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Expansion of *Phragmites australis* into tidal wetlands of North America

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Abstract

Phragmites expansion into tidal wetlands of North America is most extensive along the northern and middle Atlantic coasts, but over 80% of the US coastal wetland area occurs along the Gulf of Mexico and southern Atlantic coasts and may be susceptible to ongoing expansion. Rapid spread of *Phragmites* has been documented in freshwater (<0.5 ppt), oligohaline (0.5–5 ppt) and mesohaline (5–18 ppt) tidal wetlands. The advance of *Phragmites* into tidal wetlands of North America may have been facilitated by widespread coastal changes since European settlement, including disturbance of hydrologic cycles and nutrient regimes; the presence of *Phragmites* has become a signature of tidal wetland alteration. Although ploidy levels from $2n = 36$ to 72 have been documented for *Phragmites* throughout the continent, no genetics research to date has tested whether recent introduction of aggressive clones could account for *Phragmites* expansion. A fundamental concern regarding *Phragmites* expansion, particularly into tidal freshwater wetlands, is the observed reduction in biodiversity as many native species of plants are replaced by a more cosmopolitan species. Commensurate with a shift in habitat type is a reduction in insect, avian and other animal assemblages. Ecosystem services, including support of higher trophic levels, enhancement of water quality and sediment stabilization, however, are not diminished when a tidal wetland becomes dominated by *Phragmites*, provided that tidal flooding is retained. ©1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Phragmites australis (Cav.) Trin ex Steud (common reed), thought to have been a minor component of North American wetland plant communities for thousands of years, has

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become a dominant species in the past century. Both genetic and environmental arguments have been posed to explain the recent range expansion of *Phragmites* into terrestrial and aquatic habitats. As a biological invasion, the introduction of *Phragmites* could lead to detrimental consequences in North American tidal wetland ecosystems through alteration of resource utilization, modification of trophic structure, or change in disturbance regime (Vitousek, 1990; D'Antonio and Dudley, 1995; Mack, 1996). Because of decreased plant diversity in areas where it has spread, *Phragmites* is viewed generally as nuisance species in North America, a form of biological pollution (Cronk and Fuller, 1995). An economic and ecological basis for accepting *Phragmites* is lacking here; management programs for *Phragmites* eradication are common, whereas in Europe, scientific efforts are designed to understand and reverse *Phragmites* decline (e.g., van der Putten, 1997).

Although *Phragmites* occurs throughout non-tidal aquatic and even upland habitats, we present an overview of *Phragmites* expansion into tidal wetlands of North America. These ecosystems are valued for the numerous 'services' they provide, including flood control, water quality enhancement, and food and habitat support for commercial and recreational species of fish, shellfish and waterfowl. It is, in fact, the loss of native biodiversity and a perceived loss of socio-economic services that is a primary impetus behind management efforts to restore tidal wetland ecosystems to 'pre-*Phragmites*' structure and function. Our objectives are to introduce and describe *Phragmites* expansion and discuss current research in North America about this cosmopolitan species.

2. Phragmites distribution in tidal wetlands of North America

Phragmites currently occupies tidal and/or non-tidal habitats in large parts of Canada and all 48 of the conterminous US. The fossil record of *Phragmites* in North America is suspected to date back to the Cretaceous (e.g., Berry, 1914; Lamotte, 1952); more recently, fossil samples of *Phragmites* have been recorded from archeological sites in the Southwestern US that date to within the past 2500 years (Kaplan, 1963; Kane and Gross, 1986). In tidal wetlands of Connecticut, Niering et al. (1977) identified remains of *Phragmites* rhizomes in occasional samples of tidal marsh peat dating back 3000 years. Others have found similar remnants of *Phragmites* in north Atlantic tidal marshes 2000–4000 years old (Clark, 1986; Orson et al., 1987; G.L. Jacobson, Jr., personal communication). It is based on these records that *Phragmites* has been considered a minor native component of tidal wetland plant communities in North America (Orson et al., 1987).

The relative abundance of *Phragmites* in tidal wetlands of North America, however, has changed dramatically over the last 200 years. *Phragmites* was described as being found occasionally along ponds and marshes from the Atlantic to the Pacific coasts of Canada (Macain, 1883), but recent studies in Quebec indicate that its range has increased from local clustering of populations (Cody, 1963) to a more widespread distribution (Gervais et al., 1993). Although *Phragmites* was recorded as 'not common' in NY (Torrey, 1843) and MA (Dame and Collins, 1888), and 'rare to occasional' in CT (Graves et al., 1910), today *Phragmites* is widespread in New England and considered a nuisance species both inland and along the shoreline. Once rare in NJ (Willis, 1874), by 1910 *Phragmites* was found throughout almost the entire state (Stone, 1911). By the 1960s *Phragmites* was reported in

Table 1
Summary of coastal wetland areas and perceived status of *Phragmites* expansion throughout the conterminous US

Coastal region	Brackish/salt marsh (ha × 1000)[a]	Tidal fresh marsh (ha × 1000)[b]	Wetland types most abundant and susceptible to *Phragmites* expansion[c]	Current status of *Phragmites* expansion[c]
Northern Atlantic	27	0.7	High marsh, brackish and degraded wetlands	Extensive
Middle Atlantic	279	14	Tidal fresh, brackish and degraded wetlands	Extensive
Southern Atlantic	362	26	Tidal fresh and brackish wetlands; wildlife management wetlands	Less extensive
Gulf of Mexico	1000	40	Brackish wetlands; Mississippi River delta wetlands	Extensive
Pacific	49	5.8	Brackish wetlands of large river deltas; degraded wetlands	Less extensive

[a] Based on total salt marsh area identified by Field et al. (1991); includes marshes >18 ppt.
[b] Based on total tidal fresh marsh area identified by Field et al. (1991); may be underestimated.
[c] Based on informal polling of wetland scientists and managers.

nearly all US states with the exception of certain regions of the south Atlantic coast (Stalter, 1975).

Currently, the most expansive *Phragmites* habitats in tidal marshes of North America occur on the Atlantic coast and in the MS delta region of the Gulf of Mexico. On the Pacific coast of North America, *Phragmites* has been reported primarily from inland areas (Peck, 1941; Mason, 1957) and only occasionally is it found in tidal wetlands (M. Josselyn, personal communication), perhaps because of the relative geographic isolation of the tidal marsh habitat available for exploitation. *Phragmites* also occurs throughout Canada, but expansion has not been as rapid as in the US, likely because cold temperatures and a short growing season slow rates of vegetative growth and sexual reproduction (Victorin, 1995). In Mexico and portions of the US states of FL and TX, coastal regions are hypersaline and/or vegetated by mangrove forests that outcompete marsh vegetation. In these southern latitudes, other invasive *Phragmites*-like species, notably of the genera *Pennisetum* and *Neyraudea*, occupy some of the existing tidal marsh habitat.

The National Wetlands Inventory developed by the US Fish and Wildlife Service maintains a large, active program of mapping tidal and non-tidal US wetlands. Identification of tidal wetlands occupied by *Phragmites*, however, has not been completed at the national level (Field et al., 1991; R. Tiner, personal communication), nor is remote sensing information readily available by state or by other regional area. We completed an informal polling of scientists and wetland managers throughout coastal areas of North America and discovered that *Phragmites* expansion is known anecdotally, but total areas of *Phragmites*-impacted wetland generally are unknown (Table 1). GIS-related mapping efforts are thwarted to some extent by the common signatures of *Phragmites* with *Spartina cynosuroides* and *Zizania aquatica*. Further, the total area of tidal wetland occupied by *Phragmites* is dynamic, owing to clonal growth (area expansion) and wetland restoration efforts (area contraction).

In tidal wetlands with unimpeded water flow >18 ppt, expansion of *Phragmites* is restricted to the high marsh/upland fringe (Marks et al., 1994), a distribution influenced by environmental stressors such as depth of flooding, salinity, and sulfide effects (Hellings and Gallagher, 1992; Chambers et al., 1998). *Phragmites* is more extensive throughout natural brackish wetlands <18 ppt where salinity and sulfide effects are diminished. These growing conditions also have been created in many tidal wetlands of North America via hydrologic disturbance and alteration of tidal water flow via flood gates and culverts, effectively draining some marshes and impounding others (Roman et al., 1984; Montague et al., 1987). In addition, large tracts of tidal wetland in the US were ditched for mosquito control 50–60 years ago (Bourn and Cottam, 1950), leaving well-drained soil deposits along the ditches where *Phragmites* has since grown in (Niering and Warren, 1980). Because *Phragmites* thrives in disturbed wetland areas, the presence of *Phragmites* has become a signature of tidal wetland alteration, especially in the middle and northern Atlantic coastal regions of North America. For example, roughly one-half of the 6500 ha of tidal and brackish marshes in the state of Connecticut are considered active or potential sites of *Phragmites* expansion (P. Capotosto, personal communication), and *Phragmites* is estimated to occur in about 1500 hectares – roughly one-third – of tidal wetlands in the state of DE (W. Jones, personal communication).

Ongoing *Phragmites* expansion, however, is occurring at variable rates in newly constructed tidal wetlands (Havens et al., 1997) and in undisturbed fresh and brackish water habitats with full tidal connectivity (Rozsa, 1995; Warren and Fell, 1996; Table 2). A review by (Meyerson et al., in press(a)) found no difference in *Phragmites* stem densities growing in freshwater and brackish tidal marshes, and we found no clear evidence that recent changes in *Phragmites* abundance are different among freshwater, oligohaline and mesohaline tidal marshes (Table 2). The potential, therefore, for additional *Phragmites* expansion into undisturbed tidal freshwater and brackish wetlands of North America appears significant, especially into the large area of wetlands in the Gulf of Mexico and southern Atlantic coastal regions where *Phragmites* has most recently invaded (Table 1; Stalter, 1975).

3. Causes of *Phragmites* expansion

As has been determined for some European populations of *Phragmites* (e.g., Haslam, 1973), the primary method of *Phragmites* expansion in North American tidal wetlands is vegetative growth. Seed production and dispersion may introduce *Phragmites* into new habitats (Gervais et al., 1993), but seed viability is poor (Harris and Marshall, 1960; Fernald, 1970; Galinato and van der Walk, 1986) and most established stands expand due to rhizome spread and clonal growth. Exponential spread of *Phragmites* stands is reported from 0–3% annually by area (Rice and Stevenson, 1996; Winogrond, 1997). The dramatic expansion of this once-minor component of tidal wetland plant communities in North America may have both environmental and genetic causes.

3.1. Recent change in habitat suitability

Phragmites is an efficient colonizer of open substrate created by disturbance of tidal wetland habitat. The US human population has almost quadrupled since the turn of the

Table 2
Expansion of *Phragmites* into selected freshwater, oligohaline and mesohaline tidal marshes, documented as the change in abundance (increase in percentage of marsh covered)

Tidal marsh classification	Years of measurement	Change in *Phragmites* abundance, % cover	Source
Freshwater			
<0.5 ppt	1971–1991	0.3–2.5%	Winogrond, 1997
	1971–1991	0.1–0.5%	Winogrond, 1997
	1938–1994	16–38%	Rice and Stevenson, 1996
	1938–1994	11–24%	Rice and Stevenson, 1996
	1938–1994	2.5–6.4%	Rice and Stevenson, 1996
Oligohaline			
0.5–5 ppt	1965–1991	0.4–29%	Winogrond, 1997
	1974–1994	5–63%	Buck, 1995
	1974–1994	7.5–74%	Buck, 1995
	1985–1994	0.4–1.2%	Rice and Stevenson, 1996
Mesohaline			
5–18 ppt	1965–1991	33–73%	Winogrond, 1997
	1974–1994	12–43%	Buck, 1995
	1974–1990	11–24%	Buck, 1995
	1974–1990	6–21%	Buck, 1995
	1971–1994	0.7–7%	Rice and Stevenson, 1996
	1971–1994	1.0–2.2%	Rice and Stevenson, 1996
	1971–1991	3.2–83%	Windham, 1995
	1970–1985	9.7–24%	L. Flynn, unpublished data
	1976–1988	5.8–17%	Barrett and Niering, 1993
	1979–1993	26–45%	Bailey, 1997

century (US census data); because roughly 75% of these people live within 100 km of the coast, tidal wetland habitats are under major developmental pressures. An ongoing desire for coastal access and coastal residency has led to the construction of major seaports and transportation corridors cutting across the principle direction of tidal water flow, producing restrictions in tidal flushing by salt water at the seaward end and increases in filling at the landward end. Despite recent local, state and federal protection, coastal development accounted for 42% of estuarine wetlands loss in the US between 1975 and 1985 (Dahl and Johnson, 1991).

Expansion of *Phragmites* is on a scale comparable to the level of wetland alteration by North Americans over the last 200 years. Between the 1780s and the 1980s, 53% of all tidal and non-tidal wetlands in the conterminous US were altered, filled or destroyed (Dahl, 1990). Since European settlement in Canada, approximately 65% of Atlantic tidal salt marshes, and 80% of Pacific coast estuarine wetlands have been altered via agricultural drainage and diking, urban and industrial expansion, construction of port, road and hydroelectric facilities, and development of recreational properties (National Wetlands Working Group, 1988). *Phragmites* has expanded, albeit slowly, into many of these disturbed tidal wetland sites.

Other forms of non-human disturbance of wetlands include alteration of salinity regimes due to migration of river channels, thereby exposing freshwater vegetation to increased saltwater flows. Creation of brackish tidal habitat kills many freshwater species and creates open space quickly exploited by *Phragmites*. In some sections of the US (notably the delta region of the Sacramento River in CA) increased saltwater penetration is caused by water removal for agricultural and other uses, but land subsidence and sea level rise combine to create this effect naturally (Rejmanek et al., 1988; Rooth and Stevenson, in press). Disturbance created by large storms, wrack deposits and winter ice scouring can clear wetland habitat for *Phragmites* expansion, although the frequency of occurrence of these phenomena probably has not changed during the last 200 years.

A recent shift in nutrient availability may also be responsible for *Phragmites* expansion. With industrialization and cultural eutrophication, the quantity of nutrients discharged to tidal wetlands has increased (Ryther and Dunstan, 1971). Nitrogen borne by water and air (e.g., Yang et al., 1996) may supplement the nutrient regimes of all tidal wetland plants, but *Phragmites* may be a more efficient competitor for other limiting resources when nutrients occur in surplus (e.g., light; Levine et al., 1998). Just as increased phosphorus inputs to portions of the freshwater FL Everglades have created a shift from a *Cladium*-dominated wetland to one dominated by *Typha* (Wu et al., 1997), perhaps increases in nitrogen have stimulated a shift to tidal wetlands dominated by *Phragmites* (J.T. Morris, personal communication). It is also conceivable that *Phragmites* is capable of exploiting a form of limiting nutrient that is present but unavailable to other wetland species, giving *Phragmites* a competitive advantage through a decoupling of nutrient cycles (Meyerson et al., in press(b)).

3.2. Recent introduction of aggressive genotypes

New genotypes are hypothesized to have invaded North America sometime in the last 200 years, and the recent expansion of *Phragmites* into tidal habitats is thought to be due primarily to these more 'aggressive' forms (Metzler and Rozsa, 1987; Tucker, 1990; Rozsa, 1995). Dominance of genetic types within localized areas has been demonstrated, but no genetics research to date has provided an adequate test of the 'aggressive genotype' hypothesis. Isozyme studies of *Phragmites* now occupying expansive wetlands of the MS River Delta have identified two spatially dominant clones, one of which covers almost the entire delta region (Hauber et al., 1991). A third, more rare clone is similar to *Phragmites* populations occurring in smaller, isolated stands from the Gulf of Mexico coastal states of FL, AL, MS, LA and TX (D. Hauber, personal communication). These results suggest that the present day distribution of *Phragmites* throughout tidal wetlands of the Gulf Coast is due to vegetative growth (Hauber et al., 1991). Hybridization between the dominant delta clone and a less-dominant clone was measured at low levels, indicating that sexual reproduction occurs rarely within the delta population (Thao et al., 1994; Fournier et al., 1995). Similarly, in a study of 10 *Phragmites* populations in a watershed in MA, Keller (1998) used the RAPDs technique to demonstrate that all populations were closely related and most likely established primarily via vegetative propagules.

Karyotypic studies of North American populations of *Phragmites* indicate the presence of numerous ploidy levels (Table 3), but the ploidy level of hypothesized aggressive forms is not well-documented. In a study comparing the morphology of extant populations with historical samples obtained from herbarium collections, Besitka (1996) suggested a recent shift in ploidy levels had occurred in North American populations of *Phragmites*. The size of guard

Table 3
Summary of ploidy levels of *Phragmites australis* in North America

Country	State/province	Ploidy level	Source
USA	MS	$2n=48$, 49	Gaudreault et al., 1989[a]
	PA	4x	Besitka, 1996[b]
	NJ	4x	Besitka, 1996[b]
	CT	4x	Besitka, 1996[b]
	MA	4x, 6x	Besitka, 1996[b]
	DE	$2n=55$	Gervais et al., 1993[a]
	ME	$2n=56$	Gervais et al., 1993[a]
	FL	$2n=72$	Hauber unpublished data[a]
	LA	$2n=48$	Hauber unpublished data[a]
	FL	6x	Clevering, 1999[c], Lissner personal communication[c]
	LA	4x, 6x	Clevering, 1999[c]; Lissner personal communication[c]
	MD	4x	Clevering, 1999[c]; Lissner personal communication[c]
	WA	4x	Clevering, 1999[c]; Lissner personal communication[c]
Canada	Que.	$2n=36$,42, 45–59	Gervais, 1981; Gervais et al., 1993[a]
	Man.	$2n=48$	Löve, 1981[a]

[a] Based on chromosome counts.
[b] Based on morphological indices.
[c] Based on flow cytometry.

cells from historical samples were characteristic of hexaploids, whereas 21 of 22 extant populations from Northeastern America were more typical of the tetraploid morphology. Based on these results, Besitka (1996) suggested the tetraploid emerged in North America in the middle of the 19th century, probably introduced from Europe via trans-Atlantic shipping of goods and/or ship ballast (Burk, 1877). Further karyotypic examination will be required to support this hypothesized shift in ploidy level that is based on indirect evidence (i.e., guard cell size as an indicator of ploidy level).

Along the Gulf Coast of the US, some of the isolated stands of *Phragmites* are hexaploids, whereas the dominant *Phragmites* form in the MS delta region is a tetraploid (D. Hauber, personal communication). This result corroborates Besitka (1996) hypothesis that the tetraploid is a more aggressive form of *Phragmites*; interestingly, Hauber's isozyme analyses of tetraploids from the MS Delta versus tetraploids from the Northeast indicate they are phenotypically distinct (D. Hauber, personal communication). Studies are underway both in Europe and the US using geographically more extensive karyotypic analyses and advanced molecular techniques to provide a comprehensive genetic comparison among current and historical populations of *Phragmites* located throughout North America (D. Hauber et al., personal communication).

4. Concerns regarding expansion of *Phragmites*

Phragmites expansion represents a dramatic habitat change with direct and indirect influences on species number and type. The spread of *Phragmites* also has been equated with a perceived loss of ecosystem services – natural processes that are valued by humans and provided at no cost by tidal marshes. Relative to impacts on biodiversity, however, changes in ecosystem services do not seem to be as substantial in tidal marshes dominated by *Phragmites*.

4.1. Biodiversity

Conversion of existing tidal wetland plant communities to dominance by *Phragmites* typically decreases overall plant diversity and has a variable effect on animal diversity. The decrease in plant diversity is most dramatic in tidal freshwater marshes where over 100 species occur (Odum et al., 1984); many are native to particular freshwater wetland types. Because plant diversity is lower in brackish tidal marsh habitats, the decrease in species number is not as large. Available habitat for many animal species changes with expansion of *Phragmites*. Resting, feeding and breeding areas are diminished dramatically for migratory waterfowl (Hauber et al., 1991; G. O'Shea, personal communication). With a reduction in plant diversity and a change to vegetation structure dominated by *Phragmites*, large wading birds are excluded, many marsh specialists are replaced by generalists, and the overall species richness of birds is reduced (Benoit and Askins, 1999). The number of insect species known to feed on *Phragmites* in North America is fewer than 10, whereas over 70 are known in Europe (Haslam, 1972; Tscharntke, 1992; R.A. Casagrande, personal communication). However, density and biomass of insects can be high in *Phragmites* stands (Krause et al., 1997; Kiviat et al., submitted). The limited diversity data available for other animal groups in *Phragmites*-dominated tidal wetlands of North America show that the effect of *Phragmites* expansion and reduction/loss of pre-existing habitat on faunal richness and abundance varies by species and taxa (Meyerson et al. in press(a)).

4.2. Trophic transfer

Trophic connections in *Phragmites*-dominated marshes tend to vary as a function of tidal water flow. In tidal marshes with significant hydrologic disturbance, limited tidal exchange of water limits the transfer of energy to higher trophic levels of the adjacent estuary. *Phragmites* production may remain in these marshes and accumulate or be consumed in situ. For freshwater and brackish tidal marshes with unrestricted water flow, growth of *Phragmites* can cause small creeks on the marsh surface to fill in, thus limiting secondary production by restricting movements of fish and crustaceans into feeding areas (Roman, 1978); Smith et al. (1998), however, found no distinct differences in use of natural versus restored salt marshes by the fish *Fundulus heteroclitus* L.. Further, Fell et al. (1998) found no difference in feeding activities or food sources for *Fundulus* in *Spartina* and *Phragmites* marshes with unrestricted tidal flows. Stable isotopic analyses confirm that primary consumers of *Phragmites* detritus form a portion of the *Fundulus* diet (Wainright et al., 1998). Also, similar groups of fishes feed in *Phragmites* and *Spartina* marshes with similar flooding regimes (C. Rilling, personal communication). Unlike high-marsh species such as *Spartina patens* that form thick mats of vegetation, the spacing of *Phragmites* stems is sufficiently broad to allow fish to forage on the marsh surface.

As evidenced by standing dead biomass, *Phragmites* stems decompose slowly and appear to be of limited nutritive value to muskrats and other animals (e.g., Lynch et al., 1947; Whitman and Meredith, 1987). In contrast, the leaves have on average 2–4% nitrogen (Meyerson et al., in press(b)) and decompose quickly (Buck, 1995), indicating that some *Phragmites* production moves rapidly into secondary production. Similar to non-*Phragmites* wetlands, *Phragmites*-dominated freshwater and brackish wetlands with full tidal flows can provide a strong trophic link to fishes and invertebrates of estuaries. The observed decrease in biodiversity of birds and insects, however, suggests that some pathways for trophic transfer are different with conversion to a *Phragmites*-dominated wetland.

4.3. Water quality

The extensive literature documenting successful use of *Phragmites* in treatment wetlands (e.g., Wathugala et al., 1987; Biddlestone et al., 1991) demonstrates that chemical oxygen demand and the concentrations of dissolved and particulate nutrients and some heavy metals are reduced when water flows through *Phragmites* beds. No studies to date, however, have compared nutrient exchange in North American tidal wetlands dominated by *Phragmites* and other species. Various researchers suggest that nitrogen retention is greater in *Phragmites* wetlands (Chambers, 1997; Meyerson et al., in press(a); S. Findlay, personal communication). The accumulation of standing dead stem material supports the argument that *Phragmites* marshes are net importers of nutrients at least over the short term (years), but allocation of net production to above- and below-ground biomass for *Phragmites* relative to other tidal wetland species has not been quantified. The functional value of tidally-influenced *Phragmites* marshes as sites of water quality enhancement probably is as high as other marshes *Phragmites* replaces. Water quality enhancement by *Phragmites* may be realized in tidal wetlands <18 ppt; in tidal marshes >18 ppt, however, regular flooding by salt water restricts *Phragmites* development to higher tidal elevations, thereby limiting the opportunity for water treatment by a *Phragmites*-dominated wetland.

4.4. Sediment trapping/stabilization

Sedimentation rates in *Phragmites* marshes generally are thought to be high (Harrison and Bloom, 1977), but the impact of sediment accretion is variable. For example, many hydrologically altered tidal wetlands now dominated by *Phragmites* have undergone rapid subsidence because of increased drainage and increased peat oxidation; sedimentation in these marshes does not keep up with subsidence (R. Rozsa, personal communication). In other marshes, however, high rates of sediment trapping by *Phragmites* may exacerbate a reduction in trophic transfer between marshes and associated estuaries (Roman, 1978). As small channels fill in with sediments in *Phragmites* marshes, the tidal prism may decrease, thereby reducing access by aquatic species. Rejmanek et al. (1988) demonstrated that sedimentation in *Phragmites*-dominated marshes of the MS delta could in part offset losses of sediments resuspended by strong coastal storms. Rooth and Stevenson (in press) concluded that relative to other wetland species *Phragmites* has a greater effect on net vertical accretion of mineral and organic matter in tidal marshes subject to sea-level rise. Sea-level rise, subsidence, and erosion are the principal factors that decrease wetland elevation. In some marshes the ability of *Phragmites* to accumulate organic matter, stabilize surface sediments and trap sediments in the water column is sufficient to offset the effects of peat oxidation and localized subsidence.

5. Conclusion

Over the past century, *Phragmites* has expanded dramatically throughout tidal wetlands of North America. Both widespread environmental alteration of tidal wetland habitats and recent introduction of aggressive genotypes may contribute to *Phragmites* expansion. Historically, *Phragmites* has been an indicator of tidal wetland disturbance in North America, found where a reduction in hydrologic connectivity between tidal marsh and open water of an estuary has created suitable habitat for expansion; *Phragmites* is now expanding even into brackish and freshwater wetlands open to tidal flow. Community structure changes with the development of *Phragmites* monocultures, causing a decrease in native plant species, reduction in biodiversity and reduction in habitat for certain types of wildlife and waterfowl. With respect to other ecosystem services, however, the perception that regularly flooded tidal marshes dominated by *Phragmites* are less functional than those they replace is not supported by research to date. Ongoing expansion of *Phragmites* is expected throughout tidal wetlands of North America, particularly into large areas of southeastern US wetlands where *Phragmites* has been introduced only recently. In some instances, *Phragmites* marshes may accrete sediment better than some marshes they replace, thereby maintaining wetland habitat in the face of global sea level rise.

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