Invasion dynamics of exotic and native common reed in freshwater wetlands

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February, 2011

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements of the degree of
Master of Science

Abstract

Genetic analyses at the regional scale suggest that native haplotypes of common reed *(Phragmites australis* (Cav.) Trin. ex Steud.) have been displaced by an introduced Eurasian haplotype (M). However, the outcomes of competitive interactions at the population level between these closely related plants are unknown, especially in freshwater wetlands. The research objective was to assess and compare the spatial and temporal dynamics of the exotic (M) and native (F) haplotypes in freshwater wetlands. Specifically, the expansion patterns of each haplotype (1) into adjacent plant communities, and (2) at the intersection between exotic and native populations, were monitored for three years in permanent plots in the Lake St-Francois National Wildlife Area, Quebec, Canada. Results showed that both haplotypes were progressing, but the densification rate of the exotic haplotype was higher, suggesting greater impact on invaded plant communities. Contrary to expectations, there was no clear evidence after three years that the exotic haplotype was displacing the native haplotype where they intersected.

Keywords: biological invasion, plant competition, community dynamics, conservation area, wildlife reserve, wetland, *Phragmites australis*.

Résumé

Des analyses génétiques à l'échelle du paysage indiquent que les haplotypes indigènes du roseau commun (*Phragmites australis* (Cav.) Trin. ex Steud.) sont menacés par un haplotype européen introduit. Cependant, les interactions compétitives entre les haplotypes introduit et indigène sont peu documentées à l'échelle des populations, en particulier dans les milieux humides d'eau douce. L'objectif du projet était d'évaluer la dynamique spatiale et temporelle des haplotypes exotique (M) et indigène (F) en milieu humide d'eau douce. Spécifiquement, l'expansion des haplotypes (1) dans les communautés végétales adjacentes, ainsi qu'à (2) la zone de contact entre des populations indigènes et exotiques, a été évaluée dans des placettes de surveillance dans la Réserve de Faune du Lac St-François, Québec, Canada. Les résultats indiquent que les deux haplotypes progressent dans les communautés adjacentes, l'exotique se densifiant cependant plus rapidement que l'indigène ce qui suggère un impact plus grand sur les communautés végétales envahies. Cependant, il n'y a pas d'évidence claire après trois ans que le roseau indigène soit déplacé par le roseau exotique aux zones de contact.

Mots-clés: invasion biologique, compétition végétale, dynamique des communautés, aires protégées, réserve de faune, milieu humide, *Phragmites australis*.

Acknowledgement

I would like to thank my supervisors, Dr. Sylvie de Blois and Jacques Brisson for their patience and for the time spent on improving my research project. I would like to acknowledge Dr. Pierre Legendre for his contribution and advices for my statistical analysis.

I also would like to thank my fellow lab mates; Chaeho, Dominic, Frieda, Laura, Nathalie, Paola and Sasha for their help in various aspects of this master's project, from field work to presentation preparation. Special thanks to Sophie Taddeo who has contributed greatly to the progress of my research. Her help with the field work, our frequent exchanges and the organization of multiple «activities» provided guidance in times of need. Thanks to Laura, Sasha and Brigitte for their help reviewing this work. Thanks to my life partner, Emilie Ricard, for her support and help in revising this project.

This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by Fonds Québecois de la Recherche sur la Nature et les Technologies (FQRNT). I would also like to acknowledge the Quebec Centre for Biodiversity Science (QCSB) for funding my trip and conference fees for the 24th International Congress for Conservation Biology.

Contributions

My supervisors, Dr Sylvie de Blois and Dr Jacques Brisson provided the research question and funding. I conducted field work at Lake St-François National Wildlife Area, collected floristic data, analyzed the data, interpreted the results, and wrote the thesis, including the first draft of the manuscript for which my supervisors provided advices and editing. I presented the results of this study at two international conferences, the 24th Conference of the International Congress for Conservation Biology and the 25th Conference of the International Association of Landscape Ecology, as well as at several *Phragmites* workshops and at the McGill Symposium on Environmental Research.

Table of Contents

List of figures

List of tables

Chapter 1 – Introduction

In Europe, *Phragmites australis* (Cav.) Trin. ex Steud. is often considered as an important ecological species because it provides habitat for various wildlife. Its other ecological functions (e.g., prevention of erosion, water filtration) are also very important. Decline of native European populations is of increasing concern (Koppitz, 1999; Kuhl *et al*., 1999). In contrast, *P. australis* is an aggressive species in North America where it is currently considered as a cryptic invader. While paleoecological evidence (Orson, 1999) indicates that the species has been in North America for thousands of years, the recent progression of *P. australis* in North America is attributed to an Eurasian haplotype (M) genetically distinct from indigenous ones (Saltonstall, 2002). The progression of this exotic haplotype is astonishing and the province of Quebec is no exception. Herbarium records (Delisle *et al*., 2003) as well as landscape studies have shown that this progression occurs especially along highway drainage ditches (Hudon *et al*., 2005; Lelong *et al*., 2007; Maheu-Giroux and De Blois, 2007). These micro-wetlands are associated with a high level of disturbance which provides the required conditions for *P. australis* to spread. The progression of this exotic haplotype is expected to be linked with the decrease of haplotype (F) which is native to North America.

The invasive success of the exotic haplotype in North America can be explained by a variety of factors. Enemy release could explain part of its success. Of the over 170 species of herbivores listed in Europe that consume *P. australis*, only 26 are present in North America (Tewksbury *et al*., 2002). In addition, most of the latter are introduced, meaning that in their new environment they are more likely to become generalist species (Liu and Stiling, 2006). Establishment of *P. australis* in North America is linked with development, roads and other human activities. Because this species tolerates a wide range of environmental conditions and thrives especially well in nitrogen-rich conditions, drainage ditches in Quebec provide an excellent opportunity to spread very quickly (Maheu-Giroux and De Blois, 2007). Being a tall heliophyte, the species is advantaged in competition for light. The exotic haplotype has an important above ground density that can go up to 200 stems/m^2 (Haslam, 1972). Furthermore, it modifies the environment by reducing micro-topography and raising soil elevation, creating a drier environment (Chambers *et al*., 1999; Zedler and Kercher, 2004). All these factors confer a competitive advantage to exotic *P. australis*.

Most plant-plant interactions reported in the literature are exposing the negative effect of *P. australis* on plant abundance and diversity. Invaded communities associated with *P. australis* tend to be lower in richness and composed of less desirable species (Lavoie *et al*., 2003; Zedler and Kercher, 2004). *Spartina* sp. and *P. australis* competition dynamics have been carefully studied in the United States. While *Spartina* sp. are said to slow down *P. australis* expansion in brackish wetlands, the latter shows greater success in sites with higher salinity or sites that are not flooded (Havens *et al*., 2003). Interactions with *Typha* spp. have also been quantified. In these interactions, *P. australis* shows a greater resistance to salt and a greater plasticity than *Typha* spp., which enables it to progress in road ditches and to occupy space previously occupied by *Typha* (Bellavance, 2007; Paradis, 2008). Similar competitive interactions can be expected between the exotic haplotype and the native haplotype of *P. australis*.

Invasion patterns of *P. australis* in Quebec's freshwater wetlands are not well documented. This could be problematic because this species seems to produce even more biomass in freshwater habitats (Rice *et al*., 2000). In addition, the presence of two haplotypes competing for similar resources and space makes it even harder to define those patterns. There is circumstantial evidence that the exotic haplotype of common reed could be responsible for the displacement of the native haplotype (Wilcox *et al*., 2003; Meadows and Saltonstall, 2009). Competitive interactions at the population level have not been documented, but understanding the outcome of these interactions is essential to explain invasion patterns at the landscape scale. In addition, direct comparison between communities invaded by the exotic haplotype and communities occupied by the native haplotype is lacking. Communities should be compared in order to assess the impact of a potential replacement of the native haplotypes of reed by the exotic haplotype in natural freshwater communities.

The overall research objective was to assess at the population level the spatial and temporal dynamics of the exotic (M) and native (F) haplotypes in freshwater wetlands. Specifically, the expansion patterns of each haplotype (1) into adjacent plant communities, and (2) at the intersection between exotic and native populations, were monitored for three years in permanent plots in the Lake St-Francois National Wildlife Area (NWA), Quebec, Canada. Since the native haplotype has been present in Quebec for centuries, it was hypothesized that the species would have filled its ecological niche. The native haplotype therefore was expected to show stable populations that do not suggest invasion dynamics into adjacent plant communities. On the other hand, the exotic haplotype has been recently introduced. It presents numerous characteristics required for an invader to be successful. It was hypothesized that populations of the exotic haplotype would present invasion dynamics, i.e., rapid expansion and densification into adjacent plant communities. In order to test these two hypotheses, 18 permanent monitoring plots were set up in plant communities bordering populations of exotic or native common reed. The abundance of *P. australis* in these plots, which was zero at first, was monitored each year for three consecutive years and then compared between the two haplotypes.

While progressing, we can assume that both haplotypes will eventually come into contact. Where they do, it was hypothesized that the two haplotypes would compete for space and that the exotic haplotype, being more invasive, would displace the native one. Moreover, the level of disturbances should favor the expansion of the exotic haplotype in freshwater wetlands. In order to evaluate each haplotype's competitive capacity, five monitoring transects centered at the zone of contact between five populations of each haplotype were used, and the density of stems of each haplotype was monitored along the transects over time.

Chapter 2 - Literature review

The common reed *(P. australis)* is a worldwide ranging plant species (Chambers *et al.*, 1999). It presents various ploidy levels with the tetraploid (4x) being the most widely distributed (Lambertini *et al.*, 2006). In Europe, restoration efforts have been put forward in order to preserve this declining species (Tscharntke, 1992). Multiple genetic studies showed the diversity of this species in both phenotype and genotype allowing it to occupy various environments with different levels of success (Neuhaus *et al.*, 1993; Koppitz, 1999; Kuhl *et al.*, 1999). *P. australis* is also present in North America and has been described as a native component. Fossilized rhizomes of the species were dated as being 3000 years old, indicating the long-term and native status of the species in North America (Orson, 1999).

More recently, *P. australis* has been described as a cryptic invader in North America, having both native and exotic haplotypes. Genetic studies of chloroplast DNA and nuclear satellite DNA showed that 11 different haplotypes were native to North America and two (M and I) were introduced. Haplotype M is European and is considered invasive and problematic in North America. Haplotype I is a Gulf haplotype and can be found in the south of the United States (Saltonstall, 2002, 2003). Field experiments have already shown that the exotic haplotype M spreads faster than the gulf haplotype leading to a possible displacement of the gulf haplotype (Howard *et al.*, 2008). The Eurasian haplotype M is responsible for the marked progression of the species and is known for its aggressiveness and competitive abilities. It is believed that this haplotype is able to out-compete many native wetland plants, as well as change ecosystem functions and diversity (Chambers *et al.*, 1999; Zedler and Kercher, 2004). Hence, this haplotype causes problems in wetland conservation in northeastern North America (Lavoie *et al.*, 2003). In the Great Lakes area, this haplotype is well established and, when present at a site, it is the dominant wetland species (Trebitz and Taylor, 2007).

In Quebec, the Eurasian haplotype M was probably introduced with cargo in the 18th century and seems to have started its spread in Quebec mainly from the Montreal region (Lavoie *et al*., 2003). Looking at the species' distribution over time, it is clear that its spread in Quebec coincides with the construction of the major roads, especially highways. Herbarium records as well as genetic studies show that it is the exotic haplotype that has spread (Delisle *et al*., 2003; Lelong *et al*., 2007; Jodoin *et al*., 2008). Highway ditches serve as propagation systems for invasive wetland plants, especially because they are nutrient-rich environments (Maheu-Giroux and De Blois, 2007). Currently, the northern distributional limit of *P. australis* in Quebec seems to be limited by climate.

Studies performed so far show that *P. australis* is capable of becoming a dominant species in multiple types of environments, such as salt marshes (Silliman and Bertness, 2004; Howard *et al*., 2008), oligohaline marshes (King *et al*., 2007; Meadows and Saltonstall, 2009), and freshwater marshes (Meyerson *et al*., 2000; Meadows and Saltonstall, 2009). Many studies deal with the effects of anthropogenic disturbances on reed performance (Havens *et al*., 2003; Alvarez-Cobelas *et al*., 2008; Lelong *et al*., 2009). However, there are few studies that deal with a natural freshwater system containing undisturbed and disturbed sites and native and exotic haplotypes of reed.

2.1 Invasion dynamics

The success of invasion relies on certain factors like the release from enemies, broad tolerance to environmental stresses, efficient use of nutrients, hybridization, and allelopathy. These are some of the possible explanations that provide insights on an invasive species' success (Galatowitsch *et al*., 1999; Zedler and Kercher, 2004).

2.1.1 Enemy release

Introduced species are usually less affected by herbivory. When an exotic plant species is introduced, only a limited number of native herbivores will feed on it while most of the introduced herbivores tend to be generalist species (Liu and Stiling, 2006). Of the over 170 species of herbivores listed in Europe that consume *P. australis*, only 26 are present in North America (Tewksbury *et al*., 2002). In addition, it is unknown whether these 26 species of herbivores are specific to the introduced haplotype of *P. australis* in North America. In fact, knowledge of how specific pests are to *P. australis* in North America is fragmented. *Lepidopterans rhizedra* (native), *Phragmataecia castaneae*, *Chilo phragmitella*, and *Schoenobius gigantella* all feed on the rhizomes of *P. australis* (Tewksbury *et al*., 2002). Other species, such as *Platycephala planifrons*, are known to feed on its stem in Europe (Tewksbury *et al*., 2002). *Puccinia isiacae* of Saudi Arabia also specifically affects *P. australis* (Baka, 2004) but the fungus has not been observed in North America.

2.1.2 Tolerance to environmental stresses

The invasive *P. australis* is favored by human activities and takes advantage of perturbations (Havens *et al*., 2003; Hershner and Havens, 2008; Howard *et al*., 2008; Meadows and Saltonstall, 2009). A recent study showed that the exotic reed becomes particularly abundant in wetlands bordered by at least 15% developed areas (King *et al*., 2007). In another study, transportation and development infrastructures were able to explain 92% of its presence (Havens *et al*., 2003). Distance to roads is another important factor positively correlated to the presence of reed in some studies (Arzandeh and Wang, 2003; Lelong *et al*., 2009) as large road corridors contribute to a longer photoperiod. Common reed also presents a good tolerance to multiple natural stresses, such as hydric stress, high salinity, and high pollutant concentration (Guo *et al*., 2003; Hershner and Havens, 2008; Morris *et al*., 2008). It progresses better under low salinity conditions (Silliman and Bertness, 2004), but can survive in salinity levels of 35 g/L (Adams and Bate, 1999). This is possibly due to the very selective and efficient barrier created in the root structure (Soukup *et al*., 2006). Uptake of toxic metals, such as mercury, chrome and lead, is lower in *P. australis* than in *Spartina alterniflora*, which confirms the selective capacity of its roots (Windham *et al*., 2003). It is also capable of invading habitats of variable pH and organic matter content (Haslam, 1972; Alvarez *et al*., 2005; Lambert and Casagrande, 2006). In Europe, colonies of *P. australis* are not always easily predicted by environmental variables or flooding patterns, but natural perturbations seem to increase reed survival (Alvarez-Cobelas *et al*., 2008).

2.1.3 Nitrogen status

Nitrogen-rich conditions create optimal conditions for the growth of *P. australis* as it is able to produce more biomass (Bertness *et al.*, 2002; Rickey and Anderson, 2004). Nitrogen enrichment could be caused by human disturbances (such as roads and proximity to residential or agricultural areas). Combined effects of increased nitrogen availability and human disturbances were able to explain 90% of variation in *P. australis* distribution in Rhode Island (Minchinton and Bertness, 2003). In another study, nitrogen availability alone was able to explain 50% of the variation in *P. australis* abundance. The model explained 80% of the variation when both salinity and available nitrogen were taken into account (Silliman and Bertness, 2004). Nitrogen is a limiting nutrient in the case of *P. australis*; its invasion success is maximized where availability of this nutrient is highest, primarily near agricultural fields (Trebitz and Taylor, 2007).

2.1.4 Hybridization

Genetic studies show that cross hybridization, i.e., hybridization between individuals belonging to the same haplotype or subspecies, contributes more to the spread of the haplotype M in Quebec than previously thought (Belzile *et al.*, 2009). It results in higher genetic diversity and possibly adaptability which in turn could promote the invasiveness of the introduced species. Hybrids are intermediates between parents and can be more resistant or better adapted to a particular environment as well as more competitive. Moreover, multiple introductions of species increase the genetic diversity of the invader, and the likelihood of cross-hybridization, and is frequently the cause of invasive hybrid progression (Ellstrand and Schierenbeck, 2000). At the species level, a case study of the invasive tree species *Ulmus pumila* showed high frequency of hybridization and even introgression with native tree species *Ulmus rubra* (Zalapa *et al.*, 2010).

Intraspecific hybridization between a native and introduced haplotype of *P. australis* has been successful in a greenhouse experiment (Meyerson *et al.*, 2009), but only one very recent genetic study, based on field sampling in the Great Lakes area, suggests that hybrids can be found in nature (Paul *et al.*, 2010). This could be due to the fact that seedlings are rarely seen in field studies (Stanton, 2005) or simply do not survive (Shay and Shay, 1986). Furthermore, it would appear that both haplotypes could produce intraspecific hybrid seeds, a phenomenon that was not observed in the previously mentioned greenhouse experiment (Paul *et al.*, 2010).

2.1.5 Allelopathy

Allelopathic chemicals are naturally occurring compounds produced by an organism that can inhibit the growth of one or more of its neighbors. Examples of such processes are known (Callaway and Ridenour, 2004); successful use by introduced plants confirms the importance of the "novel weapon" hypothesis in competition and invasion ecology. For example, introduced *Centaurea maculosa* produces a chemical, racemic catechin, that reduces the growth and germination rate of three native plants of North America: *Festuca idahoensis*, *Koeleria micrantha,* and *Arabidopsis thaliana* (Bais *et al.*, 2003). Another documented example is the case of *Allaria petiolata*. The chemicals produced by this plant species interfere with mycorrhizal fungi decreasing the diversity of fungi and reducing plant growth and survival of seedlings (Callaway *et al.*, 2008). A recent laboratory study showed the potential allelopathic capacity of *P. australis* in the rhizosphere. Rhizomes of *P. australis* release gallic acid interfering with the structural proteins of roots of other plants (Rudrappa *et al.*, 2009). This acid is more efficient when transformed into mesoxalic acid due to exposure to UV in an alkaline soil. This could provide an additional tool for *P. australis* expansion into freshwater wetlands.

2.1.6 Competition for space

Asexual reproduction plays an important role in the invasion success of *P. australis*. This species can expand in all directions with the aid of rhizomes and runners (Warren *et al.*, 2001). Progression is usually rapid and creates a large, dense colony of reed possibly leading to monocultures (Zedler and Kercher, 2004). Those monocultures can be very dense colonies (up to 200 stems/m^2) and are capable of modifying certain trophic structures and, possibly, hydrological regimes (Haslam, 1972; Chambers *et al.*, 1999). In addition, studies have shown that there is an important interaction between the level of available nutrients and the removal of cover for other species. In fact, high levels of available nutrients increase all growth parameters (height, biomass) and most expansion parameters (height and biomass of advancing stems) (Minchinton and Bertness, 2003). Being one of the highest macrophytes confers this species an advantage in the competition for light. Moreover, slower litter decomposition has been shown to cause an increase of marsh elevation, the filling of small creeks and slower decomposition rate of cellulose which ultimately leads to a simplification of the marsh macro-relief (Zedler and Kercher, 2004; Stanton, 2005). Also, the fact that dead stems from the previous year tend to take a long time to decompose contributes to a drier soil that is better suited for the growth of reed. In fact, reed growth performances are higher when the level of water is low. In the Boucherville islands area, vegetative growth was greatly enhanced in the 1999-2002 time period where the mean water level was 5.72 m compared to vegetative growth of the 1996-1999 time period where the mean water level was 6.51 m (Hudon *et al.*, 2005). Annual progression speed of rhizomes in the literature varies: 0.1 m - 0.94 m (Burdick and Konisky, 2003), 0.52 m - 0.91 m (Philipp and Field, 2005), 1 m (Haslam, 1972), 0.8 m - 1.2 m (Lavoie *et al.*, 2003), 1.6 m - 2 m (Warren *et al.*, 2001) and runners can go as far as 10 m (Haslam, 1972; Rice *et al.*, 2000). Vegetative growth can be very important and this species will take advantage of any canopy opening (Zedler and Kercher, 2004).

Sexual reproduction provides opportunities for further spread, when conditions permit it. However, seed viability is low (3-7%) for the exotic haplotype (Gervais *et al.*, 1993; Maheu-Giroux and De Blois, 2007) and seedlings have been historically rarely reported in Canada. This could be attributed to the effect of low temperatures (Brisson *et al.*, 2008), shading by other plants (Havens *et al.*, 2003) or to high salinity in areas where seeds could be found (Bart and Hartman, 2003). Germination of *P. australis* seeds usually occurs in exposed areas as they are not good competitors at that stage (Stanton, 2005; Kettenring and Whigham, 2009). For example, in Manitoba, seedlings were observed but did not survive through to the next growing season (Shay and Shay, 1986). It was also recorded that this species is not an important component of the seed bank there. In addition, mature seeds could be in a state of dormancy, preventing their germination (Kettenring and Whigham, 2009). Higher temperatures, like those predicted by global warming, could mean that more seeds would germinate hence creating new opportunities for dispersal (Brisson *et al.*, 2008). A recent study shows that seed propagation could be an important vector in long range dispersal of the exotic haplotype (Belzile *et al.*, 2009). The species, which is already difficult to control as it is, is becoming even more efficient at spreading.

2.1.7 Species limiting factors

Although this species presents various tolerances and characteristics that favor it in competitive interactions, there are also factors that limit its spread. Water depth is a particularly good indicator of suitable habitat for *P. australis*. This species is restrained when the water level goes up for long periods; over 0.5 m of water, it will not be able to establish unless water level fluctuations occur. Once established in a given area, if the water level was to rise above 1 m of water, the population would not survive more than 3 years. In similar conditions, most of the well established individuals will already be dead after 2 years (Shay *et al.*, 1999). It is intolerant to prolonged flooding (Haslam, 1972; Warren *et al.*, 2001) and its cover is reduced when subjected to 100 days or more of flooding per year (Hudon *et al.*, 2005). Poor performance of *P. australis* in those limiting conditions is probably due to limited dissolved oxygen in the water when the water level rises (Amsberry *et al.*, 2000). Further, it was suggested that frost slows its progression (Jodoin *et al.*, 2008) while severe frost would kill the rhizomes (Haslam, 1972). Cold winter conditions limit expansion of *P. australis*, particularly at its northern limit in Quebec. Climate warming may alleviate some of these pressures. Lastly, it will not grow where light is limited or where light intensity is low due to shading by other plants (Shay *et al.*, 1999). For this reason, forested areas act as a particularly good barrier by limiting light intrusion in the system and providing underground competition for resources (Lelong *et al.*, 2009). Of course, it is also slowed by some other plant species like *Typha* sp. or *Spartina* sp. due to interspecific competitive interactions for resources (Amsberry *et al.*, 2000).

2.2 Impacts

2.2.1 Effect of *Phragmites* on the environment

At a large scale, *P. australis* seems to diminish overall biodiversity (Chambers *et al.*, 1999; Meyerson *et al.*, 2000; Bertness *et al.*, 2002). Studies on impacts of *P. australis* on invertebrates are numerous. Nektonic communities do not seem to be affected much by the floral shift as *P. australis* can also be used as food (Meyer *et al.*, 2001; Hanson *et al.*, 2002; Posey *et al.*, 2003; Weis and Weis, 2003). Stem epifaunal specialists are less abundant in *P. australis* dominated marshes compared to *Spartina alterniflora* dominated marshes (Weis and Weis, 2003). In addition, *P. australis* affects arthropod communities by removing the herbivores modifying species composition (Gratton and Denno, 2006). Insect communities are less diverse and species richness is lowered (Weis and Weis, 2003; Robertson and Weis, 2005), but herbicide spraying seems to restore *Odonata* and *Gastropoda* abundance (Kulesza *et al.*, 2008). Studies showed that *P. australis* seems to have a negative influence on larval and small fish survival, especially mummichog larvae (Weinstein and Balletto, 1999; Able and Ragan, 2000; Weis and Weis, 2003; Hunter *et al.*, 2006). Other fish species such as *Anguilla rostrata* or *Morone americana* are more abundant in *P. australis* dominated marshes (Warren *et al.*, 2001). One possibility is that these two species feed similarly in *P. australis* dominated marshes and in *Spartina* dominated marshes while other fish species would not. As for birds, it seems that common reed is used by some bird species for nesting while others are excluded from invaded areas (Parsons, 2003). Specialists of short vegetation marshes, such as Seaside sparrow or Saltmarsh sharp-tailed sparrow, are negatively affected by the invasion of *P. australis*. Conversely, species like Swamp sparrow that like tall vegetation, are favored by reed invasion of marshes. When comparing *Typha* sp. dominated marshes and *Phragmites* sp. dominated marshes, bird diversity is similar. Only one species, Virginia rail, was strongly correlated to the presence of *Typha* (Benoit and Askins, 1999). Algal diversity is also affected by the conversion of marshes into *P. australis* dominated marshes. *Enteromorpha* sp. and *Vaucheria* sp. are less abundant but diversity is restored after herbicide spraying (Warren *et al.*, 2001; Kulesza *et al.*, 2008).

Many case studies of *P. australis* regarding the effect on biodiversity compare communities where *Spartina* spp., *Typha* spp. or *Juncus gerardii* are the dominant plants, but non dominant plant species are also affected. Plant richness is highest in areas where *P. australis* is not present (Warren *et al.*, 2001). When present, *P. australis* is associated with other species of low conservation value (Zedler and Kercher, 2004). Available space for other plant species is limited by *P. australis*; therefore its stem abundance can be a good indicator of wetland diversity and can be used to evaluate other species' abundance. In a European study, this variable was able to explain 64% of the variation in wetland species abundance (Lenssen *et al.*, 2000). Cover patterns are also interesting. When this species is dominant, overall site diversity is minimal. When it is partially dominant, diversity is maximized, possibly due to the addition of opportunistic species to the communities. When absent, the diversity value is medium (Tulbure *et al.*, 2007). When comparing plant richness of plant communities, areas invaded by *P. australis* show the lowest richness when compared with other invasive species (*Lythrum salicaria*) or other native macrophytes (*Typha* sp.). Flood regimes, zonation and human influences may also have impacted on the richness of these communities (McGlynn, 2007). Invasion usually occurs in marshes dominated by short plants like small sedge or grass species and tends to be slowed or stopped by forested areas (Wilcox *et al.*, 2003). It has been shown that scrubs and tree seedlings (*Acer rubrum*, *Liquidambar styraciflua*, *Fraxinus pennsylvanica*, *Baccharis halimifolia*, *Iva fructescens,* and *Myrica cerifera*) can displace *P. australis* (Havens *et al.*, 2003). Thus, *P. australis* could act as an ecological engineer, creating new floating islands and replacing short grass to ultimately be displaced by scrubs and tree species. The capacity of *P. australis* to elevate its environment and dry the ground may provide the stepping stone between low marsh and forested marshes (Esselink *et al.*, 2002).

2.2.2 Specific *Phragmites*-plant interactions

More specific plant-plant interactions have been described. *Polygonum punctatum*, *Impatiens capensis*, *Sagittaria latifolia*, and *Peltandra virginica* have been found coexisting in plots with *P. australis*, but also with *Typha* spp. and *Lythrum salicaria* in brackish environments (McGlynn, 2007). One study reports that it is responsible for the displacement of two species: *Atriplex patula* var. *hastata* and *Solidago sempervirens* also in brackish environments (Minchinton *et al.*, 2006). *Panicum virginatum* can coexist with *P. australis* but its cover value has not been documented to exceed 20% in brackish water (Warren *et al.*, 2001). *Juncus gerardii* is also displaced by this species; while coexistence is rare, it has been recorded as able to occupy up to approximately 20% of the cover when it occurs in conjunction with *P. australis* (Warren *et al.*, 2001; Silliman and Bertness, 2004; Minchinton *et al.*, 2006). In some instances, surveys indicate that this species is able to slow *P. australis* progression (Amsberry *et al.*, 2000; Minchinton and Bertness, 2003). In freshwater, *Bidens cernua* was excluded while the abundances of *Sagittaria latifolia*, *Impatiens capensis,* and *Schoenoplectus tabarnaemontani* were considerably reduced. Richness and evenness remained similar between both samplings of that study (2001-2004) and similarity between the communities was 18.9% (Jaccard index) suggesting a major community structural shift due to the progression of both *P. australis* and *Typha* sp. (Tulbure *et al.*, 2007). *Carex aquatilis* and *Myrica gale* are less abundant in freshwater plots dominated by *P. australis* (Richburg *et al.*, 2001). *Lythrum salicaria* dominated communities have a higher richness. In addition, *Lythrum salicaria* density was found to be similar in communities it dominates and communities dominated by *P. australis* (Keller, 2000). However, these were static observations and do not provide insights on community alteration mechanisms.

Reed is slowed by *Spartina alterniflora* and *S. patens* in low marsh habitats (progression of only 5 cm per year compared to 30 cm in high marsh habitats) undergoing daily flooding, creating a lack of dissolved oxygen (Windham, 1999; Amsberry *et al.*, 2000; Minchinton and Bertness, 2003; Rickey and Anderson, 2004).

However, coexistence with *P. australis* was reported to be limiting *S. alterniflora* cover at 20% (Warren *et al.*, 2001). Furthermore, there is cartographic evidence of displacement of *Spartina* sp. (Havens *et al.*, 2003). In nitrogen-rich conditions (15 mg/L), *P. australis* performs better than *S. alterniflora* (Ravit *et al.*, 2007). Because nitrogen demand is lower for *Spartina* sp., the increase in availability favors *P. australis* and stimulates more of its growth (Meyerson *et al.*, 2000). Drained conditions with high levels of available nitrogen will further favor rhizomal growth of *P. australis* (Ravit *et al.*, 2007). Rhizotoxicity caused by mesoxalic acid (UV degraded gallic acid produced by *P. australis*) could also partly explain the competitive advantage of *P. australis* (Rudrappa *et al.*, 2009). Both *P. australis* and *S. alterniflora* are used as food by local fauna (Weis and Weis, 2003). In this case, the levels of water and salinity would most likely be the most limiting factors for *P. australis*.

Typha spp. are usually associated with communities that have a higher plant diversity in comparison to communities with *P. australis* (Keller, 2000; McGlynn, 2007). Some functions in the ecosystem are relatively similar between the two community types. Nesting birds and macro-invertebrate fauna are comparable (Benoit and Askins, 1999; Kulesza *et al.*, 2008). *Typha* spp. prefer organic soil to silty soil which is the opposite of *P. australis* soil requirements (Tulbure *et al.*, 2007). When comparing both species in a constant inundation condition*, Typha* shows a biomass 56% higher than *P. australis* (Boers and Zedler, 2008). Progression of *P. australis* in *Typha* spp. communities was observed (Arzandeh and Wang, 2003). In fact, *P. australis* shows a very particular spatial distribution when in contact with *Typha* spp. The number of shoots ranges from none to an almost saturated value at the zone of contact (Keller, 2000). In low marshes, when both species are present, *P. australis'* stem density is lower than *Typha's* (Amsberry *et al.*, 2000). In drainage ditches, *P. australis* also usually creates denser colonies than *Typha* spp.. When in competition for space, both species' biomass is reduced but *P. australis* shows a higher level of phenotypic plasticity, enabling it to invade different environments more easily than *Typha* spp. (Bellavance, 2007). While salinity levels of 6 g/L NaCl allows it to perform better than *Typha* spp. (Paradis, 2008), invasion rates of *P. australis* in *Typha* communities are higher when water levels are stable (Coops and Van

Der Velde, 1995). Here again, the water level and stress tolerance are of prime importance in *P. australis* invasion success.

2.3 Two haplotypes in Quebec

In Quebec, two haplotypes of *Phragmites australis* are present: an exotic haplotype (also known as *Phragmites australis subsp. australis*) and a native haplotype (also known as *Phragmites australis subsp. americanus*). Genetic studies have shown that many haplotypes of this plant can be found in North America (Saltonstall, 2002, 2003; Howard *et al.*, 2008). It would appear that there is only one exotic haplotype, haplotype M, and one native haplotype in Quebec, haplotype F (Saltonstall, 2002). Although *Phragmites australis* subsp. *australis* (exotic) and *Phragmites australis* subsp. *americanus* (native) are the same species, they have been recognized as distinct subspecies (Saltonstall *et al.*, 2004), and some traits are different and have been identified. Mainly, the lengths of the ligule, glumes and lemnas are significantly longer for the exotic haplotype. In Quebec, the native haplotype is characterized by a red stem and ligule base and there are fewer hairs on the ligule than on the ligule of the exotic haplotype. The inflorescence of the native haplotype is less dense, containing fewer seeds (Blossey, 2002; Saltonstall *et al.*, 2004).

Although their environmental requirements are generally similar, the exotic haplotype performs better than the native haplotype under high salinity. In a greenhouse experiment, the exotic haplotype survived in concentrations as high as 0.4M NaCl while the native haplotype did not survive past 0.13M NaCl (Vasquez *et al.*, 2005). The exotic haplotype is frequently associated with roads and other disturbances while the native haplotype seems to prefer undisturbed habitats (Lambert and Casagrande, 2006; Jodoin *et al.*, 2008; Meadows and Saltonstall, 2009). Water level is another important indicator since the native haplotype seems to have a higher tolerance to high water levels, when compared to the exotic haplotype (Yulan *et al.*, 2008; Meadows and Saltonstall, 2009). It is believed that their growth dynamics differ (Hanson *et al.*, 2002). It has been shown that the colonies of the exotic haplotype have higher above and below ground biomass, especially under nutrient-rich conditions (Saltonstall and Stevenson, 2007). The exotic haplotype has higher shoot height, shoot fresh weight, leaf fresh weight, and leaf cover (League *et al.*, 2006; Meadows and Saltonstall, 2009). Furthermore, the exotic haplotype develops a larger total leaf area and is more efficient in photosynthesizing, partly because it contains twice the amount of chlorophyll. When a large amount of light is available, photosynthesis is 51% more efficient in this haplotype. This also implies that it has lower water use efficiency and higher demands in total nitrogen in order to produce its maximal canopy cover. When compared to the exotic haplotype, the native haplotype appears most efficient in terms of resource use (Packett and Chambers, 2006; Mozdzer and Zieman, 2010). Nitrogen availability could be a major factor in defining the most efficient haplotype in spatial interactions.

According to herbarium data from 1910 to 1960, distribution of the native reed seems to be stable, possibly because its ecological niche has been filled. This is not the case for the exotic reed which is in continual expansion (Lavoie *et al.*, 2003; Jodoin *et al.*, 2008; Meadows and Saltonstall, 2009). Since the discovery of the native haplotype is relatively recent (Saltonstall, 2002), some earlier studies may have been unable to distinguish among the two haplotypes.

Some of the direct impacts of the invasive *P. australis* haplotype on its native counterpart include the following:

1) The invasive haplotype could exclude its native counterpart by out-competing it. Competition for similar ecological niches could drive the native reed to local extirpation or extinction. Herbarium data and surveys already reveal that the native reed may be abundant locally, but it is rare at a large scale (Saltonstall, 2002; Meyerson, 2007; Meyerson *et al.*, 2009). A study that investigates the interaction between both haplotypes is needed in order to assess whether the exotic haplotype displaces the native haplotype at the population level.

2) The native haplotype could out-compete the invasive one in the absence of disturbances and where its populations are well established and stable. Given the aggressive character and plasticity of the invasive type, this appears unlikely.

3) Co-existence of both haplotypes, but at reduced density for both, could be possible where they co-occur.

This system (exotic vs. native haplotype) provides a very interesting and unique model for understanding the dynamics that underlie invasive species' impacts on plant communities. A fine scale study could prove to be an efficient way to understand the dynamics of invasiveness and the effects caused by the replacement of a native subspecies by an exotic subspecies.

2.4 Presence of reed in the study area

The chosen study area is located in southern Quebec, near the border with the United States. It is located within the National Wildlife Area (NWA) of Lake St-François. This particular area is a remarkable wetland surrounded by agricultural fields. It provides sites that have been long disturbed by human activities, habitats that were disturbed in a recent past due to infrastructural work, sites that are not disturbed and far from agricultural lands, zones of contact where both haplotypes meet, and areas where populations of each haplotype are separated. Furthermore, the NWA is not yet entirely invaded by either haplotype of reed. Hence, it will be possible to assess invasion patterns of reed and to estimate its possible impact over time on plant communities. Currently, *P. australis* is at its northern limit of distribution in Quebec and the invasion is relatively recent in the NWA. It was observed that *P. australis* was dominant when present in emergent communities bordering islands (99.9% of dry material), but only accounted for 10.9% of the total meadow biomass (Auclair *et al.*, 1973). It is likely that the latter populations were of the native type (field obs.). In addition, a vegetation survey in the NWA done in 1993 does not mention the presence of *P. australis,* which suggests that at that time it was most likely either not yet an important or apparent component of the marsh (Jean and Bouchard, 1993).

Chapter 3 - Invasion dynamics and competitive interactions between native and exotic common reed (*Phragmites australis*) in a freshwater wetland*

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Abstract

Common reed *(Phragmites australis* (Cav.) Trin. ex Steud.) is a very efficient wetland invader. An introduced Eurasian haplotype (M) is responsible for the marked progression of the plant in North America and has several negative impacts on wetland biodiversity. Genetic analyses at the regional scale suggest that native haplotypes have been largely displaced by the exotic one, but there is still no direct evidence, at the population level, of the outcome of their competitive interactions. The research objective was to assess and compare the spatial and temporal dynamics of the exotic (M) and native (F) haplotypes in freshwater wetlands. Specifically, the expansion patterns of each haplotype (1) into adjacent plant communities, and (2) at the intersection between exotic and native populations, were monitored and compared in permanent plots located in the Lake St-Francois National Wildlife Area, Quebec, Canada. Results showed that both haplotypes were progressing, but the densification rate of the exotic haplotype was higher, suggesting greater impact on invaded communities. After three years, the exotic haplotype of reed was not clearly out-competing the native haplotype where they intersected, but further monitoring will be necessary to confirm the observed trends.

*Manuscript for submission to *Biological Invasions*.

3.1 Introduction

There are few, if any, recent documented cases of the extinction of a native plant species by an introduced plant. Examples of local plant extirpation abound and can be, among other causes, the result of direct competitive displacement by an invasive plant (Tulbure *et al.*, 2007) or indirect changes to the ecosystem that are detrimental to the native species (Chambers *et al.*, 1999; Zedler and Kercher, 2004). For instance, the tall macrophyte *Phragmites australis* (Cav.) Trin. ex Steud. is recognized as one of the most aggressive invaders of North American wetlands. It has been shown to displace *Spartina alterniflora* (Havens *et al.*, 2003) or *Typha* spp. (Arzandeh and Wang, 2003) in native or anthropogenic habitats. Ecological theory suggests that the intensity of such competitive interactions between native and introduced plants should be even stronger, with potentially greater impact on the native flora, if the interaction involves closely phylogenetically related plants that share similar traits and ecological requirements. Numerous examples of such interactions exist in the literature; sugar maple (*Acer saccharum*) and Norway maple (*Acer platanoides*) in North-eastern American forest (Wangen *et al.*, 2006), slippery elm (*Ulmus rubra*) and Siberian elm (*Ulmus pumila*) in American forest (Zalapa *et al.*, 2010), small cordgrass (*Spartina maritima*) and smooth cordgrass (*Spartina alterniflora,* native to North America) in British Isles' wetlands (Robb *et al.*, 2008), etc. Such strong interactions may lead to the introgression of the exotic species' traits into the local flora if interspecific hybridization is possible (Ellstrand and Schierenbeck, 2000; Zalapa *et al.*, 2010) and/or, in the long term, possibly to the near-extinction of the native plant (or genotype) if it ends up being displaced from most of its natural refuges by the newly introduced competitor.

The case of *P. australis* in North-east America illustrates well the challenges of understanding and managing plant invasion when congeners are involved. Paleoecological evidence confirms that the species is part of the post-glacial wetland flora of North America (Orson, 1999) and has probably been isolated from its congeners in Eurasia for thousands of years. Recent analyses have identified lineages in North America genetically and morphologically distinct from European or Asian ones but also the presence in North America of a recently introduced haplotype which is highly invasive (Saltonstall, 2002). The progression of this haplotype in North America has been remarkable particularly along coastal wetlands (Chambers *et al.*, 1999) and linear habitats such as roadsides or agricultural ditches, which serve as invasion corridors (Hudon *et al.*, 2005; Lelong *et al.*, 2007; Maheu-Giroux and De Blois, 2007). Progression of this species is usually rapid and creates vast, very dense mono-specific stands. Several studies comparing plant communities with and without *P. australis* have shown lower species richness and less desirable species (Lavoie *et al.*, 2003; Zedler and Kercher, 2004), as well as modified environments with reduced micro-topography and higher soil elevation in communities with *P. australis* (Chambers *et al.*, 1999; Zedler and Kercher, 2004). Yet, processes by which *P. australis* invades are still not well studied. Understanding the invasion patterns of *P. australis* in wetlands would require population-level studies and continued monitoring that could link the effects of this species' progression in wetlands with the decline of plant species' abundance and diversity.

If the impact of the introduced haplotype on the native fauna and flora appears significant for wetland biodiversity, the interaction with its native counterpart has been much less documented. A few studies have suggested that the exotic haplotype has been replacing the native one, but the evidence is largely indirect and based either on the relative proportion of the exotic and invasive types in historical herbarium records (Delisle *et al.*, 2003), on the observation that there are much fewer native plants collected than there are introduced ones, or on remote sensing studies showing that the introduced haplotype is occupying more space over time, leaving less available space for the native haplotype (Wilcox *et al.*, 2003; Meadows and Saltonstall, 2009). Expansion patterns at the population level for the two types of reed are just beginning to be documented and compared, and the effects of the exotic haplotype on the abundance of the native haplotype have not been quantified. Direct comparisons between communities invaded by the exotic haplotype and communities occupied by the native haplotype are also lacking. Such *in situ* observations are important to understand the fundamental dynamics of closely related plant species, one native and one invasive exotic, and therefore to quantify better their relative impact on associated plant communities and ecosystems. The presence of a native congener also greatly complicates management strategies where the two types coexist, and it is therefore essential to understand their dynamics to derive better options for conservation and control.

In this study, the spatial and temporal dynamics of the exotic (M) and native (F) haplotypes were assessed for over three years in a freshwater federally-protected wetland of southern Quebec, Canada, that may serve as one of the rare refuges for the native *P. australis*. More specifically, 1) expansion patterns of populations of each haplotype into adjacent plant communities were evaluated and compared, and 2) the outcome of competition for space where populations of the two haplotypes meet was determined. Since the native reed appears to have been present in the area historically, it was hypothesized that its population patches would be relatively stable, with little expansion of clonal patches into adjacent populations. On the other hand, the exotic haplotype having been recently introduced, rapid expansion of clonal patches into the bordering communities with time was expected. At the contact zone between colonies of the native and exotic type, it was expected that the exotic type, being more aggressive, would progressively expand over time, with a concomitant decline in the abundance of the native type. It is acknowledged from the onset that a definitive conclusion about the outcome of competitive interactions between the two haplotypes would require more years of observation than what is presented here, nevertheless these results are presented as a useful first approximation for further studies.

3.2 Methodology

3.2.1 Study area

Located between Cornwall, Ontario (45° 01' N , 74° 45' O) and Salaberry-de-Valleyfield, Quebec (45° 15' N , 74° 08' O), Lake Saint-François is a natural enlargement of the St-Lawrence River hydrological system. Its riverine wetlands are among the largest between Montreal and the Great Lakes. The study area is located at the Lake Saint-François National Wildlife Area (NWA) (45° 01' N, 74° 30' O) on the south shore of

Lake Saint-François at the border between the state of New York, USA, and the province of Quebec, Canada (Figure 3.1). Average annual temperature in the region is 6.5°C and average annual precipitation is 944.8 mm (Environnement Canada, 2009). The Lake Saint-François NWA comprises 1347 hectares of federally-protected land since 1978 (Ministère du développement durable de l'environnement et des parcs du Québec, 2009) and is within the St-Lawrence Lowland ecoregion (Ministère des ressources naturelles, 2003). In 1987, it was conferred a RAMSAR status as a remarkable wetland of the world and one of the last large remaining expanses of freshwater wetlands in the agricultural south of Quebec. It is surrounded by agricultural land with corn fields or wet meadows and low-density housing (Maheu-Giroux *et al.*, 2006). The NWA comprises several community types, including swamps dominated by shrubs such as *Alnus incana* ssp. *rugosa* (considered invasive), low marsh dominated by *Carex* spp., *Sparganium eurycarpum,* and *Typha* spp., high marsh dominated by *Carex* spp., wet prairies, upland forest, and aquatic plant communities (Létourneau and Jean, 2006).

Although protected, the ecosystems of the Lake Saint-François NWA, as most wetlands around the world, have been under increased pressure from human activities. First, the modification of the natural hydrological regime of Lake Saint-François between 1940 and 1970 through dams for various purposes has resulted in an overall increase of the water level, stabilization of mean water level at 46.6 cm (Auclair *et al.*, 1973) and a relative stabilization of annual variation in water level compared to previous conditions (from circa 50 cm to no more than 15 cm; Environment Canada, 2009). Second, man-made fires have been occurring in the NWA up to the 1970's, as evidenced by field observation and the analysis of aerial photographs (Auclair *et al.*, 1973; Jean and Bouchard, 1993; Maheu-Giroux *et al.*, 2006). With the cessation of fires, large areas of the NWA dominated by *Carex spp*. marsh have been invaded by *Alnus incana* ssp. *rugosa* (Jean and Bouchard, 1991). Third, agricultural activities around the NWA have greatly intensified in the last four decades (Maheu-Giroux *et al.*, 2006) following changes in agricultural policies and the construction of a vast network of agricultural drainage ditches to drain the rich clay soil of the region (Domon and Bouchard, 2007). At some locations and because of the slope patterns, agricultural land is being drained into watercourses flowing through the NWA. Fourth, Ducks Unlimited Canada has conducted in the 1980's work that involved digging and dredging for the creation of a network of channels to manage waterfowl habitat within the NWA. Finally, roads and trails make some parts of the NWA more accessible than others, introducing disturbances. All these changes have undoubtedly affected vegetation patterns and may have contributed to increase vulnerability to invasive species.

3.2.2 Status of *Phragmites* in the NWA

The Lake Saint-François NWA is one of the few locations in Quebec that hosts populations of both the native and exotic *P. australis* and as such may be one of the few natural refuges for the native type. It is unclear what the historical distribution of *P. australis* haplotypes was in the NWA, as the discovery of an exotic haplotype is fairly recent (Saltonstall, 2002). In a study of vegetation communities, Auclair *et al.* (1973) observed that *P. australis* was dominant when present in emergent communities bordering islands (99.9% of dry material), but only accounted for 10.9% of dry material of meadow communities. Auclair *et al.* (1976) observed a maximum biomass production of *P. australis* in plots where water level was around 1.05 m. Based on our current knowledge of *P. australis*' spatial distribution in the NWA (Taddeo and de Blois, in prep.), it would appear that the native haplotype is most likely to have been sampled in those studies. The native haplotype has been observed near water in our study area, whereas the exotic haplotype appears less tolerant of a high level of water (Hudon *et al.*, 2005; Meadows and Saltonstall, 2009). Moreover, a vegetation survey conducted in 2000 by Environment Canada (Létourneau and Jean, 2006), mainly to validate the mapping of vegetation classes gathered from satellite imagery, showed two out of 37 quadrats with *P. australis* present. Current observations in the field suggest that these were probably quadrats of exotic *P. australis*.

3.2.3 Sampling

In 2006-2007, all the colonies of exotic and native reed were mapped through extensive field sampling in the summer. Aerial surveys of the area with Ducks Unlimited served to identify isolated colonies that were hard to reach in the summer. These colonies were visited and identified in the winter. Morphological differences (e.g., reddish stem, narrower leaves and smaller inflorescence on native compared to exotic) were used to differentiate the native and exotic haplotype in the field. Tissue samples were collected on 65 specimens (37 native and 28 exotic) and were submitted to blind DNA analysis using the methodology proposed by Saltonstall *et al.* (2003). The DNA analysis performed by Annie St-Louis at the Genetic laboratory of the Phytology Department of Laval University agreed at 100% with field identification. The location of the *P. australis* colonies and their status (native or exotic) was recorded using a GPS receiver mobile mapper and then imported in an ArcView shapefile, using the Universal Transverse Projection of Mercator, zone 18. The maps produced during this extensive survey, as well as land cover/land use map produced by Environment Canada (2006), served as a basis for sampling *P. australis* in this study.

Objective 1: Evaluate and compare expansion patterns of populations of each haplotype into adjacent communities

In order to assess the relative expansion of the two haplotypes into adjacent un-invaded plant communities, a total of 18 permanent circular plots of 2 m radius were set up at three different sites in the NWA at the end of the growing season in 2007. Each site contained six expansion plots located each at the margin of a dense native *P. australis* colony (three plots) or at the margin of a dense exotic *P. australis* colony (three plots). The margin of the colony was defined at the furthest *P. australis* stem identified, and the expansion plots showed no sign of *P. australis* seedlings or stems at the time of establishment. The plots were marked using a metallic rod inserted in the middle of the plot. GPS coordinates and distances from focal landmarks were taken, and the dominant species within each plot were noted (Table 3.1). Plots at the three sampling sites (known as Hopkins, Fraser, and Avenues) were all within 52 m from a road or trail and were characterized by different levels of disturbance. Hopkins Point is a low marsh dominated by *Carex* species. The road that crosses it is not paved and not frequently used so it is considered low disturbance. Fraser Point is a marsh crossed by canals constructed in the

1980’s by Ducks Unlimited. Plots located in the Avenues are located in a marsh adjacent to a paved road and nearby low-density housing, which makes them more disturbed.

Expansion patterns were quantified using two measures: the number of *P. australis’* stems over two years in the previously unoccupied plot (densification), and the distance from the original front to the furthest stem after two years (progression). A stem count of both reed haplotypes was done within each expansion plot once in fall 2008 and again in mid-summer 2009. All the stems were examined for origin: clonal or seedling. They were all of clonal origin. In 2009, all species other than *P. australis* within the plots were also sampled using Braun-Blanquet cover classes to characterize invaded communities and to provide baseline data to assess future effect of *P. australis* on the native species. In the spring of 2010, the overall progression of *P. australis* was measured beyond the plots by measuring the distance to the farthest stem in a cross section defined by each plot (Figure 3.2a). Measurements were made perpendicular to the original front, using the center rod of the plot as a marker. Progression was noted in all sites except one native plot, site 7 of the Avenue, where no stem was found farther than the original front of 2007.

Objective 2: Determine the outcome of competition for space where the two haplotypes meet

Five competition transects were installed at two sites (Leblanc Point, Avenues) over two years to measure the outcome of competition for space where populations of the two haplotypes met (Figure 3.2b). Both sites were located along paved roads and exposed to human disturbances. The first two transects were set up in fall 2006 (one in Leblanc, one in the Avenues). Three others were set up in fall 2007 (two in Leblanc, one in the Avenues). Each transect was composed of 11 circular plots of 0.5 m radius, 2 meters apart. Each plot was dominated by either one or the other haplotype at the beginning of the monitoring period with the middle plot being where patterns of dominance would usually shift. The center of the transect (and/or the extremities) was marked, GPS coordinates were taken, and distances from landmarks measured.

Stem abundance of both reed haplotypes and cover of all other species were measured in each plot over four consecutive years (2006-2009) in the 2006 transects and over three consecutive years for the 2007 transects (2007-2009). Measurements were taken in the fall except for 2009 when they were taken in mid-summer.

3.2.4 Analysis

Expansion plots

A principal component analysis (PCA) was performed using plant cover (excluding *P. australis*) sampled in 2009 in the expansion plots to test whether plots from the same site would have similar floristic composition (and so could be considered as replicates), and whether sites could be distinguished on that basis. Data was previously transformed with the Hellinger transformation (Legendre and Gallagher, 2001).

The densification patterns into adjacent communities were represented using a quartile analysis (boxplots). Quartiles were compiled for 2008 and for 2009 using the count of *P. australis'* stems for 9 expansion plots of each haplotype (native or exotic). Moreover, a three-factor ANOVA using stem count data of 2008 and 2009 (999 permutations) was also performed to test differences in mean abundance among haplotype, site, and time (all fixed). 'Haplotype' had two classes (native, exotic), 'site' had three (Hopkins, Fraser, and Avenues) and 'time' had two (2008, 2009). Analysis was performed using «anova.3way» function for R (Legendre, 2007a).

The average distance to the furthest stem (progression) was compared among haplotypes and sites (fixed factors) using two-factor ANOVA and performed using «anova.2way» function for R (Legendre, 2007b).

Competition transect

In order to analyze spatio-temporal interactions between native and exotic populations at a fine spatial scale, stem abundances between years in each competition transect were first examined using histograms. For each transect, the percent change in total stem abundance for a given haplotype was computed using the first year as a reference point. This resulted in patterns of yearly increase or decrease in total stem abundance compared to the reference period evaluated for a total of 12 transitions (2006-2007, 2006-2008, 2006-2009, etc.) for all transects. The expectation was that the abundance of the exotic haplotype would mostly increase in transects, while the abundance of the native one would decrease. Moreover, the relative spatial progression or regression of the colony over the years was measured using quartile analysis. Starting at plot 0, the cumulative abundance of stems (25%, 50%, 75%) for a given haplotype was calculated and the position of the quartile on the transect was inferred from the patterns of cumulative abundance. This allowed quantifying whether colonies of each haplotype were gaining or losing ground.

3.3 Results

3.3.1 Expansion plots

PCA indicates some differences in plant community composition among the three sites (Hopkins, Fraser and the Avenues). The first axis explains 25.1% of variation in species composition, while the second axis explains 13.3%. Figure 3.3 confirms that sites are different when comparing their species composition and therefore could be used as replicates. *Carex lacustris* is present in most plots and usually very abundant but does not provide important information in the ordination. Most of the other species present in this ordination provide limited information, except *Calamagrostis canadensis*. This species is less frequent in the Fraser site. Other species are fairly widely distributed in all sites, meaning that the difference in composition between plots lies in the abundance of plant species in the plots rather than their presence or absence. Plots in this ordination are clearly grouped by site rather than by the haplotype of *P. australis* present nearby. Nevertheless, there seems to be a trend grouping plots of the same site and same haplotype together.

Stem abundance of *P. australis* in expansion plots after invasion in 2008-2009 was between 0 and 50 (0.96 ± 0.93 stems/m^2 on average). The abundance of the exotic *P. australis* was higher on average than the abundance of the native one (Figure 3.4; Table 3.2, effect of haplotype on stem abundance, $p = 0.033$). Overall stem abundance also varied among sites. This was mainly due to Hopkins, which had lower stem abundance than the other sites for both the native and exotic types (Table 3.2, effect of site on abundance, $p = 0.023$). The abundance of each haplotype varied marginally among sites (Table 3.2, haplotype x site, $p = 0.081$). The abundance of the exotic type was higher than the abundance of the native one at Fraser and the Avenues, but lower than the native type at Hopkins.

The effect of time on overall stem abundance was not significant (Table 3.2, effect of time, $p = 0.311$). This means that *P. australis* density overall did not change significantly between 2008 and 2009 after initial invasion. All other effects were non-significant.

The distance to the furthest stem was between 0 and 7.8 m (2.98 ± 2.03 m on average). This could be roughly estimated as 'progression speed' of 1.49 m per year on average, with small differences depending on the haplotype (1.39 m for exotic and 1.58 m for native) or site (1.04 m in Hopkins, 1.73 m in the Avenues and 1.71 m in Fraser). Even if distances were different from site to site, the permutation test of a 2-way ANOVA did not detect a significant difference in distances among sites or haplotypes (Table 3.3).

3.3.2 Competition plots

Results for competition plots are displayed using two types of figures and for each of five transects: 144 Avenue-1, 144 Avenue-2, Leblanc-1, Leblanc-2, and Leblanc-3. A histogram first represents stem abundance of each haplotype in each plot of a particular transect for each year sampled (Figures 3.5, 3.7, 3.9, 3.11, and 3.13). This gives an indication of fluctuations of stem abundance at a particular location along the transect. The second figure represents the distribution of the quartiles of stem abundance for that transect (Figures 3.6, 3.8, 3.10, 3.12, and 3.14). These figures give an indication of the overall spatial progression or regression in the distribution of abundances.

There was no clear overall trend (or ‘winner’) in the competition transects. There was no evidence of the overall competitive dominance of the exotic haplotype. In addition, differences in yearly abundance showed great fluctuations between years and between transects. Table 3.4 compiles those yearly differences in abundance. It seems that both haplotypes can benefit from competitive interactions depending on their location and on the year of sampling.

The interpretation of the spatial progression or regression in stem abundance for each haplotype was done for each transect separately. Even if there was no general trend, the exotic haplotype was clearly the most competitive in one case. In transect Leblanc-2 (Figures 3.11 and 3.12), abundance of the exotic haplotype went from 69 stems in 2007 to a total of 343 stems in 2009 compared to 69 stems of the native haplotype in 2007 that went down to 46 stems in 2009. The total abundance of the native haplotype had been in decline for the last two years of sampling, providing additional evidence of the exotic haplotype’s competitive ability in this transect. The exotic haplotype was in strong progression, while the native haplotype was losing previously occupied space. The quartile analysis showed that the exotic population had advanced toward the original zone of contact while the native population had moved away from it (Figure 3.12). These results indicate that the exotic haplotype is a better competitor in this transect.

In transect Leblanc-1 (Figures 3.9 and 3.10) on the other hand, it was the native haplotype that seemed to be the most competitive. Total abundance of stems for the native haplotype went from 119 in 2006 to 129 in 2009 but the abundance of the exotic haplotype went from 58 in 2006 to 32 in 2009. Spatial progression was obviously in favor of the native haplotype, as shown by the native population advancing toward the zone of contact. The total abundance of the exotic haplotype had been decreasing two years in a row, providing further evidence of the native haplotype’s ability to compete in that transect. All factors indicate that the native haplotype has a competitive advantage in this transect.

In the other three transects, the trend was not as clear. The related histograms indicated that both haplotypes still occupied a good proportion of each transect in 2009. In some cases, like in transect Avenue-2 (Figures 3.7 and 3.8), the exotic haplotype seemed to occupy new space but without excluding the native haplotype. Nevertheless, these changes could be simply due to inter-annual variability as no clear trend is defined for one or the other haplotype. Looking at the related quartiles analyses, the position of the populations of both haplotypes in 2009 seemed relatively stable when compared to their initial position (Figure 3.8).

In transect Avenue-2 (Figures 3.7 and 3.8) and in transect Leblanc-3 (Figures 3.13 and 3.14), the yearly pattern of change in stem abundance was similar. It decreased between 2007 and 2008 for both haplotypes and increased between 2008 and 2009 for both haplotypes. In transect Avenue-1 (Figures 3.5 and 3.6), a similar pattern of increase between 2008 and 2009 for both haplotypes is also apparent. This could indicate that competitive interactions in those two transects were not the most important driver explaining stem abundance.

3.4 Discussion

Contrary to our expectations, both haplotypes at the temporal and spatial scales of our study are expanding into adjacent communities. Above-ground progression speed of the exotic reed in this study was between 0.85 m to 2.11 m over two years. This would correspond to average annual progression speeds of about 0.42 m to 1.05 m. This seems to be similar or at the upper end of what was reported in other studies (0.1 m - 0.94 m (Burdick and Konisky, 2003), 0.52 m - 0.91 m (Philipp and Field, 2005), 1 m (Haslam, 1972), 0.8 m - 1.2 m (Lavoie *et al.*, 2003), 1.6 m - 2 m (Warren *et al.*, 2001). In addition, progression speeds between haplotypes are not significantly different. Since it was assumed that native reed has been present in the NWA for a long time, this may suggest that, just like the exotic reed, it is responding to recent disturbances or changes in environmental conditions such as increased nutrient inputs or warmer climate (Brisson *et al.*, 2008). In the Great Lakes region (Lake Superior), a study reported that the native haplotype could also be opportunistic, taking advantage of human disturbances to colonize new sites (Lynch and Saltonstall, 2002). Given that the exotic reed so far is largely confined to roads and other disturbed areas in the NWA and that our sampling sites had to include both types, all our expansion plots were within 51 m of a road or canal. This may have biased our observations for the native reed. Roads are important invasion vectors for the exotic type (Arzandeh and Wang, 2003; Lelong *et al.*, 2009), and this is also the case in the NWA, but nevertheless the native haplotype seems also to respond to the particular conditions generated by the proximity of roads or canals.

What makes a species invasive is not just its introduction into a new area, but the density it can reach once introduced, its ability to compete with the native flora, and the changes it will bring to ecosystem functions. While progression distances were not significantly different, we observed higher abundance for the exotic reed compared to the native one after two years. Even though they can progress at the same rate, their relative impact on floral communities may not be the same. The higher aerial densification rate of the exotic reed will lead to a more important canopy cover than that of the native one (Meadows and Saltonstall, 2009). Available light will be lessened in communities invaded by the exotic haplotype (Amsberry *et al.*, 2000). In the case of the native haplotype, since the density is lower, light availability might be reduced but not as much, leaving resources for other species. As for litter accumulation, since the native reed produces less aboveground biomass (Saltonstall and Stevenson, 2007), it will also produce less litter. However, higher densification rates observed aboveground may not reflect the patterns below-ground. The exotic reed produces more stems per gram of rhizome than the native one (League *et al.*, 2006). Since our survey only deals with the aerial component, densification of the rhizomes for the two haplotypes could be similar. Consequences on the floral community are still unknown and will be investigated, but we suspect that the impact on adjacent native communities will be less important for the native reed than for the exotic one.

There is one exception to the densification patterns described above and this is at Hopkins where the exotic reed reached lower levels of abundance than those of the native reed. This site is also where the marsh community is the furthest from agricultural activities and where the plant communities generally appear less disturbed, although speckled alder (*Alnus incana*) has invaded marshes here as elsewhere (Brisson *et al.*, 2006). Our measurements of water level did not reveal any significant difference between sites or haplotype (ANOVA one factor; factor site: $F = 0.0711$ and $p = 0.7936$, factor haplotype: $F = 0.1071$ and $p = 0.7483$), but measurements of water level fluctuation instead of a single measure may have shown other responses. Explaining site effect would require further investigation, but the significant patterns observed at Hopkins suggest that, even if drainage ditches or roads act as entry points, there are biotic or abiotic conditions for which the expansion of the exotic haplotype into freshwater wetlands can be relatively slow. This is good news since an improved understanding of these conditions could provide insights on how to limit further proliferation of the invasive type into native communities.

As for the competitive outcome between the two haplotypes, no clear trends have been observed at the scale of our study. Since there is no overall dominant competitor, the displacement of the native haplotype by the exotic haplotype is possible, but this could be a slow process that requires certain environmental conditions. Competitive interactions are complex and require knowledge of both soil and species interactions. While some exclusion interactions could be driven by species-species interactions, others could be due to soil properties (Wixted and McGraw, 2009). Effects of competition can also be limited to species abundance rather than species diversity (Stinson *et al.*, 2007). In this study, this could mean that, over time, the abundance of one haplotype or the other could be significantly reduced when they compete, but they may not necessarily be excluded. During three years of observation of competitive interactions between *Typha* spp. and the exotic *P. australis*, Bellavance *et al.* (2010) concluded that *P. australis* was outcompeting *Typha*, progression of *P. australis* in *Typha* stands being similar to progression in sites where vegetation had been removed.

The results of our surveys of the competition transect also reveal that site is an important driver of the competitive outcome. Indeed, interannual variation observed in stem abundance for both haplotypes and the lack of clear progression patterns seem to indicate that some environmental variables, including climatic conditions, could determine the success of one haplotype over the other. For example, yearly fluctuations in water level could advantage one haplotype over the other, slowing down the exotic haplotype in high water conditions or the native one in drier conditions (Lambert and Casagrande, 2006; Meadows and Saltonstall, 2009). A study conducted in Boucherville islands clearly indicated that the exotic *P. australis* expansion was limited by higher levels of water (Hudon *et al.*, 2005). On the other hand, maximal biomass production of the native *P. australis* was observed in plots were water levels was around 1.05 m (Auclair *et al.*, 1976). Moreover, observations of distribution patterns of the native and exotic reed at the landscape scale in the NWA show that the native reed tends to colonize areas near bodies of water whereas the exotic one is generally closer to roads (S. Taddeo, unpublished). In any case, competition patterns should be observed over a longer period of time to dilute effects of inter-annual fluctuations of environmental variables in order to fully understand competitive interactions between those haplotypes.

The displacement of the native haplotype by the exotic haplotype reported at large scale (Lelong *et al.*, 2007; Meadows and Saltonstall, 2009) does not occur in this small-scale study. In fact, it would appear that both haplotypes are in progression. At the zones of contact, no overall trends of exclusion of the native haplotype by the exotic haplotype have been detected after three years. Future observations will allow us to compare the impact of the native and exotic progression on adjacent plant communities and the outcome of competition between haplotypes, but our results already have conservation implications. First, if the native type is not necessarily excluded but may also expand in some conditions, it seems on the other hand to be more limited by pathogens than the exotic type (Lambert and Casagrande, 2007; Park and Blossey, 2008). Indeed we observed infestation on the majority of native stems and have had problems with fungi on the native stems in experimental set-ups (pers. obs.) The difference in performance between the native and exotic type, in particular because of enemy release (Tewksbury *et* *al.*, 2002; Liu and Stiling, 2006) could lead eventually to larger effect of the exotic type on native communities. Also, the main issue with the conservation of the native haplotype may not turn out to be its competitive exclusion by the exotic reed, but its hybridization with it. Hybridization is a problem for other invasive species in North America (Zalapa *et al.*, 2010) especially because hybrids are usually more aggressive than their parent plants (Ellstrand and Schierenbeck, 2000). The case of common reed is problematic because we have evidence of the possible hybridization between haplotypes in controlled conditions (Meyerson *et al.*, 2009) and some hybrid plants possibly occur in nature (Paul *et al.*, 2010). In the light of our study, the management of a hybrid would present serious challenges because the exotic haplotype is already very difficult to control when it is fully established and the native haplotype can proliferate.

Figure 3.1: Map of the study area

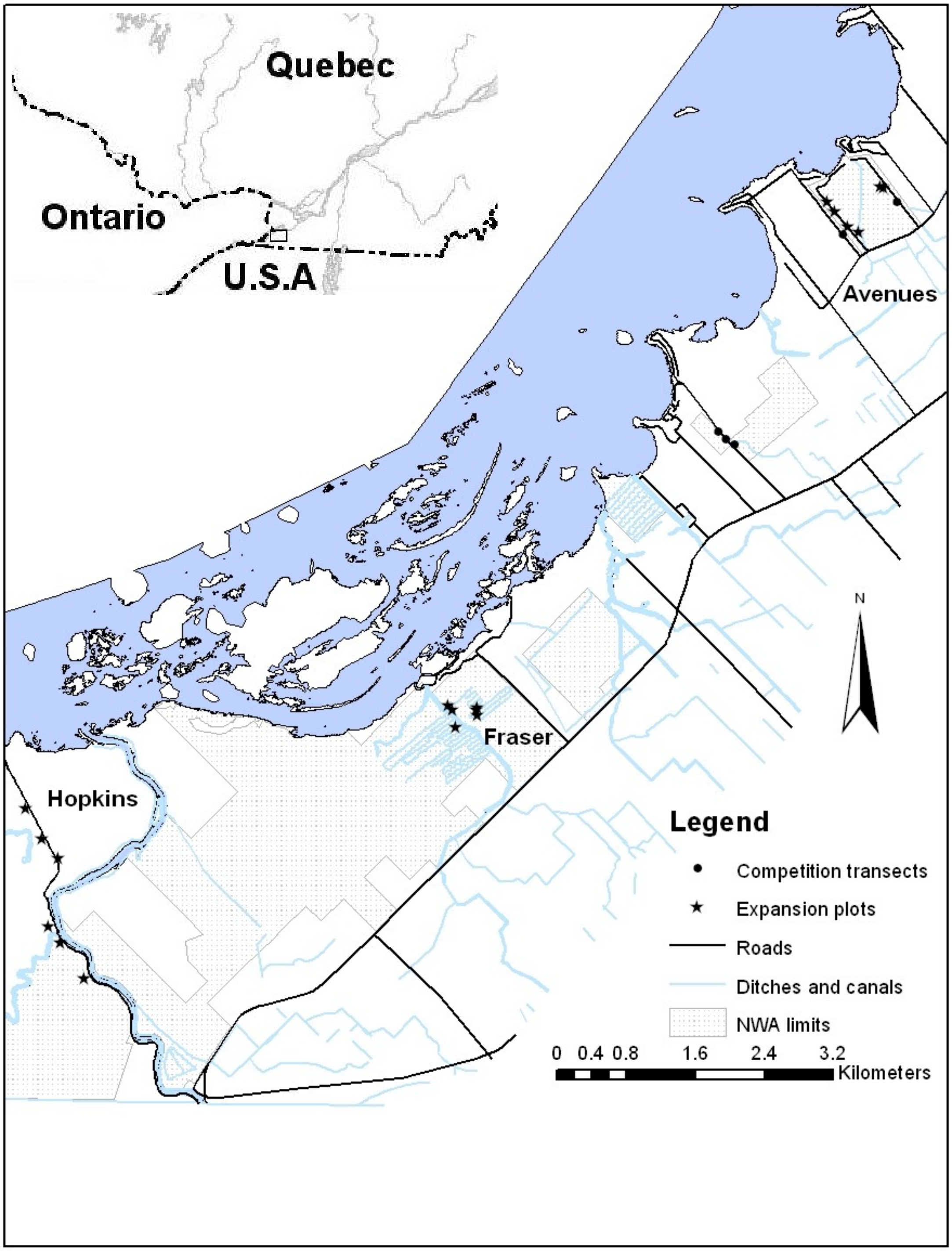
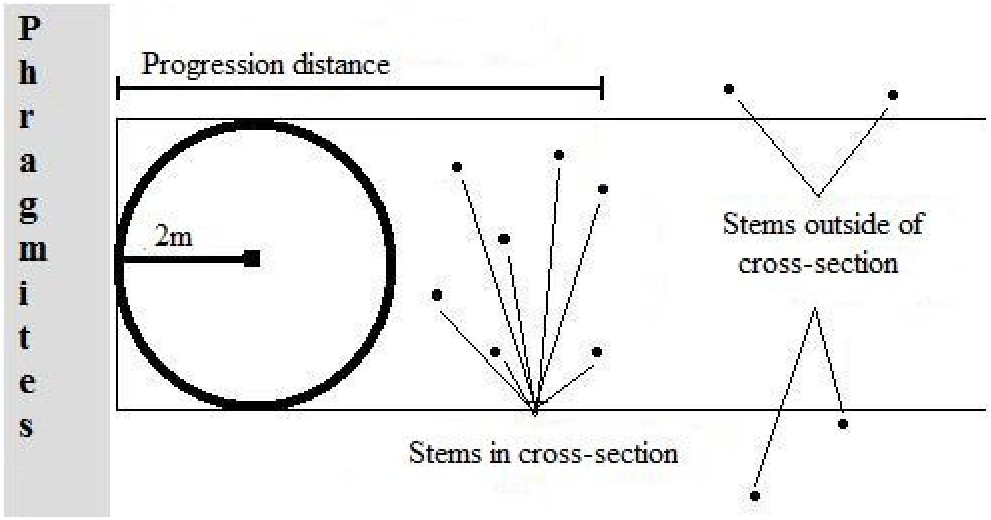

Quebec
Ontario
U.S.A
Avenues
Fraser
Hopkins
N
Legend
● Competition transects
★ Expansion plots
Roads
Ditches and canals
NWA limits
0 0.4 0.8 1.6 2.4 3.2
Kilometers

Figure 3.2: Layout a) for measuring progression distance outside expansion plots, and b) for the competition transects.

a)


P
h
r
a
g
m
i
t
e
s
Progression distance
2m
Stems outside of cross-section
Stems in cross-section

b)

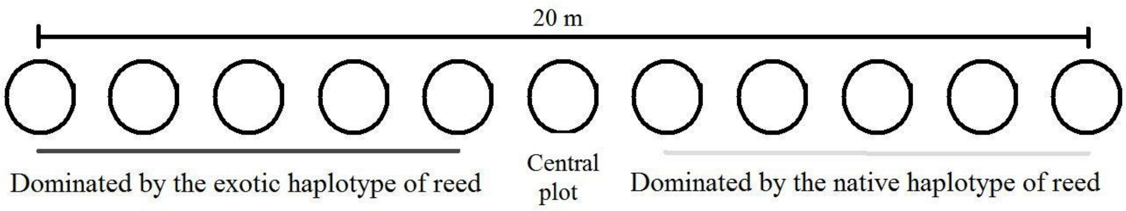

20 m
Dominated by the exotic haplotype of reed
Central plot
Dominated by the native haplotype of reed

Figure 3.3: PCA of plant cover (excluding *Phragmites* sp.) in expansion plots, July 2009. Scaling type 1 preserves distance between species. Axes explain 38.5% of total variation. Plots from Hopkins are represented by squares, plots from Fraser by circles and plots from avenues by triangles. Plots dominated by exotic haplotype (M) are in black and plots dominated by native haplotype (F) are in gray. AGGI2 (*Agrostis gigantea*), SYLAL4 (*Symphyotrichum lanceolatum* ssp. *lanceolatum* var. *lanceolatum*), CACA4 (*Calamagrostis canadensis*), CASES (*Calystegia sepium* ssp. *sepium*), EQPA (*Equisetum palustre*), GAPA3 (*Galium palustre*), IRPS (*Iris pseudacorus*), LYSA2 (*Lythrum salicaria*), ONSE (*Onoclea sensibilis*), RUOR2 (*Rumex orbiculatus*), SALIX (*Salix* sp.), SCGA (*Scutellaria galericulata*). Only most representative species are displayed.

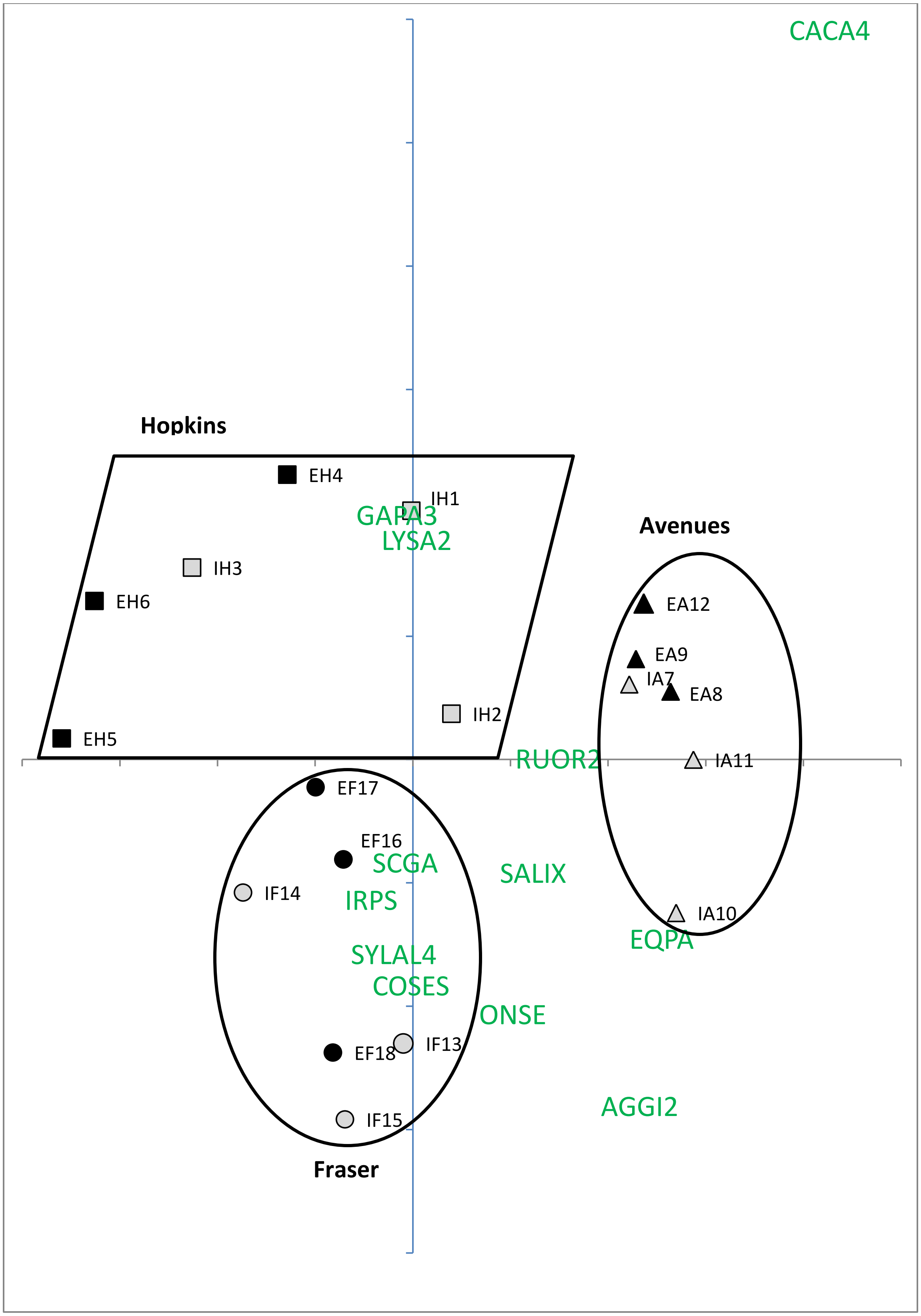

CACA4
Hopkins
EH4
IH1
GAPA3
LYSA2
IH3
EH6
IH2
EH5
Avenues
EA12
EA9
IA7
EA8
IA11
RUOR2
EF17
EF16
SCGA
SALIX
IF14
IRPS
IA10
EQPA
SYLAL4
COSES
ONSE
EF18
IF13
IF15
AGGI2
Fraser

Figure 3.4: Histograms comparing the quartiles of stem abundance between all native and exotic expansion plots (9 native and 9 exotic) in 2008 and in 2009. Initial value for all 18 plots was 0 stem in 2007. Native plots are in gray and exotic plots are in black.

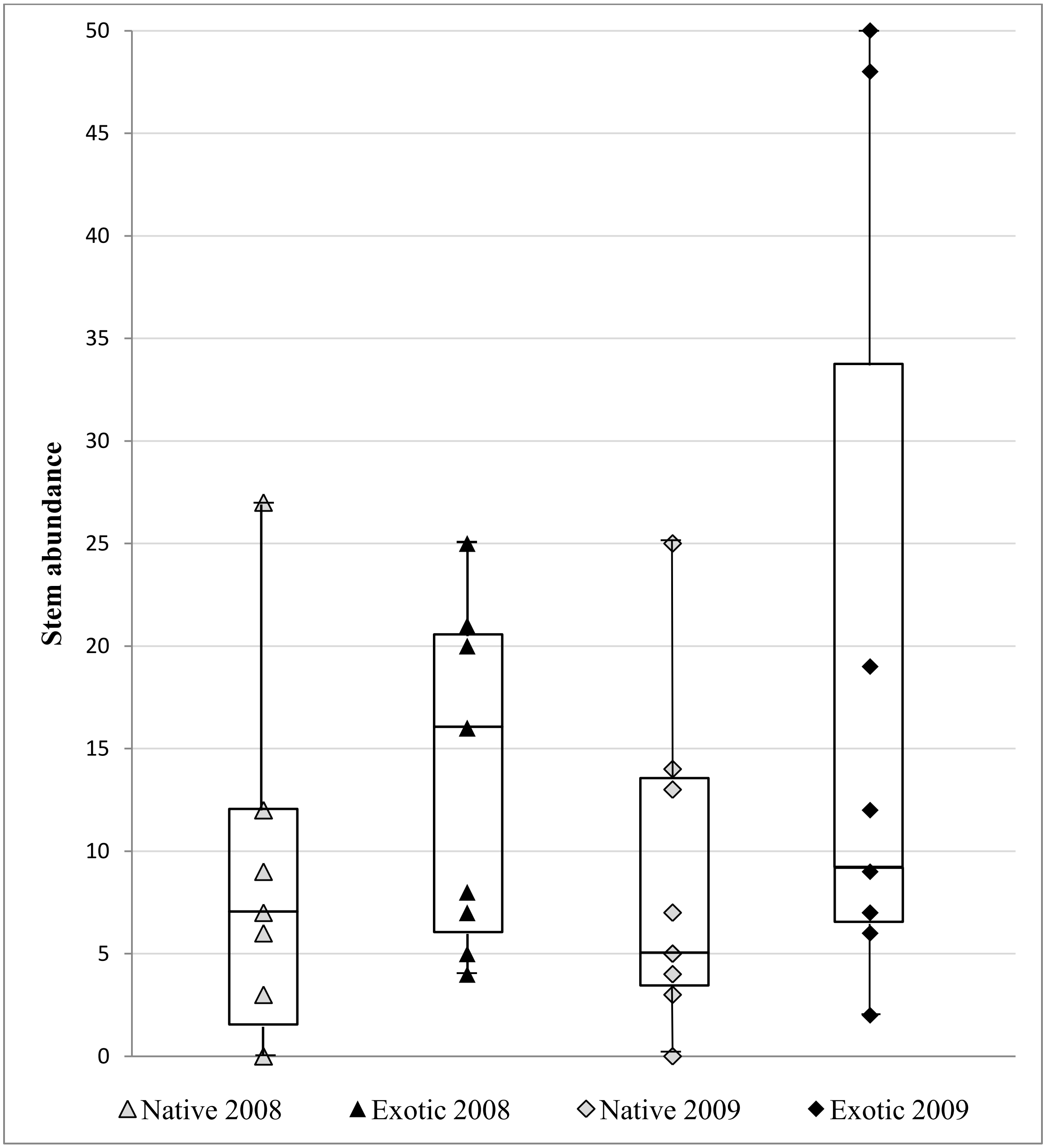

Stem abundance
0
5
10
15
20
25
30
35
40
45
50
△Native 2008
▲Exotic 2008
◇Native 2009
◆Exotic 2009

Figure 3.5: Histogram representing stem abundance of reed haplotype in the competition transect at Avenue-1. The x axis represents the position (m) of the plot on the transect. The y axis represents stem abundance for a particular year of sampling. In black, abundance of the exotic haplotype. In checked pattern, abundance of the native haplotype.

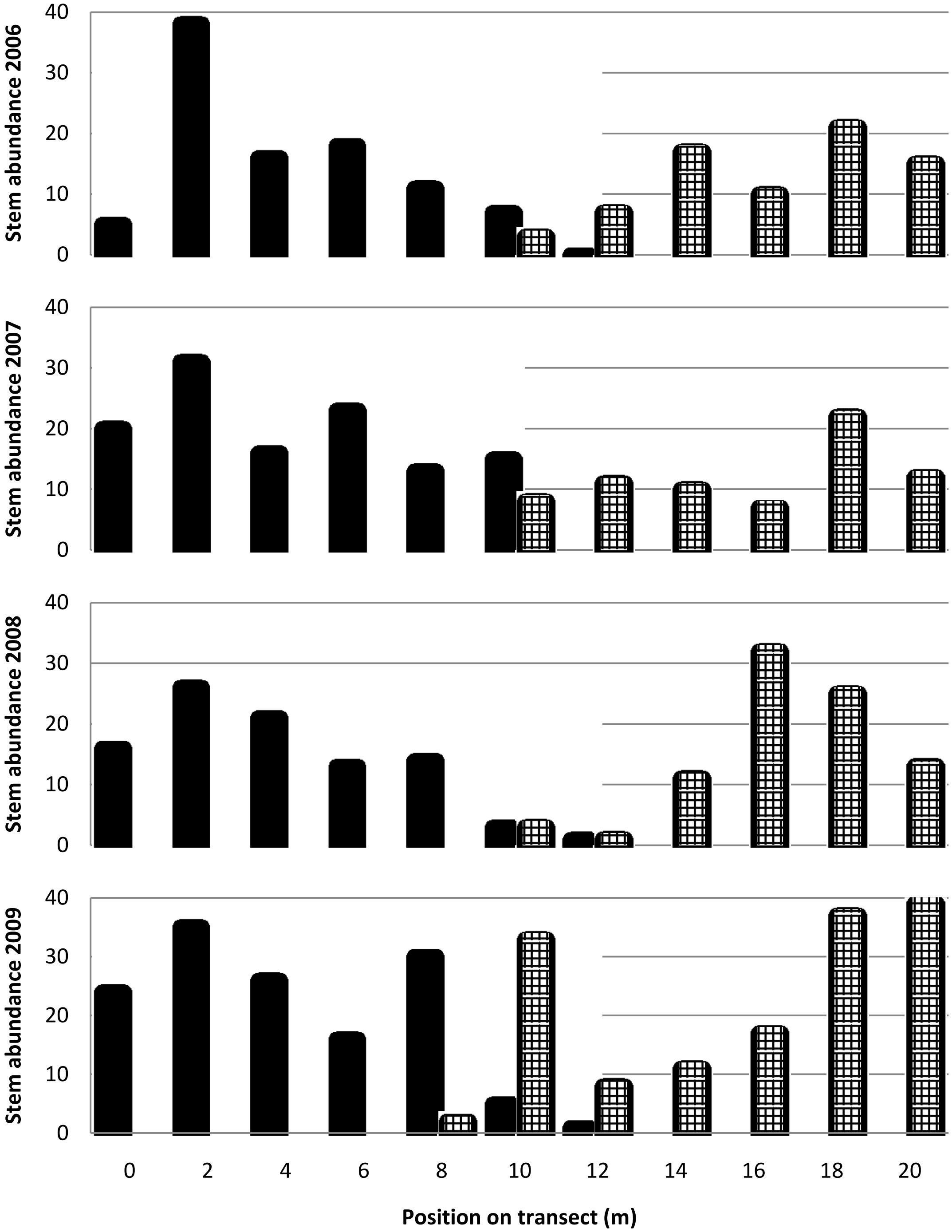
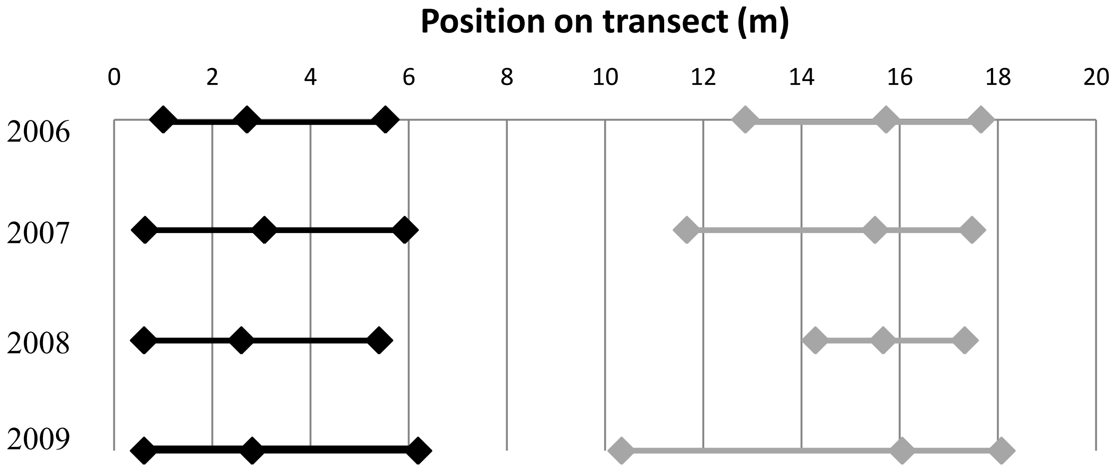

Stem abundance 2006
Stem abundance 2007
Stem abundance 2008
Stem abundance 2009
0
10
20
30
40
0
2
4
6
8
10
12
14
16
18
20
Position on transect (m)

Figure 3.6 : Diagram representing quartiles (25, 50, 75% marks) of stem abundance of reed haplotypes at Avenue-1. On the x axis, position (m) on the transect of the quartiles derived from cumulative stem abundance of the reed. On y axis, year of sampling. In black, abundance of the exotic haplotype. In gray, abundance of the native haplotype.



Position on transect (m)
0
2
4
6
8
10
12
14
16
18
20
2006
2007
2008
2009

Figure 3.7: Histogram representing stem abundance of reed haplotype in the competition transect at Avenue-2. The x axis represents the position (m) of the plot on the transect. The y axis represents stem abundance for a particular year of sampling. In black, abundance of the exotic haplotype. In checked pattern, abundance of the native haplotype.

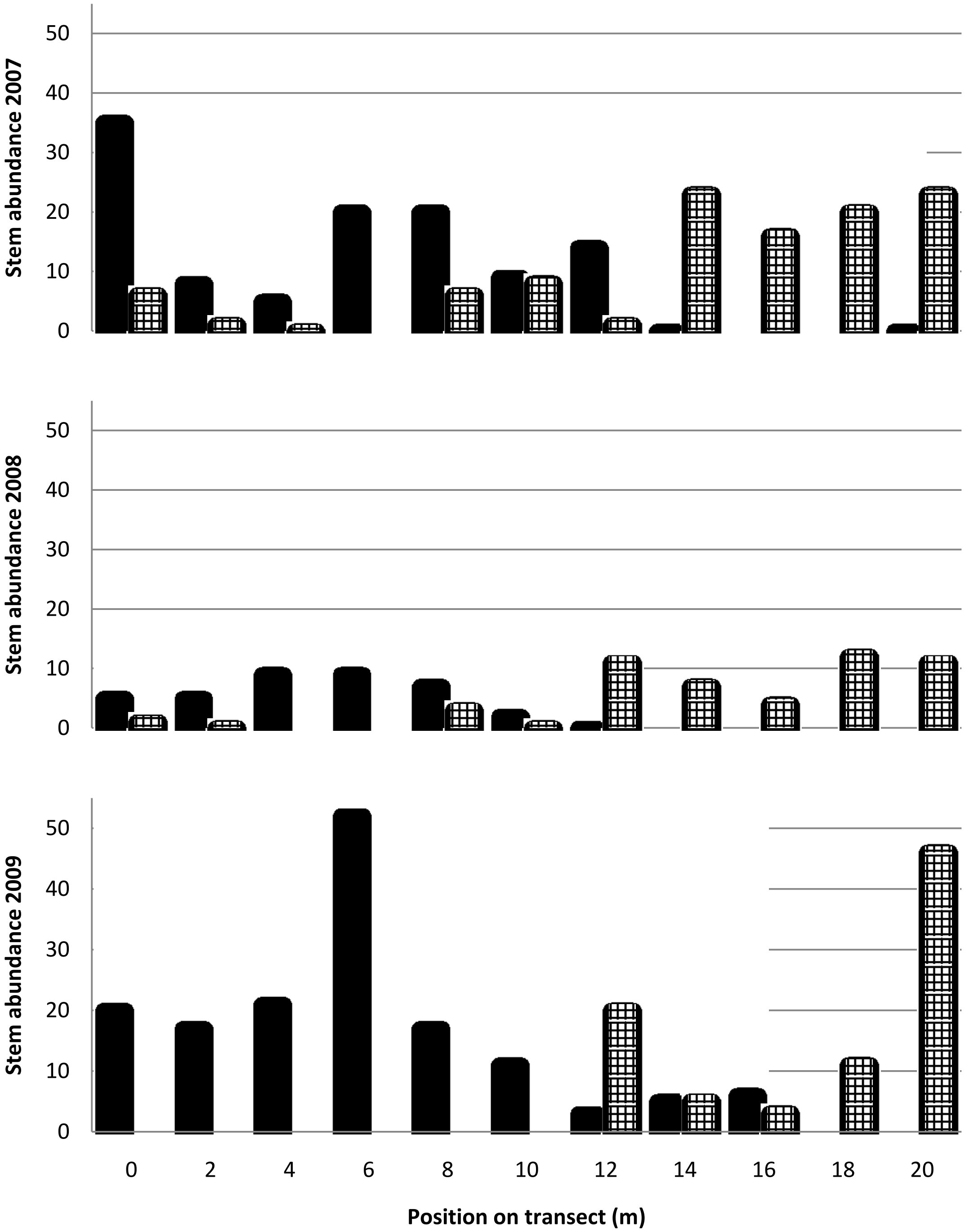

Stem abundance 2007
Stem abundance 2008
Stem abundance 2009
0
10
20
30
40
50
0
2
4
6
8
10
12
14
16
18
20
Position on transect (m)

Figure 3.8: Diagram representing quartiles (25, 50, 75% marks) of stem abundance of reed haplotypes at Avenue-2. On the x axis, position (m) on the transect of the quartiles derived from cumulative stem abundance of the reed. On y axis, year of sampling. In black, abundance of the exotic haplotype. In gray, abundance of the native haplotype.

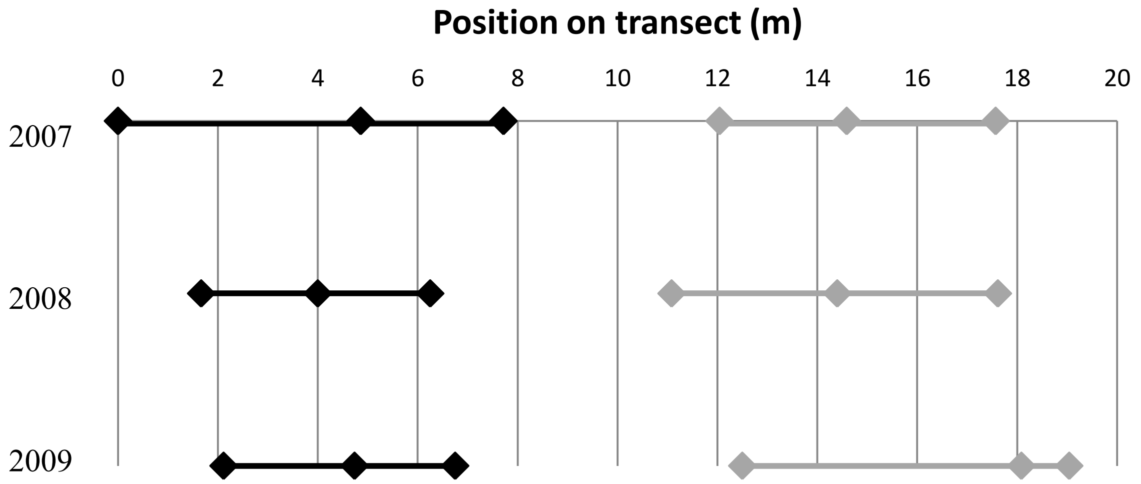

Position on transect (m)
0
2
4
6
8
10
12
14
16
18
20
2007
2008
2009

Figure 3.9: Histogram representing stem abundance of reed haplotype in the competition transect at Leblanc-1. The x axis represents the position (m) of the plot on the transect. The y axis represents stem abundance for a particular year of sampling. In black, abundance of the exotic haplotype. In checked pattern, abundance of the native haplotype.

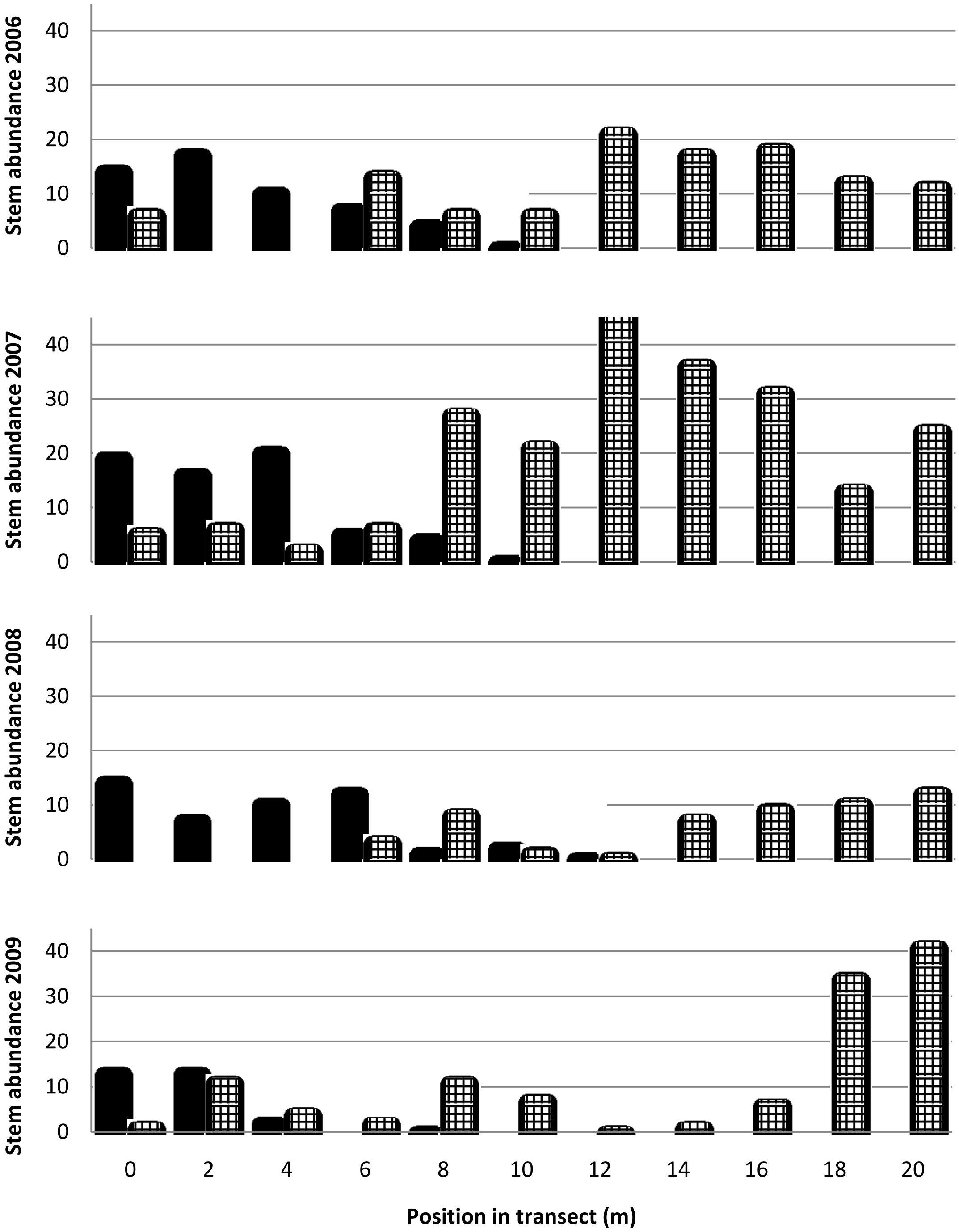

Stem abundance 2006
Stem abundance 2007
Stem abundance 2008
Stem abundance 2009
0
10
20
30
40
0
2
4
6
8
10
12
14
16
18
20
Position in transect (m)

Figure 3.10: Diagram representing quartiles (25, 50, 75% marks) of stem abundance of reed haplotypes at Leblanc-1. On the x axis, position (m) on the transect of the quartiles derived from cumulative stem abundance of the reed. On y axis, year of sampling. In black, abundance of the exotic haplotype. In gray, abundance of the native haplotype.

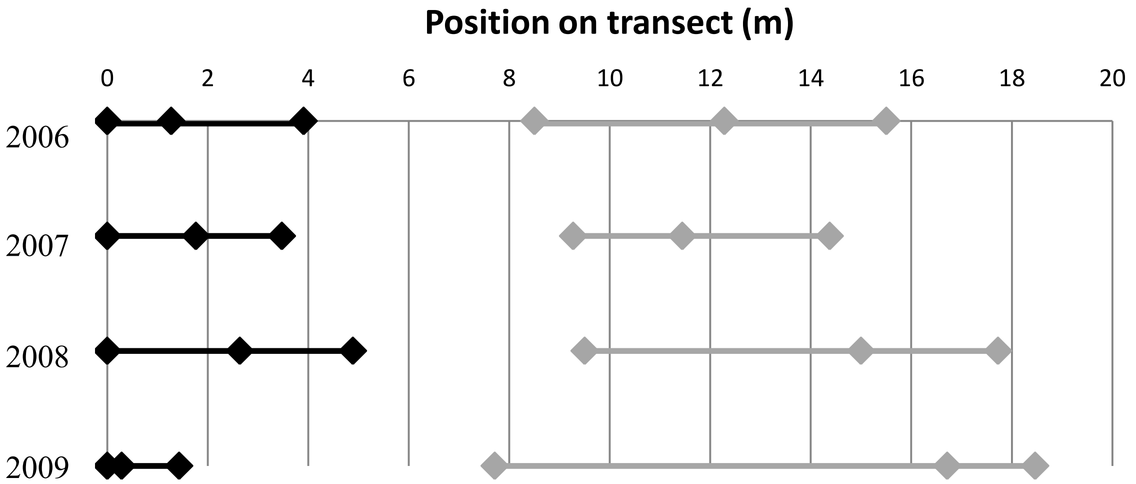

Position on transect (m)
0
2
4
6
8
10
12
14
16
18
20
2006
2007
2008
2009

Figure 3.11: Histogram representing stem abundance of reed haplotype in the competition transect at Leblanc-2. The x axis represents the position (m) of the plot on the transect. The y axis represents stem abundance for a particular year of sampling. In black, abundance of the exotic haplotype. In checked pattern, abundance of the native haplotype.

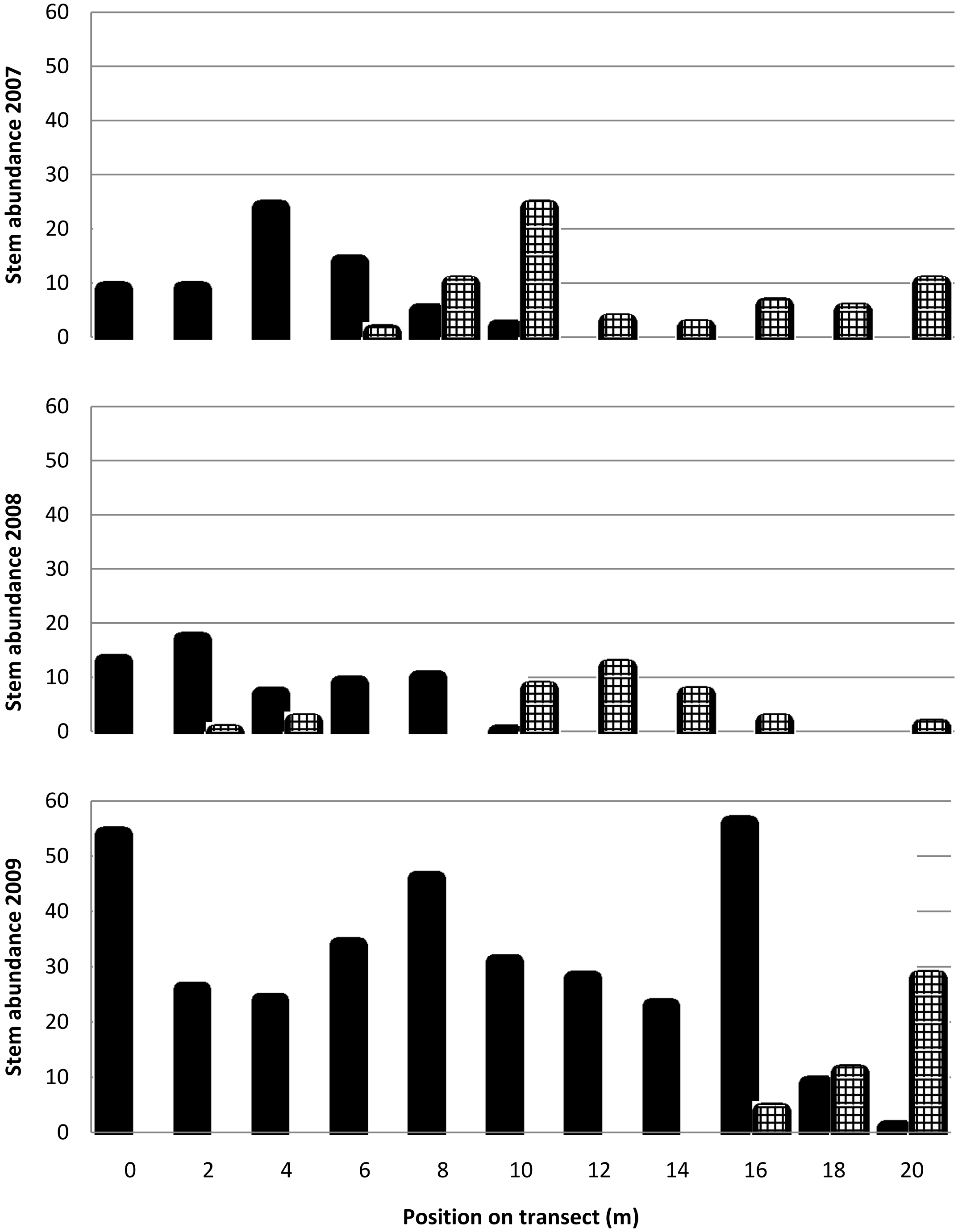

Stem abundance 2007
Stem abundance 2008
Stem abundance 2009
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
18
20
Position on transect (m)

Figure 3.12: Diagram representing quartiles (25, 50, 75% marks) of stem abundance of reed haplotypes at Leblanc-2. On the x axis, position (m) on the transect of the quartiles derived from cumulative stem abundance of the reed. On y axis, year of sampling. In black, abundance of the exotic haplotype. In gray, abundance of the native haplotype.

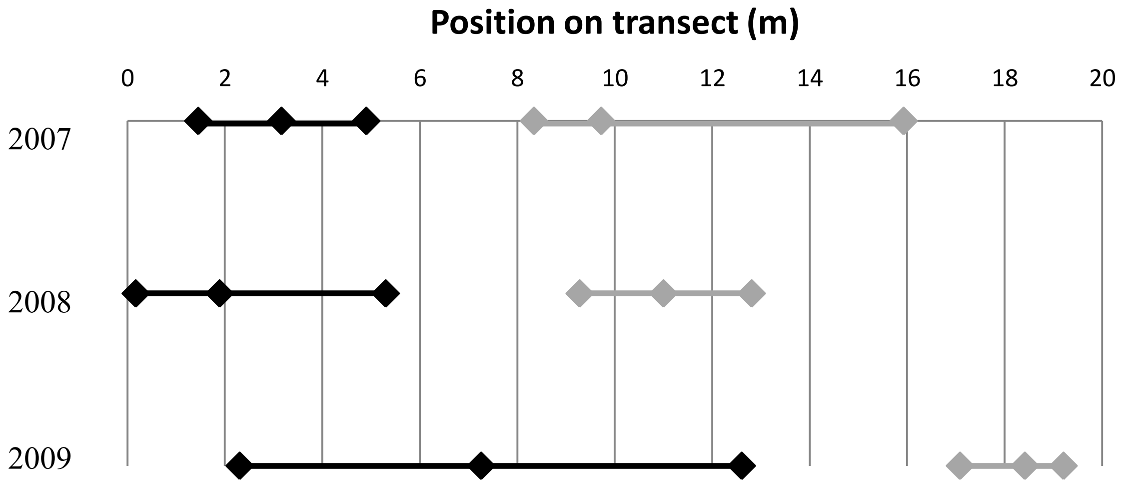

Position on transect (m)
0
2
4
6
8
10
12
14
16
18
20
2007
2008
2009

Figure 3.13: Histogram representing stem abundance of reed haplotype in the competition transect at Leblanc-3. The x axis represents the position (m) of the plot on the transect. The y axis represents stem abundance for a particular year of sampling. In black, abundance of the exotic haplotype. In checked pattern, abundance of the native haplotype.

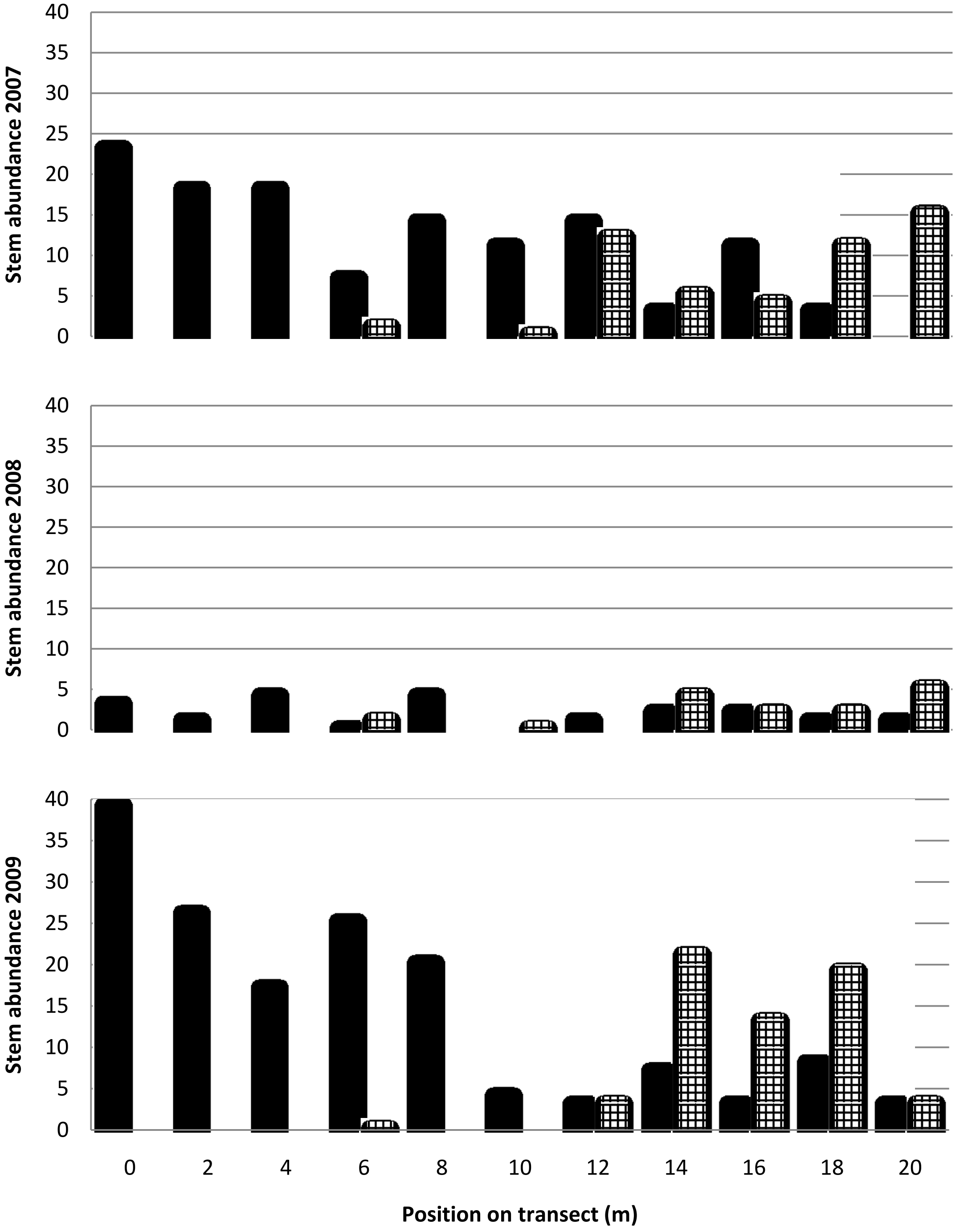

Stem abundance 2007
Stem abundance 2008
Stem abundance 2009
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
12
14
16
18
20
Position on transect (m)

Figure 3.14: Diagram representing quartiles (25, 50, 75% marks) of stem abundance of reed haplotypes at Leblanc-3. On the x axis, position (m) on the transect of the quartiles derived from cumulative stem abundance of the reed. On y axis, year of sampling. In black, abundance of the exotic haplotype. In gray, abundance of the native haplotype.

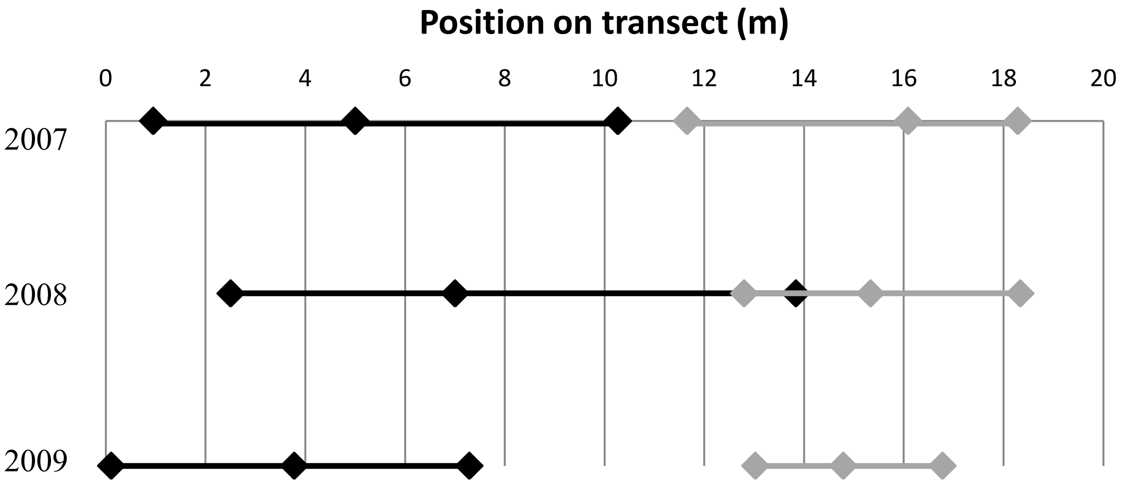

Position on transect (m)
0
2
4
6
8
10
12
14
16
18
20
2007
2008
2009

Table 3.1: Characteristics of expansion plots and their dominant species.

	Status	Site	Distance from road or canal*	Dominant plant species within plot
1	Native	Hopkins	33 m	*Carex lacustris, Lythrum salicaria, Typha* sp.
2	Native	Hopkins	15 m	*Alnus incana* ssp. *rugosa, Calamagrostis canadensis, Carex lacustris, Lythrum salicaria*
3	Native	Hopkins	51 m	*Carex lacustris, Carex* sp.*, Lythrum salicaria*
4	Exotic	Hopkins	9 m	*Carex lacustris, Carex* sp.*, Calamagrostis canadensis, Lythrum salicaria, Thelypteris palustris*
5	Exotic	Hopkins	18 m	*Alnus incana* ssp. *rugosa, Carex lacustris, Carex* sp.
6	Exotic	Hopkins	16 m	*Carex lacustris, Carex* sp.*, Thelypteris palustris*
7	Native	Avenues	52 m	*Calamagrostis canadensis, Carex lacustris, Lythrum salicaria, Onoclea sensibilis*
8	Exotic	Avenues	13 m	*Calamagrostis canadensis, Carex lacustris, Typha* sp.
9	Exotic	Avenues	16 m	*Calamagrostis canadensis, Carex lacustris, Lythrum salicaria*
10	Native	Avenues	22 m	*Calamagrostis canadensis, Carex lacustris, Lythrum salicaria, Typha* sp.
11	Native	Avenues	22 m	*Calamagrostis canadensis, Carex lacustris, Lythrum salicaria, Typha* sp.
12	Exotic	Avenues	15 m	*Calamagrostis canadensis, Carex lacustris, Lythrum salicaria, Typha* sp.
13	Native	Fraser	5 m*	*Carex lacustris, Onoclea sensibilis, Thelypteris palustris, Typha* sp.*, Rubus idaeus*
14	Native	Fraser	5 m*	*Alnus incana* ssp. *rugosa, Carex lacustris, Eupatoriadelphus maculatus maculatus, Thelypteris palustris*
15	Native	Fraser	15 m*	*Alnus incana* ssp. *rugosa, Carex lacustris, Myrica gale*
16	Exotic	Fraser	10 m	*Alnus incana* ssp. *rugosa, Carex lacustris, Carex* sp.*, Typha* sp.
17	Exotic	Fraser	9 m	*Calamagrostis canadensis, Carex lacustris, Carex sp, Typha* sp.
18	Exotic	Fraser	22 m, 10 m*	*Carex lacustris, Lythrum salicaria, Onoclea sensibilis, Typha* sp.

Table 3.2: 3-way-ANOVA results for stem abundance in expansion plots. Haplotype = native or exotic. Site = Hopkins, Fraser, or Avenues. Time = 2008 or 2009.

	d.f.	F value	Prob (perm)
Haplotype	1	4.857	0.033
Site	1	4.559	0.023
Time	1	1.039	0.311
Haplotype : Site	1	2.863	0.081
Haplotype : Time	1	0.313	0.578
Site : Time	1	0.234	0.786
Haplotype : Site : Time	1	0.365	0.707
Residual	28	NA	NA

Table 3.3: 2-way-ANOVA results for total progression distances (2008-2010). Haplotype = native or exotic. Site = Hopkins, Fraser, or Avenues.

	d.f.	F value	Prob (perm)
Haplotype	1	0.157	0.709
Site	1	1.232	0.339
Haplotype : Site	1	0.679	0.505
Residuals	14	NA	NA

Table 3.4: Number of yearly transitions for which we observed an increase or a decrease (relative to the first year of sampling) in total stem abundance in the competition transects for each haplotype. There were 2 transects sampled for 3 years and 3 transects sampled for 2 years for a total of 12 yearly transitions.

	Exotic	
Native	Increase	Decrease
Increase	3	2
Decrease	3	4

Chapter 4 – General conclusion

The preceding work is part of a long lineage of research projects, in collaboration with the «Phragmites Group», which aim to describe the invasion dynamics of common reed in Quebec. Several previous studies, especially along the road systems and along the St-Lawrence River, have been done mostly to describe the progression of *P. australis* at a landscape scale using herbarium records and field surveys. This thesis contributes to the general body of knowledge on the invasion dynamics of common reed by focusing on population patterns of the native and exotic *P. australis* at the local scale in freshwater wetlands.

This work is important because it provided a direct comparison of the invasion dynamics of both haplotypes in similar space and time frames. The NWA of Lake St-François was an ideal location to monitor such interactions. Results indicated that, contrary to what was hypothesized, both haplotypes of reed were in progression and were capable of occupying new space over time in freshwater environments. The exotic haplotype densified more rapidly, but the observed progression based on the furthest stem for the two haplotypes was generally similar. The exception was in a site with low disturbance levels where the progression speed of the exotic haplotype and its capacity to occupy space were more limited. In the case of the native haplotype, its progression speed and capacity to occupy new space were similar at all sites, indicating that all sites were possibly suitable habitats. These patterns suggest that whereas both haplotypes can expand in disturbed conditions, densification of the exotic haplotype in these conditions will result in greater impact on the invaded communities than those of the native haplotype.

This work is also important because it described competition interactions in a natural setting between these two genetically related sub-species. This should lead to a better understanding of the dynamics behind cryptic invasion like the one occurring with *P. australis* in North America. Results did not clearly demonstrate that the exotic haplotype was efficiently and consistently displacing the native haplotype in freshwater and disturbed wetland conditions. This suggests that there are conditions in which the native haplotype can be maintained. Further monitoring is needed in order to reduce the effects of the annual variability in stem abundance and to establish the possible link with environmental changes such as changes in temperature or water level. This will enable a clearer identification of the trends observed in competition interactions and will provide better long term evidence on these particular dynamics.

Chapter 5 - List of references

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Appendices

Table A1: Densification measurement data collected in expansion plots in 2008-2009.

Stem abundance	haplotype	site	sampling year
27	1	2	1
7	1	2	1
0	1	2	1
4	0	2	1
7	0	2	1
8	0	2	1
0	1	1	1
5	0	1	1
20	0	1	1
9	1	1	1
6	1	1	1
25	0	1	1
12	1	0	1
3	1	0	1
12	1	0	1
21	0	0	1
16	0	0	1
16	0	0	1
4	1	2	2
3	1	2	2
13	1	2	2
7	0	2	2
6	0	2	2
2	0	2	2
0	1	1	2
7	0	1	2
50	0	1	2
7	1	1	2
25	1	1	2
12	0	1	2
14	1	0	2
5	1	0	2
5	1	0	2
48	0	0	2
19	0	0	2
9	0	0	2

Haplotype 0 = exotic   1 = native
Site 0 = Fraser   1 = Avenues   2 = Hopkins
Sampling year 1 = 2008   2= 2009

Table A2: Progression speed data collected in expansion plots in 2009.

Progression (m)	Haplotype	Site
2	1	0
0.5	1	0
4.95	1	0
2.7	0	0
2.1	0	0
0.2	0	0
2	1	1
2.5	0	1
2.8	0	1
7.8	1	1
2.85	1	1
2.8	0	1
5.7	1	2
1.2	1	2
1.6	1	2
2.9	0	2
2.5	0	2
6.6	0	2

Haplotype 0 = exotic 1 = native

Site 0 = Hopkins 1 = Avenues 2 = Fraser

Table A3: Cover class (Braun-Blanquet classification) of each species in expansion plots for the 2009 sampling season. Plots by site: 1-6 = Hopkins, 7-12 = Avenue, and 13-18 = Fraser.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Alnus rugosa incata	0	3	2	0	6	2	0	0	0	0	0	0	0	4	6	4	3	3
Asclepias incarnata	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Aster lateriflorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Aster simplex	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Calamagrostis canadensis	2	3	0	3	0	0	2	4	2	0	2	3	0	0	0	3	3	0
Campanula aparinoides	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
Carex aquatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Carex lacustris	4	4	4	5	2	2	3	4	2	4	5	3	2	2	2	1	4	4
Cicuta bulbifera	1	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1
Convolvulus sipens	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Cornus stolonifera	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Dryopteris cristata	0	0	0	0	0	0	3	2	2	2	3	3	0	0	0	0	0	0
Dryopteris spinulosa	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Elodea canadensis	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum fluviatile	0	0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	2	0
Equisetum palustre	0	0	0	0	0	0	0	0	0	3	4	0	0	0	0	1	0	0
Eupatorium maculatum	0	0	0	1	0	0	0	2	2	1	2	2	0	2	1	1	2	1
Eupatorium perfoliatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Galium palustre	1	1	1	0	1	0	1	2	0	0	0	1	0	1	0	0	1	1
Hydrocharis morsus-ranae	0	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	1	0	0	1	0	0	1	2	1	0	0	0	1	3	2	1	1
Iris pseudacorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Lathyrus palustris	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1
Lemna minor	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopus uniflorus	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Lythrum salicaria	5	3	3	2	1	2	2	0	3	3	3	1	1	2	1	2	2	2
Myrica gale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Onoclea sensibilis	0	2	1	1	0	0	3	2	0	0	0	1	4	0	1	0	1	3
Phragmites australis americanus	2	1	2	0	0	0	0	0	0	2	2	0	2	2	2	0	0	0
Phragmites australis australis	0	0	0	2	2	1	0	2	5	0	0	2	0	0	0	4	2	2
Potentilla palustris	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0	0
Rubus idaeus	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Rumex orbiculatus	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Sagittaria latifolia	1	1	0	2	0	2	1	2	1	0	0	1	0	1	0	0	0	0
Salix sp.	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	2	0	1
Scirpus cyperinus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scirpus fluviatile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scutellaria epilobiifolia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sparginium eurycarpum	2	1	2	2	2	2	2	0	2	0	0	2	0	1	0	1	2	0
Thelypteris palustris	0	0	0	3	2	4	0	0	0	0	0	0	4	4	1	3	3	3
Typha angustifolia	3	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	2	2
Typha latifolia	0	1	0	0	0	0	3	4	2	4	2	3	2	0	2	3	1	0
graminea sp.	0	0	0	0	0	0	4	0	0	4	0	0	0	0	0	0	0	5
aster sp.	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
carex sp.	0	0	4	4	4	6	0	0	0	0	0	0	0	0	0	3	3	0
solidago sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Table A4: Stem abundance of *Phragmites australis* in competition transects for sampling years 2006-2009.

Transect	Year of sampling	Haplotype	Position on the transect (m)										
			0	2	4	6	8	10	12	14	16	18	20
Avenue-1	2006	Exotic	6	39	17	19	12	8	1	0	0	0	0
		Native	0	0	0	0	0	4	8	18	11	22	16
	2007	Exotic	21	32	17	24	14	16	0	0	0	0	0
		Native	0	0	0	0	0	9	12	11	8	23	13
	2008	Exotic	17	27	22	14	15	4	2	0	0	0	0
		Native	0	0	0	0	0	4	2	12	33	26	14
	2009	Exotic	25	36	27	17	31	6	2	0	0	0	0
		Native	0	0	0	0	3	34	9	12	18	38	40
Avenue-2	2007	Exotic	36	9	6	21	21	10	15	1	0	0	1
		Native	7	2	1	0	7	9	2	24	17	21	24
	2008	Exotic	6	6	10	10	8	3	1	0	0	0	0
		Native	2	1	0	0	4	1	12	8	5	13	12
	2009	Exotic	21	18	22	53	18	12	4	6	7	0	0
		Native	0	0	0	0	0	0	21	6	4	12	47
Leblanc-1	2006	Exotic	15	18	11	8	5	1	0	0	0	0	0
		Native	7	0	0	14	7	7	22	18	19	13	12
	2007	Exotic	20	17	21	6	5	1	0	0	0	0	0
		Native	6	7	3	7	28	22	79	37	32	14	25
	2008	Exotic	15	8	11	13	2	3	1	0	0	0	0
		Native	0	0	0	4	9	2	1	8	10	11	13
	2009	Exotic	14	14	3	0	1	0	0	0	0	0	0
		Native	2	12	5	3	12	8	1	2	7	35	42
Leblanc-2	2007	Exotic	10	10	25	15	6	3	0	0	0	0	0
		Native	0	0	0	2	11	25	4	3	7	6	11
	2008	Exotic	14	18	8	10	11	1	0	0	0	0	0
		Native	0	1	3	0	0	9	13	8	3	0	2
	2009	Exotic	55	27	25	35	47	32	29	24	57	10	2
		Native	0	0	0	0	0	0	0	0	5	12	29
Leblanc-3	2007	Exotic	24	19	19	8	15	12	15	4	12	4	0
		Native	0	0	0	2	0	1	13	6	5	12	16
	2008	Exotic	4	2	5	1	5	0	2	3	3	2	2
		Native	0	0	0	2	0	1	0	5	3	3	6
	2009	Exotic	40	27	18	26	21	5	4	8	4	9	4
		Native	0	0	0	1	0	0	4	22	14	20	4

Table A5: Coordinates of expansion plots and competition transects in the Universal Transverse Projection of Mercator, zone 18.

Expansion plots			Competition transects		
	East	North		East	North
EP1	537338	4984256	Leblanc-1	544863	4990465
EP2	537046	4984524	Leblanc-2	543895	4991704
EP3	536894	4984831	Leblanc-3	544719	4990606
EP4	536986	4985525	Avenue-1	541997	4993287
EP5	536789	4985849	Avenue-2	546135	4992884
EP6	536605	4986203			
EP7	546266	4992708			
EP8	546112	4992838			
EP9	545970	4993017			
EP10	546599	4993215			
EP11	546580	4993235			
EP12	545881	4993133			
EP13	541622	4987036			
EP14	541567	4987181			
EP15	541533	4987197			
EP16	541887	4987205			
EP17	541872	4987178			
EP18	541882	4987120			