

Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada

Yvon Jodoin^{1*}, Claude Lavoie¹, Paul Villeneuve¹, Marius Theriault¹, Julien Beaulieu² and François Belzile²

¹Centre de Recherche en Aménagement et Développement and ²Département de Phytologie, Université Laval, Québec, Québec, Canada G1K 7P4

Summary

1. Roads provide suitable conditions for the establishment and growth of exotic species. Most roads are bordered by drainage ditches forming a network of linear wetlands. Drainage ditches may serve as habitats and corridors facilitating the spread of aquatic invaders into the intersected ecosystems. The common reed *Phragmites australis* is one of these aquatic invaders frequently found in marshes and drainage ditches along roads. We hypothesized that highways have acted as corridors for the dispersal of the common reed and have contributed to the invasion of North American wetlands by this species.
2. We mapped the spatial distribution of the common reed along the highway network of the province of Quebec, Canada, where a large-scale invasion of this plant species has been reported since the 1960s. We also identified the genotype of common reed colonies using molecular tools and the main characteristics that favour the presence of the common reed in road ditches.
3. Approximately 67% of the 1359 1-km highway sections surveyed during summer 2003 in Quebec had at least one common reed colony. End to end, common reed colonies totalled 324 km, i.e. 24% of the 1359 km surveyed.
4. Common reed colonies located along the highways were largely (99%) dominated by the exotic (Eurasian) genotype (haplotype M).
5. The common reed was more abundant along highways located in warm regions, with a sum of growing degree-days ($> 5^{\circ}\text{C}$, 12-month period) ≥ 1885 , along highways built before the 1970s and in agricultural regions dominated by corn and soybean crops. Common reed colonies were larger when located along highways that were wide, built before the 1970s or in warm regions. This was particularly apparent if the roadside was bordered by a wetland. On the other hand, common reed colonies were more likely to be narrow when located near a woodland.
6. *Synthesis and applications.* Several disturbances (de-icing salts, ditch digging and agricultural nitrogen input) favour the development of large common reed colonies along roads, some of them expanding out of roadsides, particularly in wetlands. Reducing disturbances, leaving (or planting) a narrow (a few metres) hedge of trees or shrubs along highways or planting salt-resistant shrubs in roadside ditches could be efficient ways to slow the expansion of common reed or to confine the species to roadsides.

Key-words: agriculture, climate, invasive species, landscape, Quebec, restriction fragment length polymorphism, road, wetland

Introduction

In developed countries the road network extends over large areas and is particularly dense in highly populated regions

(Hawbaker *et al.* 2004). For example, in the USA public roads total more than 6.2 million km and 60% of the land area of the eastern part of the country is within 400 m of a road (Forman 2000; Riitters & Wickham 2003). Road construction and maintenance operations have major impacts on landscape and ecosystem dynamics (Forman & Alexander 1998; Trombulak & Frissell 2000; Hawbaker & Radeloff 2004). More specifically, they provide suitable conditions for the establishment and growth of exotic species (Wester & Juvik

*Correspondence author. Claude Lavoie, Centre de Recherche en Aménagement et Développement, Université Laval, Québec, Québec, Canada G1K 7P4 (fax 1 418 656 2018; e-mail claudio.lavoie@esad.ulaval.ca).

1983; Tyser & Worley 1992; Greenberg, Crownover & Gordon 1997; Johnston & Johnston 2004; Pauchard & Alaback 2004; Hansen & Clevenger 2005; Rentch *et al.* 2005). Roadsides also act as very effective corridors for plant invasions (Pyšek & Prach 1993; Gelbard & Belnap 2003; Christen & Matlack 2006; Hulme 2006; Wangen & Webster 2006). The recent extension of highway networks in some parts of the world may explain why several exotic species that had a very restricted range during the first half of the 20th century are today widespread (Delisle *et al.* 2003; Lelong *et al.* 2007).

Most roads are bordered by drainage ditches, forming a network of linear wetlands. Because of their spatial configuration, drainage ditches may serve as habitats and corridors facilitating the spread of aquatic invaders into the intersected ecosystems (Maheu-Giroux & de Blois 2007). The common reed *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) is one of these aquatic invaders frequently found in marshes and drainage ditches alongside roads (McNabb & Batterson 1991; Gervais *et al.* 1993; Delisle *et al.* 2003; Lelong *et al.* 2007; Maheu-Giroux & de Blois 2007). During the last 50 years, the number and size of common reed colonies have expanded markedly in marshes and along roads in Canada and the USA (Meyerson *et al.* 2000; Rice, Rooth & Stevenson 2000; Bertness, Ewanchuk & Silliman 2002; Lathrop, Windham & Montesano 2003; Wilcox *et al.* 2003; Hudon, Gagnon & Jean 2005). The introduction of an exotic genotype (haplotype M), associated with anthropogenic disturbances, is considered to be the leading explanation for the rapid expansion of common reed observed in North America (Saltonstall 2002). Field and experimental studies have shown that the haplotype M produces more shoots and has a higher growth rate than native haplotypes (Vasquez *et al.* 2005). It also grows taller 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.

Very few ecologists have considered the possibility that highways have acted as corridors for the common reed and contributed to the invasion of adjacent wetlands (Richburg, Patterson & Lowenstein 2001; Maheu-Giroux & de Blois 2007), which is peculiar considering that roadsides are one of the most common habitats for the species in temperate regions. Furthermore, to our knowledge, there is no recent systematic survey of the distribution of common reed colonies along roads in North America. In this study, we mapped the spatial distribution of the common reed along the highway network in the province of Quebec, Canada. The invasive genotype of common reed 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 (Lelong *et al.* 2007). We identified the genotype (native or exotic) of common reed colonies found along highways using molecular tools. We also identified the main characteristics (climate, landscape and road structure) that favour

the presence of the common reed in road ditches. We hypothesized that highway roadsides in Quebec are massively invaded by the exotic genotype of common reed, particularly in the warmest regions of the province. We also hypothesized that highway sections lying on clay soils and surrounded by marshes or agricultural lands absorbing massive inputs of fertilizers were more successfully invaded by the common reed than those lying on well-drained surface deposits and surrounded by woodlands.

Methods

STUDY AREA

For this survey of the common reed along roads in Quebec, we focused on colonies located near the 13 limited-access highways of the province, i.e. major travel corridors with separate, parallel roads for each direction of travel (total length 2800 km). The area covered by this study extended over 6° longitude and 3° latitude (Fig. 1). The climate of this large region is continental and wet, but major climatic differences can be observed within the study area. For example, the mean annual temperature at the southernmost meteorological station (Philipsburg) is 7 °C, with a mean monthly maximum (July) and minimum (January) of 21 °C and –9 °C, respectively. At this station, the sum of growing degree-days (> 5 °C) for a 12-month period totals 2170. The mean annual temperature at the northernmost station (Saint-Arsène) is 3 °C, with a mean monthly maximum (July) and minimum (January) of 18 °C and –13 °C, respectively. At Saint-Arsène, the sum of growing degree-days (> 5 °C) totals only 1451 (Environnement Canada 2002).

FIELD SURVEY

All limited-access highways in Quebec, except those on the island of Montreal (for safety reasons), were surveyed in August 2003. The distance covered by the common reed along roadsides (DCR) was first evaluated to obtain a picture of the spatial distribution of this species along highways. The time to pass by common reed colonies was estimated between two kilometre markers (two markers separated by 1 km) using a chronometer and a vehicle travelling at a constant speed (90 km h⁻¹). Colonies present in the median strip separating the two roadways of the highway were not considered for this survey for safety reasons. This timing operation was repeated every 2 km in both directions of the highway. To obtain the DCR, the time (s) was simply multiplied by the speed of the vehicle (m s⁻¹). DCR values were then transformed into a percentage of the 1-km section bordered by common reed colonies. The error associated with this method was estimated by randomly selecting 100 1-km sections and measuring the exact DCR by foot with a measuring wheel.

Once the survey was completed, a total of 260 1-km sections was selected randomly for sampling from the subset of sections containing at least one common reed colony. In the field, the common reed colony nearest the kilometre marker was recorded using a global positioning system (GPS) and sampled for genetic analyses (small leaf fragment). The roadside width and the maximum distance covered by the common reed colony (perpendicular to the road) were measured. The maximum extension of the colony away from the roadside was also measured where appropriate. The landscape structure surrounding the colony (agricultural land, old field, urban, wetland or woodland) was noted.

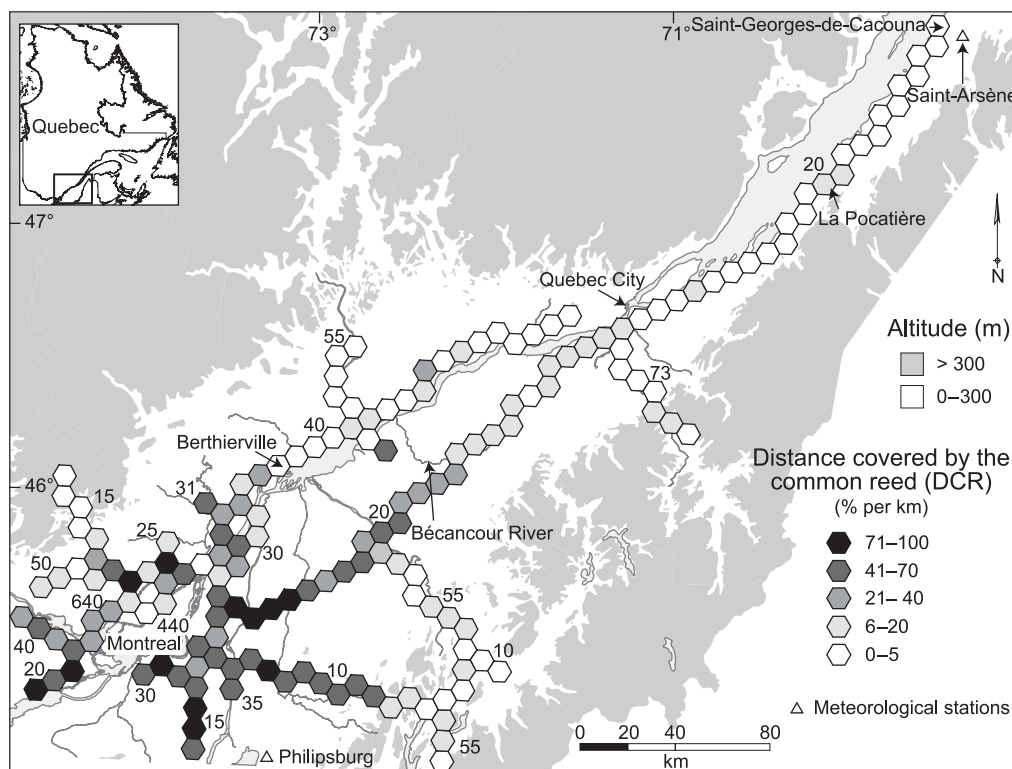


Fig. 1. Distance covered by the common reed (DCR) along roadsides of limited-access highways of Quebec in 2003. Each hexagon represents the average of DCR values (percentage of a 1-km section bordered by common reed colonies) for a 10-km long highway segment. Highway numbers and place names cited in the text are indicated.

GENETIC ANALYSES

All common reed leaf fragments were kept in a freezer (-20°C) prior to analysis. Total DNA was extracted as suggested by Edwards, Johnstone & Thompson (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 *RsaI* for *trnT* (UGU)–*trnL* (UAA) and *HhaI* for *rbcL*–*psaI*. This procedure allowed the rapid identification of native or exotic (haplotype M) genotypes of common reed (Saltonstall 2003).

GEOGRAPHICAL INFORMATION SYSTEM

All field and laboratory data were incorporated into a geographical information system (GIS), MapInfo Professional© (MapInfo Corporation 2003). Several other databases had also been incorporated into the GIS to analyse the spatial distribution of common reed. The sums of growing degree-days ($> 5^{\circ}\text{C}$, 12-month period) of the 88 meteorological stations located in the study area (Environnement Canada 2002) were used as indicators of the length of the growing season for plants. To assign a specific growing degree-day value to each 1-km section that was surveyed, a spatial interpolation of climatic data was conducted using the kriging method (Legendre & Legendre 1998) and the Vertical Mapper© software (MapInfo Corporation 2004).

A specific type of surface deposit (alluvial, fluvioglacial, lacustrine, marine or morainal) and the dominant type of the neighbouring landscape (agricultural corn and soybean, agricultural pasture,

mixed agricultural and woodlands or woodlands) were associated with each 1-km section that was surveyed. Surface deposit data were extracted from a map (1 : 1000 000) produced by the Centre de Recherches sur les Terres et les Ressources Biologiques (1996). Landscape data, sampled in 1993 and 1994, were from Jobin *et al.* (2003). The age of each 1-km road section was also calculated (Ministère des Transports du Québec 1983, 2004) and incorporated into the GIS. Finally, the presence of a woodland bordering the kilometre sections was noted using maps (1 : 50 000) produced by the Ministère des Ressources Naturelles du Canada (2003). Woodlands are important because they may prevent the expansion of common reed out of roadsides; the species does not grow well under a dense tree cover (Haslam 1972; Mal & Narine 2004).

DATA ANALYSES

We used an ordinal response regression model (ORRM; Clogg & Shihadeh 1994; Menard 1995; Hébert 1998; Guisan & Harrell 2000) to study the relationship between the DCR and (i) the surface deposit types, (ii) the landscape types, (iii) the climate, (iv) the age of the highway and (v) the presence of woodlands near a 1-km section. An ORRM was more appropriate than a multiple regression model because DCR values were not normally distributed (Weisberg 2005). Furthermore, the grouping of DCR data into a limited number of classes minimized the errors associated with the accuracy of the measuring method (chronometer).

To conduct this analysis, DCR values were first distributed into three classes (0%, 0.1–40%, 40.1–100%). In fact, the frequency distribution of DCR values had two discontinuities, one after 0% (i.e. without common reed), and the other around 40% (i.e. 40% of the

length of the 1-km section was covered by the common reed). All classes had a similar number of observations. Class homogeneity was tested using an analysis of variance. The data set was then randomly divided into two complementary subsets ($n_1 = 723$ and $n_2 = 636$), and an analysis was applied independently to each subset (Guisan & Harrell 2000) in order to enhance variables selection using simple bootstrapping. Only variables with a significance level < 0.05 in both models, and with a B coefficient similar in the two models (i.e. within the range delineated by the standard error), were retained. The magnitude of a positive (negative) B coefficient indicates the impact exercised by the independent variable on the likelihood of belonging to a class with high (low) DCR values. The ORRM was finally applied to the entire dataset ($n = 1359$) but only with significant variables. The polytomous universal model with the complementary log-log link function of the SPSS software was used to conduct the ORRM (SPSS Inc. 2003). Finally, we used a multiple regression analysis (Dodge 1999; Weisberg 2005) to study the relationship between the maximum distance covered by a common reed colony (perpendicular to the road) and (i) the surface deposit types, (ii) the landscape types, (iii) the climate, (iv) the age of the highway and (v) the width of the roadside. The multiple regression analysis was conducted with the SPSS software (SPSS Inc. 2003). Multicollinearity was tested in both models using the variance inflation factor (VIF) test (Sokal & Rohlf 1995). VIF comprises the diagonal elements of the inverse of the matrix of correlations between the independent variables. As a rule of thumb, a $VIF > 10$ indicates harmful multicollinearity. In both models, all VIF were < 5 . Finally, for each of the models (ORRM and multiple regression analysis) the spatial autocorrelation (Moran's I) was computed on the dependant variable and on the model residuals.

Results

Approximately 67% of the 1359 1-km highway sections surveyed during summer 2003 in Quebec had at least one common reed colony. End to end, the common reed colonies totalled 324 km, i.e. 24% of the 1359 km surveyed. DCR values were highest in the south-western part of the province (Fig. 1). In this region, the common reed often formed uninterrupted kilometre-long hedges along highways. The transition between regions with high and low DCR values was in most cases very rapid (Fig. 1), particularly along highways 10 (in mountainous areas), 20 (near the Bécancour River), and 40 (near Berthierville). East of Quebec City, very few roadsides were invaded by the common reed, except near La Pocatière. The difference between DCR values (chronometer) and real values (measuring wheel) was < 20 m in 62% of cases. Major mistakes (differences > 100 m) were recorded only in 12% of the 1-km sections. Furthermore, only nine out of 100 1-km highway sections (measured with a measuring wheel) were classified in the wrong DCR class, i.e. above or below the 40% value.

Common reed colonies located along highways were largely (99%) dominated by the exotic genotype (haplotype M). Only three of the 260 samples corresponded to a native (North American) genotype (Fig. 2). These were located near Lake Saint-Pierre and at Saint-Roch-des-Aulnaies, in the eastern part of the study area.

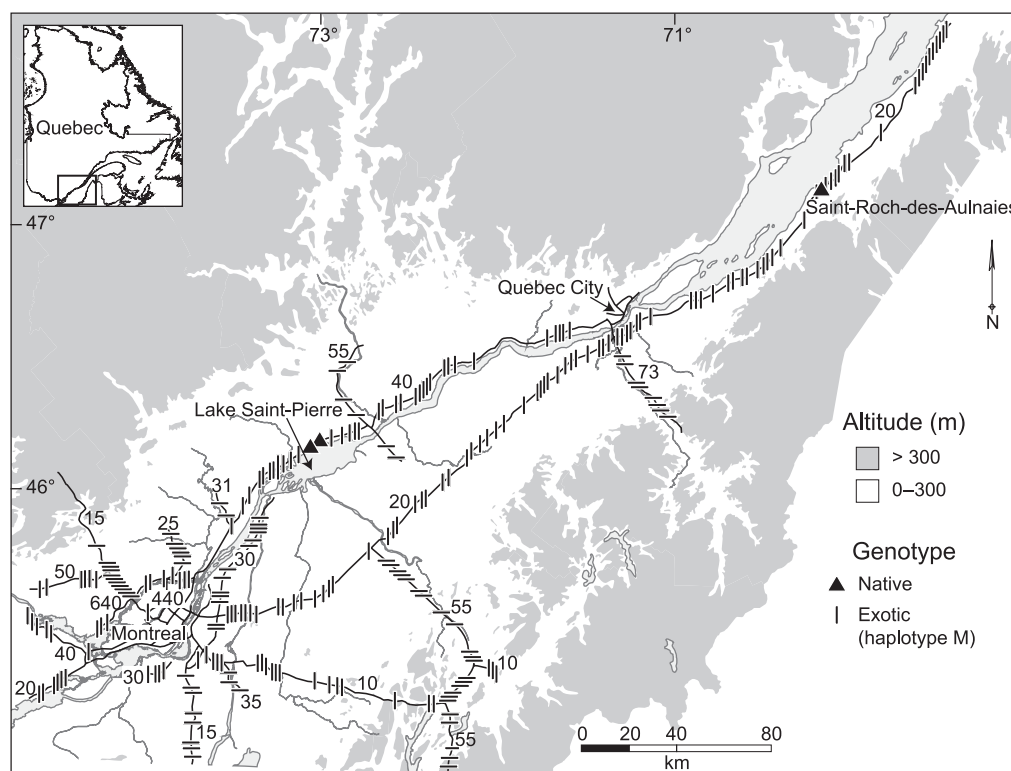


Fig. 2. Genotypes of common reed colonies along roadsides of limited-access highways of Quebec in 2003. Highway numbers and place names cited in the text are indicated.

Table 1. Results of the ordinal response regression model (ORRM) used to study the relationship between the distance covered by the common reed (DCR) along roadsides of Quebec's limited-access highways and the main environmental characteristics (climate, landscape, road structure) of southern Quebec

Significant variable	Coefficient B	SE	Wald	P
Sum of growing degree-days (> 5 °C, 12-month period)	0.354	0.019	350.4	< 0.001
Age (year) of the highway section	0.029	0.004	43.8	< 0.001
Landscape dominated by corn and soybean crops	0.654	0.168	15.2	< 0.001

Table 2. Results of the multiple regression analysis used to study the relationship between the maximum distance covered by a common reed colony (perpendicular to the road) located on a roadside of a limited-access highway in Quebec and the main environmental characteristics (climate, landscape, road structure) of southern Quebec

Significant variable	Unstandardized coefficient		Standardized coefficient	t	P
	B	SE	β_s		
Width (m) of the roadside	0.019	0.005	0.228	3.971	< 0.001
Sum of growing degree-days (> 5 °C, 12-month period)	0.072	0.018	0.227	3.942	< 0.001
Presence of a wetland near the highway section	0.741	0.214	0.200	3.455	< 0.001
Presence of a woodland near the highway section	-0.234	0.088	-0.153	-2.649	0.009
Age (year) of the highway section	0.014	0.005	0.152	2.634	0.009

The ORRM (Nagelkerke $R^2 = 0.42$, $P < 0.001$) indicated that only three variables had a significant ($P < 0.001$) influence on DCR values. The relative influence of each variable is indicated by the Wald's statistic (Table 1). The variable with the highest influence in the model was the climate, followed by the age of the highway section and the landscape. Regression coefficients (B) all had positive values. In short, the common reed was more abundant along highways located in warm regions with a sum of growing degree-days (> 5 °C) ≥ 1885 , along highways built before the 1970s and in agricultural regions where corn and soybean crops were dominant (Fig. 3). Including climate variation (interpolation of degree-days) and road age in the model was efficient to remove part of the spatial autocorrelation among adjacent DCR segments. As suggested by Fig. 1, spatial autocorrelation among adjacent observed values up to a distance of 5 km (initial Moran's $I = 0.622$, $P < 0.001$) was reduced, but still significant, when computed among the residuals ($I = 0.288$, $P < 0.001$). However, in the presence of spatial autocorrelation, the maximum likelihood estimation procedure used in the ORRM yielded asymptotically efficient estimates (Kennedy 1985).

The multiple regression model ($R^2 = 0.21$, $P < 0.001$) indicated that five variables had a significant ($P < 0.001$) influence on the maximum distance covered by a common reed colony (perpendicular to the road). The residuals of the model were non-significant ($P = 0.176$). The relative influence of each variable is indicated by the standardized coefficient (Table 2). The variable with the greatest influence in the model was the width of the roadside, followed by the climate, the landscape structure bordering the roadside (wetland or woodland), and the age of the 1-km highway section. Regression coefficients (β_s) all had positive values, except for the presence of a wood-

land in the vicinity of the roadside. In other words, a common reed colony was larger where it was located on a large roadside built in a warm region before the 1970s, particularly if the roadside was bordered by a wetland. On the other hand, a common reed colony was more likely to be narrow if it was located near a woodland.

Discussion

The exotic genotype of the common reed (haplotype M) was very abundant along the roadsides of Quebec's highways in 2003. It was, however, much more abundant along the highways located in the south-western part of the province, i.e. in the warmest regions of Quebec. Apparently, the colder climatic conditions (shorter growing seasons) of the eastern part of the province have slowed, but not prevented, the expansion of common reed colonies along the highways built in this area. Common reed was also more abundant along highways built before the 1970s. The species probably had more time to establish and spread along these highways than along those constructed later.

Common reed has several characteristics facilitating its establishment and survival in road ditches. It can tolerate the high variations in the water level of ditches (Haslam 1970; Hudon, Gagnon & Jean 2005; Pagter, Bragato & Brix 2005). It also exhibits a wide tolerance to salt (Matoh, Matsushita & Takahashi 1988; Lissner & Schierup 1997; Mauchamp & Mésleard 2001; Richburg, Patterson & Lowenstein 2001; Vasquez *et al.* 2005), which is particularly important along Quebec roads where large quantities (700 000 tons) of de-icing salt are used each winter (Soprin Experts-Conseils 1994). Indeed, high sodium levels may be observed up to 9 m

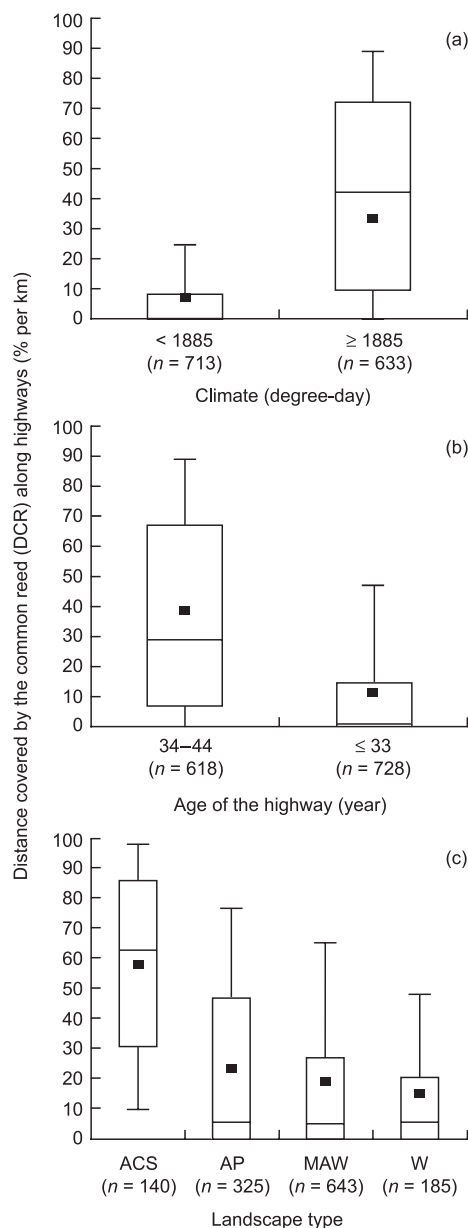


Fig. 3. Distance covered by the common reed (DCR) along roadsides of limited-access highways of Quebec in 2003, expressed as the percentage of a 1-km section bordered by common reed colonies, according to (a) the climate [sum of growing degree-days ($> 5^{\circ}\text{C}$) for a 12-month period], (b) the age of the highway and (c) the landscape surrounding the highway. Landscape types: ACS, agricultural corn and soybean; AP, agricultural pasture; MAW, mixed agricultural and woodlands; W, woodlands. In each boxplot, the mean (black square), the median (horizontal bar), 25 and 75 percentiles (box) and 10 and 90 percentiles (error bars) are indicated.

from the roadways (DiTommaso 2004). The maintenance of the road network (ditch digging and cleaning) probably contributes to the spread of common reed and to the improvement of growth conditions (more light, less competition) for the species (McNabb & Batterson 1991).

The surrounding landscape has a strong influence on the distribution of common reed. More particularly, a highway

crossing a landscape dominated by agriculture, and particularly by cash-crops such as corn and soybean, is more likely to be invaded by the common reed than a highway surrounded by woodlands. There is probably a link between fertilizers used in agriculture and common reed; nitrogen fertilization stimulates the growth of common reed biomass and accelerates the spatial expansion of colonies (Romero, Brix & ComBn 1999; Farnsworth & Meyerson 2003; Minchinton & Bertness 2003; Rickey & Anderson 2004). In the Montreal area, where the common reed is abundant, 51% of agricultural land is used to grow corn (Ministère de l'Environnement du Québec 2003). In this region, large quantities of organic (hog manure) and chemical fertilizers are spread on corn fields. Nitrogen run-off from agricultural fields is a widespread problem: high nitrate values ($0.5\text{--}1.0\text{ mg L}^{-1}$) have been recorded in tributaries of the St Lawrence River located between Montreal and Quebec City, and 34–76% of these nitrates probably result from farming activities (Painchaud 1999; Ministère de l'Environnement du Québec 2003). Considering the interconnections between drainage networks, it is probably that the common reed benefited from agricultural nitrogen inputs during its expansion along roads.

The fact that spatial autocorrelation among adjacent observed DCR values up to a distance of 5 km was still significant when computed among the residuals suggests that the common reed dissemination processes may involve additional endogenous (species dispersal, competition) or exogenous processes (environmental covariates; Dormann 2007). For instance, alpine plants with small diaspores and with adaptation for wind dispersal (such as the common reed) also show a high degree of spatial autocorrelation (Dirnböck & Dullinger 2004).

As long as the common reed remains along roadsides, the plant does not represent a major problem. Common reed may even be beneficial for road safety, because it forms effective snow fences that prevent the formation of ice on roadways (J. Gilbert, unpublished data). Problems arise when colonies expand out from roadsides, especially into agricultural lands and wetlands. To date few agricultural lands have been invaded by the common reed, but there is some evidence that this phenomenon is increasing, particularly along ditches draining corn fields (Maheu-Giroux & de Blois 2007). On the other hand, we observed several marshes located near highways that were invaded by the common reed. Colonies located in these marshes were particularly large (up to 45 m).

How can we prevent the expansion of the common reed out from roadsides? Our study showed that the common reed does not penetrate into woodlands; this species is shade intolerant (Haslam 1972). Leaving (or planting) a narrow (a few metres) hedge of trees or shrubs along highways could be an efficient way to confine the common reed to roadsides. Planting salt-resistant shrubs (alders, willows) in roadside ditches could also stop the expansion of the common reed along highways, particularly in regions where the exotic genotype of the species is not widespread. This new approach of weed control (Kim, Ewing & Giblin 2006) could be particularly useful in Canada where the use of herbicides, to date the only way to

successfully eliminate the common reed (Turner & Warren 2003; Teal & Peterson 2005), is strictly forbidden for controlling this plant species. Reducing the width of roadsides (less open space for the species) and minimizing disturbances (spreading of de-icing salt and ditch digging) may also contribute to slowing the expansion of common reed along roads.

The common reed genotype found along Quebec's highways is the same genotype invading wetlands along the Atlantic coast of the USA and having a strong impact on plant and animal diversity (Chambers, Meyerson & Saltonstall 1999; Meyerson *et al.* 2000; Saltonstall 2002). This highlights the threats facing ecosystems, and more particularly wetlands, intersected by highways; if the common reed escapes from roadsides, the probability of invasion is high.

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