Belowground Biomass of *Phragmites australis* in Coastal Marshes

Gregg E. Moore[1,2,*], David M. Burdick[1,3], Christopher R. Peter[1], and Donald R. Keirstead[4]

Abstract - The distribution of belowground biomass within monotypic stands of invasive *Phragmites australis* (Common Reed) was documented from a series of oligo-, meso-, and polyhaline coastal marshes in New Hampshire. Soil profiles were described, and live biomass was documented growing to a maximum depth of 95 cm for roots and 85 cm for rhizomes. Our data show that invasive *P. australis* utilizes a greater depth range than native graminoids (90% within the top 70 cm and top 20 cm, respectively). We corroborate prior anecdotal observations and provide further evidence illustrating the potential for this invasive plant to access resources (i.e., water and nutrients) at depths greater than the native species with which it competes.

Introduction

Phragmites australis (Cav.) Trin. ex Steudel (Common Reed) is a perennial grass with a cosmopolitan distribution that can occur in a wide range of habitats (Chambers et al. 1999, Halsam 1972). Common Reed has become an aggressive invader of tidal and non-tidal wetlands, riparian areas, agricultural lands, and other natural areas throughout the eastern United States, including New Hampshire (Chambers et al. 1999, Fell et al. 2003, Saltonstall et al. 2004). Such rapid expansion appears to be due to a Eurasian variety of *Phragmites australis* (Saltonstall 2002), which has recently been distinguished from native varieties endemic to North America, *Phragmites australis* subsp. *americanus* Saltonstall, P.M. Peterson, & Soreng (Saltonstall et al. 2004). Exotic *P. australis* appears to be a better competitor than its native cousin especially in increasing eutrophic environments, exhibiting enhanced aboveground morphology (League et al. 2006, Saltonstall and Stevenson 2007), photosynthetic production (Mozdzer and Zieman 2010, Mozdzer et al. 2010), and salinity tolerances (Vasquez et al. 2005). Invasion by exotic *P. australis* (hereafter *Phragmites*) has led to the decline or loss of local populations of native marsh grasses, rushes, and sedges, particularly in tidal marshes of New England and the Mid-Atlantic (Keller 2000, Meyerson et al. 2000). In turn, critical structural and functional alterations (e.g., floral diversity, nutrient cycling, carbon storage, and wildlife usage) have occurred in invaded tidal marshes (Benoit and Askins 2002, Findlay et al.

[1]University of New Hampshire, Jackson Estuarine Laboratory, 85 Adams Point Road, Durham, NH 03824. [2]Department of Biological Sciences, University of New Hampshire, Durham, NH 03824. [3]Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824. [4]United States Department of Agriculture Natural Resources Conservation Service, Main Street, Durham, NH 03824. [*]Corresponding author - gregg.moore@unh.edu.

2003, Keller 2000, Windham and Lathrop 1999). Accordingly, much is known about the biology, physiology, and natural history of *Phragmites* (Haslam 1972), yet effective strategies to control this plant in the United States remain a challenge to the management community (Bart et al. 2006, Burdick and Konisky 2003, Marks et al. 1994).

It has been suggested that the tall shoots of *Phragmites* contribute to its success (Haslam 1972). Often densely spaced, its shoots are capable of extending 3–4 m in height, dwarfing most native species, which range from 0.2–0.8 m in height (Meyerson et al. 2000). The substantial discrepancy in plant height allows *Phragmites* to thrive and expand by easily shading out native competitors. However, *Phragmites*' competitive ability may also be facilitated by its extensive root system, which releases phytotoxins harmful to native plant root systems (Bains et al. 2009, Rudrappa et al. 2007) and is capable of altering the rhizosphere through enhanced gas diffusion (Armstrong and Armstrong 1988, Bart and Hartman 2000) and increased soil elevation (Rooth et al. 2003, Windham and Lathrop 1999). The latter two adaptations minimize physiological stresses associated with flooded, anaerobic conditions prevalent in tidal marsh habitats. These adaptive advantages of *Phragmites* are achieved by dense, finely branched, aerenchymous roots and resilient rhizomes.

Most reports suggest *Phragmites* roots are concentrated in the upper 50 cm of the soil column, while maximum rhizome depths are reported to occur from 40 to 100 cm (Bjork 1967, Kudo and Ito 1988, Ravit et al. 2003). Isolated reports have documented rhizomes penetrating as deep as 1.5 m below the marsh surface (Haslam 1970, Lissner and Schierup 1997). Throughout these accounts, *Phragmites* roots and rhizomes appear to vary in density and depth over a range of environmental conditions. For instance, Bjork (1967) reported the maximum rooting depth of *Phragmites* was restricted in deeper stagnant waters. Vretare et al. (2001) confirmed these results, and also found the depth of rhizomes were restricted by coarse soils. Although numerous studies have described lateral growth and aboveground expansion, few studies have examined the vertical distribution of *Phragmites* roots and rhizomes, which may aid in its overall success. Of the few studies reporting on *Phragmites*' maximum rooting depth (Haslam 1970, Lissner and Schierup 1997, Ravit et al. 2003, Vretare et al. 2001), most have been conducted in Europe and were largely anecdotal, lacking quantitative data, replication, or statistical analysis.

There is evidence that the ability of the exotic variety of *Phragmites* to produce roots and rhizomes extending considerable depths may have aided recent expansion. The historical range of native *Phragmites* was typically limited to the upland edge of tidal marshes (Orson 1999), but now *Phragmites* distribution includes creek banks and the interior of tidal marshes (Moore et al. 2011, Warren et al. 2001), even in polyhaline marshes (Amsberry et al. 2000). As *Phragmites* expands into higher salinity and lower elevation areas, it may be accessing freshwater at the lower marsh contact that flows from upland groundwater to tidal creeks (Adams and Bate 1999, Wieskel and Howes 1991). This deeper freshwater resource is largely unavailable for native graminoids of the high marsh, which typically root

to 20–30 cm (Gross et al. 1991, Steinke et al. 1996, Valiela et al. 1976) and allocate 90% of their belowground biomass in the upper 20 cm of soil (Gallagher and Plumley 1979, Valiela et al. 1976, Windham 2001). In New England salt marshes, Burdick et al. (2001) suggested *Phragmites* might be accessing deeper pore water that was measurably less saline than shallower depths in the soil profile. This finding was particularly evident during late summer months when freshwater flows and water-table elevations were at their minimum. While their study provided evidence of a salinity gradient with depth, it did not document the presence or distribution of belowground roots and rhizomes within the marsh profile.

Building upon prior studies, we examined soil cores collected from ten monotypic stands of invasive *Phragmites* and one stand of the native form in coastal marshes in New Hampshire, across oligohaline, mesohaline, and polyhaline conditions. Our research 1) quantitatively documents the presence, depth range, and biomass of live roots and rhizomes within the soil profile associated with monotypic stands of *Phragmites*, 2) evaluates the potential influence of salinity regime, soil type, and variety of *Phragmites* on belowground biomass and stand properties, and 3) suggests how knowledge of belowground biomass distribution can improve monitoring strategies.

Methods

Field collection

Soil cores were collected from monotypic stands of *P. australis* at eleven coastal marsh sites within New Hampshire (Fig. 1). All sites but one (Site 3) were located within tidal marshes. Of the 11 study sites, 10 contained the invasive form of *P. australis*, whereas 1 supported the native form (Site 8), *P. australis* subsp. *americanus* (Saltonstall et al. 2004). Cores were obtained using a gouge auger (I.D. 30 mm x 100 cm; Eijkelkamp model #04.01), allowing collection of intact profiles with minimal soil mixing or compaction to 100 cm. While this coring device gathered samples more narrow in diameter than other published methods, it was preferred because it allowed for consistent and successful extraction of deep cores regardless of soil type or texture (e.g., dense clay layers, cobble, or *Phragmites* rhizomes) that can hinder coring success. Cores were described in the field using standard methods for soil classification (USDA-NRCS 2010) and texture (Thien 1979), and then grouped into either of two simplified categories, "silt" versus "sand" soils, to facilitate comparison. Soils categorized as "silt" had smooth texture (not gritty) and included textures described as silt, silt loam, clay loam, and clay, while "sand" soils were gritty to the touch and included textures described as sand loam and sandy clay loam. Sandy clay soil types were not encountered at our study sites. After descriptions were completed, soil cores were labeled, wrapped in foil, and stored at 4 °C until laboratory analysis of biomass.

Paired cores (n = 2) were collected at 9 of the sites, whereas 4 cores were taken from haphazardly selected locations at 2 of the sites: Site 7 (an exotic population) and Site 8 (a native form in the same marsh) (Fig. 1). The only native stand of *Phragmites* in New Hampshire is located in the Great Bay National

Estuarine Research Reserve. Sites were grouped into 3 habitat types according to the classification of Odum (1988) following measurements of pore-water salinity at 3 locations in the stand at a depth of 40 cm. Pore water was obtained using a 1-mm-I.D. stainless steel tubing fitted with a 60-mL plastic syringe to draw

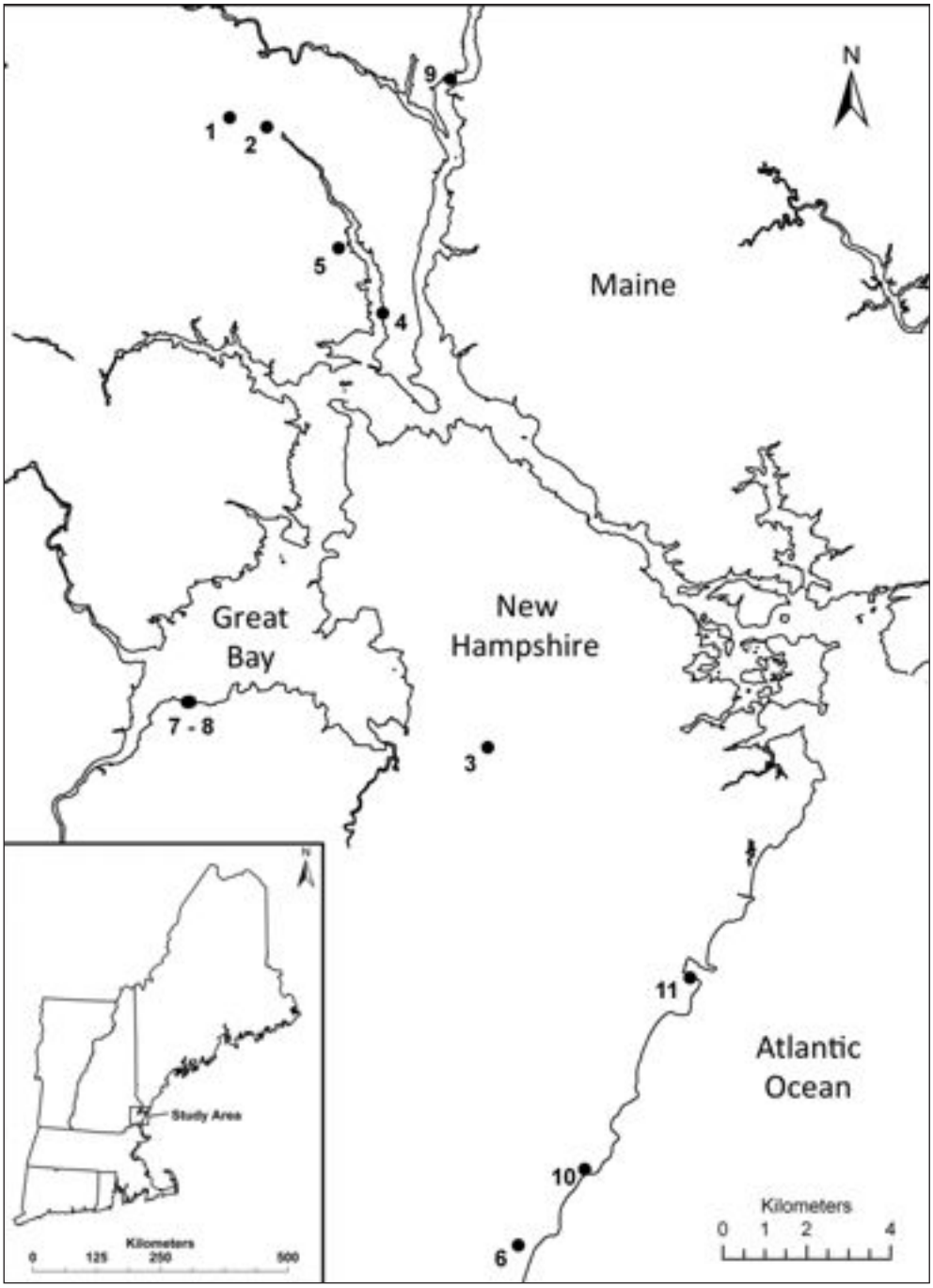


Figure 1. Study sites within Great Bay, NH and its tributaries. Black dots represent the 11 study sites.

water out of the saturated soil at the specified depth. Salinity was then measured in the field using a hand-held temperature-corrected optical refractometer that was calibrated with standard solutions (0 ppt and 15 ppt) daily. Three of the sites were determined to be fresh to oligohaline (0–5 ppt), 5 were mesohaline (5–18 ppt), and 3 were polyhaline (18–30 ppt). Collecting cores from monotypic stands insured that live root material from plants other than *Phragmites* would not be included in the sample, thus simplifying the subsequent sorting process. Two additional sets of 4 cores were collected in native marsh dominated by *Spartina patens* (Aiton) Muhl (Saltmeadow Cordgrass) (Sites 7 and 8) to provide comparable belowground biomass data. *Phragmites* stand properties were characterized at each site by counting live shoots and measuring stand height (mean of 3 tallest) within a 0.5-m^2 plot directly adjacent to each of the core sample locations.

Root and rhizome determinations

To determine the biomass contribution of live roots and rhizomes throughout the soil profile, the cores were divided into 5-cm sections from top to bottom (e.g., 0–5, 5–10, etc. to a depth of 100 cm). To facilitate sorting of organic material, sections were placed individually in shallow trays partially filled with water. Live roots and rhizomes from each core section were collected using forceps under a dissecting scope. The resulting live biomass was washed of sediment and dried at 65 °C for a minimum of 48 hours until it reached constant weight (Table 2).

Statistical analyses

One-way, fixed effects analysis of variance (ANOVA) models were used to compare belowground biomass components of entire cores, shoot density, and stem height for each salinity regime, soil type, and *Phragmites* variety. Since multiple cores (sub-samples) were taken at each site, data analysis for one-way ANOVAs were conducted by averaging sub-samples. Tests to determine the effect of *Phragmites* variety used the 4 cores from each population as replicates. Student's *t* post hoc test ($\alpha = 0.05$) was run to determine differences among means for effects deemed significant in ANOVA models. To satisfy assumptions of normality, root data were inverse transformed and rhizome data were log transformed.

To identify the potential effects of depth, sub-samples were averaged and depth data were pooled together into 20-cm increments (0–20, 20–40, 60–80, 80–100) to reduce variability (e.g., improve homoscedasticity and normality of residuals). Root and rhizome data were log transformed. A three-way fixed effects ANOVA model (depth, salinity regime, soil type) was used to compare belowground biomass (root and rhizome) over depth. To show the effects of salinity regime by soil depth and soil type by soil depth, the data were analyzed using a one-way ANOVA for each category. A post hoc Student's *t* test was run to determine differences among depths.

Results

Live roots and rhizomes were documented to a maximum depth of 95 cm and 85 cm, respectively, among the sites sampled (Table 1). Belowground biomass

Table 1. Summary data of *Phragmites* (belowground biomass and stand properties) and site characteristics (soils and salinity). Site 8 was the native variety; only one core was assessed at Site 4.

Site	Max root depth (cm)	Max rhizome depth (cm)	Total root biomass (g m^{-2})	Total rhizome biomass (g m^{-2})	Total biomass (g m^{-2})	Mean rhizome : root	Salinity category	Soil type	Salinity (ppt)	*Phragmites* average density (# m^{-2})	*Phragmites* average height (cm)
1	52.5	37.5	140	2320	2460	16.4	Oligohaline	Sand	0	82	378
2	67.5	67.5	170	1850	2020	10.5	Oligohaline	Sand	0	110	349
3	42.5	40.0	130	3030	3160	15.4	Oligohaline	Silt	0	142	345
4	70.0	75.0	420	5830	6250	13.9	Mesohaline	Sand	10	174	461
5	70.0	82.5	470	2200	2680	4.8	Mesohaline	Silt	15	90	366
6	65.0	25.0	1080	4250	5320	3.5	Mesohaline	Sand	15	174	253
7	59.8	22.5	230	430	660	2.4	Mesohaline	Sand	12	87	295
8	76.3	25.0	380	250	640	0.9	Mesohaline	Sand	17	129	234
9	65.0	47.5	120	1250	1370	10.6	Polyhaline	Silt	20	72	247
10	87.5	25.0	430	1070	1500	1.9	Polyhaline	Sand	24	220	362
11	60.0	60.0	450	2980	3430	6.0	Polyhaline	Silt	24	224	330

was observed throughout the majority of the soil profile across all pore-water salinity regimes and soil types. Root biomass ranged almost 10-fold from 120 to 1080 g m^{-2}. Rhizome biomass ranged from 250 to 5830 g m^{-2} and generally was 2- to 20-fold greater than root biomass, with one exception: the native stand (Site 8; Table 1).

Although the total live biomass (root and rhizome) was similar among the 3 salinity regimes, mean root biomass of mesohaline stands was significantly greater than that of oligohaline stands, with polyhaline sites intermediate (Table 2). Though not significant, mean rhizome biomass followed the inverse pattern. As a result, rhizome divided by root biomass produced a ratio that was significantly greater in oligohaline compared with mesohaline or polyhaline marshes. Aboveground shoot density and height also appeared to be affected by salinity, although the differences were not statistically significant (Table 2). Oligohaline stands exhibited the lowest shoot density and tallest plants, but these differences were not statistically significant (Table 2).

A comparison of native and invasive stands (n = 4) occurring at Sandy Point Marsh showed no significant difference in belowground biomass, though the native averaged 65% more roots and 42% less rhizomes than the invasive stand (Table 2). The invasive variety grew significantly taller than the native variety (P = 0.016) and apparently had lower stem densities (P = 0.058).

Both roots and rhizomes showed a pronounced decreasing trend in biomass when pooled into 20-cm depth increments (Fig. 2). Overall root biomass was greatest in the top 40 cm of the core and significantly declined thereafter. Similarly, rhizome biomass was greatest in the upper depth categories, with about two thirds of the biomass in the upper 40 cm of sediment.

When the root biomass data were analyzed by salinity regime, a decreasing trend with depth was most apparent within mesohaline sites, which demonstrated a sharp, decrease in live root biomass with depth (Fig. 3a). Oligohaline

Table 2**.** Comparison of *Phragmites* belowground biomass and stand properties by salinity regime, *Phragmites* variety, and soil type. Values are means ± 1 standard error; letters indicate differences among the means using a post-hoc Students *t*-test.

	Root biomass (g m^{-2})	Rhizome biomass (g m^{-2})	Rhizome : root	Stem density (# m^{-2})	Stem height (cm)
Salinity category					
Oligohaline	150 ± 10 a	2400 ± 340	16.8 ± 3.3 a	111 ± 17	357 ± 10
Mesohaline	520 ± 150 b	2590 ± 1080	5.0 ± 2.3 b	131 ± 19	322 ± 42
Polyhaline	330 ± 110 ab	1770 ± 610	6.4 ± 2.2 b	172 ± 50	313 ± 34
P-value	0.043	0.803	0.032	0.420	0.731
Phragmites Variety					
Native	380 ± 100	250 ± 170	0.9 ± 0.6	129 ± 14	234 ± 14 a
Invasive	230 ± 80	430 ± 260	2.4 ± 1.9	87 ± 11	295 ± 12 b
P-value	0.148	0.904	0.476	0.058	0.016
Soil Type					
Sand	410 ± 120	2280 ± 780	7.2 ± 2.5	139 ± 19	333 ± 30
Silt	290 ± 100	2370 ± 420	11.0 ± 4.0	132 ± 34	322 ± 36

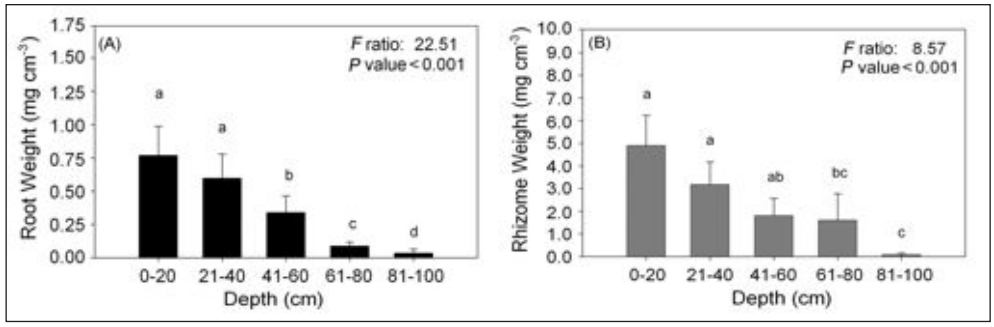
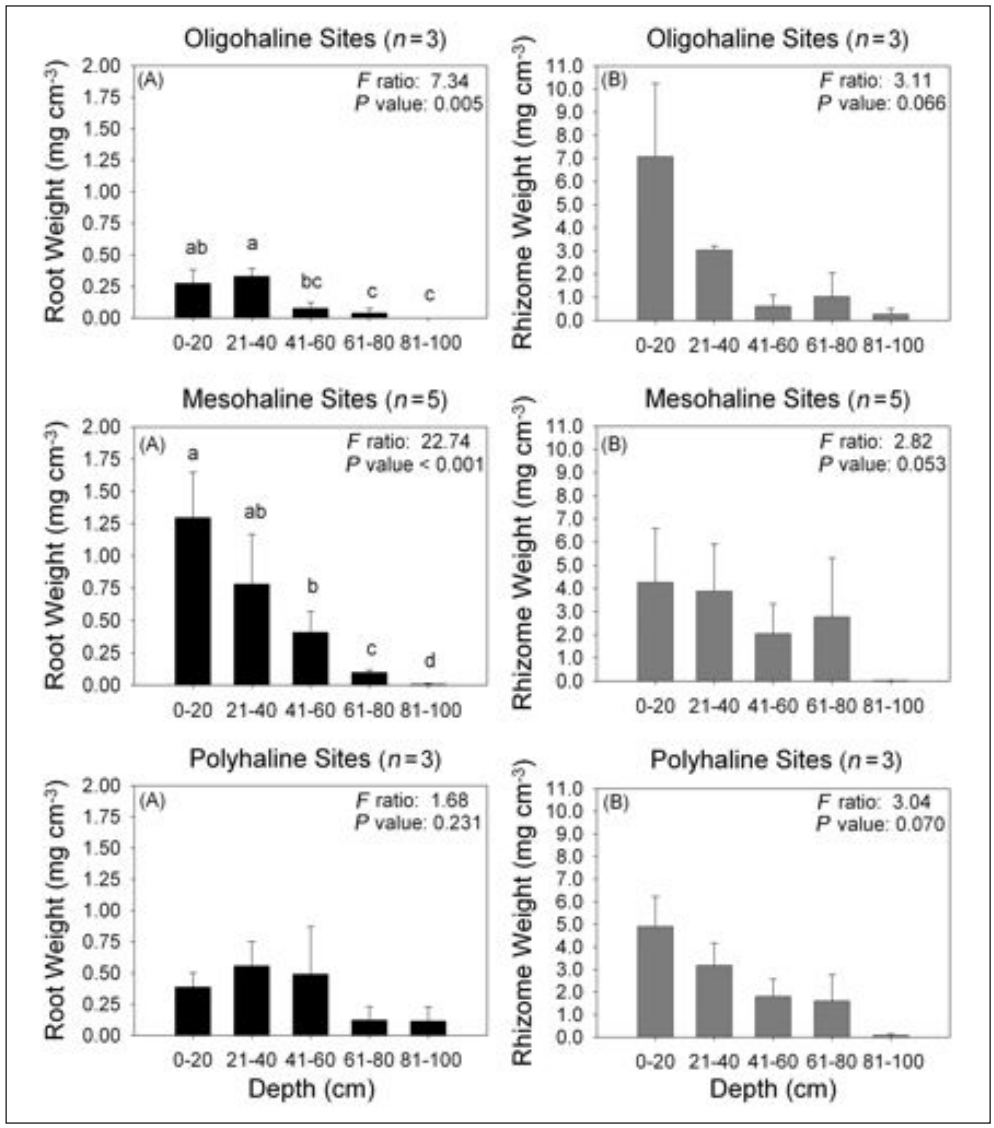


Figure 2. Average live root (A) and rhizome (B) biomass by 20-cm depth groupings in soil profile. Lowercase letters indicate differences among the means using a post-hoc Students *t*-test. Error bars are ± 1 standard error.



and polyhaline roots, however, exhibited relatively high biomass at mid-depths, peaking at the 20- to 40-cm depth range. In contrast, the biomass of live rhizomes declined sharply with depth in oligohaline sites, but was more gradual in polyhaline sites and consistent in mesohaline sites to a depth of 80 cm (Fig. 3b). When the data were sorted by soil type, live root biomass was similar in abundance in the top 60 cm for both sand and silt sites. Deeper than 60 cm, root biomass sharply declined, more so in silt sites (Fig. 4). Live rhizome biomass showed a gradual decline with depth for both soil textures.

Discussion

Several authors have noted that *Phragmites* has the ability to develop extensive roots and rhizomes that can grow rapidly (summarized in Engloner 2009, Haslam 1971, Soukup et al. 2002), reach considerable lateral length (Haslam 1972, Orson 1999, Rice et al. 2000), and penetrate deep within marsh soils (Bjork

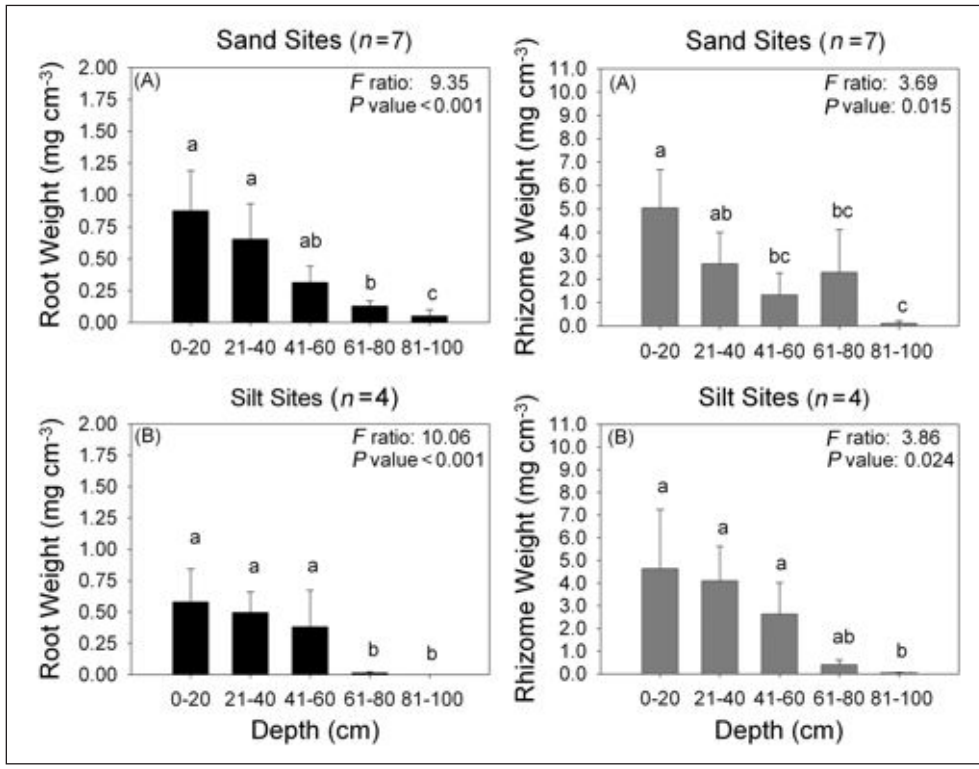


Figure 4. Live root and rhizome biomass averaged into 20-cm depth sections and grouped by (A) sand and (B) silt soil types. Lowercase letters indicate differences among the means using a post-hoc Students *t* -test. Error bars are ± 1 standard error.

Figure 3 (opposite page, lower figure). Live (A) root and (B) rhizome biomass averaged into 20-cm depth sections and grouped by pore-water salinity regime (oligohaline, mesohaline and polyhaline). Lowercase letters indicate differences among the means using a post-hoc Students *t* -test. Error bars are ± 1 standard error.

1967, Haslam 1970, Lissner and Schierup 1997, Ravit et al. 2003). All of these qualities potentially afford *Phragmites* an adaptive advantage over most native plants sharing tidal wetland habitats. In all sites sampled in this study, live roots of *Phragmites* were documented at depths greater than 40 cm and reached a maximum of 95 cm, exceeding the depth range of native graminoids (Table 3). Our study provides quantitative support for observations of *Phragmites* rooting depths noted in the literature by showing that this ability is in fact common for this species in New Hampshire and was consistently exhibited over a wide range of environmental conditions (e.g., salinity and soil texture).

In contrast, rhizomes exhibited greater variability, with rhizomes in one stand limited to soil depths as shallow as 22.0 cm, while another stand had rhizomes

Table 3. Observations of belowground biomass distribution and depth limits of *Phragmites australis* and other graminoids inhabiting tidal marsh. Percentages shown indicate proportion of total biomass contained within the denoted depth range. *observations include non-tidal sites; ** grown in experimental setting.

Source	Species	Depth of maximum biomass (cm)	Depth of maximum biomass (%)	Maximum depth (cm)
Bjork 1967	*Phragmites australis**	30		100–130 (soft substrate)
	P. australis			30 (hard/coarse substrate)
Haslam 1970	*P. australis**			50–80** up to 200
Gallagher and Plumbley 1979	*P. australis*	10–20		
Lissner and Schierup 1997	*P. australis*			35–85**
Rice et al. 2000	*P. australis*			100+
Vretare et al. 2001	*P. australis*			110**
Lynch and Saltonstall 2002	*P. australis* (var. *americanus*)			100+
Ravit et al. 2003	*P. australis*			70+
Moore et al. (this study)	*P. australis*	0–20	42	95 (roots); 85 (rhizomes)
Valiela et al. 1976	*Spartina patens*	0–15		20 (roots); 15(rhizomes)
	S. alterniflora Loisel.	0–15		20 (roots); 20 (rhizomes)
Gallagher and Plumbley 1979	*S. patens*	0–10		
Gross et al. 1991	*S. alterniflora*	0–10		30
	S. alterniflora			30
Steinke et al. 1996	*Agropyron repens* (L.) P. Beauv.	2–4		20
Windham 2001	*S. patens*			30
Saunders et al. 2006	*S. patens/ Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller	0–15		65 (roots); <15 (rhizomes)
Elsey-Quirk et al. 2011	*S. alterniflora*	0–15	86	
	S. patens	0–15	97	
	Juncus roemerianus Scheele	0–15	99	
	Distichlis spicata (L.) Greene	0–15	100	
Moore et al. (this study)	*S. patens*	0–20	92	70 (roots); 30 (rhizomes)

over 80 cm deep (Table 1). We suspect that this variability may have been due, at least in part, to the soil type, as sandy, mineral soils have been noted to inhibit deep penetration by rhizomes (Bjork 1967, Haslam 1970, Kudo and Ito 1988, Vretare et al. 2001). Additionally, the relatively narrow diameter coring device used in this study, while able to successfully obtain cores to depth, may be less likely to capture large, unevenly distributed rhizomes than more abundant roots. Nevertheless, the documentation of rhizomes across this depth range (22 to 83 cm) is consistent with less systematic observations of *Phragmites* depth in the literature (Table 3).

The distribution of belowground biomass is equally important as maximum penetration depth. We found root and rhizome biomass distributed over a greater depth range than most native plant halophytes, with 90% of the biomass occurring within the top 70 cm, versus the top 20 cm for *Spartina patens* (Fig. 2; Table 3), which has been noted co-occurring with *Phragmites* at coastal sites in New Hampshire and Massachusetts (Burdick et al. 2001, Moore et al. 2011). Windham (2001) documented similar results for *Phragmites*, finding considerable belowground biomass up to a depth 50 cm. Deep penetration of belowground biomass may allow *Phragmites* to access resources at soil depths affected less by tidal influences, thereby alleviating salinity stress and allowing it to expand its habitat range into more saline marshes.

Phragmites belowground biomass distribution may also be affected by environmental factors. Overall, a shallower depth range and significantly less biomass were found for roots in oligohaline sites compared with more saline sites (Fig. 3a), suggesting that *Phragmites* may allocate more of its resources to belowground growth to sustain itself in more physiologically taxing environments. Our findings are very similar to those documented by Soetaert et al. (2004) in Belgium and the Netherlands, who reported a total root biomass of 164 g m^{-2} in an oligohaline marsh and 414 g m^{-2} in a mesohaline marsh. Our study presents an average of 150 ± 10 g m^{-2} in 3 oligohaline marshes and 520 ± 150 g m^{-2} in 5 mesohaline marshes. The majority of rhizome biomass was also found at shallow depths for oligohaline sites, while rhizome biomass was more evenly distributed over depth in mesohaline and polyhaline regimes (Fig. 3b).

Phragmites aboveground morphology also appeared to be affected by porewater salinity, where stands tended to be taller with less dense shoots at sites lower in salinity (Table 2). This trend was shown in previous studies (Adams and Bate 1999, Chambers 1997, Hellings and Gallagher 1992, Soetaert et al. 2004), and coupled with belowground root biomass data, these trends suggest *Phragmites* may be altering its aboveground-to-root-biomass ratio based on salinity. In the more physically benign oligohaline marshes, *Phragmites* may be allocating a larger proportion of resources toward its aboveground structure to better compete for light. In more saline environments, *Phragmites* appears to commit greater resource allocation to roots. As marshes become more physically stressful (e.g., salinity, waterlogging, etc.) resource competition shifts from light to nutrients (Bertness 1991, Crain et al. 2004). The morphological plasticity of *Phragmites*

allows it to compete for belowground resources by increasing both its root biomass and depth range to potentially access fresher waters and nutrients beyond the reach of native marsh plants (Adams and Bate 1999, Burdick et al. 2001). *Phragmites* is capable of overcoming the stresses associated with greater depths (e.g., anoxia and toxic organic compounds) by developing thick hypodermal layers around its roots and rhizomes, which serve to minimize oxygen loss and promote diffusion of oxygen to more susceptible root tips (Armstrong and Armstrong 1988, Soukup et al. 2002).

While our sample size was not sufficient to make statistically robust conclusions regarding comparison of root and rhizome biomass between native and invasive forms of *Phragmites*, our data suggest native plants may invest more biomass in roots and less in rhizomes than the invasive form. A common garden experiment, using rhizomes collected from the same two stands in New Hampshire, found that native plants produced more roots than exotic plants (Holdredge et al. 2010). In other studies, League et al. (2006) found similar total belowground biomass among varieties, whereas Vasquez et al. (2005) found greater rhizome biomass associated with the invasive variety. Our results agree with Holdredge et al.'s (2010) that native stands produce more roots and fewer rhizomes, and these differences in belowground biomass allocation could help explain success of the invasive over the native variety.

Together with restoration of hydrology, increased salinity is critical in promoting re-establishment of native plant communities in tidal restoration efforts, particularly when these efforts are aimed at eliminating *Phragmites* (Bart et al. 2006, Rozsa 1995). The potential of *Phragmites* to obtain resources at soil depths beyond the reach of native marsh plants is very important in understanding competitive dynamics and especially important within a context of wetland restoration and vegetation management. Accordingly, measurement of pore-water salinity is recommended by salt marsh monitoring protocols (Drociak and Bottitta 2003, Neckles et al. 2002, Niedowski 2000, Steyer and Stewart 1992). However, none of the protocols suggest monitoring pore-water salinity throughout the range of live *Phragmites* roots documented in this study. Our findings suggest pore-water monitoring at greater depths is warranted to evaluate potential water resources available to *Phragmites* (sensu Burdick et al. 2001). Additional data can be directly obtained at greater depths or through the use of new field approaches such as electromagnetic induction that rapidly integrates pore-water salinity over a depth range of up to 150 cm (Moore et al. 2011).

Acknowledgments

We gratefully acknowledge assistance from University of New Hampshire students, including Lauren Thorpe, Quincy Blanchard, Alyson Eberhardt and Kirsten Nelson, for their participation in labor-intensive field and laboratory tasks and production of GIS-based maps. We thank David Shay of Jackson Estuarine Laboratory for assistance in collection and storage of soil samples. We also thank Howard Ginsberg (USGS Patuxent Wildlife Research Center) and two anonymous reviewers for their helpful suggestions to improve the manuscript. This work was funded in part by the United States Department of

Agriculture Natural Resources Conservation Service (Federal Award # 721428-6A380) and the New Hampshire Fish and Game Department. This paper is Contribution Number #503 from the Jackson Estuarine Laboratory and Center for Marine Biology at the University of New Hampshire.

Literature Cited

Adams, J.B., and G.C. Bate. 1999. Growth and photosynthetic performance of *Phragmites australis* in estuarine waters: A field and experimental evaluation. Aquatic Botany 64:359–367.

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

Armstrong, J., and W. Armstrong. 1988. *Phragmites australis*: A preliminary study of soil–oxidizing sites and internal gas transport pathways. New Phytologist 108:373–382.

Bains, G., A.S. Kumar, T. Rudrappa, E. Alff, T.E. Hanson, and H.P. Bias. 2009. Native plant and microbial contributions to a negative plant-plant interaction. Plant Physiology 151:2145–2151.

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., D. Burdick, R. Chambers, and J.M. Hartman. 2006. Human facilitation of *Phragmites australis* invasions in tidal marshes: A review and synthesis. Wetlands Ecology and Management 14:53–65.

Benoit, L.K., and R.A. Askins. 2002. Relationship between habitat area and the distribution of tidal marsh birds. Wilson Bulletin 114:314–323.

Bertness, M.D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. Ecology 72:138–148.

Bjork, S. 1967. Ecologic investigations of *Phragmites communis*. Studies in theoretic and applied limnology. Folia Limnologica Scandinavica 14:1–248.

Burdick, D.M., and R.A. Konisky. 2003. Determinants for expansion of *Phragmites australis,* Common Reed, in natural and impacted coastal marshes. Estuaries 26:407–416.

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

Chambers, R.M. 1997. Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. Wetlands 17:360–367.

Chambers, R.M., L.A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. Aquatic Botany 64:261–273.

Crain, M.C., B.R. Silliman, S.L. Bertness, and M.D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85:2539–2549.

Drociak, J., and G. Bottitta. 2003. A volunteer's handbook for monitoring New Hampshire salt marshes. New Hampshire Coastal Program, Portsmouth, NH. 65 pp.

Elsey-Quirk, T., D.M. Seliskar, and J.L. Gallagher. 2011. Nitrogen pools of macrophyte species in a coastal lagoon salt marsh: Implications for seasonal storage and dispersal. Estuaries and Coasts 34:470–482.

Engloner, A.I. 2009. Structure, growth dynamics, and biomass of Reed (*Phragmites australis*): A review. Flora 204:331–346.

Fell, P.E., R.S. Warren, J.K. Light, R.L. Rawson, and M. Sean. 2003. Comparison of fish and macroinvertebrate use of *Typha angustifolia*, *Phragmites australis*, and treated *Phragmites* marshes along the lower Connecticut River. Estuaries 26:534–551.

Findlay, S., P. Groffman, and S. Dye. 2003. Effects of *Phragmites australis* removal on marsh nutrient cycling. Wetlands Ecology and Management 11:157–165.

Gallagher, J.L., and F.G. Plumley. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. American Journal of Botany 66:156–161.

Gross, M.F., M.A. Hardisky, P.L. Wolf, and V. Klemas. 1991. Relationship between aboveground and belowground biomass of *Spartina alterniflora* (Smooth Cordgrass). Estuaries 14:180–191.

Haslam, S.M. 1970. The performance of *Phragmites communis* Trin. in relation to water supply. Annals of Botany 34:867–877.

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

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

Hellings, S.E., and J.L. Gallagher. 1992. The effects of salinity and flooding on *Phragmites australis*. The Journal of Applied Ecology 29:41–49.

Holdredge, C., M.D. Bertness, E. von Wettberg, and B.R. Silliman. 2010. Nutrient enrichment enhances hidden differences in phenotype to drive a cryptic plant invasion. OIKOS 119:1776–1784.

Keller, B.E.M. 2000. Plant diversity in *Lythrum*, *Phragmites,* and *Typha* marshes, Massachusetts, USA. Wetlands Ecology and Management 8:391–401.

Kudo, G., and K. Ito. 1988. Rhizome development of *Phragmites australis* in a reed community. Ecological Research 3:239–252.

League, M.T., E.P. Colbert, D.M. Seliskar, and J.L. Gallagher. 2006. Rhizome growth dynamics of native and exotic haplotypes of *Phragmites australis* (Common Reed). Estuaries and Coasts 29:269–276.

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

Lynch, E., and K. Saltonstall. 2002. Paleoecological and genetic analyses provide evidence for recent colonization of native *Phragmites australis* populations in a Lake Superior wetland. Wetlands 22:637–646.

Marks, M., B. Lapin, and J. Randall. 1994. *Phragmites australis* (*P. communis*): Threats, management, and monitoring. Natural Areas Journal 12:285–294.

Meyerson, L.A., K. Saltonstall, L. Windham, and S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetlands Ecology and Management 8:89–103.

Moore, G.E., D.M. Burdick, C.R. Peter, and D.R. Keirstead. 2011. Mapping soil porewater salinity of tidal marsh habitats using electromagnetic induction in Great Bay Estuary, USA. Wetlands 31:309–318.

Mozdzer, T.J., and J.C. Zieman. 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, T.J., J.C. Zieman, and K.J. McGlathery. 2010. Nitrogen uptake by native and invasive temperate coastal macrophytes: Importance of dissolved organic nitrogen. Estuaries and Coasts 33:784–797.

Neckles, H.A., M. Dionne, D.M. Burdick, C.T. Roman, R. Buchsbaum, and E. Hutchins. 2002. A monitoring protocol to assess tidal restoration of salt marshes on local and regional scales. Restoration Ecology 10:556– 563.

Niedowski, N.L. 2000. New York State salt marsh restoration and monitoring guidelines. New York State Department of Environmental Conservation, East Setauket, NY. 137 pp.

Odum, W.E. 1988. Comparative ecology of tidal freshwater and salt marshes. Annual Review of Ecology and Systematics 19:146–176.

Orson, R. 1999. A paleoecological assessment of *Phragmites australis* in New England tidal marshes: Changes in plant community structure during the last millennium. Biological Invasions 1:149–158.

Ravit, B., J.G. Ehenfeld, and M.M. Haggblom. 2003. A comparison of sediment microbial communities associated with *Phragmites australis* and *Spartina alterniflora* in two brackish wetlands of New Jersey. Estuaries 26:465–474.

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

Rooth, J.E., J.C. Stevenson, and J.C. Cornwell. 2003. Increased sediment accretion rates following invasion by *Phragmites australis*: The role of litter. Estuaries 26:475–483.

Rozsa, R. 1995. Tidal restoration in Connecticut. Pp. 51–65, *In* G.D. Dreyer and W.A. Neiring (Eds.). Tidal Marshes of Long Island Sound: Ecology, History, and Restoration. Bulletin No. 34. The Connecticut College Arboretum, New London, CT. 71 pp.

Rudrappa, T., J. Bonsall, J.L. Gallagher, D.M. Seliskar, and H.P. Bias. 2007. Root-secreted allelochemical in the noxious weed *Phragmites australis* deploys a reactive oxygen species response and microtubule assembly disruption to execute rhizotoxicity. Journal of Chemical Ecology 33:1898–1918.

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 United States of America 99:2445–2449.

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

Saltonstall, K., P.M. Peterson, and R.J. Soreng. 2004. Recognition of *Phragmites australis* subsp. *americanus* (Poaceae: Arundinoideae) in North America: Evidence from morphological and genetic analyses. SIDA Contributions to Botany 21:683–692.

Saunders, C.J., P. Megonigal, and J.F. Reynolds. 2006. Comparison of belowground biomass in C_3- and C_4-dominated mixed communities in a Chesapeake Bay brackish marsh. Plant and Soil 280:305–322.

Soetaert, K., M. Hoffmann, P. Meire, M. Starink, D. van Oevelen, S. Van Regenmortel, and T.J.S. Cox. 2004. Modeling growth and carbon allocation in two reed beds (*Phragmites australis*) in the Scheldt estuary. Aquatic Botany 79:211–234.

Soukup, A., O. Votrubova, and H. Cizkova. 2002. Development of anatomical structure of roots of *Phragmites australis*. New Phytologist 153:277–287.

Steinke, W., D.J. vonWillert, and F.A. Austenfeld. 1996. Root dynamics in a salt marsh over three consecutive years. Plant and Soil 185:265–269.

Steyer, G.D., and R.E. Stewart, Jr. 1992. Monitoring program for coastal wetlands planning, protection, and restoration act projects. US Fish and Wildlife Service, National Wetlands Research Center Open File Report 9341. Washington, DC. 85 pp.

Thien, S.J. 1979. A flow diagram for teaching texture by feel analysis. Journal of Agronomic Education 8:54–55.

United States Department of Agriculture - Natural Resources Conservation Service (USDA-NRCS). 2010. Keys to Soil Taxonomy. Washington, DC. 338 pp.

Valiela, I., J.M. Teal, and N.Y. Persson. 1976. Production and dynamics of experimentally enriched salt-marsh vegetation: Belowground biomass. Limnology and Oceanography 21:245–252.

Vasquez, E.A., E.P. Glenn, J.J. Brown, G.R. Guntenspergen, and S.G. Nelson. 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.

Vretare, V., S.E.B. Weisner, J.A. Strand, and W. Graneli. 2001. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. Aquatic Botany 69:127–145.

Warren, R.S., P.E. Fell, J.L. Grimsby, E.L. Buck, C.G. Rilling, and R.A. Fertik. 2001. Rates, 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.

Weiskel, P.K., and B.L. Howes. 1991. Quantifying dissolved nitrogen flux through a coastal watershed. Water Resources Research 27:2929–2939.

Windham, L. 2001. Comparison of biomass production and decomposition between *Phragmites australis* (Common Reed) and *Spartina patens* (Salt Hay Grass) in brackish tidal marshes of New Jersey, USA. Wetlands 21:179–188.

Windham, L., and R.G. Lathrop. 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.