Invasive Plant Science and Management

Roadside as Invasion Pathway for Common Reed (*Phragmites australis*)

Jacques Brisson, Sylvie de Blois, and Claude Lavoie*

Invasive Plant Science and Management 2010 3:506–514

Roadside as Invasion Pathway for Common Reed (*Phragmites australis*)

Jacques Brisson, Sylvie de Blois, and Claude Lavoie*

The rapid progression of an invasive genotype of common reed along roads and other linear infrastructures in North America provides one of the most spectacular examples of the role of transportation corridors as invasion pathways. In this paper, we discuss ecological patterns and processes in roadside habitats important for understanding the invasion dynamics of common reed from coastal areas inland. Frequent disturbances in roadsides combined with potentially high levels of nutrients from adjacent land and stress conditions (from deicing salt and other pollutants) mimic the conditions unfortunately found more and more in natural wetlands. The novel contribution of roads is the creation of linear wetlands with an unprecedented level of connectivity. Genetic evidence shows that invasion inland coincides with the intensification of the road network. Time series analysis of remote sensing data reveals impressive rates of invasion of roadsides and other linear infrastructures, suggesting prime conditions for common reed in these novel habitats. Whereas reed dispersal along roads was thought to be largely due to rhizome transport, new evidence suggests a significant contribution of sexual reproduction and seedling establishment, likely enhanced by climate warming at northern latitudes. There is little evidence that other wetland plants can slow down vegetative expansion of common reed in roadside habitats, but plant cover could prevent seedling establishment and shading by shrubs and trees limit lateral clonal expansion. The fact that common reed possibly provides water treatment and other ecosystem services in roadsides must be carefully weighed against the threat to biodiversity in natural systems. All this begs for investigating urgently if, where, and how we should intervene without compromising the great value of wetlands of conservation interest intersected by roads.

Nomenclature: Common reed, *Phragmites australis* (Cav.) Trin. ex Steud.

Key words: Corridor pathway, ecosystem services, linear wetland, plant invasion, right-of-way management, road ecology, wetland plant competition.

Transportation corridors provide relevant invasion pathways that must be assessed if we hope to manage biological invasions (Christen and Matlack 2009; Hulme et al. 2008). The proliferation of linear infrastructures with the construction of roads, railways, drainage ditches, and canals often results in novel habitats that provide a vast network of "empty niches" for exotic plant species to exploit. Ecological conditions in these habitats can select for highly stress-tolerant plant phenotypes or influence competitive plant interactions (Arteaga et al. 2009; Grant et al. 2007; Greenberg et al. 1997). Moreover, linear habitats connect ecosystems, landscapes, and regions, and therefore when invaded may contribute to increase propagule pressure in the intersected land (Findlay and Bourdages 2000; Garnier et al. 2008).

The expansion of the invasive macrophyte *Phragmites australis* (Cav.) Trin. ex Steud. (hereafter referred to by its generic name) in inland areas of North America provides one of the most spectacular examples of the role of transportation corridors as invasion pathways (Catling and Carbyn 2006; Gervais et al. 1993; Jodoin et al. 2008; Lelong et al. 2007; Maheu-Giroux and de Blois 2007). *Phragmites*' expansion in North America has been explained by anthropogenic changes to wetlands such as disturbances to hydrologic cycles, plant communities, soil, and nutrient regimes (Bart and Hartman 2000; Chambers et al. 2008; Meyerson et al. 2000; Rice et al. 2000) and by the introduction from Eurasia in the 19th century of an exotic genotype tolerant to these new ecological conditions (Saltonstall 2002). In areas where climatic and edaphic conditions allow, this introduced genotype thrives in the vast network of linear wetlands created by drainage ditches alongside transportation infrastructures and agricultural

---

DOI: 10.1614/IPSM-09-050.1

* Professor, Institut de Recherche en Biologie Végétale, Département de Sciences Biologiques, Université de Montréal, 4101 East Sherbrooke St., Montréal (QC) H1X 2B2, Canada; Associate Professor, Department of Plant Science and McGill School of Environment, McGill University, Macdonald Campus, 21,111 Lakeshore Road, Ste. Anne de Bellevue (QC) H9X 3V9, Canada; Professor, Centre de Recherche en Aménagement et Développement, Université Laval, Québec (QC) G1V 0A6, Canada. Corresponding author's E-mail: jacques.brisson@umontreal.ca

land (Jodoin et al. 2008; Maheu-Giroux and de Blois 2007). As a result, natural wetland areas that would have been otherwise relatively isolated by inhospitable upland environments have become connected and at increased risk of invasion.

In North America, the majority of the literature on *Phragmites* has focused on invasion patterns in tidal wetlands of the eastern coastal areas. In this paper, we discuss ecological patterns and processes in roadside habitats important for understanding the invasion dynamics of common reed. We believe that roadside environments provide a relevant system to investigate different aspects of biogeography, landscape ecology, and competition dynamics in relation to invasion theory. We refer to the exotic genotype of *Phragmites* (haplotype M; Saltonstall 2002), unless otherwise specified. Our focus is on *Phragmites*, but lessons can be applied to other species with somewhat similar ecological requirements and behaviors, such as *Arundo donax* L. (giant reed) or *Typha* × *glauca* Godr. (hybrid cattail). First, we present evidence of historical and current invasion patterns of *Phragmites* in road corridors. We then discuss current knowledge of *Phragmites'* establishment and propagation along roads and relate these processes to abiotic (soil chemistry) and biotic (plant interactions) factors in roadside environment. We conclude by proposing research directions that could help us decide if, where, and how we should intervene so as not to compromise the value of ecosystems intersected by roads.

Evidence for Roads as Invasion Pathway for *Phragmites*

Evidence for retracing invasion pathways for plant species comes from examination and genetic analyses of herbarium specimens and populations in the field (Delisle et al. 2003; Gervais et al. 1993; Lelong et al. 2007; Saltonstall 2002;) as well as time series analysis of established populations using remote sensing (Hudon et al. 2005; Lathrop et al. 2003; Maheu-Giroux and de Blois 2005, 2007; Rice 2000; Wilcox et al. 2003). Along the Atlantic coast of the United States, the exotic genotype of *Phragmites* (haplotype M) was likely introduced in the early 19th century from Eurasia. According to genetic evidence, after a lag of some decades, the exotic genotype rapidly spread in coastal wetlands and inland areas in the last century. Saltonstall (2002) hypothesized that this rapid expansion could have been facilitated by the construction of railroads and major roadways across North America in the late 19th and early 20th centuries. Indeed these new infrastructures would have not only accelerated the transport of propagules by cars and trains from the coast inland, but would have provided an extensive network of new habitats for the introduced genotype.

In eastern Canada, a detailed historical reconstruction of the distribution of native and exotic genotypes based on the genetic approach developed by Saltonstall (2002) allowed a test of this hypothesis. Using historical records from herbaria and from current specimens, Lelong et al. (2007) found evidence that the exotic *Phragmites* had been present in the province of Quebec at least since 1916, spreading first along the St. Lawrence River. Whether propagules were transported by water from their point of introduction or by humans traveling on or along the river is not known, but the oldest historical specimen was collected downriver, making it unlikely that transport upstream would have been unaided. The rapid expansion of the exotic genotype inland in Quebec was initiated only in the mid-1960s, and coincided with the initiation of a large highway construction program (Lelong et al. 2007). As early as the 1980s, Gervais et al. (1993) had noted the rapid invasion of roads and wetlands in Quebec, initiating one of the first extensive historical reconstructions of *Phragmites* invasion patterns inland. In four Ontario townships, historical genetic records of populations of native and exotic *Phragmites* dated the introduction of the exotic genotype back to the 1970s; the latter was much more strongly associated with roads than the native one (Catling and Carbyn 2006). More recently, in the 1990s, episodes of low water level resulted in a new surge in the establishment of the exotic genotype along the St. Lawrence River (Hudon et al. 2005) and in wetlands of the Great Lakes (Wilcox et al. 2003).

Phragmites is commonly reported as colonizing roadside habitats and other linear infrastructures, but there are still surprisingly few studies that explicitly consider roads as habitat corridors for *Phragmites*. Because of the ubiquitous presence of *Phragmites* along roadsides in eastern Canada, Jodoin et al. (2008) surveyed *Phragmites'* distribution along all major highways in the province of Quebec. The patterns they unveiled dramatically showed the extent of roadside invasion, with *Phragmites* being present in 67% of the 1,359 1-km (0.621-mile) highway sections surveyed in 2003. Not surprisingly, genetic analyses showed that only 3 out of 260 tissue samples collected along roadsides were native; all others belonging to the invasive haplotype M. In the southwestern part of the province, where climate is the warmest, *Phragmites* formed dense continuous stands, which thinned out in the northern regions, suggesting that climate was limiting or that edaphic conditions were less suitable.

Major highways are not the only road structures invaded by *Phragmites*. Lelong et al. (2009) mapped *Phragmites* populations located along all road types of a large region (1,400 km^2) of the southernmost part of Quebec. Logistic regression models using landscape metrics showed that road type was the most important factor in determining the presence of the *Phragmites* in agricultural or forest landscapes. A major road (national or regional) was more likely to be invaded by *Phragmites* than a local road, especially if the road was located on organic or clay surface deposits more typical of wetland conditions. Major roads tend to have more traffic, which may result in more propagules being transported (Gelbard and Belnap 2003). They are also surrounded by wider ditches, which correlate with increased density of *Phragmites* (S. de Blois, unpublished data).

In the agricultural regions of the St. Lawrence lowlands, the 1960s and 1970s saw not only the construction of extensive highway networks, but also the proliferation of agricultural drainage ditches. This created the conditions for a rapid intensification of agricultural activities, with the cultivation of corn and soybeans aided by fertilizers that end up partly in drainage ditches. It also contributed to increased habitat connectivity, effectively creating a dense network of linear wetlands that included roadside and agricultural ditches. Maheu-Giroux and de Blois (2005, 2007) reconstructed recent invasion patterns (1985–2002 and 1987–2002) in the linear wetlands of two landscapes. Habitats considered included roadside and railroad ditches, agricultural drainage ditches, and riparian corridors. At the beginning of the reference period, *Phragmites* populations were very sparsely distributed and found only in roadside habitats. These then served as invasion foci into other parts of the landscape. In only 15 yr, linear habitats showed spectacular invasion patterns with intrinsic rates of increase of *Phragmites* populations generally exceeding those reported for natural wetlands. Interestingly, riparian habitats were spared, being little invaded except when they intersected roads, perhaps because they were generally less disturbed than anthropogenic linear wetlands and offered fewer sites for establishment (Maheu-Giroux and de Blois 2007). A detailed network analysis of colonization events showed spatial dependence between the appearance of new distinct *Phragmites* patches and source populations in the previous time period over a range of spatial scales. The numerous new colonization events observed both within and across ditches, however, suggested a stronger than expected contribution of sexual reproduction to *Phragmites*' dispersal (Maheu-Giroux and de Blois 2007).

Establishment and Propagation along Roads

The establishment phase of *Phragmites* in nontidal freshwater marshes as well as in roadside ditches is probably the least known phase—and yet one of the most crucial—in *Phragmites* invasion. There is evidence for establishment both by sexual and vegetative means. Their respective contributions to *Phragmites*' dispersal inland and how these contributions vary in space and time remains unknown despite the relevance of this information for limiting invasion. Although our focus here is on roadsides, most of what is known about the dispersal of *Phragmites* comes from coastal wetlands, so we will draw relevant information from habitats other than roadsides as needed.

Dispersal through Vegetative Propagules. Because seed viability and seedling establishment are thought to be low at best (Gervais et al. 1993), and because rhizome fragments have a large capacity for producing new sprouts (Bart et al. 2006), it is generally assumed that, in North America, *Phragmites* establishes mainly through the transport and burial of rhizome fragments (Bart et al. 2006; Chambers et al. 1999; Small and Catling 2001). Low genetic or molecular variation in some populations has been reported as evidence of dispersal through vegetative propagules (Fournier et al. 1995; Keller 2000; Pellegrin and Hauber 1999). Potential dispersal vectors such as rodents, floodwater, or birds transporting nesting material have been proposed (Small and Catling 2001). More important sources of dispersal, however, would be through ditching, plowing, cleaning out ditches, and other human activities that provide plenty of occasions for inadvertent rhizome transport by machinery (Bart and Hartman 2003). Ailstock et al. (2001), for example, reported as personal observation an instance where "69 rhizome buds were removed from the treads of a tracked vehicle working in a *Phragmites* dominated community." Many of the *Phragmites* populations in the Charles River watershed in Massachusetts are along roadsides and near construction sites, and Keller (2000) suggested that they might have originated from deposit of fill containing rhizome fragments from distant locations. However, although inadvertent rhizome transport by machinery is a likely scenario for reed dispersal along roadsides, the evidence supporting this hypothesis is rather circumstantial. Other than anecdotal reports or unsubstantiated assertions, we found no comprehensive direct evaluation of rhizome transport and subsequent establishment in field conditions.

Dispersal through Seeds. Despite numerous early statements suggesting otherwise, *Phragmites* is capable of sexual reproduction in North America, but seed production, viability, and germination rates vary greatly and remain low or absent in many populations (Mal and Narine 2004; Tucker 1990). There is nevertheless a body of greenhouse, laboratory, and garden experiments demonstrating successful seed germination or seedling survival and growth under a range of conditions (Gervais et al. 1993; Harris and Marshall 1960; Lissner and Schierup 1997; Maheu-Giroux and de Blois 2007; Meyerson et al. 2010; Saltonstall and Stevenson 2007; Wijte and Gallagher 1996). In a survey of 77 populations in Quebec, Gervais et al. (1993) found low seed production, with an average from 0 to 5% of flowers with seeds in most locations, although a few populations showed higher production, up to 59% in one case. They also mentioned high variation in seed germination rate in laboratory conditions (from 0 to 100%), attributing much of this variability to differential damage by a fungal pathogen, *Claviceps microcephala* (Wallr.) Tul. In another study, Meyerson et al. (2010) measured germination rates of 56 to 100% in *Phragmites* from several locations in eastern North America. Germination tests showed seed viability to vary widely among roadside ditch populations in southern Quebec, but viability was overall relatively low with a mean of about 5%; seed production on the other hand was high, so low viability did not appear to be a limiting factor (Maheu-Giroux and de Blois 2007). In Europe, seed production and viability was found to vary depending on climatic conditions (McKee and Richards 1996), and the same probably holds in North America.

Successful establishment through sexual means not only depends on germination and seedling development during the first growing season, but also on the capacity to withstand the critical first winter. In Europe, the mortality rate of seedlings during the first winter is reported to be very high when the previous growth season had not been long or warm enough for the newly emerged seedlings to reach a critical size with an adequate amount of resources in their storage organ (Haslam 1975; Weisner and Ekstam 1993). This suggests that there could be a strong climatic determinant in seedling establishment, particularly at the northern limit of the species range. Gervais et al. (1993) raised doubts regarding successful establishment from sexual reproduction in Quebec based on the slow seedling development they observed in laboratory conditions.

Seedling establishment is reported to occur on moist, unvegetated bare soil (Ailstock 2001; Mal and Narine 2004; Mauchant et al 2001) and human activities such as cleaning out ditches provide perfect conditions for germination. Surprisingly, published accounts of observations of seedling establishment in freshwater wetlands or roadside habitats, especially beyond the first growing season, are rare. Brisson et al. (2008) identified unequivocally 38 *Phragmites* seedlings in roadside ditches of southern Quebec that had been disturbed; 11 seedlings survived through their second growing season. This represented, to our knowledge, the first documented record of field establishment of *Phragmites* by sexual reproduction in Canada. Previously, Harris and Marshall (1960) reported the presence of *Phragmites* seedlings in 1954 on a mud flat of Mud Lake National Wildlife Refuge (Minnesota), but no monitoring beyond the first season was reported. In addition to these two documented observations of naturally established *Phragmites* seedlings, there is also indirect but strong evidence of sexual reproduction in inland wetlands. Belzile et al. (2010) found larger than expected genetic variation among *Phragmites* patches recently established along a lake in Quebec. This very high level of genetic variation was incompatible with the hypothesis that invasion was initiated by the introduction of vegetative diaspores from a few clones, implying seed dispersal. Maheu-Giroux and de Blois (2007) observed numerous colonization events in roadside ditches of southern Quebec, especially within the period 1995–2002, that could also hardly be explained by vegetative dispersal alone. Hudon et al. (2005) similarly suspected that seed dispersal played a role in the recent accelerated progression of common reed along the St. Lawrence River (Quebec).

It is unclear whether the presence of seedlings in roadside ditches and freshwater wetlands has been simply overlooked before, notably because of the difficulty in spotting and identifying them, or whether seedling establishment is a relatively recent phenomenon, especially at the northern limit of the species range in North America. The indirect evidence mentioned above concerns populations mostly established after 1990, and the establishment episodes documented by Brisson et al. (2008) coincide with some of the warmest years on record at this latitude. Considering that climate is an alleged limiting factor for seedling establishment in Europe (Haslam 1975; Weisner and Ekstam 1993), it is entirely possible that the recent climate warming at northern latitudes played a role in facilitating seedling establishment (Brisson et al. 2008).

Lateral Expansion of *Phragmites* Patches. Whatever the mode of dispersal, vegetative or sexual, lateral expansion of established *Phragmites* patches is always through strong vegetative spread of a dense front of roots, rhizomes, and aboveground stems, eventually developing in nearly monospecific stands (Mal and Narine 2004). Physiological integration of ramets may contribute to the competitive success of *Phragmites* by allowing expansion in more stressful or less optimal habitats (Amsberry et al. 2000). Hence, it is not uncommon to see a dense *Phragmites* population in a roadside ditch expand into adjacent upland areas up to the forest margin where edaphic conditions would normally limit its growth.

Phragmites produces both horizontal and vertical rhizomes; the horizontal ones, mostly located at a depth of up to 1 m, are responsible for lateral expansion. Annual growth rates of horizontal rhizomes have been estimated to be between 0.5 and 4 m yr^{-1} (Haslam 1972). *Phragmites* also produces runners (or stolons), which can develop from a fallen aerial stem or from a vertical rhizome along with aerial shoots. Since their annual growth rate can exceed 10 m yr^{-1} (Haslam 1972), runners could play a significant role in the fast lateral expansion of *Phragmites* colonies. Runners are not common in roadsides, however, so we found no estimate of their proportional contribution to lateral expansion compared to horizontal rhizomes.

Based on the annual monitoring of lateral expansion of approximately 100 *Phragmites* colonies in roadside ditches, Lavoie (2008) reported average annual linear progressions from 0.8 to 1.2 m, depending on years. Bellavance and

Brisson (2010) monitored lateral expansion of *Phragmites* in roadsides based on the exact position of the last standing culm in eight patches and found annual progressions varying from 1.0 to 5.6 m. These values appear overall larger than those found for *Phragmites* patches in tidal wetlands, as determined by aerial photographs (Warren et al. 2001: 1.6 to 2.0 m yr^{-1} in the lower Connecticut River; Philipp and Field 2005: 0.52 to 0.91 m yr^{-1} in Delaware salt marshes) or based on field measurements (Burdick et al. 2001: -0.1 up to 0.94 m yr^{-1} depending on site, in Rowley, MA). Both Bellavance and Brisson (2010) and Lavoie (2008) found a difference in expansion between years, suggesting climatic control. Other factors that may affect expansion include abiotic conditions and competitive interactions.

Ecological Effects in Roadside Invasion

Several ecological factors relevant to roads influence *Phragmites* dispersal or expansion. Moving vehicles act as dispersal vectors by transporting seeds (Hodkinson and Thompson 1997; Von der Lippe and Kowarik 2007; Wace 1977; Zwaenepoel et al. 2006). Road construction involves the transport of large quantities of soil that can contain *Phragmites* rhizomes. Ditch cleaning or roadfill create large areas of barren soil that provide ideal conditions for seedling establishment. Mowing and vegetation management, by removing native plant cover and woody species, favor *Phragmites*, which is resistant to mowing unless it is repeated very frequently (Derr 2008).

Two sets of ecological factors relevant to roads deserve particular attention. First, soil conditions are suspected to be an important determinant of the success of *Phragmites* along roads. Second, biotic interactions with other plant species are worth considering since they have important management implications.

Roadside Soil Chemistry. *High Nutrient Levels.* Fertilizer nutrients leaching from nearby agricultural land and nitrogen from vehicles' nitrous oxide emissions result in high nutrient level in roadside ditches (Angold 1997; Cale and Hobbs 1991). *Phragmites*' growth and performance benefit more than most of its competitors from nutrient enrichment (Ravit et al. 2007; Rickey and Anderson 2004). Rickey and Anderson (2004) suggest that reducing nitrogen in roadsides may aid in controlling *Phragmites.*

Soil Pollutants. Roadside ditches typically carry a large variety and quantity of pollutants. Typical contaminants include several heavy metals, often derived from gasoline additives including lead, aluminum, iron, cadmium, copper, manganese, nickel, zinc, and others (Trombulak and Frissell 2000). Organic pollutants and hydrocarbons are also frequent contaminants in road corridors. Plants species have differential susceptibilities and responses to pollutants, but there is no doubt that *Phragmites* is very tolerant to a wide range of contaminants. This high tolerance is certainly one of the reasons, along with high productivity and a deep root system, for the wide use of *Phragmites* in constructed wetlands for wastewater treatment (Brisson and Chazarenc 2009; Tanner 1996; Yang et al. 2007).

High Salinity. The amount of deicing salt used for security purposes on roads and highways can be very high in regions with severe winters (up to 700,000 metric tons] each year in the province of Quebec alone; Jodoin et al. 2008). Much of this salt simply washes out in roadside ditches, increasing salinity levels, with large variation depending on season and rainfall (Richburg 1999; Wilcox 1986a). High salinity in roadsides significantly impacts plant survival and growth and community composition (Hughes et al. 1975; Lumis et al. 1976), even allowing maritime halophytic plants to establish far from marine coasts (Moore 1982). *Phragmites* tolerates brackish water, as demonstrated by its severe invasive status in coastal tidal wetlands of eastern North America (Farnsworth and Meyerson 2003; Lissner and Schierup 1997). It has therefore been suggested that the increased salinity due to deicing salt is an important factor contributing to *Phragmites* invasion in roadside ditches by reducing competition from salt-intolerant species (Catling and Carbyn 2006; Jodoin et al. 2008; Maheu-Giroux and de Blois 2007; McNabb and Batterson 1991; Zedler and Kercher 2004).

There has been a large number of experiments measuring or comparing the effect of salinity on *Phragmites* at various stages of development (Bart and Hartman 2003; Paradis 2008; Vasquez et al. 2006; Wijte and Gallagher 1996). *Phragmites* is sensitive to high salinity compared to real halophytes such as *Spartina* spp., but it tolerates a wide range of salinity conditions in the fresh-to-brackish spectrum, with little effect on biomass (Meyerson et al. 2000). There is experimental evidence that a moderate level of salinity may provide an additional competitive advantage to *Phragmites* (see next section), but in a Massachusetts wetland impacted by deicing salt, *Phragmites* abundance was not well correlated with elevated salt concentration (Richburg 1999). More field evidence is needed to assess the real impact of salinity in facilitating roadside invasion.

Plant Interactions. *Phragmites* may displace native plant species with negative impacts on biodiversity (Keller 2000; Meyerson et al. 2000; Silliman and Bertness 2004). On the other hand, competition with plants may prevent *Phragmites* establishment or slow down invasion, suggesting prevention strategies (Minchinton and Bertness 2003).

Plant Cover to Prevent Establishment. Because *Phragmites* germination and early seedling growth is poor under competition (Haslam 1971), establishment is best on bare ground. This represents a valuable prospect for preventing *Phragmites* seedling establishment in roadsides and other disturbed sites. Encouraging the rapid development of a competitive plant cover, either by facilitating natural restoration or by introducing suitable plant species, represents a promising alternative that could be less environmentally costly than attempting to control well-established *Phragmites* stands.

Shading by Woody Plants. Because *Phragmites* is intolerant of shade, it is either absent, or has reduced density, height, or proportion of flowering shoots under shrub or tree canopy. Therefore planting woody species along roadsides could help limit *Phragmites* expansion (Havens et al. 2003). This may offer another preventive strategy to reduce the density of *Phragmites* within and outside the corridor when the presence of shrubs or trees is compatible with road operation and safety.

Competition with Other Herbaceous Wetland Species. There are numerous studies on the competition between *Phragmites* and other co-occurring wetland species. Several involve exclusively halophyte species of coastal wetlands (Amsberry et al. 2000; Rickey and Anderson 2004; Wang et al. 2006), whereas others examine plants that may also occur in roadside habitats such as cattails (*Typha* spp.) (Bellavance and Brisson 2010; Konisky and Burdick 2004; Szczepanska and Szczepanski 1982). The cattails *Typha latifolia* L., *Typha angustifolia* L. and their hybrid *Typha* ×*glauca* Godr. are widespread in North America (and Europe) and dense stands of cattails alternating with stands of *Phragmites* are common sights in roadside ditches of the St. Lawrence lowlands. Given their similar niche and traits, competition should be intense at the zone of contact between these populations. Moreover, competitive outcomes vary depending on environmental conditions, including nutrient status and salinity. Like *Phragmites*, cattails are tolerant of disturbance and salinity (especially *T. angustifolia* and *T.* ×*glauca*) (Konisky and Burdick 2004), so the use of deicing salt has also been suspected of promoting spread of *Typha angustifolia* and *T.* ×*glauca* in roadside ditches outside their native range (Galatowitsch et al. 1999). Cattails have dense rhizomes and strong vegetative spread, they form large nearly monospecific stands, and they are considered invasive in many areas (Shih and Finkelstein 2008). Like *Phragmites*, they have strong competitive impact on other plants; the determination of the competitive hierarchy of 26 wetland plants in North America assessed against a common indicator (phytometer) species ranked *Phragmites* and *Typha* ×*glauca* (the only cattail species tested in this study) respectively fourth and first under high-nutrient status (Keddy et al. 2000). If there are species that could slow down the vegetative spread of *Phragmites*, cattails certainly appear to be good candidates (Bellavance and Brisson 2010). Experiments testing *Phragmites*–*Typha* interactions, however, provided mixed results. In Europe, a pair-wise competition experiment showed *T. latifolia* to be a better competitor than *Phragmites* (Szczepanska and Szczepanski 1982). A field experiment in New England salt marshes including salinity and flooding as stressors also found a small (but nonsignificant) competitive advantage of cattail (this time *T. angustifolia*) over *Phragmites* (Konisky and Burdick 2004). On the other hand, mesocosm competition experiments monitoring lateral expansion and biomass showed *Phragmites* to outcompete *Typha* spp. with or without increased salinity (Bellavance and Brisson 2010; Paradis 2008). The latter results corroborated observations and experiments on interactions between *Phragmites* and cattails conducted in roadside ditches. Monitoring several zones of contact between patches over 3 yr in ditches, Bellavance and Brisson (2010) showed that *Phragmites* was consistently progressing over cattails. Moreover, in roadside ditches, the progression rate of *Phragmites* against cattail was found to be relatively similar to its progression rate in zones where all plants were removed, suggesting that cattails had little impact in slowing down *Phragmites*.

In mesocosms, *Phragmites* was superior to cattails at all salinity levels tested, but its competitive advantage was greatest at an intermediate salinity level (Paradis 2008). In conclusion, there was little effect of competition from co-occurring herbaceous wetland species on *Phragmites*' clonal expansion in the disturbed context of roadside ditches, even from highly competitive species such as cattails.

Research Directions

In a review of invasion pathways, Hulme et al. (2008) argued for a better understanding of the role of transport infrastructure (“corridor pathway” sensu Hulme et al. 2008) in the introduction and dispersal of alien species. Other weedy or invasive species than *Phragmites* colonize transportation corridors. For example, Olson et al. (2009) reported that the invasive hybrid *Typha* ×*glauca* was favored under roadside ditch conditions. Also, highway drainage ditches may have facilitated the migration of purple loosestrife (*Lythrum salicaria* L.), increasing its ability to invade wetland sites (Wilcox 1986b). Species of the genus *Fallopia*, some of which are among the worst invaders in the world, have been associated with roadsides and now wetlands in North America (Richards et al. 2008). There are, in addition, several other weedy species thriving in the drier portions of transportation rights-of-way. The case of *Phragmites* and these other successful invaders highlights the strong interaction between roadside environmental conditions and species traits, which results in the selection of highly successful invaders. Frequent disturbances in roadsides combined with potentially high level of nutrients but also stress conditions (e.g., salt and other pollutants) mimic the conditions unfortunately found more and more in natural wetlands. The novel contribution of roads, however, is the creation of linear wetlands with unprecedented level of connectivity, which benefits even species that depend mostly on clonal propagation. It would be wise, therefore, to monitor the road environment for exotic plant species with the same diligence with which we would monitor ballast water for aquatic species, that is, *before* these species become a nuisance.

Most of what we have learned about *Phragmites* biology, ecology, and impact on biodiversity come from coastal wetlands or from studies in native habitats of Europe or Asia. There is less information about freshwater ecosystems and even less so about linear habitats. We do not know, for instance, the relative contribution of sexual reproduction vs. vegetative propagation to establishment in linear habitats or in the wetlands that they intersect. Determining establishment modes is tremendously important for management because prevention measures will differ depending on whether *Phragmites* establishes mostly by seeds or mostly vegetatively. For example, establishing a competitive plant cover may inhibit *Phragmites* seed germination and seedling growth but is probably much less efficient against invasion through vegetative means. Moreover, climate change is likely to have an impact on the reproductive and establishment potential of *Phragmites* and this should be investigated.

Transportation right-of-way managers are increasingly aware of the impacts the infrastructures they manage have on adjacent land uses, especially when the adjacent land is a nature reserve or is cultivated. There may be incentives in controlling *Phragmites* within ditches when the species affects drainage or to prevent contamination of adjacent land. It is still unclear, however, how *Phragmites* specifically invades the natural wetlands that roads intersect. Roads bring propagules to an area but will these always eventually colonize adjacent undisturbed wetlands? Is it that the road brings also disturbances, creating the conditions for the establishment of *Phragmites*? In this case, will invasion be confined only to areas immediately affected by roads? These questions are important because if *Phragmites* has little chance of invading undisturbed sites, this may suggest management strategies to confine *Phragmites* within the transportation corridor with minimal impact on biodiversity. Such strategies may include using barriers of shrubs or trees or reducing as much as possible disturbances to adjacent land when constructing roads.

Road networks bring together *Phragmites* colonies that were previously isolated. Not only could this increase genetic diversity in the exotic *Phragmites* populations, but connected road networks may also increase the chance of bringing together exotic and native *Phragmites* populations. Although hybrids in the wild remain to be found, the fact that they can be produced under experimental conditions using hand pollination techniques confirms that both lineages can interbreed (Meyerson et al. 2010). Decline of the native *Phragmites* subspecies may occur through genetic swamping if hybridization occurs in the field (Meyerson et al. 2010).

Finally, there is a debate about whether or nor invasive species should be controlled at all given the ecosystems services some provide and *Phragmites* is a case in point (Hershner and Havens 2008, 2009; Martin and Blossey 2009; Weis and Weis 2003). The question is even more relevant when invasion takes place in artificial habitats such as roadside ditches, which have low conservation value. Along roadsides, *Phragmites* can provide useful services by trapping nutrients, pollutants, and sediments, or acting as windbreaks. Of course, the risk of invasion to nearby natural wetlands may largely override the benefits of not controlling *Phragmites* in roadside ditches to retain some ecological services. The chosen management strategy will largely depend on conservation priorities and on how trade-offs, say between water filtration and biodiversity conservation, are assessed. All this begs for investigating urgently if, where, and how we should intervene to maximize the services we consider important without compromising the value of ecosystems of particular interest. Understanding how *Phragmites* invades roads, ecosystems, and landscapes provides a great opportunity to address this important task.

Literature Cited

Ailstock, M., C. Norman, and P. Bushmann. 2001. Common reed *Phragmites australis*: control and effects upon biodiversity in freshwater nontidal wetlands. Restor. Ecol. 9:49–59.

Amsberry, L., M. A. Baker, P. J. Ewanchuk, and M. D. Bertness. 2000. Clonal integration and the expansion of *Phragmites australis*. Ecol. Appl. 10:1110–1118.

Angold, P. G. 1997. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. J. Appl. Ecol. 34: 409–417.

Arteaga, M. A., J. D. Delgado, R. Otto, J. M. Fernandez-Palacios, and J. R. Arevalo. 2009. How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. Biol. Invas. 11:1071–1086.

Bart, D., D. Burdick, R. Chambers, and J. M. Hartman. 2006. Human facilitation of *Phragmites australis* invasions in tidal marshes: a review and synthesis. Wetl. Ecol. Manag. 14:53–65.

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

Bart, D. and J. M. Hartman. 2003. The role of large rhizome dispersal and low salinity windows in the establishment of common reed, *Phragmites australis*, in salt marshes: new links to human activities. Estuaries 26:437–444.

Bellavance, M.-È. and J. Brisson. 2010. Spatial dynamics and morphological plasticity of common reed (*Phragmites australis*) and cattails (*Typha* sp.) in freshwater marshes and roadside ditches. Aquat. Bot. 93:129–134.

Belzile, F., J. Labbé, M.-C. Leblanc, and C. Lavoie. 2010. Seeds strongly contribute to the spread of the invasive genotype of the common reed (*Phragmites australis*). Biol. Invasions. 12:2243–2250.

Brisson, J. and F. Chazarenc. 2009. Maximizing pollutant removal in constructed wetlands: should we pay more attention to macrophyte species selection ? Sci. Total Environ. 407:3923–3930.

Brisson, J., É. Paradis, and M.-È. Bellavance. 2008. New evidence of common reed (*Phragmites australis*) sexual reproduction in eastern Canada: a consequence of the recent global warming ? Rhodora 110: 225–230.

Burdick, D. M., R. Buchsbaum, and E. Holt. 2001. Variation in soil salinity associated with expansion of *Phragmites australis* in salt marshes. Environ. Exp. Bot. 46:247–261.

Cale, P. and R. J. Hobbs. 1991. Condition of roadside vegetation in relation to nutrient status. Pages 353–362 *in* D. A. Saunders and R. J. Hobbs, eds. 1991. Nature Conservation 2: The Role of Corridors. Chipping Norton, Australia: Surrey.

Catling, P. M. and S. Carbyn. 2006. Recent invasion, current status and invasion pathway of European common reed, *Phragmites australis* subspecies *australis*, in the southern Ottawa district. Can. Field-Nat. 120:307–312.

Chambers, R. M., K. J. Havens, S. Killeen, and M. Berman. 2008. Common reed *Phragmites australis* occurrence and adjacent land use along estuarine shoreline in Chesapeake Bay. Wetlands 28: 1097–1103.

Chambers, R. M., L. A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. Aquat. Bot. 6:261–273.

Christen, D. C. and G. R. Matlack. 2009. The habitat and conduit functions of roads in the spread of three invasive plant species. Biol. Invasions 11:453–465.

Delisle, F., C. Lavoie, M. Jean, and D. Lachance. 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. J. Biogeogr. 30:1033–1042.

Derr, J. F. 2008. Common reed (*Phragmites australis*) response to mowing and herbicide application. Invasive Plant Sci. Manag. 1: 12–16.

Farnsworth, E. J. and L. A. Meyerson. 2003. Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. Wetlands 23:750–762.

Findlay, C. S. and J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conserv. Biol. 14: 86–94.

Fournier, W., D. P. Hauber, and D. A. White. 1995. Evidence of infrequent sexual propagation of *Phragmites australis* throughout the Mississippi River delta. Amer. J. Bot. 82:71. [Abstract]

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

Garnier, A., S. Pivard, and J. Lecomte. 2008. Measuring and modelling anthropogenic secondary seed dispersal along roadverges for feral oilseed rape. Basic Appl. Ecol. 9:533–541.

Gelbard, J. L. and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv. Biol. 17:420–432.

Gervais, C., R. Trahan, D. Moreno, and A. M. Drolet. 1993. *Phragmites australis* in Quebec—geographic distribution, chromosome numbers and reproduction. Can. J. Bot. 71:1386–1393.

Grant, E. H. C., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecol. Lett. 10:165–175.

Greenberg, C. H., S. H. Crownover, and D. R. Gordon. 1997. Roadside soils: a corridor for invasion of xeric scrub by nonindigenous plants. Nat. Area. J. 17:99–109.

Harris, S. W. and W. H. Marshall. 1960. Experimental germination of seed and establishment of seedlings of *Phragmites communis*. Ecology 41:395.

Haslam, S. M. 1971. The development and establishment of young plants of *Phragmites communis* Trin. Ann. Bot. 35:1059–1072.

Haslam, S. M. 1972. Biological flora of the British Isles. *Phragmites communis* Trin. J. Ecol. 60:585–610.

Haslam, S. M. 1975. The performance of *Phragmites communis* Trin. in relation to temperature. Ann. Bot. 39:881–886.

Havens, K. J., H. Berquist, and W. I. Priest. 2003. Common reed grass, *Phragmites australis*, expansion into constructed wetlands: are we mortgaging our wetland future? Estuar. Coast. 26:1559–2723.

Hershner, C. and K. J. Havens. 2008. Managing invasive aquatic plants in a changing system: strategic consideration of ecosystem services. Conserv. Biol. 22:544–550.

Hershner, C. and K. J. Havens. 2009. Ecosystem services and management of invasive species in a changing system: response to Martin and Blossey. Conserv. Biol. 23:497–498.

Hodkinson, D. J. and K. Thompson. 1997. Plant dispersal: the role of man. J. Appl. Ecol. 34:1484–1496.

Hudon, C., P. Gagnon, and M. Jean. 2005. Hydrological factors controlling the spread of common reed (*Phragmites australis*) in the St. Lawrence River (Québec, Canada). Écoscience 12:347–57.

Hughes, T. D., J. D. Butler, and G. D. Sanks. 1975. Salt tolerance and suitability of various grasses for saline roadsides. J. Environ. Qual. 4: 65–68.

Hulme, P. E., S. Bacher, M. Kenis, S. Klotz, I. Kuhn, D. Minchin, W. Nentwig, S. Olenin, V. Panov, J. Pergl, P. Pysek, A. Roques, D. Sol, W. Solarz, and M. Vila. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J. Appl. Ecol. 45:403–414.

Jodoin, Y., C. Lavoie, P. Villeneuve, M. Theriault, J. Beaulieu, and F. Belzile. 2008. Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. J. Appl. Ecol. 45:459–466.

Keddy, P. A., C. Gaudet, and L. H. Fraser. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. J. Ecol. 88:413–423.

Keller, B. 2000. Genetic variation among and within populations of *Phragmites australis* in the Charles River watershed. Aquat. Bot. 66: 195–208.

Konisky, R. A. and D. M. Burdick. 2004. Effects of stressors on invasive and halophytic plants of New England salt marshes: a framework for predicting response to tidal restoration. Wetlands 24:434–447.

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

Lavoie, C. 2008. The common reed (*Phragmites australis*): a threat to Quebec's wetlands? Québec, Canada: Report prepared for the Government of Quebec's Interministerial Committee on the Common Reed and for Ducks Unlimited Canada. 41 p.

Lelong, B., C. Lavoie, Y. Jodoin, and F. Belzile. 2007. Expansion pathways of the exotic common reed (*Phragmites australis*): a historical and genetic analysis. Divers. Distrib. 13:430–437.

Lelong, B., C. Lavoie, and M. Thériault. 2009. Quels sont les facteurs qui facilitent l'implantation du roseau commun (*Phragmites australis*) le long des routes du sud du Québec? Écoscience 16:224–237.

Lissner, J. and H. H. Schierup. 1997. Effects of salinity on the growth of *Phragmites australis*. Aquat. Bot. 55:247–260.

Lumis, G. P., G. Hofstra, and R. Hall. 1976. Roadside woody plant susceptibility to sodium and chloride accumulation during winter and spring. Can. J. Plant Sci. 56:853–859.

Maheu-Giroux, M. and S. de Blois. 2005. Mapping the invasive species *Phragmites australis* in linear wetland corridors. Aquat. Bot. 83: 310–320.

Maheu-Giroux, M. and S. de Blois. 2007. Landscape ecology of *Phragmites australis* invasion in a network of linear wetlands. Landsc. Ecol. 22:285–301.

Mal, T. K. and L. Narine. 2004. The biology of Canadian weeds. 129. *Phragmites australis* (Cav.) Trin. ex Steud. Can. J. Plant Sci. 84: 365–396.

Martin, L. J. and B. Blossey. 2009. A framework for ecosystem services valuation. Conserv. Biol. 23:494–496.

Mauchant, A., S. Blanch, and P. Grillas. 2001. Effects of submergence on the growth of *Phragmites australis* seedlings. Aquat. Bot. 69: 147–164.

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

McNabb, C. D. and T. R. Batterson. 1991. Occurrence of the common reed, *Phragmites australis*, along roadsides in lower Michigan. Mich. Academician 23:211–220.

Meyerson, L. A., K. Saltonstall, L. Windham, E. Kiviat, and S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetl. Ecol. Manag. 8:89–103.

Meyerson, L. A., D. V. Viola, and R. N. Brown. 2010. Hybridization of invasive *Phragmites australis* with a native subspecies in North America. Biol. Invasions 12:103–111.

Minchinton, T. E. and M. D. Bertness. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. Ecol. Appl. 13:1400–1416.

Moore, P. D. 1982. Coastal plants take to the road. Nature (Lond.) 297: 537–538.

Olson, A., J. Paul, and J. R. Freeland. 2009. Habitat preferences of cattail species and hybrids (*Typha* spp.) in eastern Canada. Aquat. Bot. 91:67–70.

Paradis, E. 2008. Effet de la salinité sur la compétition entre le roseau (*Phragmites australis*) et les quenouilles (*Typha* spp.). M.Sc. thesis. Montréal, Canada: Université de Montréal. Département de sciences biologiques. 103 p. + ann p.

Pellegrin, D. and D. Hauber. 1999. Isozyme variation among populations of the clonal species, *Phragmites australis* (Cav.) Trin. ex Steudel. Aquat. Bot. 63:241–259.

Philipp, K. R. and R. T. Field. 2005. *Phragmites australis* expansion in Delaware Bay salt marshes. Ecol. Eng. 25:275–291.

Ravit, B., J. G. Ehrenfeld, M. M. Häggblom, and M. Bartels. 2007. The effects of drainage and nitrogen enrichment on *Phragmites australis*, spartina alterniflora, and their root-associated microbial communitie. Wetlands 27:915–927.

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

Richards, C. L., R. L. Walls, J. P. Bailey, R. Parameswaran, T. George, and M. Pigliucci. 2008 Plasticity in salt tolerance traits allows for invasion of novel habitat by Japanese knotweed s. l. (*Fallopia japonica* and *F.* ×*bohemica*, Polygonaceae). Am. J. Bot., 95:931–942.

Richburg, J. A. 1999. Water chemistry, *Phragmites* invasion, and changing plant communities at Kampoosa Bog, Stockbridge, Massachusetts. M.S. thesis. Amherst, MA: University of Massachusetts.

Rickey, M. A. and R. C. Anderson. 2004. Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata*. J. Appl. Ecol. 41:888–896.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proc. Nat. Acad. Sci. U. S. A. 99:2445–2449.

Saltonstall, K. and J. C. Stevenson. 2007. The effect of nutrients on seedling growth of native and introduced *Phragmites australis*. Aquat. Bot. 86:331–336.

Shih, J. G. and S. A. Finkelstein. 2008. Range dynamics and invasive tendencies in *Typha latifolia* and *Typha angustifolia* in eastern North America derived from herbarium and pollen records. Wetlands 28: 1–16.

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

Small, E. and P. M. Catling. 2001. Poorly known economic plants of Canada—29. Common reed, *Phragmites australis* (Cav.) Trin. ex Steud. Can. Bot. Assoc. Bull. 34:21–26.

Szczepanska, W. and A. Szczepanski. 1982. Interactions between *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha latifolia*. Ekologia Polska 30:165–186.

Tanner, C. C. 1996. Plants for constructed wetland treatment systems—a comparison of the growth and nutrient uptake of eight emergent species. Ecol. Eng. 7:59–83.

Trombulak, S. C. and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14: 18–30.

Tucker, G. C. 1990. The genera of Arundinoideae (Graminae) in the southeastern United States. J. Arnold Arbor. 71:145–177.

Vasquez, E. A., E. P. Glenn, G. R. Guntenspergen, J. J. Brown, and S. G. Nelson. 2006. Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. Am. J. Bot. 93: 1784–1790.

Von der Lippe, M. and I. Kowarik. 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv. Biol. 21: 986–996.

Wace, N. 1977. Assessment of dispersal of plant species—the car-borne flora in Canberra. Proc. Ecol. Soc. Aust. 10:167–186.

Wang, Q., C. H. Wang, B. Zhao, Z. J. Ma, Y. Q. Luo, J. K. Chen, and B. Li. 2006. Effects of growing conditions on the growth of and interactions between salt marsh plants: implications for invasibility of habitats. Biol. Invasions 8:1547–1560.

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

Weis, J. S. and P. Weis. 2003. Is the invasion of the common reed, *Phragmites australis*, into tidal marshes of the eastern US an ecological disaster? Mar. Pollut. Bull. 46:816–820.

Weisner, S. E. B. and B. Ekstam. 1993. Influence of germination time on juvenile performance of *Phragmites australis* on temporarily exposed bottoms—implications for the colonization of lake beds. Aquat. Bot. 45:107–118.

Wijte, A. H. and J. L. Gallagher. 1996. Effect of oxygen availability and salinity on early life history stages of salt marsh plants. 2. Early seedling development advantage of *Spartina alterniflora* over *Phragmites australis* (Poaceae). Am. J. Bot. 83:1343–1350.

Wilcox, D. A. 1986a. The effects of deicing salts on vegetation in Pinhook Bog, Indiana. Can. J. Bot. 64:865–874.

Wilcox, D. A. 1986b. Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. Environ. Manag. 13: 365–370.

Wilcox, K. L., S. A. Petrie, L. A. Maynard, and S. W. Meyer. 2003. Historical distribution and abundance of *Phragmites australis* at Long Point, Lake Erie, Ontario. J. Gt. Lakes Res. 29:664–680.

Yang, Q., Z. H. Chen, J. G. Zhao, and B. H. Gu. 2007. Contaminant removal of domestic wastewater by constructed wetlands: effects of plant species. J. Integr. Plant Biol. 49:437–446.

Zedler, J. B. and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Crit. Rev. Plant Sci. 23:431–452.

Zwaenepoel, A., P. Roovers, and M. Hermy. 2006. Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic Appl. Ecol. 7:83–93.

Received July 29, 2009, and approved December 4, 2009.