THE LANDSCAPE ECOLOGY OF THE INVASIVE SPECIES *PHRAGMITES AUSTRALIS* IN ANTHROPOGENIC LINEAR WETLANDS

By

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Abstract

The recent and rapid expansion of *Phragmites australis* in North America provides an opportunity to relate dispersal patterns to landscape structure. Linear wetlands, such as roadside or agricultural ditches, may serve as corridors that facilitate dispersal at the landscape scale, but there is little quantitative information on patterns of invasion in these habitats. Remote sensing data, GIS, and field observations were used (1) to assess the feasibility of mapping populations of *P. australis* in linear wetlands and (2) to quantify and explain recent invasion patterns of *P. australis* in two periurban areas of southern Québec. An accuracy assessment demonstrated the reliability of aerial photographs to map populations in linear habitats. The intrinsic growth rate observed is high compared to those reported in natural wetlands. Spatial analysis revealed that colonization events are not constrained by the network's configuration. Logistic regressions confirmed the effect of road corridors on the spread of *P. australis*.

Résumé

L’expansion rapide et récente de *Phragmites australis* en Amérique du Nord fournit une opportunité unique permettant de relier des patrons de dispersion à la structure du paysage. Les milieux humides linéaires, comme les fossés de drainage routiers ou agricoles, serviraient de corridors d’invasion, mais il y a peu de données quantitatives sur les patrons de dispersion dans ces habitats. La télédétection, un SIG, et des observations de terrain ont été utilisés pour (1) quantifier la précision de la cartographie de *P. australis* dans des habitats linéaires à partir de photos aériennes et (2) pour caractériser et expliquer les patrons d’invasion dans les habitats linéaires de deux paysages périurbains. L’analyse de la cartographie a démontré la fiabilité des photos aériennes. Le taux de croissance des populations est élevé comparé à celui rapporté en milieu naturel. Des régressions logistiques ont confirmé l’effet des routes sur la dispersion de *P. australis.*

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Authors' contributions

The general introduction, chapter 1, and the general conclusion were written by the candidate and edited by his supervisor, Dr. Sylvie de Blois (Dept. of Plant Science of McGill University and McGill School of Environment). Dr. de Blois also co-authored chapter 2 and 3. Processing of remote sensing data, integration of data into the GIS, sampling designs, data collection, statistical analysis and interpretation were all performed by the candidate under the supervision of Dr. de Blois. Chapter 2 has been submitted to "Aquatic Botany" and has been accepted for publication. Chapter 3 will be submitted shortly to "Landscape Ecology". Funding for this research project was provided by Dr. de Blois through an NSERC grant and from the Ministère des Transports du Québec. Bruce Gélinas assisted the candidate for two weeks in the summer 2004 for conducting the accuracy assessment reported in chapter 2. Myosotis Bourgon Desroches performed the germination tests reported in chapter 3.

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List of Abbreviations

AIC	Akaike Information Criterion
GCP	Ground Control Point
GIS	Geographic Information Systems
GPS	Global Positioning System
LC/LU	Land Covers / Land Uses
NAD	North American Datum
PCA	Principal Component Analysis
RMSE	Root Mean Square Error
ROW	Right-of-Way
SC	Schwarz Criterion
UTM	Universal Transverse Mercator

GENERAL INTRODUCTION

The recent and aggressive invasion of an introduced genotype of the emergent macrophyte *Phragmites australis* (Cav.) Trin. ex Steud., in Québec and other parts of North America provides an exceptional opportunity to relate landscape structure to patterns of plant invasion. The species colonizes anthropogenic linear wetlands, such as roadsides and agricultural ditches, that potentially serve as dispersal corridor and foci of invasion in the landscape that they intersect (Bart and Hartman 2000; Catling et al. 2003; Gervais et al. 1993). Adverse consequences of this biological invasion include blockage of drainage structures, competition with adjacent agricultural crops, reduction in plant species richness and associated fauna, and possibly ecosystem functions (Buttery and Lambert 1965; Chambers et al. 1999; Keller 2000; Weinstein and Balletto 1999; Windham and Lathrop 1999).

The investigation of the spatio-temporal dynamics of *P. australis* can provide insights into the ecological processes that facilitate or hinder invasion. Moreover, because the timely detection and monitoring of invasive species may be critical to control efforts, managers of natural and anthropogenic systems need detailed information on the dynamics of invasion patterns. In spite of the omnipresence of linear wetlands in agricultural and periurban landscapes, there is to date no quantitative information on the invasion dynamics of *P. australis* in these habitats. This requires information on changes in spatial patterns over time, which is best provided by remote sensing data. The monitoring of an emergent macrophyte in such narrow landscape elements, however, remains a challenge.

The overall objectives of this study were:

1) To assess the feasibility of mapping populations of *P. australis* in narrow linear wetlands using remote sensing data.
2) To quantify and explain recent invasion patterns of *P. australis* in two periurban areas of southern Québec, focusing on the interaction between the network of linear wetlands and the adjacent land uses.

In this thesis, I present in the first chapter an overview of the current knowledge on *P. australis* invasiveness, discuss techniques for monitoring the species at the landscape scale and consider the effect of landscape structure on biological invasion. To fulfill the first objective, an accuracy assessment of maps obtained from large-scale aerial photographs was conducted and results for panchromatic and colour photographs at the same spatial resolution were compared. Aerial photographs were chosen because they are still the most available and cost-effective remote sensing data source for time-series analysis of emergent macrophytes. Because of the structure of our target habitats and the characteristics of the target species, the errors in photointerpretation and classification were potentially high and had to be rigorously assessed. Sources of mapping errors were identified and analyzed by logistic regressions. Results of those analyses are presented in chapter 2. To my knowledge, this study is the first to report a detailed methodology and an accuracy assessment for mapping invasive plants in linear habitats.

To fulfill the second main objective, I conducted a landscape scale analysis of invasion patterns in two periurban areas of southern Quebec, Canada, focusing on the interaction between the network of linear wetlands and the adjacent land uses. Invasion patterns within the network of linear habitats were first reconstructed from historical remote sensing data (1985-2002 and 1987-2000) using the knowledge acquired in the second chapter. Colonization events, which are crucial to understand the spread of the species, were analysed using spatial statistics. Finally a predictive model of *P. australis* occurrence in linear wetlands was tested using landscape, landscape dynamicity, biotic, and abiotic variables. The results are presented in chapter 3.

This study provides the first quantitative evaluation of *P. australis* dynamics in linear wetlands and is one of the first to relate landscape structure to patterns of plant invasion, an important and novel issue in landscape and invasion ecology. Moreover, the results provide insights on the ecological and landscape processes that can explain these patterns and provide land managers with spatial information that can increase the efficiency of management practices to control invasion in these habitats.

CHAPTER 1: Literature Review

Introduction

Because of its worldwide distribution, *Phragmites australis* is one of the most extensively studied wetland species in the world (Brix 1999). In fact, when the keyword "Phragmites australis" is typed in a scientific database research engine (Web of Science® V-3.0), more than 900 entries are found. This literature review focuses on the invasive behaviour of this plant in North America and related subjects. I will briefly review current knowledge on *P. australis* invasiveness and give pertinent background information. Then, I will discuss techniques for monitoring this species at the landscape scale. Finally, I will end this literature review by considering the effect of landscape structure on biological invasion.

Phragmites australis

Species distribution and description

The name of the genus *Phragmites* is derived from the Greek word *phragm,* which refers to the plant's fencelike growth. There are three species from this genus: *Phragmites karka* (Retz.) Trin. ex Steud., *Phragmites mauritianus* Kunth, and *Phragmites australis* (Cav.) Trin. ex Steud. The first inhabits regions of Polynesia, Australia, tropical Asia and West Africa. The second occupies central Africa and the third thrives in all temperate zones of the world, from the tropics to the 70th parallel (Haslam 1972; Marie-Victorin 1995; Mousseau 1987). Hence, *P. australis* is one of the most widespread species (Tucker 1990) and one of a few that can truly be regarded as cosmopolitan (Den Hartog et al. 1989). Reed, common reed, common grass, cane grass, reed grass, roseau cane, and roseau commun are some of the usual vernacular names for this species (Darbyshire et al. 2000; Marie-Victorin 1995).

P. australis is a hemicryptohpyte, perennial, with an annual stem that can grow to heights ranging from 1 to 4 metres. The glabrous stem has a round shape and wear knots (Marie-Victorin 1995; Mousseau 1987; Rameau 1993). Intercalary meristems, located at the base of each internodes, enable fallen stems to curve upwards and continue their growth (Dahlgren et al. 1985). Aerial shoots arise from the rhizomes and are located under the soil surface. Rhizomes can grow to depth of 2 m, while roots can reach 80 cm or more in depth (Haslam 1970; Lissner and Schierup 1997). Rhizomes are also known to survive low temperatures, fire, water stress, and damage by disease or predators (Hocking et al. 1983). Irrespective of sites conditions, dissimilarity between different clones are to be expected (Pauca-Comanescu et al. 1999). *P. australis* is a highly polymorphic species that demonstrates a high degree of phenotypic and physiologic plasticity (Hocking et al. 1983; Rolletschek et al. 1999).

In Canada, *P. australis* is present in all provinces (Mal and Narine 2004). Historically, this plant was described as being found occasionally along ponds and marshes from the Atlantic to the Pacific coasts of Canada (Macoun 1883). According to the fossil record, it has been a minor component of wetlands for a long period and can be considered native to North America (Hansen 1978; Niering et al. 1977). Its abundance has increased dramatically only in the last 150 years (Saltonstall 2002) and this once innocuous plant is now considered a nuisance species (Chambers et al. 1999; Gervais et al. 1993; Mal and Narine 2004). In Québec, *P. australis* distribution expanded from previously scattered locations to form a near continuum in less than 50 years (Gervais et al. 1993). The northern limit of the species distribution, known to be situated near Anticosti Island, has remained unchanged since (Rousseau 1974).

Biology-ecology

P. australis can be found in numerous sites, ranging from freshwater, alkaline and brackish environments (Haslam 1971, 1972). Roadside ditches, railroad, piles of dredge spoil and wherever slight depression holds water are typical locations to find *P. australis* (Ricciuti 1983). Usually associated with disturbed areas (Rice et al. 2000; Roman 1984), this plant has been documented to invade relatively undisturbed wetland ecosystems (Chambers et al. 1999; Phillips 1987; Windham and Lathrop 1999). In both cases, *P. australis* is forming extensive and dense mono-specific stands but can be associated with other species from the following genera: *Typha, Glyceria, Spartina, Carex, Nymphaea, Juncus, Myrica, Triglochin, Calamagrostis, Polygonum, Scirpus, Galium* and *Phalaris* (Riemer 1976). Once well established, *P. australis* nevertheless easily outcompetes other plant species (Marks et al. 1994). In fact, observations of the colonization of a reclaimed polder area in the Netherlands has shown that *P. australis* became the dominant species after only 3 years (over previously dominant *Typha latifolia* and *Senecio congestus*) despite fewer initial seedlings (Clevering and van der Toorn 2000).

The aggressive nature of *P. australis* is a direct reflection of the adaptive features of its life cycle. This macrophyte reproduces primarily vegetatively through a vigorous system of rhizomes and stolons (Best et al. 1981; Hara et al. 1993; Marks et al. 1994). Stolons, also called "legehalme" (long runners), can play a significant role in clonal growth as they can extend to distances of 10-15 meters per growing season and can develop from both aerial stems and rhizomes (Haslam 1969; Weaver 1960). *P. australis* is said to have a clonal habit because rhizomes remain physiologically integrated which allows clones to move and access resources (Hara et al. 1993). Hence, clonal integration enables the species to escape stresses and to support new shoots along invasion fronts (Bart and Hartman 2000). Clones and colonies are long-lived as they can persist for over 100 years (Haslam 1972; Rice et al. 2000) and perhaps more than 1000 years by vegetative reproduction (Rudescu et al. 1965). Dispersal and colonization of new habitats may rely on rhizome fragments transported by tides, storm waters, ice, and animals (Mal and Narine 2004; Marks et al. 1994). Once established both linear clonal growth and circular clonal growth of *P. australis* stands can be observed (Lathrop et al. 2003; Warren et al. 2001).

Sexual reproduction of *P. australis* has been reported from various regions of the world but seed set is highly variable among populations and viability is generally low (Björk 1967; Gervais et al. 1993; Ishii and Kadono 2002; McKee and Richards 1996; Vézina 1989). In the Montréal region, the species generates viable seeds in a proportion of less than 1% of the total number of flowers produced in one growing season (Vézina 1989). Independently of the latitude where the plant grows in Québec, *P. australis* can produce viable seeds (Gervais et al. 1993) but it is generally assumed that northern populations of *P. australis* produce less seeds than their southern counterparts (Marie-Victorin 1995; Small and Catling 2001). Some evidence suggested that establishment from sexual propagules could become a significant means of dispersal when associated with anthropogenic activities that disturb soils or remove vegetation cover (Ailstock et al. 2001). The principal dispersal vector of sexual propagules is wind (anemochory) and seeds are usually dispersed during the winter months, but hydrocory and zoochory by redwinged blackbirds (*Agelaius phoeniceus*) have also been reported (Coops and van der Velde 1995; Haslam 1969). Various causes have been suggested for the poor fertility of *P. australis* but given its high clonal propagation and self-incompatibility, pollen limitation may be the most important factor contributing to the low seed productivity (Ishii and Kadono 2002). Some authors suggested that the species was not able to form a persistent seed bank (Ter Heerdt and Drost 1994) but results from other studies found that seeds can remain viable in the soil for periods of 2 to 5 years (Clevering and van der Toorn 2000; Hürlimann 1951).

Causes and consequences of invasive behaviour

In Europe, *P. australis* decline is observed and the regression of large colonies of this species is thought to be associated with eutrophication and development (Ostendorp 1989). The paradox lies in the fact that in North America, *P. australis* expansion is thought to be associated with disturbances and development (Roman 1984). Recent historical trends in our region have facilitated the spread of this species. The second half of the 20th century was characterized in southern Québec by the intensification of agriculture from traditional dairy farming to cereal crops. This has led to the straightening of streams and to extensive drainage of agricultural fields and wetlands to better accommodate cereal crop production (Jobin et al. 2003). Drainage of agricultural fields benefited from generous governmental subsidies, which peaked in the late 1970's (Domon et al. 1993). Phosphorus being the limiting nutrient in *P. australis* stands, the intensification of agriculture with associated increase in fertilizers uses has provided numerous disturbed habitats in which this species is not nutrient limited (Auclair et al. 1976; Lippert et al. 1999; Minchinton and Bertness 2003). The expansion of the highways systems in Québec also occurred during those decades, almost all highways in Québec being built between 1963 and 1983 (Ministère des Transports du Québec 1983). Those historical disturbances are suspected to have played a major role in the invasion process of *P. australis* (Delisle et al. 2003). Moreover, wetlands of urban landscapes are more susceptible to common reed invasion because large volumes of water pass quickly through them, thus destabilizing substrates and leaving it opened for colonization (Burdick and Konisky 2003; Marks et al. 1994; Silliman and Bertness 2004). Activities associated with the maintenance of roads and ditches favoured the dispersal of this species by fragmenting and displacing rhizomes over large distances (Ailstock et al. 2001; Gervais et al. 1993). The application of de-icing salts during winter months has also been linked to the increased abundance of *P. australis* over *Typha sp*. (Galatowitsch et al. 1999; Richburg et al. 2001).

It has recently been demonstrated, through the study of chloroplast DNA sequences, that an introduced genotype from Europe was responsible for the current North American invasion (Saltonstall 2002). In the 1800s, *P. australis* was collected in places where ships ballast were dumped (Burk 1877). Ships carrying goods from Europe are likely to have introduced the European genotype in North America. This alien genotype has now virtually eliminated the majority of native populations along the Atlantic coast of North America (Saltonstall 2003a) but has only become frequent in the Canadian landscape over the past 20 years (Catling et al. 2003). Moreover, hybridization between the European and native genotype is not likely to occur and native *P. australis* populations are genetically pure (Saltonstall 2003b). Native lineages of North America have now been recognized as a subspecies of *P. australis* called *Phragmites australis* subsp. *americanus* Saltonstall, P.M. Peterson & Soreng (Saltonstall et al. 2004). The enemy release hypothesis (relief of biotic pressure) could explain the invasive behaviour of the introduced genotype as less than 10 species of insects are known to feed on *P. australis* in North America whereas over 70 are known in Europe (Haslam 1972; Tscharntke 1992). Yet native populations of common reed have also been reported to spread in at least one location in Lake Superior, thus stressing the importance of disturbances and increased nutrient loads as factors that promote *P. australis* growth (Lynch and Saltonstall 2002).

South of the border, states and federal governments of the United-States have listed *P. australis* as a noxious weed (US Department of Agriculture, 2003). In Canada, legal status is missing, but the species is becoming a serious nuisance in prime agricultural land of southern Quebec and central Canada, where it obstructs drainage ditches and competes with adjacent crops (Maheu-Giroux and de Blois in press). *P. australis* is now outcompeting other plant species, causing the accretion of sediment, altering hydrology and soil properties, causing subsidence of tidal wetlands, and reducing habitat heterogeneity (Buttery and Lambert 1965; Chambers et al. 1999; Keller 2000; Weinstein and Balletto 1999; Windham and Lathrop 1999). The main deleterious effect of mono-specific stands of *P. australis* is the resulting reduction in plant species richness. In fact, *P. australis* affects plant diversity more than flowering-rush (*Butomus umbellatus*) and purple loosestrife (*Lythrum salicaria*) in the St-Lawrence wetlands (Lavoie et al. 2003). The resulting shift in the composition of wetland native plant communities ultimately result in the reduction of the associated fauna (Chambers et al. 1999; Walton 2000). However, some ecosystems functions might still be maintained following *P. australis* invasion (Chambers et al. 1999; Lathrop et al. 2003; Weis and Weis 2003). This plant has also impacted human activities by blocking drainage structure and invading agricultural crops (Grandtner 1999; Small and Catling 2001). In Québec alone, the Ministère des Transports spends millions of dollars annually on roadside vegetation management to maintain visibility and clear drainage ditches (Y. Bédard, Ministère des Transports du Québec; pers. comm.).

P. australis is resistant to most eradication practices such as burning, mowing, and cutting if they are not undertaken continuously over several years (Marks et al. 1994; Warren et al. 2001). A generally prescribed eradication method is the application of herbicides, generally an isopropylamine salt of glyphosate such as Rodeo^{TM} (Marks et al. 1994). Other possible management practices include drainage/flooding, increased salinity and application of plastic mulch but are generally difficult to implement in areas of conservation value or in agricultural settings (Marks et al. 1994). Hence, the control/eradication of *P. australis* is both cost and time-consuming.

P. australis and linear wetlands

The literature regarding *P. australis* invasion of linear wetlands is scarce and mostly anecdotal. Although it has long been recognised that roadsides linear wetlands played a major role in the range expansion of *P. australis* (Bart and Hartman 2000; Catling et al. 2003; Gervais et al. 1993), no study has quantitatively assessed their role in invasion dynamics. To my knowledge, only once has *P. australis* been studied in linear wetlands and this study focused on the relation between population structure and the elapsed time since the last ditch clean-up (Boszke et al. 2005). In almost all cases where

P. australis was studied outside natural settings, authors have concentrated their research efforts on the species' ability to capture and store nutrients and heavy metals, this plant being used worldwide in water treatment wetlands (Kadlec and Knight 1996). Nevertheless, linear wetlands can also be recognised as valuable habitats for plant species (Boutin et al. 2003; Bunce and Hallam 1993) although the floristic value of ditch vegetation is affected by managements practices (Best 1993; Novàkovà 1997; Twisk et al. 2003). Moreover, plant distribution patterns in linear wetlands seem to be related to habitat quality and presence of seed sources at short distances (Geertsema and Sprangers 2002). In roadsides verges of Québec, plant diversity can be relatively high compared to adjacent land-uses and as much as 13% of Québec's flora can be found in transportation corridors (Bédard and Trottier 2003).

Remote sensing of invasive species

In the context of plant invasion, scientists and land managers need efficient methods to detect and appraise the severity of infestations (Byers et al. 2002). Remote sensing offers significant avenues to gather information in a timely manner over large areas (Underwood et al. 2003). This technique is based on measuring the electromagnetic energy reflected or emitted by the surface of a geographic space (Caloz and Collet 1997). Remote sensing data sources can also easily be incorporated in GIS and the combination of both enables managers and ecologists to efficiently study aquatic macrophyte distributions over time and at the landscape scale (Remillard and Welch 1993). Nevertheless, best classification accuracies using remote sensing data are achieved usually by categorizing vegetation according to phenotypes (life-forms) and not species (Valta-Hulkkonen et al. 2003). It remains therefore a challenge to detect specific invasive species, especially herbaceous species in the initial stages of invasion when populations are small but control effort could be most efficient.

Satellite images offer the opportunity for automated image processing, large spatial coverage and a good spectral resolution (i.e. number of spectral bands). Auda et al. (2002) studied the potential use of satellite imagery to detect an agricultural weed, *Ambrosia artemisiifolia* L., but concluded that satellite remote sensing data are not operational given their actual characteristics. Recent advances in satellite technology are promising and the spatial resolution of the youngest generation of satellites (IKONOS launched in 1999 and QUICKBIRD launched in 2001) are comparable to aerial photographs at scales of 1/15000-1/20000 (eMap International Inc. 2002). Nevertheless, the spatial resolution of those satellites is still not sufficient enough to detect *P. australis* in narrow linear habitats.

Large-scale photographs may in many cases remain the best, if not the only option to detect and map invasive herbaceous species. In most areas, aerial photographs can offer fine spatial resolution at relatively low cost compared to satellite images and usually provide a long-term record for time-series analysis (Shay et al. 1999). Rowlinson et al. (1999) compared the accuracy of remote sensing data sources (aerial videography, aerial photography, and satellite imagery) for identifying and classifying alien invasive vegetation in riparian zones and concluded that the most accurate and cost-effective data source was panchromatic aerial photographs at a scale of 1/10 000.

Aerial photographs have already been successfully used to study the dynamics of *P. australis* in natural wetlands (Havens et al. 1997; Kotschy et al. 2000; Krumscheid et al. 1989; Lathrop et al. 2003; Rice et al. 2000; Warren et al. 2001; Weisser and Parsons 1981; Wilcox et al. 2003). However, those studies were mostly descriptive and did not provide an accuracy assessment of the distribution maps used. Despite an attempt by Lathrop et al. (2003) to describe colonization events and subsequent growth of *P. australis*, none of those studies used spatial statistics or spatially-explicit models to quantitatively measure patterns of growth, colonization, die-back, or distribution.

Landscape ecology of invasive species

Remote sensing and GIS have greatly facilitated the emergence and recognition of the scientific discipline of landscape ecology by facilitating data acquisition and processing (Turner et al. 2001). Landscape ecology has been defined in at least three ways by Forman and Godron (1986), Urban et al. (1987), and Turner (1989). I will use throughout this project the definition of Turner (1989); landscape ecology being the study of “the effect of pattern on process”. This definition entails that a landscape is defined at any scales relative to the organism or process under study (Wiens 1989). Given that habitat loss and fragmentation may facilitate the spread of invasive species (With 2002) and that landscape factors are important in biological invasions, it is surprising that few studies (Deckers et al. (2005) is a notable exception) have addressed biological invasion at the landscape scale (Vankat and Roy 2002). A primary reason to explain the void in application of landscape ecology principles is the lack of unifying theory relating the effect of landscape conditions to biological invasions (Vankat and Roy 2002). To fill this gap, With (2002) recently outlined six ways in which landscape structure can affect biological invasions and invasibility of communities (see Lonsdale (1999) for the concept of invasibility):

(1) Thresholds in landscape structure (patterns of disturbances for instance) could accelerate the spread of exotic species (With and King 1999).

(2) Different stages of invasion may be affected in different ways by landscape structure. For example, Bergelson et al. (1993) demonstrated that fragmentation could reduce establishment success but enhance dispersal.

(3) Species interactions can be altered by landscape structure (Fagan et al. 1999) in a way that could facilitate the growth of exotic species.

(4) Satellite populations (nascent foci) that greatly accelerate invasion speed (Moody and Mack 1988) may be promoted by a fragmented landscape structure.

(5) Native species may fail to evolve adaptive strategies in fragmented landscapes because they function as overall population sinks from more intact landscapes. Alternatively, landscape fragmentation could enhance competitive abilities of exotic species as their genetic diversity is enhanced by continual dispersal/introduction in fragmented landscapes (Dietz et al. 1999).

(6) Finally, landscape dynamics (in space and time) could create windows of opportunity for the establishment, growth, and reproduction of alien species by creating temporary disturbances or increase in nutrient availability (Davis et al. 2000).

Roadside and railway verges are know to act as dispersal corridor for grassland plants (Tikka et al. 2001). Exotic species are also known to use linear features of the landscape such as roads, streams, and power line cuts as dispersal corridor (Parendes and Jones 2000; Pauchard and Alaback 2004; Stiles and Jones 1998). However to my knowledge, the corridor function of linear wetlands has been demonstrated only once for an invasive species, *Lythrum salicaria* (Wilcox 1989). Trombulak and Frissell (2000) described three mechanisms that enable the dispersion of exotic species via roadsides; roads facilitate the spread of alien species (1) by altering local environmental conditions, (2) by disturbing the habitat or removing native species, and (3) by facilitating the movement of dispersal vectors (animal or human).

Wetlands are particularly interesting for studying exotic plants as those landscape elements are particularly susceptible to invasion. Wetlands represent less than 6% of the globe surface but are the host of the 24% most invasive plants of the world (Zedler and Kercher 2004). Vulnerability to invasion of wetlands have been related to their landscape sink function (Zedler and Kercher 2004). They accumulate debris, sediments, water, pollutants, and nutrient all of which promote invasive plant spread by creating disturbances and supplying invaders with the resources they need. This explanation is consistent with the theory developed by Davis et al. (2000) which states that a plant community become more susceptible to plant invaders whenever there is an increase in the amount of unused resources. Hence, eutrophic linear wetlands of urban and agricultural landscapes are highly vulnerable to *P. australis* invasion and the knowledge gained from this project could be applied to other invasive plant species thriving in linear wetlands.

Conclusion

P. australis is spreading aggressively and displacing native communities. Plant diversity is greatly reduced and this species is also affecting human activities by blocking drainage structures and invading agricultural crops. Aerial photographs seems to be the best remote sensing data source available to investigate the spatio-temporal dynamics of *P. australis* at the landscape scale but no accuracy assessment backed this affirmation until now. Anthropogenic linear wetlands are suspected to have greatly accelerated the spread of this species. Hence, monitoring *P. australis* in those habitats could greatly improve our knowledge on the structure and function of linear wetlands, the literature concerning *P. australis* in those anthropogenic habitats being virtually non-existent. Moreover, very few studies have linked landscape structure to invasive spread and it will be of great interest to apply landscape ecology theories to *P. australis* dynamics in networks of linear wetlands. This research will therefore fill a knowledge gap that could provide managers and policy-makers with insights on alternatives for vegetation control.

CONNECTING TEXT

The first objective of this thesis is to assess the reliability of aerial photographs for the monitoring of *P. australis* in narrow linear habitat. Chapter 2 will address this issue.

CHAPTER 2: Mapping the invasive species *Phragmites australis* in linear wetland corridors

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Abstract

The detection and monitoring of invasive species at the initial stage of invasion is often critical to control/eradication efforts. In the case of *Phragmites australis*, anthropogenic linear wetlands such as roadside and agricultural ditches are believed to play a key role in invasion patterns. Accurate remote sensing of an aquatic macrophyte in such narrow habitats, however, remains a challenge. We used large-scale (1/8000) panchromatic and color aerial photographs to produce different distribution maps of *P. australis* in a network of linear wetlands. Accuracy assessments were conducted to compare the two classifications and sources of errors were identified using logistic regressions. Different thresholds of stem abundance (1%, 5%, 20%, and 40%) were used in the error matrices to determine the stem abundance at which our classification is optimized. Results show that color images are much better in enabling the detection of *P. australis*. Producer's accuracy ranges from 44% to 71% (depending on the selected threshold of stem abundance) for color images and from 16% to 28% for panchromatic images. User's accuracy ranges from 84% to 55% for color photographs and from 51% to 28% for panchromatic photographs. Generally, the mapping of vigorous populations is more accurate. The presence of *Typha sp*. is the main source of commission errors. Landscape context also affects the mapping accuracy. We discuss the relevance of our results for mapping invasion patterns in narrow linear wetlands.

Keywords: Common reed; biological invasion; linear habitat; agricultural weed; accuracy assessment; road ecology.

Introduction

In the context of plant invasion, scientists and land managers need efficient methods to detect and appraise the severity and progression of infestations (Byers et al. 2002). In spite of recent promising advances in the use of remote sensing tools such as hyperspectral imagery (Underwood et al. 2003), large-scale photographs, because of their availability for time-series analysis and relative low cost, are still largely used for mapping wetland vegetation changes (Shay et al. 1999). Best classification accuracies using this type of data, however, are achieved usually by categorizing vegetation according to life-forms and not species (Valta-Hulkkonen et al. 2003). Another significant problem arises when invasive species, especially herbaceous ones, are confined to narrow linear habitats such as drainage ditches or riparian corridors. Linear habitats may act as dispersal corridors and invasion foci into the land that they intersect (Bart and Hartman 2000), but their spatial structure makes accurate mapping of invasion patterns particularly challenging compared to natural wetlands.

This study reports on the feasibility of mapping populations of *Phragmites australis* (common reed), an emergent macrophyte, in narrow linear wetlands of eastern Canada using aerial photographs. We define linear wetlands as linear, highly connected features of the landscape such as roadside, railroad, or agricultural drainage ditches that can support permanent or transient populations of hydrophytic plant species. Common reed has been expanding rapidly in wetlands of North-Eastern America following the introduction of a competitive non-native strain (Saltonstall 2002). Evidence from field survey (Catling et al. 2003) and examination of herbarium records (Delisle et al. 2003) also show an extensive colonization of linear anthropogenic wetlands, especially along highways and agricultural lowlands. Although several studies have quantified common reed invasion patterns in natural wetlands using remote sensing (Havens et al. 1997; Kotschy et al. 2000; Krumscheid et al. 1989; Rice et al. 2000; Weisser and Parsons 1981; Wilcox et al. 2003), the potential of aerial photographs to map common reed in narrow linear habitats has never been assessed to our knowledge. Errors in photointerpretation and classification are potentially high in these habitats and must be rigorously assessed. We therefore conducted an accuracy assessment of maps obtained from large-scale aerial photographs, comparing the results for panchromatic and color photographs at the same spatial resolution. The sources of mapping errors were identified and analyzed by logistic regression.

Methods

Study area

We focused our investigation on periurban/agricultural landscapes with heterogeneous land-covers, and where *P. australis* is growing in a complex network of linear wetlands. The study site was chosen primarily according to the availability of large-scale aerial photographs. The selected site is situated in Saint-Bruno-de-Montarville (45^o30’N, 73^o19’W) on the south shore of Montréal (Québec, Canada) and encompasses an area of 1162 hectares. It is primarily composed of agricultural fields, residential zones, forests, old-fields, and commercial/industrial zones. Small rivers, highways, and railroads pass through it.

Remotely sensed data sources

Preliminary examinations of color aerial photographs have shown that images acquired in early spring (late April - early May) have the greatest potential of distinguishing *P. australis* populations. At that time of the year, the vegetation is turning green again while *P. australis* populations from the previous growing season appear beige, young shoots not being visible yet. The most recent coverage available was flown in spring 2002 in color photographs at a scale of 1:8000. To also evaluate the accuracy of panchromatic photographs, we converted the color 2002 photographs to panchromatic format.

Construction of the photo-map

The aerial photographs were first scanned at a resolution of 600 dpi and saved in Tagged Image File Format (TIFF). The images where then rectified with ArcGIS 9 (Environmental Systems Research Institute Inc., Redlands CA, USA), using an average of 16 Ground Control Points (GCPs) per photograph. This procedure is necessary before the images can be used as geo-referenced photo-maps (Bolstad 1992; De-Leeuw et al. 1988). GCPs were taken with an Alto-G12^{TM} global positioning system (GPS), in Universal

Tranverse Mercator (UTM, NAD 1983), which registers geographical coordinates with a sub-meter precision. In order to avoid distortions occurring at the edge of each photograph, we cropped the overlapping part of each image prior to mosaicking. We did not ortho-rectify the images because the study site is situated on a flat terrain. After the rectification and geo-referencing procedure, we imported the images in ENVI 4.0 (Research Systems Inc., Boulder CO, USA) to mosaic them. The resulting pixels have a corresponding ground resolution of 0.33 m. We calculated the Root Mean Square Error (RMSE) resulting from the geo-referencing and rectification procedure, digitising phase, and subjectivity of polygons boundaries as described in Green and Hartley (2000). The resulting RMSE is equivalent to 1.66 meter.

Training sites were established on a small but representative portion of the mosaic in a preliminary study. An independent observer conducted the photo-interpretation of the two mosaics to minimize biases in the interpretation. The panchromatic mosaic contains less spectral information than the color mosaic and was thus classified first. *P. australis* polygons, all linear wetlands (roadsides ditches, railroad ditches, and agricultural ditches), and other potential *P. australis* habitats (wet patches and river banks) were manually digitized on-screen (Figure 1).

Field sampling and accuracy assessment

We conducted an accuracy assessment of our two classifications using a stratified random sampling scheme to allocate the samples. The stratification was made using two categories of interest: *P. australis* polygons and all other habitats (linear wetlands, wet patches, and river banks). Each point was located at least 1.66 meter inside the *P. australis* polygons to avoid bias associated with positional errors. Points falling in the training area where disregarded. A total of 347 points were sampled (*P. australis* = 237, potential habitats = 110) for the color mosaic and 297 points (*P. australis* = 181, potential habitats = 116) for the panchromatic mosaic. This discrepancy occurs because the interpretation of the color mosaic resulted in more *P. australis* polygons being digitized.

Field sampling was performed in mid-July 2004, before full bloom. We located the sampling points with a MobileMapper^{TM} GPS (1 meter accuracy) and a circular plot (radius = 1 m) was used as the sampling unit. In order to characterize the digitized *P.*

australis polygons we measured the height, stem abundance (% cover), and inflorescence abundance of *P. australis* (% cover), as well as abundance of other plant species using semi-quantitative cover classes.

We constructed several error matrices to compare our classifications with information obtained by ground-truthing. Those matrices were used to compute overall accuracies, producer's accuracies, and user's accuracies. Overall accuracy is the sum of the correctly classified samples divided by the total of samples and is a measure of agreement. For a specific category, producer's accuracy is a measure of omission error (population present in the field at the time of sampling but omitted on the map) whereas user's accuracy is a measure of commission error (population identified as *P. australis* on the map but not present in the field at the time of sampling). *P. australis* has been reported to grow as much as 2.6 meters per growing season in linear wetlands of southern Québec (C. Lavoie, unpublished data). For that reason and to acknowledge the existence of a two year lag between photo acquisition and field sampling, we used different stem abundance thresholds (1%, 5%, 20%, and 40%) in the accuracy assessment for a population to be recorded as present in the field. For instance, in the case of a 5% threshold, only sampling units that had $\geq$ 5% stem cover and that had been classified as *P. australis* population during photointerpretation were considered as correctly classified on our map. Using these thresholds allows us to identify the stem cover abundance at which our classification accuracy is optimized. However the way those thresholds are defined will also affect producer's and user's accuracies. Proportional allocation was not used in the design of our sampling scheme which resulted in unequal inclusion probabilities. In the perspective of finite population sampling we corrected the estimates of the different parameters using the equations given in Stehman (1995) and Stehman and Czaplewski (1998). Confidence intervals were derived from the formulas in Singh and Mangat (1996) for overall accuracy. Stehman (1995) advocates the use of the Taylor linearization technique to calculate confidence intervals for the producer's and user's accuracy. Nevertheless, this method is cumbersome to implement because of the theoretical calculation needed to program the derivatives (Sitter 1992). The bootstrap percentile method (Efron 1979) is known to give equivalent results as the Taylor linearization technique and is thus preferred (Li and Maddala 1999). The confidence intervals were estimated using MatLab 7.0 (MathWorks Inc., Natick MA, USA) with 4000 bootstrap replications.

Data analysis

We used logistic regression to identify which variables could best predict omission errors and commission errors. Two logistic regressions (one modeling omission errors and the other modeling commission errors) were performed for each data set. We decided to analyse separately the two types of errors because some variables measured on the reed population, such as stem abundance, could not be included in the analysis of commission errors. Logistic regression was used to test the occurrence of an omission error with respect to the following variables: stem abundance, and the presence of other dominant plant species. Only plant species with a relative cover of more than 5% were included: *Lythrum salicaria, Typha sp., Salix sp., Fraxinus sp.,* and *Solidago sp*. We also included one contextual variable with four classes to characterize the landscape position of sampling points. They were: right-of-way (highway, roads, and railroad), agricultural fields, urbanized areas (residential, commercial, and industrial zones), and old-fields. Theses classes are related to the habitat structure and management practices that can both influence the detection of *P. australis*. To facilitate interpretation of the results we recoded the classes of the contextual variable that were found significant in preliminary analysis as binary variables and excluded the non-significant ones. The height and the inflorescence abundance of a population where not included because they were exhibiting strong collinearity with the stem abundance.

To test the occurrence of a commission error we used the same variables as for the occurrence of omission errors excluding the stem abundance variable because it is always equal to 0 in the case of a commission error. To select the best model among alternative ones we compared the Akaike Information Criterion (AIC) (Akaike 1973) and the Schwarz Criterion (SC) (Schwarz 1978) for the full model, and the ones resulting from forward selection, backward selection, and stepwise selection. The forward selection procedure consistently produces the smallest AIC and SC for the four analyses. Following the principle of parsimony we excluded from the models selected by the forward procedure any variable that had marginal influence. Logistic regressions were performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA). Our four analyses exhibited a separation of data points, consequently the maximum likelihood estimates may not exist and are not reliable (Albert and Anderson 1984; Santner and Duffy 1986). To circumvent that particularity we used exact conditional logistic regressions to obtain the true estimates (Cox 1970). The Wald statistic was used to test the significance of the regression criterion. Note that for exact conditional logistic regression, this statistic is conditional on the other parameters of the model, including the intercept.

For our error models, we used a lower threshold stem abundance of 5% measured in the field to record *P. australis* as present. This takes into account the time lag between photo acquisition and field sampling and can be considered conservative.

Results

Accuracy assessment: panchromatic images

Overall accuracy ranged from 71% (1% stem abundance) to 87% (40% stem abundance) but no statistically significant differences (α=0.05) where found across the range of stem abundances for overall accuracy (Figure 2). Omission and commission errors are fairly high. For producer's accuracy, we report accuracy ranging from 16% (1% stem abundance) to 28% (40% stem abundance). A non-significant trend is observed between the producer's accuracy and the stem abundance threshold. User's accuracy ranges from 51% (1% stem abundance) to 28% (40% stem abundance). The trend suggesting that user's accuracy decreases as the stem abundance increases is here significant. This decrease is mostly due to the fact that 72% of *P. australis* polygons on the map have a stem abundance in the field below the maximum threshold (40%). Thus, they were considered misclassified at this particular threshold, even when common reed was present.

Accuracy assessment: color images

Overall accuracy ranged from 77% (1% stem abundance) to 88% (40% stem abundance) but those differences are not statistically significant (Figure 2). Moreover when comparing the overall accuracy, for each stem abundance thresholds, between the panchromatic images and the color images no significant differences are found. Producer's accuracies range from 44% (1% stem abundance) to 71% (40% stem abundance). Significant differences between the stem abundance thresholds are only found between the 40% threshold and the 1% and 5% threshold, but not with the 20% threshold. User's accuracy scores range from 84% (1% stem abundance) to 55% (40% stems abundance) and only the 40% threshold is statistically different from the other thresholds. Significant differences are found between the classification based on the panchromatic images and the classification based on the color images for both the producer's and user's accuracies at each density thresholds.

Logistic regression

Panchromatic images: omission errors

The forward procedure of the logistic regression produced a non-significant model with three variables included (stem abundance, *Solidago sp*., and the contextual variable). Only the stem abundance variable was found significant and we therefore excluded the other variables from the model. The result of the exact conditional logistic regression has shown that the stem abundance has marginal influence (score X^2=3.51, p=0.0607) on the detection of *P. australis*. The fitted model is:

OMISSION ERRORS = INTERCEPT - 1.91*(STEM ABUNDANCE)

According to the logistic regression model, the probability (*p*= log (CCP/(1-CCP))) of committing an omission error decreases as stem abundance increases. Confidence intervals for the odds/ratio parameter are 0.92 to 60.48 (95% C.I.) which indicates that the positive effect of this variable on the detection of a population is not significant even though this effect is likely to occur. This model predicts accurately 53.2% of all samples.

Panchromatic images: commission errors

No samples being located in old-fields, the contextual variable has only three classes in this analysis. One variable (*Fraxinus sp.*) originally retained by the forward selection procedure was disregarded in the model since it had only marginal influence and was not significant. The final model is composed of the following variable: *Typha sp*. (score X^2=17.29, p=<0.0001), agricultural fields (score X^2=14.23, p=0.0002), *Lythrum salicaria* (score X^2=8.16, p=0.0043), and *Solidago sp*. (score X^2=6.97, p=0.0083). The fitted model is:

COMMISSION ERRORS = INTERCEPT + 9.57*(TYPHA SP.) +
2.41*(AGRICULTURAL FIELDS) + 11.65*(LYTHRUM SALICARIA) +
10.64*(SOLIDAGO SP.)

The probability of doing a commission error thus increases with the presence of other macrophytes (mainly *Typha sp*., but also *Lythrum salicaria* and *Solidago sp*.) and when the sample is situated in an agricultural field. This model accurately predicts 91.3% of the samples. (No separation of data points occurred with this model.)

Color images: omission errors

The model retained is composed of two variables: stem abundance (score X^2=35.41, p=<0.0001) and old-field (score X^2=18.41, p=<0.0005). A preliminary forward procedure included stem abundance, contextual, and *Solidago sp.* but the last variable was disregarded because it was not significant. The significant class of the categorical variable is the one indicating that the sample is located in an old-field.

OMISSION ERRORS = INTERCEPT - 5.34*(STEM ABUNDANCE) + 3.50 *(OLD-FIELD)

The probability of an omission error decreases with stem abundance and increases when the reed population is situated in an old-field. This model predicts accurately 80.3% of the samples. Note that only 20 omissions errors were recorded for a total of 180 samples for this analysis.

Color images: commission errors

The variables retained by the forward selection procedure are: *Typha sp.* (score X^2=75.51, p=<0.0001) and *Fraxinus sp*. (score X^2=21.03, p=0.0052). The model goes as follow:

COMMISSION ERRORS = INTERCEPT + 5.99*(TYPHA SP.) + 5.36*(FRAXINUS SP.)

The probability of committing a commission error increases with the abundance of both *Typha sp*. and *Fraxinus sp.* The Wald statistic informs us that the effect of *Typha sp*. is considerably more important than the effect of *Fraxinus sp*. This model accurately predicts 67.3% of our samples.

Discussion

Color photographs are far superior in enabling the detection of *P. australis* populations, as indicated by the producer's and user's accuracy of this category compared to the panchromatic images. The spectral resolution is therefore a determinant factor in enabling the photo-interpreter to distinguish the populations. Given the thresholds used, our classification is optimized for populations having a stem abundance threshold varying from 20% to 40% on color photographs. This is the threshold at which the best compromise between omission and commission errors is achieved. The large scale (1/8000) of the color photographs is therefore adequate to obtain accurate maps of the distribution of *P. australis* in these linear habitats and provides a reference scale for other studies in similar conditions, especially when other remote sensing approaches such as hyperspectral imagery or airborne videography are not an option. Panchromatic photographs at the same scale (1/8000) do not have a sufficient spatial resolution to obtain a reliable map, but the lack of spectral resolution could potentially be compensated by using larger scale panchromatic photographs.

A number of factors affect the mapping accuracy of *P. australis* in linear wetlands. On color images, less vigorous populations are the ones that are more often omitted. For panchromatic images the trend relating vigor and correct classification is only marginally significant. The classification on this data set being inaccurate, errors might be distributed randomly or other factors such as illumination or contrast could be more meaningful in explaining the patterns observed. Regarding landscape context, populations thriving in old-fields are generally omitted compared to other types of habitats when using color images. This could be explained by the lack of contrast between *P. australis* and the dead plants left in these habitats which are not managed. As well, *P. australis* tends to be overestimated in agricultural ditches compared to other habitats when panchromatic images are photo-interpreted, possibly because of the combined effect of poor spectral resolution and the fact that the ditches are narrower in agricultural fields. Because of similar spectral signatures, *P. australis* can be confounded with *Typha* sp. on both panchromatic and color photographs, leading to commission errors. It may be possible to discriminate between the two macrophytes particularly in the case of adjacent populations, using training samples of *Typha* sp., but this remains to be assessed. On color photographs stems of *Fraxinus sp.*, when present at the shrub stage, seems to provide a spectral signature similar to that of *P. australis*, whereas on panchromatic images, other herbaceous species such as *Solidago sp.* and *L. salicaria* also lead to an overestimation of *P. australis*.

Like many suburban areas in North America, our study site is a very dynamic landscape and is constantly threatened by increased urbanization. As much as 12.7% of all points visited were not included in the analysis because of new residential constructions, road or railroad work, etc. Adding to this effect are the management practices to control *P. australis* by land-owners. *P. australis* is cut, sprayed with herbicide, and burned to limit its expansion (pers. observ.). Those practices result in less vigorous stands or possibly in stands that have disappeared altogether, resulting in an underestimation of the classification accuracy.

Since the exotic strain of *P. australis* shows aggressive behavior, it is especially important to be able to recognize early stages of invasion when control measures may be more efficient. We are currently estimating the rate of progression in linear habitats and historical photographs are often panchromatic ones. Compared to panchromatic images, color aerial photographs at the scale used in this study or at larger scale should provide adequate maps of *P. australis* populations in linear wetlands, even at relatively low stem abundance. For these images, accuracy level compares with those considered generally acceptable for remote sensing data. Because color photographs tend to be more recent, photointerpreting first recent color photographs when available and then older panchromatic ones, when analyzing temporal pattern, could help diminish mapping errors. In any case, because of the potential significant errors associated with mapping macrophytes in linear habitats, we recommend using a methodology similar to ours to provide a measure of map accuracy whenever possible.

Figure 1: Distribution map of *P. australis* populations in linear wetlands and other potential habitats (from color aerial photographs) of Saint-Bruno-de-Montarville, Québec, Canada (45°30’N, 73°19’W)

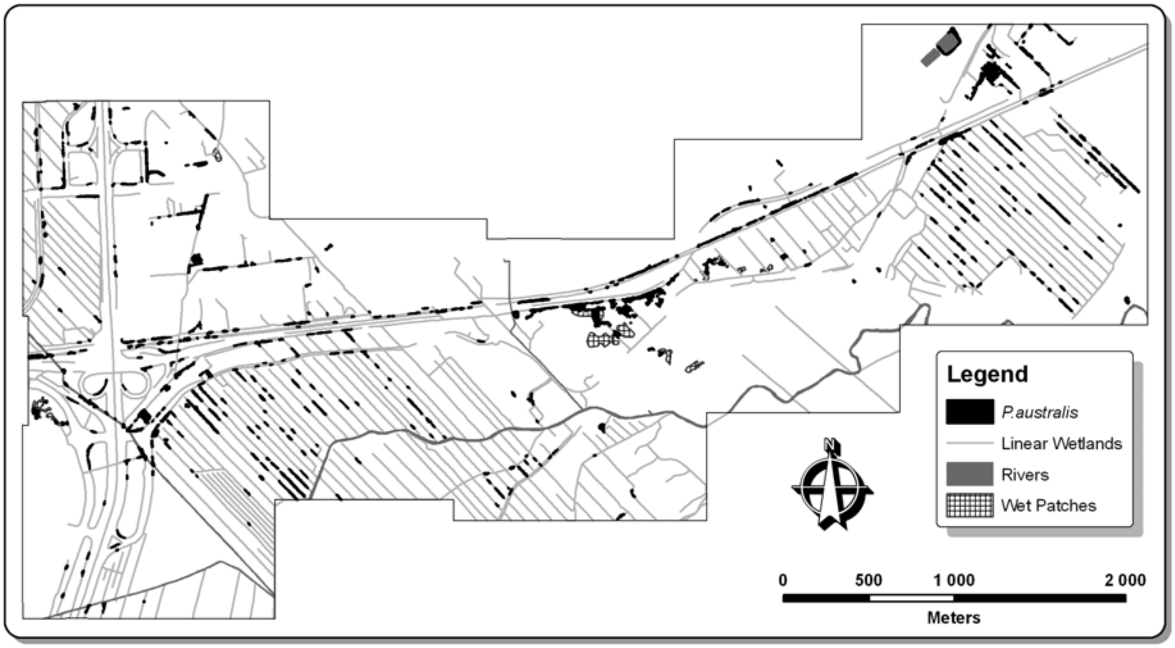
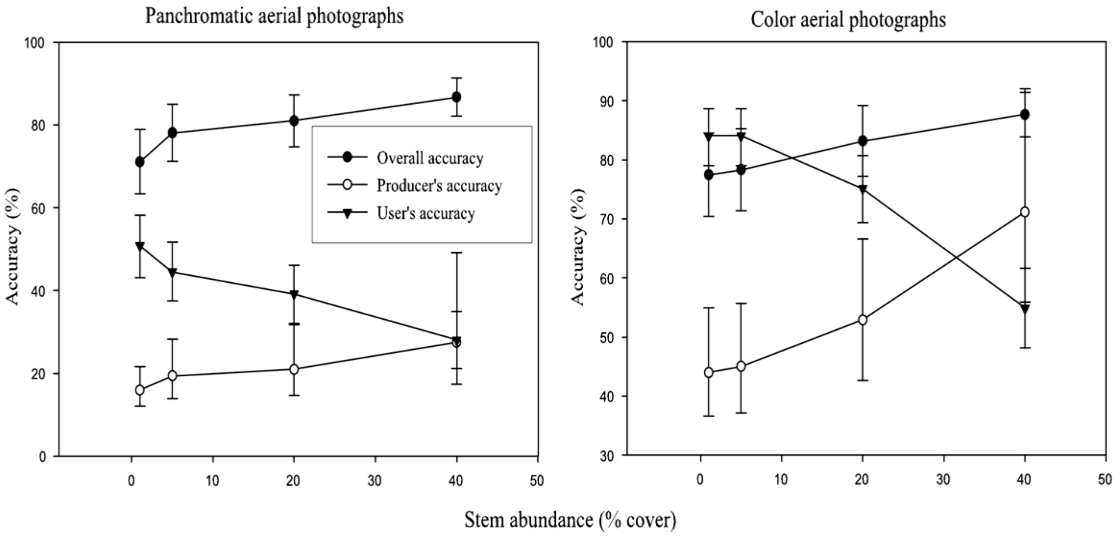


Figure 2: Accuracy assessment results for the panchromatic and color images at different thresholds of stem abundance



CONNECTING TEXT

Chapter 2 demonstrated that aerial photographs are a reliable remote sensing data source to distinguish *P. australis* populations in linear wetlands. The developed methodology was then used to reconstruct and explain invasion patterns of *P. australis* in linear wetlands. This second objective will be addressed in Chapter 3.

CHAPTER 3: Landscape ecology of *Phragmites australis* invasion in a network of anthropogenic linear wetlands

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Abstract

The interaction between landscape structure and spatial patterns of plant invasion has been little addressed by ecologists despite the new insights it can provide. Because of their spatial configuration as highly connected networks, linear wetlands such as roadside or agricultural ditches, have the potential to serve as corridors that facilitate dispersal of invasive wetland species at the landscape scale and subsequent invasion into the natural or anthropogenic ecosystems that they intersect. In this study, we conduct a landscape scale analysis of *Phragmites australis* invasion patterns (1985-2002 and 1987-2002) in two periurban areas of southern Québec, Canada, focusing on the interaction between the network of linear anthropogenic wetlands and the adjacent land-uses. Our results show very high intrinsic growth rates of *P. australis* populations in linear habitats compared to those reported for natural wetlands. Roadside habitats are the first invaded landscape elements and serve as foci of invasion into other linear habitats and adjacent land-uses. Spatial point pattern analysis adapted to network suggests that dispersal is not necessarily constrained by the linear dimension of the network. A logistic regression model shows that the effect of roads and the disturbances associated with them overrides other landscape variables to explain *P. australis’* occurrence in this system. Given the high rates of invasion observed, managers of transportation right-of-way (ROW) should carefully monitored expansion patterns especially when the ROWs intersect landscape of conservation or economic value.

Keywords: Invasive species, agricultural weed, network-*K* function, road ecology, spatial pattern analysis.

Introduction

The interaction between landscape structure and spatial patterns of plant invasion has been little addressed by ecologists despite the new insights and opportunities it can provide (With 2002). The recent and rapid expansion of *Phragmites australis* (Cav.) Trin. ex Steud. (common reed*),* an emergent macrophyte showing invasive behaviour in wetlands of eastern North America provides a unique opportunity to relate invasion patterns to landscape structure. *P. australis* is considered a noxious weed at the federal and state level in the United States (US Department of Agriculture, 2003). In Canada, legal status is missing but the species is becoming a nuisance in prime agricultural land where it obstructs drainage ditches and competes with adjacent crops. In natural wetlands, it can replace native plant species (Keller 2000; Lavoie et al. 2003; Saltonstall 2002) and may affect habitat quality and possibly ecosystem functions (Weinstein and Balletto 1999). As populations continue to spread aggressively, the species is therefore receiving increased attention for its ecological and economic effect on both natural and anthropogenic systems.

Several studies have quantified invasion patterns of *P. australis* mostly in coastal wetlands using remote sensing in order to get insights into the processes that facilitate invasion (Havens et al. 1997; Kotschy et al. 2000; Krumscheid et al. 1989; Lathrop et al. 2003; Rice et al. 2000; Weisser and Parsons 1981; Wilcox et al. 2003). However, other types of habitats often largely ignored in ecological studies (Forman and Alexander 1998), can play an important role in invasion patterns at the landscape scale. In central Canada (Quebec and Ontario), evidence from field survey (Catling et al., 2003) and examination of herbarium records (Delisle et al. 2003) show an extensive colonization by *P. australis* of linear anthropogenic wetlands, especially along highways and agricultural lowlands. Genetic evidence (Y. Jodoin, unpubl. data) recently confirmed that linear wetlands, such as roadside or agricultural ditches, are mostly invaded by an exotic non-native strain that seems highly competitive (Saltonstall 2002), especially in disturbed habitats. Because of their spatial configuration as highly connected networks, linear wetlands have the potential to serve as corridors that facilitate dispersal at the landscape scale and subsequent invasion into the natural or anthropogenic ecosystems that they intersect. This suggests that the effective management of *P. australis* at the landscape scale has to take into account the interaction between natural and anthropogenic habitats, but there is still little evidence on the structure and function of linear anthropogenic wetlands and invasion patterns in anthropogenic habitats have yet to be assessed.

In this study, we conduct a landscape scale analysis of *P. australis* invasion patterns in two periurban areas of southern Québec, focusing on the interaction between the network of linear anthropogenic wetlands and the adjacent landscape. Specifically, we (1) provide a detailed reconstruction of invasion patterns from historical remote sensing data, (2) analyse colonization events using spatial point pattern analysis adapted to network, and (3) test a predictive model of *P. australis* occurrence in the network of linear wetlands that incorporates landscape variables. Our study also provides a detailed example of a methodological approach for the study of spatial patterns in linear habitats.

Materials and methods

Description of study sites

The study was conducted in two periurban landscapes of southern Quebec, Canada. The first landscape (1326 hectares) is situated on the south shore of Montréal, near Saint-Bruno-de-Montarville, hereinafter refer to as St-Bruno, (45°30’N, 73°19’W) and the second one (1446 hectares) is in the eastern tip of Laval Island (45°39’N, 73°36’W), about 27 km North-West of St-Bruno (Figure 3). The two study sites were chosen according to the following criteria: 1) presence of *P. australis* populations, 2) heterogeneous land-uses/land-covers (LU/LC), 3) complex network of linear wetlands, and 4) availability of historical large-scale aerial photographs. Genetic analyses using RFLP technique (Saltonstall 2003c) have demonstrated that *P. australis* populations of both landscapes are from the invasive European genotype, haplotype “M” (Y. Jodoin., unpublished data). One highway (Highway 30, built in 1975), a major road (route 116, built in 1940 but widened to 4 lanes in 1959), and a railroad (one of the oldest railroad built by the Canadian National at the end of the 19th century) are passing through St-Bruno. In Laval, a railroad (also built at the end of the 19th century by the Canadian National), and two avenues (Avenue Marcel-Villeneuve built in 1989 and Avenue Lortie built in 1984) are crossing the landscape. The proximity of those agro-forested landscapes to the city of Montréal has also greatly contributed to the increase in urbanization pressure in the last two decades. Hence, the two study areas are dynamic landscapes with heterogeneous LU/LC threatened by urban sprawl.

Data collection

Large-scale aerials photographs were used to reconstruct *P. australis* invasion. Images from 1985 (1/5 000; panchromatic), 1988 (1/5 000; panchromatic), 1995 (1/10 000; panchromatic), and 2002 (1/8 000; color) were available for St-Bruno and from 1987 (1/5 000; panchromatic), 1993 (1/10 000; panchromatic), 1995 (1/10 000; panchromatic), 1997 (1/5 000; panchromatic), 2001 (1/10 000; panchromatic), and 2002 (1/8 000, color) for Laval. Distribution maps of *P. australis* and landscape characteristics were obtained from aerial photographs and integrated into ArcGIS 9 (Environmental Systems Research Institute Inc., Redlands CA, USA) according to the methodology proposed by Maheu-Giroux and de Blois (in press), which includes an accuracy assessment that supports the validity of the mapping (84% of populations on the map are actually on the ground). A total of 236 aerial photographs were scanned, rectified, geo-referenced, and mosaicked to obtain the 10 final photo-maps (St-Bruno has 4 and Laval has 6).

Ten categories of LU/LC were derived from the photo-maps by manual delineation: 1) Agricultural, 2) Commercial, 3) Transportation Right-of-Way, 4) Forest, 5) Old-Field, 6) Industrial, 7) Water Bodies, 8) City Parks and Golf, 9) Residential, and 10) Wet patches. The latter is loosely defined as areas that maintains a high water table, permanently or occasionally during the year. The complex network of anthropogenic linear wetland, i.e. roadsides ditches, railroad ditches, agricultural ditches, etc. was also digitized, as well as linear wetlands with woody vegetation (> 2m). Soils maps were obtained from the "Institut de Recherche et de Développement en Agroenvironnement" (IRDA) who digitized the original governmental maps (Agriculture Canada 1952, 1991).

Landscape characteristics

Both landscapes are mostly agricultural (corns and soybean production in rotation) and crossed by rivers and small streams. They nevertheless differ in their dynamics, soils conditions, degree of colonization by *P. australis*, and date of construction of major roads. To gain information on the landscape context in which invasion was occurring, we quantified those differences by calculating descriptive statistics for each landscape related to:

1) Edaphic conditions; we derived from the soil maps the percentage of total area covered by specific drainage conditions for the two landscapes to test their effect on *P. australis'* spatial distribution. Drainage definitions (Lamontagne and Nolin 1997) refer to the internal drainage of the soil and takes principally into account the slope, texture, vertical water flow speed, and retention capacity of the soil.

2) Length of linear wetlands with woody vegetation; the percentage of the total network of linear wetlands with woody vegetation was obtained from the GIS.

3) Network characteristics; to assess the dynamics of the network of linear wetlands, we calculated the length of this network for each available year. The degree of connectivity of the network was estimated using the Gamma index (γ). This index describes the extent to which nodes of the network are connected and is calculated by dividing the number of actual links between the nodes by the maximum potential number of links. It can therefore be expressed as percentage of connectivity, i.e. connected nodes.

4) LC/LU changes: we performed a Principal Component Analysis (PCA) on the time series of observations of the total area of each LC/LU and network length. Those descriptors were first centered and standardized to ensure homogeneous dimensions and the scaling was focused on inter-sample distances (distance biplots) to enable accurate representation of the relationship between samples and descriptive variables (Legendre and Legendre 1998).

P. australis invasion pattern analysis

We used a logarithmic growth equation, $N = N_0 e^{r t}$ (Wilson and Bossert 1971), to analyze changes in the total area of *P. australis* for each landscape (where N is the total area of *P. australis* and t is the time difference in year). We solved the equation to obtain r, the intrinsic growth rate of *P. australis*. This equation normalizes area change to enable comparison of landscapes differing in their total areas. Rate of spread (% of linear wetlands invaded/year) in linear wetlands of the different LU/LC were also calculated for each year, landscape, and LU/LC.

Because clonal growth of *P. australis* is said to be the major means of population growth and spread (Mal and Narine 2004), especially at our latitude, we expected to observe mostly the contiguous expansion of existing patches rather than the establishment of new patches away from source populations. A preliminary inspection of distribution maps, however, suggested that the establishment of new patches was more frequent than expected. The establishment of new patches likely contributes significantly to the rapid spread of the species at the landscape scale. The spatial patterns of establishment of new patches were therefore investigated using variants of the cross-*K* Function, a bivariate second-order spatial point pattern analysis, which is an extension of the traditional *K*-Function for bivariate data set (Ripley 1976). Population polygons were converted to points using their centroids to accommodate the fact that this function used point-referenced data.

The cross-*K* function was used to test whether colonization events occurred closer, randomly, or uniformly in relation to the source populations. In a linear habitat, however, distances can be calculated in two ways: linearly through the network, or in two-dimensions, i.e., assuming colonization events are not necessarily constrained by the linear dimension of the network. For instance, depending on the spatial structure of the network, the location of a patch relative to another could be measured as 1000 m if we follow the network (one dimension), but only 100 m in two-dimensions. Both distances may account for different dispersal processes (e.g., water transport of rhizomes within the network vs seed dispersal by dominant wind or human--mediated displacement of propagules). In the first instance, the network cross-K function (Deckers et al. 2005; Okabe and Yamada 2001; Spooner et al. 2004a; Spooner et al. 2004b), will calculate distances between points using network (linear) distances (1D). In the second case, the more traditional version of the network cross-K function, the cross-K function (2D) will calculate distances between points using the Euclidean distances. One of the assumptions of the latter function, however, i.e., the homogeneity of habitats, is clearly violated in this case (e.g., *P. australis* will not establish in the middle of a road). We nevertheless chose to explore spatial patterns using both functions, acknowledging the limitations of the Euclidian distances in this context.

The network cross-*K* Function was computed using an ESRI ArcMap extension, SANET – v 2.0 (Okabe et al. 2004). It was not possible to calculate confidence envelopes using Monte Carlo simulations with this version of SANET but we can nevertheless obtained it from the binomial distribution (Okabe et al. 2004). No edge effect (Haase 1995) adjustments are necessary using the network cross-*K* function since edge effects are intrinsically taken into account in the network distances computations (Okabe and Yamada 2001). An *R* package, “Spatstat” (Baddeley and Turner 2005), was used to calculate the 2-D cross-*K* Function. Confidence intervals were constructed using 1000 Monte Carlo simulations that followed a Poisson distribution. To correct for edge effect we used the translation correction (Ohser 1983).

Dispersal process

Seed dispersal as well as human- or animal-mediated displacement of propagules could produce patterns that would be clumped but not necessarily constrained by the linear dimension of the network. The literature, however, suggests that sexual reproduction is highly variable among populations (Gervais et al. 1993; Haslam 1972) and could be non-significant at our latitude (Marie-Victorin 1995). To quantify the potential contribution of sexual reproduction, we performed germination tests on 28 populations (14 for each landscape) in laboratory conditions. Seeds were collected in late January 2005 and were stored in a cold chamber at 5ºC until used. For each population, three replicates of 30 seeds sown in Petri dishes (2520 seeds sown, with a filter paper at the bottom and soaked with distillate water) were used to determine the germination rate. Petri dishes were placed in a growth chamber for three weeks with a photoperiod of 12 hours. We also implemented a thermoperiod (12h) with a 20ºC amplitude and a mean temperature of 20ºC to simulate conditions maximizing germination rate (Ekstam et al. 1999). Germinated seeds were counted after 14 days.

Predictive model of *P. australis* occurrence at the landscape scale

Multiple logistic regression analysis was used to model the occurrence of *P. australis* in the network of linear wetlands using land cover/land use, edaphic, and vegetation variables. The networks of each landscape were first divided in 32 053 ten-meter long segments (19253 segments for Laval and 12797 segments for St-Bruno) and each segment was assigned presence/absence data for *P. australis* The mutually non-exclusive LC/LU variables tested are: (1) Agricultural, (2) Transportation ROW, (3) Urban areas (industrial, commercial, golf, city park, and residential areas), (4) Old-field, (5) Forest, (6) Water bodies, and (7) Wet patches. We also included the dynamic dimension by incorporating LU/LC changes observed on the photo-maps. Changes in specific LU/LC were regrouped into broader categories: (8) Agricultural intensification (i.e. old-fields returned to cultivation), (9) Land abandonment (agricultural field abandoned), (10) Urbanization, (11) Road constructions and road work, and (12) a disturbance category that included all major soil disturbances and changes in hydrology. The distance to a transportation ROW was also recorded for each segment (13). To accommodate possible non-linear responses for the distance variable, we also tested its square and cubic terms. Finally, drainage conditions (14) obtained from the soil maps and the presence of ligneous vegetation (15) for each segment were tested in the regression. None of those variables exhibited strong collinearity (≥ 0.60).

Preliminary analyses modeling the occurrence of *P. australis* using all observations demonstrated that the mapped residuals were highly positively autocorrelated, which was to be expected in this linear system. This lack of independence between pairs of neighboring observations violates the independence assumption of classical tests of significance (Legendre 1993; Legendre and Fortin 1989). The large number of observations (32 053 segments), however, allowed us to select a subset of the data to remove as much as possible the spatial dependence among observations. Even though it entails a net loss of information, it also help us avoid pseudoreplication (Hurlbert 1984). We used Moran's *I* (Moran 1950) to determine the linear distance at which spatial independence is attained. In our case, computational limitations proscribed the use of all observations as the distance matrix will be too large (32 053 * 32 053 elements). Therefore, we stratified our sampling by calculating the autocorrelation function for a dozen of the most invaded linear wetlands in each landscape, making sure that the locations of those linear wetlands were representative of the exhibited habitat heterogeneity (the mean length of the selected linear wetland is 1391 m. for St-Bruno and 1140 m. for Laval). The number of distance classes was selected to obtain classes representing a distance of around 50 meters in order to compare correlograms more easily and measure more precisely fine-scale autocorrelation. Distances were calculated using network distances and all calculations were done with the "AUTOCOR" function of the

“Progiciel R”- v 4.0 (Casgrain and Legendre 2004). The progressive Bonferroni correction was used to account for multiple tests (Hewitt et al. 1997). The distribution maps were made so as to include 50% of samples at each site and 50% of them in *P. australis* populations. Observations were randomly drawn at a minimum network distance of 300 m for St-Bruno and 200 m for Laval. Those distances were determined by inspection of the Moran’s *I* correlogram. We used a total of 200 observations, 100 per landscape, to perform our logistic regression. This corresponds to the maximum number of points that we could sample keeping the minimum network distance specifications.

We tested our model on the two landscapes together and each one separately. Logistic regressions were performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA) and variables were selected using the stepwise selection procedure. We performed 10 logistic regressions on 10 different randomly drawn sets of observations to guarantee that our sampling distribution was both stable and representative. The Wald statistic was used to test the significance of the regression criterion and Nagelkerke R^2 (Nagelkerke 1991), a coefficient of determination for logistic regression, was used to assess the model goodness of fit. Residuals of this regression were mapped and inspected to ensure that no spatial autocorrelation remained.

Results

Landscape characteristics

Drainage conditions (Figure 4) in St-Bruno are worse than in Laval. In the latter, 69% of the total area shows a moderate drainage, whereas bad drainage conditions occupy 79% of the St-Bruno landscape. Linear wetlands harboring woody vegetation represents 5 % of the network length in St-Bruno compared to 19% in Laval. The linear wetland networks of both landscapes have increased in length at the beginning of the time period with a maximum attained in 1988 for St-Bruno (154 km) and in 1993 for Laval (234 km) (Table 1). Increases in network length are mostly due to the drainage of former old-fields for agricultural purposes in St-Bruno and by the construction of a new road in Laval. After reaching a peak, the length of networks decreases by about 14% in each landscape. In St-Bruno this decrease is caused mostly by residential constructions and in Laval by residential constructions and the filling of drainage ditches after agricultural abandonment. Regarding the connectivity of the two networks (Table 2), the γ index informs us that about 39.6% of all nodes are connected in St-Bruno at the beginning of the reference period. After that, connectivity decreases continuously to a low of 36.2% of nodes connected. In Laval, the maximum connectivity is 40.5%, attained in 1993 after the new road was constructed. Subsequently, the degree of connectivity diminished to a low of approximately 38.8% in 2001, followed by a small increase in 2002. Although, the degree of connectivity is higher in Laval, the mean link length is smaller in St-Bruno (170 meters vs. 124 meters in 2002, respectively). Thus, even if the Laval network is more connected, longer distances need to be traveled before finding a connection.

The biplot of the PCA for St-Bruno (Figure 5) informs us of the major LU/LC changes. The first axis explains 70% of the variation and combined with the second axis, as much as 92.4% of the variation is explained. At the beginning, a more agricultural and forested landscape was present. Changes occurred primarily trough the urbanization (both industrial, commercial, and residential) of the landscape and the shift of old-fields or agricultural areas to city parks and golf (Figure 6). Wet patches have seen their areas increased until 1995, when they were filled following urbanization.

The first axis of the Laval biplot (Figure 7) explains 66.1% of the variation. When combined with the second axis, a total of 87.6% of the variance is explained. The Laval site has seen its landscape shift from old-field and industrial zones to urbanized (residential and commercial) and agricultural areas (Figure 8). Some old-fields were also left undisturbed and became forested. A road (4.6 km) was also constructed on agricultural fields and forested areas in 1989. The increase in wet patches between 1997 and 2001 is due to the blockage of drainage features of the railroad which has caused the flooding of old-fields.

P. australis invasion patterns

St-Bruno exhibits a severe invasion and the rapidity of *P. australis* spread is impressive (Figure 9). Laval is also invaded, although to a lesser extent (in the total invaded area) than St-Bruno (Figure 10). Both sites exhibit exponential growth curves of *P. australis* populations. The annual intrinsic growth rate of *P. australis* for each landscape is very high: ranging from 0.1957 to 0.3632 yr^{-1} for St-Bruno and from 0.1900 to 0.5400 yr^{-1} for Laval (Table 3). Maximum intrinsic growth rates are observed after the initial establishment of the first populations in both landscapes and decreased afterward. The two sites were relatively non-invaded at the beginning of the reference period and populations occur mostly in the transportation ROW at that time. Interestingly, natural riparian habitats are not invaded by *P. australis*, except when they cross transportation ROW. Moreover, agricultural areas of St-Bruno are heavily invaded compared to the ones in Laval. In both landscapes, invasion first occurs from the roads into the other intersected land uses/land cover such as agricultural areas.

Depending on landscape context, the linear structures show different rates and extent of invasion. In St-Bruno, commercial linear wetlands are the most rapidly invaded landscape elements (40% of their length invaded in 2002) but they only represent 1.5% of all linear wetlands (Figure 11). Industrial (16% in 2002) and transportation ROW (13% in 2002) follow. Transportation ROWs, however, represent 30% of all linear wetlands in St-Bruno. Other linear structures invaded are within agricultural (8.5% in 2002), residential (6% in 2002), forest (1.5% in 2002), and old-field (1%) LC/LU. The LC/LU of the Laval landscape that is most invaded is the transportation ROW (22.5% in 2002) and they represent 7.3% of all linear wetlands of this landscape (Figure 9**).** Linear wetlands situated in old-fields (3.5% in 2002) are also invaded, as well as agricultural fields (<1%). Most of the invaded old-fields in the Laval landscape are situated near an industrial plant that was demolished and abandoned.

Colonization events in St-Bruno occurred at a yearly mean distance of 105 meters/year whereas in Laval, they did so at a mean distance of 115 meters/year, but these estimates are skewed by rare long-distance events. If the top 5% longest dispersal events are removed, establishment occurred at a mean distance of 27 meters/year in St-Bruno and 77 meters/year in Laval. The lower distance dispersal of St-Bruno is caused by the fact that distances are calculated from the closest source population. Therefore, the higher population density of St-Bruno is affecting the estimates.

The cross-K function analysis reveals that colonization events generally occur closer to source populations than expected from complete spatial randomness, both using network and Euclidean distances (Table 4). One notable exception is the period between 1988 and 1995 in Saint-Bruno where a repulsion phenomenon is observed at distance of

20 meters and more using network distance. However, when using Euclidean distance the opposite phenomenon is observed, attraction at scale of 95 meter and more. The subsequent period in Saint-Bruno is exhibiting randomness in establishment pattern for small scale (0-135 meters) and attraction at larger scale. The cross-*K* function was not calculated for the period 1985-1988 in St-Bruno because there were too few populations to have valid estimates (4 colonization events). For the Laval landscape, attraction is the spatial phenomenon observed in all cases. However, randomness is generally observed at small scales (0-20 meters) using Euclidean distances but this might be an artefact of the network configuration.

A biologically relevant summary of the association/randomness/repulsion is to calculate the proportion of colonization events in excess/deficit compared to a random distribution (Dixon 2002). We divided the observed value of the function (*K*(d)) by the expected value of the function (E *K*(d)) at the same distance to obtain this summary. We report this summary for distances of 50m., 75m., and 100m., because they cover the range of distances observed between parallel segments of linear wetlands (Table 5). Thus, we can learn that, at a distance of 50 meters, the Euclidean distance method always account for more association, 5% more than with the network distance. The same is true at distance of 75 meters and 100 meters except for period corresponding to the initial establishment of populations. Generally, the patterns observed suggest that dispersion of *P. australis* is not strongly constrained by the linear dimension of the network.

Dispersal process

Regarding the contribution of sexual reproduction to dispersal, seeds of populations in St-Bruno germinated at a rate of 6.6% (maximum rate is 27.1% and minimum rate is 0%) whereas population in Laval had a germination rate of 2.7% (maximum is 11.3% and minimum is 0%). The difference between the germination rate of St-Bruno and Laval is statistically significant, as determined by a t-test ($\alpha = 0.05$). We also estimated, by weighing seeds and inflorescences (35 panicles), that a single inflorescence can produce an average of 13 000 seeds. The contribution of sexual reproduction to dispersal in this landscape appears therefore potentially significant.

Predictive model of *P. australis* occurrence at the landscape scale

Following preliminary analyses with logistic regressions we retained in our final model only the variables that consistently showed a significant effect in the random draws. The stepwise selection procedure retained the following variables: the "distance to the transportation ROW" (the linear term) (score X^2=11.25, p=0.0008) and the "road construction and road works" variables (score X^2=7.41, p=0.0065). The model is:

$$P.\ AUSTRALIS = \text{INTERCEPT} - 0.00191(\text{ROW DISTANCE}) + 2.8441(\text{ROAD CONSTRUCTION/WORK})$$

According to the model, the probability (p= log (*P. australis*/(1-*P. australis*))) of occurrence of a *P. australis* population decreases as we travel farther from transportation ROW and increase where road construction/work has been done. This model, which includes observations from both landscapes, accurately predicts 69% of our observations and Nagelkerke R^2 is equal to 0.43. Separate runs of the logistic regressions for each landscape demonstrated that the significant effects observed were mostly driven by the Laval landscape. None of the variables were significant for the St-Bruno landscape.

Discussion

Because they intersect various land-uses, linear habitats have the potential to serve as corridor of invasion facilitating the spread of *P. australis* at the landscape scale. Our results show that, at least for these landscapes, roadside habitats, more than any other types of linear wetlands that we analysed, were more likely to drive invasion patterns. Moreover, the overall rates of invasion in our landscapes generally seem to exceed those reported for natural wetlands even if lateral growth of linear wetlands populations is constrained. For instance, *P. australis* populations in tidal marshes of the upper Chesapeake Bay (USA) had intrinsic growth rates ranging from 0.0065 to 0.2123 yr^{-1} (Rice et al. 2000) and in brackish marsh of Delaware, New Jersey, and New York they had intrinsic growth rates ranging from 0.0024^{-1} to 0.2537 yr^{-1} (Lathrop et al. 2003). At Long Point in Lake Erie (Ontario, Canada) populations had intrinsic growth rates ranging from –0.74 to 0.50 yr^{-1} (Wilcox et al. 2003). Several factors could explain these patterns. Undoubtedly, the highly disturbed and nutrient-rich nature of linear wetlands makes them an ideal habitat for *P. australis*. This is especially true when they intersect agricultural lands which tend to be an important source of nutrient, especially phosphorus. Whereas *P. australis* is considered a nuisance when it competes with native species or alters ecosystem functions in natural wetlands (Weinstein and Balletto 1999), in linear habitats, it may just act as an obvious indicator of eutrophication and may serve to capture, at least temporarily, the heavy load of nutrients and herbicides before it reaches aquatic ecosystems (Naylor et al. 2003; Schroder et al. 2005; Sun et al. 1999). This 'ecosystem service' may come at the cost of saturating the landscape with propagules that will eventually reach more pristine wetlands.

The different types of LC/LU that we considered corresponds to different management units, from minimal to no intervention along abandoned fields to possibly aggressive management in agricultural ditches (cut, burn, herbicide drift). The extent to and the rate at which linear wetlands of different landscape elements are invaded may reflect the degree of disturbances or control to which they are submitted. Observing these patterns can also provide insights into future trends. For instance, industrial areas that have been heavily disturbed but then abandoned in Laval also show high extent of invasion. On the other hand, agricultural ditches in Laval are relatively non-invaded compared to other linear wetlands. These patterns contrast with the rate and extent of invasion observed in agricultural areas of St Bruno. We expected differences in edaphic and drainage conditions to play a role (St-Bruno is generally a wetter site) but this was not supported by the logistic regression. It may be worthwhile in this case to rule out differences in the internal structure of the drainage ditches (width, depth, etc.) or differences in management practices by farmers. Since both landscapes, however, tend to support similar intensive crops, it may then be only a matter of time until we observe similar patterns of invasion in agricultural land in Laval. Given the speed at which the populations spread, it seems therefore important to control the smallest patches to avoid having to deal with populations that will eventually be beyond control in agricultural land.

Roadside ditches, especially along highways, tend to be generally larger and deeper than the other types of linear structures considered (pers. obser). Like wetlands, they act as sinks that collect nutrients, sediments, seeds, propagules, heavy metals, pesticides, salts, etc. (Zedler and Kercher 2004) from the surrounding landscape and these functions are compounded by the fact that they are connected to most other linear features within the landscape and that they intersect many different types of land uses. *P. australis* is exhibiting large environmental tolerance to such conditions (Pauca-Comanescu et al. 1999; Rolletschek et al. 1999). These spatial and ecological characteristics are reflected in the extent to which roadside wetland habitats are invaded in both studied landscapes. *P. australis* is usually cut in ROW transportation during regular maintenance operation and heavy machinery is sometimes used when the ditch has to be cleared. Obviously, from the temporal patterns observed, vegetation management does little to curb *P. australis* invasion. In contrast, the riparian habitats of small streams and rivers are not encroached by *P. australis*, except when they cross transportation ROW, even though our field observations suggested that the former could have been potential habitats. It is possible that differences in disturbance regimes and competitive vegetation in the riparian habitats contribute to slow down invasion rates. Again these differences are worth investigating in the field, first because they may suggest potential control strategy using other native competitive species (de Blois et al. 2004), and they may also suggest ways to mitigate invasion along natural areas when they intersect roads.

One should always be cautious in trying to infer processes from spatial patterns. In our landscapes, point pattern analysis show scale dependence effect that could partly be related to the spatial configuration of the network itself. For instance, parallel linear wetlands are separated by a distance that varies, depending on the landscape context; between 20 and 25 meters for ditches of transportation ROW, and between 35 and 75 meters for agricultural ditches. This may contribute to the clumping patterns observed at Euclidian distances which reflect the spatial arrangement of the network as much as dispersal events. However, if colonization was mostly done within the same segment of the network close to a source population, we would expect to observe more clumping using the network function than when we would using the Euclidian distance. Yet, in most cases, the reverse is true. The transport of propagules does not seem to be strongly constrained by the linear dimension of the network, which suggests a significant contribution of dispersal event across ditches. Dispersal agents would be animals or humans transporting propagules (rhizome and stolon fragments) across fields or roads.

Although the contribution of sexual reproduction has not been investigated in these types of habitats, it is generally assumed that sexual reproduction is extremely variable between populations and between years and even rare in many populations (Mal and Narine 2004). In fact, well-resourced plants, such as the ones thriving in eutrophic linear wetlands, may produce more seeds (McKee and Richards 1996) than populations in natural wetland habitats that are resource limited. Our populations show relatively high potential for producing seeds (as many as 13 000 seeds per inflorescence, from 350 to 800 viable) which would be easily transported to safe sites in the landscape. In our study, the most infested landscape is also the one that shows significantly higher germination rates. Disturbances in linear wetlands or wet patches will facilitate the establishment of *P. australis* as seeds only successfully colonize bare soils (Ailstock et al. 2001). If invasibility increases with increased propagule pressure (Foxcroft et al. 2004; Rouget and Richardson 2003), infested roads harbouring prolific populations that benefit from nutrient input from agricultural areas, chances are that the seeds will eventually take advantage of open sites in the intersected wetlands. This hypothesis has been partly verified by our data on the interaction between transportation ROW and riparian habitats, but we would need more evidence at the regional scale to corroborate these findings.

Our model shows that the effect of roads and the disturbances associated with them overrides any other potential variables, including drainage, in these systems. It seems that highly interconnected linear wetlands are thus forming a relatively homogenous habitat suitable for the establishment, growth, and reproduction of *P. australis* and that roads are the main vector of invasion at the landscape scale. Given the recent historical trend in agriculture intensification and highway construction in our area, that anthropogenic linear wetlands are periodically disturbed, and that *P. australis* is exhibiting large environmental tolerance (Pauca-Comanescu et al. 1999; Rolletschek et al. 1999), it is expected that linear wetlands will continue to be particularly susceptible to invasion. However, some landscapes, as demonstrated in this study, may be experiencing a peak in invasion as sites become saturated. At the regional scale, the species may be still expanding. Managers of transportation ROW should carefully monitor expansion patterns especially when the ROWs intersect landscape of conservation or economic value. Given the high rates of invasion, they should act as early as possible to limit establishment into adjacent land.

Figure 3: Location map of the St-Bruno and Laval landscapes

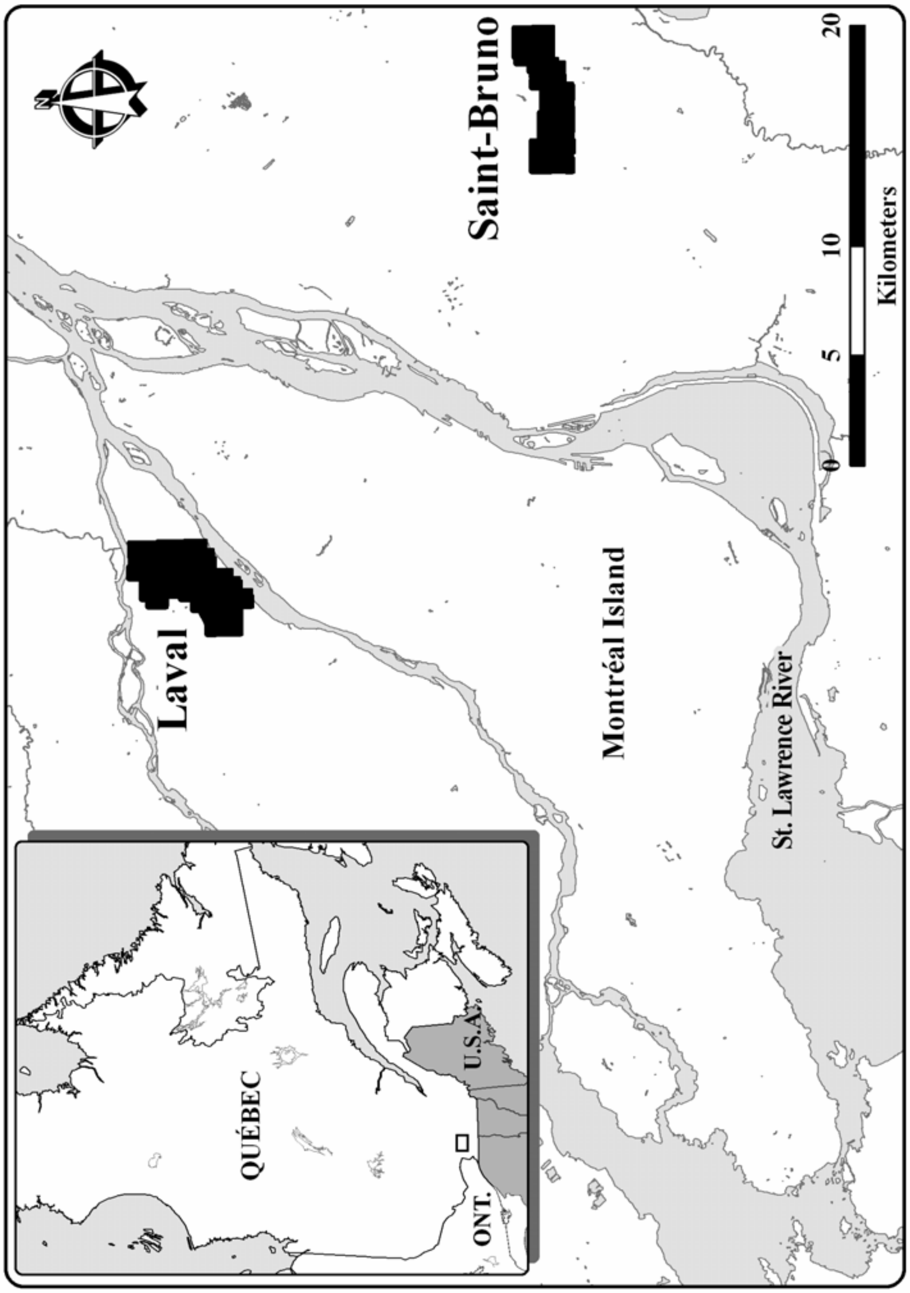

Figure 4: Drainage conditions of the St-Bruno and Laval landscapes

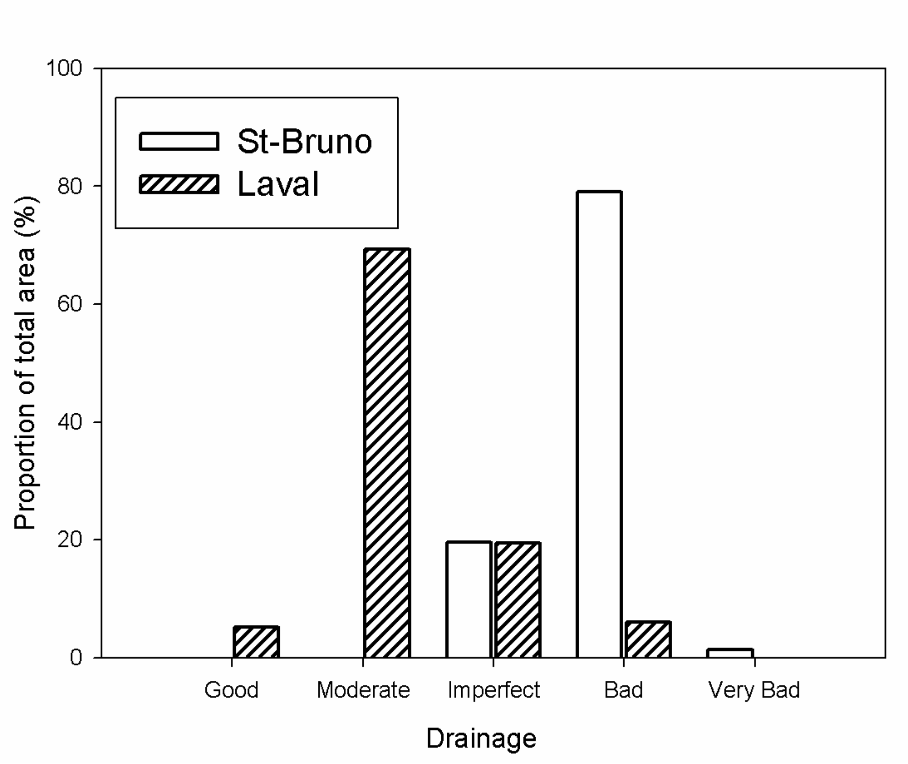

Figure 5: PCA of a time series of observation of LC/LU changes in the St-Bruno landscape

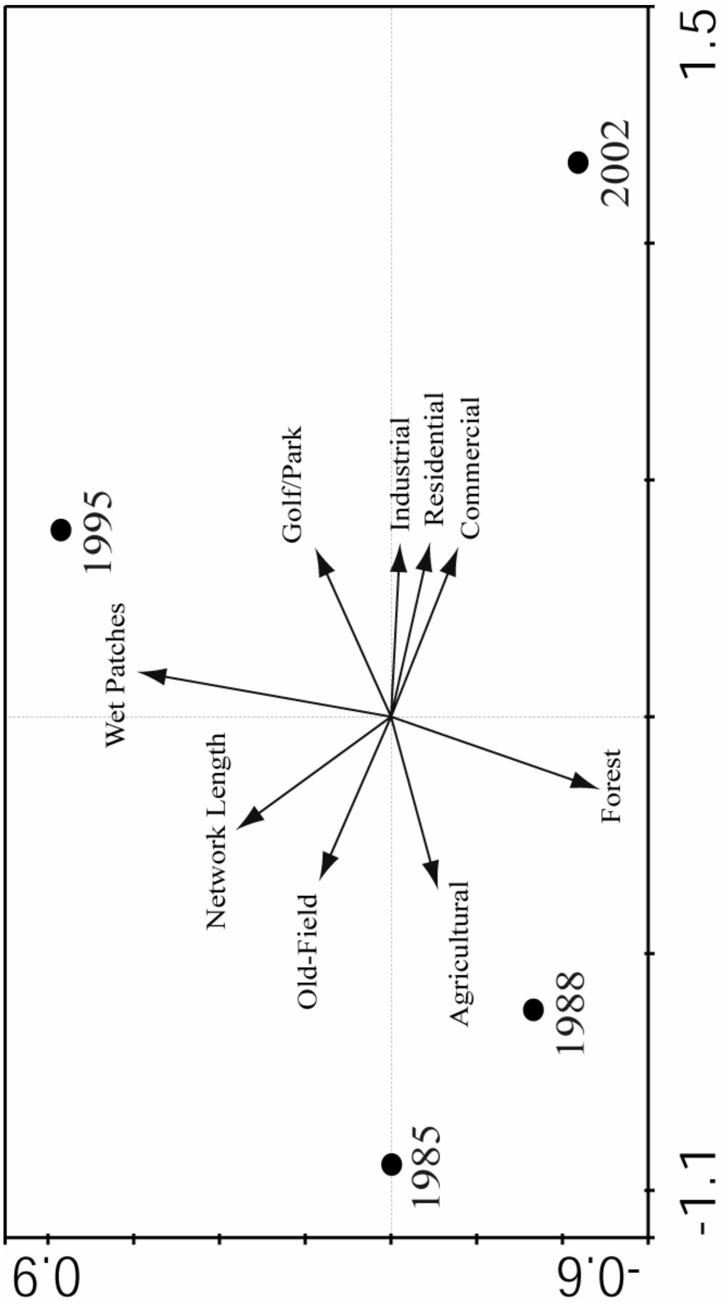

Figure 6: Landscape dynamicity exhibited by the LC/LU maps for the covered period at the St-Bruno landscape

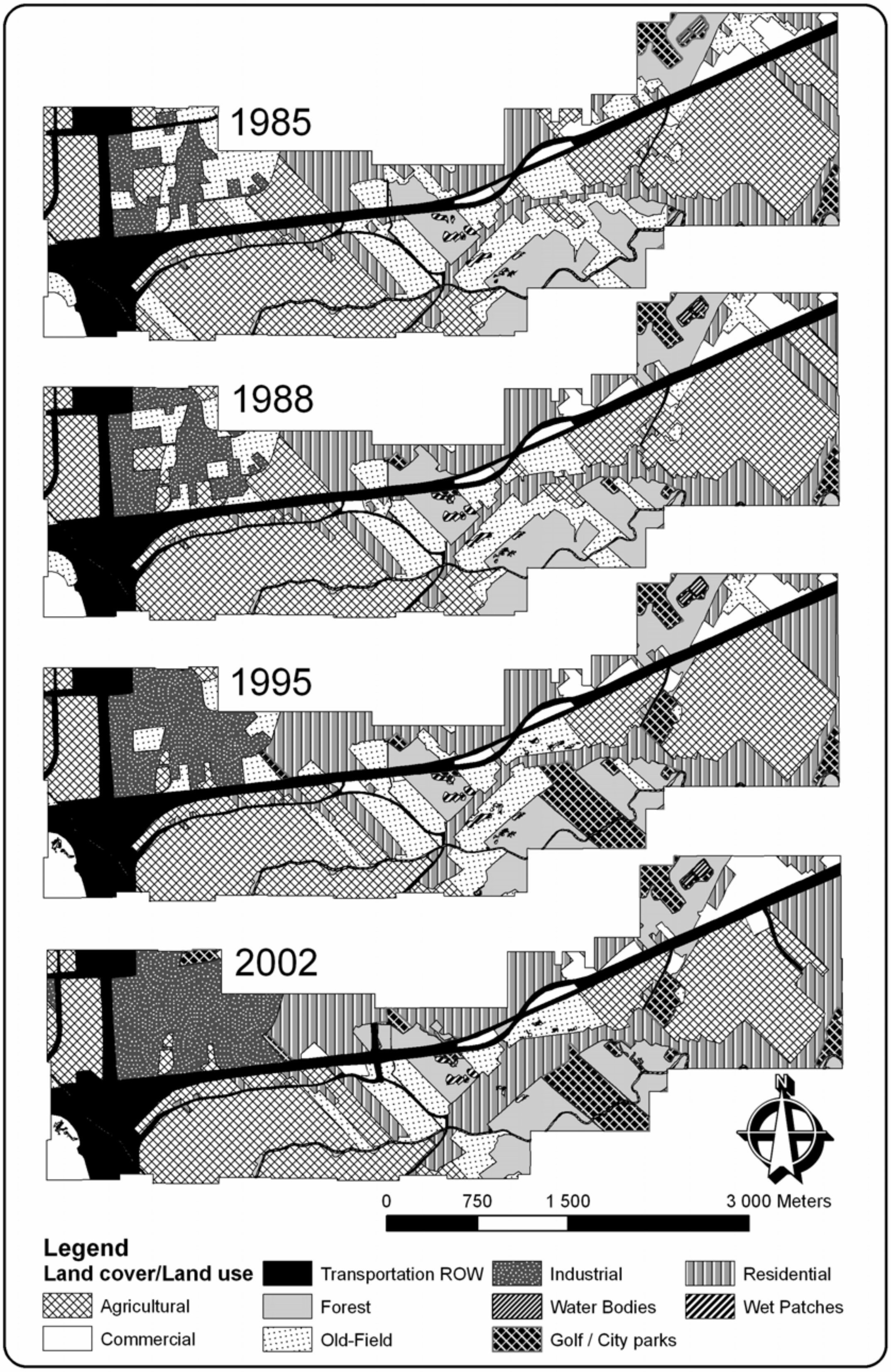
1985
1988
1995
2002
N
0
750
1 500
3 000 Meters
Legend
Land cover/Land use
Transportation ROW
Industrial
Residential
Agricultural
Forest
Water Bodies
Wet Patches
Commercial
Old-Field
Golf / City parks

Figure 7: PCA of a time series of observations of LC/LU changes in the Laval landscape

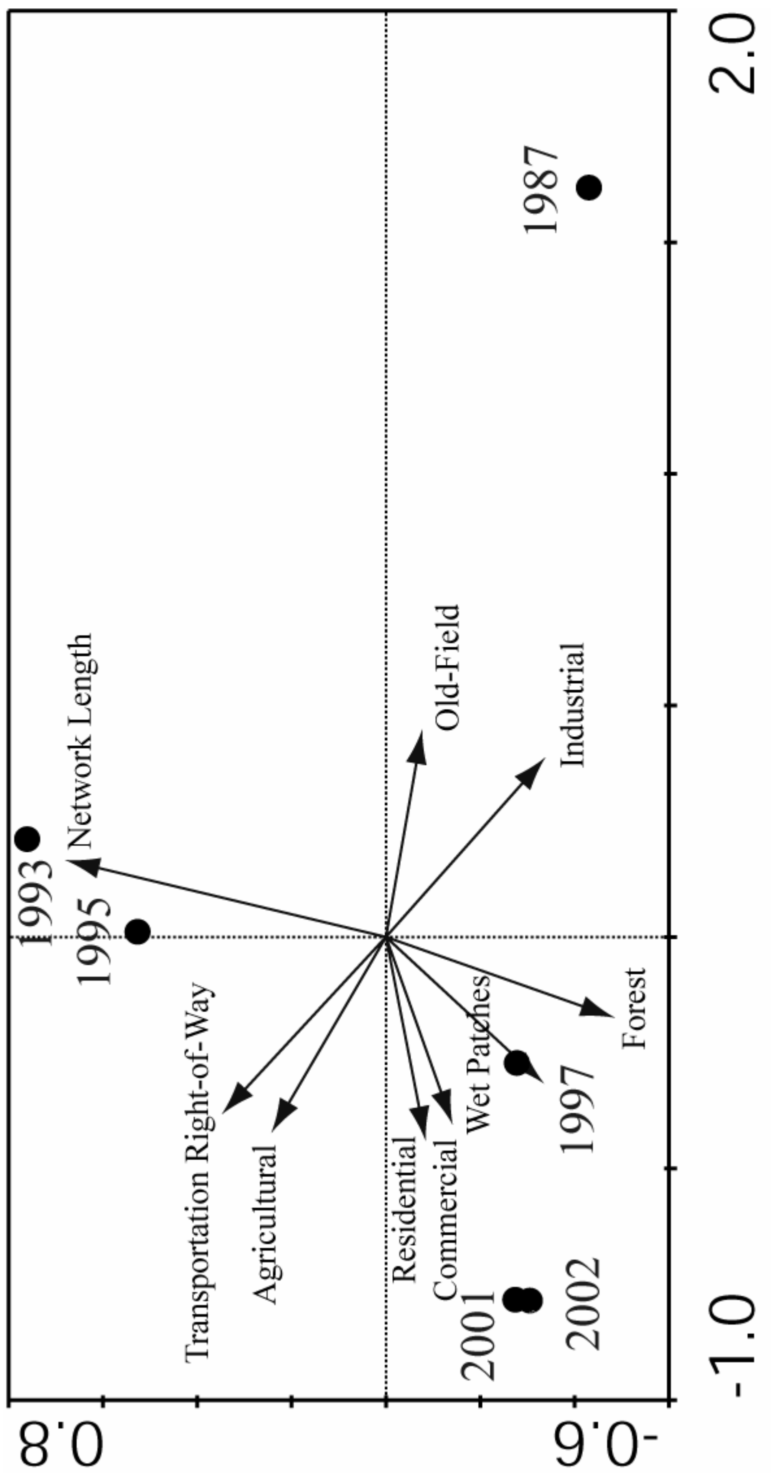

Figure 8: Landscape dynamicity exhibited by the LC/LU maps for the covered period at the Laval landscape

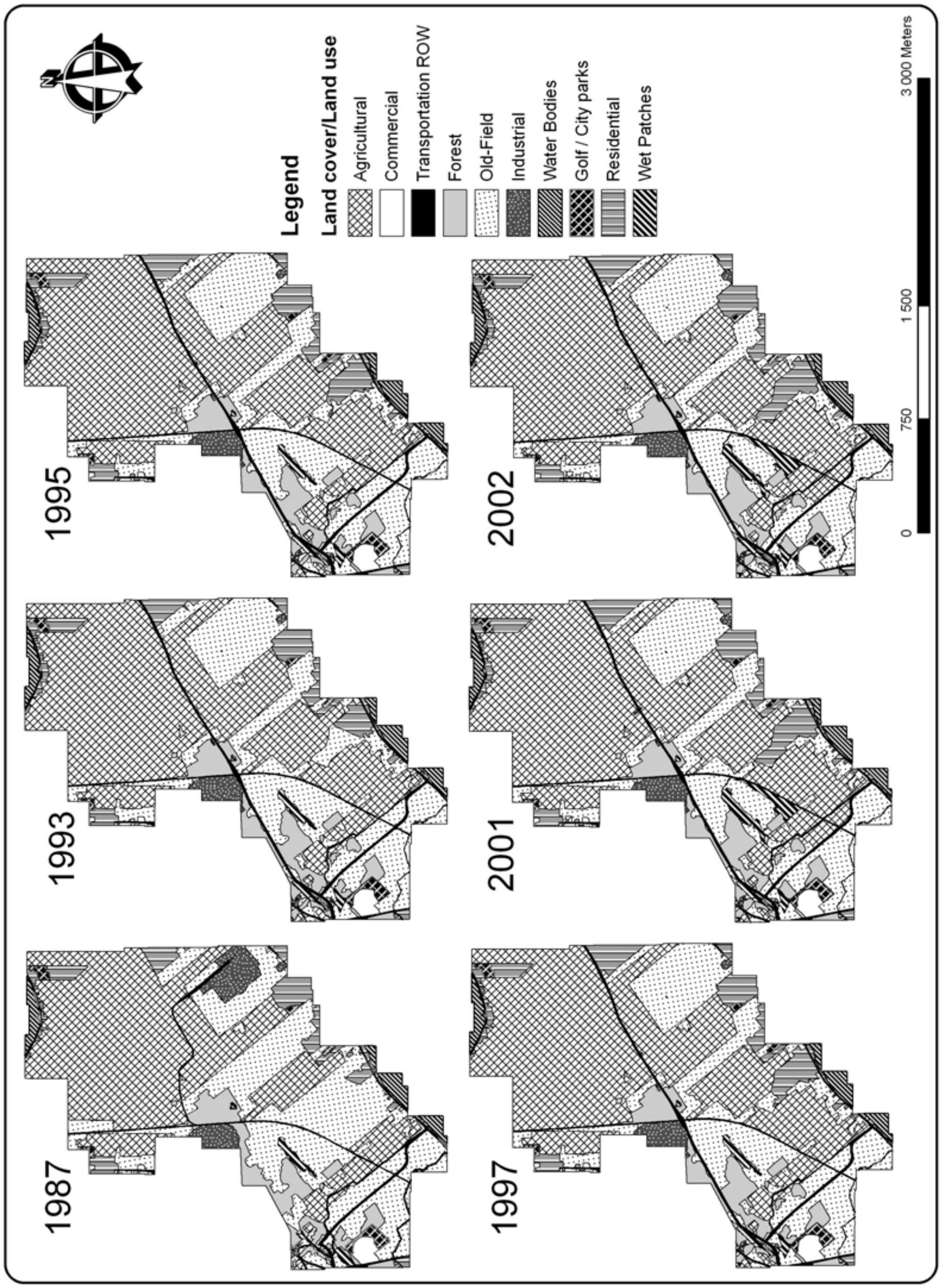

Figure 9: Distribution maps of *P. australis* for the St-Bruno landscape

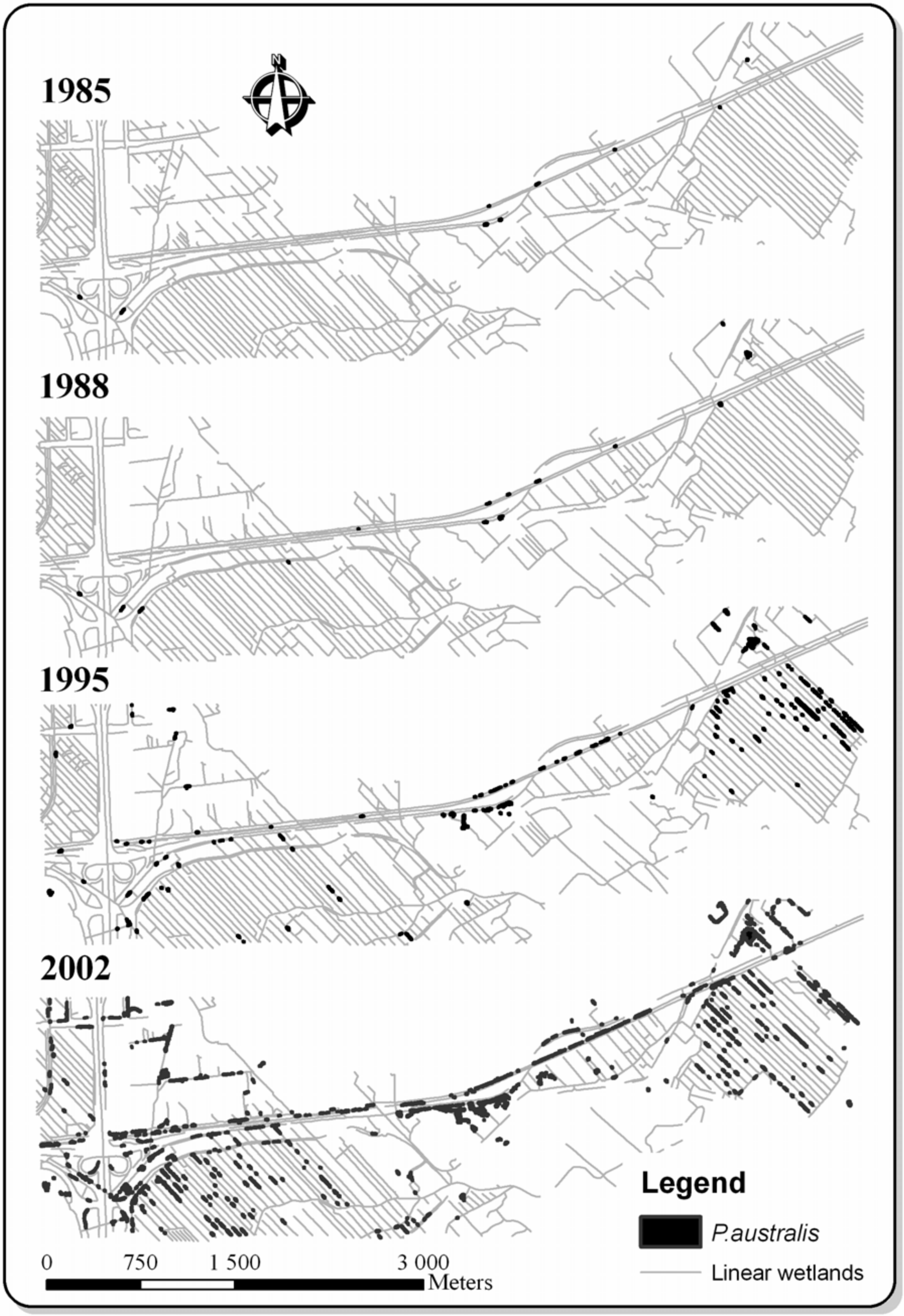
1985
1988
1995
2002
N
0
750
1 500
3 000
Meters
Legend
P.australis
Linear wetlands

Figure 10: Distribution maps of *P. australis* populations in the Laval landscape

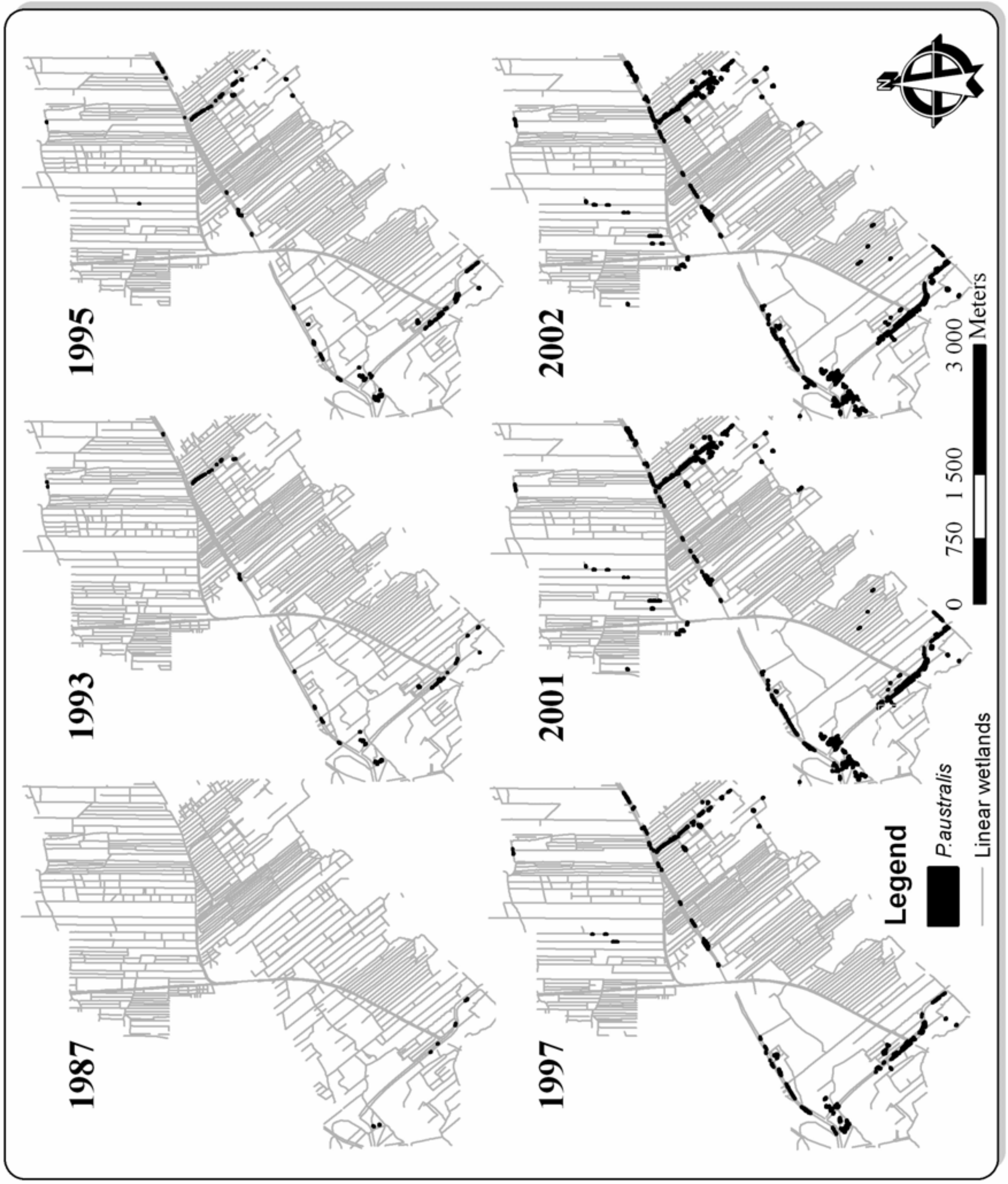

Figure 11: Rate of invasion of different LC/LU for both landscapes

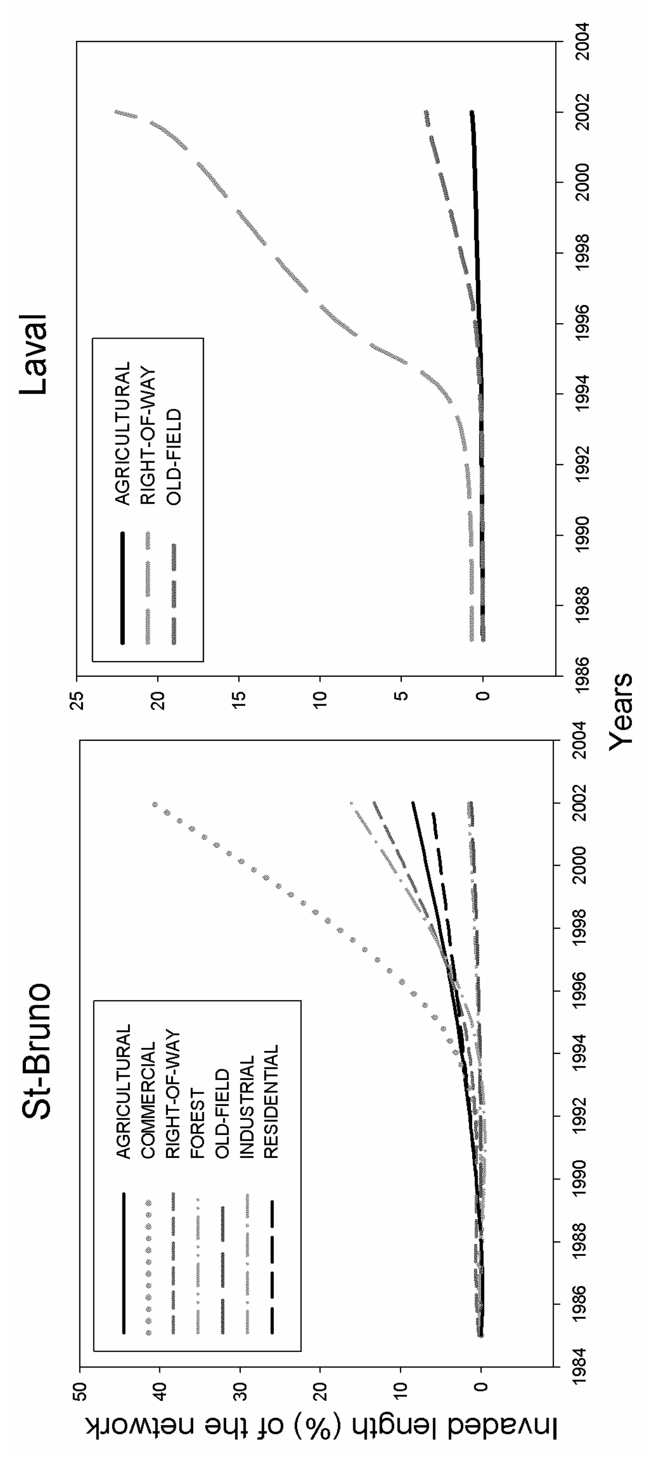

Table 1: Network length (km) fluctuations in time for both landscapes

Fluctuations in the total network length of both landscapes			
St-Bruno		**Laval**	
Date	Length (Km)	Date	Length (Km)
		1987	212.7
1985	147.7	1993	234.6
1988	154.1	1995	222.6
1995	153.8	1997	202.1
2002	133.5	2001	203.4
		2002	202.3

Table 2: Networks connectivity (gamma index) dynamics for both landscapes

Gamma connectivity index for both landscapes			
St-Bruno		**Laval**	
Date	Gamma index	Date	Gamma index
		1987	0.40
1985	0.40	1993	0.41
1988	0.38	1995	0.40
1995	0.38	1997	0.39
2002	0.36	2001	0.39
		2002	0.39

Table 3: Historical intrinsic growth rate of the St-Bruno and Laval landscapes

Intrinsic rates of increase (/yr)			
St-Bruno		Laval	
		1987-1993	0.4308
1985-1988	0.3438	1993-1995	0.5400
1988-1995	0.3632	1995-1997	0.4394
1995-2002	0.1957	1997-2001	0.2590
		2001-2002	0.1900

Table 4: Synthesis of the degree of association/repulsion, determined by the cross-K function, of colonization events for both landscape

Spatial dependence between colonization events and source populations							
		Network distances (m)			**Euclidean distances (m)**		
		Association*	Randomness	Repulsion*	Association*	Randomness	Repulsion*
St-Bruno							
	1988-1995	---	0-20 m	20m and up	95 m and up	0-95 m	---
	1995-2002	135 m and up	0-135 m	---	24 m and up	0-24 m	---
Laval							
	1987-1993	18 m and up	---	---	21 m and up	---	---
	1993-1995	6 m and up	---	---	18 m and up	10-18 m	---
	1995-1997	24 m and up	0-24 m	---	16 m and up	6-16 m	
	1997-2001	0 m and up	---	---	20 m and up	4-20 m	---
	2001-2002	4 m and up	---	---	20 m and up	9-20 m	---

* Spatial dependence is considered at the $\alpha = 0.05$ significance level

"---": signify that the type of spatial dependence is not applicable

Table 5: Proportion of colonization found in excess/deficit for both landscape using network and Euclidean distances at 50 m, 75 m, and 100 m

Proportion (%) of colonization events in excess or deficit compared to a random process							
		50m		75m		100m	
		Network	**Euclidean**	**Network**	**Euclidean**	**Network**	**Euclidean**
St-Bruno							
	1988-1995	-0.9	**-0.1**	-0.8	**0.6**	**1.4**	1.2
	1995-2002	0.0	**0.8**	0.1	**0.9**	0.1	**0.7**
Laval	1987-1993	32.2	**33.3**	**36.2**	32.8	**26.6**	19.8
	1993-1995	8.5	**17.8**	7.1	**11.3**	9.5	**10.5**
	1995-1997	7.0	**17.2**	5.9	**10.6**	6.0	**9.2**
	1997-2001	4.8	**8.3**	4.7	**6.7**	4.4	**5.3**
	2001-2002	8.3	**16.8**	5.7	**10.7**	5.4	**7.3**

* Bold numbers indicate more association of colonization events

GENERAL CONCLUSION

The remote sensing monitoring methodology developed for *P. australis* in this study is accurate enough to obtain reliable distribution maps and could be applied to other similar species (i.e. giant reed, *Arundo donax*) in other types of linear habitats such as field margins and small streams. *P. australis* spread in networks of anthropogenic wetlands in our study area is generally more rapid than the ones reported for natural wetlands. Hence, linear wetlands are and will continue to be highly susceptible to *P. australis* invasion because the suspected conditions that cause this vulnerability such as disturbances and nutrient loads are unlikely to change in the short-term. Transportation ROWs are generally the first invaded landscape elements and served as foci of invasion into the intersected landscape. However, the configuration of the network of linear wetlands is not constraining the dispersal of *P. australis* as our data suggest that sexual reproduction might have been underestimated in this type of habitat. The developed predictive model of *P. australis* occurrence also stresses the importance of transportation ROWs as their effect overrides other landscape variables and drove invasions patterns in the studied landscapes. Given the high rates of invasion observed, an advice to managers of transportation ROWs should be to monitor carefully expanding populations especially when the ROWs intersect landscape of conservation or economic value. In agricultural settings, it is strongly recommended to control as soon as possible new patches to avoid having to deal with populations that will eventually be beyond control, with significant economical loss.

REFERENCES

Agriculture Canada 1952. Carte des sols des Îles de Montréal - Jésus - Bizard, Québec. Services des fermes expérimentales, Ottawa, Canada, 1/50 000.

Agriculture Canada 1991. Carte pédologique du Comté de Chambly. Unité de cartographie et des systèmes d'information, Centre de recherches sur les terres, Direction générale de la recherche, Ottawa, Canada, 1/20 000.

Ailstock M., Norman C. and Bushmann P. 2001. Common reed *Phragmites australis*: Control and effects upon biodiversity in freshwater nontidal wetlands. *Restoration Ecology* 21: 49-59.

Akaike H. 1973. Information theory and an extension of the maximum likelihood principles. *2nd International Symposium on Information Theory*, p.267-281. Akademia Kiado, Budapest, Hungary.

Albert A. and Anderson A. 1984. On the existence of maximum likelihood estimates in logistic regression models. *Biometrika* 17: 1-10.

Auclair A.N.D., Bouchard A. and Pjazxkowski J. 1976. Plant standing crop and productivity relations in a *Scirpus-Equisetum* wetland. *Ecology* 57: 941-952.

Auda Y., Blasco F., Gastelly-Etchegorry J.P., Marty G. and Déchamp C. 2002. Éssai préliminaire de détection des champs d'ambroisie par télédétection spatiale. *Revue française d'allergologie et d'immunologie clinique* 42: 533-538.

Baddeley A. and Turner R. 2005. Spatstat: an *R* package for analyzing spatial point patterns. *Journal of Statistical Software* 12: 1-42.

Bart D. and Hartman J.M. 2000. Environmental determinants of *Phragmites australis* expansion in a New Jersey salt marsh: an experimental approach. *Oikos* 89: 59-69.

Bédard Y. and Trottier D. 2003. La gestion de la végétation des corridors autoroutiers: la nouvelle approche québécoise. *Service des inventaires et du plan, Direction de Québec, Ministère des Transports du Québec*, Québec, Canada. 10 pp.

Bergelson J., Newman J.A. and Floresroux E.M. 1993. Rates of weed spread in spatially heterogeneous environments. *Ecology* 74: 999-1011.

Best E.P.H. 1993. The impact of mechanical harvesting regimes on the species composition of Dutch ditch vegetation: a quantitative approach. *Journal of Aquatic Plant Management* 31: 148-154.

Best E.P.H., Zippin M. and Dassen J.H.A. 1981. Growth and production of *Phragmites australis* in Lake Vechten (The Netherlands). *Hydrobiological Bulletin, Netherlands Hydrobiological society* 15: 165-174.

Björk S. 1967. Ecological investigations of *Phragmites communis*: studies in theoretical and applied limnology. *Folia Limnologica Sandinavia* 14: 1-248.

Bolstad P.V. 1992. Geometric errors in natural resources GIS data: tilt and terrain effects in aerial photographs. *Forest Science* 33: 367-380.

Boszke P., Bociag K. and Szmeja J. 2005. Population structure and regeneration of *Phragmites australis* (Cav.) Trin. ex Steud. in flood control ditches in the depression wetland (Zulawy Wislane, northern Poland). *Polish Journal of Ecology* 53: 3-12.

Boutin C., Jobin B. and Belanger L. 2003. Importance of riparian habitats to flora conservation in farming landscapes of southern Quebec, Canada. *Agriculture, Ecosystems & Environment* 94: 73-87.

Brix H. 1999. Genetic diversity, ecophysiology and growth dynamics of reed (*Phragmites australis*). *Aquatic Botany* 64: 179-184.

Bunce R.G.H. and Hallam J. 1993. The ecological significance of linear features in agricultural landscapes in Britain. *In* Bunce R.G.H., Ryskowski L. and Paoletti M.G. (eds.), *Landscape ecology and agroecosystems*, 11-19. Lewis Publishers, Boca Raton, USA.

Burdick D. and Konisky R.A. 2003. Determinants of expansion for *Phragmites australis*, common reed, in natural and impacted coastal marshes. *Estuaries* 26: 407-416.

Burk I. 1877. List of plants recently collected on ship's ballast in the neighbourhood of Philadelphia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 29: 105-109.

Buttery B.R. and Lambert J.M. 1965. Competition between *Glycera maxima* and *Phragmites communis* in the region on Surlington Broad I. The competition mechanism. *Journal of Ecology* 53: 163-181.

Byers J.E., Reichard S.H., Randall J.M., Parker I.M., Smith C.S., Lonsdale W.M., Atkinson I.A.E., Seastedt T.R., Williamson M., Chornesky E. and Hayes D. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16: 630-640.

Caloz R. and Collet C. 1997. Geographic information systems (GIS) and remote sensing in aquatic botany: methodological aspects. *Aquatic Botany* 58: 209-228.

Casgrain P. and Legendre P. 2004. Le Progiciel R - Version 4.0. Université de Montréal, Montréal, Canada.

Catling P.M., Schueler F.W., Robichaud L. and Blossey B. 2003. More on *Phragmites australis* - native and introduced races. *Canadian Botanical Association Bulletin* 36: 4-7.

Chambers R.M., Meyerson L.A. and Saltonstall K. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany* 64: 261-273.

Clevering O.A. and van der Toorn J. 2000. Observations of the colonization of a young polder area in the Netherlands with special reference to the clonal expansion of *Phragmites australis*. *Folia Geobotanica* 35: 375-387.

Coops H. and van der Velde G. 1995. Seed dispersal, germination and seedling growth of six helophyte species in an experimental water-depth gradient. *Freshwater biology* 34: 13-20.

Cox D.R. 1970. Analysis of binary data. Chapman and Hall, New York, USA. 142 pp.

Dahlgren R.M.T., Clifford H.T. and Yeo P.F. 1985. The families of the Monocotyledons: structure, evolution, and taxonomy. Springer-Verlag, Berlin, Germany. 520 pp.

Darbyshire S.J., Favreau M. and Murray M. 2000. Common and scientific names of weeds in Canada. *Research Branch, Agriculture and Agri-Food Canada*, Ottawa, Canada. 132 pp.

Davis M.A., Grime J.P. and Thompson J.D. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528-534.

de Blois S., Brisson J. and Bouchard A. 2004. Herbaceous covers to control tree invasion in rights-of-way: Ecological concepts and applications. *Environmental Management* 33: 606-619.

Deckers B., Verheyen K., Hermy M. and Muys B. 2005. Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium. *Ecography* 28: 99-109.

De-Leeuw A.J., Veugen L.M.M. and Van Stokkom H.T.C. 1988. Geometric correction of remotely-sensed imagery using ground control points and orthogonal polynomials. *International Journal of Remote Sensing* 9: 1751-1759.

Delisle F., Lavoie C., Martin J. and Lachance D. 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. *Journal of Biogeography* 30: 1-11.

Den Hartog C., Kvet J. and Sukopp H. 1989. Reed a common species in decline. *Aquatic Botany* 35: 1-4.

Dietz H., Fischer M. and Schmid B. 1999. Demographic and genetic invasion history of a 9-year-old roadside population of *Bunias orientalis* L. (Brassicacea). *Oecologia* 120: 225-234.

Dixon P.M. 2002. Ripley's *K* function. *In* El-Shaarawi A.H. and Piegorsch W.W. (eds.), *Encyclopedia of Environmetrics*, 1796-1803. John Wiley & Sons, Chichester, England.

Domon G., Bouchard A. and Gariépy M. 1993. The dynamics of the forest landscape of Haut-Saint-Laurent (Québec, Canada): interactions between biophysical factors, perceptions and policy. *Landscape & Urban Planning* 25: 53-74.

Efron B. 1979. Bootstrap methods: another look at the Jackknife. *The Annals of Statistics* 7: 1-26.

Ekstam B., Johannesson R. and Milberg P. 1999. The effects of light and number of diurnal temperature fluctuations on germination of *Phragmites australis*. *Seed Science Research* 9: 165-170.

eMap International Inc. 2002. QUICKBIRD - Aerial photography comparison report. *Prepared by David K. Nale for Digital Globe*, London, England. 39 pp.

Fagan W.E., Cantrell R.S. and Cosner C. 1999. How habitat edges change species interactions. *The American Naturalist* 153: 165-182.

Forman R.T.T. and Alexander L.E. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207-231.

Forman R.T.T. and Godron M. 1986. Landscape ecology. John Wiley & Sons, New York, USA. 640 pp.

Foxcroft L.C., Rouget M., Richardson D.M. and Mac Fadyen S. 2004. Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. *Diversity and Distributions* 10: 427-437.

Galatowitsch S.M., Anderson N.O. and Ascher P.D. 1999. Invasiveness in wetland plants in temperate North America. *Wetlands* 19: 733-755.

Geertsema W. and Sprangers J. 2002. Plant distribution patterns related to species characteristics and spatial and temporal habitat heterogeneity in a network of ditch banks. *Plant Ecology* 162: 91-108.

Gervais C., Trahan R., Moreno D. and Drolet A.M. 1993. *Phragmites australis* in Québec - Geographic distribution, chromosome number and reproduction. *Canadian Journal of Botany / Revue Canadienne de Botanique* 71: 1386-1393.

Grandtner M.M. 1999. Ecology and use of *Phragmites communis* in eastern Canada. *Bulletin Kansai Organisation for Nature Conservation* 21: 289-299.

Green D.R. and Hartley S. 2000. Integrating photointerpretation and GIS for vegetation mapping: some issue of error. *In* Alexander R. and Millington A.C. (eds.), *Vegetation mapping: from patch to planet*, 103-134. John Wiley & Sons, Chichester, England.

Haase P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. *Journal of Vegetation Science* 6: 575-582.

Hansen R.M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* 4: 302-319.

Hara T., Van Der Toorn J. and Mook J.H. 1993. Growth dynamics and size structure of shoots of *Phragmites australis*, a clonal plant. *Journal of Ecology* 81: 47-60.

Haslam S.M. 1969. The development and emergence of buds in *Phragmites communis* Trin. *Annals of Botany* 33: 127-131.

Haslam S.M. 1970. The performance of *Phragmites communis* Trin. in relation to water supply. *Annals of Botany* 34: 867-877.

Haslam S.M. 1971. Community regulation in *Phragmites communis* Trin. I. monodominant stands. *Journal of Ecology* 59: 65-73.

Haslam S.M. 1972. *Phragmites communis* Trin. biological flora British Isles. *Journal of Ecology* 60: 585-610.

Havens K.J., Walter I. and Berquist H. 1997. Investigation and long-term monitoring of *Phragmites australis* within Virginia's constructed wetland sites. *Environmental Management* 21: 599-605.

Hewitt J.E., Legendre P., McArdle B.H., Thrush S.F., Bellehumeur C. and Lawrie S.M. 1997. Identifying relationships between adult and juvenile bivalves at different spatial scales. *Journal of Experimental Marine Biology and Ecology* 216: 77-98.

Hocking P.J., Finlayson C.M. and Chick A.J. 1983. The biology of Australian weed. 12. *Phragmites australis* (Cav.) Trin. Ex Steud. *Journal of the Australian Institute of Agricultural Research* 49: 123-132.

Hurlbert S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.

Hürlimann H. 1951. Zur Lebensgeshichte des Schilfs an den Ufern der Schweizer Seen. *Beitrage zur Geobotanischen Landesaufnahme der Schweiz* 30: 1-132.

Ishii J. and Kadono Y. 2002. Factors influencing seed production of *Phragmites australis*. *Aquatic Botany* 72: 129-141.

Jobin B., Beaulieu J., Grenier M., Bélanger L., Maisonneuve C., Bordage D. and Filion B. 2003. Landscape changes and ecological studies in agricultural regions, Quebec, Canada. *Landscape Ecology* 18: 575-590.

Kadlec R.H. and Knight R.L. 1996. Treatment Wetlands. Lewis Publishers, Boca Raton, USA. 893 pp.

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

Kotschy K.A., Rogers K.H. and Carter A.J. 2000. Patterns of change in reed cover and distribution in a seasonal riverine wetland in South Africa. *Folia Geobotanica* 35: 363-373.

Krumscheid P., Stark H. and Peintinger M. 1989. Decline of reed at Lake Constance (Obersee) since 1967 based on interpretations of aerial photographs. *Aquatic Botany* 35: 57-62.

Lamontagne L. and Nolin M.C. 1997. Dossier des noms de sols du Québec 1997 : SISCan (Système d'information des sols au Canada). *Agriculture et Agroalimentaire Canada, Direction générale de la recherche*, Sainte-Foy, Canada. 59 pp.

Lathrop R.G., Windham L. and Montesano P. 2003. Does Phragmites expansion alter the structure and function of marsh landscapes? Patterns and processes revisited. *Estuaries* 26: 423-435.

Lavoie C., Jean M., Delisle F. and Letourneau G. 2003. Exotic plant species of the St Lawrence River wetlands: a spatial and historical analysis. *Journal of Biogeography* 30: 537-549.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659-1673.

Legendre P. and Fortin M.-J. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.

Legendre P. and Legendre L. 1998. Numerical Ecology. Elsevier Science, Amsterdam, Netherlands. 853 pp.

Li H. and Maddala G.S. 1999. Bootstrap variance estimation of non-linear functions of parameters: an application to long-run elasticities of energy demand. *The Review of Economics and Statistics* 81: 728-733.

Lippert I., Rolletschek H., Kuhl H. and Kohl J.G. 1999. Internal and external nutrient cycles in stands of *Phragmites australis* - a model for two ecotypes. *Hydrobiologia* 409: 343-348.

Lissner J. and Schierup H.H. 1997. Effects of salinity on the growth of *Phragmites australis*. *Aquatic Botany* 55: 247-260.

Lonsdale W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522-1536.

Lynch E.A. and Saltonstall K. 2002. Paleoecological and genetic analyses provide evidence for recent colonization of native *Phragmites australis* populations in a lake superior wetland. *Wetlands* 22: 637-646.

Macoun J. 1883. Catalogue of Canadian Plants Part 1: Polypetale. Dawson Brothers, Montréal, Canada. 203 pp.

Maheu-Giroux M. and de Blois S. Mapping the invasive species *Phragmites australis* in linear wetland corridors. *Aquatic Botany*: in press

Mal T.K. and Narine L. 2004. The biology of Canadian weeds. 129. *Phragmites australis* (Cav.) Trin. ex Steud. *Canadian Journal of Plant Science* 84: 365-396.

Marie-Victorin F.E.C. 1995. Flore Laurentienne. Les Presses de l'Université de Montréal, Montréal, Canada. 1083 pp.

Marks M., Lapin B. and Randall J. 1994. *Phragmites australis (P.communis)*: Threats, Management, and Monitoring. *Natural Areas Journal* 14: 285-294.

McKee J. and Richards A.J. 1996. Variation in seed production and germinability in Common reed (*Phragmites australis*) in Britain and France with respect to climate. *New Phytologist* 133: 233-243.

Minchinton T.E. and Bertness M.D. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. *Ecological Applications* 13: 1400-1426.

Ministère des Transports du Québec 1983. Les autoroutes du Québec: dates de construction ou de mise en service. *Gouvernement du Québec*, Québec, Canada. 31 pp.

Moody M.E. and Mack R.N. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25: 1009-1021.

Moran P.A.P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37: 17-23.

Mousseau P. 1987. Synthèse des connaissances sur le phragmite commun (*Phragmites communis*). *Hydro-Québec*, Région de Maisonneuve, Canada. 55 pp.

Nagelkerke N.J.D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78: 691-692.

Naylor S., Brisson J., Labelle M.A., Drizo A. and Comeau Y. 2003. Treatment of freshwater fish farm effluent using constructed wetlands: the role of plants and substrate. *Water Science & Technology* 48: 215-222.

Niering W.A., Warren R.S. and Weymouth C.G. 1977. Our dynamic tidal marshes vegetation changes as revealed by peat analysis. *Connecticut Arboretum Bulletin* 22: 2-12.

Novàkovà J. 1997. Agricultural impact of linear vegetation formations: species richness, stand trophy, and plant strategies. *Ekolôgia-Bratislava* 16: 395-402.

Ohser J. 1983. On estimators for the reduced second moment measure of point processes. *Mathematische Operationsforschung und Statistik, series Statistics* 14: 63-71.

Okabe A., Okunuki K. and Shiode S. 2004. SANET: a toolbox for spatial analysis on a network - Version 2.0. Centre for Spatial Information Science, University of Tokyo, Tokyo, Japan.

Okabe A. and Yamada I. 2001. The K-function method on a network and its computational implementation. *Geographical Analysis* 33: 271-290.

Ostendorp W. 1989. 'Die-back' of reeds in Europe- a critical review of literature. *Aquatic Botany* 35: 5-26.

Parendes L.A. and Jones J.A. 2000. Role of light availability and dispersal in exotic plant invasions along roads and streams in the H.J. Andrews experimental forest, Oregon. *Conservation Biology* 14: 64-75.

Pauca-Comanescu M., Clevering O.A., Hanganu J. and Gridin M. 1999. Phenotypic differences among ploidy levels of *Phragmites australis* growing in Romania. *Aquatic Botany* 64: 223-234.

Pauchard A. and Alaback P.B. 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. *Conservation Biology* 18: 238-248.

Phillips J.D. 1987. Shoreline processes and establishment of *Phragmites australis* in a coastal plain estuary. *Vegetatio* 71: 139-144.

Rameau J.C., D. Mansion, G. Dumé, A. Lecointe, J. Timbal, P. Dupont & K. Keller 1993. Flore forestière française, guide écologique illustré. Tome 2: Montagnes. Institut pour le développement forestier, France. 2421 pp.

Remillard M.M. and Welch R. 1993. GIS technologies for aquatic macrophytes studies: Modelling applications. *Landscape Ecology* 8: 163-175.

Ricciuti E.R. 1983. The all too common, common reed. *Audubon Magazine* September: 65-66.

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

Richburg J.A., Patterson W.A. and Lowenstein F. 2001. Effects of road salt and *Phragmites australis* invasion on the vegetation of a western Massachusetts calcareous lake-basin fen. *Wetlands* 21: 247-255.

Riemer D.N. 1976. Long-term effects of glyphosate applications to *Phragmites communis*. *Journal of Aquatic Plant Management* 14: 39-43.

Ripley B.D. 1976. The second-order analysis of stationarity point processes. *Journal of Applied Probability* 13: 255-266.

Rolletschek H., Rolletschek A., Kuehl H. and Kohl J.-G. 1999. Clone specific differences in a *Phragmites australis* stand II. Seasonal development of morphological and physiological characteristics at the natural site and after transplantation. *Aquatic Botany* 64: 247-260.

Roman C.T., W.A. Niering & R.S. Warren 1984. Salt marsh vegetation change in response to tidal restriction. *Environmental Management* 8: 141-150.

Rouget M. and Richardson D.M. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *The American Naturalist* 162: 713-724.

Rousseau C. 1974. Géographie floristique du Québec-Labrador. Presses de l'Université Laval, Québec, Canada. 798 pp.

Rowlinson L.C., Summerton M. and Ahmed F. 1999. Comparison of remote sensing data sources and techniques for identifying and classifying alien invasive vegetation in riparian zones. *Water SA* 25: 497-500.

Rudescu L., Niculescu C. and Chivu I.P. 1965. Monographia stufului den delta Dunarii (Monograph of the common reed in the Danube delta). *Editura Academie Republicii Socialiste*, Bucuresti, Romania. 542 pp.

Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences* 99: 2445-2449.

Saltonstall K. 2003a. Genetic variation among north American populations of *Phragmites australis*: implications for management. *Estuaries* 26: 444-451.

Saltonstall K. 2003b. Microsatellite variation within and among North American lineages of *Phragmites australis*. *Molecular Ecology* 12: 1689-1702.

Saltonstall K. 2003c. A rapid method for identifying the origin of North American *Phragmites* populations using RFLP analysis. *Wetlands* 23: 1043-1047.

Saltonstall K., Peterson P.M. and Soreng R.J. 2004. Recognition of *Phragmites australis* subsp. *americanus* (Poaceae: Arundinoideae) in North America: Evidence from morphological and genetic analyses. *Sida, Contribution to Botany* 21: 683-692.

Santner T.J. and Duffy E.D. 1986. A note on A. Albert and J.A. Anderson's conditions for the existence of Maximum Likelihood Estimates in logistic regression models. *Biometrika* 73: 755-758.

Schroder P., Maier H. and Debus R. 2005. Detoxification of herbicides in *Phragmites australis*. *Zeitschrift fur Naturforschung - A Journal of Bioscience* 60: 317-324.

Schwarz G. 1978. Estimating the dimension of a model. *Annals of Statistics* 6: 461-464.

Shay J.M., De Geus P.M.J. and Kapinga M.R.M. 1999. Changes in shoreline vegetation over a 50-year period in the Delta Marsh, Manitoba in response to water levels. *Wetlands* 19: 413-425.

Silliman B.R. and Bertness M.D. 2004. Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. *Conservation Biology* 18: 1424-1434.

Singh R. and Mangat N.S. 1996. Elements of Survey Sampling. Kluwer Academic Publishers, Dordrecht/Boston/London. 388 pp.

Sitter R.R. 1992. A resampling procedure for complex survey data. *Journal of the American Statistical Association* 87: 755-765.

Small E. and Catling P.M. 2001. Poorly known economic plants of Canada-29. Common reed, *Phragmites australis* (Cav.) Trin. ex Steud. *Canadian Botanical Association Bulletin* 34: 21-26.

Spooner P.G., Lunt I.D. and Briggs S.V. 2004a. Spatial analysis of anthropogenic disturbance regimes and roadside shrubs in a fragmented agricultural landscape. *Applied Vegetation Science* 7: 61-70.

Spooner P.G., Lunt I.D., Okabe A. and Shiode S. 2004b. Spatial analysis of roadside *Acacia* populations on a road network using the network K-function. *Landscape Ecology* 19: 491-499.

Stehman S.V. 1995. Thematic map accuracy assessment from the perspective of finite population sampling. *International Journal of Remote Sensing* 16: 589-593.

Stehman S.V. and Czaplewski R.L. 1998. Design and analysis for thematic map accuracy assessment: fundamental principles. *Remote Sensing of Environment* 64: 331-344.

Stiles J.H. and Jones R.H. 1998. Distribution of the red imported fire ant, *Solenopsis invicta*, in road and powerline habitats. *Landscape Ecology* 335: 335-346.

Sun G., Gray K.R., Biddlestone A.J. and Cooper D.J. 1999. Treatment of agricultural wastewater in a combined tidal flow-downflow reed bed system. *Water Science & Technology* 40: 139-146.

Ter Heerdt G.J.J. and Drost H. 1994. Potential for the development of marsh vegetation from the seed bank after drawdown. *Biological Conservation* 67: 1-11.

Tikka P.M., Högmander H. and Koski P.S. 2001. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology* 16: 659-666.

Trombulak S.C. and Frissell C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18-30.

Tscharntke T. 1992. Fragmentation of *Phragmites* habitats, minimum viable population size, habitat suitability, and local extinction of moths, midges, flies, aphids, and birds. *Biological Conservation* 6: 530-535.

Tucker G.C. 1990. The genera of Arundinoideae (Gramineae) in the South-Eastern United States. *Journal of the Arnold Arboretum (Harvard University)* 71: 145-177.

Turner M.G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171-197.

Turner M.G., Gardner R.H. and O'Neil R.V. 2001. Landscape ecology in theory and practice. Springer-Verlag, New York, USA. 404 pp.

Twisk W., Noordervliet M.A.W. and ter Keurs W.J. 2003. The nature value of the ditch vegetation in peat areas in relation to farm management. *Aquatic Ecology* 37: 191-209.

U.S. Department of Agriculture 2003. Natural Resources Conservation Service. 2003, May 9. http://plants.usda.gov/.

Underwood E., Ustin S. and DiPietro D. 2003. Mapping nonnative plants using hyperspectral imagery. *Remote Sensing of Environment* 86: 150-161.

Urban D.L., O'Neil R.V. and Shugart H.H. 1987. Landscape ecology. *Bioscience* 37: 119-127.

Valta-Hulkkonen K., Pellikka P., Tanskanen H., Ustinov A. and Sandman A. 2003. Digital false colour aerial photographs for discrimination of aquatic macrophyte species. *Aquatic Botany* 75: 71-88.

Vankat J.L. and Roy D.G. 2002. Landscape invasibility by exotic species. *In* Gutzwiller K.J. (ed.) *Applying landscape ecology in biological conservation*, 171-191. Springer-Verlag, New York, USA.

Vézina L. 1989. Effet de la coupe, du travail du sol et du fractionnement des rhizomes sur la regénération du phragmites commun. *Phytoprotection* 70: 15-23.

Walton D.P. 2000. The impact of *Phragmites* on rare species and natural communities. *Phragmites in Virginia: A Management Symposium, Virginia Department of Conservation and Recreation, Division of Natural Heritage and The Chesapeake Bay Commission*, p. 5. Richmond, USA.

Warren R.S., Fell P.E., Grimsby J.L., Buck E.L., Rilling G.C. and Fertik R.A. 2001. Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within tidelands of the lower Connecticut River. *Estuaries* 24: 90-107.

Weaver J.E. 1960. Flood plain vegetation of the central Missouri Valley and contacts of woodland with prairie. *Ecological Monographs* 30: 37-64.

Weinstein M.P. and Balletto J.H. 1999. Does the common reed, *Phragmites australis*, affect essential fish habitat? *Estuaries* 22: 793-802.

Weis J.S. and Weis P. 2003. Is the invasion of the common reed, *Phragmites australis*, into tidal marshes of the eastern US an ecological disaster? *Marine Pollution Bulletin* 46: 816-820.

Weisser P.J. and Parsons R.J. 1981. Monitoring *P. australis* increases from 1937 to 1976 in the Siyai Lagoon (Natal, South Africa) by means of air photo interpretation. *Bothalia* 13: 553-556.

Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Wilcox D.A. 1989. Migration and control of purple loosestrife (*Lythrum salicaria*) along highway corridors. *Environmental Management* 13: 365-370.

Wilcox K.L., Petrie S.A., Maynard L.A. and Meyer S.W. 2003. Historical distribution and abundance of *Phragmites australis* at Long Point, Lake Erie, Ontario. *Journal of Great Lakes Research* 29: 664-680.

Wilson E.O. and Bossert W.H. 1971. A primer of population biology. Sinauer Associates Inc., Stanford, Connecticut, USA. 192 pp.

Windham L. and Lathrop R.G. 1999. Effects of *Phragmites australis* (common reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. *Estuaries* 22: 927-935.

With K.A. 2002. The Landscape Ecology of Invasive Spread. *Conservation Biology* 16: 1192-1203.

With K.A. and King A.W. 1999. Dispersal thresholds in fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14: 73-82.

Zedler J.B. and Kercher S. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* 23: 431-452.

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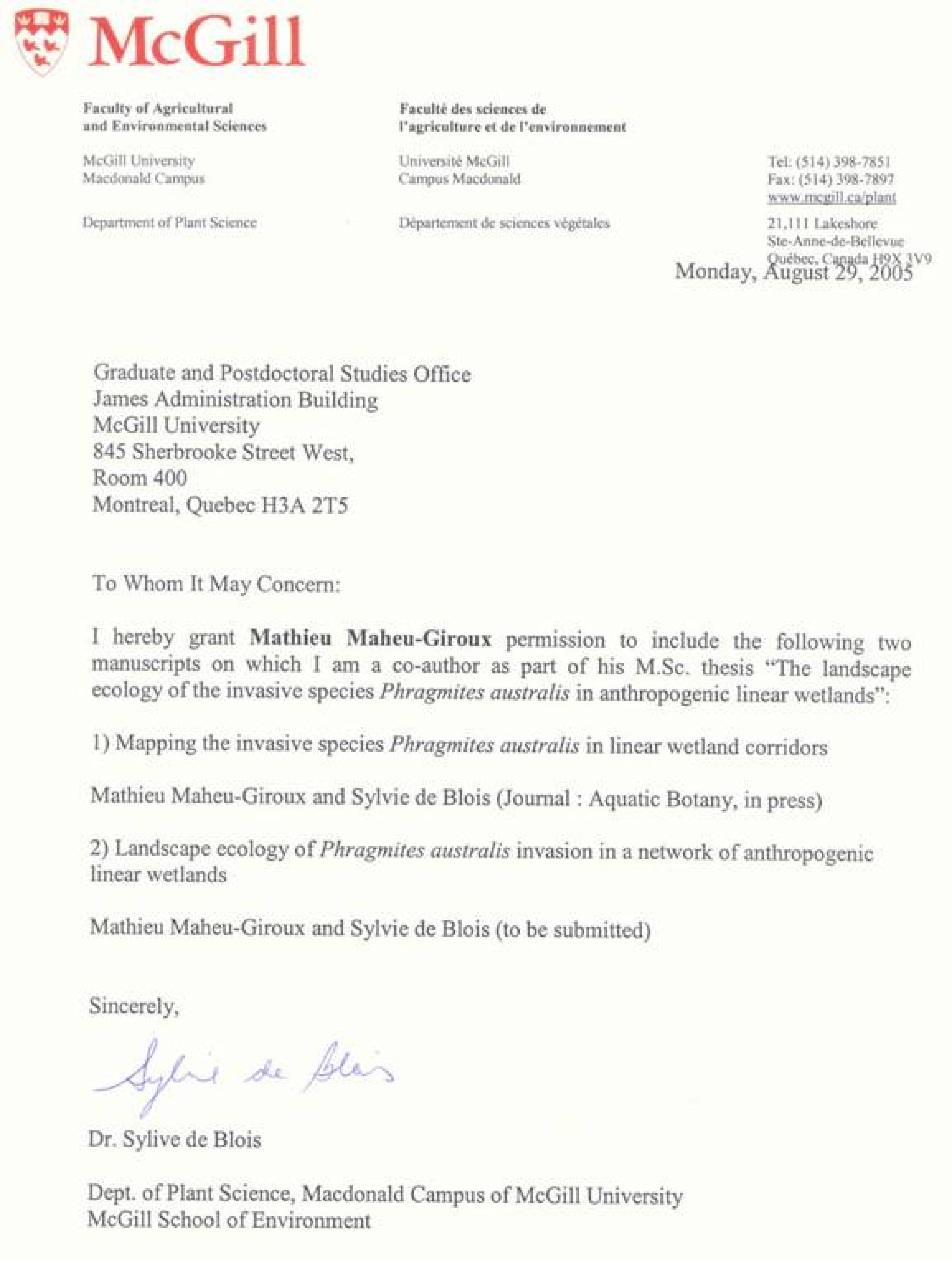

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I hereby grant **Mathieu Maheu-Giroux** permission to include the following two manuscripts on which I am a co-author as part of his M.Sc. thesis "The landscape ecology of the invasive species *Phragmites australis* in anthropogenic linear wetlands":

1) Mapping the invasive species *Phragmites australis* in linear wetland corridors

Mathieu Maheu-Giroux and Sylvie de Blois (Journal : Aquatic Botany, in press)

2) Landscape ecology of *Phragmites australis* invasion in a network of anthropogenic linear wetlands

Mathieu Maheu-Giroux and Sylvie de Blois (to be submitted)

Sincerely,

Sylvie de Blois

Dr. Sylive de Blois

Dept. of Plant Science, Macdonald Campus of McGill University
McGill School of Environment

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