



A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America

L.A. Meyerson¹, K. Saltonstall², L. Windham³, E. Kiviat⁴ & S. Findlay⁵

¹Yale University, School of Forestry and Environmental Studies, 301 Prospect Street, New Haven, CT 06511, U.S.A. (E-mail: laura.ahearn@yale.edu); ²Yale University, Department of Ecology and Evolutionary Biology, 165 Prospect Street, New Haven, CT 06520-8106, U.S.A.; ³Rutgers University, Department of Ecology, Evolution, and Natural Resources, New Brunswick, NJ 08903, U.S.A.; ⁴Hudsonia, Ltd., Bard College, P.O. Box 5000, Annandale, NY 12504-5000, U.S.A.; ⁵Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545-0129, U.S.A.

Received 1 September 1998; accepted in revised form 15 May 1999

Key words: biomass, biogeochemistry, nontidal marsh, *Spartina*, species richness, tidal marsh, *Typha*, wildlife habitat

Abstract

This paper compares the available North American literature and data concerning several ecological factors affecting *Phragmites australis* in inland freshwater, tidal fresh, and tidal brackish marsh systems. We compare aboveground productivity, plant species diversity, and sediment biogeochemistry; and we summarize *Phragmites* effects on faunal populations in these habitats. These data suggest that *Phragmites* aboveground biomass is higher than that of other plant species occurring in the same marsh system. Available data do not indicate any significant difference in the aboveground *Phragmites* biomass between marsh types, nor does there appear to be an effect of salinity on height. However, *Phragmites* stem density was significantly lower in inland non-tidal freshwater marshes than in tidal marshes, whether fresh or brackish. Studies of the effects of *Phragmites* on plant species richness suggest that *Phragmites* dominated sites have lower diversity. Furthermore, *Phragmites* eradication in freshwater sites increased plant diversity in all cases. *Phragmites* dominated communities appear to have different patterns of nitrogen cycling compared to adjacent plant communities. Aboveground standing stocks of nitrogen (N) were found to be higher in *Phragmites* sites compared to those without *Phragmites*. Porewater ammonium (NH_4^+) did not differ among plant cover types in the freshwater tidal wetlands, but in brackish marshes NH_4^+ was much higher in *Spartina* spp. than in neighboring *Phragmites* stands. Faunal uses of *Phragmites* dominated sites in North America were found to vary by taxa and in some cases equaled or exceeded use of other robust emergent plant communities. In light of these findings, we make recommendations for future research.

Introduction

Phragmites australis (Cav.) Trin. ex. Steud. (common reed) is increasingly viewed as a wetland pest species due to its rapid population expansions over the past century and its ability to quickly dominate marsh plant communities throughout the United States (Roman et al., 1984; Marks et al., 1994). The characteristically dense growth of *Phragmites* has several significant effects on the systems that it invades, which alter the available resources to other plants and animals. Plant height, stem density, and detrital accumulation com-

bine to reduce light at the marsh surface soil and air temperatures within *Phragmites* stand. These factors may inhibit the germination or establishment of other plant species as well as slow decomposition of organic material. In addition, low light levels in *Phragmites* stands resulting from this biomass accumulation can significantly delay spring thawing of marsh substrates, further preventing establishment of non-*Phragmites* plant species.

Other potential effects of *Phragmites* invasions include altered edaphic conditions, increased vertical accretion of marsh substrates, changes in floral diversity,

modified nutrient cycling, and changes in animal populations depending upon taxa (Harrison and Bloom, 1977; Metzler and Rosza, 1987; Sinicrope et al., 1990; Marks et al., 1994; Chambers 1997; Rooth and Stevenson, 1998). *Phragmites* has a broad salinity tolerance and colonizes both freshwater and brackish marsh environments, often forming near-monocultures. It is easily dispersed via water and readily colonizes disturbed sites, but it is also known to invade pristine areas (Phillips, 1987; Marks et al., 1994; Windham, 1995). Some of the characteristics of *Phragmites* that make it such an effective invasive plant are vegetative reproduction via rhizomes and rapid recovery after damage to aboveground growth.

It is interesting to note that despite the disparate abiotic environments and vastly different plant assemblages of freshwater and brackish systems, *Phragmites* flourishes in both environments. While much has been written about *Phragmites* in North America, surprisingly few data have been published on its ecology, particularly for freshwater marsh systems. This paper reviews available literature on the ecology of *Phragmites* in both freshwater and brackish wetlands in North America and compares the effects of *Phragmites* on those ecosystems. The factors selected for comparison reflect those aspects that researchers have considered important up to this time. More explicitly, this paper will examine the extent to which *Phragmites* in both types of environments (a) differs in aboveground plant growth, (b) affects total plant species diversity, (c) changes the biogeochemistry of sediment porewater, and (d) alters faunal populations. While other important ecological functions of *Phragmites* have been documented (e.g., increased evapotranspiration, photosynthetic rates, etc.), the available data are insufficient to develop generalizations and will not be included in this analysis.

Data used for this review were gathered from both published and unpublished studies of systems where *Phragmites* was a dominant species. In some cases data are from a single site due to the lack of other comparative information. We recognize that the lack of replicate studies that examine similar variables makes it difficult to form generalizations about the functioning of *Phragmites* in different habitats. However, the primary purpose of this review is to synthesize the existing data and identify avenues for future research.

While many studies in North America have been conducted on *Phragmites* ecology and management, knowledge of this species' effects on plant and animal communities remains incomplete. The mechanisms

used by *Phragmites* to establish and maintain dominance of marsh ecosystems are not clearly understood. Some data indicate potentially different strategies for *Phragmites* in fresh and brackish systems (Chambers, 1997; Templer et al., 1998), but the research necessary to conclusively establish these differences has not been undertaken. Two areas of future research that have the potential to affect management and restoration efforts are an improved understanding of how *Phragmites* differs in inland fresh, fresh tidal, and brackish tidal marshes, and the identification of the ecological indicators of *Phragmites* effects. This paper is an initial effort to begin this process.

The marsh environment

Marsh systems in estuaries occur along a complex and dynamic gradient. Salinities range from <0.5 ppt for freshwater tidal marshes and up to 30 ppt for brackish systems and are highly variable both seasonally and annually (Odum, 1988). Salinity is the dominant factor in determining the distribution of most plant species along the estuarine gradient (Odum, 1988). Generally, salt marsh systems have a low plant species diversity and a high incidence of zonation or single species dominance (Bertness, 1991). The opposite is true for freshwater tidal systems, which have relatively high plant species diversity and habitat overlap among species, though dominance by individual species may occur in a seasonal sequence (Odum, 1988).

Because freshwater tidal marshes are usually associated with rivers, they may have a greater tidal range than salt marshes. This is primarily caused by the restriction of the tidal water as it moves up the river channel (Odum, 1988). This tidal influence generally creates a regular, stable hydrologic regime over the long term that influences species diversity and productivity of the marsh. Inland freshwater marshes are also highly productive systems and are largely controlled by their hydrologic regime which can be highly variable, depending on the balance between water inputs (e.g., precipitation) and outputs (e.g., evapotranspiration; Mitsch and Gosselink, 1993).

Physiology and ecology of *Phragmites* growth

Seed germination

Although *Phragmites* produces large quantities of seeds, germination rates tend to be variable but are

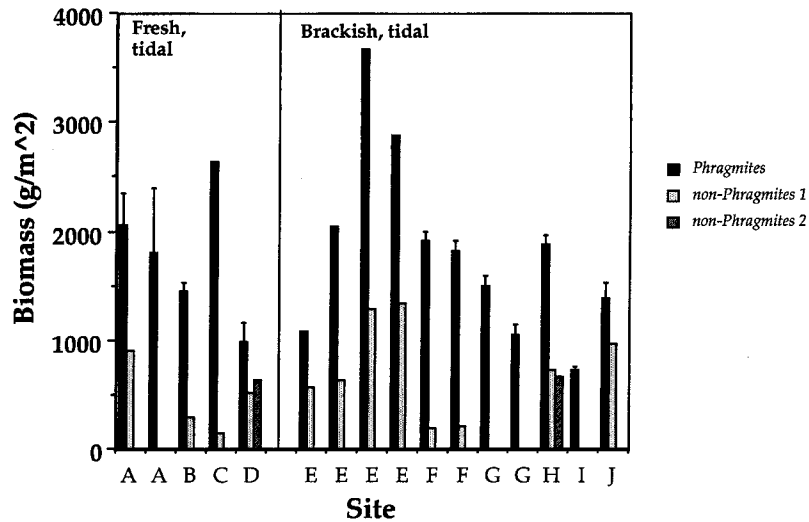


Figure 1. Biomass data for *Phragmites* vs. non-*Phragmites* plant species within a marsh site. In fresh tidal sites, non-*Phragmites* 1 refers to *Typha* sp. And non-*Phragmites* 2 refers to *Lythrum salicaria*. In the brackish sites, non-*Phragmites* 1 and 2 refer to *Spartina patens* and *S. alterniflora*. Error bars represent standard error (not available for all data). Site locations and data sources are as follows: A) Chapman Pond, CT: Findlay, unpub. Data; B) Chapman Pond, CT: Meyerson 2000; C) Chester Creek, CT: Meyerson 2000; D) Tivoli North Bay, NY: Temple et al., 1998; E) Great Island/Lower Connecticut River, CT: Buck, 1995; F) Mullica River, NJ: Windham, 1995; Sussex County/Milford, DE: Tyranski, 1977; H) Blackbird Creek Marsh, DE: Roman and Daiber, 1984; I) Lac des Alenares, LA: Hopkinson et al., 1978; J) Lewes, DE: Linthurst et al., 1978.

generally low (Harris and Marshall, 1960; Galinato and van der Valk, 1986; Tucker, 1990; Marks et al., 1994). Low seed viability may be due to the self-incompatibility of *Phragmites* and its tendency to grow in large homogeneous clones that are genetically identical (Tucker, 1990). Salinity and temperature are other important abiotic factors regulating seed germination rates (Galinato and van der Valk, 1986). In laboratory experiments, Wijte and Gallagher (1996) found that although *Phragmites* seed germination is inhibited by salinities of 25 ppt, germination is stimulated by salinities of 5 to 10 ppt. In the field, *Phragmites* is restricted to regions in the marsh where salinity is abated by freshwater inputs or well-drained soils (Wijte and Gallagher, 1996). However, in the 5–10 ppt range, *Phragmites* has a competitive advantage over other upland marsh species (e.g., *Iva frutescens*, *Solidago sempervirens*, etc.; Wijte and Gallagher, 1996).

Biomass

The availability of biomass data on *Phragmites* in North America is very limited and mainly exists for the aboveground portion, but several patterns do emerge. The dense clonal growth of *Phragmites* and its great height makes this reed highly productive. Live aboveground biomass of *Phragmites* (range

980–2642 g dw m⁻² in freshwater tidal marshes, 727–3663 g dw m⁻² in brackish marshes) is higher than that of other plant species in all studies used in this analysis (range 152–900 g dw m⁻² in freshwater tidal marshes, 194–1340 g dw m⁻² in brackish marshes; Figure 1). Dead culms of *Phragmites* can remain standing for two or more years with the result that total aboveground standing biomass (live and dead) is even higher for *Phragmites* than other marsh species (Roman and Daiber, 1984; Meyerson, unpub. data). In addition, in *Phragmites* stands with little or no tidal flushing (e.g., higher elevation sites, inland marshes), slowly decomposing detritus can accumulate so that total aboveground biomass (live, dead standing, detritus) in established stands further increases (Meyerson, 2000).

While salt marshes and the higher elevations of freshwater tidal marshes usually maintain at least a partial litter layer throughout the year, the lower and middle elevations of freshwater tidal marshes may be dominated by bare mudflats during the late winter and spring due to rapid decomposition (Odum, 1988). When *Phragmites* colonizes these zones, they function similarly to the upland tidal or brackish sites by retaining a year-round aboveground vegetation cover.

The available data presented in Figure 1 do not indicate any significant differences in live aboveground

Table 1. Summary of available data on *Phragmites australis* growth in three marsh types. (* indicates no available data).

Site	Density (culms-m ²)	Height (cm)	Salinity (ppt)	Data source Data source
Fresh, non-tidal				
Delta Marsh, Manitoba	28	191	<0.5	Thompson and Shay, 1985
Yale-Myers Marsh, Eastford, CT	26	380	<0.5	Meyerson, 1997
		272	<0.5	Meyerson, 1997
Stenners Run Wildlife Mgmt. Area, MD	13		*	Ailstock et al., 1990
Fresh, tidal				
Chapman Pond, CT	46	335	<0.5	Meyerson, unpub. data.
Chester Creek, Chester, CT	34	208	<0.5	Meyerson, unpub. data
Brackish/salt, tidal				
Pine Creek Estuary, Fairfield, CT	11	182	*	Bongiorno et al., 1984
Bodie Island and Pea Island, NC	104	345	*	Boone et al., 1987
Great Island, CT River, CT	54	280	4	Buck, 1995
Great Island, CT River, CT	*	245	4.5	Buck, 1995
Ben Marvin's Creek CT River, CT	125	235	10	Buck, 1995
Upper Island, CT River, CT	89	175	11.5	Buck, 1995
Fishing Bay/Greens Island Waterfowl Mgt. Complex, MD	67	*	*	Ailstock et al., 1990
	78	*	*	Ailstock et al., 1990
Charles E. Wheeler Salt Marsh, Milford, CT	*	208	15.6	Chambers, 1997
Sussex County, DE	105	*	*	Tyrawski, 1977
	71	*	*	Tyrawski, 1977
Milford, DE	79	*	*	Tyrawski, 1977
Demarest-Lloyd Memorial State Park, S. Dartmouth, MA	94	*	*	Davis and Briggs, 1986
Lewes, DE	93	*	*	Linthurst et al., 1978

Phragmites biomass between freshwater tidal and brackish tidal marshes. However, the limited freshwater data presented in Table 1 suggest that the density of stems in freshwater non-tidal marshes is substantially lower than in freshwater tidal and brackish tidal marshes (T-test, $T = -20.25$, $p < 0.001$). One possible explanation is that tidal wetlands may provide better habitat for *Phragmites* due to nutrient loading provided by tidal inundation (Mitsch and Gosselink, 1993), since aboveground biomass is closely related to the nutrient status of the substrate (Gorham and Pearsall, 1956). The regular flooding of tidal marshes imports nutrient-rich sediments which results in more vigorous plant growth (Buttery and Lambert, 1965). In contrast, inland wetlands receive only seasonal hydro-pulses from precipitation and runoff (Gosselink and Turner, 1978; Mitsch and Gosselink, 1993), and therefore less frequent nutrient inputs. Stresses and lower

nutrient availability due to irregular flooding should cause more resources to be allocated to belowground production in inland systems (Fitter, 1997). Differences in biomass and stem density between freshwater tidal and brackish marshes might become more apparent if total biomass data were available.

The negative impact of salinity on *Phragmites* is often cited as a major factor in successfully controlling the spread of *Phragmites*, especially in salt marsh restoration efforts where tide gates are replaced or removed (Roman et al., 1984; Sinicrope et al., 1990; Hellings and Gallagher, 1992; Marks et al., 1994). However, no significant differences were detectable with the data presented in Table 1. The lack of differences in culm density and height growth between the marsh types could be explained in several different ways. Because detailed sampling strategies of many studies were not reported, we could not de-

termine how sampling reflected heterogeneity of the marsh continuum (e.g., upland fringe to marsh edge). This lack of standardization may have weakened our ability to detect a statistically significant salinity effect. Another explanation may be that *Phragmites* tolerates such a wide range of salinity levels that the fresh-brackish separation is not sufficient to cause a difference in biomass (Hellings and Gallagher, 1992; Marks et al., 1994). Further, in brackish marshes, it is not known to what extent *Phragmites* clones in the upland fringe are supporting ramets in the lower portion of the marsh (Amsberry, 1997). Finally, because *Phragmites* rhizomes can penetrate to deep groundwater resources (Haslam, 1970), the impact of salinity may be diminished in some cases.

Plant diversity

Spread of Phragmites

Few comparative data are available regarding plant diversity in tidal marshes prior to the recent expansion of *Phragmites* throughout North America. However, paleoecological data suggest that species diversity in historical salt marsh systems is similar to what is found today in undisturbed systems (Niering et al., 1977; Clark, 1986). Although *Phragmites* has been part of the North American flora for at least 3500 years, its historical distribution is thought to have been limited to the upland border of the salt marsh (Orson et al., 1987).

Today *Phragmites* is prevalent across North America and is found in both coastal and inland marsh habitats. Studies performed in Connecticut comparing un-impounded and impounded brackish marsh systems have clearly showed that human alteration of natural hydrological cycles allowed *Phragmites* to enter the system and quickly dominate (Harrison and Bloom, 1977; Roman et al., 1984). Similarly, freshwater diversion from coastal freshwater wetlands, such as those in Hackensack Meadowlands (Sipple, 1971), can lead to saltwater intrusion and facilitate *Phragmites* expansion. Other factors thought to influence the spread of *Phragmites* include mechanical disturbance, pollution, coastal development, and the introduction of an aggressive genotype (Marks et al., 1994; Chambers et al., 1999). However, invasions have also occurred in many sites where human influence is not as apparent, and they may in fact occur in sites that have not been subject to human disturbance (Phillips, 1987; Marks et al., 1994; Windham, 1995).

Effects on diversity

Phragmites has become an aggressive colonizer of both freshwater and brackish systems. In most cases it excludes other plants and rapidly dominates the marsh. Clonal integration is one factor allowing it to penetrate into micro-habitats of poorer quality while maintaining vigorous growth in adjacent high quality areas of more optimal conditions (Amsberry, 1997). The overall result of *Phragmites* establishment is usually a reduction in plant species richness, particularly in the more diverse freshwater marsh systems. In brackish systems, where plant species diversity is generally low, the primary effect is to change the structure and function (e.g., nutrient cycling, wildlife utilization) of the marsh.

Studies examining changes in vegetation diversity over time show that when *Phragmites* enters the system, overall species diversity within the marshes declines (Stalter and Baden, 1994). These results are also supported by anecdotal evidence obtained by talking to land managers across North America who have observed the effects of *Phragmites* invasion on their sites (Chambers et al., 1999). Similarly, studies comparing *Phragmites*-dominated to *Phragmites*-free regions within the same marsh have demonstrated higher species diversity in *Phragmites*-free regions in all marsh types; this is particularly evident in freshwater non-tidal marshes where the total number of species in *Phragmites*-free regions shows a twofold increase over *Phragmites*-dominated areas (Figure 2). Further, in sites dominated by *Phragmites*, relatively high plant diversity can be recorded throughout a stand (e.g., East Harbor State Park, OH), but individuals of other species are often sterile, widely scattered, and do not represent viable populations of the species (J. McCormac, pers. comm.).

Data on species richness pre- and post-*Phragmites* invasion were not available. However, the studies presented in Figure 3 support the notion that the overall effect of *Phragmites* invasions is a decrease in plant biodiversity, particularly in freshwater marshes. Following *Phragmites* eradication treatments, colonization rates of other marsh plants are rapid, and in most cases species diversity markedly increases. Species diversity in freshwater sites rises quickly, possibly due to germination of seeds in the soil being released by higher light levels (Galinato and van der Valk, 1986). In contrast, a brackish site had a reduction in plant species diversity (Figure 3). However, the long-term stability of these plant communities is not known since

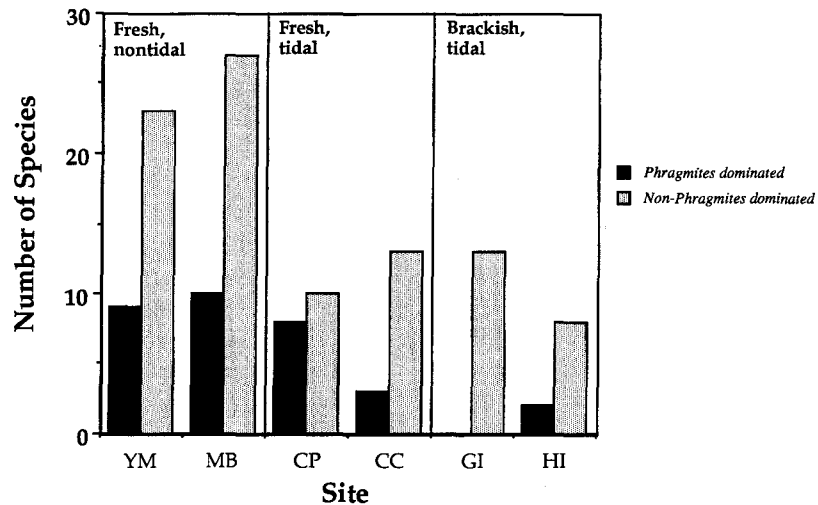


Figure 2. Total number of plant species found in *Phragmites* vs. non-*Phragmites* stands within a marsh site. Dominant plant species for non-*Phragmites* stands are *Typha* for YM, CP, and CC, *Carex* for MB, and *Spartina patens* for GI and HI. Site locations and data sources are as follows: YM = Yale-Myers marsh, Union, CT: Meyerson, unpub. data; MB = Moore Brook, CT: Kiviati unpub. data; CP = Chapman Pond, CT: Meyerson, unpub. data; CC = Chester Creek, CT: Meyerson, unpub. data; GI = Great Island, CT: Fertik, 1995; HI = Hog Island, NJ: Windham, 1995.

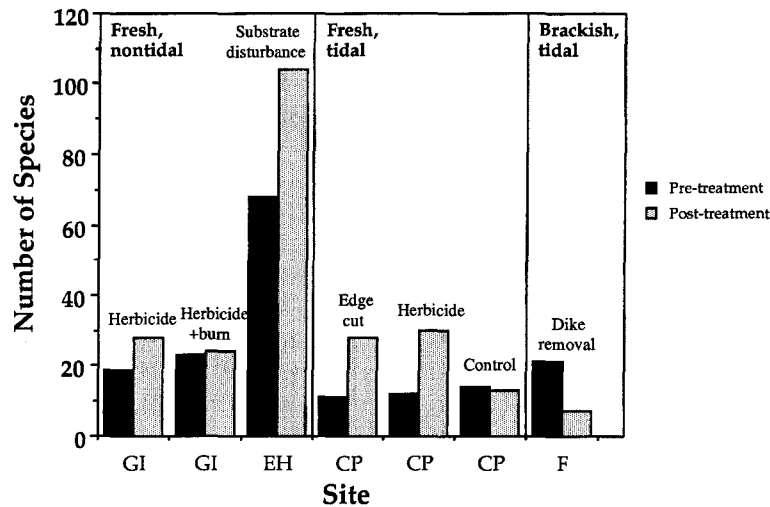


Figure 3. Changes in plant species richness in *Phragmites* marshes before and after *Phragmites* control procedures. Types of control measures are as indicated. Site locations, time since control procedure, and data sources are as follows: GI = Greens Island, MD, +2 years: Ailstock et al., 1990; EH = East Harbor State Park, OH, +3 years: McCormac, 1994; CP = Chapman Pond, CT +1 year: The Nature Conservancy CT Chapter, unpub. data; F = Fairfield, CT +3 years: Bongiorno et al., 1984.

re-invasion of *Phragmites* frequently occurs at many sites in the absence of repeated treatments (Farnsworth and Meyerson, submitted).

Biogeochemistry of *Phragmites* in freshwater and brackish tidal marshes

At the ecosystem level, *Phragmites* may have a significant effect on nutrient cycling (Windham, 1995; Chambers, 1997; Windham and Ehrenfeld, 1997; Templer et al., 1998; Windham and Ehrenfeld, 1998; Meyerson et al., in press). While *Phragmites* leaves decompose relatively rapidly, its stems decompose

more slowly than tissues of other plant species that *Phragmites* displaces (Tyrawski, 1977; Buck, 1995; Windham and Ehrenfeld, 1998; Meyerson, 2000). The accumulation of this refractory detritus may also impoverish *Phragmites*-invaded sites by binding limiting nutrients in organic material and making them unavailable to other plants (Ahearn-Meyerson and Vogt, 1997; Meyerson et al., in press). The high biomass of *Phragmites*, therefore, has the potential to significantly alter nutrient cycling in the systems that it invades. Sequestration of other nutrients in living and dead biomass is also greater in *Phragmites* relative to other species (Meyerson, 1997; Templer et al., 1998; Meyerson 2000).

The effects of *Phragmites* on nitrogen cycling have received the most attention because nitrogen is commonly the most limiting nutrient in tidal marshes (Mitsch and Gosselink, 1993). Aboveground standing stock nitrogen (N) may be doubled or tripled by the invasion of *Phragmites* (Figure 4), suggesting a concomitant higher uptake of nitrogen. This relationship is probably not driven by increased N in tissues, but by large increases in biomass due to *Phragmites* invasion (Figure 1). The average tissue N concentration is variable from both *Phragmites* and non-*Phragmites* sites (Figure 5). Notably, the tissues of *Phragmites* differ in nitrogen content (leaves = 2–4%N, culms = 0.5–1%N), and culms decompose much more slowly than leaves. The N concentrations of *Spartina* and *Typha* tissues range from 1–2% for *Typha* and 1–4% for *S. patens*. The wide variability in N concentrations for all species in Figure 5 is probably the result of differences in nutrient availability at each site.

Porewater ammonium (NH_4^+) is the most common form of inorganic N in both freshwater and brackish marsh systems. Figure 6 shows porewater profiles of August NH_4^+ concentrations in stands of *Phragmites* and the two species it is displacing: *Typha*, spp. in freshwater marshes and *Spartina*, spp. in brackish marshes. Porewater NH_4^+ does not differ substantially among plant species in the freshwater marshes (Figures 6a, b), although there is a trend toward higher NH_4^+ concentrations in *Phragmites*-dominated sites. In brackish marshes, porewater NH_4^+ concentrations in stands of *Spartina* spp. are much higher than neighboring *Phragmites* stands (Figures 6c, d). Ammonium concentrations beneath *S. patens* also increases with depth, suggesting ammonium accumulation below the rooting depth in stands of *Spartina* (Figure 6d).

The most direct explanation for the low NH_4^+ in the sediment under *Phragmites* in brackish marshes

is the greater *Phragmites* demand for N relative to either of the *Spartina* species. In some ways, it may be expected that the higher standing stock N with *Phragmites* (and concomitant higher N uptake) should result in lower flux rates of N measured as lower porewater NH_4^+ concentrations in all tidal marshes. Porewater concentrations, however, are determined not only by biological uptake and supply rates, but also by chemical adsorption to available soil exchange sites. Therefore, variations between the porewater profiles of fresh and brackish marshes may result from differences in chemical properties of the sediment.

For instance, an increase in salinity corresponds with increases in the presence of free sodium ions (Na^+). Because Na^+ quickly attaches to soil exchange sites, higher salinity soils have more exchange sites filled with Na^+ , and these are therefore unavailable as adsorption sites for other ions (Seitzinger et al., 1991). We extracted bulk soil cores with 2M KCl in the laboratory for exchangeable NH_4^+ . Porewater NH_4^+ concentrations increased following these KCl extractions for freshwater soils (<0.5 ppt NaCl) but did not increase for brackish marsh soils (6–8 ppt NaCl).

The KCl extractions suggest that plant effects on porewater concentrations of NH_4^+ in freshwater marshes are buffered through available exchange sites in the soil so that available NH_4^+ is not in the porewater, but on exchange sites. In brackish marshes, exchange sites are filled with Na^+ , and any NH_4^+ in excess of plant demand remains in the porewater. Therefore, if *Phragmites* demand results in lower porewater NH_4^+ relative to *Spartina*, the difference in NH_4^+ remains in the porewater pool. In tidal freshwater marshes, any difference in plant demand on porewater NH_4^+ is masked by adsorption of excess NH_4^+ to available exchange sites. In freshwater sites, porewater NH_4^+ concentrations are similar under the different plant communities despite the difference in plant demand. Because porewater NH_4^+ is more likely to adsorb to soil in freshwater marshes, the influence of *Phragmites* on marsh NH_4^+ export may be greater in brackish marshes than in tidal freshwater systems.

Another mechanism for low NH_4^+ concentrations may be the increase in coupled nitrification-denitrification rates under *Phragmites* due to higher redox potentials that support NO_3^- production and, eventually, its dissimilatory reduction. Potential nitrification rates ($\text{NH}_4^+ > \text{NO}_3^-$) on whole-core laboratory incubations were three-fold greater in *Phragmites* soils than *S. patens* soils (Windham and Ehrenfeld,

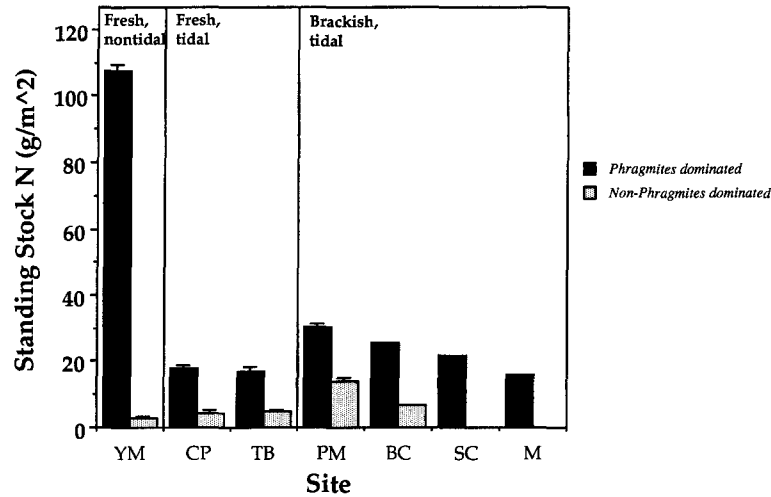


Figure 4. Total amount of nitrogen in aboveground plant tissue. Calculated as tissue %N in aboveground whole-plant tissues \times aboveground biomass g/m^2 . Error bars represent standard error. Site locations and data sources are as follows: YM=Yale-Myers marsh, Union, CT: Meyerson, unpub. data; CP=Chapman Pond, CT: Meyerson, unpub. data; TB=Tivoli Bay, NY: Templer et al., 1998; PM=Piermont marsh, NJ: Windham and Ehrenfeld, unpub. data; BC=Blackbird Creek, DE: Roman and Daiber, 1984; SC=Sussex County, DE: Tyrawski, 1977; M=Milford, DE: Tyrawski, 1977.

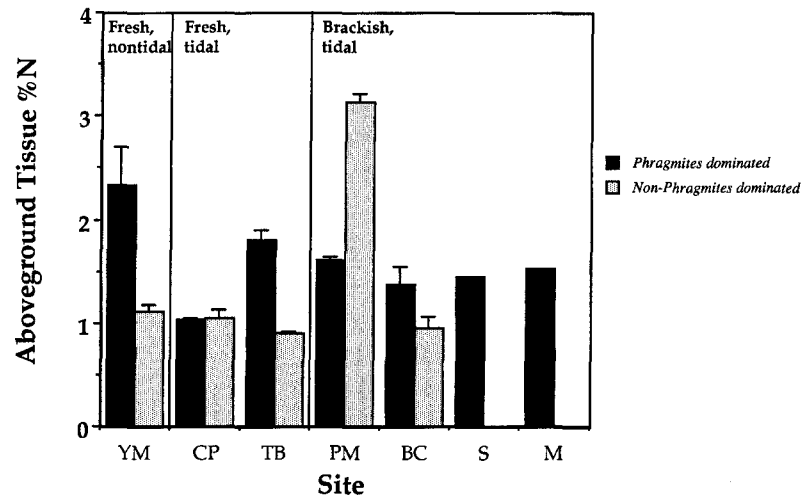


Figure 5. Concentration of nitrogen in aboveground plant tissue. Tissue %N determined at peak biomass (August) with CHN analyzer or sulfuric acid digestion. Error bars represent standard error. Site locations and data sources are as in Figure 4.

1998). Porewater nitrate (NO_3^-) concentrations were consistently below detection limits, so that if any nitrate was produced in the soils, it was quickly removed.

Whereas several mechanisms may explain the lower NH_4^+ concentrations detected in the porewater of *Phragmites* communities, increased mineralization rates may also be occurring so that the total available pools of NH_4^+ may in fact be higher than initial analyses suggest in brackish systems. Potential ammoni-

fication rates (NH_4^+ supply rates) were up to three-fold greater for *Phragmites* than *S. patens* in a brackish marsh (Windham and Ehrenfeld, 1998). Because no seasonal differences were found between *Phragmites* porewater NH_4^+ concentrations in this brackish marsh, NH_4^+ supply and consumption appear to be tightly coupled. In a tidal freshwater marsh on the Hudson River, Otto et al. (1999) found no difference in denitrification enzyme activity among three plant species (*Phragmites*, *Typha*, and *Lythrum salicaria*). There

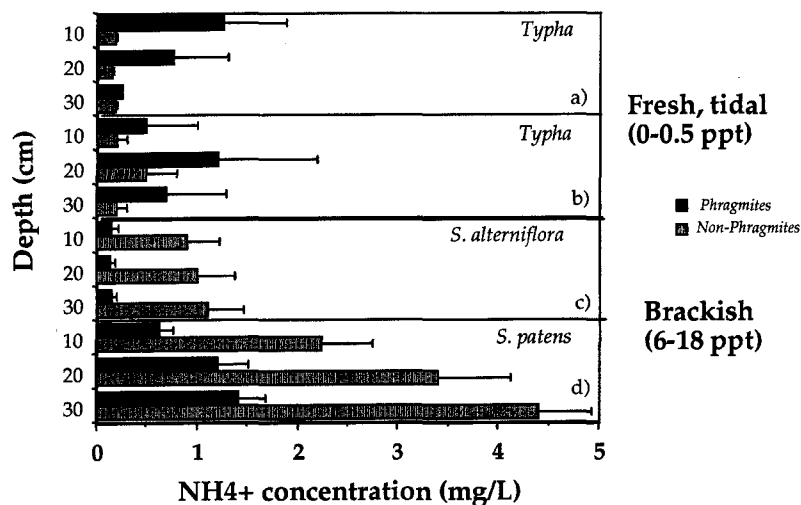


Figure 6. Porewater ammonium concentrations. Samples were collected by sippers or porewater equilibrators from 10–30 cm deep in the soil. Ammonium concentrations are displayed in mg/L. Error bars denote standard error. A) Meyerson, unpub. data from Chapman Pond, CT; B) Templer et al., 1998 from Tivoli Bay, NY; C) Chambers 1997 from Charles Wheeler Marsh, Milford, CT; D) Windham and Ehrenfeld, unpub. data from Hudson River, NY

were only sporadic differences among plants in potential net nitrogen mineralization. It remains to be seen whether it is possible to generalize that the presence of *Phragmites* affects nitrogen cycling processes in brackish marshes and not in freshwater tidal systems. It is clear, however, that differences among plants can influence an array of nutrient cycling processes and pools.

In addition to direct litter and plant biomass effects, *Phragmites* has the potential to indirectly influence several aspects of nutrient cycling. Oxidation of the rhizosphere is likely to be greater under *Phragmites*, due to convective through-flow of gases (Armstrong and Armstrong, 1988) and higher transpiration rates (sensu Dacey and Howes, 1984), which may cause phosphorous and other limiting nutrients to become bound and thus less available. In stands of declining *Phragmites* in Europe, it has been suggested that a lack of oxygen supplied via convection increases the dissimilatory reduction of nitrate to ammonium (Nijburg and Laanbroek, 1997) rather than to nitrogen gas. This would act to increase N availability in sediments of declining reed stands. Similarly, Sorrell et al. (1997) report that *Phragmites* die-back leads to more anaerobic sediments and consequently greater rates of methane release.

Biogeochemical processes may also influence *Phragmites* invasions. In brackish tidal marshes, Chambers (1997) and Chambers et al. (1999) found positive correlations between sulfide concentrations

and both NH_4^+ concentrations and species composition in brackish marshes. These studies noted the exclusive presence of *S. alterniflora* in areas of high sulfide/high NH_4^+ /high salt concentrations, and a decrease in *Phragmites* height with increasing sulfide concentrations. Due to sulfide-inhibition of NH_4^+ uptake, *Phragmites* may be restricted from high sulfide areas in brackish and salt marshes.

Animal use

In North America, monocultures of *Phragmites* are generally considered to provide poor quality habitat for wildlife and to support a low diversity of fauna (Roman et al., 1984; Kiviat, 1987). While many animals reportedly use *Phragmites* stands in North America (Table 2), few quantitative data are available on animal density or biomass in *Phragmites* stands, and few studies compare these factors to other marsh plant communities. There is currently insufficient information to contrast wildlife use in brackish and freshwater marsh environments because freshwater studies are scarce.

About 50 species of North American birds have been reported to breed in *Phragmites* communities. In contrast to the European bird fauna (Berthold et al., 1993), there are no *Phragmites* specialists in North America, though *Phragmites* is a characteristic nesting habitat for the marsh wren (*Cistothorus palustris*)

Table 2. Examples of animal use of *Phragmites* in North America.

Animals	Use	References
Mammals		
Muskrat	Regionally important food, but less so than <i>Typha</i> ; may degrade habitat	Howard et al., 1978; Whitman & Meredith, 1987.
Other mammals	White tailed deer, eastern cottontail use <i>Phragmites</i> stands in winter	Eggers and Reed, 1987.
Birds		
Breeding	Many species breed in <i>Phragmites</i> ; a few studies indicate lower densities than in other robust graminoids e.g., <i>Typha</i> , <i>Scirpus</i> , <i>Spartina</i> ; no reed specialists, but some graminoid specialists. Edges used by waterfowl.	e.g., Ward, 1942; Anderson et al., 1984; Schneider, 1992; Hudson, 1994; Brawley, 1995; Benoit, 1997.
Insectivory	A few insectivores e.g., black-capped chickadee (<i>Parus atricapillus</i>), commonly forage in <i>Phragmites</i>	Kiviat, pers. obs.
Non-breeding roosts	Swallows (Hirundinidae), European starling (<i>Sturnus vulgaris</i>), blackbirds (Icteridae)	Meanley, 1993; Kiviat, pers. obs.
Other non-breeding use	Ring-necked pheasant (<i>Phasianus colchicus</i>), Yuma clapper rail (<i>Rallus longirostris yumanensis</i>), brown-headed cowbird (<i>Molothrus ater</i>)	Anderson et al., 1984; Eggers and Reed, 1987.
Water bird foraging	Water birds use pools in <i>Phragmites</i> ; low use by blue-winged teal (<i>Anas discors</i>) broods	Bennett, 1938; Buchsbaum, 1997.
Reptiles		
Bog turtle	<i>Phragmites</i> is believed to degrade the habitat of the threatened bog turtle (<i>Clemmys muhlenbergii</i>)	M.W. Klemens, pers. comm.
Amphibians		
Bullfrog	More bullfrogs (<i>Rana catesbeiana</i>) along <i>Phragmites</i> - or <i>Arundo donax</i> -dominated sections of river bank than other communities	Clarkson and deVos, 1986
Fishes		
Fishes	Mummichog (<i>Fundulus heteroclitus</i>) & other small fishes forage about equally in <i>Phragmites</i> and non- <i>Phragmites</i> marsh on the Connecticut River estuary. More fish in <i>Spartina alterniflora</i> than in <i>Phragmites</i> at the same elevations in a southern New Jersey estuary	Fell et al. 1998; Rilling et al., 1999; Able, in press.
Insects		
Insects: Homoptera	Aphid (<i>Hyalopterus pruni</i>) and scale (<i>Chaetococcus phragmitidis</i>) density and biomass can be high; scale is a <i>Phragmites</i> specialist	Buckley & Ristich, 1977, Krause et al. 1997; Kiviat et al., unpub. data.
Insects: butterflies	Some favored, others displaced by <i>Phragmites</i> . One skipper, <i>Ochlodes yuma</i> , occurs in the western states and is a <i>Phragmites</i> specialist	Scott et al., 1977; Opler and Krizek, 1983; Kunstler, no date; D. Wagner, pers. comm.
Other terrestrial insects	Density, biomass, species richness variable; some are specialists; comparisons to other graminoids are variable	Fell et al., 1996; Krause et al., 1997; Kiviat et al., unpub. data.
Arachnids		
Spiders (Aranea)	More abundant in <i>Phragmites</i> than in other graminoids, individual species variable	Fell et al., 1996.
Harvestmen (Opiliones)	Less abundant in <i>Phragmites</i> than in other graminoids	Fell et al., 1996.
Mites	Phytophagous mites abundant	Buckley and Ristich, 1977.
Crustacea		
Isopods & amphipods	Different taxa more or less abundant in <i>Phragmites</i> compared to non- <i>Phragmites</i> marsh	Fell et al., 1996.
Mollusks		
Mollusks	More taxa more abundant in <i>Phragmites</i> than other graminoids	Fell et al., 1996.

(Burger, 1985; Cadman et al., 1987; Brawley, 1995), red-winged blackbird (*Agelaius phoeniceus*) (Yasukawa and Searcy, 1995) and yellow-headed blackbird (*Xanthocephalus xanthocephalus*) (Twedt and Crawford, 1995). However, these three species also nest in a wide variety of other plant communities dominated by graminoids, forbs, or shrubs. Near the ground, *Phragmites* culms are strong enough to support large nests of herons and egrets which otherwise nest in woody plants (Burger, 1985). In addition, edges along *Phragmites* communities can be important habitat for nesting ducks (Ward, 1942).

Birds also use *Phragmites* for roosting and foraging, but these activities have apparently been studied even less than breeding. Most use appears to be at stand edges rather than in the interior (Cross and Fleming, 1989; Benoit, 1997), although Benoit (1997) argues that the tall, dense growth of *Phragmites* along creek banks may, in fact, inhibit bird use of these edges. Red-winged blackbirds commonly roost in *Phragmites* during the non-breeding season (Meanley, 1993; Kiviat, pers. obs.). Black-capped chickadee (*Parus atricapillus*) appears to be the species that forages most commonly in *Phragmites* during the non-breeding season in the Hudson Valley of New York (Kiviat, pers. obs.).

Two recent studies of tidal marshes in Connecticut have indicated that the species composition and abundance of avian marsh specialists (i.e., those species that exclusively or primarily nest in marshes (Benoit and Askins, 1999) is similar in *Phragmites*- and *Typha*-dominated areas (Brawley, 1995; Benoit, 1997). There is one exception: Virginia rail is significantly more abundant in *Typha* than in *Phragmites* (Benoit and Askins, 1999). Benoit and Askins (1997) found that the number of marsh specialists using *Phragmites* was not significantly different than the numbers using short-grass marsh (*Spartina*, *Juncus gerardi*, *Distichlis*) areas. However, the species composition did differ; *Phragmites* contained marsh wren and swamp sparrow while short-grass meadow had seaside and sharp-tailed sparrows. In addition, several of the birds that used the short-grass areas were categorized as state-listed (endangered, threatened, or of special concern) while those that used *Phragmites* were more common. Marsh birds that are state-listed in Connecticut appear to be adapted to short-grass vegetation and do not breed in *Phragmites* stands due to their structure (Benoit and Askins, 1999). Marsh specialists, however, are only one group of birds that use marshes. Many herons, bitterns, ducks, rails, gulls,

terns, and shorebirds are also found there (L. Benoit, pers. comm.). Benoit and Askins (1999) found that the average number of species per plot was significantly lower in *Phragmites*-dominated wetlands compared to short-grass meadows.

It has been suggested that *Phragmites* impedes animal movement due to its high stem density and sizable culm height (Ward, 1942; Benoit and Askins, 1999; J. Collins, pers. comm.). Predatory mammals may also have difficulty moving through *Phragmites* communities or, in so doing, make noise that warns birds (D. Smith, pers. comm.). *Phragmites* growing in a mixed plant community, very large pools surrounded by *Phragmites* (Buchsbaum, 1997), or edges of *Phragmites* stands (Cross and Fleming, 1989) often appear to be better habitat for breeding or non-breeding birds than the interior of dense *Phragmites* stands. However, Benoit and Askins (1999) found that *Phragmites* pools were not utilized by birds, while those in other plant community types were.

Phragmites is also used by a number of animal species for protective cover. While reed may have limited value for muskrat (*Ondatra zibethicus*), standing dead culms can provide protection during winter storms when tidal marshes are swept by storm tides (Lynch et al., 1947). Pools of water isolated by *Phragmites* growth can also provide protection to flightless ducks during the summer wing molt (Ward, 1942).

Few vertebrates eat *Phragmites*, probably because culms and leaves are highly siliceous and thus unpalatable and indigestible (Lanning and Eleuterius, 1985; Kiviat, 1994). Muskrat can feed intensively on *Phragmites* rhizomes, although they are thought to prefer other foods such as the carbohydrate-rich *Typha* rhizomes (Daiber, 1982). The song sparrow (*Melospiza melodia*) is the only North American bird reported to consume *Phragmites* seeds (Marks et al., 1994).

On the Quinnipiac and Connecticut Rivers, there was a dramatic decrease in muskrat populations between 1965 and 1990 (Benoit and Askins, 1999). A similar decline occurred in the tidal Hudson River in the mid-1970s. During this time, *Phragmites* populations on these rivers expanded (Benoit, 1997, Winogron and Kiviat, 1997). It is unclear whether *Phragmites* expansion caused muskrat declines by replacing more important food plants, whether muskrat declines facilitated *Phragmites* expansion via reduced grazing on *Phragmites*, or whether other independent factors were responsible. Muskrats may benefit ducks, rails, wetland birds, and songbirds in tidal marshes by creating pools and bare patches on the marsh surface when

they harvest the vegetation (usually *Typha*) to feed and build their lodges. One consequence of the decrease in muskrat populations is that these pools and bare patches have decreased, and, in turn, so has potential wetland bird habitat (Benoit and Askins, 1999).

Terrestrial insect density, biomass, and species richness in *Phragmites* dominated communities can be high or low, depending on the species. Unlike Europe, where *Phragmites* supports many specialized phytophagous insects (Haslam, 1972; Tschardt, 1992), only 10–20 species are commonly found on *Phragmites* in North America, and most of these are generalists. Aphids or scale insects can reach high densities and biomasses in some *Phragmites* communities which may exceed those recorded on other plant species. For example, in early spring at a Hudson River fresh-tidal marsh, insect density and biomass were significantly higher on *Phragmites* than on either *Typha angustifolia* or *Lythrum salicaria*. Insect density was 1570, 198, and 60 m⁻², and insect biomass was 2.59, 0.695, and 0.169 g m⁻² (means of five 0.25 m² samples per plant community on *Phragmites*, *T. angustifolia*, and *L. salicaria* respectively; T-test, n = 10, p < 0.05 for both *Phragmites* vs. *Typha* and *Phragmites* vs. *L. salicaria*; Kiviat, unpub. data). Reed scale (*Chaetococcus phragmitidis*) comprised 98% of the biomass on *Phragmites* and did not occur on the other two plants. Such phytophagous insects may attract predators such as spiders and insectivorous birds.

In tidal wetlands, macrobenthos use is approximately equal in *Phragmites* and other plant communities, and there was no significant difference in the number of fish and the amount of prey biomass consumed by fish using a *Phragmites* versus non-*Phragmites* dominated high marsh (Table 2). Data on fish, aquatic invertebrates, and terrestrial invertebrates are limited to a few studies conducted on the Connecticut River estuary and the Hudson River estuary. Fell et al. (1998) and Rilling et al. (1999) found that both the brackish and freshwater *Phragmites* marshes of the lower Connecticut River estuary provide similar habitat and usable food resources as *Phragmites*-free marshes, at least for typical tidal marsh invertebrates and for the mummichog (*Fundulus heteroclitus*).

Conclusions

The goal of this review was to compare the ecosystem functions of marsh communities dominated

by *Phragmites*. Although available data are limited and incomplete in many cases, it appears that while aboveground productivity may be similar in brackish and freshwater marshes, *Phragmites* impacts these systems in different ways.

In brackish marshes, plant diversity is generally low. As a result, colonization by *Phragmites* does not significantly effect overall floral diversity. However, the physical structure and quantity of the aboveground plant component of the marsh increases. This, in turn, affects sediment porewater chemistry of the marsh by sequestering nitrogen in the aboveground biomass which, in typical short-grass brackish marsh systems, would otherwise have been made available to other species or exported to the nearby estuary. Aboveground plant growth patterns also may affect habitat quality for some wildlife species, specialized marsh birds in particular, which are unable to adapt to the taller, more robust structure of *Phragmites*.

In both tidal and non-tidal freshwater marshes, plant diversity is high and formation of a *Phragmites* monoculture can affect the marsh system in several ways. Plant species diversity is decreased, which may contribute to loss of rare species already threatened by small population size. In tidal marshes, sediment porewater NH₄⁺ flux may be affected by increased litter levels on the marsh surface which can act as a cap to marsh sediments, preventing loss of NH₄⁺ from sediment porewater via tidal flushing (Bowden, 1987). As with brackish marshes, certain animal species may be displaced in freshwater systems due to structural changes in the aboveground flora.

This review suggests several opportunities for additional research. Most studies to date have been conducted in *Phragmites*-dominated marshes. It would be desirable to compare those sites with systems where *Phragmites* is present but not dominant. This may elucidate some of the environmental factors which facilitate or inhibit *Phragmites* invasion and spread, such as competition, nutrients, salinity, water flow, and herbivory. The factors and mechanisms by which *Phragmites* invades and attains dominance may, in fact, be found to differ among inland freshwater, freshwater tidal and brackish tidal marshes.

It is noteworthy that the majority of the studies used in this analysis were performed in brackish marsh systems. Much less research on *Phragmites* has been undertaken in either freshwater inland or freshwater tidal marshes, yet it is apparent that *Phragmites* is spreading rapidly in many of these systems. In all marsh types, more manipulative field experiments

are necessary to reveal the mechanisms that lead to successful *Phragmites* invasion. For instance, while biomass is an obvious indicator of *Phragmites* success, it does not reveal the underlying mechanisms.

In conclusion, although the negative impacts of *Phragmites* on marsh systems in North America are often referred to in the literature, there is a shortage of quantitative data available to compare systems, both within and between marsh types. Much of the data cited herein were collected in the northeastern U.S.; therefore it is not clear how widely the results of these studies may apply to *Phragmites* environments in other geographic areas. Much past and current research, particularly in the field of tidal marsh restoration, is driven by concerns about adverse ecosystem impacts due to *Phragmites* invasion. However, few data have been published, and the unpublished literature is difficult to obtain. Additional studies comparing the effect of *Phragmites* on marsh systems are badly needed to provide a scientific basis for management decisions and to better understand the causes and effects of *Phragmites* spread.

Acknowledgements

We thank Dr K. Vogt, Dr R. Chambers, Dr J. Ehrenfeld, F.A.B. Meyerson, J. Hall, L. Benoit, C. Rilling, and two anonymous reviewers for their comments on drafts of this manuscript. We also thank F. Baumgarten, S. Braden, J. Collins, M. Gara, M.W. Klemens, J. Morrill and students, D. Raphael, D. Smith, J. Stainkamp, D. Wagner, and M.-A. White. Partial funding for this research was provided by The Nature Conservancy, Connecticut Chapter, Long Island Sound Fund administered by the Connecticut Department of Environmental Protection, through the sale of Long Island Sound license plates and contributions, and by Grant #98-26 from the Marsh Ecology Research Program administered by the Academy of Natural Sciences and funded jointly by the Connecticut Sea Grant College Program and New Jersey Public Service and Gas Company.

References

- Able, K.W. in press. Measures of juvenile fish habitat quality from a National Estuarine Research Reserve. American Fisheries Society Symposium 22 (Bethesda, MD).
- Ahearn-Meyerson, L. and Vogt, K.A. 1997. Considerations for restoring structure, function, and diversity to an ecosystem colonized by invasive plants: A *Phragmites* case study. In: MacDonald, K. and Weinman, F. (eds.), Wetland and Riparian Restoration: Taking a Broader View. Contributed papers and selected abstracts. pp. 257-258. Society for Ecological Restoration International conference, Seattle Washington.
- Ailstock, M.S., Suman, T.W. and Williams, D.H. 1990. Environmental impacts, treatment methodologies and management criteria for establishment of a statewide policy for the control of the marsh plant *Phragmites*: Year 2. Environmental Center, Anne Arundel Community College, Arnold, MD. Unpub. report. 54 pp.
- Amsberry, L. 1997. Mechanisms of invasion of *Phragmites australis* into salt marshes: the importance of clonal integration. Unpub. B.S. Thesis, Brown University, Providence, Rhode Island. 33 pp.
- Anderson, B.W., Ohmart, R.D., Meents, J.K. and Hunter, W.C. 1984. Avian use of marshes on the Lower Colorado River. In: Warner, R.E. and Hendrix, K.M. (eds.), California Riparian Systems; Ecology, Conservation, and Productive Management. pp. 598-604. University of California Press, Berkeley, California.
- Armstrong, J. and Armstrong, W. 1988. *Phragmites australis* - A preliminary study of soil-oxidizing sites and internal gas transport pathways. New Phytologist 108: 373-382.
- Bennett, L.J. 1938. The Blue-Winged Teal; Its Ecology and Management. Collegiate Press, Ames, Iowa. 144 pp.
- Benoit, L.K. and Askins, R.A. 1999. Impact of the Spread of *Phragmites* on the distribution of birds in Connecticut Tidal Marshes. Wetlands 19: 194-208.
- Berthold, P., Kaiser, A., Querner, U. and Schlenker, R. 1993. Analysis of trapping figures at Mettnau Station S. Germany with respect to the population development of small birds. A 20 years summary. 34th Report of the MRI-program. Journal of Ornithology 134: 283-299.
- Bertness, M.D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72: 138-148.
- Bongiorno, S.F., Trautman, J.R., Steinke, T.J., Kawa-Raymond, S. and Warner, D. 1984. A study of restoration in Pine Creek salt marsh, Fairfield, Connecticut. Proceedings of the 11th Annual Conference on Wetlands Restoration and Creation, Hillsborough Community College Institute of Florida Studies. pp. 10-19.
- Boone, J., Furbish, E. and Turner, K. 1987. Control of *Phragmites communis*: results of burning, cutting and covering with plastic in a North Carolina salt marsh. Technical Report No. 41, Athens, National Park Service, Cooperative Park Studies Unit.
- Bowden, W.B. 1987. The biogeochemistry of nitrogen in freshwater wetlands. Biogeochemistry 4: 313-348.
- Brawley, A.H. 1995. Birds of Connecticut's tidal wetlands: Relating patterns of use to environmental conditions. Unpub. M.A. thesis, Connecticut College, New London. 87 pp.
- Buchsbaum, R. 1997. Return of the native or what? Sanctuary 36(3): 12-15.
- Buck, E.L. 1995. Selected environmental factors and the spread of *Phragmites australis*. Unpub. Honors Thesis. New London, Connecticut College. 67 pp.
- Buckley, E.H. and Ristich, S.S. 1977. Rooted vegetation of the estuary. In: Weinstein, L.H. (ed.), An Atlas of the Biologic Resources of the Hudson Estuary. pp. 10-33. Boyce Thompson Institute for Plant Research, Yonkers, New York.
- Burger, J. 1985. Habitat selection in temperate marsh-nesting birds. In: Cody, M.L. (ed.), Habitat Selection in Birds. pp. 253-281. Academic Press, Orlando, Florida.
- Buttery, B.R. and Lambert, J.M. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. Journal of Ecology 53: 163-181.

- Cadman, M.D., Eagles, P.F.J. and Helleiner, F.M. 1987. Atlas of breeding birds of Ontario. University of Waterloo Press, Ontario, Canada.
- Chambers, R.M. 1997. Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. *Wetlands* 17: 360–367.
- Chambers, R.M., Meyerson, L.A. and Saltonstall, K. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany* 64: 261–273.
- Chambers, R.M., T.J. Mozdzer and J.C. Ambrose. 1999. Effects of salinity and sulfide on the distribution of *Phragmites australis* and *Spartina alterniflora* in a tidal saltmarsh. *Aquatic Botany* 62: 161–169.
- Clark, J.S. 1986. Late-Holocene vegetation and coastal processes at a Long Island Sound tidal marsh. *Journal of Ecology* 74: 561–578.
- Clarkson, R.W. and deVos, J.C. 1986. The bullfrog, *Rana catesbiana* Shaw, in the lower Colorado River, Arizona-California. *Journal of Herpetology* 20: 42–49.
- Cross, D.H. and Fleming, K.L. 1989. Control of *Phragmites* or common reed. Fish and Wildlife Leaflet 13.4.12. U.S. Fish and Wildlife Service, Washington, D.C. 5 pp.
- Dacey, J.W.H. and Howes, B.L. 1984. Water uptake by roots controls water table movement and sediment oxidation in short *Spartina* marsh. *Science* 224: 487–489.
- Daiber, F.C. 1982. Animals of the Tidal Marsh. Van Nostrand Reinhold, New York. 442 pp.
- Davis, A.N. and Briggs, T.L. 1986. Dispersion patterns of aerial shoots of the common marsh reed *Phragmites australis* (Poaceae). *Rhodora* 88: 325–330.
- Eggers, S.D. and Reed, T.L. 1987. Wetland plants and plant communities of Minnesota and Wisconsin. U.S. Army Corps of Engineers, St. Paul District.
- Farnsworth, E. and Meyerson, L. submitted. Species composition and inter-annual dynamics of a freshwater tidal plant community following removal of the invasive grass, *Phragmites australis*: a four-year study. *Biological Invasions*.
- Fell, P.E., Weissbach, S.P., Zuckerman, B. and Fell, S.P. 1996. Macroinvertebrates in *Phragmites*-dominated and *Phragmites*-free marsh regions at Chapman Pond and utilization by fish of tidal creeks situated along the salinity gradient of the lower Connecticut River system. Unpub. Report, Connecticut College, New London. 17 pp.
- Fell, P.E., Weissbach, S.P., Jones, D.A., Fallon, M.A., Zeppieri, J.A., Faison, E.K., Lennon, K.A., Newberry, K.J. and Reddington, L.K. 1998. Does invasion of oligohaline tidal marshes by reed grass, *Phragmites australis* (Cav.) Trin. ex Steud. affect the availability of prey resources for the mummichog *Fundulus heteroclitus*? *Journal of Experimental Marine Biology and Ecology* 222: 59–77.
- Fertik, R.A. 1995. Distribution of dominant angiosperms on the tidelands of the lower Connecticut River estuary in relation to salinity and hydroperiod. Unpub. report, New London, Connecticut College. 17 pp.
- Fitter, A. 1997. Nutrient Acquisition. In: Crawley, M.J. (ed.), *Plant Ecology*, 2nd edition. pp. 51–72, Blackwell Science, Oxford.
- Galinato, M.I. and van der Valk, A.G. 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. *Aquatic Botany* 26: 89–102.
- Gorham, E. and Pearsall, W.H. 1956. Production Ecology III. Shoot production in *Phragmites* in relation to habitat. *Oikos* 7: 206–214.
- Gosselink, J.G. and Turner, R.E. 1978. The role of hydrology in freshwater wetland ecosystems. In: Good, R.E., Whigham, D.F. and Simpson, R.L. (eds.), *Freshwater Wetlands: Ecological Processes and Management Potential*. pp. 63–78. Academic Press, Inc., San Diego, California.
- Harris, S.W. and Marshall, W.H. 1960. Experimental germination of seed and establishment of seedlings of *Phragmites communis*. *Ecology* 4: 395.
- Harrison, E.Z. and Bloom, A.L. 1977. Sedimentation rates on tidal salt marshes in Connecticut. *Journal of Sedimentary Petrology* 47: 1484–1490.
- Haslam, S.M. 1970. The performance of *Phragmites communis* Trin. in relation to water supply. *Annals of Botany (Lond.)* 34: 867–877.
- Haslam, S.M. 1972. Biological Flora of the British Isles: *Phragmites communis* Trin. *Journal of Ecology* 60: 585–610.
- Hellings, S.E. and Gallagher, J.L. 1992. The effects of salinity and flooding on *Phragmites australis*. *Journal of Applied Ecology* 59: 41–49.
- Hopkinson, C.S. and Gosselink, J.G. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. *Ecology* 59: 760–769.
- Howard, R., Rhodes, D.G. and Simmers, J.W. 1978. A review of the biology and potential control techniques for *Phragmites australis*. Unpub. report prepared for the Dredged Material Research Program. Environmental Laboratory, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi. 80 pp.
- Hudson, K. 1994. American robins nesting in *Phragmites*. *Bird Observer* 22: 153–155.
- Kiviat, E. 1987. Common reed (*Phragmites australis*). In: Decker, D. and Enck, J. (eds.), *Exotic Plants with Identified Detrimental Impacts on Wildlife Habitats in New York*. pp. 22–30. New York Chapter, The Wildlife Society, Annandale, New York.
- Kiviat, E. 1994. Reed, sometimes a weed. *News from Hudsonia* 10:4–6.
- Krause, L.H., Rietsma, C. and Kiviat, E. 1997. Terrestrial insects associated with *Phragmites australis*, *Typha angustifolia*, and *Lythrum salicaria* in a Hudson River tidal marsh. In: Nieder, W.C. and Waldman, J.R. (eds.), *Final Reports of the Tibor T. Polgar Fellowship Program 1996*. pp. V-1–V-35, Hudson River Foundation and New York State Department of Environmental Conservation – Hudson River National Estuarine Research Reserve.
- Kunstler, D.S. No date. Butterflies of Bayswater Point State Park & Dubos Point Park, Rockaway Peninsula, Queens County, New York. Unpub. report to the New York City Audubon Society. 13 pp.
- Lanning, F.S. and Eleuterius, L.N. 1985. Silica and ash in tissues of some plants growing in the coastal area of Mississippi USA. *Annals of Botany (Lond.)* 56: 157–172.
- Linhurst, R.A. and Reimold, R.J. 1978. Estimated net aerial primary productivity for selected estuarine angiosperms in Maine, Delaware and Georgia. *Ecology* 59: 945–955.
- Lynch, J.J., O'Neil, T. and Lay, D.W. 1947. Management significance of damage by geese and muskrats to Gulf Coast marshes. *Journal of Wildlife Management* 11: 5–76.
- Marks, M., Lapin, B. and Randall, J. 1994. *Phragmites australis* (*P. communis*): Threats, management, and monitoring. *Natural Areas Journal* 14: 285–294.
- McCormac, J.S. 1994. Lake Erie Protection Fund, Final Report. Project # LEPF-93-04.
- Meanley, B. 1993. The Patuxent River wild rice marsh. Privately published. 69 pp.
- Metzler, K. and Rozsa, R. 1987. Additional notes on the tidelands of the Connecticut River. *Newsletter of the Connecticut Botanical Society* 15: 1–6.

- Meyerson, L.A. 1997. Competition between *Phragmites australis* and *Typha latifolia* in a freshwater marsh ecosystem. Unpub. report to The Nature Conservancy, Connecticut Chapter. Middletown, CT, 33 pp.
- Meyerson, L.A. 2000. The impact of *Phragmites australis* on nutrient pools in two Connecticut River freshwater marshes. Final report to the office of long island sound programs. Connecticut Dep.
- Meyerson, L.A., Vogt, K.A. and Chambers, R.M. in press. Linking the success of *Phragmites australis* to the decoupling of ecosystem nutrient cycles. In: Weinstein, M.P. and Kreeger, D.A. (eds.), Concepts and Controversies in Tidal Marsh Ecology, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Mitsch, W.J. and Gosselink, J.G. 1993. Wetlands. 2nd ed. Van Nostrand Rheinhold, New York. 722 pp.
- Niering, W.A., Warren, R.S. and Weymouth, C.G. 1977. Our dynamic tidal marshes: Vegetation changes as revealed by peat analysis. Connecticut Arboretum Bulletin 12: 22.
- Nijburg, J.W. and H.J. Laanbroek. 1997. The fate of 15N-nitrate in healthy and declining *Phragmites australis* stands. Microbial Ecology 34: 254–262.
- Odum, W.E. 1988. Comparative ecology of tidal freshwater and salt marshes. Annual Review of Ecology and Systematics 19: 147–176.
- Opler, P.A. and Krizek, G.O. 1984. Butterflies east of the Great Plains. Johns Hopkins University Press, Baltimore, Maryland. 295 pp.
- Orson, R.A., Warren, R.S. and Niering, W.A. 1987. Development of a tidal marsh in a New England river valley. Estuaries 10: 20–27.
- Otto, S.P.M., Groffman, S.E.G., Findlay and Arreola, A.E. 1999. Invasive plant species and microbial processes in a tidal freshwater marsh. Journal of Environmental Quality 28: 1252–1257.
- Phillips, J.D. 1987. Shoreline processes and establishment of *Phragmites australis* in a coastal plain estuary. Vegetatio 71: 139–144.
- Rilling, G.C., Fell, P.E. and Warren, R.S. 1999. Fish use of brackish tidal wetlands on the lower Connecticut River: a comparison of a *Phragmites australis*-dominated vs. a restored high marsh. Final Report to the Connecticut Department of Environmental Protection, Hartford, CT.
- Roman, C.T. and Daiber, F.C. 1984. Aboveground and belowground primary production dynamics of two Delaware Bay tidal marshes. Bulletin of the Torrey Botanical Club 3: 31–41.
- Roman, C.T., Niering, W.A. and Warren, R.S. 1984. Salt marsh vegetation changes in response to tidal restrictions. Environmental Management 8: 141–150.
- Schneider, K.J. and Pence, D.M. (eds.). 1992. Migratory nongame birds of management concern in the Northeast. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts. 403 pp.
- Scott, J.A., Shields, O. and Ellis, S.L. 1977. Distribution and biology of pleistocene relict: *Ochlodes Yuma* (Hesperiidae) Journal of the Lepidoptera Society 31: 17–22.
- Seitzinger, S.P., Gardner, W.S. and Spratt, A.K. 1991. The effect of salinity on aquatic sediments: implications for benthic nutrient recycling. Estuaries 14: 167–174.
- Sinicrope, T.L., Hine, P.G., Warren, R.S. and Niering, W.A. 1990. Restoration of an impounded salt marsh in New England. Estuaries 13: 25–30.
- Sipple, W.S. 1971. The past and present flora and vegetation of the Hackensack Meadows. Bartonia 41:4–56.
- Sorrel, B.K., H. Brix, H. Schierup, and B. Lorenzen. 1997. Die-back of *Phragmites australis*: influence on the distribution and rate of sediment methanogenesis. Biogeochemistry 36: 173–188.
- Stalter, R. and Baden, J. 1994. A twenty-year comparison of vegetation of three abandoned rice fields, Georgetown County, South Carolina. Castanea 59: 69–77.
- Templer, P., Findlay, S. and Wigand, C. 1998. Sediment chemistry associated with native and non-native emergent macrophytes of a Hudson River marsh ecosystem. Wetlands 18: 70–78.
- Thompson, D.J. and Shay, J.M. 1985. The effects of fire on *Phragmites australis* in the Delta Marsh, Manitoba. Canadian Journal of Botany 63: 1864–1869.
- Tscharntke, T. 1992. Fragmentation of *Phragmites* habitats, minimum viable population size, habitat suitability, and local extinction of moths, midges, flies, aphids, and birds. Conservation Biology 6: 530–535.
- Tucker, G.C. 1990. The genera of Arundinoideae (Gramineae) in the southeastern United States. J. Arnold Arbor. 71: 145–163.
- Twedt, D.J. and Crawford, R.D. 1995. Yellow-headed blackbird (*Xanthocephalus xanthocephalus*). Birds of North America (192): 1–28.
- Tyravski, J.M. 1977. A study of the common reedgrass (*Phragmites communis* Trin.) in the coastal zone of Delaware. Unpub. M.S. Thesis, Marine Studies, University of Delaware, 164 pp.
- Ward, E. 1942. *Phragmites* management. Transactions of the North American Wildlife Conference 7: 294–298.
- Whitman, W.R. and Meredith, W.H. 1987. Introduction. In: Proceedings of a Symposium on Waterfowl and Wetlands management in the Coastal Zone of the Atlantic Flyway. Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife and the Delaware Coastal Management Program. pp. 5–10.
- Wijte, H.B.M. and Gallagher, J.L. 1996. Effect of oxygen availability and salinity on early life history stages of salt marsh plants. I. Different germination strategies of *Spartina alterniflora* and *Phragmites australis* (Poaceae). American Journal of Botany 83: 1337–1342.
- Windham, L. 1995. Effects of *Phragmites australis* invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. Unpub. M.S. thesis. Rutgers, New Brunswick, NJ. 61 pp.
- Windham, L. and Ehrenfeld, J.G. 1997. Effects of *Phragmites australis* invasion on dissolved nitrogen retention in brackish tidal marsh of the eastern U.S. Bulletin of the Ecological Society of America 78(4 supp): 208.
- Windham, L. and Ehrenfeld, J.G. 1998. Effects of *Phragmites australis* invasions on nitrogen cycling in brackish tidal marsh of the eastern U.S. In: Bulletin of the Conference on Concepts and Controversies in Tidal Marsh Ecology, Vineland, New Jersey. pp. 46.
- Winogrand, H. and Kiviat, E. 1997. Invasions of *Phragmites australis* in the tidal marshes of the Hudson River. In: Nieder, W.C. and Waldman, J.R. (eds.), Final Reports of the Tibor T. Polgar Fellowship Program 1996. pp. VI-1–VI-29, Hudson River Foundation and New York State Department of Environmental Conservation – Hudson River National Estuarine Research Reserve.
- Yasukawa, K. and Searcy, W.A. 1995. Red-winged blackbird (*Agelaius phoeniceus*). Birds of North America (184): 1–28.