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Exotic plant species of the St Lawrence River wetlands: a spatial and historical analysis

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Abstract

Aim To evaluate the importance (number of species, plant cover) of the exotic flora in seven well-defined sectors of one of the most important transportation waterways in North America. To determine the impact of exotic species on wetland plant diversity and reconstruct the spread of some invasive species.

Location St Lawrence River, southern Québec.

Methods The exotic flora (vascular plants) of wetlands bordering the St Lawrence River was studied using 713 sampling stations (25 m^2) along a 560-km long corridor.

Results Exotic species represent 13.7% of the vascular flora of the St Lawrence wetlands. The relative plant cover occupied by exotic species is high in some of the fluvial sectors (42–44%), but low (6–10%) in the estuarine sectors. Wetlands (marshes) surrounding islands were particularly susceptible to invasion by exotic plants. Historical, abiotic and landscape factors may explain the differences observed between sites. Purple loosestrife (*Lythrum salicaria* L.) is the most common exotic species of the St Lawrence wetlands, but other species, namely flowering-rush (*Butomus umbellatus* L.) and reed canary grass (*Phalaris arundinacea* L.) are much more invasive. There is no linear relationship between the exotic species cover and the diversity of wetland plants; low diversity sites can be dominated by either exotic or native plant species. In the other sites, exotic species generally have little impact on plant communities and can contribute to increase diversity. Common reed (*Phragmites australis* (Cav.) Trin. ex Steudel) and reed canary grass, both considered as exotic species in this study, clearly have a stronger impact on plant diversity than flowering-rush and purple loosestrife.

Main conclusions This study shows that the global impact of an invader cannot be adequately evaluated with only a few highly invaded sites. While nationwide strategies have been developed to control exotic species, large surveys are essential to adapt them to regional particularities.

Keywords
Butomus umbellatus, diversity, exotic species, herbarium specimens, invasive species, *Lythrum salicaria*, *Phalaris arundinacea*, *Phragmites australis*, St Lawrence River, wetlands.

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INTRODUCTION

In North America, exotic wetland weeds are among the most aggressive invaders of natural ecosystems. Several species, such as water hyacinth [*Eichhornia crassipes* (Mart.) Solms], purple loosestrife (*Lythrum salicaria* L.), and Eurasian watermilfoil (*Myriophyllum spicatum* L.), are believed to change vegetation structure, reduce the diversity of native plant species and associated wildlife, and alter the basic biogeochemical functions of wetlands (Aiken *et al.*, 1979; Gaudet & Keddy, 1988; Mehra *et al.*, 1999; Blossey *et al.*, 2001). Moreover, many species, including water hyacinth, Eurasian watermilfoil, and European frogbit (*Hydrocharis morsus-ranae* L.), slow boat traffic and curtail recreational activities (Aiken *et al.*, 1979; Catling & Porebski, 1995; Mehra *et al.*, 1999). In the United States, costs associated with the control of introduced wetland weeds are estimated at 145 million dollars per year (Pimentel *et al.*, 2000).

Rivers used for transport are particularly susceptible to invasion by wetland weeds, as sailing vessels often carry exotic seeds or rhizomes in solid or water ballast (Aiken *et al.*, 1979; Thompson *et al.*, 1987; Mills *et al.*, 1997). The banks of these rivers are densely populated, and other vectors, such as horticulture, can also contribute to the introduction of exotic plants (Thompson *et al.*, 1987; Catling & Porebski, 1995; Reichard & White, 2001). As rivers function as corridors for plant dispersal (Pyšek & Prach, 1993; Johansson *et al.*, 1996), the spread of introduced wetland species is usually a very rapid phenomenon (Thompson *et al.*, 1987; Catling & Porebski, 1995; Lachance & Lavoie, 2002). Although there is a large amount of literature about invasive wetland plants, there are very few works dealing with the biogeography of exotic species along major river systems (Planty-Tabacchi *et al.*, 1996; Mills *et al.*, 1997). Most studies focus on a small number of highly invaded wetlands and provide little information about the factors favouring or limiting the spread of exotic species along a riparian corridor (Johansson & Nilsson, 1993; Johansson *et al.*, 1996). Furthermore, without an extensive database covering a large part of a river system, it is difficult to assess the global impact of exotics on the biodiversity of invaded ecosystems.

In this study, we analysed the exotic flora of wetlands bordering the St Lawrence River, one of the two most important transportation waterways in North America, along with the Mississippi–Missouri system. The St Lawrence River is travelled by more than 19,000 commercial ships per year, carrying a total of 100 million tons of goods (Centre Saint-Laurent, 1996). We used more than 700 sampling stations along a 560-km long corridor to evaluate the importance (number of species, plant cover) of the exotic flora in seven well-defined fluvial and estuarine sectors of the river. We also determined the impact of exotic species on wetland plant diversity and used more than 1900 herbarium specimens to reconstruct the spread of three invasive species to gain an appropriate historical perspective. We hypothesized that the largest concentrations of exotic species would be located near Montréal and Québec City, the two main ports and urban areas bordering the river. We also hypothesized a negative linear relationship between the exotic species cover and both the species richness and the diversity of wetland plants. To our knowledge, this is the first extensive biogeographical survey of wetland exotic flora bordering a major river system.

METHODS

Field sampling

For the survey of the exotic flora of the St Lawrence River wetlands, we used a large database that was collected by the Centre Saint–Laurent (Environment Canada) from 3 July to 25 August 2000 (fluvial section of the river) and from 23 July to 24 August 2001 (estuarine sections). This database (M. Jean & G. Létourneau, unpublished data) was created to validate the interpretation of remote sensing images (MEIS-II) taken in 2000, and covering St Lawrence wetlands. The 713 sampling stations were spread along a 560-km long corridor (Fig. 1) from Cornwall (45.0° N, 74.3° W) to Trois-Pistoles (48.1° N, 69.1° W).

To select the position of sampling stations, the St Lawrence River was divided into seven sectors on the basis of available information about the distribution of wetlands (Létourneau & Jean, 1996): five in the fluvial section of the river (from Cornwall to the outlet of Lake St Pierre), where there are large concentrations of wetlands, one in the freshwater estuary (from the outlet of Lake St Pierre to Montmagny), and one in the brackish estuary (from Montmagny to Trois-Pistoles). In the estuarine sections, there are no major wetland concentrations. Wetlands are distributed along the north and south shores of the St Lawrence River in the freshwater estuary but only along the south shore in the brackish estuary. Downstream of Trois-Pistoles, there are very few wetlands and they are sparsely distributed (Centre Saint-Laurent, 1996). In each sector, existing vegetation maps (Létourneau & Jean, 1996) were used to delineate each marsh (wetland dominated by emergent herbaceous vegetation) or swamp (dominated by trees or shrubs) and to identify all vegetation communities present in those wetlands. At each site, a minimum of one sampling station per vegetation community was randomly positioned using a geographical information system. During the summers of 2000 and 2001, sampling stations were located in the field using a differential global positioning system. The final positions of stations were adjusted *in situ* to ensure that they covered a homogeneous vegetation community and were then recorded with the global positioning system. Additional stations were sampled to cover vegetation communities that were not reported in previous inventories.

The wetland type corresponding to each station was noted (Buteau *et al.*, 1994) and a 5 × 5 m quadrat was delineated. All vascular plant species present in the quadrat were identified and their respective cover was estimated using a semi-quantitative scale: <1%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75% and 76–100% (Jean & Bouchard, 1993). The water level was measured but only when it was above the soil

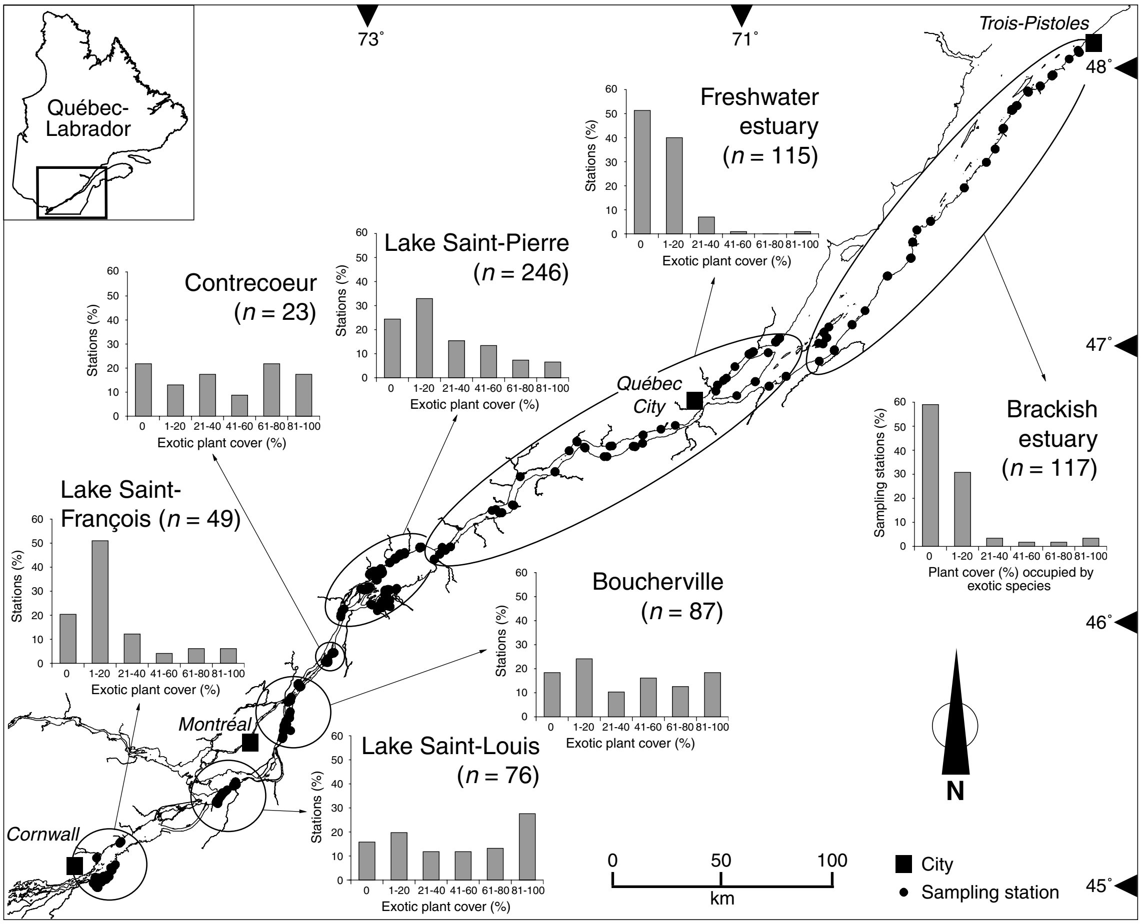

Figure 1 Spatial distribution of the cover occupied by exotic vascular plant species in the wetlands of the St Lawrence River. For each sector of the river, the percentage of sampling stations with a specific relative exotic cover (20%-classes) is indicated.

surface. Otherwise, it was simply characterized as below the soil surface.

Data analysis

All vascular plant species sampled were classified as native or exotic according to various botanical sources, mainly Rousseau (1968, 1974) and Marie-Victorin (1995). We decided to consider reed canary grass (*Phalaris arundinacea* L.) and common reed (*Phragmites australis* (Cav.) Trin. ex Steudel) as exotic species. Both species are native to North America (Dore & McNeill, 1980; Marks *et al.*, 1994; Merigliano & Lesica, 1998) but there is a growing body of evidence that the recent expansion of the cover and of the distribution of these plants in North American wetlands is the result of introduced cultivars or of invasive hybrids of North American and European genotypes (Dore & McNeill, 1980; Marks *et al.*, 1994; Chambers *et al.*, 1999; Rice *et al.*, 2000; Maurer & Zedler, 2002). Based on previous reports (Morency, 1966; Deschamps, 1968; Cantin & Blais, 1976; Tessier *et al.*, 1981; Mousseau, 1987), both species are clearly invasive in St Lawrence wetlands.

The percentage of flora (number of species) represented by exotic species was calculated for each sector of the river. For plant cover data, the median value of each class of the semi-quantitative scale was used. For each sampling station, the median values of the cover of all exotic species were totalled, and the result was divided by the sum of the median values of all species identified (native and exotic). We then determined the percentage of plant cover occupied by exotic species, i.e. the relative exotic cover. As the cover of exotic species is highly variable between stations, a global assessment of the exotic cover for a particular sector or site was performed. The exotic cover was calculated by totalling the median values of the exotic species cover from all stations and dividing the result by the sum of the median values of all species sampled in all stations of the sector or site.

Median values of plant cover data were also used to evaluate the impact of exotics on species richness and diversity of native vascular plants. Sampling stations were grouped (10%-classes) according to the relative plant cover occupied by exotic species. Box plots were constructed to illustrate the relationship between the importance of the exotic species cover and both the associated species richness and the Shannon diversity index (Magurran, 1988). The median values of plant cover data were used to calculate the index, which incorporated native and exotic plant species. Regressions between species richness, diversity and exotic plant cover were calculated using SPSS software (SPSS Inc., 1999). Four exotic species (common reed, flowering-rush (*Butomus umbellatus* L.), purple loosestrife, reed canary grass) are considered highly problematic in Canada and eastern North America (White *et al.*, 1993; Chambers *et al.*, 1999). The impact of these plants on species richness and diversity were therefore estimated, but only at stations where the species cover was higher than 50%, i.e. at stations strongly dominated by these exotic species. Species richness and diversity values were compared using the notched box plot method of Velleman & Hoaglin (1981).

Historical analysis

In order to evaluate the impact of exotic species on native wetland plant communities, it is necessary to have an estimate of the year of arrival of the main invaders in each sector of the St Lawrence River. The year of arrival distinguishes recent invaders from old ones, the latter being more likely to have large impacts on plant communities because those colonies are well-established and have had time to develop ecological interactions with native species. Using herbarium specimens from the five main herbaria of Québec (MT, MTMG, QFA, QUE, SFS) and the two herbaria of the Canadian Government (CAN, DAO), we reconstructed the spread of three species that were *a priori* considered to be the most invasive plants of the St Lawrence wetlands, i.e. flowering-rush, purple loosestrife and common reed. Each herbarium specimen was checked for possible misidentification and the specimen number, sampling location, year of sampling, and habitat characteristics were recorded. Only specimens collected in Québec were examined and any duplicates and specimens with imprecise information about sampling location were discarded. Data on selected specimens were incorporated into a geographical information system to reconstruct the evolution of the distribution of the three species during the last 200 years. Furthermore, literature on botanical surveys conducted in the St Lawrence River wetlands was carefully consulted for any mention of exotic species and their abundance.

RESULTS

Spatial distribution of exotics

Thirty-nine exotic and 246 native vascular plant species were sampled in wetlands along the St Lawrence River. In 2000–2001, exotic species represented 13.7% of the vascular flora of the St Lawrence wetlands. The proportion of exotic species (Table 1) was lowest in the Lake St François sector (9%) and highest in the Contrecœur sector (24%). Elsewhere, it ranged from 15% to 18%. The relative plant cover of exotic species was low in the Lake St François sector (18%) but rose sharply in the Montréal and Contrecœur areas (42–44%), where only 16–22% of sampling stations had no exotic species (Fig. 1). In the Lake St Louis, Boucherville and Contrecœur sectors, exotic species occupied 60–100% of the plant cover in 31–41% of sampling stations. In the Lake St Pierre sector, where half of the St Lawrence River wetlands are located, the relative cover occupied by exotic species was 27%. Downstream from Lake St Pierre, although exotic species still represented 16–18% of the vascular flora, their relative cover was only 6–10%. In the freshwater and brackish estuaries, more than 90% of the sampling stations exhibited a relative exotic cover of <20%.

Some sites were more susceptible than other sites to invasion by exotic plants, in particular wetlands surrounding islands. For example, in the de la Paix (Lake St Louis), Dufault, aux Fermiers, St Jean, and Verte (Boucherville), and Cardin, du Moine, and Lamarche (Lake St Pierre) islands, the relative exotic plant cover (all stations considered) ranged from 50% to 71%. Such high exotic covers have never been recorded in wetlands bordering the main shores of the St Lawrence River, with the exception of a few isolated stations. On the other hand, the only site in the freshwater

Table 1 Overview of the native and exotic vascular flora of the St Lawrence River wetlands, Québec, Canada

Sector	Total wetland area (ha)	Sampling stations (*n*)	Native species (*n*)	Exotic species (*n*)	Exotic species (% flora)	Relative exotic plant cover (%)
Lake St François	4356*	49	88	9	9.3	17.8
Lake St Louis	598*	76	59	11	15.7	43.6
Boucherville	473*	87	86	17	16.5	41.7
Contrecœur	670*	23	25	8	24.2	44.3
Lake St Pierre	16 762*	246	99	17	14.7	27.1
Freshwater estuary	7760†	115	95	18	15.9	6.2
Brackish estuary	4180†	117	87	19	17.9	10.0

*Unpublished data from M. Jean & G. Létourneau.
†Data from Centre Saint-Laurent (1996).

Table 2 Relative plant cover occupied by exotic vascular plant species in the wetlands of seven sectors of the St Lawrence River, Québec, Canada. Cover is presented according to the water levels of the summers of 2000 and 2001

Sector	Relative exotic plant cover (% and *n* sampling stations)	
	Stations with water level below soil surface	Stations with water level above soil surface
Lake St François	33.6% (13)	12.9% (36)
Lake St Louis	65.3% (25)	34.3% (51)
Boucherville	43.1% (37)	40.4% (50)
Contrecœur	61.8% (7)	37.3% (16)
Lake St Pierre	30.7% (80)	25.3% (166)
Freshwater estuary	10.9% (51)	1.9% (64)
Brackish estuary	11.3% (100)	0.4% (17)

estuary with a relative exotic cover higher than 6% was the Cap Tourmente National Wildlife Area (18%, all stations considered), located in the extreme northeast. In the brackish estuary, there were few sites with a relative exotic cover higher than 6%, and cover was always <19%, except in Trois-Pistoles (27%). The relative exotic cover also seemed to be influenced by water level. Except in the Boucherville and Lake St Pierre areas, the exotic cover was much higher at stations with a water level below the soil surface (Table 2). It should be noted that in each sector of the river, minimal variations of the water level (0–11 cm) were registered during the sampling periods (Environment Canada, unpublished data).

Purple loosestrife was by far the most common exotic species of the St Lawrence wetlands (Fig. 2, Table 3). In each sector, it placed among the four most frequently sampled species (native or exotic). The percentage of sampling stations where this species occurred declined from Lake St François (57%) to Contrecœur (26%), and then rose downstream (30–39%). Flowering-rush and reed canary grass were also very common in the wetlands, but mainly from Lake St Louis to Lake St Pierre. Locally, other exotic species were widespread: European frogbit (Lake St François), common reed (Boucherville), and Eurasian watermilfoil (Contrecœur, Lake St Pierre).

Although purple loosestrife was the most common exotic species, flowering-rush and reed canary grass were much more invasive: 40% of the sampling stations where these species were present were dominated (>50% of absolute plant cover) by those plants, compared with 9% for purple loosestrife (Fig. 2). Another exotic, common reed, occurred infrequently in the wetlands, but was highly invasive once established.

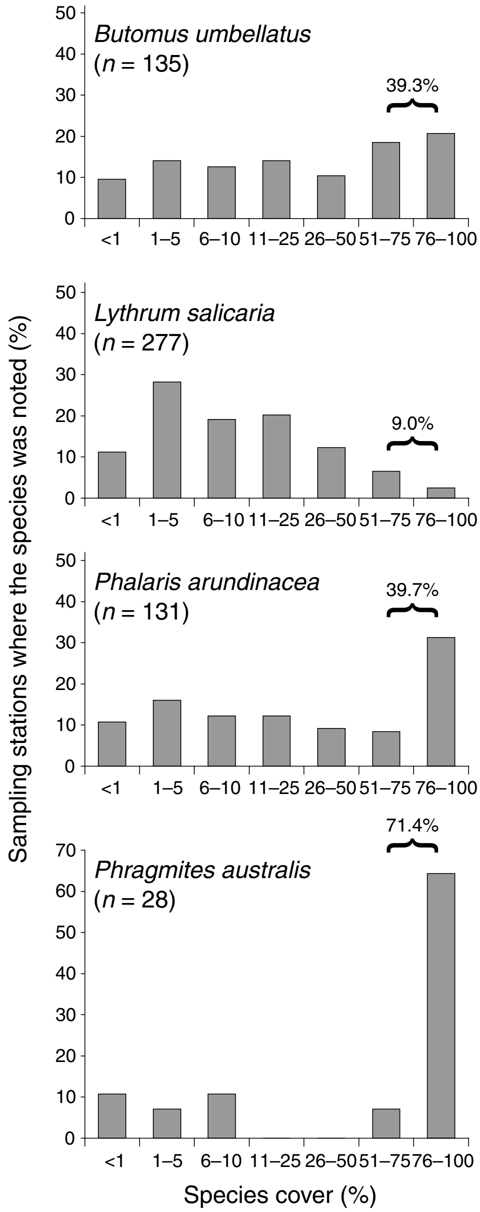

Figure 2 Distribution of sampling stations according to the absolute cover occupied by four exotic vascular plant species found in the St Lawrence River wetlands: flowering-rush (*Butomus umbellatus* L.), purple loosestrife (*Lythrum salicaria* L.), reed canary grass (*Phalaris arundinacea* L.) and common reed [*Phragmites australis* (Cav.) Trin. ex Steudel]. Only sampling stations where the species was noted are considered.

Impact of exotics on species richness and diversity

As exotic species cover was only significant from Lake St Louis to Lake St Pierre, we used the 432 stations in this part of the St Lawrence River to evaluate the impact of exotic flora on the species richness and diversity of wetland plant communities. The exclusion of the estuarine sectors from this analysis prevented amalgamation of tidal and non-tidal vegetation communities. From Lake St Louis to Lake St Pierre, there is a significant but weak negative linear relationship ($F = 36.08$, $P < 0.0001$, $R^2 = 0.075$) between the number of native plant species per sampling station and the

Table 3 Five most frequent vascular plant species and species with the highest total cover in the wetlands of seven sectors of the St Lawrence River, Québec, Canada. Exotic species are marked with an asterisk. Rank and associated values of other exotic species are also indicated

Sector	Frequency: Species	Frequency: Percentage of sampling stations where the species was noted	Plant cover: Species	Plant cover: Sum of median values of species cover (%) for all stations
Lake St François	1. *Lythrum salicaria* L.*	57.1	1. *Carex lacustris* Willd.	785
	2. *Hydrocharis morsus-ranae* L.*	32.7	2. *Typha angustifolia* L.	548
	2. *Sparganium eurycarpum* Engelm.	32.7	3. *Calamagrostis canadensis* (Michx.) Nutt.	441
	4. *Typha latifolia* L.	30.6	4. *Lythrum salicaria* L.*	407
	5. *Carex lacustris* Willd.	28.6	5. *Sparganium eurycarpum* Engelm.	399
	32. *Phalaris arundinacea* L.*	8.2	10. *Phragmites australis* (Cav.) Trin. ex Steudel*	300
	32. *Phragmites australis* (Cav.) Trin. ex Steudel*	8.2	11. *Hydrocharis morsus-ranae* L.*	293
	66. *Butomus umbellatus* L.*	2.0	17. *Phalaris arundinacea* L.*	220
			43. *Butomus umbellatus* L.*	18
Lake St Louis	1. *Lythrum salicaria* L.*	47.4	1. *Phalaris arundinacea* L.*	1608
	2. *Butomus umbellatus* L.*	39.5	2. *Butomus umbellatus* L.*	1391
	3. *Phalaris arundinacea* L.*	36.8	3. *Lythrum salicaria* L.*	1113
	4. *Sparganium eurycarpum* Engelm.	32.9	4. *Bolboschoenus fluviatilis* (Torrey) S. Sojak	831
	5. *Bolboschoenus fluviatilis* (Torrey) S. Sojak	21.1	5. *Sparganium eurycarpum* Engelm.	782
	26. *Phragmites australis* (Cav.) Trin. ex Steudel*	5.3	21. *Phragmites australis* (Cav.) Trin. ex Steudel*	99
Boucherville	1. *Lythrum salicaria* L.*	42.5	1. *Phalaris arundinacea* L.*	1138
	2. *Phalaris arundinacea* L.*	35.6	2. *Butomus umbellatus* L.*	927
	3. *Bolboschoenus fluviatilis* (Torrey) S. Sojak	34.5	3. *Bolboschoenus fluviatilis* (Torrey) S. Sojak	902
	4. *Sagittaria latifolia* Willd.	26.4	4. *Lythrum salicaria* L.*	852
	5. *Scirpus lacustris* L.	25.3	5. *Phragmites australis* (Cav.) Trin. ex Steudel*	807
	8. *Butomus umbellatus* L.*	24.1		
	10. *Phragmites australis* (Cav.) Trin. ex Steudel*	16.1		
Contrecœur	1. *Sparganium eurycarpum* Engelm.	47.8	1. *Butomus umbellatus* L.*	518
	2. *Butomus umbellatus* L.*	43.5	2. *Sparganium eurycarpum* Engelm.	359
	3. *Typha angustifolia* L.	30.1	3. *Scirpus lacustris* L.	223
	4. *Lythrum salicaria* L.*	26.1	4. *Typha angustifolia* L.	214
	5. *Scirpus lacustris* L.	21.7	5. *Myriophyllum spicatum* L.*	171
	8. *Myriophyllum spicatum* L.*	16.0	9. *Lythrum salicaria* L.*	108
	8. *Phalaris arundinacea* L.*	16.0	11. *Phragmites australis* (Cav.) Trin. ex Steudel*	88
	19. *Phragmites australis* (Cav.) Trin. ex Steudel*	4.0	15. *Phalaris arundinacea* L.*	78
Lake St Pierre	1. *Bolboschoenus fluviatilis* (Torrey) S. Sojak	41.9	1. *Bolboschoenus fluviatilis* (Torrey) S. Sojak	2621
	2. *Sagittaria latifolia* Willd.	41.5	2. *Sparganium eurycarpum* Engelm.	2341
	3. *Lythrum salicaria* L.*	39.0	3. *Butomus umbellatus* L.*	2191
	4. *Scirpus lacustris* L.	35.8	4. *Typha angustifolia* L.	2128
	5. *Sparganium eurycarpum* Engelm.	35.0	5. *Nymphaea odorata* Aiton.	2045
	8. *Butomus umbellatus* L.*	28.0	10. *Myriophyllum spicatum* L.*	1618
	12. *Myriophyllum spicatum* L.*	19.9	11. *Phalaris arundinacea* L.*	1533
	13. *Phalaris arundinacea* L.*	17.5	12. *Lythrum salicaria* L.*	1325
	14. *Rorippa amphibia* (L.) Bess.*	15.9	16. *Rorippa amphibia* (L.) Bess.*	684
	16. *Hydrocharis morsus-ranae* L.*	13.4	17. *Hydrocharis morsus-ranae* L.*	517
	81. *Phragmites australis* (Cav.) Trin. ex Steudel*	0.4	43. *Phragmites australis* (Cav.) Trin. ex Steudel*	88

Table 3 *continued*

	Frequency		Plant cover	
Sector	Species	Percentage of sampling stations where the species was noted	Species	Sum of median values of species cover (%) for all stations
Freshwater estuary	1. *Schoenoplectus pungens* (Vahl) Palla	53.0	1. *Schoenoplectus pungens* (Vahl) Palla	3706
	2. *Lythrum salicaria* L.*	33.0	2. *Spartina pectinata* Link.	1258
	3. *Sagittaria latifolia* Willd.	31.3	3. Sagittaria latifolia Willd.	972
	3. *Zizania aquatica* var. *brevis* Fassett	31.3	4. *Zizania aquatica* var. *brevis* Fassett	905
	5. *Sagittaria rigida* Pursh.	27.0	5. *Vallisneria americana* Michx.	691
	20. *Phalaris arundinacea* L.*	11.3	15. *Lythrum salicaria* L.*	397
	67. *Butomus umbellatus* L.*	1.7	16. *Phalaris arundinacea* L.*	372
			68. *Butomus umbellatus* L.*	15
Brackish estuary	1. *Spartina alterniflora* Loisel.	36.7	1. *Spartina alterniflora* Loisel.	2426
	2. *Lythrum salicaria* L.*	29.9	2. *Spartina pectinata* Link.	993
	3. *Salicornia europaea* L.	21.3	3. *Schoenoplectus pungens* (Vahl) Palla	963
	4. *Hordeum jubatum* L.	19.7	4. *Calamagrostis canadensis* (Michx.) Nutt.	838
	5. *Calamagrostis canadensis* (Michx.) Nutt.	18.8	5. *Spartina patens* (Ait.) Mühl.	812
	28. *Phalaris arundinacea* L.*	6.8	12. *Lythrum salicaria* L.*	439
	39. *Phragmites australis* (Cav.) Trin. ex Steudel*	3.4	16. *Phragmites australis* (Cav.) Trin. ex Steudel*	350
	69. *Butomus umbellatus* L.*	0.9	19. *Phalaris arundinacea* L.*	247
			83. *Butomus umbellatus* L.*	3

relative exotic cover (Fig. 3). There is no significant linear relationship between the Shannon diversity index and the relative exotic cover ($F = 0.32$, $P < 0.572$, $R^2 = 0.001$). However, there is a strong significant quadratic relationship between diversity and exotic plant cover ($F = 178.48$, $P < 0.0001$, $R^2 = 0.452$). Data are distributed along an arc: stations with low (≤10%) or high exotic cover (>90%) exhibit low diversity indexes. This relationship can be explained by the fact that 92% of the stations with a high exotic cover (>90%) were dominated (>50% absolute plant cover) by a single exotic species (Fig. 4). Furthermore, 43% of the stations with a low exotic cover (≤10%) were dominated by a single native species, such as *Bolboschoenus fluviatilis* (Torrey) S. Sojak or *Typha angustifolia* L. Furthermore, the impact of a massive establishment (>50% of absolute plant cover) of reed canary grass or common reed on native species richness, and especially on plant diversity, seems to be more significant than the impact of flowering-rush or purple loosestrife (Fig. 5).

Reconstruction of the spread of invasive species

A total of 2667 herbarium specimens (common reed: 577; flowering-rush: 622; purple loosestrife: 1468) were examined in this study. Data from 1965 specimens were used to reconstruct the evolution of the distribution of the three species in Québec (Fig. 6). Very few specimens were sampled before 1926; flowering-rush was first collected in 1905 (Montréal), purple loosestrife in 1883 (Québec City) and 1890 (Montréal), and common reed in 1820 (Montréal and Québec City), 1880 (Lake St Jean), and 1882 (Gaspésie Peninsula). It is possible that purple loosestrife was present near Québec City as early as 1865 (Rousseau, 1968). Between 1926 and 1950, flowering-rush and purple loosestrife spread rapidly along the St Lawrence River. During the last 50 years, some isolated colonies of flowering-rush became established in Gaspésie and Lake St Jean, but the spatial distribution of this species did not change much during this period. On the other hand, purple loosestrife seemed to continue its expansion, particularly in the south-western part of the province. Common reed expanded its range mainly after 1950.

DISCUSSION

Biogeography of exotic species

Exotic species represent only a small fraction (*c.* 14%) of the vascular flora of the St Lawrence River wetlands. For example, exotic species constitute *c.* 20–27% of the total vascular flora of the Québec–Labrador peninsula and Ontario (Rousseau, 1968, 1974; Brunton & Di Lablo, 1989; Rapoport, 2000). In France and western North America, exotic species typically represent 24–30% of the flora of riparian habitats (Planty-Tabacchi *et al.*, 1996). The proportion of exotic species is also fairly constant along the waterway. The

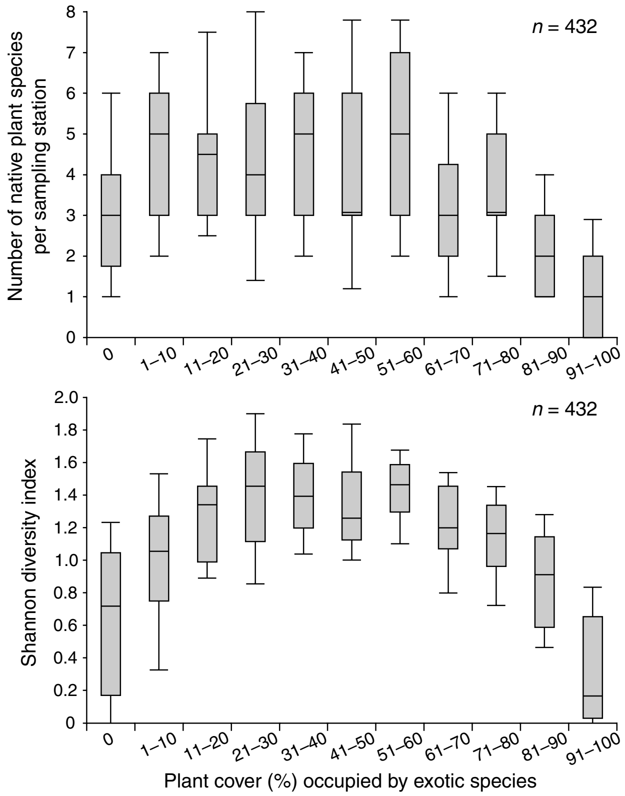

Figure 3 Number of native plant species per sampling station and Shannon diversity index according to the relative cover (10%-classes) occupied by exotic vascular plant species. Only stations sampled in the wetlands of the fluvial section of the St Lawrence River, from Lake St Louis to Lake St Pierre, are considered. For each plant cover class, the median (horizontal bar), 25 and 75 percentiles (box), and 10 and 90 percentiles (error bars) are indicated.

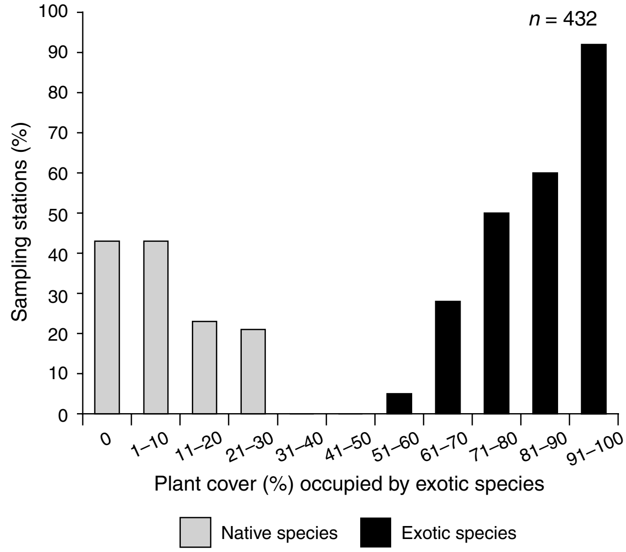

Figure 4 Percentage of sampling stations dominated (>50% absolute plant cover) by a single exotic or native vascular plant species in each 10%-class of relative exotic plant cover. Only stations sampled in the wetlands of the fluvial section of the St Lawrence River, from Lake St Louis to Lake St Pierre, are considered.

higher proportion observed in the Contrecœur sector is more likely related to the low number of sampling stations than to an increase in the number of exotic species; numerous native vascular plants that are not widespread were consequently not recorded. This constant proportion of exotic species contrasts strongly with what has been observed in riparian habitats (10-year flood zone) where the percentage of exotic species usually increases with the distance from the river source (Planty-Tabacchi *et al.*, 1996).

Documenting the proportion of exotic species provides an incomplete picture of the level of invasion in the St Lawrence wetlands. The relative exotic cover appears to be a more appropriate measurement since, unlike the proportion of exotic species, major differences in the exotic plant cover were detected between the sectors of the river. The highest cover is recorded in the Montréal area whereas the estuarine sectors have a very low exotic plant cover. Several factors may explain the differences observed:

(1) *Historical factors:* Montréal is an old city (founded in 1642) and its port has been an important shipping centre since 1830 (Centre Saint-Laurent, 1996). It is likely that several aquatic plants were accidentally introduced near Montréal because of the release of ship ballast (Rousseau, 1968; Lachance & Lavoie, 2002): in the mid-ninteenth century, more than 54% of the 1200 British vessels docking each year at Montréal and Québec City only carried ballast (Hamelin & Roby, 1971. This ballast, probably gravel, rock, and moist sand from tidal flats (Thompson *et al.*, 1987), was released near ports and replaced with wood products on the return voyage. The release of ship ballast may explain why one of the most invasive plants of St Lawrence wetlands, the flowering-rush, was introduced near Montréal at the beginning of the twentieth century, possibly from Asia (Anderson *et al.*, 1974). On the other hand, Québec City (founded in 1608) is older and its port was more important than that of Montréal before 1860 (Lemelin, 1981). More than 43% of the vascular flora of Québec City is composed of exotic species (Baillargeon, 1981). However, and contrary to our expectations, the exotic plant cover is very low in wetlands of the Québec City area, although the main invasive species have been present since 1820 (common reed), 1883 (purple loosestrife), and 1922 (flowering-rush).

(2) *Abiotic factors:* the low exotic plant cover downstream of Lake St Pierre is probably explained in part by the high-amplitude tides of the freshwater estuary. At Grondines, 60-km downstream of the outlet of Lake St Pierre, the mean tide amplitude is 2.8 m, and reaches 5.6 m near Québec City (Centre Saint-Laurent, 1996). It is likely that the major tides of the freshwater estuarine sector hamper the establishment of large colonies of exotic plants and of other native species (Gauthier,

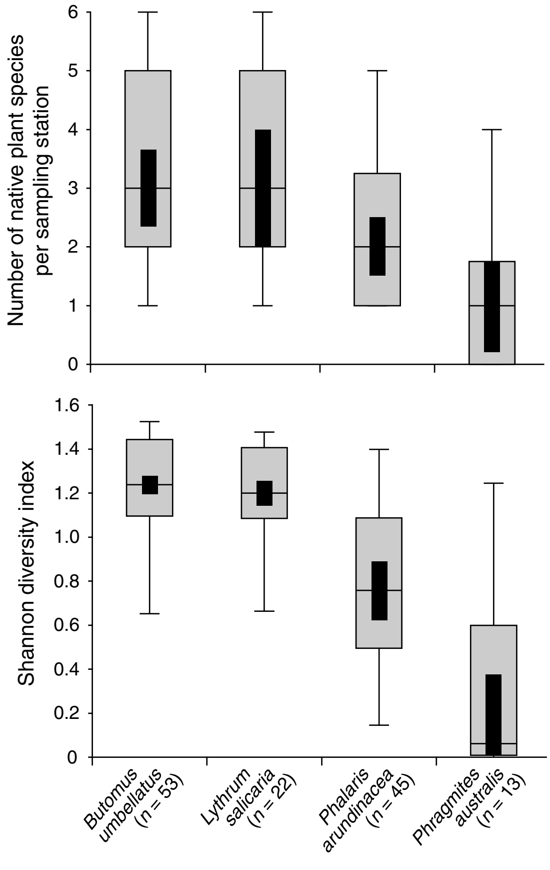

Figure 5 Respective impact on the number of native plant species per sampling station and Shannon diversity index by four exotic vascular plant species: flowering-rush (*Butomus umbellatus* L.), purple loosestrife (*Lythrum salicaria* L.), reed canary grass (*Phalaris arundinacea* L.) and common reed [*Phragmites australis* (Cav.) Trin. ex Steudel]. Only stations sampled in the wetlands of the fluvial section of the St Lawrence River (from Lake St Louis to Lake St Pierre) and where the species cover was >50% are considered. For each species, the median (horizontal bar), 25 and 75 percentiles (box), and 10 and 90 percentiles (error bars) are indicated. Black boxes are notched box plots. Two groups whose notched box plots do not overlap can be said to be significantly different at the 5% level (Velleman & Hoaglin, 1981).

1980). In the brackish estuary, the salinity of the surface water changes from <1–2‰ to 15‰ over a 60-km distance (Centre Saint-Laurent, 1996). This rapid increase probably precludes the establishment of large colonies of exotic plants inside the tidal zone (Lachance & Lavoie, 2002), as suggested by the very low exotic plant cover at sampling stations with a water table above the soil surface.

(3) *Landscape factors and disturbances:* the exotic plant cover is higher in the wetlands surrounding islands than in those bordering the main shores of the St Lawrence River. From Lake St Louis to Contrecœur, marshes and swamps are almost exclusively located near islands (Centre Saint-Laurent, 1996) and consequently, more than 85% of sampling stations were located in those wetlands. No island was sampled in the Lake St François sector and the proportion of sampling stations located near islands decreased from Lake St Pierre (26%) to the estuarine sectors (10–12%) where most wetlands are located near the main shores of the river. It is unclear why wetlands surrounding islands are more susceptible to invasion by exotic species but the various disturbances affecting these islands may offer an explanation. Between 1972 and 1976, Lake St Louis was affected by high water levels (Robichaud & Drolet, 1998), which severely damaged the forested swamps located in the de la Paix islands. Swamps were replaced by large open areas later colonized by purple loosestrife and reed canary grass (Dryade, 1985; Jean *et al.*, 1992; Buteau *et al.*, 1994). Other islands downstream were not as severely affected by the 1972–76 high water levels. However, since 1968, they experienced a significant drop (from 4 to 1.5 m) in the amplitude of the annual water level (Robichaud & Drolet, 1998). In addition, most of these islands are intensively used for agriculture (Photosur Géomat Inc., 1991), so the cumulative effects of these disturbances could explain the high cover of exotic species.

Purple loosestrife is considered to be the most invasive exotic plant species in Québec (White *et al.*, 1993) so it is not surprising that it is the most frequent exotic species in the St Lawrence wetlands. Interestingly, only 9% of the stations containing this species have a purple loosestrife cover >50%, yet several reports indicate that this species tends to form dense monocultures (Thompson *et al.*, 1987; Mal *et al.*, 1992). However, recent studies have shown that monocultures of purple loosestrife are uncommon in nature (Keller, 2000; Farnsworth & Ellis, 2001; Morrison, 2002) and the present study supports this assertion.

To our knowledge, this study is the first to document the importance of flowering-rush populations over a large area; dense populations (>50% cover) of this species are much more common than those of purple loosestrife. Another invasive species, reed canary grass, is also widespread, but this phenomenon is not recent. Large populations of reed canary grass were observed in the wetlands of the Montréal, Contrecœur, and Lake St Pierre areas as early as 1931 (Marie-Victorin, 1943; Morency, 1966; Deschamps, 1968; Cantin & Blais, 1976; Tessier *et al.*, 1981). On the other hand, common reed populations are infrequent in the St Lawrence wetlands. However, some colonies recently expanded in the Boucherville sector: between 1980 and 1999, the area occupied by dense common reed populations rose from 1 to 25 ha. This increase may be associated with a drop in the annual water level amplitude (Robichaud & Drolet, 1988; I. Jetté & M. Jean, unpublished data).

Exotic species and plant richness and diversity

We initially hypothesized a negative linear relationship between the cover of exotic species and both the species

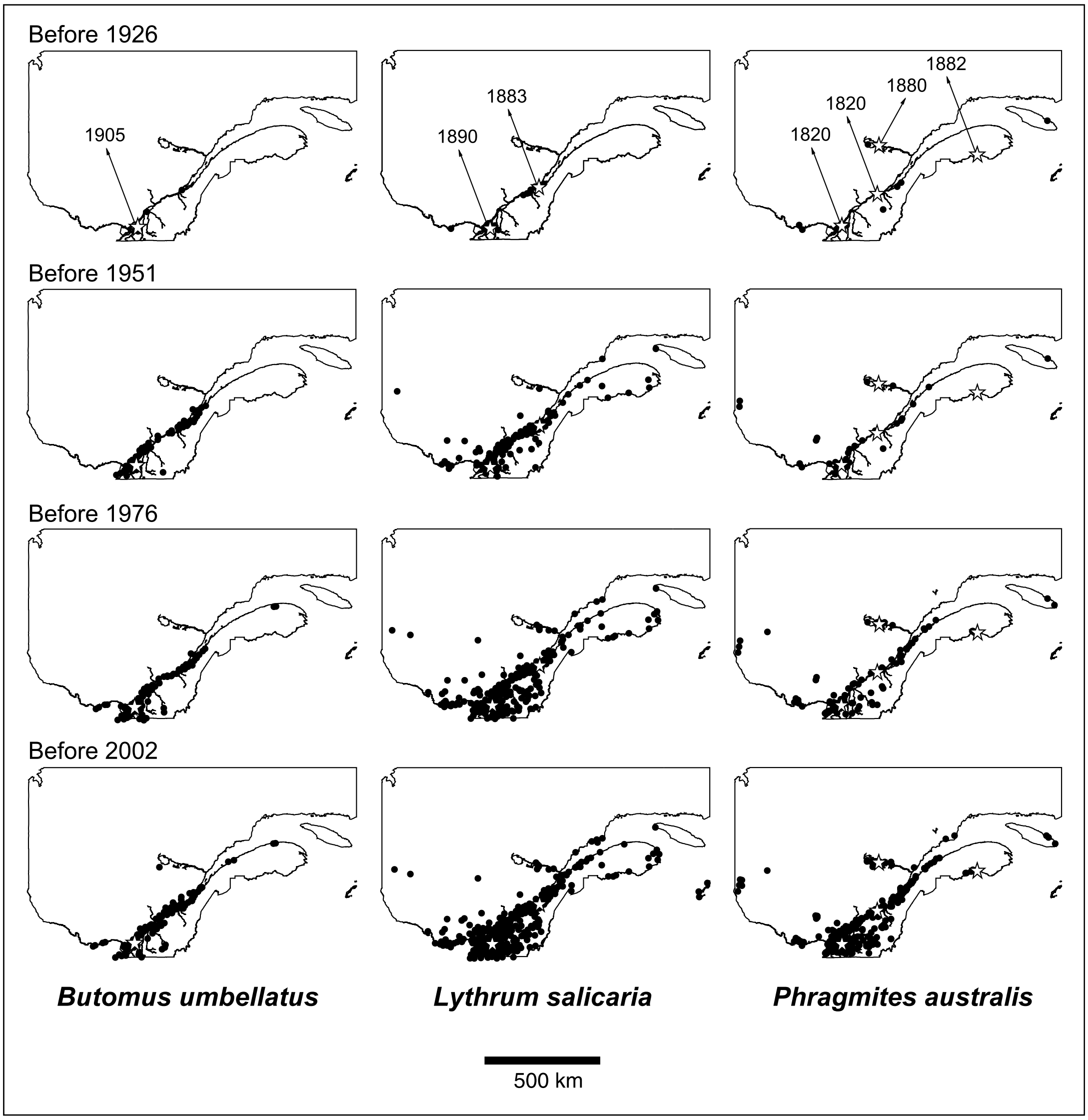

Figure 6 Herbarium specimens (black dots) of flowering-rush (*Butomus umbellatus* L.), purple loosestrife (*Lythrum salicaria* L.) and common reed [*Phragmites australis* (Cav.) Trin. ex Steudel] sampled in Québec before 1926, 1951, 1976, and 2002, respectively. The year and location (white stars) of the oldest herbarium specimens are indicated.

richness and the diversity of wetland plants. There is a weak linear relationship between exotic cover and species richness, which may reflect the impact of exotic plants on native species (Levine & D'Antonio, 1999). However, there is no linear relationship between the relative exotic cover and the diversity of wetland plants. In fact, low diversity sites can be dominated by either an exotic or a native plant species. In other sites, exotic species seem to impact little on plant communities and can contribute to increase diversity. The St Lawrence wetlands are naturally species-poor (Groupe de travail national sur les terres humides, 1988) and resistance to invasion by exotic species seems to be related to the presence of dense populations of native species rather than to high diversity levels. This strongly supports earlier observations suggesting that low diversity sites are hard to invade when they are dominated by one or a few species (Levine & D'Antonio, 1999; Stohlgren *et al.*, 1999; Meiners *et al.*, 2001).

Common reed and reed canary grass clearly affect plant diversity more than flowering-rush and purple loosestrife. There are numerous studies showing that these grasses eliminate native plants once established (Auclair *et al.*, 1973; Apfelbaum & Sams, 1987; Gaudet & Keddy, 1988; Marks *et al.*, 1994; Keller, 2000; Meyerson *et al.*, 2000; Green & Galatowitsch, 2001). Our study is the first attempt to determine whether flowering-rush threatens the diversity of wetland plant communities in North America. Although there is a high number of dense flowering-rush populations along the St Lawrence River, this species has not demonstrated a strong impact on wetland plant diversity, at least in comparison with common reed and reed canary grass. Unlike grasses, the growth form of the flowering-rush probably prevents this species from occupying all the available space, thereby allowing the establishment and survival of other wetland plants.

The impact of purple loosestrife populations on wetland plant diversity has recently been the subject of a vigorous debate (Anderson, 1995; Hager & McCoy, 1998; Blossey *et al.*, 2001). Experimental studies strongly suggest that purple loosestrife is a very competitive plant, which eliminates native species (Gaudet & Keddy, 1988; Weiher *et al.*, 1996; Mal *et al.*, 1997), but this phenomenon has rarely been observed in nature (Anderson, 1995; Treberg & Husband, 1999; Keller, 2000; Farnsworth & Ellis, 2001). Our data do not support the hypothesis that purple loosestrife reduces wetland plant diversity, at least at its north-eastern distribution limit. While this species has been widespread along the St Lawrence River for the last 75 years, dense monospecific stands are rare and sites with a purple loosestrife cover >50% have a Shannon diversity index that differs little from most other stations, except those dominated by either an exotic or a native plant species. Keller (2000) suggested that invasion of purple loosestrife may consist of a first step, in which the plant forms very dense stands, and of a second step, in which colonies decline and allow the reestablishment of native wetland plants. This scenario is plausible for the St Lawrence wetlands: dense colonies described in the 1940s in the Lake St Pierre area (Louis-Marie, 1944) were no longer present 60 years later (Gratton *et al.*, 1998; this study).

CONCLUSIONS

This survey of the exotic plants of the St Lawrence River wetlands demonstrates the importance of perspective. For example, while purple loosestrife is widespread in southern Québec, few sites along the St Lawrence River have been invaded by this species. Nationwide strategies that have been developed to control purple loosestrife could be totally inappropriate at a regional level. This work and other field studies also question the presumed detrimental impact of this species on native wetland plant communities. On the other hand, common reed is highly competitive once established. This species is rare in the wetlands outside the Montréal area, but recent evidence suggesting the spread of colonies is worthy of attention: it is much easier to control a regional invasion by curbing the growth of small nascent colonies than large well-established populations (Moody & Mack, 1988). The invasive potential of some plant species should also be reconsidered: the Canadian Botanical Conservation Network (www.rbg.ca/cbcn) classifies both flowering-rush and reed canary grass as 'low level invasive', which does not reflect their status in the St Lawrence wetlands. In summary, the global impact of an invader cannot be determined by focusing on few highly invaded sites.

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REFERENCES

Aiken, S.G., Newroth, P.R. & Wile, I. (1979) The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. *Canadian Journal of Plant Science*, **59**, 201–215.

Anderson, M.G. (1995) Interactions between *Lythrum salicaria* and native organisms: a critical review. *Environmental Management*, **19**, 225–231.

Anderson, L.C., Zeis, C.D. & Alam, S.F. (1974) Phytogeography and possible origins of *Butomus* in North America. *Bulletin of the Torrey Botanical Club*, **101**, 292–296.

Apfelbaum, S.I. & Sams, C.E. (1987) Ecology and control of reed canary grass (*Phalaris arundinacea* L). *Natural Areas Journal*, **7**, 69–74.

Auclair, A.N., Bouchard, A. & Pajaczkowski, J. (1973) Plant composition and species relations on the Huntingdon Marsh, Quebec. *Canadian Journal of Botany*, **51**, 1231–1247.

Baillargeon, G. (1981) *Zonation et modification de la composition de la flore vasculaire dans une région urbaine: la colline de Québec*, Unpublished MSc Thesis, p. 206. Université Laval, Québec City.

Blossey, B., Skinner, L.C. & Taylor, J. (2001) Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation*, **10**, 1787–1807.

Brunton, D.F. & Di Labio, B.M. (1989) Diversity and ecological characteristics of emergent beach flora along the Ottawa River in the Ottawa-Hull region, Québec and Ontario. *Naturaliste canadien*, **116**, 179–191.

Buteau, P., Dignard, N. & Grondin, P. (1994) *Système de classification des milieux humides du Québec*, p. 25. Ministère de l'Énergie des Mines et des Ressources du Canada & Ministère des Ressources naturelles du Québec, Québec City.

Cantin, M. & Blais, P. (1976) *La végétation des îles de Contrecœur*, p. 70. Environnement Canada, Québec City.

Catling, P.M. & Porebski, Z.S. (1995) The spread and current distribution of European frogbit, *Hydrocharis morsus-ranae* L., in North America. *Canadian Field-Naturalist*, **109**, 236–241.

Centre Saint-Laurent (1996) *Rapport-synthèse sur l'état du Saint-Laurent*, Vol. 1, *L'écosystème du Saint-Laurent*, p. 594. Environnement Canada & Éditions MultiMondes, Montréal.

Chambers, R.M., Meyerson, L.A. & Saltonstall, K. (1999) Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany*, **64**, 261–273.

Deschamps, L. (1968) *Étude floristique de l'île Sainte-Thérèse et des îles avoisinantes*, Unpublished MSc Thesis, p. 253. Université de Montréal, Montréal.

Dore, W.G. & McNeill, J. (1980) *Grasses of Ontario*, p. 566. Agriculture Canada, Ottawa.

Dryade (1985) *Étude complémentaire de la végétation du lac Saint-Louis et du lac des Deux-Montagnes: groupes écologiques, patrons d'inondation, clés de potentiel et plans de gestion*, p. 603. Le Groupe Dryade, Québec City.

Farnsworth, E.J. & Ellis, D.R. (2001) Is purple loosestrife (*Lythrum salicaria*) an invasive threat to freshwater wetlands? Conflicting evidence from several ecological metrics. *Wetlands*, **21**, 199–209.

Gaudet, C.L. & Keddy, P.A. (1988). A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.

Gauthier, B. (1980) Les limites phytogéographiques du Saint-Laurent. *Provancheria*, **11**, 1–103.

Gratton, L., Labrecque, J. & Bérubé, D. (1998) *Étude écologique des terres du ministère de la Défense nationale à Nicolet*, p. 32. Ministère de l'Environnement et de la Faune du Québec, Québec.

Green, E.K. & Galatowitsch, S.M. (2001) Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha* × *glauca*). *Canadian Journal of Botany*, **79**, 170–178.

Groupe de travail national sur les terres humides (1988) *Terres humides du Canada*, p. 425. Environnement Canada, Ottawa & Polyscience Publications, Montréal.

Hager, H.A. & McCoy, K.D. (1998) The implications of accepting untested hypotheses: a review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation*, **7**, 1069–1079.

Hamelin, J. & Roby, Y. (1971) Histoire économique du Québec, 1851–1896, p. 436. Fides, Montréal.

Jean, M. & Bouchard, A. (1993) Riverine wetland vegetation: importance of small-scale and large-scale environmental variation. *Journal of Vegetation Science*, **4**, 609–620.

Jean, M., D'Aoust, M., Gratton, L. & Bouchard, A. (1992) *Impacts of water level fluctuations on wetlands: Lake St Louis case study*, p. 79. Institut de recherche en biologie végétale, Montréal.

Johansson, M.E. & Nilsson, C. (1993) Hydrochory, population dynamics and distribution of the clonal aquatic plant *Ranunculus lingua*. *Journal of Ecology*, **81**, 81–91.

Johansson, M.E., Nilsson, C. & Nilsson, E. (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, **7**, 593–598.

Keller, B.E.M. (2000) Plant diversity in *Lythrum, Phragmites*, and *Typha* marshes, Massachusetts, U.S.A. *Wetlands Ecology and Management*, **8**, 391–401.

Létourneau, G. & Jean, M. (1996) *Cartographie des marais, marécages et herbiers aquatiques le long du Saint-Laurent par télédétection aéroportée*, p. 101. Environnement Canada, Montréal.

Lachance, D. & Lavoie, C. (2002) Reconstructing the biological invasion of European water-horehound, *Lycopus europaeus* (Labiatae), along the St Lawrence River, Québec. *Rhodora*, **104**, 151–160.

Lemelin, A. (1981) *Le déclin du port de Québec et la reconversion économique à la fin du 19e siècle*, p. 45. Département d'économique, Université Laval, Québec City.

Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.

Louis-Marie, P. (1944) *La salicaire dans le Québec*, p. 46. Institut agricole d'Oka, Oka.

Magurran, A.E. (1988) *Ecological diversity and its measurement*, p. 179. Princeton University Press, Princeton.

Mal, T.K., Lovett-Doust, J., Lovett-Doust, L. & Mulligan, G.A. (1992) The biology of Canadian weeds. 100. *Lythrum salicaria*. *Canadian Journal of Plant Science*, **72**, 1305–1330.

Mal, T.K., Lovett-Doust, J. & Lovett-Doust, L. (1997) Time-dependent competitive displacement of *Typha angustifolia* by *Lythrum salicaria*. *Oikos*, **79**, 26–33.

Marie-Victorin, F. (1943) Observations botaniques sur les effets d'une exceptionnelle baisse de niveau du Saint-Laurent durant l'été de 1931. *Contributions de l'Institut botanique de l'Université de Montréal*, **48**, 21–28.

Marie-Victorin, F. (1995) *Flore laurentienne*, 3rd edn, p. 1093. Presses de l'Université de Montréal, Montréal.

Marks, M., Lapin, B. & Randall, J. (1994) *Phragmites australis* (*P. communis*): threats, management, and monitoring. *Natural Areas Journal*, **14**, 285–294.

Maurer, D.A. & Zedler, J.B. (2002) Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. *Oecologia*, **131**, 279–288.

Mehra, A., Farago, M.E., Banerjee, D.K. & Cordes, K.B. (1999) The water hyacinth: an environmental friend or pest? A review. *Resource and Environmental Biotechnology*, **2**, 255–281.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography*, **24**, 633–644.

Merigliano, M.F. & Lesica, P. (1998) The native status of reed canarygrass (*Phalaris arundinacea* L.) in the inland Northwest, USA. *Natural Areas Journal*, **18**, 223–230.

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E. & Findlay, S. (2000) A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management*, **8**, 89–103.

Mills, E.L., Scheuerell, M.D., Carlton, J.T. & Strayer, D.L. (1997) Biological invasions in the Hudson River basin: an inventory and historical analysis, p. 51. New York State Museum, Albany.

Moody, M.E. & Mack, R.N. (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.

Morency, M. (1966) *Étude floristique des îles de la Paix*, Unpublished MSc Thesis, p. 225. Université de Montréal, Montréal.

Morrison, J.A. (2002) Wetland vegetation before and after experimental purple loosestrife removal. *Wetlands*, **22**, 159–169.

Mousseau, P. (1987) *Synthèse des connaissances sur le Phragmite commun* (Phragmites communis) p. 55. Hydro-Québec, Vice-présidence Environnement, Montréal.

Photosur Géomat Inc. (1991) *Cartographie de l'utilisation riveraine des sols de Cornwall à Tadoussac par télédétection*, p. 26. Environnement Canada, Montréal.

Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience*, **50**, 53–65.

Planty-Tabacchi, A.-M., Tabacchi, E., Naiman, R.J., Deferrari, C. & Décamps, H. (1996) Invasibility of species-rich communities in riparian zones. *Conservation Biology*, **10**, 598–606.

Pyšek, P. & Prach, K. (1993) Plant invasion and the role of riparian habitats: a comparison of four species alien to central Europe. *Journal of Biogeography*, **20**, 413–420.

Rapoport, E.H. (2000) Remarks on the biogeography of land invasions. *Revista Chilena de Historia Natural*, **73**, 367–380.

Reichard, S.H. & White, P. (2001) Horticulture as a pathway of invasive plant introductions in the United States. *BioScience*, **51**, 103–113.

Rice, D., Rooth, J. & Stevenson, J.C. (2000) Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. *Wetlands*, **20**, 280–299.

Robichaud, A. & Drolet, R. (1998) *Rapport sur l'état du Saint-Laurent. Les fluctuations des niveaux d'eau du Saint-Laurent*, p. 171. Équipe conjointe bilan, Sainte-Foy.

Rousseau, C. (1968) Histoire, habitat et distribution de 220 plantes introduites au Québec. *Naturaliste canadien*, **95**, 49–169.

Rousseau, C. (1974) *Géographie floristique du Québec-Labrador*, p. 798. Presses de l'Université Laval, Québec City.

SPSS Inc. (1999) *SPSS for Windows*. Release 10.0.0., SPSS Inc., Chicago, IL.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.

Tessier, C., Maire, A. & Aubin, A. (1981) Étude de la végétation des zones riveraines de l'archipel des Cent-îles du fleuve Saint-Laurent, Québec. *Canadian Journal of Botany*, **59**, 1526–1536.

Thompson, D.Q., Stuckey, R.L. & Thompson, E.B. (1987) *Spread, impact, and control of purple loosestrife* (Lythrum salicaria) *in North American wetlands*, p. 55. US Fish & Wildlife Service, Washington, DC.

Treberg, M.A. & Husband, B.C. (1999) Relationship between the abundance of *Lythrum salicaria* (purple loosestrife) and plant species richness along the Bar River, Canada. *Wetlands*, **19**, 118–125.

Velleman, P.F. & Hoaglin, D.C. (1981) *Applications, basics, and computing of exploratory data analysis*, p. 354. Duxbury Press, Boston.

Weiher, E., Wisheu, I.C., Keddy, P.A. & Moore, D.R.J. (1996) Establishment, persistence, and management implications of experimental wetland plant communities. *Wetlands*, **16**, 208–218.

White, D.J., Haber, E. & Keddy, C. (1993) *Plantes envahissantes des habitats naturels du Canada*, p. 136. Environnement Canada & Musée canadien de la nature, Ottawa.

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