 and 2001, prior to the initial sampling event, average July lake levels in Lakes Erie and Michigan/Huron dropped 19 and 35 cm, respectively, to levels that were 28 to 55 cm below average (Table 4). The rapid water level decline exposed large areas of lake bottom along their shorelines. Lake Ontario experienced no such decrease; its lake level increased slightly between 1999 and 2001 and was close to the long-term average in 2001. *Phragmites* cover increased an average of only 1.25% in the Lake Ontario sites, as opposed to 7.4% in the sites on Lakes Michigan, Huron, and Erie (F=2.74, df=1, p=0.09).

Table 4 July Great Lakes water level from 1999–2006 (USCOE, http://www.lre.usace.army.mil/greatlakes/)

Year	July water level (meters above IGLD 1983)		
	Michigan/Huron	Erie	Ontario
1999	176.40	174.23	74.81
2000	176.13	174.27	75.24
2001	176.05	174.04	74.97
2002	176.33	174.25	75.19
2003	176.04	174.19	75.05
2004	176.37	174.35	75.09
2005	176.19	174.23	74.95
2006	176.14	174.29	74.98
Record High	177.39	175.03	75.66
Record Low	175.78	173.45	74.14
Long term average	176.60	174.32	74.99

Discussion

Our research demonstrated that *Phragmites* invasion can occur very rapidly: *Phragmites* cover greatly expanded at four of our five Lake Huron sites in only 2 years (all first sampled in 2003). All of the Lake Huron sites are in Saginaw Bay, which is characterized by lakebed wetlands with gently sloping bathymetry (Burton et al. 2002; Mink and Albert 2002). All of our Lake Huron sites were open-coast wetlands, with emergent vegetation relatively exposed to wave action (Johnston et al. 2007a). Wetlands with direct exposure to wave action usually have sandy soils, which is conducive to *Phragmites* expansion. The gentle slope of Saginaw Bay plus the presence of mineral substrates creates very fertile sand flats when lake levels drop. In healthy coastal wetlands these newly exposed flats would be colonized by native, early successional species that are adapted to these cycles, such as *Bidens cernua* L. (Wilcox et al. 2007). However, the newly exposed flats created by rapidly receding water levels, as occurred in Lakes Michigan and Huron, provided excellent substrate for introduced *Phragmites* colonization. In other regions, *Phragmites* seedlings can germinate on exposed bottoms without standing water, but cannot colonize submerged or densely vegetated substrates (Weisner and Ekstam 1993).

Neuman Road is the only Lake Huron site we revisited that did not experience increase in *Phragmites* cover. In contrast, the nearby White Feather Creek site had increases in *Phragmites* cover despite comparable agricultural index in the watershed, water level change, and amount of change in bare soil. One of the major differences between the two sites is the small watershed area of Neuman Road, which might result in lower total nutrient inputs from the watershed.

Previous studies have suggested that once it has invaded, *Phragmites* alters soil properties and nutrient pools (Windham and Lathrop 1999; Ehrenfeld 2003; Windham and Meyerson 2003). In the present study we did not detect significant differences in nutrients from soil water of vegetation (total nitrogen and SRP) between *Phragmites* and non-*Phragmites* stands. This could be due to the fact that the invasion process is in its early stages (some of the sites were invaded in periods as short as 2 years) and it is too early to detect any changes.

On Lake Erie, *Phragmites* increased in cover at Presque Isle, Otter Creek, Bay Creek, and Little Lake Creek, remained unchanged at Toledo Beach, and decreased in cover at Kelly Doty Drain. All of our Lake Erie sites with the exception of Presque Isle were located at the western end of Lake Erie, which has been altered by construction of dikes for wetland water level control (Johnston et al. 2007b). These structures disrupt the natural flow and water level fluctuations and may have influenced changes in *Phragmites* cover at these sites.

Phragmites did not change in cover at our sites located on Lake Ontario. This is one of the Great Lakes where water level did not drop between 1999 and 2001, and our findings show that *Phragmites* expanded more at Great Lakes coastal wetlands where there was a drop in water levels early in the decade. Lake Ontario sites had primarily organic and clay soils (Johnston et al. 2009b). The GLEI project showed that the invasive *Typha* X *glauca* is an indicator species of organic soil and a common species on Lake Ontario wetlands (Johnston et al. 2009b; Vaccaro et al. 2009). *Typha* spp. could also generate their own organic matter substrate, as they are known to form floating mats of organic matter (Hogg and Wein 1988). The competition between the two species might prevent *Phragmites* from invading those wetlands.

Although *Phragmites* tolerates most soil conditions (Global Invasive Species Database), we found that *Phragmites* occurred predominantly on sandy soils (60% of the plots where it occurred), similar to our previous study (Tulbure et al. 2007). This could also be due to the fact that *Phragmites* invades newly exposed substrates where sandy soils are prevalent.

Our focus on wetlands that already contained *Phragmites* in 2001–2003 was intentional, because those wetlands would be expected to experience more rapid invasion by *Phragmites* than wetlands lacking an internal source of *Phragmites* propagules. However, the exclusion of *Phragmites*-free wetlands from our sample design means that these findings cannot be extrapolated to all Great Lakes coastal wetlands without further research.

The fact that none of the samples we analyzed in this present study came from native *Phragmites* populations suggests that non-native genotypes are common in wetlands of the southern Great Lakes coast. The non-native genotype displays an aggressive behavior and has a greater ability to ventilate the root system with atmospheric oxygen (Tulbure 2008). To our knowledge, there is no evidence to suggest that the native *Phragmites* inhabited the wetlands that were sampled in this study. However, there still are native *Phragmites* populations in the region, at Bark Bay (Lynch and Saltonstall 2002) and other Lake Superior wetlands (Natalie Wright, Univ. of Minnesota, *personal communication*), and in Ohio (John Mack, Ohio EPA, *personal communication*). This underlies the need to identify the origins of populations especially in areas where they are sympatric (Saltonstall 2003).

Mixed model results showed that a combination of plot and site level variables were the most useful predictors of *Phragmites* change. Decreases in bare soil at plots with high increase in *Phragmites* suggest that the bare substrate was colonized by *Phragmites* rather than other species. Change in water depth was another predictor of *Phragmites* increase in cover, with a greater increase in *Phragmites* cover at plots where there was a decrease in water level. *Phragmites* is generally found in shallower water or areas not permanently inundated, but it is also favored by wide water-level fluctuations and is known to survive in water as deep as 2 m (Squires and van der Valk 1992; Herrick and Wolf 2005).

Phragmites invades and spreads when water levels drop and temperatures rise in Lake Erie (Wilcox et al. 2003) and Lake Michigan-Huron (Pengra et al. 2007; Tulbure et al. 2007). Recently, Brisson et al. (2008) found evidence of sexual reproduction in the non-native *Phragmites* at sites with newly exposed substrate of eastern Canada. The authors attributed the phenomenon to the recent climate change towards warmer years (Brisson et al. 2008). The substrate exposed by declining water levels in the Great Lakes provides new germination opportunities for rapid colonization by invasive wetland plant species. Under most climate models Great Lakes water levels are projected to decline (Chao et al. 1999). Stream runoff will also drop (International Joint Commission 2003). Water level in Lake Michigan-Huron Basin is anticipated to drop by as much 1.38 m due to decreased precipitation and increased air temperature and evapotranspiration (Lofgren et al. 2002). The frequency and duration of low water levels could increase, dropping water levels below historic lows (International Joint Commission 2003). Given these projections it is very likely that *Phragmites* is going to expand and thrive at most Great Lakes coastal wetlands where water levels drop, adding to the multiple stresses that these ecosystems are facing. Once established, *Phragmites* populations cause biodiversity loss and are extremely difficult to eradicate (Havens et al. 1997). Monitoring coastal wetlands where water level has dropped and controlling *Phragmites* at early stages of invasion are essential for maintaining healthy wetlands along the Great Lakes coast. Our work underscores the need to collect baseline vegetation data and revisit sites often to monitor *Phragmites* invasion.

In contrast to previous studies of *Phragmites* invasion in individual wetlands, this study is, to our knowledge, the first to investigate rates and causes of *Phragmites* invasion in multiple Great Lakes wetlands spanning a large range of geographic and abiotic conditions. Understanding how natural and anthropogenic abiotic factors drive changes in coastal wetlands is important and can help managers focus their efforts in areas where they are needed the most. Documenting vegetation shifts in time is especially important in dynamic systems such as Great Lakes coastal wetlands that experience water level fluctuations and changes in emergent vegetation.

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