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BIODIVERSITY
RESEARCH

Expansion pathways of the exotic common reed (*Phragmites australis*): a historical and genetic analysis

Benjamin Lelong[1], Claude Lavoie[1]*, Yvon Jodoin[1] and François Belzile[2]

[1]*Centre de Recherche en Aménagement et Développement,* [2]*Département de phytologie, Université Laval, Québec, Québec, Canada G1K 7P4*

*Correspondence: Claude Lavoie, Centre de Recherche en Aménagement et Développement, Université Laval, Québec, Québec, Canada G1K 7P4. Tel.: 1-418-656-2131 ext. 5375; Fax: 1-418-656-2018; E-mail: claude.lavoie@esad.ulaval.ca

ABSTRACT

Using 779 herbarium and modern specimens, we reconstructed the spread of the common reed (*Phragmites australis*) in Quebec, Canada, where large-scale invasion of this plant species has been reported since the 1960s. All specimens were genetically differentiated using molecular tools to identify the genotype (native or exotic). The exotic genotype (haplotype M) has been present in Quebec as early as 1916, but it was rare prior to the 1970s and was almost exclusively restricted to the shores of the St. Lawrence River. The exotic genotype spread inland only after the beginning of the 1970s. In less than 20 years, a complete shift occurred, from the dominance of native genotypes to the dominance of the exotic genotype. Today, more than 95% of common reed colonies found in Quebec are dominated by the haplotype M. It is especially abundant along roads, but colonies present in marshes are also dominated by the exotic genotype. This study provides evidence that, in Quebec, the development of the highway network in the 1960s and 1970s strongly contributed to the inland expansion of the exotic genotype. Moreover, it shows the usefulness of molecular techniques for reconstructing the spread of an invader. Without the use of molecular tools, the reconstruction of invasions of exotic taxa would be impossible because of the lack of clear phenotypic differences between genotypes.

Keywords

Herbarium specimen, invasive species, *Phragmites australis*, restriction fragment length polymorphism, river, road.

INTRODUCTION

Until recently, biogeographical studies relied on classical means (field data, museum specimens) to describe and analyse the distribution of species around the globe. During the last 20 years, genetics has opened additional avenues to ecologists and biogeographers. These avenues could not be explored without the resolution provided by sophisticated molecular tools. Recent developments in the field of molecular ecology have been particularly useful to biologists studying invasive species. Several questions may not be adequately answered without the use of molecular tools: What is the area of origin of the invader? (Downie, 2002; Genton *et al.*, 2005); Which expansion pathways are used by the invader? (Scotti *et al.*, 2000; Bryan *et al.*, 2005; Wüster *et al.*, 2005); How quickly are new regions occupied by the invader? (Saltonstall, 2002; Wüster *et al.*, 2005). Molecular tools are especially useful to discriminate between native and exotic populations of invaders that cannot otherwise be differentiated based on morphological traits (McIvor *et al.*, 2001; Saltonstall, 2002). This aspect is particularly important because native and exotic populations often behave differently; the exotic genotypes may be expanding (and should be controlled), while the native ones become rare (and should be the object of conservation plans).

Common reed (*Phragmites australis* [Cav.] Trin. ex Steud; Poaceae) is one of these invasive species that, in North America, has both native and exotic populations. Until the beginning of the 20th century, this aquatic plant species, although widespread on the continent, was not particularly common in wetlands (Orson *et al.*, 1987; Chambers *et al.*, 1999; Orson, 1999). However, during the last 50 years, the number and size of common reed colonies have markedly expanded in the freshwater (Meyerson *et al.*, 2000; Rice *et al.*, 2000; Wilcox *et al.*, 2003; Hudon *et al.*, 2005), brackish (Meyerson *et al.*, 2000; Rice *et al.*, 2000; Lathrop *et al.*, 2003), and salt (Bertness *et al.*, 2002) marshes of Canada and the USA. Common reed invasions often have severe consequences for plant and animal diversity and may alter the ecological functions of wetlands (Keller, 2000; Meyerson *et al.*, 2000; Lathrop *et al.*, 2003; Rooth *et al.*, 2003; Windham & Meyerson, 2003; Mal & Narine, 2004; Silliman & Bertness, 2004; Minchinton *et al.*, 2006).

Several ecologists and biogeographers (Chambers *et al.*, 1999; Galatowitsch *et al.*, 1999; Rice *et al.*, 2000; Bertness *et al.*, 2002;

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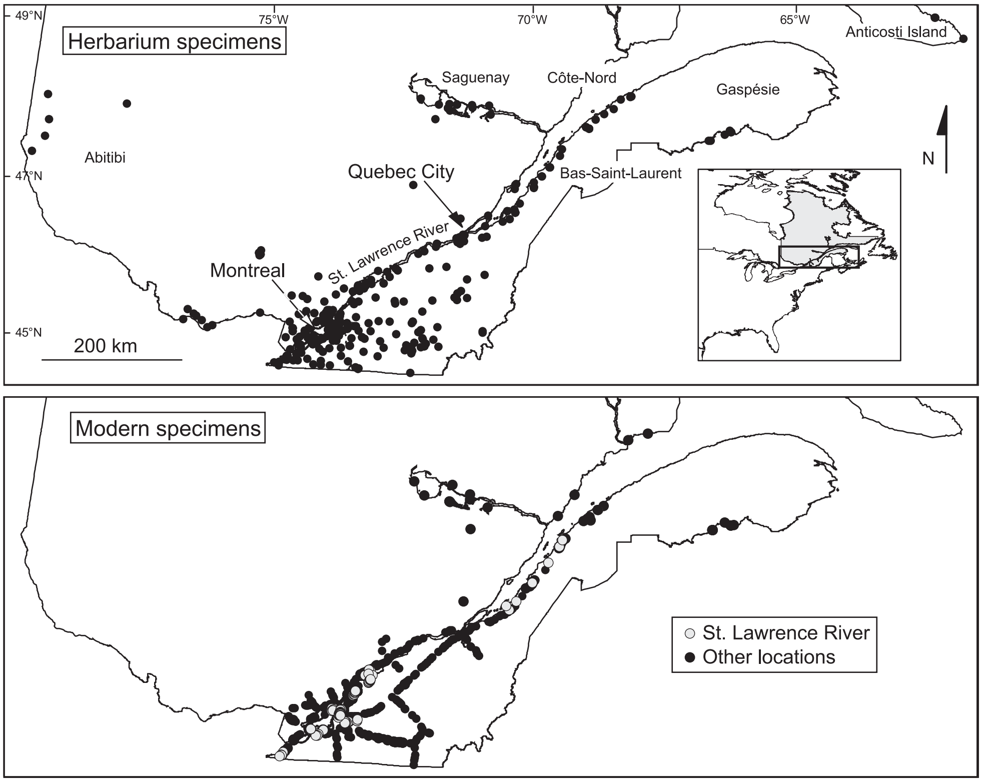

Figure 1 Spatial distribution of herbarium and modern common reed (*Phragmites australis*) specimens used to reconstruct the spread of the species in Quebec (Canada). Modern specimens sampled along the St. Lawrence River or in other locations (i.e. mainly along roads, some of these roads being located near the St. Lawrence River) are differentiated. Place names cited in the text are indicated.

Minchinton, 2002; Delisle *et al.*, 2003; Minchinton & Bertness, 2003; Hudon *et al.*, 2005) have attempted to understand why this species, present in North America for thousands of years (Orson *et al.*, 1987; Orson, 1999; Pederson *et al.*, 2005), has suddenly adopted an invasive behaviour allowing it to form dense monospecific stands covering hundreds of hectares. Several hypotheses have been raised (altered hydrology, anthropogenic disturbances, eutrophication, changing salinity levels), but they have so far failed to provide answers that are entirely satisfactory. On the other hand, using DNA sequencing, Saltonstall (2002) showed that the North American invasion by the common reed coincided with the introduction of an exotic genotype (haplotype M) along the eastern coast of North America. In some regions, the exotic genotype has completely replaced the native ones in less than 60 years.

The introduction of an exotic genotype (associated with anthropogenic disturbances) is considered to be the leading explanation for the rapid expansion of common reed observed in the 20th century. Field and experimental studies have already shown that haplotype M produces more shoots and has a higher growth rate than native haplotypes in both freshwater and saline environments (Vasquez *et al.*, 2005). It also grows taller, exhibits greater fresh biomass, and produces more leaf and stem biomass than its native counterparts (League *et al.*, 2006). Unfortunately, these studies do not shed light on the pathways used by the exotic common reed genotype in its spread. How has this genotype spread over such large areas? What are the main dispersal vectors? Are there any factors triggering invasions? A highly detailed biogeographical study can answer these questions. In this study, we used herbarium and modern specimens to reconstruct the spread of common reed in the province of Quebec, Canada, where a large-scale invasion has been reported since the 1960s (Delisle *et al.*, 2003; Hudon *et al.*, 2005). All specimens were genetically differentiated using molecular tools to identify the genotype (native or exotic). Since the common reed is mainly found along roads in Quebec (Jodoin, 2006), we hypothesized that the large-scale development of the provincial road network in the 1960s and 1970s was responsible for the rapid expansion of the exotic genotype.

METHODS

To reconstruct the spread of common reed in Québec, we used all the herbarium specimens that were stored in the four main herbaria of Québec (MT, QFA, QUE, SFS) and in the two herbaria of the Canadian Government (CAN, DAO). Each herbarium specimen was checked for possible misidentification, and the specimen number, sampling location, year of sampling, habitat characteristics, and name(s) of collector(s) were recorded. Only specimens collected in Quebec were examined (Fig. 1). Geographical coordinates (latitude, longitude) of sampling sites were identified as precisely as possible using the *Topos sur le web*

Figure 2 Common reed (*Phragmites australis*) colonies in Quebec (Canada); native genotype in a marsh near Restigouche (a); exotic genotype in a marsh at Lake Saint-François (b); exotic genotype along a highway near Montreal (c). Photographs: B. Lelong and C. Savage.

database (Commission de Toponymie du Québec, 2005). Any duplicates and specimens lacking precise information regarding the sampling location or date were discarded. A small leaf fragment was also taken from the specimens for genetic analyses.

To obtain a recent picture of the spatial distribution of common reed genotypes in Quebec, we sampled common reed colonies present in two habitat types, i.e. along roads and in marshes (Figs 1 & 2). A colony located in a marsh adjacent to a road (i.e. beyond the drainage ditch of the road) was classified as a marsh population. In 2000 and 2001, all common reed colonies present along the St. Lawrence River — where most marshes in the province are located — were recorded with a global positioning system (Lavoie *et al.*, 2003). These colonies, and newly established ones (Hudon *et al.*, 2005), were revisited in the summers of 2004 and 2005, and a small leaf fragment was taken from individuals located at the centre of each colony for genetic analysis. For common reed along roads, we focused our study on colonies located near the 13 limited-access highways of the province (total length: 2800 km). During the summer of 2003, the presence of colonies between each kilometre marker was noted. Once the survey was completed, a total of 260 kilometres were randomly selected for sampling from the kilometre segments containing at least one common reed colony. In the field, the first common reed colony found after crossing the kilometre marker that was selected was sampled (small leaf fragment) and recorded using a global positioning system.

According to the herbarium specimen database, some regions located far from the highway network of the province (Bas-Saint-Laurent, Côte-Nord, Gaspésie, Saguenay) contained few common reed colonies (Fig. 1). We hypothesized that these regions were less susceptible to invasion by the exotic genotype of common reed because of their remoteness from the highway network. To test this hypothesis, we revisited all historical common reed colonies identified in these regions during the summer of 2005. Once found, each colony was recorded with a global positioning system and sampled (small leaf fragment). It should be noted that considering the lack of precision of most herbarium specimen labels, we cannot be sure that the colony sampled in the field was exactly the same as that sampled several decades ago.

All leaf fragments (from herbarium or modern specimens) were kept in a freezer (−20 °C) prior to analysis. Total DNA was extracted as suggested by Edwards *et al.* (1991), and two non-coding regions of the chloroplast genome (*trnT* (UGU) — *trnL* (UAA) and *rbcL* — *psaI*) were amplified by polymerase chain reaction as described in Saltonstall (2003). Restriction site polymorphism was detected by digesting the amplicons with *Rsa*I for *trnT* (UGU) — *trnL* (UAA) and *Hha*I for *rbcL* — *psaI*. This procedure allowed the rapid identification of native or exotic (haplotype M) genotypes of common reed (Saltonstall, 2003).

All data were incorporated into a geographical information system, ARCGIS™ (ESRI, 2005). Maps indicating the spatial distribution of common reed genotypes during six time periods (before 1950, 1950–59, 1960–69, 1970–79, 1980–89, and after 1989) were produced. Furthermore, using the geographical information system, we superimposed a 10 × 10-km grid on a map of Quebec. The earliest mention of an exotic herbarium specimen of common reed (haplotype M) was recorded in each 100-km^2 cell. The cumulative number of occupied 100-km^2 cells was then plotted against time to construct an invasion curve (*sensu* Pyšek & Prach, 1993). Invasion curves were constructed using raw and square-root-transformed data to detect any significant lag in the dispersal of the species (Crooks, 2005).

RESULTS

A database incorporating 282 herbarium specimens and 529 modern specimens was created for this study (Fig. 1). We were able to identify the genotype (exotic or native) of all specimens, except 32 of the 282 herbarium specimens (11%) that were too badly preserved to extract DNA. Few specimens (39) were collected before 1950, but they nevertheless indicate that the species was probably well established at that time in the Montreal region and in some remote areas like Abitibi, Anticosti, Gaspésie, and Saguenay (Fig. 3). The oldest native common reed specimen

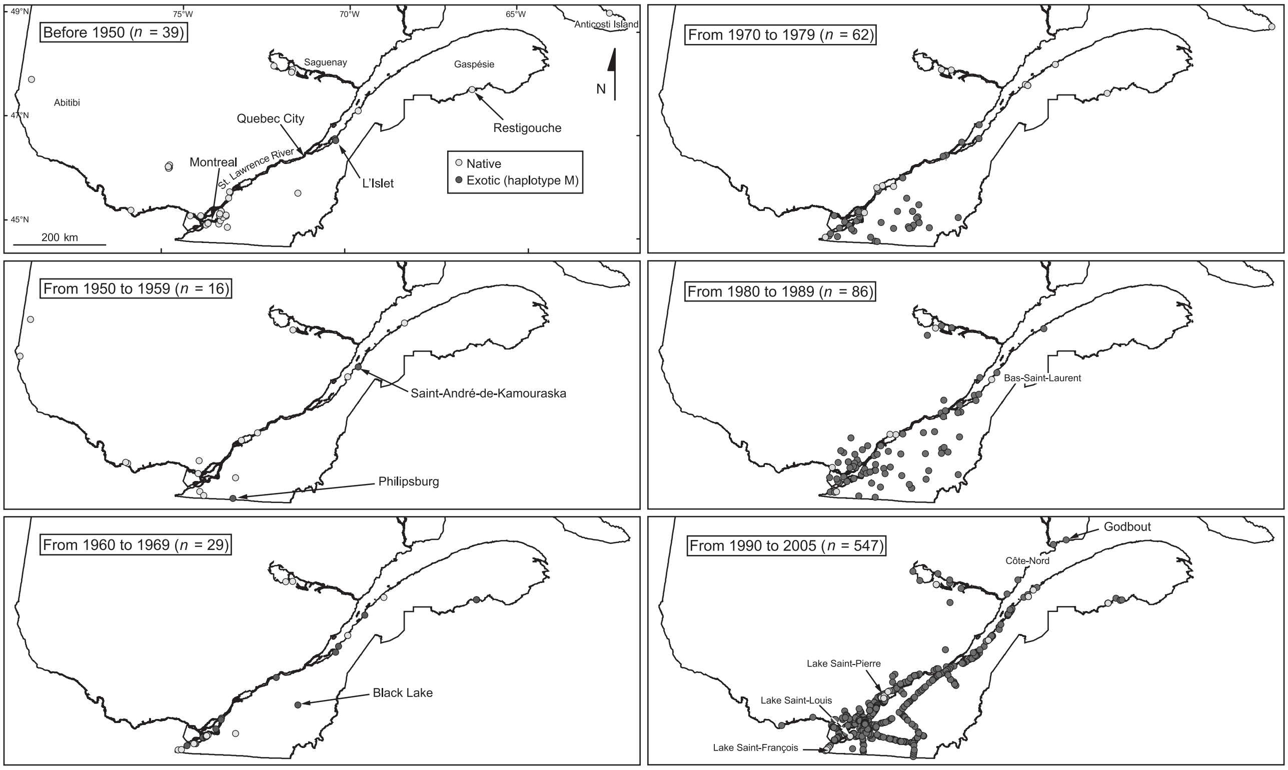

Figure 3 Location of common reed (*Phragmites australis*) specimens collected in Quebec (Canada) before 1950, from 1950 to 1959, from 1960 to 1969, from 1970 to 1979, from 1980 to 1989, and from 1990 to 2005, respectively. Genotypes (native or exotic) are differentiated. Place names cited in the text are indicated.

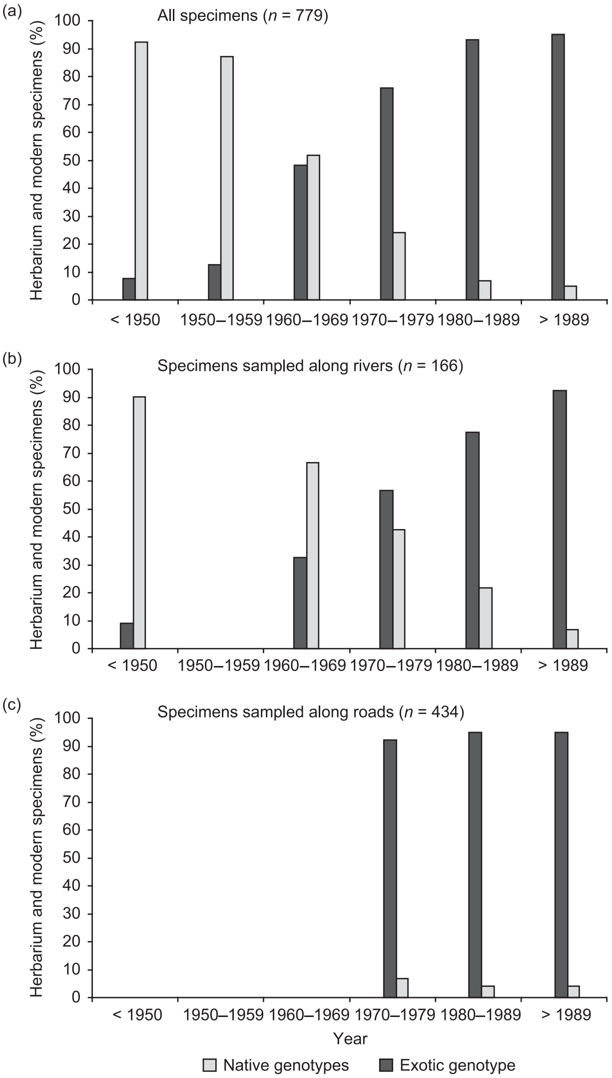

Figure 4 Proportion of common reed (*Phragmites australis*) specimens with the native or exotic genotype sampled in Quebec (Canada) before 1950, from 1950 to 1959, from 1960 to 1969, from 1970 to 1979, from 1980 to 1989, and from 1990 to 2005, respectively; all specimens sampled (a); specimens sampled only along rivers (b); specimens sampled only along roads (c). Two few specimens were collected along rivers in the 1950s (3) and along roads before the 1970s (5) to calculate reliable proportions.

was collected on the shore of a river in Restigouche (Gaspésie) in 1882. The oldest exotic (haplotype M) common reed specimen was collected at L'Islet, near Quebec City, in 1916. However, more than 92% of the common reed specimens sampled before 1950 were native (Fig. 4).

From 1950 to 1959, few changes occurred in the spatial distribution of common reed in Quebec. Only two additional exotic colonies were sampled during this period, one at Philipsburg, near the US border, in 1952, and the other along a road near L'Islet (Saint-André-de-Kamouraska) in 1955. The native genotype still dominated common reed colonies during this decade. This situation changed during the 1960s. Several new exotic colonies appeared, although almost exclusively along the St. Lawrence River. Only one exotic colony became established inland (Black Lake) in 1965. Approximately half of the common reed colonies sampled from 1960 to 1969 were exotic. However, the native genotype still dominated the colonies established along rivers.

The exotic common reed genotype spread inland mainly from the beginning of the 1970s. The specimens that were not collected along major waterbodies were only found along roads, and were almost exclusively (93%) exotic. Along rivers, the proportion of exotic colonies exceeded that of native colonies for the first time. The exotic common reed established in the marshes of St. Lawrence River with a salinity ranging from 0‰ to 24‰ (Bourget, 1997). The spread of the exotic genotype continued from 1980 to 2005. For the first time, the exotic common reed colonies were sampled in the Saguenay (1985) and Bas-Saint-Laurent (1987) regions. The northernmost exotic common reed colony found in Quebec was sampled at Godbout (Côte-Nord) along a road in 2004. From 1990 to 2005, 95% of common reed colonies sampled (including the modern specimens collected for this study) were exotic. This proportion was almost as high for colonies sampled along rivers (93%) as along roads (96%). Only 26 native common reed colonies have been sampled since 2000 in Quebec: some in regions that are far from the provincial highway network (Bas-Saint-Laurent, Gaspésie, Saguenay), and others along the St. Lawrence River (Lake Saint-François, Lake Saint-Louis, Lake Saint-Pierre) in the southern part of the province.

The invasion curve produced with all the exotic common reed herbarium specimens (Fig. 5) suggests a long lag (1916–61) between the introduction of the exotic genotype and its spread through the province of Quebec. This lag may not be real, especially if the growth of the exotic common reed population increases exponentially (Crooks, 2005). However, the lag remained even after a square-root transformation of data (the curve is still concave, and does not form a straight line), which strongly suggests that the prolonged lag is real, and not merely the representation of an inherent lag arising from dynamics early in the invasion process, when population sizes and occupied area are small (Crooks, 2005). It should be noted that the abrupt rise in the invasion curve (arithmetic scale) observed in 1985 is the result of the collection of a large number of common reed herbarium specimens to study chromosome numbers and reproductive aspects of several Quebec populations (Gervais *et al.*, 1993).

DISCUSSION

The exotic common reed genotype (haplotype M) has been present in Quebec since at least 1916, but it was rare prior to the 1970s and was almost exclusively restricted to the shores of the St. Lawrence River. The exotic genotype spread inland only after the beginning of the 1970s. In less than 20 years, a complete shift occurred, from the dominance of native genotypes to the dominance of the exotic genotype (haplotype M). Today, more than 95% of common reed colonies found in Quebec are dominated by the haplotype M. It is especially abundant along roads, but

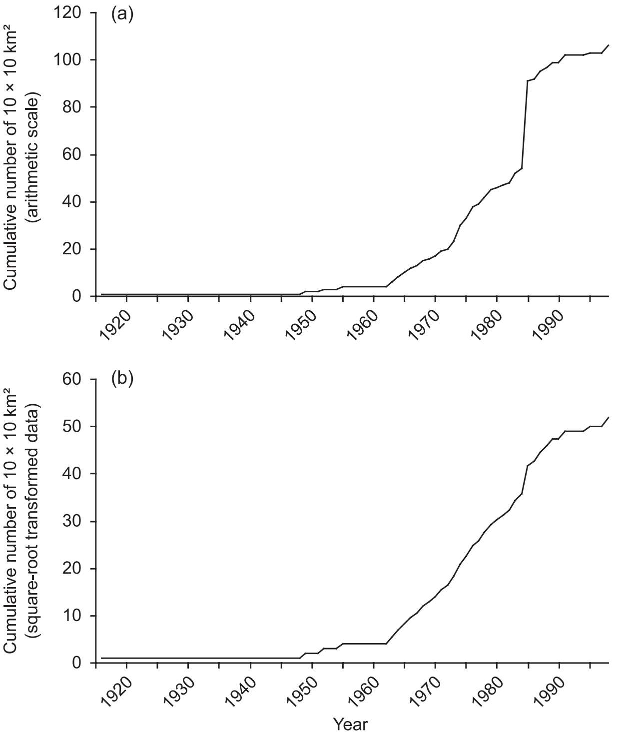

Figure 5 Invasion curves (*sensu* Pyšek & Prach, 1993) of the exotic genotype (haploytpe M) of common reed (*Phragmites australis*) in Quebec (Canada). Results are expressed as the cumulative number of 100-km^2 cells occupied by at least one herbarium specimen over time; arithmetic scale (a); square-root transformed data (b).

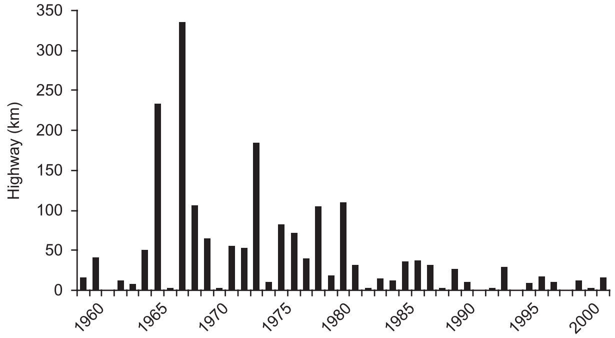

Figure 6 Length of the highway network constructed each year in Quebec (Canada) since the beginning of the construction program. Data (updated) from Ministère des Transports du Québec (1983).

colonies present in the marshes located along the St. Lawrence River are also dominated by the exotic genotype. Some native colonies still persist in regions located far from the highway network. However, the exotic common reed exists even there.

As with many other exotic plant species (Delisle *et al.*, 2003), the St. Lawrence River contributed to the spread of the exotic common reed genotype. However, there was a long lag (45 years: 1916–61) between the first mention of the exotic common reed in Quebec and the spread of the genotype. This lag cannot be attributed to low levels of herbarium specimen collection because in Quebec the most intense collection periods of the 20th century were recorded between 1930 and 1940 and from 1950 to 1985 (Delisle *et al.*, 2003). Which factors triggered the spread of the genotype along the St. Lawrence River and, later, inland? Recent studies conducted in the wetlands of the St. Lawrence River have shown that low water levels greatly facilitate the establishment and growth of new common reed colonies in marshes (Hudon *et al.*, 2005). Common reed exhibits a wide tolerance to water level fluctuations, giving this species a competitive advantage over most other aquatic plant species (Chambers *et al.*, 2003; Hudon *et al.*, 2005; Pagter *et al.*, 2005). The water level of the St. Lawrence River was exceptionally low at the beginning of the 1960s. For instance, at Lake Saint-Pierre, the river flow was only about 6000–6100 m^3 s^{-1}, compared to a maximum of 20,343 m^3 s^{-1} in 1976. Such low values were only reached twice from 1932 to 2001, i.e. in the mid-1930s and in the 1960s (Cantin & Bouchard, 2002). It is thus likely that the low water levels of the 1960s contributed to the spread and establishment of common reed. Wetland disturbances may also be responsible for this phenomenon. From 1945 to 1976, more than 3649 ha of wetlands were disturbed (drainage, dredged deposit, excavation, landfill) along the St. Lawrence River for agriculture, housing, and road construction, and to create the St. Lawrence Seaway (Centre Saint-Laurent, 1996). Such disturbances may have contributed to the establishment of common reed colonies by spreading rhizome fragments and eliminating competition by other wetland plants. However, the link between local disturbance and common reed establishment or expansion in wetlands remains to be substantiated (Rice *et al.*, 2000; Bart & Hartman, 2003; Silliman & Bertness, 2004; Hudon *et al.*, 2005).

There is a striking coincidence between the inland expansion of the exotic genotype of common reed (initiated about 1965) and the development of the highway network in Quebec. Most highways of the province were built between 1964 and 1979 (Fig. 6). Today, the roadsides of these highways are highly invaded by the exotic genotype, especially in the Montreal area where common reed forms hedges several kilometres long (Jodoin, 2006). The creation of highly interconnected linear wetlands (road ditches) that extend over hundreds of kilometres, and the maintenance of the highway network (ditch digging, roadside mowing) probably contributed to the spread of common reed and to the improvement of growth conditions (more light, less competition) for the species (Maheu-Giroux & de Blois, 2005, 2007; Jodoin, 2006). Moreover, more than 700,000 tons of de-icing salt are spread over Quebec roads every winter (Jodoin, 2006). High sodium levels may be observed up to 9 m from the highways (DiTommaso, 2004). The high salt tolerance of the haplotype M (Vasquez *et al.*, 2005) likely gives it a strong competitive advantage over other plants present in road ditches, such as cattails (*Typha* spp.).

CONCLUSION

The invasion history of the exotic common reed genotype in Quebec is a good example of a 'sleeper weed' phenomenon. A sleeper weed is an invasive plant that arrives in a region, naturalizes, and remains localized for some periods of time before the population suddenly increases and starts to spread and become seriously invasive (Groves, 2006). Our study provides evidence that in Quebec, the development of the highway network strongly contributed to the spread of the exotic genotype from populations established in riparian habitats. The case of the common reed in Quebec corroborates the fluctuating resource hypothesis of invasibility proposed by Davis *et al.* (2000), i.e. most plant invasions are caused by a change in the availability of a resource. In this case, the resource is a habitat (highways) forming long corridors, which suddenly became available to a plant species that was particularly well adapted to the harsh growth conditions characterizing roadsides. Our study highlights the increasing importance of roads for invasive plants, not only as conduits, but also as habitats (Pyšek & Prach, 1993; Gelbard & Belnap, 2003; Christen & Matlack, 2006; Wangen & Webster, 2006). Moreover, it shows the usefulness of molecular techniques for reconstructing the spread of an invader. Without these techniques, the reconstruction of the invasions of exotic taxa would be impossible due to the lack of clear phenotypic differences between genotypes.

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