Invited Review

SPECIAL ISSUE: *Phragmites australis* in North America and Europe

Physiological ecology and functional traits of North American native and Eurasian introduced *Phragmites australis* lineages

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Abstract. Physiological ecology and plant functional traits are often used to explain plant invasion. To gain a better understanding of how traits influence invasion, studies usually compare the invasive plant to a native congener, but there are few conspecific examples in the literature. In North America, the presence of native and introduced genetic lineages of the common reed, *Phragmites australis*, presents a unique example to evaluate how traits influence plant invasion. We reviewed the literature on functional traits of *P. australis* lineages in North America, specifically contrasting lineages present on the Atlantic Coast. We focused on differences in physiology between the lineage introduced from Eurasia and the lineage native to North America, specifically seeking to identify the causes underlying the recent expansion of the introduced lineage. Our goals were to better understand which traits may confer invasiveness, provide predictions of how these lineages may respond to interspecific competition or imminent global change, and provide guidance for future research. We reviewed published studies and articles in press, and conducted personal communications with appropriate researchers and managers to develop a comparative dataset. We compared the native and introduced lineages and focused on plant physiological ecology and functional traits. Under both stressful and favourable conditions, our review showed that introduced *P. australis* consistently exhibited greater ramet density, height and biomass, higher and more plastic relative growth rate, nitrogen productivity and specific leaf area, higher mass specific nitrogen uptake rates, as well as greater phenotypic plasticity compared with the native lineage. We suggest that eco-physiological and other plant functional traits elucidate potential mechanisms for the introduced lineage’s invasiveness under current and predicted global change conditions. However, our review identified a disconnect between field surveys, experiments, natural competition and plant ecophysiology that must be addressed in future field studies. Given the likelihood of hybridization between lineages, a better understanding of plant traits in native, non-native and hybrid lineages is needed to manage current invasions and to predict the outcome of interactions among novel genotypes. Comparative physiology and other plant functional traits may provide additional tools to predict the trajectory of current and potential future invasions.

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Keywords: Conspecific; global change; invasive; nitrogen; nitrogen productivity; phenotypic plasticity; relative growth rate; specific leaf area; wetland.

Introduction

Plant invasions threaten biodiversity and ecosystem services worldwide (Vitousek et al. 1997). Numerous studies have investigated plant invasion by comparing non-native species with closely related native congeners, and subsequently relating plant invasiveness to the differences in plant traits among the species compared (McDowell 2002; Deng et al. 2004; Drenovsky et al. 2012; Caplan and Yeakley 2013). A potential issue with this approach is that congeneric comparisons can be confounded by phylogenetic differences (Harvey 1996). Although not always possible, the ideal approach for assessing how strongly plant traits contribute to invasiveness would minimize phylogenetic differences, specifically by using conspecific individuals that are present in the same geographic range. In North America, multiple conspecific lineages of the common reed, Phragmites australis (hereafter Phragmites), co-exist (Saltonstall 2002). This provides a unique opportunity to identify the heritable traits and ecophysiological differences that may contribute to invasion success.

Cosmopolitan in distribution (Haslam 1972), P. australis is one of the most studied wetland plants due in part to its perceived benefits and threats to ecosystem services. In North America, Phragmites is often considered a nuisance species (but see Kiviat 2013) as invasion results in a loss of habitat (Chambers et al. 1999; Weinstein and Balleto 1999), reductions in species richness and diversity (Chambers et al. 1999; Bertness et al. 2002) and alterations to biogeochemical cycles (Windham and Lathrop 1999; Meyerson et al. 2000; Windham and Ehrenfeld 2003). Elsewhere, Phragmites is either managed or preserved for shoreline stabilization (Benner et al. 1982), faunal habitat (Poulin et al. 2002) or building materials (Haslam 2010). It is also an important species in wetland-based wastewater treatment systems (Vymazal et al. 2006; Brisson and Chazarenc 2009).

Phragmites australis consists of dozens of distinct genetic lineages (Saltonstall 2002), seven of which are found in North America (Saltonstall 2002; Meyerson et al. 2012). While the genus Phragmites has a history of gene flow (Lambertini et al. 2012), North American genetic lineages have been geographically separated for millennia. The relatively recent introduction of the Eurasian lineage (haplotype M) most likely occurred in the 19th century (Saltonstall 2002). Historically, the North American native subspecies (P. australis subsp. americanus; hereafter ‘native Phragmites’) (Saltonstall 2002) was considered to be a minor component of both tidal and non-tidal wetlands throughout North America (Marks et al. 1994; Chambers et al. 1999). The cryptic invasion of P. australis subsp. australis, or haplotype M (hereafter ‘introduced Phragmites’), threatens a wide range of habitats across North America, including tidal fresh wetlands (Rice et al. 2000), brackish wetlands (Windham and Lathrop 1999; McCormick et al. 2010b), salt marshes (Silliman and Bertness 2004), fens (Richburg et al. 2001), roadside ditches (Brisson et al. 2010) and freshwater coastal wetlands (Tulbure et al. 2007; Tulbure and Johnston 2010). Recent work has also identified four additional lineages of Phragmites along the North American Gulf Coast, including a hybrid between the Gulf Coast native lineage (P. australis subsp. berlanderii) and the introduced Eurasian lineage (Lambertini et al. 2012).

The presence of conspecific lineages of Phragmites along the Atlantic Coast of North America provides a unique opportunity to identify the heritable traits that confer success to invasive plants. Past research has demonstrated that multiple introductions of Phalaris arundinacea resulted in increased genetic variation and contributed to invasion in the introduced range (Lavergne and Molofsky 2007). Earlier studies of Phragmites in Europe identified population- and/or clone-specific differences in plant phenotype and physiological traits (Raffleschek et al. 1999; Lessmann et al. 2001; Hansen et al. 2007). However, until recently, it was not possible to attribute these differences to a particular genetic lineage. Current molecular tools now provide a framework to assess ecological questions based on evolutionary history, potential speciation due to geographical separation and/or hybridization (Meyerson et al. 2010; Lambertini et al. 2012). In North America, the introduced Eurasian lineage (haplotype M) is generally considered to be invasive and responsible for the increased dominance of Phragmites throughout the North American wetlands. At the same time, native Atlantic Coast lineages are in decline (Saltonstall 2002). Owing to separations in flowering phenology (which limit hybridization) and lack of intermediate morphological forms (Saltonstall 2003, 2011), intraspecific lineages can be used to understand which plant traits may confer invasiveness.

Physiological plant traits and responses to abiotic conditions can influence the spatial distribution of plants from the species to the population level (Chapin and Oechel 1983; Reich et al. 1999; Lavergne and Molofsky 2007). When identifying plant traits that may confer invasiveness,
spurious interpretations can be avoided by restricting contrasts to those within genera or species. Previous studies have shown that differences in traits such as maximum photosynthetic rate ($A_{max}$) (Lavergne and Molofsky 2007; Mozdzer and Zieman 2010), specific leaf area (SLA) (McDowell 2002; Mozdzer and Zieman 2010) and relative growth rate (RGR) (Vasquez et al. 2005) can greatly influence the ability of a plant to be successful under a variety of environmental conditions. Here we use a literature review to identify key differences in plant ecophysiology, intraspecific competition and responses to global change factors that distinguish North American native from introduced lineages (haplotype M) of the common reed, *Phragmites australis*. We also highlight areas of future research necessary to understand interactions in the field with regard to intraspecific and intrageneric competition.

**Methods**

We reviewed the peer-reviewed literature and unpublished theses that directly compared native and introduced *Phragmites* lineages, and conducted interviews with individuals involved in *Phragmites* research and management. We only included studies that focused on native and non-native lineages along the Atlantic Coast, where clear genetic differences between the lineages had been demonstrated (Saltonstall 2011). We excluded work prior to 2002 in our review because the native and introduced lineages were typically not differentiated prior to that date. To take into account potential differences in abiotic environment, experimental set-up and differences in propagule source (seed versus rhizome), we relativized data for each trait by calculating the per cent difference between the two lineages. This was specifically calculated as the mean trait value of the introduced lineage minus the mean trait value of the native lineage, divided by the mean trait value of the native lineage, and multiplied by 100. Positive values indicated a greater advantage to the introduced *Phragmites* and negative values indicated a greater advantage to the native *Phragmites*. For data obtained from field studies we calculated mean ramet density (ramets m$^{-2}$), leaf area per ramet (cm$^2$ ramet$^{-1}$), ramet height and aboveground biomass (g m$^{-2}$). When published data were available, we also calculated mean SLA (cm$^2$ g$^{-1}$) and mean nitrogen productivity (NP; RGR per unit gram of nitrogen).

**Results**

**Comparative morphology**

While ramet densities varied, mass per ramet and mass on a ground area basis were always greater in the introduced lineage. Introduced *Phragmites* produced from 15 to 191 % more biomass under field conditions and from 69 to 286 % higher biomass under experimentally controlled conditions (Table 1). There were no instances where the native type produced more biomass than the introduced type. Such differences are due to plants being taller under both field (6–30 %) and experimental (14–49 %) conditions (Table 1); i.e. they support a larger photosynthetic canopy (36–38 % under field conditions (Table 1) and 14–314 % under experimental conditions (Table 2)).

Mean ramet densities of the introduced lineage were significantly higher than those of the native lineage (Fig. 1) in both field and experimental settings (Tables 1 and 3), although ramet densities were highly variable for both lineages. Even when the densities of the native and introduced *Phragmites* are similar, ramets of the introduced lineage are most often taller (Table 1, Fig. 1). In the field, ramets were 6–10 % taller, and had a 36–38 % greater leaf area per ramet (Table 1). Density was also greater in introduced versus native *Phragmites* (95–322 %) in growth chamber experiments where carbon dioxide (CO$_2$) and nitrogen (N) were manipulated (Table 3). In addition, introduced plants were 13–20 % taller (Table 3) in both field and manipulative experiments.

**Canopy differences**

Phenotypic differences in colour and canopy structure are indicative of physiological differences. Native *Phragmites* is characteristically yellow–green in colour, whereas the introduced lineage is more blue–green in colour throughout North America (Blossey 2002; Mozdzer and Zieman 2010; Swearingen and Saltonstall 2010). In Atlantic Coast populations, the characteristic yellow–green colour of the native lineage was related to it having 143 % lower chlorophyll content and 14 % thicker leaves (lower SLA) (Table 1) than the introduced lineage (Mozdzer and Zieman 2010). We report anywhere from 12 to 80 % lower light-saturated rates of photosynthesis ($A_{max}$) (Table 4) than the introduced population due to lower chlorophyll content and lower SLA (Mozdzer and Zieman 2010) translating into the observed lower RGR (Vasquez et al. 2005; Mozdzer and Megonigal 2012). Given the consistently observed phenotypic differences among North American native populations, it is likely that differences in photosynthetic physiology are similar across North American native populations.

Investment in both light-harvesting capacity (leaf area ramet$^{-1}$) and fast growth (SLA and RGR) differentiates the two lineages. The introduced lineage had a 14–33 % greater SLA, and this difference in SLA is consistent among populations for plants grown under field experimental conditions (Tables 1 and 2). Consistent with theory (Ceulemans 1989; Westoby 1998), increased SLA also corresponds to higher RGRs (10–116 %; Table 2) of...
the introduced lineage under current and predicted elevated CO₂ and N pollution conditions. In addition, on a per ramet basis, introduced Phragmites had anywhere from 36 % to over 300 % greater leaf area than the native type (Tables 1 and 2). While both lineages have high photosynthetic rates (Mozdzer and Zieman 2010), the introduced lineage has anywhere from 12 to 80 % greater rates of photosynthesis per unit leaf area (Table 4). To illustrate the potential ecological significance of these photosynthetic rates on potential plant growth, we used data on mean ramet density, mean size of the photosynthetic canopy and mean photosynthetic rates (Table 1 and Fig. 1) to calculate stand-scale photosynthesis rates. Assuming full light penetration to all leaves on an individual plant, we found that the introduced lineage would fix 83 % more CO₂ per ramet per second (Fig. 2) than the native lineage. By taking into account the Phragmites density per unit area, our analysis suggests that introduced Phragmites has the potential to fix 112 % more C on a stand scale than native Phragmites (Fig. 2).

Belowground

Only a few studies have investigated belowground differences between native and introduced Phragmites, yet trait differences associated with belowground allocation have the potential to magnify differences in growth potential. The non-native lineage had a greater ratio of belowground : aboveground biomass, allocating 46–89 % more biomass belowground both proportionally and in absolute terms under ambient nutrient conditions (Table 2), but when grown from rhizomes, the introduced lineage allocated 54–100 % more biomass belowground than did the native lineage (Table 3). Of this belowground allocation, Mozdzer and Megonigal (2012) reported that the introduced lineage allocated...
proportionally more biomass to both roots (root mass fraction) and rhizomes (rhizome mass fraction) than the native lineage. Thus, higher rates of nutrient acquisition and clonal expansion may come from greater resource allocation belowground to both rhizomes and roots.

Nutrient uptake, plant N demand and N metabolism

A study comparing the partitioning of glutamine synthetase (GS) activity, a proxy for nitrogen use efficiency (NUE) (see reviews by Oaks 1992; Andrews et al. 2004), demonstrated that the leaf/root partitioning of GS activity of a Phragmites-dominated habitat was the highest recorded in a natural system. Although there was no significant difference between Phragmites lineages, both had among the highest leaf/root GS activity measured in land plants, scoring higher than transgenic plants that were modified to express this trait (Hazelton et al. 2010). The comparably high NUE was reflected in several studies that have shown similar vigour and assimilation of N at low concentrations (Holdredge et al. 2010; Mozdzer et al. 2010; Mozdzer and Megonigal 2012). Both lineages have higher affinities for ammonium when compared with dominant tidal wetland plants and both use multiple forms of organic N. Phragmites australis may therefore have access to a pool of nutrients that is not used by competing plants (Mozdzer et al. 2010). While both lineages have high affinities for N, native Phragmites has a higher affinity for NH₄⁺, but uptake rates saturate at a lower N concentration (Mozdzer et al. 2010). Thus, under low nutrient conditions, both lineages would be expected to perform equally well (Holdredge et al. 2010; Mozdzer et al. 2010). However, as anthropogenic N loading increases, the advantage clearly shifts to introduced Phragmites (Holdredge et al. 2010; Mozdzer et al. 2010), as demonstrated by the greater vigour relative to the native lineage for all measured traits and metrics (Table 3).

Mozdzer and Megonigal (2012) found that only the introduced lineage, and not the native lineage of Phragmites, can alter its N metabolism to match a variety of N availability conditions. In particular, under low N availability, the introduced lineage changes plant NP, an integrative term of nutrient use efficiency, dramatically altering N metabolism to match growing conditions. In contrast, the native lineage has a nearly static NP for low-N environments. Data from the Vasquez et al. (2005) study reveal the same pattern (Table 4), with the introduced Phragmites exhibiting a greater NP under ambient and high-salinity conditions.

### Table 2. Relative differences between North American Atlantic Coast native and Eurasian introduced Phragmites from manipulative experiments including common garden, transplant and greenhouse studies. Relative difference was calculated as the mean trait value of the introduced lineage minus the mean trait value of the native lineage, divided by the mean trait value of the native lineage, and multiplied by 100. *Total density including expansion tillers from this study was used in this calculation. †Means were not significantly different in the original study.*

| Variable | Propagule source | Site     | Relative difference | Citation                  |
|----------|------------------|----------|---------------------|----------------------------|
| Plant density (ramets experimental unit⁻¹) | Rhizome | MD         | 224                 | Mozdzer and Megonigal (2012) |
|          | Seed             | MD        | 121                 | Saltonstall and Stevenson (2007) |
|          | Rhizome          | AZ        | 77                  | Saltonstall and Stevenson (2007) |
|          | Rhizome          | RI        | 99                  | Holdredge et al. (2010)⁠ |
| Total biomass (g experimental unit⁻¹) | Rhizome | MD         | 265                 | Mozdzer and Megonigal (2012) |
|          | Seed             | MD        | 286                 | Saltonstall and Stevenson (2007) |
|          | Rhizome          | RI        | 69                  | Holdredge et al. (2010)⁠ |
| Plant height (cm) | Rhizome | MD         | 34                  | Mozdzer and Megonigal (2012) |
|          | Seed             | MD        | 49                  | Saltonstall and Stevenson (2007) |
|          | Rhizome          | AZ        |                     | Vasquez et al. (2005)⁠ |
| Belowground : aboveground (R : S) | Rhizome | MD         | 89                  | Mozdzer and Megonigal (2012) |
|          | Seed             | MD        | 46                  | Saltonstall and Stevenson (2007) |
| Leaf area (cm² ramet⁻¹) | Rhizome | Denmark    | 14⁠b               | Hansen et al. (2007) |
|          | Rhizome          | MD        | 314                 | Mozdzer and Megonigal (2012) |
| Specific leaf area (cm² g⁻¹) | Rhizome | VA         | 33                  | Mozdzer and Zieman (2010) |
|          | Rhizome          | Denmark   | 15⁠b               | Hansen et al. (2007) |
|          | Rhizome          | MD        | 33                  | Mozdzer and Megonigal (2012) |
Global change effects
The most striking differences between the North American native and introduced lineages are when they are experimentally exposed to global change factors such as anthropogenic N pollution, elevated CO₂ or salinity. In particular, introduced *Phragmites* had a greater physiological and morphological plasticity under both stressful and resource-rich conditions, resulting in its designation as a ‘Jack-and-master’ strategist (Mozdzer and Megonigal 2012). Because of this greater plasticity, introduced *Phragmites* had a greater density with added N (85–168 %), salinity (873 %) and elevated CO₂ (193–322 %); introduced plants are 13–20 % taller and have 182–201 % greater leaf area per ramet (Table 3). As a consequence of increased density, height and leaf area, the introduced lineage produced anywhere from 151 to 250 % more total biomass (aboveground + belowground) (Table 3). Of the biomass produced, the introduced lineage allocated 54–100 % proportionally more belowground (Table 3).

Discussion

Physiological ecology and invasiveness of the introduced *Phragmites*
Our review confirms that introduced and native *Phragmites* lineages differ both physiologically and morphologically. Introduced plants are generally taller and occur in greater densities, which results in greater productivity in the introduced lineage in nearly every study. The taller and denser canopies (Meadows 2006; Mozdzer and

![Figure 1. Mean values (± SE) for density (A), biomass (B), culm height (C) and leaf area per culm (D) for *P. australis* lineages native to the North American Atlantic Coast and introduced from Eurasia. All data come from naturally occurring ecosystems. Mean values and standard errors were calculated from the studies that appear in Table 1. The number of studies summarized in (A)–(D) was \( n = 3 \), \( n = 3 \), \( n = 6 \) and \( n = 2 \), respectively.](image-url)
Zieman 2010; Mozdzer and Megonigal 2012) and thick litter layer (Holdredge and Bertness 2011) in stands of the introduced lineage cumulatively result in reduced light availability. The introduced *Phragmites* may also transmit oxygen to rhizomes and roots more efficiently (Tulbure et al. 2012), a feature that would potentially give it a belowground competitive advantage by ameliorating the anaerobic rhizosphere of saturated soils. As a consequence of its greater biomass, introduced *Phragmites* may be more effective at immobilizing N; thus it may limit the N available to competitors (Meyerson et al. 2000; Windham and Meyerson 2003) or facilitate invasion through competitive exclusion (Holdredge and Bertness 2011).

The higher ramet density of the introduced lineage, observed in both field and experimental settings, suggests differences in clonal strategies. The introduced lineage initially spreads through guerilla growth, sending out individual stolons. It then transitions to phalanx growth, resulting in the formation of dense patches that exclude other vegetation (Windham and Lathrop 1999; Amsberry et al. 2000). In contrast, the native lineage does not always exhibit phalanx growth, as demonstrated by the fact that native *Phragmites* stands are interspersed with other species (E. L. G. Hazelton and V. Douhovnikoff, pers. comm.).

Table 3. Effects of salinity, N and elevated CO₂ on relative differences between North American Atlantic Coast native and Eurasian introduced *Phragmites* in manipulative field and greenhouse studies. Relative difference was calculated as the mean trait value of the introduced lineage minus the mean trait value of the native lineage, divided by the mean trait value of the native lineage, and multiplied by 100. *Means were not significantly different in the original study.

| Variable | Propagule source | Treatment | Site | Relative difference | Citation |
|----------|------------------|-----------|------|---------------------|----------|
| Density (ramets experimental unit⁻¹) | Rhizome | N | MD | 168 | Mozdzer and Megonigal (2012) |
| | Seed | N | MD | 95 | Saltonstall and Stevenson (2007) |
| | Rhizome | Field + N | RI | 100* | Holdredge et al. (2010) |
| | Rhizome | Salinity | AZ | 873 | Vasquez et al. (2005) |
| | Rhizome | CO₂ | MD | 322 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ + N | MD | 193 | Mozdzer and Megonigal (2012) |
| Total biomass (g or g m⁻²) | Rhizome | N | MD | 171 | Mozdzer and Megonigal (2012) |
| | Rhizome | N | MD | 108 | Saltonstall and Stevenson (2007) |
| | Rhizome | Field + N | RI | 250 | Holdredge et al. (2010) |
| | Rhizome | CO₂ | MD | 171 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ + N | MD | 151 | Mozdzer and Megonigal (2012) |
| Plant height (cm) | Rhizome | N | MD | 20 | Mozdzer and Megonigal (2012) |
| | Seed | N | MD | 16 | Saltonstall and Stevenson (2007) |
| | Rhizome | CO₂ | MD | 20 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ + N | MD | 13 | Mozdzer and Megonigal (2012) |
| Belowground : aboveground (R : S) | Rhizome | N | MD | 100 | Mozdzer and Megonigal (2012) |
| | Seed | N | MD | 0 | Saltonstall and Stevenson (2007) |
| | Rhizome | CO₂ | MD | 90 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ + N | MD | 54 | Mozdzer and Megonigal (2012) |
| Leaf area (cm² ramet⁻¹) | Rhizome | N | MD | 201 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ | MD | 196 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ + N | MD | 182 | Mozdzer and Megonigal (2012) |
| Specific leaf area (cm² g⁻¹) | Rhizome | N | MD | 28 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ | MD | 13 | Mozdzer and Megonigal (2012) |
| | Rhizome | CO₂ + N | MD | 5 | Mozdzer and Megonigal (2012) |
per unit area, which thereby increases its potential for invasion (Holdredge et al. 2010).

Given the consistent phenotypic differences in North American native populations, we hypothesize that differences in photosynthetic physiology are similar across North American native populations. We base this on the fact that the native population has lower $A_{\text{max}}$ rates compared with the introduced population, which is due to lower chlorophyll content and lower SLA (Mozdzer and Zieman 2010) translating into a lower RGR (Vasquez et al. 2005; Mozdzer and Megonigal 2012). More common garden and field studies are needed, especially across

| Variable                                      | Experiment type | Treatment    | Site   | Relative difference | Citation                          |
|-----------------------------------------------|-----------------|--------------|--------|---------------------|-----------------------------------|
| N uptake rate ($\mu$mol g$^{-1}$ h$^{-1}$)    | Lab             | NH$_4$       | VA     | 50                  | Mozdzer et al. (2010)              |
|                                               | Lab             | Urea-N (DON) | VA     | 0                   | Mozdzer et al. (2010)              |
|                                               | Lab             | Glycine (DON)| VA     | 30$^a$              | Mozdzer et al. (2010)              |
|                                               | Lab             | Glutamic acid (DON) | VA | 28$^a$              | Mozdzer et al. (2010)              |
| Nitrogen productivity (g gN$^{-1}$ day$^{-1}$) | Chamber         | Control      | MD     | 118                 | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | N            | MD     | 26                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$       | MD     | 81                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$ + N   | MD     | 111                 | Mozdzer and Megonigal (2012)       |
|                                               | Garden          | Control (0.02 M) | AZ  | 21                  | Vasquez et al. (2005)$^b$         |
|                                               | Garden          | Salinity (0.17 M) | AZ | 34                  | Vasquez et al. (2005)$^b$         |
|                                               | Field           | None         | ME     | 12                  | Hazleton et al. (2010)$^b$        |
|                                               | Field           | None         | MD     | 33                  | Mozdzer et al. (2010)             |
|                                               | Greenhouse      | None         | VA     | 80                  | Mozdzer et al. (2010)             |
|                                               | Garden          | None         | Denmark | 12$^b$            | Hansen et al. (2007)              |
| Leaf : root GS activity                       | Chamber         | Control      | MD     | 116                 | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | N            | MD     | 30                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$       | MD     | 57                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$ + N   | MD     | 36                  | Mozdzer and Megonigal (2012)       |
|                                               | Garden          | Control      | AZ     | 10                  | Vasquez et al. (2005) (0.02 M)    |
|                                               | Garden          | Salinity     | AZ     | 25                  | Vasquez et al. (2005) (0.13 M)    |
| $A_{\text{max}}$ ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) | Chamber         | Control      | MD     | 80                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | N            | MD     | 30                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$       | MD     | 57                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$ + N   | MD     | 36                  | Mozdzer and Megonigal (2012)       |
|                                               | Garden          | Control      | AZ     | 10                  | Vasquez et al. (2005) (0.02 M)    |
|                                               | Garden          | Salinity     | AZ     | 25                  | Vasquez et al. (2005) (0.13 M)    |
| Relative growth rate (g g$^{-1}$ day$^{-1}$)  | Chamber         | Control      | MD     | 116                 | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | N            | MD     | 30                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$       | MD     | 57                  | Mozdzer and Megonigal (2012)       |
|                                               | Chamber         | CO$_2$ + N   | MD     | 36                  | Mozdzer and Megonigal (2012)       |
|                                               | Garden          | Control      | AZ     | 10                  | Vasquez et al. (2005) (0.02 M)    |
|                                               | Garden          | Salinity     | AZ     | 25                  | Vasquez et al. (2005) (0.13 M)    |
| Ventilation efficiency (mL min$^{-1}$ Pa$^{-1}$ m$^{-2}$) | Field          | None         | MD     | 320                 | Tulbure et al. (2012)             |
multiple populations and study sites, to validate this observation with regard to potential differences in chlorophyll content, accessory pigments and SLA.

Increased light-harvesting capacity (leaf canopy per ramet) and higher growth rates (SLA and RGR) are indicative of underlying physiological strategies. In particular, the greater and plastic SLA and higher RGR of introduced Phragmites have been suggested as factors driving its invasion (Mozdzer and Zieman 2010; Mozdzer and Megonigal 2012). Although leaf-level photosynthetic rates respond immediately to local environmental conditions (Lessmann et al. 2001), traits such as SLA, which combine physiological and biochemical processes, are slower to respond (Callaghan et al. 1992) and are excellent predictors of potential plant growth (Ceulemans 1989). While the lower SLA of the native lineage should confer some resistance to herbivory, herbivory by invertebrates seems to be greater on native populations (Lambert and Casagrande 2007; Lambert et al. 2007), suggesting that the decreased SLA did not evolve for herbivory defence. Lower SLA could be attributed to an adaptation for slower growth under nutrient-limited conditions, where plants invest more in longer-lived structures.

The greater resource allocation belowground (to both rhizomes and roots) in the introduced lineage may result in both higher rates of nutrient acquisition and high rates of clonal expansion, contributing to both growth and clonal expansion. Historically, clonal integration and resource sharing were prominent hypotheses used to explain the invasiveness of introduced Phragmites (Amsberry et al. 2000). However, given the recent findings of high within-patch genetic diversity (McCormick et al. 2010a, b), and different potential growth strategies between native and introduced Phragmites (E. L. G. Hazelton and V. Douhovnikof, unpubl. data), more research is needed to conclusively determine the importance of resource sharing, and whether there are differences among native and introduced lineages. Resource sharing and a greater ability to efficiently exchange gases between aboveground and belowground organs (Tulbure et al. 2012) may provide a mechanism to facilitate establishment and expansion in environments such as salt marshes that have pronounced stress gradients and limit plant distributions.

Our review showed that both Phragmites lineages are adapted to N-limited environments, and that both lineages have a similar high-affinity transport system, which is an adaptation to N limitation (Crawford and Glass 1998). However, the difference in performance under high N indicates that the introduced lineage may be shifting to a more efficient low-affinity transport system than the native lineage. The ability to respond to changing nutrient conditions has been suggested as one of the competitive advantages of the introduced Phragmites, while the native lineage becomes N saturated and is not able to exploit eutrophic conditions (Mozdzer et al. 2010). Yet, the introduced Phragmites is not at a complete disadvantage in low-N environments, due to its plastic N productivity (Mozdzer and Megonigal 2012). These studies indicate that the vigour of introduced Phragmites will increase with anthropogenic nutrient pollution, and provide evidence that the competitive ability of introduced Phragmites may be linked to plastic nutrient use strategies under lower nutrient availability.

Taken together, the physiological and other functional trait advantages of the introduced lineage (greater density, ramet height and biomass, higher RGR and SLA, and high N uptake under high anthropogenic N loading) are major factors driving its invasiveness in North America.
**Competition between native and introduced *Phragmites***

The overall superior performance of introduced *Phragmites* suggests that it would outcompete the native *Phragmites* in mixed populations. Indeed, the increase in abundance of introduced *Phragmites* with the concomitant decrease in the native one at the landscape scale is often interpreted as being the result of direct competition (Saltonstall 2002; Lelong et al. 2007). However, processes other than competitive exclusion may result in similar patterns. For example, a disturbance causing the removal of native *Phragmites* may facilitate the establishment of the introduced lineage. In such cases, better dispersal, establishment and expansion of introduced *Phragmites*, and not direct resource competition, would be responsible for the observed shift in relative abundance at the landscape scale.

If competitive exclusion occurs, the most direct field evidence would come from the contact zone of adjoining native and introduced stands. Competitive outcomes would be revealed by the spatial dynamics at that contact zone over time as one lineage progresses to the detriment of the other. Such studies remain rare, and their results are inconclusive or contradictory. In a study in the Lac Saint-François Reserve of southern Quebec, five contact zones of neighbouring stands growing in freshwater wetlands were surveyed for up to 5 years (S. de Blois et al., unpubl. data). The survey did not reveal a clear pattern of progression of the introduced over the native lineages, or that the introduced patches were increasing over the course of the survey. Instead, there were variations in progression or regression between sites and between years, with only a slight (and non-significant) net advantage for the introduced lineage.

Meadows (2006) surveyed five transects crossing the contact zones in each of two cases of adjoining stands of native and introduced *Phragmites* in Delaware. During the 2 years of the survey, there appears to have been an increase in the relative density of the native lineage over the introduced lineage in the ‘mixed’ zone of one site and a small decrease in the native lineage at the other site, although interannual changes in density for either lineage were not significant. Meadows (2006) also measured the expansion rate of adjoining stands of native and introduced *Phragmites* located in a different Delaware site. Comparing the position of the most distant culm outside the leading edge of the stands positioned the previous year, he found that the introduced stand expanded by 1.11 m, while the adjoining native stand contracted or was displaced by 1.59 m.

Classical garden or greenhouse competition experiments using seedlings or transplants, with various combinations of mixed and pure populations, represent the most direct approach to evaluate competitive interaction between two plant species (Gibson et al. 1999; Holdredge et al. 2010). We found one such study in our review; Holdredge et al. (2010) transplanted native and introduced *Phragmites* plants to a common field, and manipulated both the identity of competitors and fertilization. Although they found no evidence of suppression of the native lineage after 2 years, their results suggest that, under high-nutrient conditions, the invasive lineage would displace the native lineage over time by producing more biomass and expanding at a faster rate.

In a mesocosm competition experiment, S. de Blois et al. (unpubl. data) compared the expansion of native or introduced *Phragmites* grown in one half of the mesocosms into the opposite, competitor-occupied half, as well as expansion into mesocosms with unoccupied (control) halves. While the absolute performance of introduced *Phragmites* in terms of biomass and ramet density was superior to the native one under all circumstances, there was no statistical difference in the overall percentage of decrease in performance caused by the presence of the competitor. For example, expansion into the opposite compartment 1 year after a central panel was removed, as measured by aboveground biomass, was approximately 65 % lower for both subspecies in competition mesocosms compared with the control. By producing more biomass and a larger number of culms, the results nonetheless suggest that the relative competitive effect of the introduced *Phragmites* on the native one would increase over time. Because a decline in the native lineage has been related to an increase in the introduced lineage, there is still a need for more experimental research on competition between the lineages in order to clarify the conditions that may lead to competitive exclusion.

**Responses to global change factors (anthropogenic N pollution and CO₂)**

Our review finds that introduced *Phragmites* is a ‘Jack-and-master’ of change, which is a similar characterization to that of a super weed (Baker 1965). In other words, the introduced lineage outperforms the conspecific native lineage under both stressful and resource-rich conditions. Inherently higher RGRs, greater and plastic SLA, and plastic NP are suggested to be the physiological mechanisms unique to the introduced lineage that enhance its invasive ability under current and future conditions (Mozdzer and Megonigal 2012). More research is needed to elucidate the reasons behind the greater plasticity and ecological fitness of introduced *Phragmites*. Whether its plasticity and fitness are related to a history of multiple introductions (Hauber et al. 2011),...
hybridization (Freeland et al. 2010; Meyerson et al. 2010; Lambertini et al. 2012) or evolution of increased competitive ability (Blossey and Notzold 1995) is still unclear (but see Guo et al. 2013). This focus area would greatly benefit from an investigation of heritable changes in gene expression via an epigenetic approach (Nicotra et al. 2010).

Our literature survey suggested that introduced Phragmites will continue to expand its range and become more abundant in response to continuing change in the global environment. In particular, anthropogenic N pollution benefits the introduced lineage; it has a stem density that is 181% higher, produces 85–171% more biomass and has ramets that are 13–20% taller under elevated N (Table 3). In addition, N had profound effects on the introduced lineage by producing a canopy with 200% greater photosynthetic area (Table 3). These differences in growth can be attributed to the greater N uptake capacity of the introduced lineage (Mozdzer et al. 2010) coupled to a greater allocation belowground for nutrient acquisition (Tables 2 and 3). Plastic NP (Mozdzer and Megonigal 2012) may be the underlying cause for the disproportionate response under current and predicted N availabilities. This is congruent with correlations of introduced Phragmites expansion throughout New England (Bertness et al. 2002) and Chesapeake Bay (King et al. 2007; Chambers et al. 2008) with anthropogenic N pollution.

As C3 plants, both Phragmites lineages should benefit from elevated CO2 (Ainsworth and Long 2005). In growth chamber experiments (Mozdzer and Megonia 2012), both lineages responded positively to elevated CO2. However, the introduced lineage had the greatest biomass response to CO2, which was about 45% greater than the control treatment. This suggests, but does not demonstrate, that it is likely that elevated CO2 will also favor the introduced genetic lineage in the field. Elsewhere, only a handful of studies have investigated CO2 responses in Phragmites. Neither the growth chamber study on Phragmites japonica or Phragmites communis (Kim and Kang 2008) nor field experiments with Phragmites within a Sphagnum peatland (Milla et al. 2006) demonstrated any significant effects of elevated CO2 on Phragmites growth. It is most likely that the elevated CO2 growth response in Kim and Kang’s (2008) study was limited by pot volume, which is a well-documented phenomenon (Thomas and Strain 1991). A mini-FACE experiment in Europe by Milla et al. (2006) concluded that vascular plants in peatlands, including Phragmites, are not very responsive to elevated CO2. The lack of CO2 response by Phragmites in the mini-FACE study was likely attributable to the CO2 concentration at the position of the tall Phragmites canopy being close to ambient levels and/or a combination of nutrient limitation and immobilization by the Sphagnum layer (Milla et al. 2006). Alternatively, it is also possible that the introduced Phragmites lineages in North America are physiologically different from those in Eurasia.

In short-term studies, rising CO2 and anthropogenic N pollution seem to benefit the introduced lineage with respect to both expansion and establishment. In particular, the introduced lineage outperformed the native lineage for every measurable metric (Table 4); the introduced lineage exhibited a more plastic NP and SLA and an inherently higher RGR (Richburg et al. 2001) The introduced lineage also exhibits a ‘Jack-and-master’ phenotypic and physiological plasticity (sensu Richards et al. 2006), suggesting that it had greater ecological fitness under both stressful and resource-rich conditions. These results suggest that the introduced lineage will only become more competitive in the future.

Conclusions

Given the high genetic diversity within native and introduced Phragmites populations (McCormick et al. 2010a; Saltonstall 2011), the underlying question is what caused the introduced lineage to become so invasive in North America? Our review clearly identifies gaps in our knowledge. Additional studies are needed to determine whether there has been an evolution of increased competitive ability (Blossey and Notzold 1995) given potential physiological differences between North American and Eurasian populations. An alternative explanation is that there has been gene flow among North American native and introduced populations that made the introduced lineage more invasive and/or plastic than it is outside of North America. Given the amount of gene flow recently demonstrated in Gulf Coast populations (Saltonstall 2011; Lambertini et al. 2012), and the discovery of new genetic lineages (Lambertini et al. 2012), this possibility should be further evaluated.

Finally, our review shows that direct studies of competitive interactions between the native and the introduced Phragmites are few, and that conclusions from the laboratory and field observations do not always concur. The assumed superiority of introduced Phragmites does not necessarily hold in mixed or adjoining populations under pristine conditions, and inconclusive or even opposing results have occasionally been observed. Certainly, more experiments or surveys of adjoining populations are necessary to examine how physiological and morphological characteristics translate into a competitive advantage of the introduced lineage over the native Phragmites when they are naturally co-occurring. Acknowledging the disconnect between laboratory and field observations, we still observe profound differences in response to global
change factors such as CO₂ and N pollution. Thus, our analysis of comparative ecophysiology and functional traits allows us to predict its likely trajectory. Given the differential response of native and introduced Phragmites, we hypothesize that the competitive advantage will shift to more strongly favour the introduced lineage, especially when competition is coupled with anthropogenic N pollution and rising CO₂.

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Contributions by the Authors
T.J.M. performed the meta-analysis of the published studies. T.J.M., J.B. and E.L.G.H. contributed to the interpretation and writing of the manuscript.

Conflicts of Interest Statement
None declared.

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Literature Cited
Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. New Phytologist 165: 351 – 371.

Amsberry L, Baker MA, Ewanchuk PJ, Bertness MD. 2000. Clonal integration and the expansion of Phragmites australis. Ecological Applications 10:1110 – 1118.

Andrews M, Lea PJ, Raven JA, Lindsey K. 2004. Can genetic manipulation of plant nitrogen assimilation enzymes result in increased crop yield and greater N-use efficiency? An assessment. Annals of Applied Biology 145:25 – 40.

Baker HG. 1965. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL, eds. The genetics of colonizing species. New York: Academic Press, 147 – 169.

Benner CS, Knutson PL, Brochu RA, Hurme AK. 1982. Vegetative erosion control in an oligohaline environment Currucuck Sound, North Carolina. Wetlands 2:105 – 117.

Bertness MD, Ewanchuk PJ, Silliman BR. 2002. Anthropogenic modification of New England salt marsh landscapes. Proceedings of the National Academy of Sciences of the USA 99:1395 – 1398.

Blossey B. 2002. Phragmites: common reed. Morphological differences between native and introduced genotypes. http://www.invasiveplants.net/Phragmites/Morphology.htm.

Blossey B, Notzold R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. Journal of Ecology 83:887 – 889.

Brison J, Chazarenc F. 2009. Maximizing pollutant removal in constructed wetlands: should we pay more attention to macrophyte species selection? Science of the Total Environment 407: 3923 – 3930.

Brison J, de Blois S, Lavoie C. 2010. Roadside as invasion pathway for common reed (Phragmites australis). Invasive Plant Science and Management 3:506 – 514.

Callaghan TV, Carlsson BA, Jonsdottir IS, Svensson BM, Jonasson S. 1992. Clonal plants and environmental change—introduction to the proceedings and summary. Oikos 63:341 – 347.

Caplan J, Yearley JA. 2013. Functional morphology underlies performance differences among invasive and non-invasive ruderal Rubus species. Oecologia 173:363 – 374.

Ceulemans R. 1989. Genetic variation in functional and structural productivity components in Populus. In: Lambers H, Cambridge ML, Konings H, Pons TL, eds. Causes and consequences of variation in growth rate and productivity in higher plants. The Hague: SPB Academic Publishing, 69 – 85.

Chambers RM, Meyerson LA, Saltonstall K. 1999. Expansion of Phragmites australis into tidal wetlands of North America. Aquatic Botany 64:261 – 273.

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

Chapin FS III, Oechel WC. 1983. Photosynthesis, respiration, and phosphorus absorption by Carex aquatilis ecotypes along latitudinal and local environmental gradients. Ecology 64:743 – 751.

Crawford NM, Glass ADM. 1998. Molecular and physiological aspects of nitrate uptake in plants. Trends in Plant Science 3:389 – 395.

Deng X, Ye WH, Feng HL, Yang OH, Cao HL, Hui KY, Zhang Y. 2004. Gas exchange characteristics of the invasive species Mikania micrantha and its indigenous congenger M. cordata (Asteraceae) in south China. Botanical Bulletin of Academia Sinica 45:213 – 220.

Drenovsky RE, Grewell BJ, D’Antonio CM, Funk JL, James JJ, Molinari N, Parker IM, Richards CL. 2012. A functional trait perspective on plant invasion. Annals of Botany 110:141 – 153.

Freeland JR, Paul J, Vochon N, Garroway CJ. 2010. Molecular data provide strong evidence of natural hybridization between native and introduced lineages of Phragmites australis in North America. Biological Invasions 12:2967 – 2973.

Gibson DJ, Connolly J, Hartnett DC, Weidenhamer JD. 1999. Designs for greenhouse studies of interactions between plants. Journal of Ecology 87:1 – 16.

Guo W-Y, Lambertini C, Li X-Z, Meyerson LA, Brix H. 2013. Invasion of Old World Phragmites australis in the New World: precipitation and temperature patterns combined with human influences design the invasive niche. Global Change Biology 19:3406 – 3422.

Hansen DL, Lambertini C, Jampeetong A, Brix H. 2007. Clone-specific differences in Phragmites australis: effects of ploidy level and geographic origin. Aquatic Botany 86:269 – 279.
Harvey PH. 1996. Phylogenies for ecologists. *Journal of Animal Ecology* **65:**255–263.

Haslam SM. 1972. *Phragmites communis* Trin. (Arundo phragmites L., Phragmites australis (Cav.) Trin. ex Steudel) (in biological flora of the British Isles). *Journal of Ecology* **60:**585–610.

Haslam SM. 2010. A book of reed. Tresaith, UK: Forrest Text.

Hauber DP, Saltonstall K, White DA, Hood CS. 2011. Genetic variation in the common reed, *Phragmites australis*, in the Mississippi River delta marshes: evidence for multiple introductions. *Estuaries and Coasts* **34:**851–862.

Hazelton ELG, Knight TJ, Theodose TA. 2010. Glutamine synthetase partitioning in native and introduced salt marsh grasses. *Marine Ecology Progress Series* **414:**57–64.

Holdredge C, Bertness MD. 2011. Litter legacy increases the competitive advantage of invasive *Phragmites australis* in New England wetlands. *Biological Invasions* **13:**423–433.

Holdredge C, Bertness MD, von Wettberg E, Silliman BR. 2010. Nutrient enrichment enhances hidden differences in phenotype to drive a cryptic plant invasion. *Oikos* **119:**1776–1784.

Kim SY, Kang H. 2008. Effects of elevated CO2 on below-ground processes in temperate marsh microcosms. *Hydrobiologia* **605:**123–130.

King RS, Deluca WV, Whigham DF, Marra PP. 2007. Threshold effects of coastal urbanization on *Phragmites australis* (common reed) abundance and foliar nitrogen in Chesapeake Bay. *Estuaries and Coasts* **30:**469–481.

Kivist E. 2013. Ecosystem services of *Phragmites* in North America with emphasis on habitat functions. *AoB PLANTS* Splt008; doi:10.1093/aobpla/splt008.

Lambert AM, Casagrande RA. 2007. Susceptibility of native and non-native common reed to the non-native mealy plum aphid (Homoptera: aphididae) in North America. *Environmental Entomology* **36:**451–457.

Lambert AM, Winiasiik K, Casagrande RA. 2007. Distribution and impact of exotic gall flies (*Lipara* sp.) on native and exotic *Phragmites australis*. *Aquatic Botany* **86:**163–170.

Lambertini C, Mendelsohn IA, Gustafsson MH, Olesen B, Riis T, Kiviat E. 2013. Ecosystem services of *Phragmites australis* spread in brackish wetlands in Chesapeake Bay, Maryland (USA). *Wetlands* **30:**67–74.

McCormick MK, Kettenring KM, Baron HM, Whigham DF. 2010a. Extent and reproductive mechanisms of *Phragmites australis* spread in estuaries with differing degrees of development: genetic patterns, Allee effects and interpretation. *Journal of Ecology* **98:**1369–1378.

McDowell SCL. 2002. Photosynthetic characteristics of invasive and noninvasive species of Rubus (Rosaceae). *American Journal of Botany* **89:**1431–1438.

Meadows RE. 2006. Aboveground competition between native and introduced *Phragmites* in two tidal marsh basins in Delaware. MS Thesis, Delaware State University, Dover.

Meyerson LA, Vogt KA, Chambers RM. 2000. Linking the success of *Phragmites* to the alteration of ecosystem nutrient cycles. In: Weinstein MP, Kreeger DA, eds. *Concepts and controversies in tidal marsh ecology*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 827–844.

Meyerson LA, Viola DV, Brown RN. 2010. Hybridization of invasive *Phragmites australis* with a native subspecies in North America. *Biological Invasions* **12:**103–111.

Meyerson LA, Lambertini C, McCormick MK, Whigham DF. 2012. Hybridization of common reed in North America? The answer is blowing in the wind. *AoB PLANTS* **2012:**pls022; doi:10.1093/aobpla/pls022.

Milla R, Cornellissen JHC, van Logtestijn RSP, Toet S, Aerts R. 2006. Vascular plant responses to elevated CO2 in a temperate lowland Sphagnum peatland. *Plant Ecology* **182:**13–24.

Mozdzer TJ, Mcgionigal JP. 2012. Jack-and-Master trait responses to elevated CO2 and N: a comparison of native and introduced *Phragmites australis*. *PLoS One* **7:**e42794.

Mozdzer TJ, Ziemer JC. 2010. Ecophysiological differences between genetic lineages facilitate the invasion of non-native *Phragmites australis* in North American Atlantic coast wetlands. *Journal of Ecology* **98:**451–458.

Mozdzer TJ, Ziemer JC, McGlothery KJ. 2010. Nitrogen uptake by native and invasive temperate coastal macrophytes: importance of dissolved organic nitrogen. *Estuaries and Coasts* **33:**784–797.

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathiesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15:**684–692.

Oaks A. 1992. A reevaluation of nitrogen assimilation in roots. *Science* **42103–111.

Pockett CR, Chambers RM. 2006. Distribution and nutrient status of holotypes of the marsh grass *Phragmites australis* along the Rappahannock river in Virginia. *Estuaries and Coasts* **29:**1222–1225.

Poulin B, Lefebvre G, Moucharmp A. 2002. Habitat requirements of passinones and reseeded management in southern France. *Biological Conservation* **107:**315–325.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Grescham C, Volin JC, Bowman WD. 1998. Generality of leaf trait relationships: a test across six biomes. *Ecology* **80:**1955–1969.

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

Richards CL, Boosdarof D, Muth NZ, Gurveitch J, Pigliucci M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* **9:**981–993.
Richburg JA, Patterson WA, Lowenstein F. 2001. Effects of road salt and Phragmites australis invasion on the vegetation of a western Massachusetts calcareous lake-basin fen. Wetlands 21: 247–255.

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

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

Saltonstall K. 2003. Genetic variation among North American populations of Phragmites australis: implications for management. Estuaries 26: 444–451.

Saltonstall K. 2007. Comparison of morphological variation indicative of ploidy level in Phragmites australis (Poaceae) from eastern North America. Rhodora 109: 415–429.

Saltonstall K. 2011. Remnant native Phragmites australis maintains genetic diversity despite multiple threats. Conservation Genetics 12: 1027–1033.

Saltonstall K, Stevenson JC. 2007. The effect of nutrients on seedling growth of native and introduced Phragmites australis. Aquatic Botany 86: 331–336.

Silliman BR, Bertness MD. 2004. Shoreline development drives invasion of Phragmites australis and the loss of plant diversity on New England salt marshes. Conservation Biology 18: 1424–1434.

Swearingen J, Saltonstall K. 2010. Phragmites field guide: distinguishing native and exotic forms of common reed (Phragmites australis) in the United States. In: W. G. W. Plant Conservation Alliance, ed. http://www.nps.gov/plants/alien/pubs/index.htm.

Thomas RB, Strain BR. 1991. Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon-dioxide. Plant Physiology 96: 627–634.

Tulbure MG, Johnston CA. 2010. Environmental conditions promoting non-native Phragmites australis expansion in Great Lakes Coastal Wetlands. Wetlands 30: 577–587.

Tulbure MG, Johnston CA, Auger DL. 2007. Rapid invasion of a Great Lakes coastal wetland by non-native Phragmites australis and Typha. Journal of Great Lakes Research 33: 269–279.

Tulbure M, Ghioca DM, Johnston CA, Whigham DF. 2012. Inventory and ventilation efficiency of nonnative and native Phragmites australis (common reed) in tidal wetlands of the Chesapeake Bay. Estuaries & Coasts 35: 1353–1359.

Vasquez EA, Glenn EP, Brawn JJ, Guntenspergen GR, Nelson SG. 2005. Salt tolerance underlies the cryptic invasion of North American salt marshes by an introduced haplotype of the common reed Phragmites australis (Poaceae). Marine Ecology Progress Series 298: 1–8.

Vitousek PM, DAntonio CM, Loope LL, Rejmanek M, Westbrooks R. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16.

Vymazal J, Greenway M, Tonderski K, Brix H, Mander U. 2006. Constructed wetlands for wastewater treatment. In: Verhoeven JTA, Beltman B, Bobbink R, Whigham DF, eds. Wetlands and natural resource management. Ecological Studies 190. New York: Springer, 69–96.

Weinstein MP, Balletto JH. 1999. Does the common reed, Phragmites australis, affect essential fish habitat? Estuaries 22: 793–802.

Westoby M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. Plant and Soil 199: 213–227.

Windham L, Ehrenfeld JG. 2003. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. Ecological Applications 13: 883–896.

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

Windham L, Meyerson LA. 2003. Effects of common reed (Phragmites australis) expansions on nitrogen dynamics of tidal marshes of the northeastern US. Estuaries 26: 452–464.