The Eco-physiological and Genetic Basis of Invasiveness

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INTRODUCTION

The invasion of ecosystems by alien species is a key driver of global environmental change and many invasive plant species attain sufficiently high abundance to alter ecosystem structure and function (Meffin *et al.* 2010). Thus, attempts have been made to plausibly explain why some alien species undergo a profound shift in their ecological fortune, from being minor components of their native ecosystems to becoming devastating dominants of non-native habitats (Callaway and Maron 2006). To untangle this ecological mystery, the prediction and management of already established and future species invasions undoubtedly holds promise (Hulme, 2003). Research efforts to resolve this paradox have primarily focused on identifying a syndrome of traits that promote invasiveness of alien species in their non-native range(s). Though a multitude of traits contributing to species invasiveness has been recognised, attempts to identify key traits that promote invasiveness of alien species have not yet ceased (Kolar and Lodge, 2001; Pysek and Richardson, 2007). In fact, a number of studies has been carried out to compare the traits of both invasive alien plant species and non-invasive plant species under common environmental conditions (Pysek and Richardson, 2007). Besides conventional morphological, reproductive and physiological traits, recent developments in molecular biology have enabled an exploration of the relationship between the amount of nuclear DNA (genome size) and other molecular attributes and the invasiveness of species (Ekrt *et al.* 2009). Combining the results of these studies in a single meta-analysis enabled Van Kleunen *et al.* (2010) to show that invasive plant species generally have higher values for performance-related traits characterising physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness than non-invasive plant species. This extensive study also pointed out that despite a steady increase, the number of studies comparing traits of invasive and non-invasive species grown under common environmental conditions is still relatively low and very heterogeneous with respect to the type of traits measured and the design of the study. Most studies have included only one or a few species pairs, and each of these studies consequently has a low number of replicates and thus is of limited value. A notable exception, however, is a study of Grotkopp and Rejmanek (2007), which measured seedling growth rates of 15 invasive alien tree species and 13 non-invasive alien tree species. Such experimental multi-species comparisons (also see Van Kleunen *et al.* 2007) considerably increase our power to test which traits are consistently associated with invasive alien species.

Recent studies have showed that invasive species suppress the diversity of native species in their non-native regions but not at home (Shah and Reshi, 2014). The studies so far, though, support the questions of why and how invasive species expand their range in non-native regions, but why these species become rarer in their native regions is still an open question. The advent of new tools in molecular genetics during the past two decades has opened additional avenues to ecologists and biogeographers to address such questions and obtain novel insights into the ecology of invasive species. Molecular tools are especially useful to discriminate between native and exotic populations of invaders that cannot otherwise be differentiated based on morphological traits (Saltonstall, 2002). Population genetics analyses have significantly contributed towards addressing questions of the origin and expansion of invasive species (Sakai *et al.* 2001). Such genetic approaches are being widely used to help control exotic haplotypes and conserve the native species in invaded regions.

Keeping in view the importance of trait analysis studies in the prediction and management of alien invasive species, this book aims to compare the traits of native and invasive aquatic plant species growing in various freshwater ecosystems globally. This focus on aquatic invasive plant species is because of the fact that the biological diversity of freshwater ecosystems is increasingly threatened by the introduction and rapid spread of invasive alien species (Zedler and Kercher, 2004; Olden *et al*. 2006). Recent studies (Johnson *et al*. 2008) have also indicated that the decline and extinction of species in freshwater ecosystems is greater than in terrestrial or marine environments and it is largely due to hydrological alterations and biological invasions. While the focus has been on the study of various facets of plant invasions in terrestrial ecosystems, aquatic habitats have received little attention with respect to the extent and impact of alien invasive species and the traits that promote invasiveness of alien species in these ecosystems (Zedler and Kercher, 2004).

INVASION OF AQUATIC ECOSYSTEMS

Understanding the factors associated with species invasiveness has been a challenging task for ecologists, and given the many interlinked elements of invasion ecology, there is no single structure for a broad review (Richardson and Pysek, 2006). While most of the previous studies regarding the success of invasives have been largely ecological, ecologists have now begun to focus on another potential explanation for the success of invaders: rapid evolutionary change (Bossdorf *et al.* 2005). Considerable research interest has been generated in recent years in developing the predictions of the features of species that enable them to become invasive (Stohlgren and Schnase, 2006; Wani *et al.* 2018).

While humans have greatly facilitated the invasion of aquatic alien species through international shipping and trade, aquarium releases and canal construction etc. (Rahel, 2002), flowing river waters act as natural conduits for the transport of propagules of alien species (Lavoie *et al.* 2003) across geographical and political boundaries. Aquatic habitats, usually being resource-rich, are particularly more vulnerable to the spread of invasive alien species (Zedler and Kercher, 2004) and many aquatic plants are characteristically invasive (Richardson *et al.* 2000). Once established, these invasive species impair ecological processes, such as the level of the water table, fire regimes, soil quality and nutrient cycling, thereby influencing the flow and chemistry of water, blocking drainage pipes, impeding navigation, and hindering commercial and recreational fishing. Invasive macrophytes often have negative effects on aquatic biodiversity, especially fish and macro-invertebrate communities (Keast, 1984; Lyons, 1989); yet some studies demonstrate that they may also be used positively by macro-invertebrates as well as fish (Cyr and Downing, 1988; Chilton, 1990; Bickel and Closs, 2008). Although biological invasions have been implicated as a principal cause of freshwater extinctions (Miller *et al.* 1989; Witte *et al.* 1992), researchers are confronted with the question of whether non-indigenous species drive or follow ecological changes leading to biodiversity loss (Didham *et al.* 2005).

In freshwater systems, invasion studies are relatively difficult due to the interaction of myriad stressors with invasive species. Habitat alteration facilitates invasions and exacerbates their impacts by increasing the connectedness of watersheds, thereby reducing native competitors and predators and increasing habitat homogenisation to the benefit of opportunistic invaders (Moyle and Light, 1996; Scott, 2006; Johnson *et al.* 2008). Impoundment and reservoir construction have been shown to promote the replacement of endemic riverine species by cosmopolitan lentic species that would otherwise be poorly suited to natural river flows (Duncan and Lockwood, 2001). In fact, the interaction of invasion and land use has homogenised freshwater biota across multiple spatial scales (Duncan and Lockwood, 2001).

Invasive species often have a set of traits associated that promote invasiveness such as small, short-lived seeds that can germinate without pre-treatment (e.g. freezing), with short juvenile periods and short intervals between large seed crops, a relatively large size, a longer flowering period, vegetative reproduction and perfect flowers (Crawley, 1987, 1989; Perrins *et al.* 1992). The relative competitive performance of native versus invasive species often depends on environmental conditions (Daehler, 2003). A similarity in climate between native and target regions has long been recognised as a basic requirement for successful invasion (Scott and Panetta, 1993). The establishment and spread of alien plants are sometimes limited by an imperfect climate match (Pysek *et al.* 2003). Fluctuations in the availability of resources can also play an important role in the invasion process (Davis *et al.* 2000; Davis and Pelsor, 2001). Furthermore, it is expected that invasive processes increase due to global climate change (di Castri, 1990; Sukopp, 1998; Dukes and Mooney, 1999; Pysek *et al.* 2002a), fragmentation of natural ecosystems (Rajmanek and Richardson, 1996; Falinski, 1998; Alpert *et al.* 2000) and growing urbanisation (Klotz, 1990; Sukopp, 1998; McKinney, 2002). Ecosystems with anthropogenic disturbances, such as cities or densely populated areas, contain high numbers of alien species (di Castri, 1989; Falinski, 1998; Pysek *et al.* 1998; Sukopp, 1998; McKinney, 2002), whereas natural or near-natural ecosystems (like natural forests or bogs) display a certain ecological resistance against the introduction of alien species (Elton, 1958; Rejmanek, 1989; Falinski, 1998). Some studies on local scales show that a high species richness of alien plants is coupled with a low species richness of native plants in man-dominated habitats (Mclntyre and Lavorel, 1994; Hoffmann, 1998).

In Kashmir (Himalayas), freshwater ecosystems comprise a sizeable area and support a rich biodiversity. Although several studies have been carried out on macrophytic diversity in different lentic and lotic freshwater bodies of Kashmir (Zutshi, 1975; Kak, 1990; Gopal and Chamanlal, 1991; Gopal and Zutshi, 1998), very little is known about the extent of invasion (Reshi *et al.* 2008). On the other hand, a relatively richer body of literature exists on the widespread invasion of non-native species and their impacts in aquatic systems elsewhere (Gollasch, 2002; Genovesi and Shine, 2004; Gollasch and Nehring, 2006; Lodge *et al.* 2006; Minchin, 2007).

CHARACTERISTICS OF AQUATIC INVASIVE SPECIES

Invasions by exotic species are now happening at an alarming rate (Ricciardi, 2007). The Canadian Wildlife Service defines an invasive species as a non-native species that has moved into a new habitat. These species grow and reproduce so aggressively that they displace some of the original components of the native community (White *et al.* 1993). Their spread is often associated with human activities, which enable them to have a wider range of distribution than unconditional dispersal. Invasive species can be introduced unintentionally (e.g. through inadvertent dispersal via cars or boats) or intentionally (e.g. as ornamental plants or for medicinal purposes). Several investigators have tried to find common characteristics of biological invaders (e.g. Hayes and Barry, 2008; Whitney and Gabler, 2008). A high dispersal rate, high fecundity, fast growth rate, early fruiting, vegetative reproduction and a wide range of tolerance to environmental conditions were all characteristics commonly found in invasive plants (Rejmanek, 1989. However, others have showed that there were no significant differences in the characteristics that separate invasive species from native and non-invasive species (Goodwin *et al.* 1999), and that predictors of invasibility could vary from species to species (Daehler, 2003). Goodwin *et al.* (1999) noted that the size of the native range was a more efficient variable from which to predict invasion success.

The introduction of invasive species into new habitats is the second greatest cause of biodiversity loss worldwide, after habitat degradation (Wilcove *et al.* 1998). Wilcove *et al.* (1998) stated that invasive species are one of the main stressors to native species. Yet, Gurevitch and Padilla (2004) confirmed that there is no concrete evidence to suggest that invasive species can cause extinctions and that it is the combination of invasion with other stressors (e.g. pollution, habitat destruction) that causes extinctions. Ricciardi (2004) suggested that invasive species can cause local extirpations at the population level. Nevertheless, several impacts of invasive species on habitat diversity have been well documented. Because they compete for space and resources, invasive species may negatively affect native species richness, although impacts tend to vary with invaders (Hejda *et al.* 2009). Moreover, hybridisation between native and invasive species was shown to enhance invasiveness in certain plant species (e.g. *Spartina maritima X Spartina alterniflora, Mentha arvensis X Mentha aquatica, Amelanchier humilis X Amelanchier 'clade B'*; Ellstrand and Schienrenbeck, 2000). Invasive species may have considerable social impacts, mostly on human health but also on our appreciation of the environment (Canadian Food Inspection Agency, 2008). The problem is also of particular concern in terms of biodiversity protection. In fact, 44 of the plant species at high risk in Canada are threatened by exotic species (Canadian Food Inspection Agency, 2008).

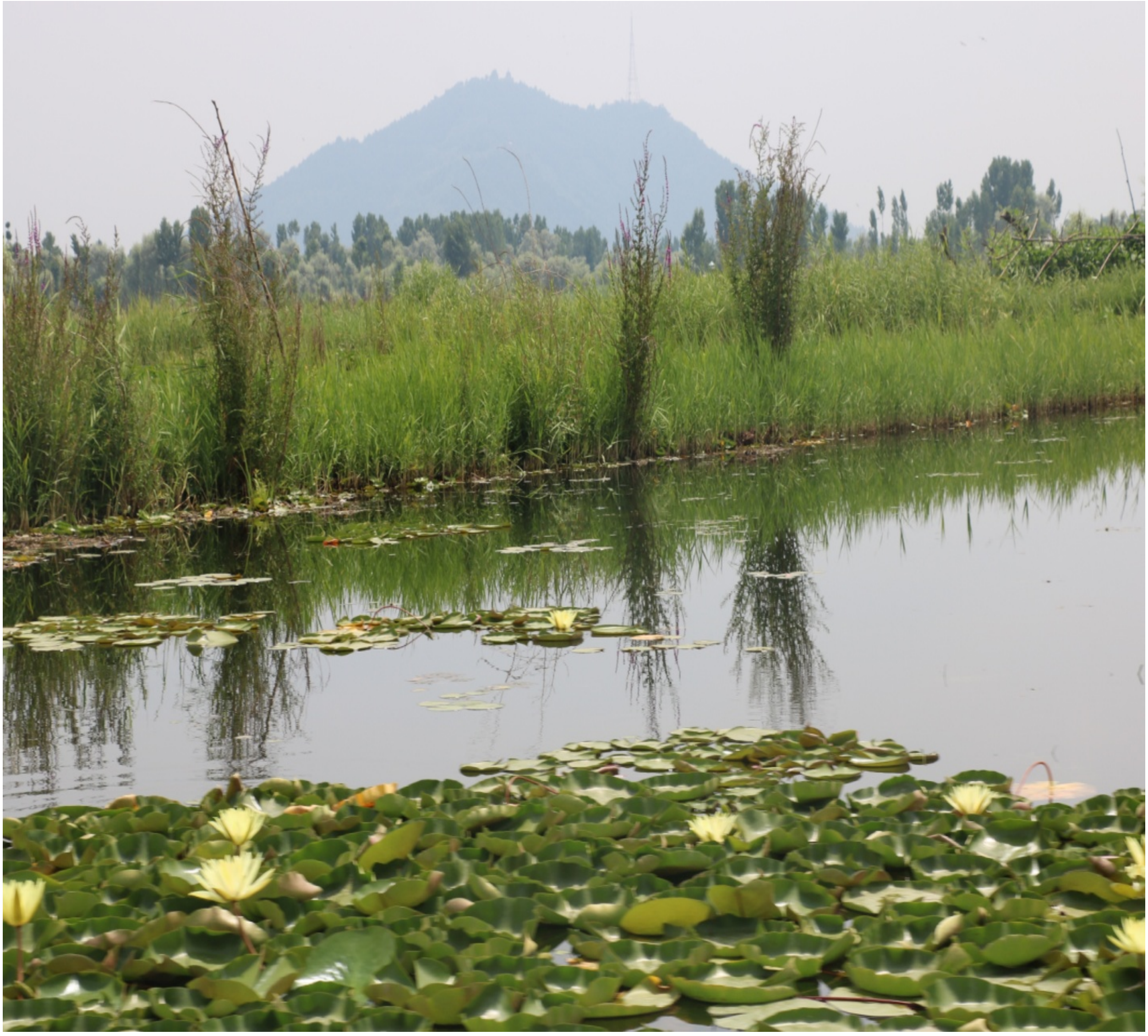
VULNERABILITY OF AQUATIC SYSTEMS TO INVASION

Attempts at identifying functional characteristics of successful plant invaders were only marginally successful, so other studies have tried to predict invasion success based on the habitat characteristics and community composition. The "efficient use" hypothesis states that invasive species are more efficient than native ones in terms of photosynthetic efficiency and biomass allocation or that they make a better use of resources (Zedler and Kercher, 2004). The "enemy release" hypothesis suggests that exotic species are more successful in their introduced range of distribution because they escape from natural enemies and develop novel competitive abilities in a new environment, unlike native species (Mitchell and Power, 2003; Keane and Crawley, 2002). The "diversity-invasibility" hypothesis proposes that more diverse plant communities are less easily invaded because they offer less availability of resources (Knops *et al.* 1999). However, Van Holle and Simberloff (2005) showed in an experimental design that plant species richness did not affect invasion success at a small scale. Finally, the "fluctuating resource" hypothesis states that fluctuations in resource supply can reduce competitive pressure and invasions are thus facilitated (Davis *et al.* 2000). In a review of literature, Theoharides and Dukes (2007) found that size and distribution of suitable habitat patches, landscape heterogeneity and dispersal corridors are all factors that facilitate the invasion success of exotic species at the landscape level. Principles of island biogeography theory, which describe factors that affect the species diversity of a specific community on islands, may be applied to other systems for a better understanding of the mechanism of biological invasion. Usually, there are more invasive species in small patches than in large patches, and invasive species in large patches are mainly distributed near the edges (Harrison *et al.* 2001). Similarly, at a broader scale, unfragmented landscapes tend to be less invaded than fragmented ones (Parendes and Jones, 2000). This is explained by the fact that the greater the length of contact between a pristine area and adjacent land uses, the greater the propagule pressure. Propagule pressure is a composite term of propagule number and propagule size (e.g. rhizome, abundance of seeds) in an introduction effort, and the number of introductions of invasive species.

Corridors may increase the invasibility of a site by increasing its patchwork connectivity with sources of propagules (Parendes and Jones, 2000). Rhizomes float on dead material (Minchinton *et al.* 2006) and rivers transport seeds, which may later be dispersed through floods (Egertson *et al.* 2004). The density of roads can also be linked with the spread of invasive species (Tyser and Worley, 1992; Lelong *et al.* 2009). Roads may favour invasion by creating new habitats in the roadsides. As they are commonly disturbed by pollutants and dust, clear-cutting, and inputs of de-icing salt, roadsides are harsh environments that can only be colonised by disturbance-adapted species (Tyser and Worley, 1992; Christen and Matlock, 2006). These areas represent open habitats free of vegetation and constitute ideal conditions for the establishment of invasive species (Tyser and Worley, 1992; Christen and Matlock, 2006). Traffic density along roads can also have an impact on the density of invasive species. In fact, deserted roads have been reported to be less invaded than frequently used ones (Parendes and Jones, 2000). The properties of adjacent land uses may also have significant impacts on the invasibility of a given site. The nature of land uses surrounding a given site may affect propagule pressure. Research conducted in 302 reserves in the Czech Republic showed that protected areas surrounded by homogenous or pristine land uses were less invaded than those surrounded by heterogenous lands (Pysek *et al.* 2002).

Wetlands surrounded by farms receive more nutrients which is reported to favour invasion and allows these species to grow more rapidly and form abundant colonies (Bertness *et al.* 2002; Bobbink *et al.* 2006). Moreover, isolated patches of habitat surrounded by farms are more exposed to propagules than patches surrounded by forest which provide a shade tolerance against some exotic communities (Theoharides and Dukes, 2007). An increase in population density around a given territory may also facilitate its invasibility, as more infrastructure is needed to support larger populations (McKinney, 2002). The development of infrastructure (e.g. houses, roads, parking) threatens the local diversity that is not adapted to such turbulence and therefore this favours tolerant invasive species (Hansen *et al*. 2007).

INVASIVE PLANT SPECIES IN WETLANDS



Wetlands are among the world's most invaded habitats (Bobbink *et al.* 2006). In the Canadian Great Lakes region, wetlands within agricultural and urban landscapes are the areas most exposed to several negative impacts of changes in sedimentation rates, hydrologic cycles (e.g. retention time), nutrient enrichment and soil compaction (Detenbeck *et al.* 1999).

Indian lakes and wetlands with fewer herbivores, an increase in nutrient inputs and greater vegetation removal were all considered as factors for enhancing the invasive capacities of *Phalaris arundinacea, Lythrum salicaria, Typha X glauca, P. australis* and *Myriophyllum spicatum.* The increased content of nitrogen, phosphorus and potassium was associated with a decrease in plant diversity, as it allows certain species to grow taller, shade competitors and produce more litter which leads to the formation of monocultures (Drexler and Bedford, 2002). The occurrence of monocultures of exotic species in aquatic systems was attributed to high concentrations of sediment and water nutrient levels that characterised wetlands located close to farms (Zedler and Kercher, 2004). Wetlands with hydrological disturbances are more susceptible to invasion and are characterised by a downturn in diversity of native species (Zedler and Kercher, 2004).

Attempts to control invasive species can be both costly and time consuming. Blossey (1999) pointed out possible negative impacts on regional flora and the environment that were induced by forms of control of invasive species, especially chemical control. Thus, some authors have recommended that prevention is often the most cost-effective way to control invasive species (Thuiller *et al.* 2005). To be able to efficiently allocate limited resources to prevent or control invasions, managers of protected areas need spatially explicit information about the risks and negative impacts of invasions (Byers, 2002a). Among different foci that risk assessments may have, identifying pathways of introduction is often designated as being crucial because it enables managers to identify potential sources of propagules (Byers, 2002b).

The common reed (*Phragmites australis*) is a cosmopolitan, hydrophytic grass found in wetlands and estuaries throughout the continental United States (Chambers *et al.* 1999). It presents various ploidy levels, with the tetraploid (4x) being the most widely distributed (Lambertini *et al.* 2006). A number of studies have shown the phenotypic and genotypic diversity of this species, allowing it to occupy various environments with different levels of success (Koppitz, 1999; Kuhl *et al.* 1999). *P. australis* is invasive in India and is also present in North America where it is described as a native. Fossilised 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 nuclear satellite DNA and chloroplast DNA showed that two haplotypes (M and I) were introduced to North America and 11 different haplotypes were native to this region. Haplotype M is European in origin and is considered invasive and problematic in North America. Haplotype I is believed to have originated from south of the United States and from parts of Asia, and is the most widespread haplotype along the Gulf Coast of the United States (Saltonstall, 2002, 2003a). I Meyerson *et al.* (2010 reported evidence of an additional invasion by another introduced haplotype (L), further complicating the description and history of these non-native *Phragmites* in North America. Field experiments have shown that the exotic haplotype M spreads more rapidly than the gulf haplotype, leading to the quick replacement of the latter (Howard *et al.* 2008). Rapid growth of the Eurasian haplotype M is responsible for the marked progression of the species, which is known for its competitive abilities and aggressiveness. It is believed that this haplotype is able to limit the establishment of more slowly growing native wetland plants, as well as change ecosystem functions and diversity (Chambers *et al.* 1999; Zedler and Kercher, 2004). Hence, this haplotype causes serious wetland conservation problems in north-eastern North America (Lavoie *et al.* 2003). In the *Phragmites*-dominant Great Lakes area, this haplotype is a well-established wetland species (Trebitz and Taylor, 2007).

In Quebec, the Eurasian haplotype M was most likely introduced via 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 change over time and space, it is clear that its spread in Quebec generally coincides with the major road construction. Genetic studies, as well as herbarium records, show that it is the spread of exotic haplotype (Delisle *et al.* 2003; Lelong *et al.* 2007; Jodoin *et al.* 2008). Ditches along highways have been shown to 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 is limited because of recent changes in climate.

Studies performed so far have shown that *P. australis* is capable of becoming a dominant species in multiple types of environment, such as salt marshes (Silliman and Bertness, 2004; Howard *et al.* 2008), freshwater marshes (Meyerson *et al.* 2000; Meadows and Saltonstall, 2009) and oligohaline marshes (King *et al.* 2007; 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 only a few studies that deal with a natural freshwater system containing disturbed and undisturbed sites, and exotic and native haplotypes of reed.

INVASION DYNAMICS IN AQUATIC SYSTEMS

The success of an invasion relies on certain factors like the broad tolerance to environmental stresses, release from enemies, hybridisation, efficient use of nutrients 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).

Introduced species are usually less affected by herbivory. When an exotic plant species is introduced from multiple continents, only a limited number of native herbivores will prefer to feed on it while most of the introduced herbivores tend to be generalist species (Liu and Stiling, 2006). Out of 170 species of herbivores listed in Europe that consume *P. australis*, only 26 are present in North America (Tewksbury *et al.* 2002). In addition, there is no clear evidence whether these 26 species of herbivores are specific to the introduced haplotype of *P. australis* in North America. In fact, knowledge of how specific that pests are to *P. australis* in North America is fragmented.

Lepidopterans rhizedra (native), *Phragmataecia castaneae*, *Schoenobius gigantella*, and *Chilo phragmitella* 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).

The invasive *P. australis* benefits from human activities and disturbances and takes greater advantage of perturbations (Havens *et al.* 2003; Howard *et al.* 2008; Hershner and Havens, 2008; Meadows and Saltonstall, 2009). A study showed that the exotic reed becomes predominantly abundant in wetlands delimited by at least 15%-developed areas (King *et al.* 2007). In another study, development infrastructure and transportation were thought to be responsible for 92% of the reeds' presence (Havens *et al.* 2003). Another important factor was a positive correlation between the distance to roads and the presence of the reed (Arzandeh and Wang, 2003; Lelong *et al.* 2009), as large road corridors contribute to a longer photoperiod. The common reed also displays a good tolerance to multiple natural stresses, such as high salinity, hydric stress and high pollutant concentrations (Guo *et al.* 2003; Morris *et al.* 2008; Hershner and Havens, 2008). It performs better under low salinity conditions (Silliman and Bertness, 2004), but can also survive in high salinity levels of 35 g/L (Adams and Bate, 1999). Uptake of toxic metals, such as lead, chromium and mercury, 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, the locations of 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).

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 can be caused by human disturbances (such as agricultural activity, roads and proximity to residential areas). The combined effects of human disturbances and increased nitrogen availability were able to explain more than 90% of the 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 a variation of 80% when both available nitrogen and salinity were taken into account (Silliman and Bertness, 2004). Nitrogen is the most common limiting nutrient in the case of *P. australis*; its invasion success is maximised where this nutrient is present in higher concentrations, primarily near agricultural fields (Trebitz and Taylor, 2007).

Genetic studies have shown that cross-hybridisation, i.e. hybridisation between individuals belonging to the native and invasive species, contributes more to the spread of the haplotype M in

Quebec than previously thought (Belzile *et al.* 2009). It results in greater genetic diversity and adaptability, which in turn have been found to promote invasiveness of the introduced species. Hybrids are intermediates between parents and can be more adapted to the particular environment as well as more competitive. Moreover, multiple introductions of invasive species increase the genetic diversity of the invader and the likelihood of hybridisation, and are frequently the cause of invasive hybrid progression (Ellstrand and Schierenbeck, 2000). At the species level, a case study of the invasive *Ulmus pumila* showed an unexpectedly high level of hybridisation and even genetic introgression with native tree species *Ulmus rubra* (Zalapa *et al.* 2010).

Intra-specific hybridisation of invasive *P. australis* with a native haplotype has been successful in a greenhouse experiment (Meyerson *et al.* 2000, but only one genetic study, based on field sampling in the Great Lakes area, suggests that hybrids can be found in nature (Paul *et al.* 2010b). 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 invasive and native haplotypes could produce intra-specific hybrid seeds, a phenomenon that was not observed in the previously mentioned greenhouse experiment (Paul *et al.* 2010a).

Allelopathic chemicals are released by an organism into the environment that can inhibit the growth of one or more of its neighbours. Examples of such processes are well known (Callaway and Ridenour, 2004); the 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: *Koeleria micrantha*, *Festuca idahoensis*, and *Arabidopsis thaliana* (Bais *et al.* 2003). Another well-documented example is the case of *Allaria petiolata*. The chemicals released by this plant species reduce plant growth and the survival of seedlings and interfere with mycorrhizal fungi, decreasing the diversity of fungi (Callaway *et al.* 2008). A recent 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 the expansion of *P. australis* into freshwater wetlands.

Asexual reproduction plays an important role in the establishment, growth and maintenance of *P. australis*. This species can expand in all directions with the help of runners and rhizomes (Warren *et al.* 2001). The rapid progression of this exotic haplotype forms a dense colony of reed, possibly leading to monocultures (Zedler and Kercher, 2004). These monocultures can be very dense (>180 stems/m^2) and are capable of changing trophic structures and, most probably, hydrological regimes (Haslam, 1972; Chambers *et al.* 1999). In addition, a number of studies have shown that there is a significant interaction between the amount of available nutrients and the removal of cover for other species. When the level of available nutrients is high, it can maximise all growth parameters (biomass, height) and most expansion parameters (biomass of advancing stems and height) (Minchinton and Bertness, 2003). Being one of the highest macrophytes confers this species an advantage in the competition for light. Moreover, a slower rate of decay has been shown to cause an increase in marsh elevation, the slower decomposition rate of cellulose and the filling of small creeks, 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 to the growth of reed. In fact, reed growth is relatively faster when the level of water is low. In the Boucherville islands area, maximum vegetative growth was recorded in the 1999–2002 time period when the mean water level was 5.72 m compared to 1996–1999 when the mean water level was 6.51 m (Hudon *et al.* 2005). The annual progression speed of rhizomes varies in the literature: 0.52 m to 0.91 m (Philipp and Field, 2005), 0.1 m to 0.94 m (Burdick and Konisky, 2003), 1 m (Haslam, 1972), 1.6 m to 2 m (Warren *et al.* 2001), 0.8 m to 1.2 m (Lavoie *et al.* 2003), 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 very few studies have reported seedlings in Canada. This could be attributed to the effect of high salinity, shading by other plants (Havens *et al.* 2003) or to low temperatures in areas where seeds could be found (Brisson *et al.* 2008; Bart and Hartman, 2003). Invasive *P. australis* seeds can speed up the germination rate, usually 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 failed to survive through to the next growing season (Shay and Shay, 1986). It was also observed that this species is not an important component of the seed bank there. In addition, mature seeds can have very low viability, preventing their germination (Kettenring and Whigham, 2009). Higher temperatures, like those predicted by climate change could mean that more seeds will germinate, hence creating new opportunities for dispersal (Brisson *et al.* 2008). A recent study has shown that seed propagation could be an important vector in long-distance dispersal of the invasive haplotype (Belzile *et al.* 2009). The species, which is already very resistant to control measures, is becoming even more competent at spreading.

Although this species presents broad ecological tolerances and characteristics that favour 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 restricted when the water level rises for long periods; it will not be able to establish itself in water deeper than 0.5 m unless water level fluctuations occur. Once established in an area, if the water level rises above 1 m, the population will not survive more than three years. In similar conditions, most of the well-established individuals will already be dead after two 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 these limiting conditions is probably due to limited dissolved oxygen in the water when the water level rises (Amsberry *et al.* 2000). Further, it has been suggested that frost slows its progression (Jodoin *et al.* 2008), while severe frost can kill the rhizomes (Haslam, 1972). Cold winter conditions limit the 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, *P. australis* is also slowed by some other plant species like *Typha* sp. or *Spartina* sp. due to inter-specific competitive interactions for resources (Amsberry *et al.* 2000).