

Inventory and Ventilation Efficiency of Nonnative and Native *Phragmites australis* (Common Reed) in Tidal Wetlands of the Chesapeake Bay

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Abstract Nonnative *Phragmites* is among the most invasive plants in the U.S. Atlantic coast tidal wetlands, whereas the native *Phragmites* has declined. Native and nonnative patches growing side by side provided an ideal setting for studying mechanisms that enable nonnative *Phragmites* to be a successful invader. We conducted an inventory followed by genetic analysis and compared differences in growth patterns and ventilation efficiency between adjacent native and nonnative *Phragmites* stands. Genetic analysis of 212 patches revealed that only 14 were native suggesting that very few native *Phragmites* populations existed in the study area. Shoot density decreased towards the periphery of native patches, but not in nonnative patches. Ventilation efficiency was 300 % higher per unit area for nonnative than native *Phragmites*, likely resulting in increased oxidation of the rhizosphere and invasive behavior of nonnative *Phragmites*. Management of nonnative *Phragmites* stands should include mechanisms that inhibit pressurized ventilation of shoots.

Keywords Patch inventory · Intragenic physiological differences · Intrapatch biomass allocation · Pressurized ventilation · Ventilation efficiency · Invasive wetland plants · *Phragmites* · Chesapeake Bay

Introduction

Phragmites australis (Cav.) Trin. ex Steud. is a perennial grass found on every continent with the exception of Antarctica (Tucker 1990). *Phragmites* can grow in a variety of freshwater and brackish wetlands, but it can also colonize and expand in drier conditions (Global Invasive Species Database; <http://www.issg.org>). Paleological evidence suggests that *Phragmites* is native to North America (Niering et al. 1977; Orson 1999) but was historically a minor constituent of the U.S. wetlands (Chambers et al. 1999). Molecular studies conducted by Saltonstall (2002) have shown that there are three distinct lineages of *Phragmites* currently occurring in North America: the native subspecies (Saltonstall et al. 2004), the lineage introduced from Eurasia (hereafter nonnative *Phragmites*), and the Gulf Coast lineage (Lambertini et al. 2012; Saltonstall 2002, 2003). In recent years, the nonnative *Phragmites* has proliferated in brackish and tidal freshwater wetlands on the Atlantic coast (McCormick et al. 2010), whereas the native *Phragmites* has declined in the same region (Saltonstall 2003; Vasquez et al. 2005).

The recent expansion of *Phragmites* into brackish tidal wetlands on the US East Coast has been attributed to the introduction of the nonnative lineage, but factors such as disturbance (Bart and Hartman 2000, 2003; Minchinton and Bertness 2003) and anthropogenic modifications within wetlands (Johnston et al. 2008; Maheu-Giroux and de Blois 2007; McNabb and Batterson 1991) or on adjacent upland areas (King et al. 2007; Minchinton and Bertness 2003;

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Tulbure 2008; Tulbure and Johnston 2010) facilitate *Phragmites* invasion. Once established, nonnative *Phragmites* forms large stands, with shoots up to 3–4 m tall. Nonnative *Phragmites* has high biomass (Meyerson et al. 2000), displaces native vegetation, and changes ecosystem processes (Chambers et al. 1999; Ehrenfeld 2003).

Situations where patches of native and nonnative *Phragmites* grow side by side in the field represent a unique opportunity to study intraspecific differences because comparative studies can provide important information on the invasive behavior of introduced populations (Daehler and Strong 1996; Seliskar and Gallagher 2000; Seliskar et al. 2002). Despite the potential benefits of understanding mechanisms that impart invasiveness in *Phragmites* when conducting studies comparing native and nonnative *Phragmites*, to our knowledge, only a limited number of studies have been conducted in the U.S.A., of which the majority were greenhouse studies. These studies showed that nonnative *Phragmites* emerges from rhizomes earlier in the season, grows taller, and has greater biomass (Holdredge et al. 2010; League et al. 2006; Meadows and Saltonstall 2007; Mozdzer et al. 2010), can tolerate higher salinity levels (Vasquez et al. 2005), and has higher rates of photosynthesis than native *Phragmites* (Mozdzer and Zieman 2010).

We briefly outline the a priori theoretical and empirical support for each of our goals and hypotheses which were to:

1. Identify native and nonnative *Phragmites* stands growing side by side in the field: Finding stands of native and nonnative *Phragmites* growing in close proximity was not a trivial task as there are apparently few tidal wetlands on the Mid-Atlantic Coast where native *Phragmites* occurs (Saltonstall 2003; Vasquez et al. 2005). Because one of our goals was to compare native and nonnative *Phragmites* that occurred in the same wetlands, the first objective of our study was to conduct a geographic survey and genetic analysis of *Phragmites* in Chesapeake Bay to locate and identify adjacent native and nonnative *Phragmites* stands.
2. Compare native and nonnative *Phragmites* patches that were growing close to each other, a priori hypothesizing that:
 - (a) Nonnative *Phragmites* displays greater clonal growth (i.e., produces more stems and biomass per unit area) towards the edge of the clones: *Phragmites* can reproduce both sexually and vegetatively. Although the ability to reproduce sexually increases the potential for colonizing new sites, the shift in resource allocation towards clonal growth facilitates the establishment and survival of populations (Sakai et al. 2001). Plant species with clonal growth often exhibit greater growth at the edge of patches (Lambrecht-McDowell and Radosevich 2005; Parker 2000; Wikberg and Svensson 2003), and rapid shoot initiation allows

ruderal species to spread (Grime 1977). Previous studies showed that nonnative *Phragmites* grows in denser stands than does native *Phragmites* (Meadows and Saltonstall 2007), but there have not been any studies in which the shoot density between native and nonnative stands has been compared at the leading edge of the expansion of patches (i.e., density at the edge of a patch versus density toward the center of the patch).

- (b) Nonnative *Phragmites* has greater ventilation efficiency per unit area than native *Phragmites*: The mechanisms of internal pressurization and convective gas flow are important adaptations of wetland plants to growth in anoxic substrates (Brix et al. 1992; Cronk and Fennessy 2001). Pressurized ventilation represents a bulk flow of oxygen and requires a pressure gradient between two ends of a pathway with an exit to the atmosphere (Colmer 2003). In *Phragmites*, oxygen enters via the leaf sheath stomata of green stems, flows to the roots along the intercellular spaces of the green shoots, and flows back to the atmosphere via senesced culms (Armstrong and Armstrong 1991; Colmer 2003; Rolletschek et al. 1999). Therefore, high densities of pressurizing living and dead culms play an important role in delivering oxygen to belowground organs as well as removing gases (e.g., carbon dioxide) associated with belowground respiration. The convective flow-through mechanism has been described for several wetland species (Armstrong and Armstrong 1991; Brix et al. 1992) and lower per stand ventilation efficiency has been observed in declining *Phragmites* stands in Europe (Ostendorp 1989). One factor behind the recent expansion of nonnative *Phragmites* in brackish tidal wetlands in the U.S.A. may be its ability to more efficiently transport oxygen to roots. The ability to efficiently deliver oxygen to roots could be especially important in coastal wetlands that are enriched by eutrophication and could result in a decline in the native lineage for reasons similar to those that have been responsible for the decline of *Phragmites* in Europe—as the substrate becomes more reduced due to eutrophication, *Phragmites* is unable to supply enough oxygen to the rhizosphere (van der Putten 1997).

Methods

Native and Nonnative *Phragmites* Survey and Study Site

A field survey of 212 *Phragmites* stands was conducted in eastern Maryland U.S.A. (Fig. 1) during summer 2006. Leaf samples were collected from the 212 *Phragmites* patches and

identified as native or nonnative lineage using the genetic analysis described in Tulbure et al. (2007) that was based on Saltonstall's (2002) protocol. The survey targeted suspected locations of native *Phragmites* and was not intended to be random or otherwise representative of the area.

We selected three pairs of native and introduced stands identified during the survey that were located along King's Creek in Talbot County, Maryland (Fig. 1), northeast of the town of Easton near the Nature Conservancy's King's Creek Preserve site (The Nature Conservancy; www.nature.org). The site is a tidal freshwater wetland that drains into the Choptank River, a subestuary of Chesapeake Bay. The pairs of stands selected were within meters of each other and close to the creek, with no standing water present but waterlogged soils. A previous study at the wetland showed that there were no differences in porewater ammonium and phosphate, the primary limiting nutrients to *Phragmites*, between native and nonnative stands (Mozdzer and Ziemann 2010). Therefore, we assume that any differences between native and nonnative *Phragmites* would be due to genetic differences alone.

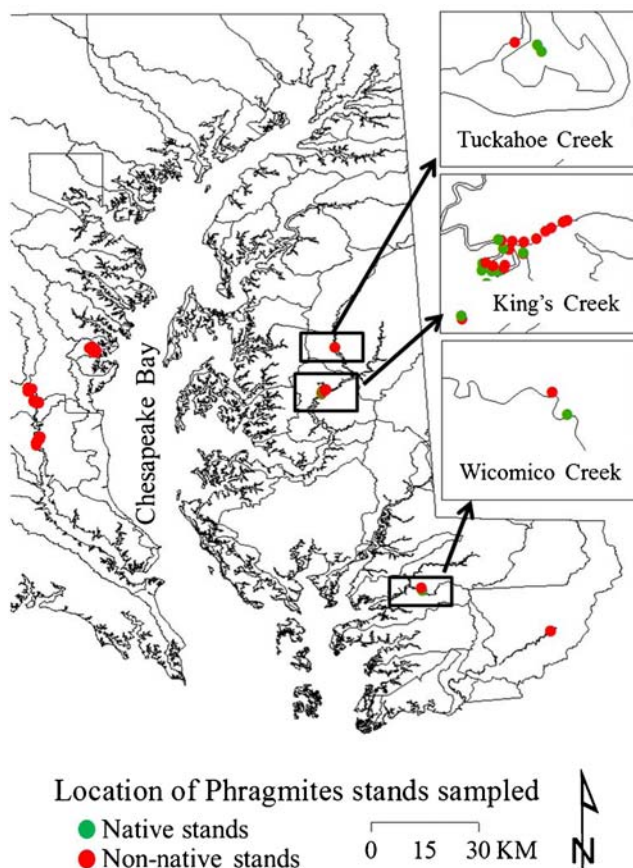


Fig. 1 Location of *Phragmites* stands sampled around Chesapeake Bay. The three insets represent the areas where we identified native *Phragmites* stands

Clonal Study and Pressurized Ventilation

A north–south transect was placed across each of the six patches, and the transects were divided into three zones of equal length. The zones are hereafter referred to as center, intermediary, and edge. In August 2006, we harvested all aboveground biomass in three 0.25-m² quadrats in each zone. Biomass from each quadrat was divided into living (green) and senesced (brown) shoots and then oven dried at 60 °C for 48 h. Gas flow parameters were measured on randomly chosen stems (18 per lineage) in each stand following the methodology described in Rolletschek et al. (1999). Pressurization of the lacunal air in the shoots was measured with a digital manometer (HM35, Revue Thommen AG, Switzerland) and gas flow rate was measured with a flow meter (Gilmond Instruments, Inc., USA). The static pressure differential of the living culm (*P_{culm}*) and the cutoff at the base, the stubble (*P_{stubble}*), was measured with a gas connection directly to the manometer. The dynamic pressure differential (*P_d*) and the gas flow rate (*F_d*) were measured with the culm connected to the stubble with the manometer in parallel and the flow meter in series (Rolletschek et al. 1999). Ventilation efficiency (*sensu* Rolletschek et al. 1999) was determined as the effective ventilation per unit area. The effective ventilation parameter, $F_d/(P_d - P_{stubble})$ represents the flow rate (*F_d*) standardized by the effective pressure differential ($P_d - P_{stubble}$). Shoot height, circumference at the base of the stem, and number of leaves per shoot were also recorded for the same stems used in the ventilation study.

Biomass, density, and ventilation efficiency data were analyzed using Generalized Linear Mixed-Effects Models to examine how lineage (native or nonnative *Phragmites*) and location within a patch (edge, intermediary, or center) affect total stem density as well as new and old culm density, biomass, and ventilation efficiency. Lineage was treated as a fixed effect, while stand was treated as a random effect nested in lineage. When testing several a priori working hypotheses, AIC is the method of choice over null hypothesis testing (Anderson et al. 2001). We used an information theoretic approach based on the second-order Akaike's Information Criterion corrected for small sample size, AIC_c (Burnham and Anderson 2002). Models were run using the *glmer* function in the *lme4* package in the software R (R Development Core Team 2008).

Results

Survey of Native and Nonnative *Phragmites*

PCR/RFLP genetic analysis of leaf samples revealed that only 14 *Phragmites* stands out of the 212 Chesapeake Bay stands sampled were native. None of the samples collected from the

western shore of Chesapeake Bay (167) were native patches (Fig. 1). Eleven native and 20 nonnative patches were identified at the King's Creek site and, as already described, native and nonnative patches growing side by side were identified. The other three native stands were from Tuckahoe Creek (two stands) and Wicomico Creek (one stand). All native patches identified as part of this study were located on the eastern shore of Chesapeake Bay (Fig. 1).

Clonal Study and Pressurized Ventilation

The mean diameter of the nonnative stands was 30 % greater, but the difference was not significant (Table 1). Shoot circumference was 15 % greater for nonnative *Phragmites*, the number of green leaves was 37 % greater, and the shoot length was 16 % higher for nonnative than native *Phragmites* (Table 1). Mean aboveground biomass was substantially greater for nonnative than native *Phragmites* (Table 2), and the difference was significant ($F=69.12$, $df=1$, p -value=0.01). Biomass per unit area decreased by 45 % from the center towards the edge in patches of the native lineage and differences between the three zones were significant (one-way ANOVA $F=2.41$, p -value=0.1, $df=2$; Table 2). There were no significant biomass differences among zones within stands of the nonnative lineage. The nonnative *Phragmites* always had significantly greater biomass in each of the three zones compared to the native lineage, and stem density was significantly greater for the nonnative lineage ($F=9.75$, $df=1$, p -value=0.03) within each of the three zones (Table 2). Nonnative *Phragmites* had almost twice as many green stems as the native lineage ($F=6.16$, $df=1$, p -value=0.06; Table 2). The standing dead density of stems was approximately four times greater for the nonnative lineage compared to the native *Phragmites* ($F=14.01$, $df=1$, p -value=0.02; Table 2). Information theoretic model selection based on AICc revealed strong support from the data for the influence of lineage (i.e., whether *Phragmites* patches were native or nonnative) on biomass, total stem density, new and old stem density, and ventilation efficiency (Table 3). Ventilation efficiency was 300 % higher for nonnative than native *Phragmites* (nonnative *Phragmites*, 1.85 ± 0.5 mL min⁻¹ Pa⁻¹ m⁻²; native *Phragmites*, $0.44\pm$

0.4 mL min⁻¹ Pa⁻¹ m⁻²), whereas effective ventilation of single stems was approximately 200 % for nonnative than native *Phragmites* (nonnative *Phragmites*, 0.016 ± 0.004 mL/min Pa⁻¹; native *Phragmites*, 0.007 ± 0.004 mL/min Pa⁻¹).

Discussion

This study advances scientific knowledge about *Phragmites* in several ways. This is the first study showing differences in ventilation efficiency between native and nonnative *Phragmites*. Also, we inventoried the lineage of *Phragmites* stands on both shores of Chesapeake Bay, expanding upon earlier work characterizing the eastern shore (Meadows and Saltonstall 2007). Finally, our *Phragmites* stand characterization is novel in comparing the allocation of stem density and biomass in native versus introduced *Phragmites* stands.

Once established, *Phragmites* can change environmental conditions to create more favorable conditions for growth and reproduction (Rudrappa et al. 2007). We found that nonnative *Phragmites* had greater ventilation efficiency per unit area than native stands. This was likely created by the fact that introduced *Phragmites* had higher pressurized gas flow rates, denser growth pattern, and greater number of old culms which act as efflux culms. The flow rates measured were at the lower range of values measured for *Phragmites* in Europe (Rolletschek et al. 1999). Results of the pressurized ventilation study demonstrated that nonnative *Phragmites* had the potential to oxidize the substrate more than native *Phragmites*. While not measured in the field, one consequence of the higher ventilation rates would be more efficient oxidation of the substrate and a less reduced substrate in stands of nonnative *Phragmites*, which in the long run would improve sediment condition.

The convective flow-through pressurized ventilation mechanism has been described for several wetland species (Armstrong and Armstrong 1991), and *Phragmites* was shown to have the highest flow rate when compared to 13 other wetland plants (Brix et al. 1992). This mechanism may offer a competitive advantage over species relying exclusively on diffusive gas transport (Brix et al. 1992). Higher

Table 1 Characteristics of nonnative and native *Phragmites* stands at King's Creek (MD) measured in August 2006 (mean \pm SE)

	Nonnative	Native	F statistic	df	p-value	Sample size, n
Shoot length (cm)	300.58 \pm 15.13	260.12 \pm 14.52	3.72	1	0.12	18
Shoot circumference (cm)	2.71 \pm 0.11	2.30 \pm 0.11	6.31	1	0.06	18
Number of green leaves per shoot	13.50 \pm 1.43	8.48 \pm 1.42	6.19	1	0.06	18
Diameter (m) of native and nonnative stands	32.67 \pm 8.83	23.13 \pm 4.23	0.95	1	0.38	3

Table 2 Differences in above ground biomass and stem density within the three zones of a stand (center, intermediary, and edge) for nonnative and native *Phragmites*

	Nonnative				Native			
	Center	Intermediary	Edge	Per stand	Center	Intermediary	Edge	Per stand
Biomass (mean \pm SE) as dry weight (g m^{-2})	2,410.4 \pm 69.7	2,868.8 \pm 106.0	2,667.5 \pm 72.6	2,649 \pm 80.0	974.6 \pm 45.0	708.0 \pm 38.4	545.5 \pm 26.1	742.7 \pm 35.4
Density of new culms (# stems m^{-2})	96.9 \pm 21.2	72.4 \pm 10.2	83.6 \pm 10.7	84.3 \pm 8.5	48.4 \pm 6.5	37.3 \pm 6	49.3 \pm 12.5	45 \pm 5
Density of old culms (# stems m^{-2})	31.6 \pm 4.9	56.0 \pm 14.7	37.3 \pm 10.0	41.6 \pm 6.3	9.3 \pm 3.0	10.7 \pm 2.2	8.0 \pm 3.0	9.3 \pm 1.6
Total stem density (# stems m^{-2})	128.4 \pm 14.8	128.0 \pm 15.3	120.9 \pm 16.3	126.0 \pm 31.3	57.8 \pm 11.6	48.0 \pm 11.2	57.3 \pm 9.0	54.4 \pm 20.2

ventilation efficiency can also benefit the nonnative *Phragmites* by oxidizing potentially toxic compounds in the rhizosphere (Armstrong and Armstrong 1991). Efficient ventilation would oxidize sulfides, allowing *Phragmites* to grow in brackish wetlands with higher sulfide concentrations (Cronk and Fennessy 2001). Although nonnative *Phragmites* can tolerate higher salinity levels than native *Phragmites* (Vasquez et al. 2005), it cannot tolerate high sulfide concentrations (Bart and Hartman 2003; Chambers et al. 1998; Wijte and Gallagher 1996). By supplying oxygen to nitrifying bacteria, the nitrification of ammonium is increased (Armstrong and Armstrong 1991), which could benefit the plant, nitrate being mentioned as a primary cause for increased introduced *Phragmites* abundance (Marks et al. 1994). Future studies should collect soil redox data and relate them with ventilation efficiency and stand characteristics.

Our survey of Chesapeake Bay *Phragmites* stands revealed that surprisingly few stands, all located on the eastern shore, were of the native lineage (Fig. 1). Meadows and Saltonstall

(2007) reported that native *Phragmites* was much more common on the Maryland eastern shore than in Delaware or southern New Jersey, but they did not search for stands along the western shore of Chesapeake Bay. Although subsequent work by co-author Whigham and colleagues had identified a stand of native *Phragmites* along Parker's Creek on the western shore of Chesapeake Bay, it was in an area with very little shoreline or upland development, atypical of the western shore. Upland development and disturbance in wetlands have been reported as factors contributing to the spread of nonnative *Phragmites* (Bertness et al. 2002; King et al. 2007; Meadows and Saltonstall 2007; Minchinton and Bertness 2003), often at the expense of the native subspecies (Saltonstall 2003). We cannot attribute causality to the low proportion of native stands, but it is clear that the introduced lineage is far more prevalent than the native lineage around Chesapeake Bay. The rapid expansion of the nonnative *Phragmites* (McCormick et al. 2010) potentially could result in the complete elimination of the native haplotype when they co-occur.

Table 3 AICc-based model selection for (1) total stem density, (2) new culm density, (3) old culm density, (4) biomass, and (5) ventilation efficiency. Generalized Linear Mixed-Effect Models used site as a random factor and included Lineage (Lin) and Location within stand (L) as fixed factors. We show the number of predictor variables (K), AICc differences (Δ) and Akaike weights ($\hat{\omega}$)

Model rank	Model	K	AICc	Δ	$\hat{\omega}$
Total stem density (# stems m^{-2})	Lin + L	3	624.1	32.0	0.001
	Lin	2	592.1	0.0	0.999
	L	2	606.1	14.0	0.009
New culms (# new stems m^{-2})	Lin + L	3	624.1	32.0	0.001
	Lin	2	592.1	0.0	0.999
	L	2	606.1	14.0	0.009
Old culms (# old stems m^{-2})	Lin + L	3	575.2	29.3	0.004
	N	2	545.9	0.0	0.996
	L	2	557.2	11.3	0.003
Biomass	Lin + L	3	962.8	32.6	0.008
	Lin	2	930.2	0.0	0.999
	L	2	944.8	14.6	0.006
Ventilation Efficiency (per m^{-2})	Lin + L	3	823.5	27.9	0.008
	Lin	2	795.6	0.0	0.992
	L	2	805.5	9.9	0.007

The growth of the native and introduced stands within meters of one another at King's Creek made this site the ideal setting for our study because edaphic conditions were similar, therefore any differences observed could be attributed to differences in lineage. Even though sampling nonnative and native *Phragmites* pairs at different locations would have been desirable, we could not locate other native and nonnative *Phragmites* growing side by side at other sites besides King's Creek. As expected, nonnative *Phragmites* had greater biomass and stem density per unit area than the native *Phragmites*, similar to the findings of previous studies (League et al. 2006; Meadows and Saltonstall 2007; Mozdzer and Zieman 2010; Vasquez et al. 2005), which increase the competitiveness and the ability of the nonnative *Phragmites* to compete for resources such as light and space.

Rapid vegetative growth is one of the qualities of successful weeds (Baker 1974; Sakai et al. 2001), allowing them to maintain vigorous growth in their current habitat (Eriksson 1994). A greater growth rate towards the periphery of patches has been shown to be inversely related to the time of stand recruitment and clone density (Hartnett and Bazzaz 1985; Parker 2000). We predicted that the stands of nonnative *Phragmites* would exhibit greater clonal vigor (number of stems and biomass) towards the edge of the clones. We observed that biomass decreased toward the periphery of native stands but not stands of the nonnative lineage, nor did stem density per unit area change with increasing distance from the center of stands (Table 2). However, *Phragmites* stands sampled here have been established at King's Creek for several decades, very likely during the 1980s (Rice et al. 2000), and lack of vigor could be related to patch age. To further test our prediction that introduced stands would have greater clonal vigor with increasing distance from the center of the stand, future studies would either have to compare the clonal growth in stands of *Phragmites* of different ages or use newly established stands and measure parameters of clonal vigor during several years immediately after establishment.

Studies documenting differences between native and nonnative *Phragmites* are essential for a sound management of *Phragmites*. This study explored one aspect of *Phragmites* invasion, namely mechanisms employed by *Phragmites* to sustain its invasion.

Once established, *Phragmites* is difficult to control as it displaces native vegetation and changes wetland properties. This study is the first one to show that nonnative *Phragmites* has a higher ability to send oxygen to the rhizosphere than native *Phragmites*, a physiological attribute that clearly benefits nonnative *Phragmites* and provides a partial explanation for its success. While testing with an experimental approach should be conducted, our results suggest that once established, along with other management practices (e.g., herbicide treatment), measures targeted at inhibiting the pressurized ventilation mechanism, such as completely removing the culms

which act as influx/efflux culms, followed by flooding for a long period of time can reduce *Phragmites* success.

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