Hydrological factors controlling the spread of common reed (*Phragmites australis*) in the St. Lawrence River (Québec, Canada)[1]

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Abstract: The spread of *Phragmites australis* between 1980 and 2002 was documented from seven series of aerial photographs and remote sensing images covering the Grandes Battures Tailhandier (Boucherville Islands, St. Lawrence River, Québec, Canada). Over the 23-y period, the colonized surface rose exponentially from 0.86 to 32.6 ha, corresponding to an 18% annual increase. This increase resulted mostly from vegetative growth, although the establishment of new colonies — most likely resulting from seed germination — allowed longer-range dispersion. Hydrological factors, especially the water level and duration of flooding over the growth season (July 1 to October 31) of the previous year, favoured the spread of colonies. Gains were highest the year following low water-level conditions and in a southerly direction, whereas they were reduced when plants grew at more than 1.5 m above mean water level or when they were flooded for more than 100 d during the previous growing season. The rate of surface colonization observed at Boucherville Islands was compared to that recorded at four other fluvial sites. Between Cornwall and Trois-Rivières, the noticeable increase in the number of colonized sites since 1980 suggests that low water levels in 1995, 1999, and 2001 favoured the establishment of colonies of *P. australis* along the shores of the St. Lawrence River.
Keywords: common reed, marshes, *Phragmites australis*, St. Lawrence River, vegetative growth, wetlands.

Résumé : L'expansion des colonies de *Phragmites australis* a été suivie entre 1980 et 2002 sur sept séries de photographies aériennes et d'images satellitaires couvrant les Grandes Battures Tailhandier (îles de Boucherville, fleuve Saint-Laurent, Québec, Canada). En 23 ans, la superficie occupée par la graminée s'est accrue de façon exponentielle, passant de 0,86 à 32,6 ha, ce qui correspond à une augmentation de 18% par an. L'accroissement de superficie résulte surtout de la propagation végétative, quoique l'apparition de nouvelles colonies (probablement issues de la germination de graines) permette la dispersion de la plante sur de plus grandes distances. L'hydrologie, particulièrement les faibles niveaux du fleuve et la durée d'inondation au cours de la saison de croissance (1er juillet au 31 octobre) de l'année précédente, favorisent l'expansion des colonies. Les gains maximaux surviennent l'année suivant une saison de bas niveaux d'eau et se font vers le sud. L'expansion est faible lorsque les plantes poussent à plus de 1,5 m au dessus du niveau moyen de l'eau ou lorsque les plantes ont été inondées pendant plus de 100 jours lors de l'année précédente. Le taux d'accroissement de la surface colonisée par *P. australis* observé aux îles de Boucherville a été comparé aux valeurs de quatre autres sites fluviaux. Entre Cornwall et Trois-Rivières, l'accroissement notable du nombre de sites colonisés depuis 1980 suggère que les bas niveaux d'eau de 1995, 1999 et 2001 ont favorisé l'établissement de colonies le long des rives du Saint-Laurent.
Mots-clés : croissance végétative, fleuve Saint-Laurent, marais, milieux humides, *Phragmites australis,* roseau commun.

Nomenclature: Marie-Victorin, 1995.

Introduction

Phragmites australis (previously *P. communis*, here-after *Phragmites*) is a tall perennial grass, indigenous to North America, that occurs in marshlands worldwide, from the tropics to the 70th parallel. It is widespread in Québec and particularly common in the St. Lawrence River Valley and along highways (Delisle *et al.*, 2003). Over the past decade, the species has vigorously expanded in eastern North America (Chambers, Meyerson & Saltonstall, 1999), probably following the introduction of a more aggressive European genotype (Saltonstall, 2002) favoured by anthropogenic disturbances (Warren *et al.*, 2001).

The main cause for concern of a *Phragmites* invasion is the decrease of plant (Lavoie *et al.*, 2003) and faunal habitat (Helling & Gallagher, 1992; Lindsay *et al.*, 2000) diversity, as this species tends to form dense, monospecific stands. *Phragmites* marshes offer poor-quality habitats for larval and juvenile fish (Meyer, Johnson & Gill, 2001), whose mobility is reduced by the progressive clogging of shallow-water areas following litter and sediment accumulation (Chambers, Meyerson & Saltonstall, 1999). Dense colonies produce a large litter biomass that increases sediment accretion and bottom aggradation, leading to the progressive drying out of littoral zones. The proliferation of *Phragmites* reduces avian diversity by limiting available nesting and feeding habitat for waterfowl (Benoît & Askins, 1999; Chambers, Meyerson & Saltonstall, 1999). In addition to reducing potential avian shelter and the structural heterogeneity of riparian habitats, *Phragmites* also modi-

fies faunal food quality and thus the structure of food webs that may be supported by wetlands. For ducks, geese, and muskrats, *Phragmites* has a lower nutritive value than *Typha* spp., *Scirpus* spp. (*Schoenoplectus* spp.), and *Polygonum* spp., the taxa it replaces (Marks, Lapin & Randall, 1994; Chambers, Meyerson & Saltonstall, 1999). *Phragmites* appears to take advantage of various types of disturbances that destabilize natural wetland communities, decrease competition, and create open spaces that are then available for new seedling establishment (Marks, Lapin & Randall, 1994; Lindsay *et al.,* 2000).

This study examines the recent expansion of the species along the St. Lawrence River shoreline in light of the cumulative effects of physical, chemical, and hydrological disturbances of the past decades. The objectives were to quantify the spread of *Phragmites* in the St. Lawrence River over the past few decades, with particular attention to the Boucherville Islands (Figure 1), and to assess the role of hydrological effects on its vegetative propagation. To meet these objectives, we tested three hypotheses regarding the effects of readily quantifiable hydrological changes on the colonization and spread of *Phragmites* in the Boucherville Islands.

Hypothesis 1: The sediments of St. Lawrence River wetlands fall within the range of characteristics favourable to growth of *Phragmites* and do not limit its ability to spread. *Phragmites* grows on a wide range of soil types. It is often the first plant to colonize inhospitable grounds, such as drainage ditches along roads (Lavoie *et al.,* 2003) or dredged spoils (Marks, Lapin & Randall, 1994; Rice, Rooth & Stevenson, 2000). Many sites colonized by *Phragmites* in the St. Lawrence River have been modified, excavated, or filled-in, including dredged spoil deposits from the navigation channel (Gratton, 1996). *Phragmites* grows on soils with a wide range of organic matter, nutrient concentrations (Haslam, 1972), and pH (Shay & Shay, 1986). Colonization is facilitated by high levels of nutrients (Chambers, Meyerson & Saltonstall, 1999; Lindsay *et al.,* 2000), especially nitrogen originating from urban areas and farmlands (Haslam, 1972; Galatowitsch, Anderson & Ascher, 1999).
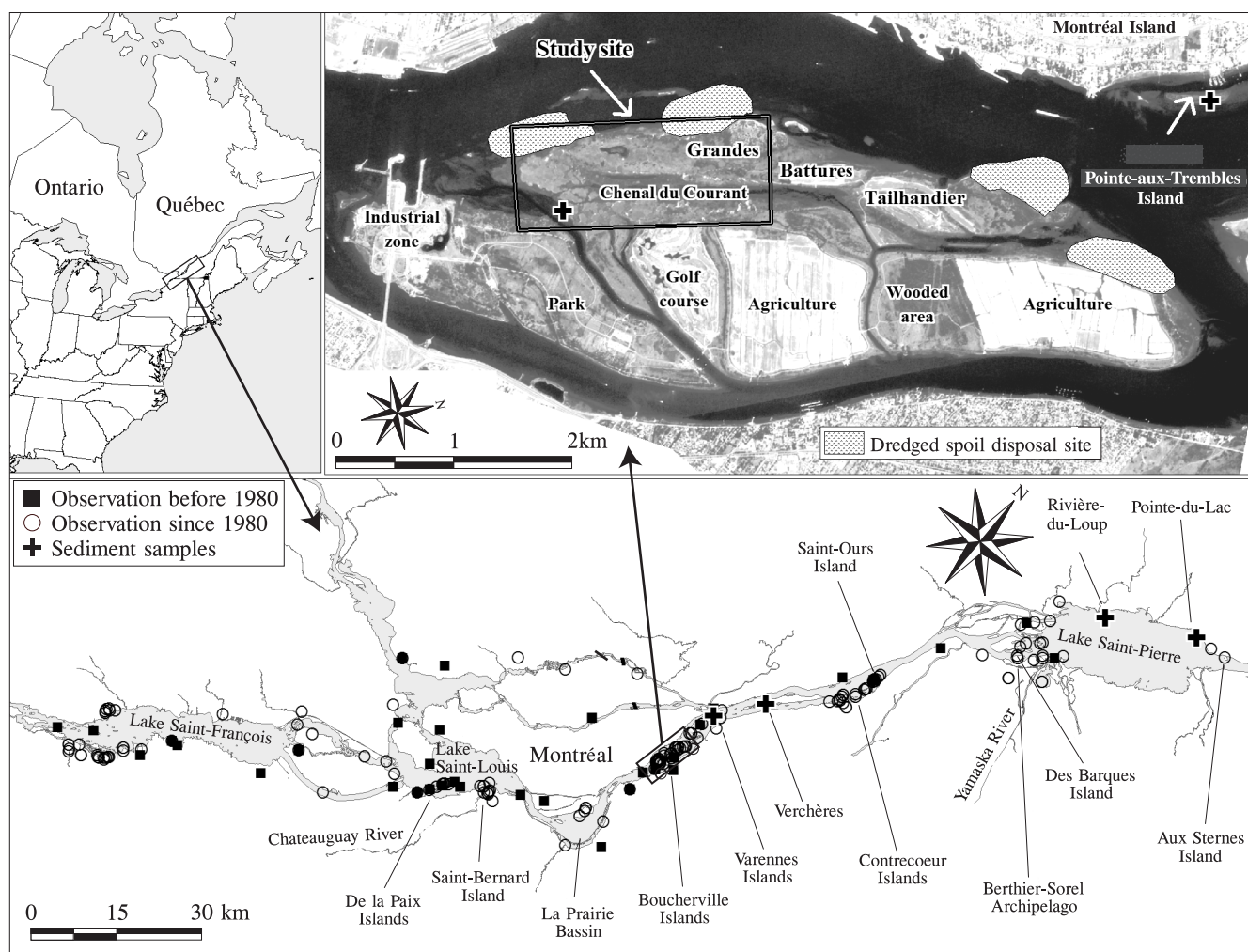

FIGURE 1. Study site location (insert) and other sites colonized by *Phragmites australis* in the St. Lawrence River between Lake Saint-François and Lake Saint-Pierre. Symbols indicate whether first mention occurred before (black squares) or after (open circles) 1980. Repeated observations (black circles) are also shown. Crosses indicate the sites at which sediment samples were collected.

Hypothesis 2: Gains in colonized surface area resulting from rhizomatous growth are larger than those resulting from seed germination. Although *Phragmites* produces a large number of seeds, the species rarely reproduces sexually (Mauchamp, Blanch & Grillas, 2001), since seeds are often sterile or develop slowly (Gervais *et al.*, 1993). On the other hand, vegetative expansion of aerial stolons or underground rhizomes can reach up to 10 m per year in established colonies (Mal & Narine, 2004). Colonies initially occupying favourable high marsh areas are able to propagate vegetatively into less hospitable lower marshes through clonal integration (Amsberry *et al.*, 2000).

Hypothesis 3: Vegetative expansion of *Phragmites* colonies is determined by the water-level conditions (depth, number of days with flood) prevailing during the growth season of the previous year. On a seasonal basis, *Phragmites* stems reach their maximum height and biomass in mid-summer (late July to mid-August). In the latter part of the growing season, energy is allocated to horizontal rhizome production and underground energy stores to sustain the germination of buds that will regenerate the colony over the following spring. At the end of the summer and until the onset of winter, horizontal rhizomes develop from the vertical rhizomes supporting the above-ground stems (Haslam, 1972; Lindsay *et al.*, 2000).

Hydrological disturbances have been suggested as a possible cause of *Phragmites* proliferation (Haslam, 1972; Marks, Lapin & Randall, 1994; Chambers, Meyerson & Saltonstall, 1999; Galatowitsch, Anderson & Ascher, 1999; Rice, Rooth & Stevenson, 2000; Meyer, Johnson & Gill, 2001; Warren *et al.*, 2001; Wilcox *et al.*, 2003). Once a site has been colonized, water-level conditions determine the productivity (Yamasaki & Tange, 1981; Hellings & Gallagher, 1992; Vretare *et al.*, 2001) and the propagation rate (Galatowitsch, Anderson & Ascher, 1999; Shay, de Geus & Kapinga, 1999; Rice, Rooth & Stevenson, 2000; Warren *et al.*, 2001; Wilcox *et al.*, 2003) of colonies. The amount of lateral, rhizomatous expansion in any given year thus likely reflects the hydrological conditions of the previous years.

Methods

STUDY AREA

The study focused on the upstream part of the Grandes Battures Tailhandier (Tailhandier Flats) and the partially dried river bed of Chenal du Courant, in the Boucherville Islands (Figure 1), located in the St. Lawrence River (Québec, Canada) between the cities of Montréal (west bank) and Boucherville (east bank). The Grandes Battures Tailhandier include wetlands, mainly high marshes; they have been used as a disposal site for dredged spoil by the Montréal Port Authority, which delegated management of the site to the Canadian Wildlife Service of Environment Canada in 1998 to ensure the protection of resident wildlife. The Boucherville Islands also comprise a provincial park, a golf course, corn fields, and a managed pond for waterfowl. Until 1980, the Tailhandier marshes were dominated by *Phalaris arundinacea, Typha angustifolia, Butomus umbellatus, Bolboschoenus fluviatilis,* and *Schoenoplectus* spp. (Pilon *et al.*, 1980). Since then, however, the site has been progressively taken over by *Phragmites*, a process that is the subject of this study.

ACQUISITION OF LAND-USE, SEDIMENT, AND HYDROLOGICAL DATA

Land-use information, location of dredged spoil disposal sites in the Boucherville Islands, and identification of sites colonized by *Phragmites* in the St. Lawrence River prior to and after 1980 were gathered from aerial photographs, maps, a literature review, and databases and verified by telephone interviews. Detailed methods and results can be found in Hudon *et al.* (2005). Sediment samples from the upper 10 cm were collected in 2000 and 2001 in Boucherville ($n = 40$) and in wetlands located on the islands of Pointe-aux-Trembles ($n = 27$), Varennes ($n = 31$), Verchères ($n = 25$), and two sites on the north shore of Lake Saint-Pierre (Rivière-du-Loup, $n = 22$ and Pointe-du-Lac, $n = 29$) (Figure 1). At each site, samples were taken at regular intervals along transects perpendicular to the shoreline in the elevation belt at which *Phragmites* can occur. At the Boucherville site, sediment samples were taken at approximately 100 m from the nearest *Phragmites* colony; those areas were subsequently invaded. Other sites also supported the same plant assemblages but were, and remained, free of *Phragmites*. Percentage of volatile solids (organic combustible compounds), nutrients (Kjeldahl organic nitrogen and total phosphorus), and pH were determined (APHA, 1995).

Daily water levels at Montréal Harbour (Jetty No. 1, gauging station 15520) were obtained for the 1977-2002 period (DFO, 2003). The source data, referenced to the International Great Lakes Datum of 1985 (IGLD85, 5.560 m) were adjusted to mean sea level (MSL, 5.579 m). A numerical elevation model (1×1 m horizontal and 10 cm vertical resolution) of the study area was derived from laser topometry data (LIDAR, Light Detection And Ranging) (IJC, 2001) and used in conjunction with daily water levels to calculate three hydrological variables (mean water height, number of wet/dry transitions, and number of days flooded) for each pixel of the study area. Hydrological variables were calculated for the entire growing season (April 1 to October 31) and for the period of horizontal rhizome growth (July 1 to October 31) of each year between 1979 and 2002.

ASSESSMENT OF *PHRAGMITES* PROPAGATION

Phragmites areal cover over 7 y was assessed from aerial photographs (1980, 1988, 1994, 1995, and 1999; 1:5,000 to 1:15,000, black and white or colour, stereoscopic) and remote sensing (vertical videography of 1996 with a resolution of 3 m and multispectral IKONOS of 2002 with a resolution of 4 m) images of the Boucherville Islands taken from July to October. The location of the colonies was determined visually by stereoscopic photo-interpretation of aerial photographs and on computer screen for remote sensing images. Among three observers delineating a surface of about 0.03 ha, error was estimated at about 10%. Aerial photographs and delineated colonies were digitized, corrected for distortion, georeferenced, and assembled into a mosaic using the Geomatica software (PCI Geomatics Enterprises, Toronto, Ontario, Canada). The resolution for all maps was adjusted to 1 m

to correspond to the 1-m grid of the elevation model. It was assumed that observed colonies were dense enough to permit extrapolation for the images of lower resolution. For each annual cover, *Phragmites* colonies were digitized as individual polygons using the MapInfo geographic information system (MapInfo Corporation, Troy, New York, USA). Each year's data was compiled into a separate layer of information that was then superimposed onto the numerical elevation model of the study site. This sequential process allowed us to determine the number and elevation of pixels in which *Phragmites* remained absent (0, 0), appeared (0, 1), disappeared (1, 0) and persisted (1, 1) for each period between consecutive aerial photographs/remote sensing images. Spatial statistics (total surface area, number and surface of old and new colonies, perimeter, etc.) were assessed for each image using ArcView with the Spatial Analyst module (Environmental Systems Research Institute, Redlands, California, USA). Differences in spatial statistics between each pair of consecutive images were used to assess mean annual gains stemming from vegetative growth (two variables) and from dispersion (two variables). Vegetative growth was quantified using the rate of total areal gains (colonization, ha·y⁻¹) and the progression rate of the edge of persistent colonies (progression, m·y⁻¹), as the ratio of annual total surface gain to the total perimeter of the (> 40) colonies on every image. Gains stemming from dispersion were assessed using the mean annual rate of appearance of new colonies (new colonies·y⁻¹) and the proportion of total areal gains resulting from the appearance of new colonies (% ha·y⁻¹), although some of the increase may be due to vegetative progression during multi-year intervals.

Modeling *Phragmites* vegetative propagation from hydrology

Hypothetical factors controlling the vegetative progression of *Phragmites* were included in a spatial model (Table I): distance to the closest colony of *Phragmites* (m), slope (m·m⁻¹ vertical) and orientation (degrees from the north) of progression, and factors representing the hydrology of the previous year's growing season (average height with respect to the water level, number of days flooded, and number of wet/dry transitions). The growing seasons of 1994 and 1995, which were characterized by average (6.39 m) and low (5.76 m) water levels, respectively, were considered to explain the progression observed in 1995 and 1996. Individual pixels were sampled according to a cohort (prospective) sampling plan

(Hosmer & Lemeshow, 2000). For each year, 500 pixels were randomly selected within each 1-m interval of a 10-m-wide belt located around *Phragmites* colonies, for a total sample of 10,000 pixels. The changes of state (*i.e.,* appearance or disappearance) from one year to the next were related to our selected factors using logistic regression. Separate models were derived to explain the probability of colony retreat (from where *Phragmites* were present) and advancement (to where they were absent). The net gains of *Phragmites* resulting from the sequential application of both models were validated by comparing the predicted surface to that measured on our images for varying time intervals.

Results

Sediment and hydrological characteristics

The first hypothesis, concerning the suitability of Boucherville Islands and river sediments to sustain *Phragmites*, was tested by assessing the characteristics of sediments found in St. Lawrence River wetlands with respect to the plant's tolerance range as reported in the literature. River sediments exhibited a broad range of pH levels (4.9 to 7.7). They also contained low to moderate percentages of organic matter (0.4 to 14.6%) and wide-ranging concentrations of total phosphorus (0.42 to 1.60 mg P·g⁻¹ dry sediment) and organic nitrogen (0.2 to 5.5 mg N·g⁻¹ dry sediment).

Average annual water-levels near Montréal have decreased by about 50 cm over the last 25 y; daily minimum and maximum values have also declined (Figure 2). Hydrological conditions for the years in our *Phragmites* dataset vary considerably, including years of high (> 6.8 m: 1980, 1996), intermediate (6.3 to 6.8 m: 1988, 1994), and low (≤ 6.2 m: 1995, 1999, 2001) annual levels. In conjunction with the low relief of the study site, which rises linearly between 5.0 and 8.0 m, the large range of water level results in widely different flooding conditions from year to year. Applying the numerical elevation model to maximum (in 1986: 7.16 m) and minimum (in 2001: 5.82 m) mean annual water-level conditions showed that about a third of the study site (≤ 6.25 m) was constantly flooded in 1986, whereas the same area was flooded for fewer than 40 d in 2001.

Assessment of *Phragmites* propagation

Phragmites is mentioned in some pre-1960 studies of the St. Lawrence River flora (Pageau, 1959), although it

Table I. Description of *Phragmites australis* average annual vegetative progression and dispersion between 1980 and 2002 on the Grandes Battures Tailhandier (Boucherville Islands), assessed by photo interpretation.

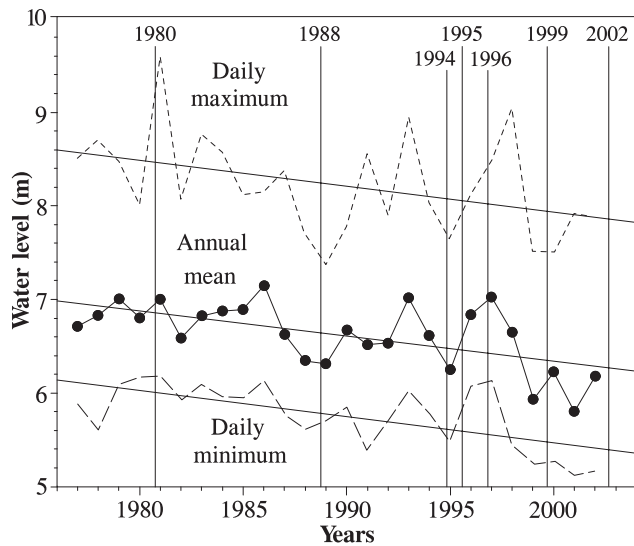| Interval	Surface at the end of the interval (ha)	Rate of vegetative progression		Dispersion	
		Surface gains of established colonies (ha·y⁻¹)	Linear progression of the edge of colonies (m·y⁻¹)	Dispersion gains (% total)	Annual number of new colonies (new colonies·y⁻¹)
1980-1988	4.52	0.46	1.13	10.4	2.1
1988-1994	15.34	1.80	1.73	30.5	14.5
1994-1995	16.09	0.75	0.47	14.1	21
1995-1996	19.85	3.76	2.28	1.6	10
1996-1999	23.19	1.35	0.67	6.9	11.3
1999-2002	32.63	3.15	1.68	9.7	5.6

FIGURE 2. Annual variations in mean, minimum, and maximum daily water levels of the St. Lawrence River at Montréal harbour (Jetty No. 1) between 1977 and 2002, as well as overall trend for the period. Occasions on which *Phragmites australis* surface cover in Boucherville Island was measured are shown.

was "neither very frequent, nor very developed" (Dansereau, 1959). Numerous newly colonized sites in Lake Saint-Louis, La Prairie Basins, Varennes, Contrecoeur, and the Berthier-Sorel Archipelago (Figure 1) were added to the list after 1980.

The first colonies appeared at Boucherville in 1980 (0.86 ha) and were located in the bed of Chenal du Courant, a natural flood channel located west of the Grandes Battures Tailhandier (Figures 1 and 3). Colonies were numerous (> 50), small (< 0.15 to 0.3 ha), and scattered along the SW/NE axis, corresponding to predominant current and wind directions. These first colonies were located within previously established marsh plant assemblages in the bed of Chenal du Courant, well away from dredged spoil deposits and the modified shores of the park and golf course.

Between 1980 and 1988, early colonies grew and merged such that more than half of the area was covered by large (> 0.21 ha) colonies. Average gains in total surface area and in distance at the edge of colonies were low (Table I). Seventeen new, small (< 0.06 ha) colonies appeared more than 1 km north of those observed in 1980, on Grandes Battures Tailhandier *per se*. By 1994,
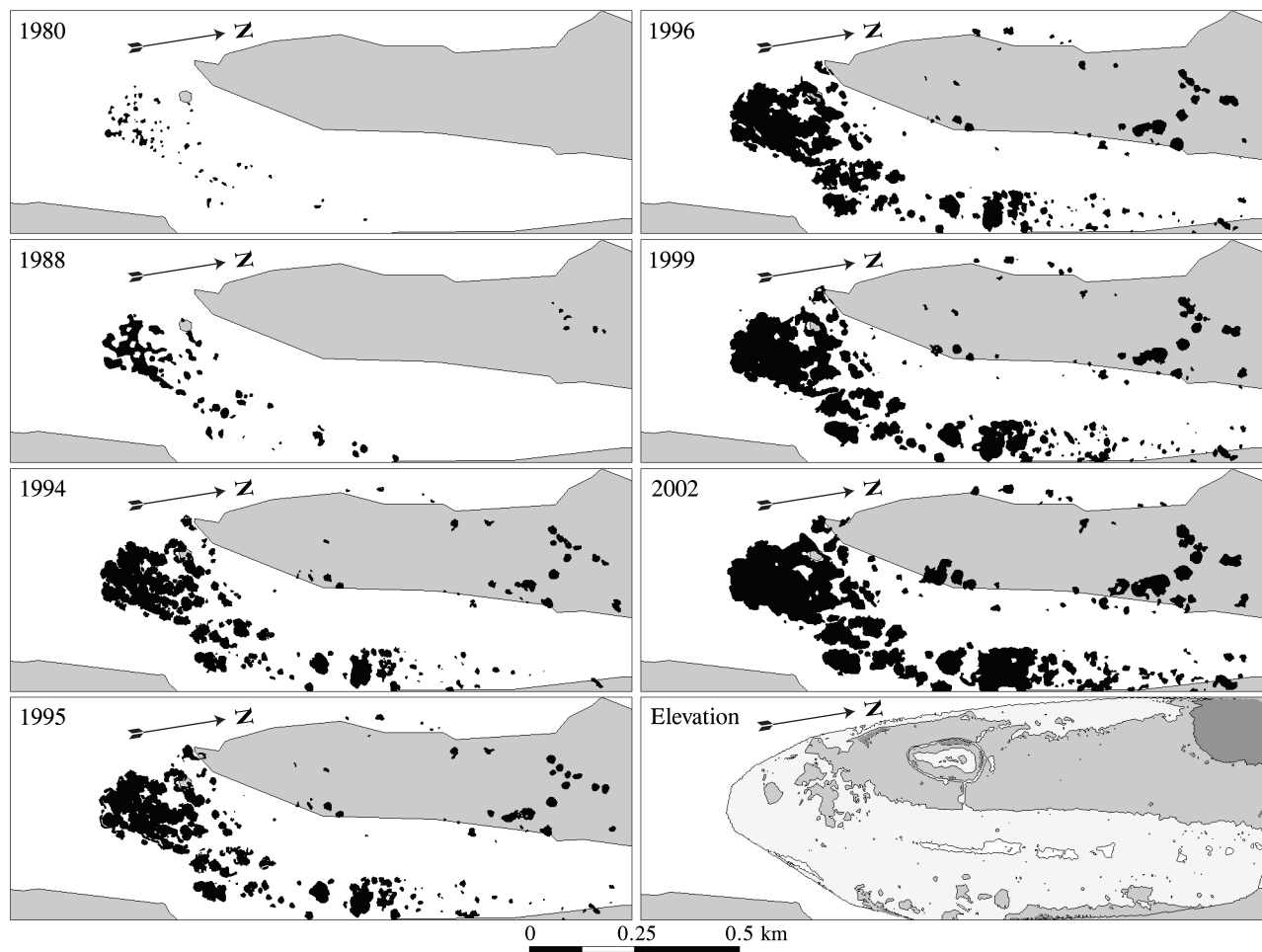

FIGURE 3. Distribution of *Phragmites australis* between 1980 and 2002. Dry land identified on topographical maps, which corresponds roughly to ground higher than 6.5 m (in grey), is shown for reference on all maps. Elevation map showing the areas above 5.5 m (light grey), 6.5 m (medium grey), and 7.5 m (dark grey).

previously established colonies encompassed > 70% of the colonized territory, which covered the entrance of Chenal du Courant entirely. All indicators of vegetative progression and dispersion exhibited higher values than in the previous period. Dispersion appeared particularly important during the 1988-1994 period, as 30.5% of total gains in surface area resulted from new colonies. In total, 87 new colonies were observed in the SW/NE axis of Chenal du Courant (next to the golf course), as well as on the western shore of Grandes Battures Tailhandier, next to dredged spoil deposits.

The two subsequent time intervals are particularly revealing as they represent estimates of colonized surface over consecutive annual periods (1994-95 and 1995-96), thus showing the large interannual variability of *Phragmites* rate of increase. Vegetative gains displayed a five-fold variation between years, with much higher values over the 1995-96 period. Conversely, 1994-95 represented a more active period of dispersal than 1995-96, as 21 new colonies were formed (twice as many as in 1995-96), representing 14% of gains in total surface area for that year (seven times that of 1995-96).

During the last two intervals (1996-99 and 1999-2002) vegetative gains exhibited a three-fold increase, whereas the number of new colonies per year decreased two-fold between consecutive periods. In summary, the largest gains in surface area resulted from vegetative propagation of existing colonies (88% on average), although the formation of new colonies away from established ones could represent up to 30% of total surface gains (as during 1988-1994). The distance of progression of the edge of colonies was highly variable through time; the highest values (> 4 m·y^{-1}) were recorded in 1995-96 and 1999-2002. Overall, the surface area colonized by *Phragmites* over time grew exponentially ($r^2 = 0.96$, $n = 7$, $P < 0.0001$) at a rate of 18% per year, suggesting that *Phragmites* will colonize all the area available on the Grandes Battures Tailhandier (135 ha) before the year 2009, leaving only higher ground to other species.

Effects of hydrology on *Phragmites* propagation

Highly significant negative relationships were found between mean water levels during the previous growing season and the rise in surface area of the colonies as well as with the distance gained at their edge (Table II), revealing that *Phragmites* vegetative propagation is accelerated during the year following a drop in mean water levels. In contrast, the number of new colonies (Table I) was not correlated to water levels.

The effects of hydrological conditions on *Phragmites* propagation were examined more closely over the 1994-95 and 1995-96 intervals, coinciding with a 63-cm drop in mean water levels (July 1 to October 31) between 1994 and 1995. Flooding of *Phragmites* in water 10-90 cm deep in 1994 resulted in little vegetative growth in 1995, whereas the rates of vegetative growth were three-fold higher in 1996, following the 1995 drop in water levels. The largest gains were observed for colonies located 40-60 cm above average water levels. Similar observations were made when comparing the small gains observed under 1996-99 levels (mean water level = 6.51 m) with the high rate of vegetative growth recorded in the 1999-2002 period (mean water level = 5.72 m).

Modeling *Phragmites* propagation

To explain the rate of progression of the edge of colonies, the key factors established by logistic regression were the north/south component of the direction of propagation, the number of days during which the colonies were submerged, and the average water level above- or belowground during the growing season of the previous year. *Phragmites* was dominant under brief (*e.g.,* 20 d total) and shallow (*e.g.,* plants located 15 cm above average water level) flooding conditions and in the southerly direction, but was less successful under extended (over 90 d) flooding conditions. Of the other factors examined, neither the east/west component of the propagation direction, the ground slope, nor any crossed variables was statistically significant despite the large sample (> 30,000 pixels) used. The seasonal variability in water level, expressed as the number of wet/dry transitions, was not related to *Phragmites* dynamics and was thus omitted from further analyses.

We looked for environmental factors explaining the advancement of the edge of *Phragmites* colonies when it dominates its competitors. Three explanatory variables were significant in the logistic regression: the logarithm of the distance to the nearest colony, the north/south component of the direction of propagation, and the average water level above- or belowground (Figure 4a). Gains were more important in the southerly direction, but the advance of the edge of colonies was constrained by deeper flooding.

A similar approach was used to develop a separate model explaining the retreat of the edge of *Phragmites* colonies (Figure 4b). The explanatory variables in this case were the distance from the edge of the colony inwards, the average height of the water level above- or belowground, and flood duration. In this model, the probability of retreat is higher for plants that are flooded for long periods or, conversely, are located too far above the water level. Thus, plants located well within the colonies and that sustain a moderate duration of flooding are virtually immune to extirpation. With the flooding conditions

Table II. Equations linking mean water level during the previous season with the mean annual rate of total surface gain and the rate of progression of the edge of *Phragmites australis* colonies over the subsequent growing season, for two time intervals.

| Dependent variable	Intercept	Slope	Time interval	Adjusted r^2 (p)
Mean annual rate of progression of the edge of colonies (m·y^{-1})	9.54	−1.27	April 1 to October 31	0.56 (0.05)
Mean annual rate of total surface gains (ha·y^{-1})	20.67	−2.91	April 1 to October 31	0.90 (< 0.01)
Mean annual rate of progression of the edge of colonies (m·y^{-1})	10.20	−1.44	July 1 to October 31	0.52 (0.06)
Mean annual rate of total surface gains (ha·y^{-1})	22.87	−3.40	July 1 to October 31	0.91 (< 0.01)
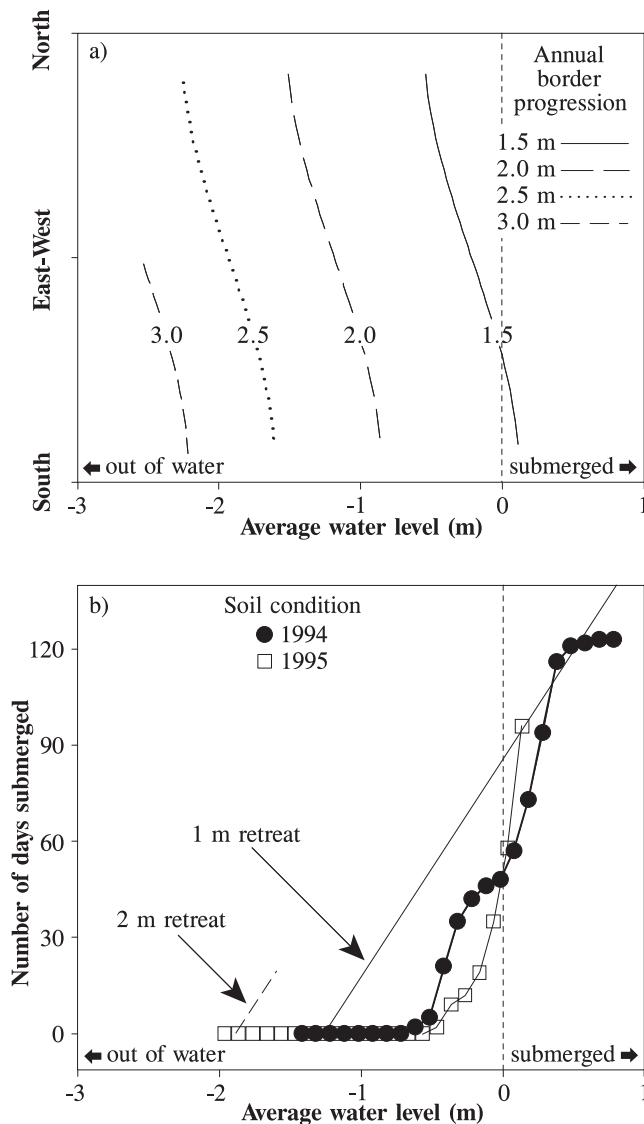
FIGURE 4. Curves describing the magnitude of annual shifts in the edge of *Phragmites australis* colonies. The distance of border progression or retreat depends on the average water level at the plant's location. a) Progression distance is also a function of the new shoots' location relative to the colony as expressed by the north-south component of the direction of propagation. b) Retreat distance on the other hand is affected by the total flooding duration. Hydrological conditions recorded in 1994 and 1995 at Boucherville that enabled us to predict the retreat of colonies observed in 1995 and 1996 are shown.

predicted sequentially on each consecutive time interval (years) as if they were of equal probability. A comparison of observed *Phragmites* distribution in 1999 with its predicted distribution for the same year from the initial colony distribution in 1996 (projected over three years) revealed major fine-scale differences in distribution with the predicted colony outlines having dampened features compared to observations.

Although the detailed geographic distribution of *Phragmites* expansion is not well predicted by our model, the predicted global change in colonized surface at the scale of the study area (135 ha) was relatively accurate. The comparison of all possible projections to the observed changes revealed that total predicted surface gains tend to be conservative and to underestimate the overall progression, although not significantly. For example, predictions of colonized surface area differed from observations by + 127% (1994-95) and -43% (1995-96) for single-year projections, whereas the relative difference dropped to less than 25% for 3-y (1996-99) to 8-y (1994-2002) projections.

Discussion

ECOLOGY OF *PHRAGMITES* PROPAGATION

HYPOTHESIS 1: CONDITIONS FAVOURABLE TO PHRAGMITES IMPLANTATION AND GROWTH

Phragmites can grow under a wide range of nutrient concentrations (Romero, Brix & Comín, 1999). In our results, nutrient concentrations, percentage of organic matter, and pH in sediments from St. Lawrence wetlands were well within the range of tolerance for the species. Seven percent (n = 10, from the two Lake Saint-Pierre sites) of all samples fell below the optimum-growth threshold of pH 5.5 (Shay & Shay, 1986), although *Phragmites* has been shown to tolerate pH values as low as 2.9 (Small & Catling, 2001). All other sediment characteristics measured in the St. Lawrence were well within *Phragmites*'s tolerance range.

The presence of *Phragmites* at certain sites in the St. Lawrence would thus likely depend upon the availability and successful implantation of seeds and/or rhizomes, circumstances that may result from anthropogenic disturbances. Land alteration and disruption of natural shorelines have been shown to favour colonization by *Phragmites* in Delaware Bay (Chambers, Meyerson & Saltonstall, 1999).

The study site at Boucherville is one of the few remaining wetlands in the Greater Montréal area, where more than 80% of wetlands have been eliminated since European settlement (Kessel-Taylor, 1984). The area directly surrounding the Grandes Battures Tailhandier has been subjected to numerous alterations, including dredged spoil deposits, shoreline landfills for development, and excavation of a pond for waterfowl in 1999. Many St. Lawrence River islands colonized by *Phragmites*, particularly the outer islands of Contrecoeur, Saint-Ours, and Aux Sternes have been built entirely with clay excavated from the navigation channel (DOT, 1994). At Des Barques Islands, the presence of *Phragmites* coincided with dredged spoil deposits (Gratton, 1998). *Phragmites*

experienced in 1994 and 1995 (Figure 4b), colonies located higher above the water table, especially in 1995, or that were flooded extensively, receded by one or two metres. Most of the colonies considered were not affected by such conditions.

The application of the models to an initially circular colony of *Phragmites* illustrates the advance and retreat of the edge of a colony located on a regular slope ranging from 1.5 m above the water to a depth of 1.5 m below (Figure 5a). The net gains after the results of advance and retreat models were combined using the probabilities from the domination model are shown on Figure 5b. When applying the same models to distributions of *Phragmites* observed on aerial photographs, retreat and advance were
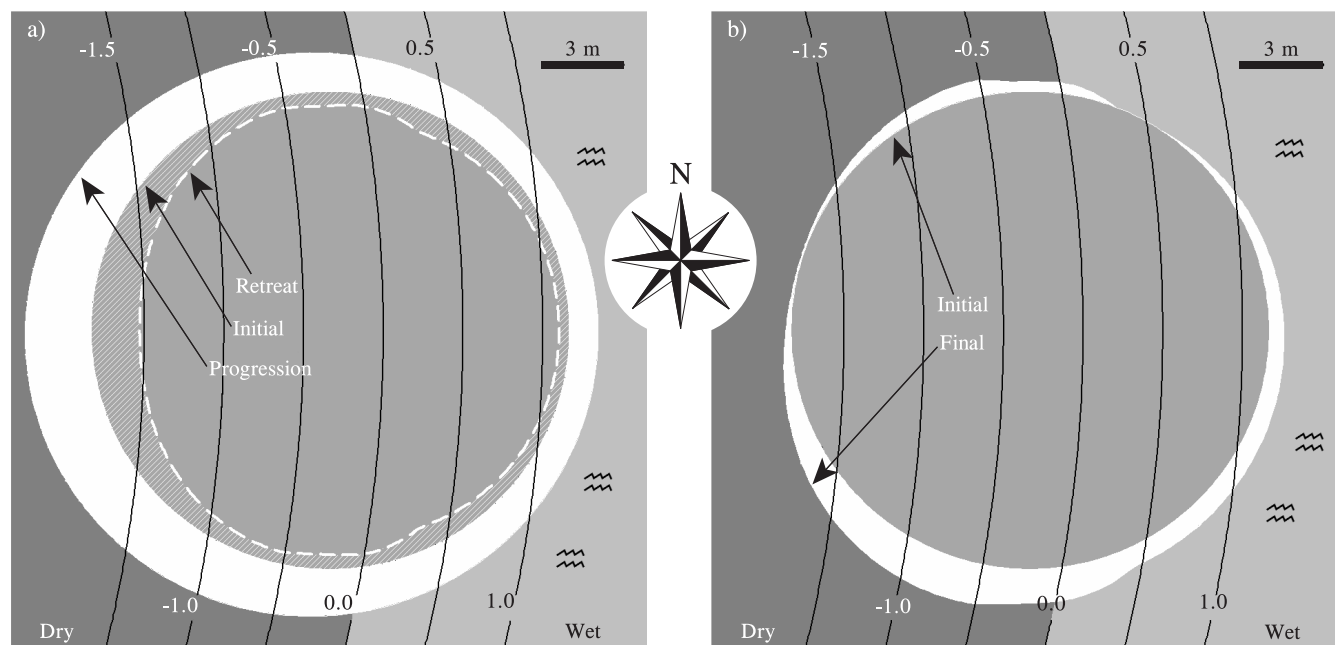
FIGURE 5. Illustration of how *Phragmites australis* colonies shift as a result of the combined progression and retreat of their borders according to our models. At the beginning of 1994, a circular colony is located on a steep slope straddling the water margin. During the growing season, the colony will be exposed to mean water levels shown as isolines. a) The colony is predicted to progress (expanded white area) or retreat (dotted line, hatched zone) as predicted by the models described by Figures 4a,b. b) Net border movement is obtained by combining progress and retreat proportionally to their modeled probability of dominance. In the water zone represented here, the hydrological conditions experienced in 1994 always resulted in net surface gains in 1995, albeit variable depending on the position.

colonization rates for the entire Boucherville Archipelago were lower than rates observed at five other sites in the St. Lawrence River. Although all colonized sites have been subjected to various degrees of anthropogenic disturbance, including shoreline modification, nutrient input, and hydrological alterations (Hudon *et al.,* 2005), there is no obvious correspondence between *Phragmites* propagation and a given type of modification at the scale of individual sites. This is in accordance with the analysis of Rice, Rooth, and Stevenson (2000), concluding that the linkage between local disturbance and expansion is not clear.

The first colonies at Boucherville were detected in the partially filled bed of the natural flood channel (Chenal du Courant). This suggests that *Phragmites*'s initial implantation at the site resulted either from wind-dispersed seeds or from drifting rhizome fragments. The year of introduction also remains uncertain: although colonies were visible on aerial photographs taken in 1980 (this study), *Phragmites* was not mentioned in an inventory conducted in the late 1970s (Pilon *et al.,* 1980), possibly because colonies were small and located well within the dense beds of *Typha angustifolia* and *Phalaris arundinacea*, which dominated Boucherville wetlands at that time.

HYPOTHESIS 2: GAINS THROUGH VEGETATIVE CLONAL GROWTH ARE MORE IMPORTANT THAN COLONY DISPERSION VIA SEED GERMINATION

Once *Phragmites* has colonized a site, vegetative propagation is the main avenue of colonization, although seed germination could also serve as a dispersal mechanism. Examination of colony distribution and propagation at Boucherville revealed that most gains (88% on aver-

age) in surface area resulted from clonal expansion, which was adequately modeled over time. This result is in accordance with the conclusions of Amsberry *et al.* (2000), who demonstrated the importance of clonal integration in colonizing less favourable locations. The appearance of very small colonies at large distances (> 1 km) from previously established ones could indeed result from either the drift of rhizome fragments or the germination of seeds. Although seeds have variable fertility (Gervais *et al.,* 1993), the probability of seed germination should increase with the total number of seeds produced, which likely becomes considerable near a well-established stand.

HYPOTHESIS 3: EFFECTS OF HYDROLOGY ON VEGETATIVE PROPAGATION

Our results showed the effects of hydrology on the vegetative propagation of *Phragmites*, derived from the analysis of aerial photographs, remote sensing images, and from modeling. This species exhibited a wide tolerance to the magnitude and duration of flooding and drainage conditions. *Phragmites* persists under dry conditions (1 m above the water table) and tolerates flooding in 20 cm of water for 90 d. Conversely, we observed a retreat of *Phragmites* colonies under conditions either too dry ($\geq$ 1.5 m above the water table) or too wet (flooding with > 0.5 m of water). *Phragmites* propagation was observed in the belt of elevation in which water-level variations were greatest. *Phragmites* can also temporarily withstand adverse water-level conditions, to resume its advance when favourable conditions return. For an established colony, the probability of disappearance was lowest for plants located near the centre of the colony and for those located between 1 m above and 0.5 m below the

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mean water level of the previous growing season (July 1 to October 31).

MODELING *PHRAGMITES* PROPAGATION

There are few modeling studies of *Phragmites*. De Swart *et al.* (1994) developed a logistic regression model predicting the realized niche; that is, the immersion conditions dominated by four marsh species, including *Phragmites*. The absence of a lag period in the model was proposed to explain its weaknesses in forecasting plant abundance and the lack of upslope propagation of flooded colonies. Our results support their hypothesis, inasmuch as local hydrological conditions occurring over the previous growing season were significantly related to the propagation of *Phragmites*, among other important local factors that we could not account for. Such limitations illustrate the inherent difficulty of capturing ecosystem complexity through a set of simple rules (Guisan & Zimmermann, 2000; Higgins, Richardson & Cowling, 2001; Higgins, Lavorel & Revilla, 2003). Nonetheless, since actual propagation or retreat differed from our model predictions in a spatially autocorrelated way, we hypothesize that important factors influencing local clone growth — such as microtopography, litter biomass, drainage, and possibly competition from other species — are not randomly distributed. This is a common feature of spatial models: although they are not biased, their detailed predictions may not resemble observations, since the noise added to average predicted values is often autocorrelated (Goovaerts, 1997).

In spite of its inability to predict the shape of expanding colonies, our model succeeded in identifying important factors acting at a larger scale, such as hydrology and direction of propagation (a proxy for exposure to sun), which represented the main objective of this study. *Phragmites* does not grow well in the shade (Shay, de Geus & Kapinga, 1999); cool weather and low light intensities can also slow its growth (Haslam, 1972). In that respect, it is possible that the effect of climate could be combined with that of water level to affect *Phragmites* propagation, as hot, dry, and sunny summers often come with low water levels, all factors stimulating vegetative growth (Wilcox *et al.,* 2003).

At 1 to 5 m in height (Marie-Victorin, 1995), *Phragmites* is one of the tallest marsh plants. This confers upon it a strong advantage in the competition for light (Lindsay, 2000), since dense stands may block up to 99% of incident radiation (Hudon, 2004). *Phragmites*'s southerly propagation thus reflects its heliophilic character since, in this direction, its mature stems do not shade new ones, whereas towards the north, competitors more tolerant to shade may maintain themselves or even gain ground against it.

FUTURE CONSIDERATIONS FOR ST. LAWRENCE RIVER RIPARIAN ECOSYSTEMS

The results of the present study and other published information underscore the important elements of feedback existing between *Phragmites* and its environment, especially hydrology. In the St. Lawrence River system, shoreline alteration, excavation of the navigation channel, and water level regulation have reduced the magnitude of floods, decreased circulation in shallow littoral areas, and reduced the efficiency of the river in flushing sediments and organic matter downstream. These changes have led to the progressive clogging of side channels and shallow lateral areas (Hudon, 2004), a phenomenon amplified by the proliferation of *Phragmites* and other dense emergents such as *Typha* spp.

As *Phragmites* colonies mature, overall plant biomass and litter accumulation increase; both factors further reduce water circulation and increase sediment and organic matter retention within dense stands. Over time, the conditions become less favourable for *Phragmites* growth, selecting for better adapted competing species (van der Werff, Simmers & Kay, 1987). In addition, reduced water circulation and organic sediment build-up may accentuate root anoxia and production of organic acids, both factors potentially explaining *Phragmites* die-back in European wetlands (van der Putten, 1997). Paradoxically, control measures like excavation of ditches, removal of aboveground biomass, or litter fire may facilitate *Phragmites* maintenance over time by improving water circulation and removing excessive organic matter from dense stands (Ostendorp, 1999). Well-maintained drainage ditches along highways may thus have been the initial reservoir allowing the spread of *Phragmites* in other habitats. In the St. Lawrence River, propagation of *Phragmites* might have been further facilitated by the destabilization of its natural wetland assemblages under the cumulative impacts of hydrological and shoreline alterations. The large increase in the number of colonized sites since 1980 indicates that the species is in expansion along the shores of the St. Lawrence River. Given the importance of riparian ecosystems, *Phragmites*'s proliferation and its effects on species diversity and habitat structure should be closely monitored in the future, especially in light of future modifications to hydrology, shoreline encroachment, and channel dredging.

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