J. Great Lakes Res. 29(4):664–680
Internat. Assoc. Great Lakes Res., 2003

Historical Distribution and Abundance of *Phragmites australis* at Long Point, Lake Erie, Ontario

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ABSTRACT. *Recent expansion of* Phragmites australis *throughout many Great Lakes wetlands has caused concern among resource managers because it is thought to degrade waterfowl habitat and reduce biodiversity. Wetlands at Long Point, Lake Erie, have some of the most important habitats for staging waterfowl on the Great Lakes and anecdotal evidence suggests that* Phragmites *has been expanding rapidly in some of these wetlands. To make informed management decisions, a better understanding of historical changes in distribution and abundance of this species is needed, as well as the ability to identify which plant species/communities* Phragmites *is replacing. Long Point's wetland communities were digitally mapped from aerial photographs from 1945 to 1999. The aerial extent of* Phragmites *stands was measured by digitizing vegetation boundaries, ground-truthing, and analyzing the data using a GIS. A geometric growth formula was used to determine the intrinsic rate of change of* Phragmites *over time.* Phragmites *abundance fluctuated throughout the period (1945: 4 ha; 1955: 7.7 ha; 1964: 69 ha; 1968: 3.6 ha; 1972: 15.1 ha; 1978: 17.7 ha; 1985: < 4 ha; 1995: 18 ha; 1999: 137 ha), but its abundance increased exponentially between 1995 and 1999 (137 ha; intrinsic rate of growth in area = +0.50/yr). The species/communities that were most often replaced by* Phragmites *between 1995 and 1999 were* Typha *spp. (33.8%), marsh meadow (31%), sedge/grass hummock (10.8%), and other mixed emergents (9.6%). Of 31 stands analyzed within the study area, 28 (90%) were of a non-native strain of* Phragmites australis *(haplotype M) that has been rapidly expanding throughout the Atlantic region of the United States. We suggest that the recent rapid expansion of* Phragmites *at Long Point is the direct result of this exotic invasion, and that it has been facilitated by both declines in Great Lakes water levels and increases in ambient air temperatures; anthropogenic and natural disturbances have possibly also contributed. Given the invasive nature of the exotic genotype, combined with future global warming predictions,* Phragmites *probably will continue to rapidly expand throughout lower Great Lakes coastal wetlands.*

INDEX WORDS: *Biodiversity, common reed, Great Lakes, invasive species, Lake Erie, Long Point,* Phragmites australis, *wetland.*

INTRODUCTION

Phragmites australis (Cav.) Trin. ex Steudel (hereafter *Phragmites*) is a tall cane-like perennial grass that grows in aquatic, semi-aquatic, and terrestrial habitats (Marks *et al.* 1994). It reproduces sexually and asexually and its superior competitive abilities allow it to quickly displace other wetland and marsh meadow plants (Roman *et al.*

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1984, Marks *et al.* 1994, Chambers *et al.* 1999). Formation of a *Phragmites* monoculture causes changes in wetland floral diversity, alters edaphic conditions, increases vertical accretion of marsh substrates, modifies nutrient cycling, and affects plant and animal populations (Meyerson *et al.* 2000). *Phragmites* has been present in North America for at least 3,000 years (Niering and Warren 1980), but it has expanded rapidly along the Atlantic Coast during the past century (Meyerson *et al.* 2000) and is now regarded as an aggressive invader (Marks *et al.* 1994, Chambers *et al.* 1999, Rice *et al.* 2000).

More recently, *Phragmites* has expanded throughout many lower Great Lakes coastal wetlands, including Long Point, Lake Erie. This could be problematic because the ecological integrity of lower Great Lakes coastal wetlands has already been severely compromised by drainage, degradation, and the introduction of exotic species (Crowder and Bristow 1998, Smith *et al.* 1991, Herdendorf 1992, Prince *et al.* 1992, Knapton and Petrie 1999, Petrie and Francis 2003). For instance, less than 5% of western Lake Erie's original wetlands remain (Herdendorf 1987). Consequently, the spread of monospecific stands of *Phragmites* throughout remaining wetlands may threaten important food resources and habitat for wetland-dependent wildlife and plants, including rare species.

Several hypotheses have been proposed to explain the dramatic increases in *Phragmites* along the eastern seaboard of Canada and the United States (Chambers *et al.* 1999); habitat manipulations and disturbances or stresses such as pollution (Marks *et al.* 1994), increased wetland salinity from road de-icing salts (McNabb and Batterson 1991), and changes in hydrologic regimes (Marks *et al.* 1994) and seasonal temperature (see Haslam 1971*a*, Zemlin *et al.* 2000). At least one non-native genotype has been introduced from Europe and it appears to be contributing to the rapid growth and spread of *Phragmites* along the Atlantic coast and throughout the lower Great Lakes (Saltonstall 2002).

Scientists, resource managers, and the general public have proposed that measures be implemented to control *Phragmites* at Long Point and elsewhere throughout the lower Great Lakes. Before *Phragmites* control measures can be justified and implemented, however, a basic understanding of its historical rates of expansion and present distribution are needed. Thus, the purpose of this study was to: 1) document the historic and current distribution and rates of expansion of *Phragmites* at Long Point (1945–1999), 2) determine which plant species/communities it has been replacing, and. 3) propose ideas (hypotheses) why *Phragmites* is rapidly expanding on the lower Great Lakes.

Study Area

Long Point is a 35 km sandspit extending into the eastern basin of Lake Erie (80°30′ E, 42°35′ N to 80°03′ E and 42°33′ N) (Fig. 1). The spit partially encompasses and protects a 280,000 ha lacustrine embayment (Inner Bay) and 24,000 ha of palustrine wetlands (Petrie 1998). Long Point also consists of sand dunes, ponds, forest, and savanna and is one of the most extensive wild areas left in southwestern Ontario (Reznicek and Catling 1989).

This diverse range of habitats, along with the relatively pristine nature of Long Point, make it important to a wide range of migratory and resident wildlife. Long Point is one of the most important waterfowl staging areas in eastern North America (Dennis *et al.* 1984, Wilcox 1994, Wilcox and Knapton 1994, Petrie 1998, Petie *et al.* 2002). Birdlife International has designated Long Point as a globally significant Important Bird Area, primarily because of its importance to migratory songbirds. Long Point hosts a number of rare species including 31 that have been identified as Endangered, Threatened, or of "Special Concern" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2003). Long Point is also one of the most important waterfowl staging areas in eastern North America (Dennis *et al.* 1984, Wilcox 1994, Wilcox and Knapton 1994, Petrie 1998, Petrie *et al.* 2002).

METHODS

The study area included four wetland complexes; Big Creek Marsh (1,192 ha), Crown Marsh (566 ha), Long Point Company Marsh (hereafter Company Marsh) (2,661 ha) and the Tip of Long Point (3,064 ha) (Fig. 1). Wetland vegetation was mapped from historical aerial photos of Long Point (1945, 1955, 1964, 1968, 1972, 1978, 1985, 1995, 1999). For a description of how parity was maintained between years with different scales of aerial photography, see Snell and Cecile Environmental Research (1992) or Hebb (2003).

Aerial photos were interpreted using a mirror stereoscope based on the classification system de-

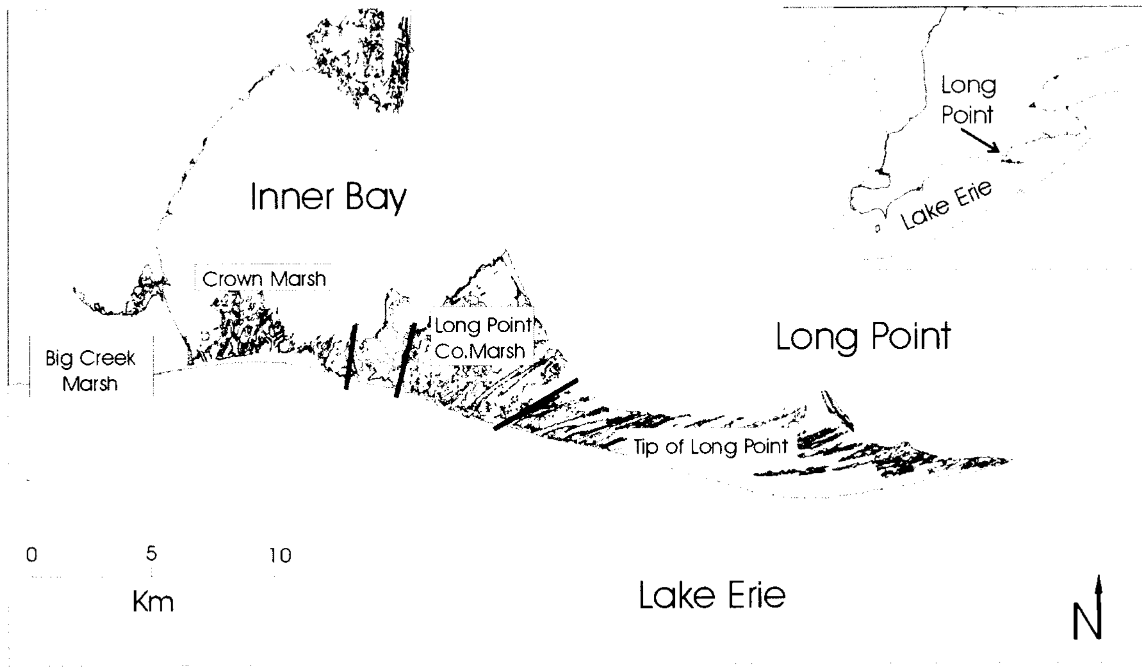

FIG. 1. Study area and geographic location of Long Point, Lake Erie, Ontario.

veloped by Snell and Cecile Environmental Research (1992). The classes are: open water; submergents, emergents, meadow; open bog; and trees and shrubs. Emergents are further divided into three categories: flat wet emergents (e.g., *Nuphar, Nymphaea, Lemna, Zizania*); tall, dense possibly drier emergents (*Typha, grass-sedge hummocks, Phragmites*); and a mixture of the former two or conditions between. Wherever possible, single-species communities were identified separately, e.g., *Phragmites, Typha* spp.. Monospecific *Phragmites* stands were distinguished on the aerial photos by their medium gray tone and solid, fine texture as well as their height (also see Rice *et al.* 2000). Community boundaries and types were outlined on aerial photos using a grease pencil and then field-checked during August and September 1999. Locations of the boundaries were then transferred onto clear plastic overlay sheets registered to Ontario Base Maps (OBM) at a scale of 1:10 000. Each year was overlain on the previous years' coverage to detect real changes in community size and type. This step was also essential to obtain ground control points required for entry into a geographic information system. Ground control points are features such as road intersections that can be located on aerial photographs and for which ground coordinates can be obtained from maps, global positioning systems, or traditional ground surveys (Rice *et al.* 2000).

Vegetation boundaries for each of the nine survey occasions were then digitized using GIS software. Line files created for each time period were projected into UTM Zone 17 and brought into ARC/INFO. Polygon topology was constructed for each year and each separate OBM sheet was joined to create a single file for each year. Labels were added to each polygon to identify vegetation classes. Spatial analysis focused on summarizing the total area colonized by *Phragmites* for each year. This analysis was then performed and compared for each of the four wetland complexes in the study area (Fig. 1).

Changes in *Phragmites* abundance between survey occasions were further analyzed using a geometric or logarithmic growth equation (Rice *et al.* 2000). A geometric growth formula normalizes area change so changes over time within small areas are more comparable to area changes over time within large areas. The following logarithmic growth equation was used (Wilson and Bossert 1971) as described in Rice *et al.* (2000):

$$N = N_0 e^{rt} \quad (1)$$

where:

N = Total area at time 1

N_0 = Total area at time 0

e = 2.718281828 which is the base of the natural logarithm

t = Difference (years) between time 1 and time 0 corresponding to each time interval.

The equation was solved for r which is the intrinsic annual rate of *Phragmites* area increase per year. The intrinsic rate of increase was calculated for the entire study area as well as for the four wetland complexes separately.

The Geoprocessing option in Arcview was used to calculate the area of each plant species/community that was displaced by *Phragmites* between 1995 and 1999. An Arcview option called "UNION 2 themes" was chosen, then 1999 was used as the base year and was overlaid with 1995 coverage. A new field was added to the table and areas were recalculated based on this new union.

Linear regression analysis (Wilkinson 1988) was used to determine if there was a relationship between *Phragmites* abundance and mean annual Lake Erie water levels (Canadian Hydrographic Service, Department of Fisheries and Oceans) and annual, mean ambient air temperature taken at Erie, Pennsylvania (National Oceanic and Atmospheric Administration, Asheville, North Carolina) during the year that *Phragmites* abundance was quantified, the previous year, the mean of the current and previous year, and the mean of the previous two, three, four, and five years.

In 2002, Bernd Blossey of Cornell University developed a diagnostic service to determine whether a particular stand/clone of *Phragmites* is a native or introduced haplotype (http://www.invasiveplants.net/diag/diagnostic.asp). Samples were collected from 31 different *Phragmites* stands from throughout the study area and submitted for analysis. An attempt was made to collect samples from numerous different geographic locations, habitat types, and water depths.

RESULTS

Phragmites Distribution and Abundance 1945–1999

In 1945 there were 54.1 ha of *Phragmites* in the 22,229 ha Long Point study area (Table 1). Several small stands were located in Big Creek Marsh (Fig. 2), no *Phragmites* was distinguished from Crown Marsh aerial photography (Fig. 3), numerous large stands (> 1 ha in size) were located in the interior of the Company Marsh (Fig. 4), and only a few small stands were located on the Tip of Long Point (Fig. 5).

By 1955, *Phragmites* abundance had dropped to 7.7 ha, 7.5 ha of which was in the Big Creek Marsh (Table 1, Fig. 2). No stands were identified in the Crown Marsh, Company Marsh, or on the Tip of Long Point. The rate of change between 1945 and 1955 was –19%/yr. By 1964, *Phragmites* increased in abundance to 69.5 ha (Table 1), the largest stands were in interior areas of the Crown Marsh (Fig. 3) and along the western shore of the Company Marshes (Fig. 4). One large stand (5 ha) was located in the Big Creek Marsh (Fig. 5) and very little *Phragmites* occurred on the Tip of Long Point (Fig. 6). The rate of change in *Phragmites* abundance between 1955 and 1964 was +24%/yr.

There was a substantial decline in *Phragmites* abundance between 1964 and 1968 (–74%/yr). By 1968, the large *Phragmites* stands in the Crown and Company marshes were completely gone; *Phragmites* was only present in the Big Creek Marsh at that time. Between 1968 and 1972, *Phragmites* increased within the Big Creek Marsh but remained almost non-existent in the other marsh complexes. Little change in *Phragmites* distribution was observed between 1972 and 1978 (Table 1). By 1985, *Phragmites* abundance had again declined to less than 4 ha (Figs. 2, 3, 4, 5) (–0.22%/yr). Although a few small stands remained in the Big Creek Marsh, no *Phragmites* stands were observed in the Crown or Company marshes. *Phragmites* area increased to 18 ha by 1995 (+16%/yr); a number of small scattered stands occurred in the Big Creek and Crown marshes (Figs. 2, 3), whereas *Phragmites* had shifted to the southern portions of the Long Point Company Marsh and on the Tip of Long Point (Figs. 4, 5). *Phragmites* area increased exponentially between 1995 (18 ha) and 1999 (137 ha) (+50%/yr). Within the Big Creek Marsh, only a few small *Phragmites* stands occurred, most of which were located along the raised dykes. The Crown Marsh supported numerous *Phragmites* stands of various sizes, whereas the Long Point Company Marsh and the Tip of Long Point supported extensive stands which were located primarily along the southern portions of the Point in what was identified as meadow or cattail habitat in 1995 (Figs. 3, 4, 5).

TABLE 1. Historical changes in* Phragmites australis *distribution and abundance at Long Point, Lake Erie, 1945–1999.

	Total Wetland Area	Area of *Phragmites* (ha)									Intrinsic Rate of Increase/Decrease in Area							
		1945	1955	1964	1968	1972	1978	1985	1995	1999	1945–1955	1955–1964	1964–1968	1968–1972	1972–1978	1978–1985	1985–1995	1995–1999
Big Creek Marsh	1,192	12.6	7.5	11.7	3.1	13.9	17.4	2.9	0.8	3.7	–0.05	0.05	–0.33	0.37	0.04	–0.26	–0.14	0.38
Crown Marsh	566	0.0[1]	0.0	24.8	0	0	0.11	0.1	0.9	13.1	n/a[2]	n/a	n/a	n/a	n/a	–0.01	0.23	0.67
Company Marsh	2,661	39.6	0.0	29.3	0	1.1	0.2	0.0	14.8	85.7	n/a	n/a	n/a	n/a	–0.28	n/a	n/a	0.44
Tip of Long Point	3,064	1.3	0.0	0.9	0	0.1	0	0	1.3	27.9	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0.76
Entire Study Area	22,229	54.1	7.7	69.5	3.6	15.1	17.7	3.8	18.4	136.5	–0.19	0.24	–0.74	0.36	0.03	–0.22	0.16	0.50

[1]0.0—No stands were evident from aerial photography

[2]n/a—Intrinsic rate of increase can not be calculated, because Total area at time 0 (N_0) = 0 which results in a divisor of 0.0.

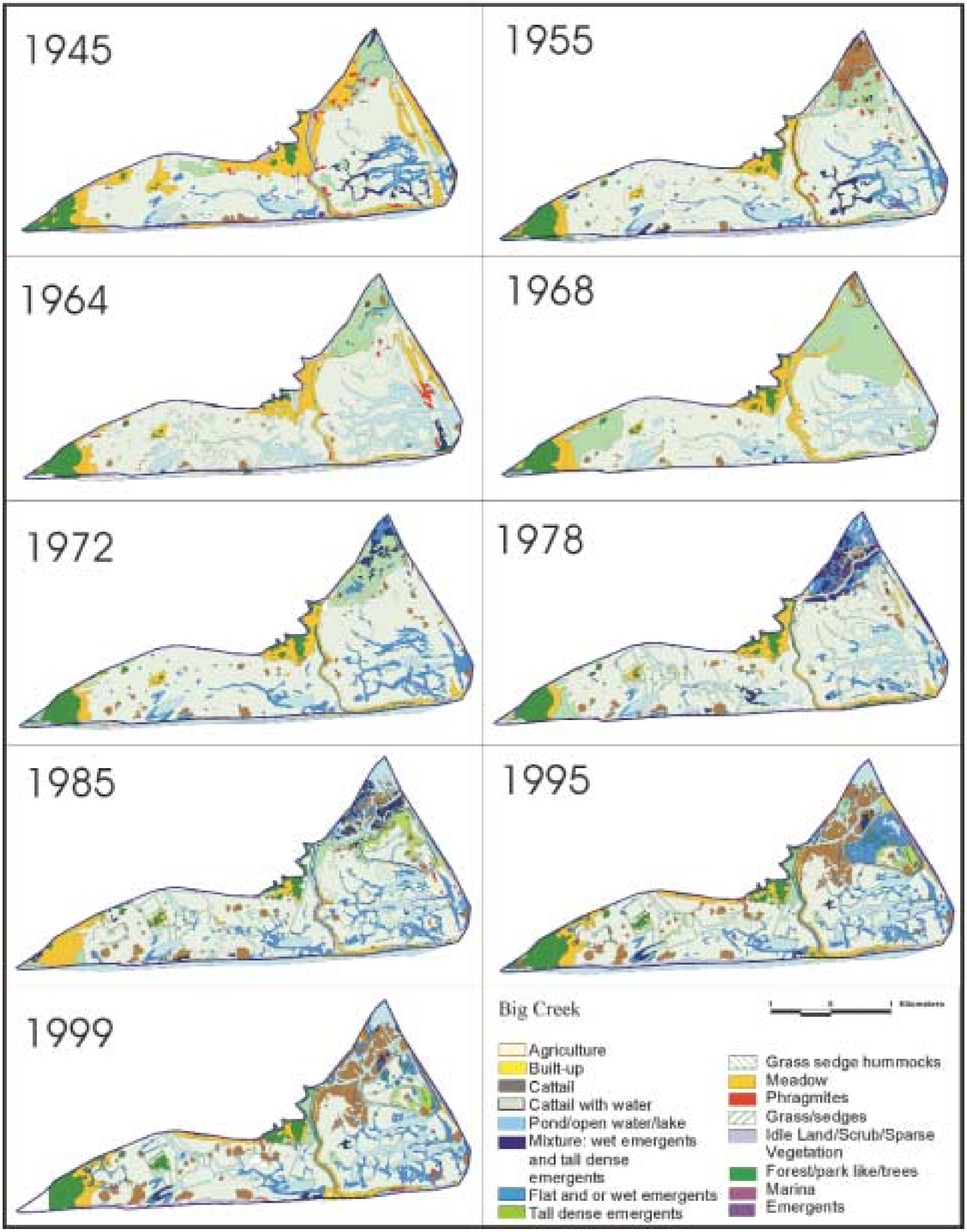

FIG. 2. **Phragmites australis** *distribution in the Big Creek Marsh, Long Point, Lake Erie, 1945–99.*

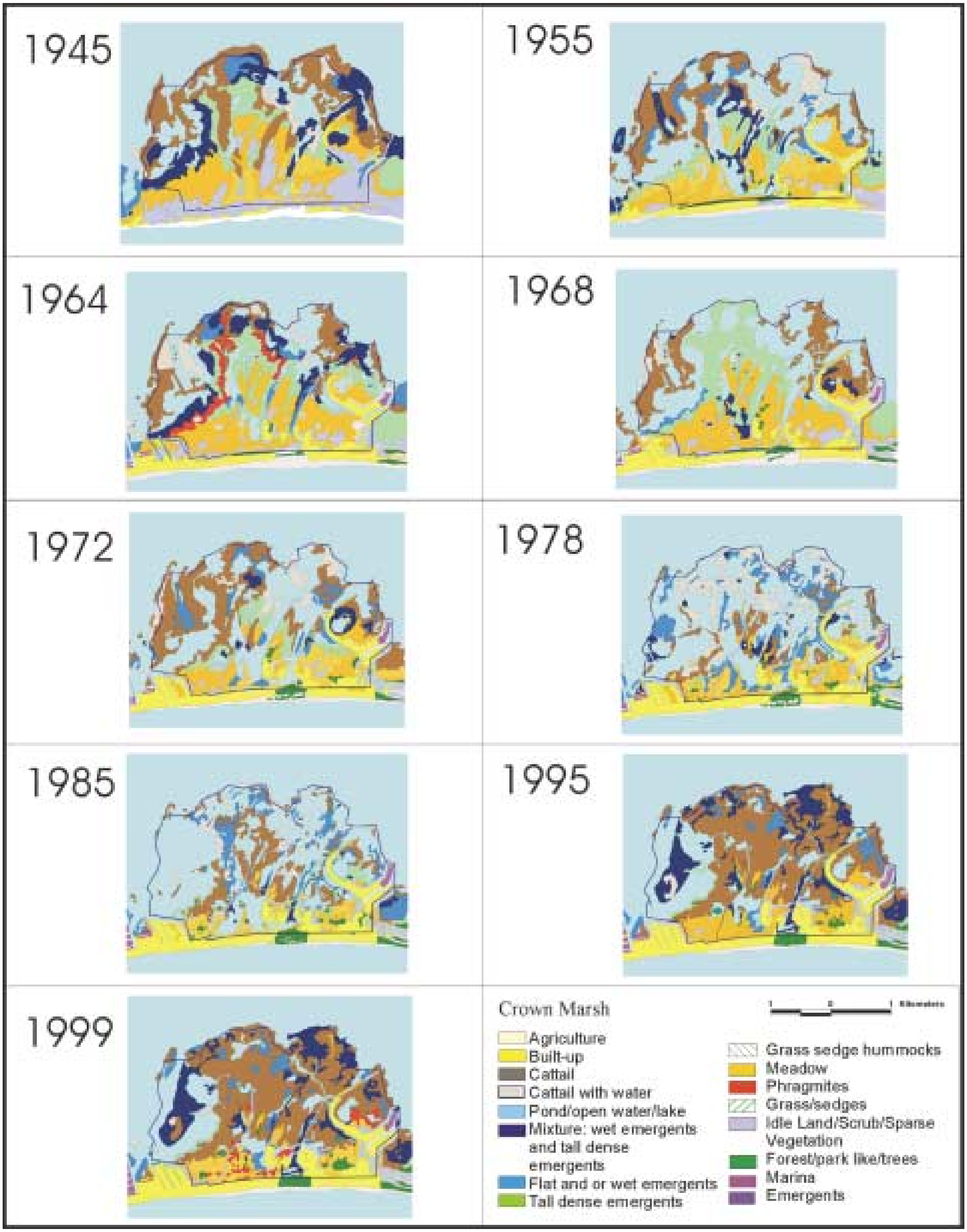

FIG. 3. **Phragmites australis** *distribution in the Crown Marsh, Long Point, Lake Erie, 1945–99.*

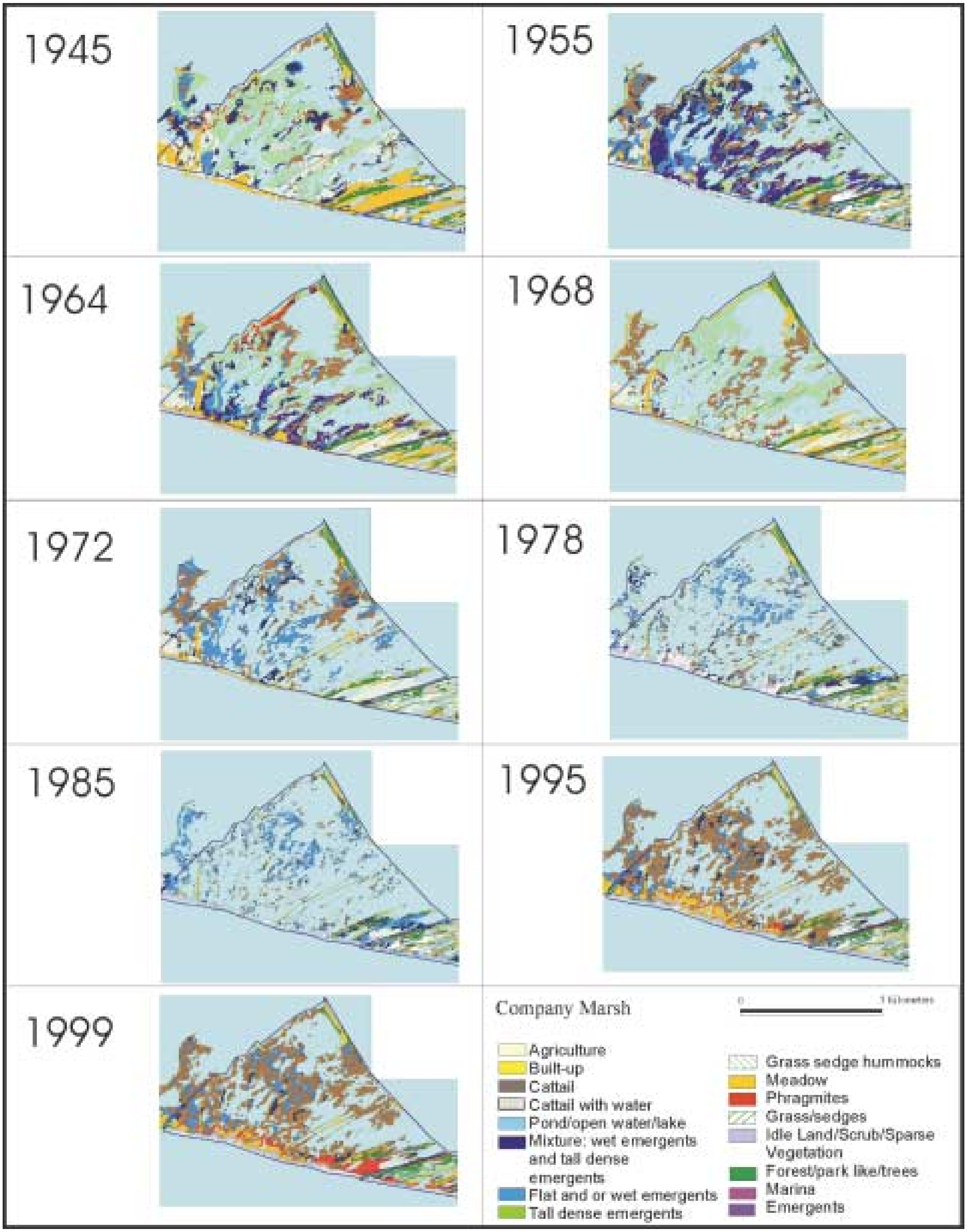

FIG. 4. **Phragmites australis** *distribution in the Long Point Company Marsh, Long Point, Lake Erie, 1945–99.*

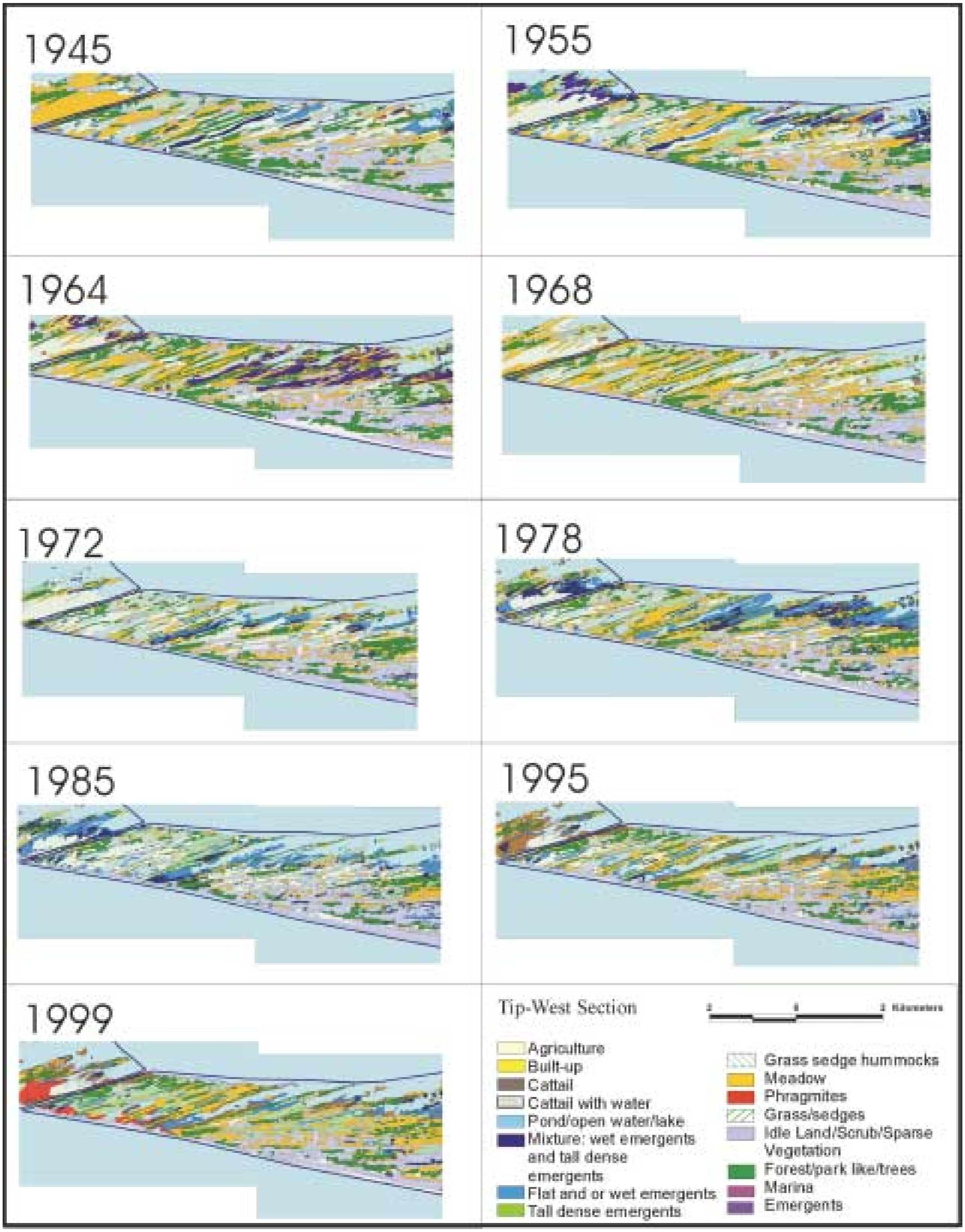

FIG. 5a. **Phragmites australis** *distribution at the Tip of Long Point, Lake Erie, West Section 1945–99.*

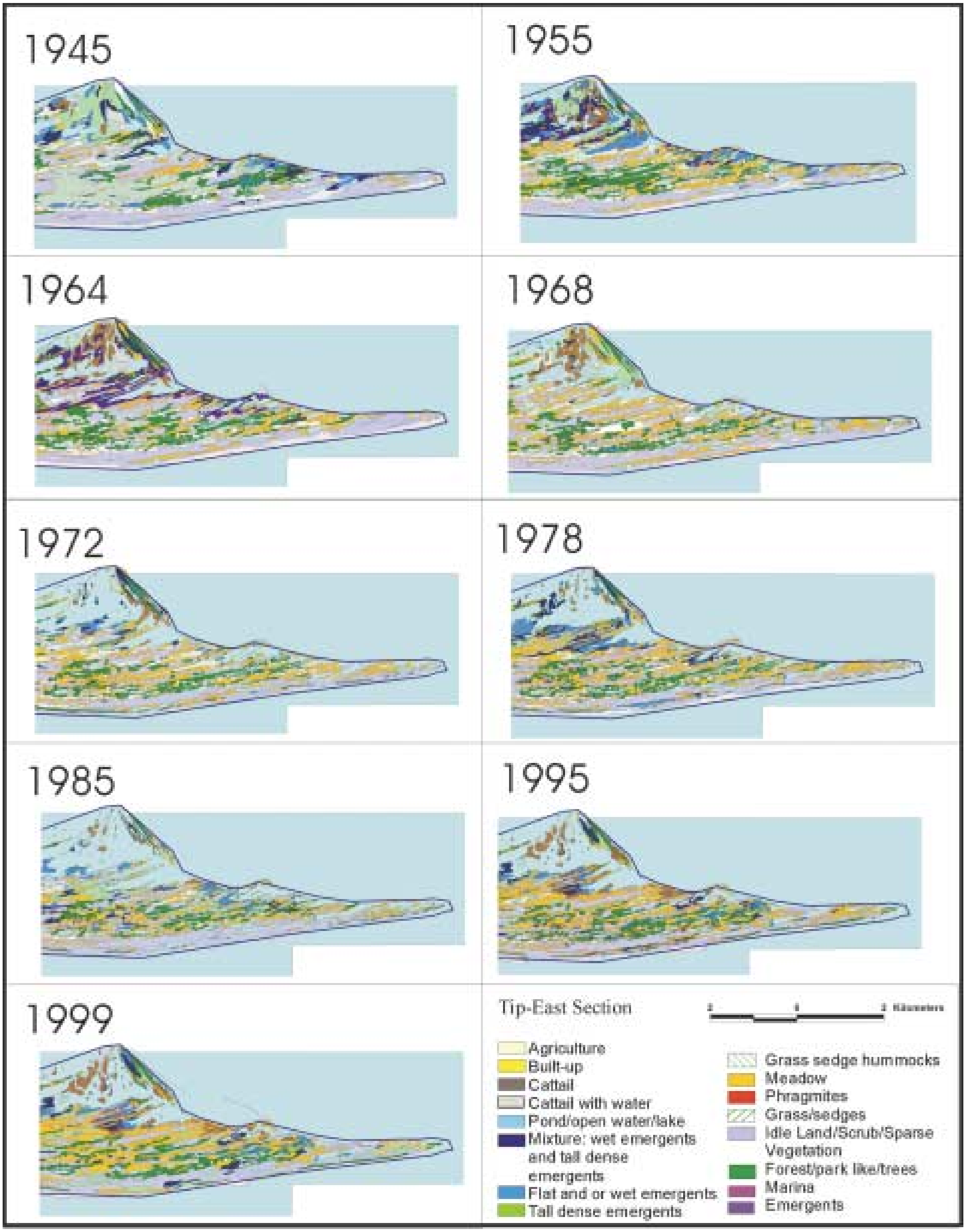

FIG. 5b. **Phragmites australis** ***distribution at the Tip of Long Point, Lake Erie, East Section 1945–99.***

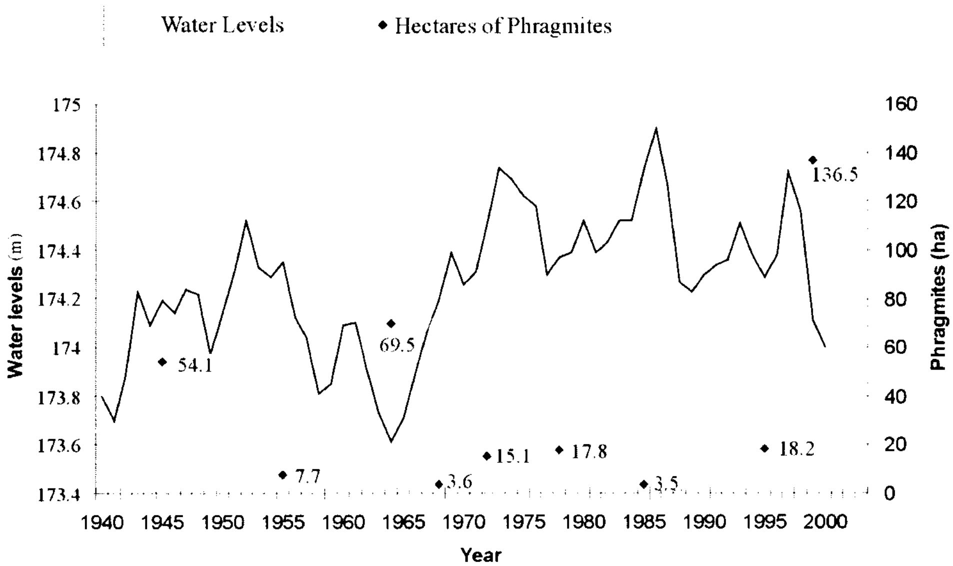

FIG. 6. Relationship between mean annual Lake Erie water levels and the abundance of* Phragmites australis *at Long Point, Ontario, 1945–99. Water level data supplied by the Canadian Hydrographic Service, Department of Fisheries and Oceans.

Communities Replaced by *Phragmites*

The primary plant species/communities that were replaced by *Phragmites* between 1995 and 1999 were *Typha* spp. (33.8%), marsh meadow (31%), sedge/grass hummock (10.8%), other mixed emergents (9.6%), open water (6.4%), transition between sand and vegetation (4.1%), scrub (1.7%), and mixed grassland/woodland (1.7%) (Table 2). Plant species/communities replaced by *Phragmites* also varied by wetland complex (Table 2). Marsh meadow was the primary community replaced by *Phragmite*s in both Big Creek Marsh (36%) and the Crown Marsh (56%) (Table 2). In the Company Marsh, *Typha* spp. (48%) was the primary community replaced, followed by marsh meadow (35.9%). On the Tip of Long Point, grass/sedge hummocks was the primary community replaced by *Phragmites* (39.5%).

TABLE 2. Types of plant species/communities replaced by* Phragmites australis *in four wetland complexes at Long Point, Lake Erie, Ontario, 1995–1999.

	Total Area Replaced (ha)	Big Creek Marsh (%)	Crown Marsh (%)	Company Marsh (%)	Tip of Long Point (%)
Cattail	41.1	16.5	23	48.1	6.0
Meadow	37.7	27.8	57.6	35.9	10.0
Other Emergents/submergents	11.7	18.1	11.2	8.8	6.0
Sedge/grass Hummocks	13.1	17.5	—	0.6	44.0
Open Water	7.6	12.2	6.7	4.4	10.0
Transition between sand and vegetation/sand	2.9	4.4	—	0.3	16.0
Idle Land/sparse veg/scrub	2.1	1.5	tr*	1.1	4.0
Mixed grassland/woodland	2.1	0.3	tr	0.2	3.0
Total area replaced	118.3 ha	3.4 ha	12.2 ha	73.4 ha	26.7 ha

*tr = < 0.1%

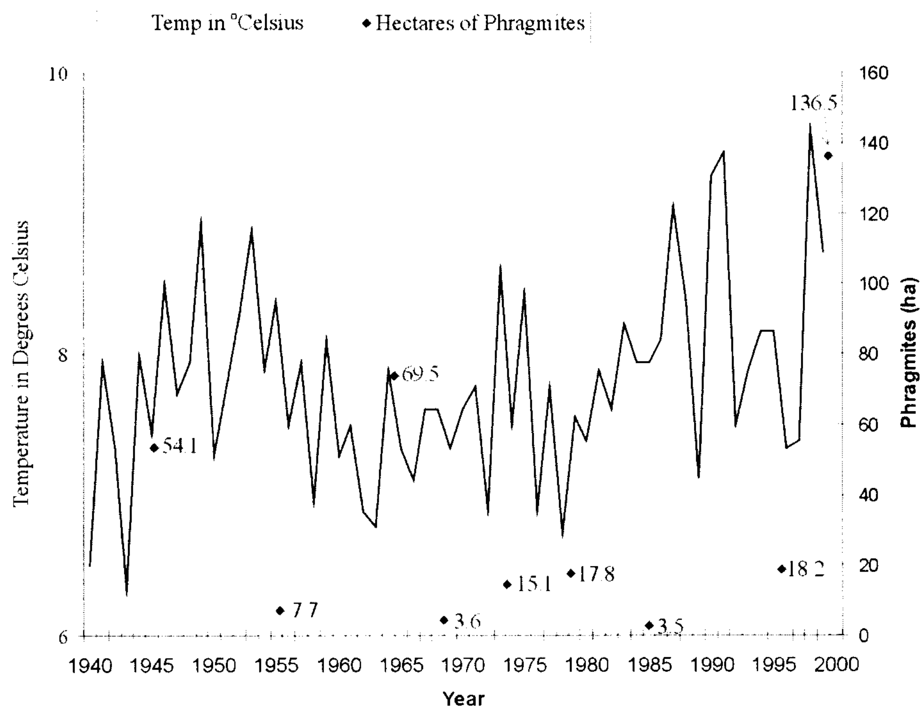

FIG. 7. Relationship between mean annual ambient air temperature and the abundance of* Phragmites australis *at Long Point, Ontario, 1945–99. Ambient temperatures for Erie Pennsylvania supplied by the National Oceanic and Atmospheric Administration.

Influence of Water Levels, Ambient Temperature and Introduced Genotype

Lake Erie experienced large between-year fluctuations in mean water levels and ambient air temperature throughout the study period (1945–99, Figs. 6, 7). Although it appears as though high water levels are associated with low *Phragmites* abundance (Fig. 6), none of the relationships between current and recent year's water levels tested were statistically significant (Table 3). *Phragmites* abundance was more strongly and negatively correlated with mean ambient temperature of the previous 3 years (r^2 = 0.480, P = 0.039) than it was for that of the current year or any of the other year combinations tested (Table 4) (Fig. 7). Of 31stands that were tested, only three (10%) were identified as the native genotype of *Phragmites*. The three native stands occurred in the Big Creek Marsh, Long Point Company Marsh, and near the tip of Long Point (Fig. 8).

TABLE 3. Results of regression analysis for* Phragmites *abundance vs water levels.

Source	*df*	Mean square	*f*-ratio	r^2	*b*	*p*
Current year	1	43,340	2.015	0.287	–77.22	0.215
Previous year	1	102	0.034	0.007	13.99	0.861
Mean of current & previous year	1	1,108	0.395	0.073	–45.28	0.557
Previous 2 years	1	791	0.276	0.052	38.68	0.622
Previous 3 years	1	701	0.243	0.046	39.14	0.643
Previous 4 years	1	620	0.214	0.041	36.98	0.663
Previous 5 years	1	532	0.182	0.035	33.53	0.687

TABLE 4. Results of regression analysis for* Phragmites *abundance vs. ambient air temperatures.

Source	*df*	Mean square	*f*-ratio	r^2	*b*	*p*
Current year	1	3,255	1.84	0.208	30.55	0.217
Previous year	1	4,977	3.27	0.318	33.51	0.114
Mean of current & previous year	1	5,459	3.76	0.349	42.80	0.094
Previous 2 years	1	6,581	5.09	0.421	58.44	0.059
Previous 3 years	1	7,508	6.47	0.480	106.94	0.039
Previous 4 years	1	2,464	1.31	0.158	93.93	0.290
Previous 5 years	1	586	0.273	0.037	–54.65	0.618

DISCUSSION

Historical Changes in *Phragmites* Distribution and Abundance

As would be expected in a freshwater ecosystem characterized by cycles of flooding and drying, the distribution of *Phragmites* at Long Point was very dynamic from 1945 to 1999. However, *Phragmites* distribution increased exponentially between 1995 and 1999. We suggest that, while recent increases in ambient temperatures and decreases in Lake Erie water levels have probably contributed to this expansion, the invasion of an exotic genotype of *Phragmites australis* is most likely the ultimate cause.

Big Creek Marsh

Prior to the mid-1980s, Phragmites was concentrated along a raised dyke and areas surrounded by meadow habitat in the Big Creek Marsh. In 1984, much of the area where *Phragmites* had occurred was dyked to facilitate a cycle of periodic drawdowns followed by reflooding. This probably eliminated many previously occuring stands and possibly has suppressed *Phragmites* growth since that time. *Phragmites* remained virtually unchanged in Big Creek Marsh in 1995 and 1999, possibly due to water level management and low levels of natural disturbance; of the four wetland complexes studied, Big Creek Marsh receives the most protection from the destructive wave action of Lake Erie and Inner Long Point Bay.

Crown Marsh

Although no *Phragmites* stands were detected in the Crown Marsh in 1945 or 1955, large stands had developed along the northwest shore by 1964.

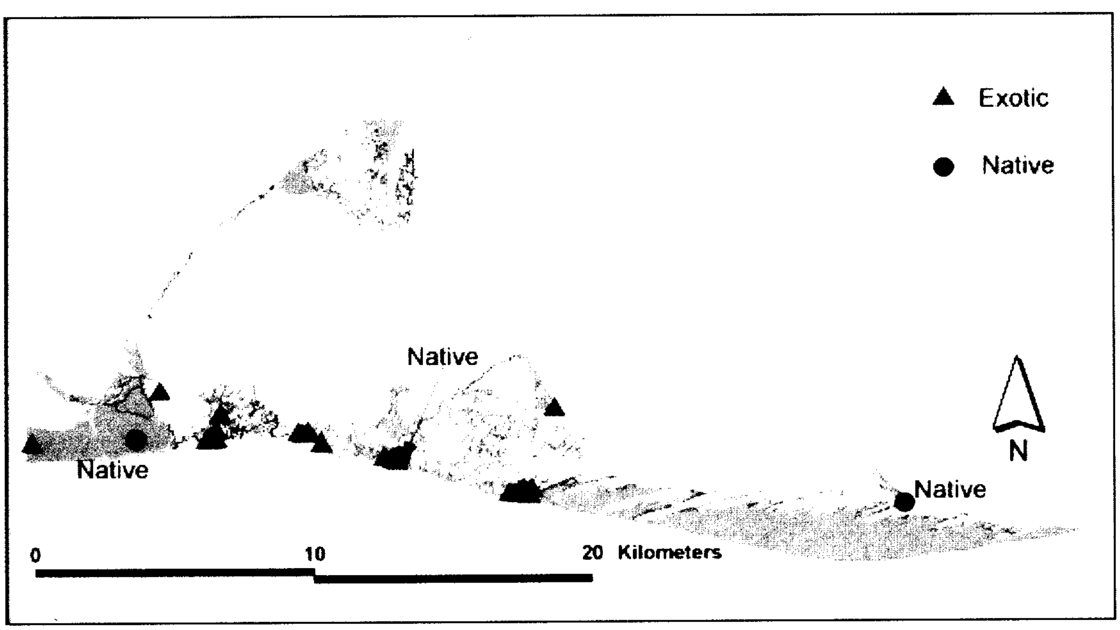

FIG. 8. Geographic location of introduced (*n *= 28) and native (*n *= 3) stands of* Phragmites australis *at Long Point, Lake Erie, Ontario, 2003.

These large stands occurred on mudflats exposed during low water levels. The appearance of these large stands is not surprising because *Phragmites* seeds are shed from November to January and are among the first propagules to reach exposed sites (Marks *et al.* 1994). Marks *et al.* (1994) also noted that newly exposed sites may be colonized by seeds or by rhizome fragments dispersed by wave action. High water levels from the late-1960s to mid-1980s virtually eliminated *Phragmites* from the Crown Marsh. *Phragmites* has a low tolerance for wave and current action, which can break its culms and impede rhizome bud formation (Haslam 1971*b*). New stands appeared by 1995 and increased substantially until 1999. Because all seven stands tested from the Crown Marsh, as well as five from the neighboring Long Point Provincial Park, were of the introduced genotype, we suggest that recent rapid expansion is primarily due to the competitive abilities of this genetic variant.

The Long Point Company Marsh

The most substantial changes in distribution and abundance of *Phragmites* occurred in the Company Marsh. In 1945, *Phragmites* was scattered in the interior of the marsh and was mainly growing in areas surrounded by other tall, dense emergents. By 1955, *Phragmites* had disappeared from the Company Marsh, but large stands returned to the North Shore by 1964 when water levels were low. By 1968, water levels had increased and only a few small stands remained. The large stands along the shore were probably eliminated by wave and current action. By 1995, new stands had appeared on the south shore for the first time. These *Phragmites* stands appear to be in wash-over areas where sand and silt were deposited from Lake Erie, as well as areas where substantial anthropogenic disturbances (berm construction) occurred in the 1980s. *Phragmites* flourished between 1985 and 1999 along the south shore where it colonized exposed soils and replaced *Typha* spp. and meadow communities. This rapid expansion is typical of *Phragmites* as the production of long, extensive rhizomes enables it to spread up to 10 m in a single growing season (Haslam 1971*c*). Consequently, *Phragmites* can quickly dominate large areas extending for acres, as it has in the Long Point Company Marsh. Twelve of thirteen (92%) *Phragmites* stands tested from the Company Marsh were of the introduced genotype. Therefore, we suggest that natural and anthropogenic disturbances in the southern portions of the Company Marsh provided optimum conditions for the introduced genotype of *Phragmites* to colonize and expand rapidly.

Tip of Long Point

During the eight sampling periods between 1945 and 1995, *Phragmites* never exceeded 1.5 ha at the tip of Long Point. By 1999, however, the area had increased considerably to 27.9 ha and stands had appeared along the south shore where they replaced grass/sedge hummock communities and meadow. This area also has experienced considerable wash-over from Lake Erie. Consequently, the recent expansion closer to the Tip of Long Point also is likely due to the availability of primary successional sites, combined with recent arrival of the introduced genotype.

Possible Causes of *Phragmites* Expansion

Water depth is one of the factors that controls *Phragmites* distribution and abundance (Haslam1971*c*, Marks *et al*. 1994). Ostendorp (1990) studied *Phragmites* growth in relation to water levels at Lake Constance, Germany, and concluded that the combination of flooding during the growing phase and mechanical damage by waves was responsible for reductions in *Phragmites*. Shay (1984) also found that high water levels from 1953–58 eliminated hundreds of hectares of *Phragmites* at Delta Marsh, Manitoba, but dry conditions following water level regulation in 1959 led to rapid expansion. Although results were not significant, evidence suggests that *Phragmites* abundance at Long Point may be negatively correlated with Lake Erie water levels. For example, *Phragmites* abundance was highest during the 1960s and late 1990s when water levels were well below long-term average (see Fig. 6).

Phragmites shoot elongation during the main growth phase correlates positively with average daily temperatures (Zemlin *et al*. 2000). Although *Phragmites* abundance at Long Point was not related to the current years' temperature, it was positively correlated with the mean temperature of the previous 3 years. This is consistent with the results of Zemlin *et al*. (2000), because shoot growth was not evident by aerial photo interpretation until the following year. Therefore, increased global temperatures over the last two decades may also have contributed to increases in *Phragmites* distribution and abundance at Long Point since 1985. It has been predicted that global temperatures will continue to rise and that a doubling of atmospheric CO_2 will lower the Great Lakes by 0.5 to 2.5 m (Lenters 2001). Therefore, if global warming predictions are realized and temperatures continue to increase, this may contribute to further *Phragmites* expansion on the Great Lakes.

Recent DNA research has confirmed that a European genotype of *Phragmites* has displaced native North American types as well as expanded to regions previously not known to have *Phragmites* (Saltonstall 2002). Although the invasive haplotype was restricted to portions of the Atlantic coast during the early 20th century, it had established on portions of the lower Great Lakes by the 1960s. Saltonstall (2002) identified the non-native genotype as well as two North American genotypes at Long Point. Of 31 stands we subsequently had tested, 28 (90%) were of the introduced genotype of *Phragmites australis* (Bernd Blossey, Cornell University, Pers. Comm.). The invasive lineage is considered to be very competitive and aggressive because it rapidly replaced native *Phragmites* in the marshes of Connecticut and Massachussets (Saltonstall 2002). Given the rapid expansion of *Phragmites* at Long Point, and the fact that the introduced genotype now dominates, we suggest that a similar phenomenon is presently occurring at Long Point, and possibly throughout other wetlands of the lower Great Lakes. This competitive exclusion and rapid expansion has quite possibly been further facilitated by decreased water levels and increased ambient temperatures (Haslam 1971*c*, Zemlin *et al.* 2000, Williams and Lyon 1997).

Wetland Communities Replaced by *Phragmites*

Phragmites stem height, density, and litter accumulation combine to reduce light and soil surface air temperatures (van der Valk 1986, Rice *et al*. 2000, Meyerson *et al*. 2000). These factors inhibit the establishment of other plant species and slow the decomposition of organic materials (van der Valk 1986, Rice *et al*. 2000, Meyerson *et al*. 2000). Studies examining changes in vegetation diversity over time show that overall species diversity within marshes declines when *Phragmites* enters a system (Meyerson *et al*. 2000). It has been further suggested that *Phragmites* replaces more desirable species such as *Spartina cynosuroides*, *Zizania aquatica*, and *Spartina patens* (Havens *et al*. 1997). No previous studies have determined which plant species *Phragmites* displaces in Great Lakes coastal marshes; we also were unable to effectively ascertain such detailed, species-specific wetland dynamics from aerial photos. However, the most frequent plant communities that were replaced by *Phragmites* between 1995 and 1999 at Long Point were marsh meadow, *Typha* spp., other mixed emergents, and grass/sedge hummocks. Given that only 10% of the *Phragmites* stands sampled were native, the non-native haplotype is quite possibly also replacing native *Phragmites* at Long Point, as it has in the marshes of Connecticut and Massachussets (Saltonstall 2002).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

When seeds germinate and become established, young *Phragmites* plants usually persist for at least 2 years in a small, rather inconspicious state, resembling many other grasses (Marks *et al.* 1994). Spreading rhizomes also are likely indistinguishable from aerial photographs. *Phragmites*, therefore, probably occupied a much larger area than could be detected on aerial photos. The recent, rapid expansion of *Phragmites* at Long Point and other lower Great Lakes wetlands is probably due to the introduction of an invasive European genotype, combined with decreased water levels and increased ambient air temperatures. Given the superior competitive capabilities of the invasive genotype (Saltonstall 2000), we suggest that *Phragmites* will continue to expand rapidly on the lower Great Lakes and that management options may then need to be investigated.

Marsh meadow and cattail were the communities most often replaced by *Phragmites* between 1995 and 1999. Development of a *Phragmites* monoculture changes the structural complexity of wetlands and can impact plant species diversity (Meyerson *et al.* 2000). This could contribute to loss of rare plant species and compromise the suitability of wetland habitats for wildlife (Meyer 2003). However, Meyerson *et al*. (2000) noted that, while *Phragmites* stands are considered to be associated with low faunal diversity in North America, few quantitative data are available on animal density or diversity in *Phragmites* and few studies exist that compare these factors to other marsh plant communities. Thus, additional studies comparing the effect of *Phragmites* on marsh systems are needed to provide a scientific basis for management decisions and to better understand the causes and effects of *Phragmites* expansion.

ACKNOWLEDGMENTS

Financial support was provided by the Long Point Waterfowl and Wetlands Research Fund, through funding provided by the Bluff's Hunting Club. Other key financial and logistical contributors included the Waterfowl Research Foundation, Trillium Foundation, Eastern Habitat Joint Venture, Fuller Foundation, Canadian Wildlife Service of Environment Canada, and Bird Studies Canada. We thank Bernd Blossey (Cornell University) for identifying native vs. non-native *Phragmites*, Liz Snell for advice on aerial photo interpretation, Gary McCullough (CWS, Environment Canada), Lynda Mortsch (Meteorological Service of Canada, Environment Canada), and Andrea Hebb (Environment Canada Atmospheric Adaptation Centre, University of Waterloo) provided historical GIS coverage of Long Point, Bill Baskerville of the Long Point Region Conservation Authority provided digitizing advice and use of GIS facilities, David Walmsley helped collect *Phragmites* samples, and Andrew Couturier of Bird Studies Canada contributed GIS analysis advice. Shannon Badzinski, Leslie Lovett-Doust, and Steve Wilcox provided helpful comments on the manuscript.

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Submitted: 27 December 2002
Accepted: 19 September 2003
Editorial handling: Patricia Chow-Fraser