Journal of the Torrey Botanical Society 134(1), 2007, pp. 99–107

Distribution of native and introduced *Phragmites australis* in freshwater and oligohaline tidal marshes of the Delmarva Peninsula and southern New Jersey[1]

Robert E. Meadows[2,3]
Delaware Division of Fish & Wildlife, Newark, DE 19702

Kristin Saltonstall
Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD 21613

MEADOWS, R. E. (Delaware Division of Fish & Wildlife, Newark, DE 19702) AND K. SALTONSTALL (Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD 21613). Distribution of native and introduced *Phragmites australis* in freshwater and oligohaline tidal marshes of the Delmarva Peninsula and Southern New Jersey. J. Torrey Bot. Soc. 134: 99-107. 2007.—We surveyed freshwater and oligohaline portions of tidal river systems in Delaware, the eastern shore of Maryland, and southern New Jersey for native and introduced *Phragmites australis* populations. Populations of native *P. australis* occur along the major rivers of the eastern shore of Maryland, particularly the Choptank and Nanticoke Rivers, and were common along river and creek edges and typically less dense than introduced *P. australis*. In contrast, few native populations occur along rivers in Delaware and southern New Jersey where introduced *P. australis* dominates. These differences in distribution of native *P. australis* could be due to the magnitude of human impacts and the timing of invasion of introduced *P. australis* into these systems. The presence of so many populations of native *P. australis* on the eastern shore of Maryland is unique today as the subspecies has all but disappeared from much of its historical range along the Atlantic Coast.

Key words: anthropogenic impacts, Delaware, diversity, invasive plant, Maryland, New Jersey.

Freshwater tidal marshes of North America are typically diverse communities which are rarely dominated by single species (Odum 1988). However, most marshes along the Atlantic coast of North America have been greatly impacted by human perturbations and these disruptive changes have been paralleled by the rapid spread of *Phragmites australis* Cav. Trin ex. Steud (common reed) across the region. This invasion has been of great concern to both private and public land owners and managers since invasive *P. australis* typically will rapidly exclude other vegetation and form a monoculture.

Historically, *Phragmites australis* was found throughout much of North America, except in the southeastern United States. Along the Atlantic coast, preserved rhizome materials indicate that it grew along the borders of salt marshes, typically in mixed communities along with other grasses, sedges, and forbs (Kraft 1971, Niering et al. 1977, Orson 1999). Waksman et al. (1943) found *P. australis* remains in freshwater peat cores throughout New Jersey and herbarium specimens collected in the 1800's indicate that *P. australis* was likely found both in tidal freshwater systems and inland non-tidal communities in the region (Meadows and Saltonstall pers. obs).

Genetic studies have shown that invasive *Phragmites australis* populations are introduced in origin, probably having been brought to North America from Eurasia in colonial times (Saltonstall 2002, 2003a, b). This introduced lineage (Haplotype M, hereafter referred to as introduced *P. australis*) has high above- and belowground biomass (Meyerson et al. 2000) and spreads via transport of rhizome fragments or by seed dispersal (Haslam 1972, Bart and Hartman 2003). Although seed viability is typically low and varies interannually (Saltonstall unpub. data), thousands of seeds are produced by each plant, providing ample seed source with potential for colonization of new sites. Establishment at new sites is facilitated by soil disturbance and eutrophic conditions (Bertness et al. 2002, Bart

---

[1] Research support was provided by the Delaware Division of Fish & Wildlife (REM), the Adkins Arboretum, and Horn Point Laboratory (KS).

[2] Special thanks to Dr. Kimberly Hunter of Salisbury University for assistance with genetic analyses. We also thank Lori Staver, Jefferson S. Hall, and two anonymous reviewers for their comments on the manuscript. This is Contribution #4023 from the University of Maryland Center for Environmental Sciences.

[3] Author for correspondence: E-mail: Robert.Meadows@state.de.us

Received for publication January 16, 2006, and in revised form August 30, 2006.

and Hartman 2003, Minchinton and Bertness 2003). Once established, introduced *P. australis* typically spreads rapidly throughout a site and forms a tall dense monoculture which excludes most other plants and may change habitat quality for wildlife (Meyerson et al. 2000). In contrast, native *P. australis* (*P. australis* subsp. *americanus* Saltonstall, P.M. Peterson and Soreng, Saltonstall et al. 2004) is thought to have lower biomass, be less dense, and disperse less easily than the introduced lineage. Few studies have been done on the biology of native *P. australis* however, and these patterns are yet to be confirmed. Despite the overlap in distribution, there is very little evidence for hybridization between native and introduced *P. australis* (Saltonstall 2003b). The reason for this is unknown but differences in ploidy, phenology, pollen compatibility, or other factors may be inhibiting viable crosses between the two subspecies.

Although native *Phragmites australis* was found historically along the Atlantic coast, *P. australis* populations are now dominated by the introduced lineage (Saltonstall 2003a) which is probably the most aggressive invader in coastal marsh habitats of the region. Until recently, only a few relict native *P. australis* populations were known to occur in the mid-Atlantic region, including one found near Allen, MD and several along the Rappahannock River near Chance, VA (Saltonstall 2002, 2003a). Given the rarity of native *P. australis* elsewhere along the Atlantic coast, we sought to map the extent of its distribution in the area. Here we report the results of a regional survey for native *P. australis*. Although qualitative in nature, these data indicate differences in the growth habit as well as overlap in the habitat of native and introduced *P. australis* growing in natural environments. We also report the occurrence of two previously unidentified genetic haplotypes of native *P. australis*.

Methods. STUDY AREA. The study area encompassed the Delmarva Peninsula which is comprised of Delaware (DE), the eastern shore of Maryland (MD), and the eastern shore of Virginia (VA; Fig. 1). It stretches nearly 200 miles in length and is surrounded on three sides by water. Human population density is low and agriculture drives the economy, as it has since colonial times. However, residential development in the region has increased dramatically in the past 50 years (Chesapeake Bay Program 2004). The study area extends to the east to include southern New Jersey (NJ), a mostly rural agricultural area comparable to the southern Delmarva.

SURVEY METHODS. We surveyed freshwater and oligohaline-mesohaline (< 5 to 15‰) tidal marsh systems on the Delmarva Peninsula and in southern NJ for native and introduced *Phragmites australis* populations in October and November of 2002 and 2003 (Fig. 1). Major river systems with extensive emergent marsh communities in this salinity regime were targeted as these were the most likely to harbor native *P. australis* based on the current knowledge of its distribution (Saltonstall 2003a). While the range of salinities varied in the portions of the rivers that we surveyed between systems, annual mean values are typically less than 5‰ at the closest monitoring stations (MD DNR 2004).

For the purposes of this survey, we define a population as a continuous *Phragmites australis* stand with no obvious physical connection to adjacent populations. As such, a population may contain only a few culms or may extend uninterrupted over several acres. While this definition may allow genetically identical clones to be counted as separate populations or a large continuous stand comprised of multiple genetically different clones to be counted as a single population, the nature of our survey methods prevented delineation of the physical boundaries of each genetically distinct clone. Where mixed stands of native and introduced plants occurred, one population of each type was counted.

Populations were classified as either native or introduced on the basis of morphology. Characters used to distinguish the two population types included degree of senescence (introduced plants remained green well into November while native plants had already senesced), culm color (maroon or bright yellow color indicated native), degree to which leaf sheaths were attached to the culms (introduced plants retain their leaf sheaths on the culm while natives tend to drop their leaves and leaf sheaths after senescing), and presence/absence of culm spots (native plants may have black spots near the nodes; Blossey 2002, Saltonstall et al. 2004). Green leaf samples

amatically in the past
'ay Program 2004). The
) the east to include
(NJ), a mostly rural
arable to the southern

/e surveyed freshwater
aline (< 5 to 15‰)
ι the Delmarva Penin-
NJ for native and
australis populations
ıber of 2002 and 2003
ystems with extensive
unities in this salinity
s these were the most
P. australis based on
e of its distribution
ıile the range of sali-
tions of the rivers that
systems, annual mean
than 5‰ at the closest
D DNR 2004).
this survey, we define
ontinuous *Phragmites*
no obvious physical
populations. As such,
in only a few culms or
ted over several acres.
nay allow genetically
counted as separate
ge continuous stand
genetically different
s a single population,
ey methods prevented
cal boundaries of each
. Where mixed stands
d plants occurred, one
was counted.
ssified as either native
basis of morphology.
inguish the two popu-
degree of senescence
ained green well into
e plants had already
(maroon or bright
ative), degree to which
ached to the culms
ı their leaf sheaths on
nd to drop their leaves
ıescing), and presence/
ıative plants may have
nodes; Blossey 2002,
. Green leaf samples

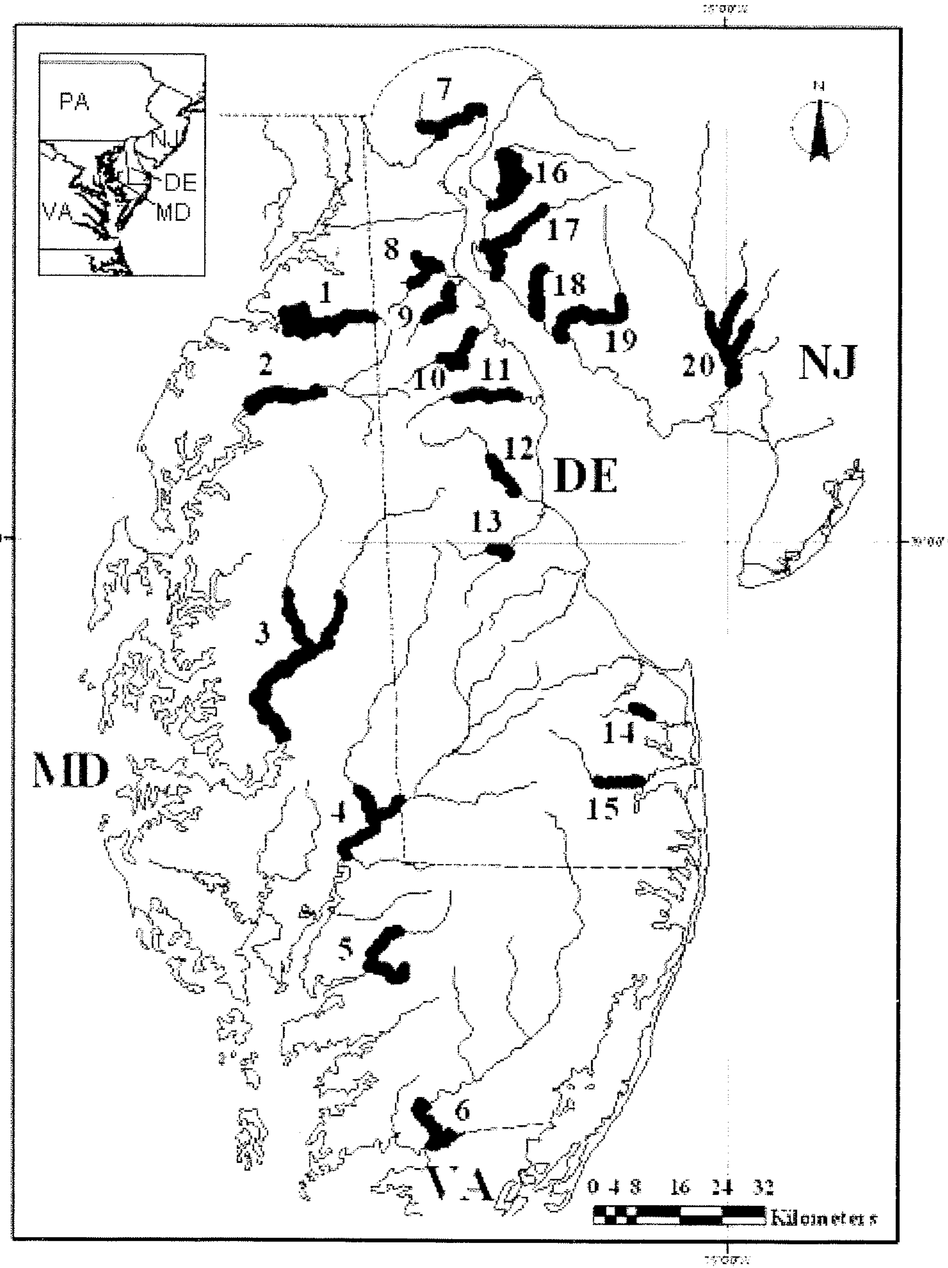

FIG. 1. Map of the Delmarva Peninsula and southern New Jersey. Surveyed sections of rivers are marked with a heavy line. Rivers are indicated as follows: MD: 1) Sassafras River; 2) Chester River; 3) Choptank River; 4) Nanticoke River; 5) Wicomico River; 6) Pocomoke River; DE: 7) Christina River; 8) Appoquinimink River; 9) Blackbird Creek; 10) Smyrna River; 11) Leipsic River; 12) St. Jones River; 13) Murderkill River; 14) Love Creek; 15) Indian River; NJ: 16) Salem River; 17) Alloway-Hope Creeks; 18) Stow Creek; 19) Cohansey River; 20) Maurice River.

were periodically collected and genetic analysis was done to confirm native status (see below).

Along all rivers in DE, NJ, and on the Sassafras and Chester Rivers in MD (Fig. 1), native populations were noted and coordinates logged on a GPS but no other data collected. Along the Choptank, Nanticoke, Pocomoke, and Wicomico Rivers in MD all *Phragmites australis* populations (native and introduced) were recorded, with GPS coordinates logged.

The size of each population was estimated visually within several broad size classes (e.g., < 0.1 ha, 0.1-0.2 ha, 0.2-0.5 ha, 0.5-1 ha, 1+ ha), as was stem density which we divided into three categories: sparse (< 10 stems m^{-2}), moderate (10-50 stems m^{-2}), and dense (> 50 stems m^{-2}). The position of each population relative to river/creek banks, marsh interior, or upland edge was also noted.

GENETIC ANALYSIS. To verify the native/introduced identification of *Phragmites australis* populations, a restriction fragment length polymorphism (RFLP) assay which distinguishes the two subspecies was done on 41 leaf tissue samples (27 putative native and 16 putative introduced based on morphology) collected in the survey. Restriction enzymes were used to cut two noncoding chloroplast DNA (cpDNA) regions and the sizes of the resulting DNA fragments were used to distinguish between native and introduced samples (Saltonstall 2003c). All samples confirmed native using the RFLP assay were analyzed further by sequencing the *trnT*A-*trnL*b intron and the *rbc*L-*psa*I noncoding cpDNA regions, following the protocols of Saltonstall (2002), to determine their haplotype. Each haplotype represents the combined DNA sequence from the two cpDNA regions and unique combinations are identified by letter designations. Native samples are distinguished from introduced ones by five mutations which all native haplotypes share, in addition to the mutations which distinguish haplotypes within the native subspecies (Saltonstall 2002). Sequences were aligned using Sequencher 4.1 (Genecodes) and compared to previously identified haplotypes for differences.

Results. We surveyed over 360 km of shoreline along the main channels of the rivers in addition to a large amount of marsh area up side creeks and channels off the rivers. Native *Phragmites australis* was present throughout the study area and covered more marsh habitat than introduced populations along some rivers in MD (Table 1). More large native populations were found than large introduced ones but native populations tended to have lower stem density than introduced populations (Fig. 2). We found native *P. australis* growing most often along river and creek banks in emergent marsh habitat and less frequently in marsh interiors or along upland edges (Fig. 3). We also observed that native populations appear to prefer lower salinity habitats. As we moved downstream within each river system we encountered fewer native populations and those that we did find were more likely to grow along side creeks and channels extending up into the marshes.

Introduced *Phragmites australis* was found growing along nearly all river systems surveyed and was more common than the native in all watersheds (Table 1). However, where quantified, the average size of introduced populations was often smaller than native ones (Table 1, Fig. 2). Introduced *P. australis* was frequently found along river and creek edges but, unlike native *P. australis*, was also common in the mid-marsh and along upland edges of the marsh (Fig. 3).

DELAWARE AND NEW JERSEY. Despite having surveyed over 200 km of river habitat, only 23 native *Phragmites australis* populations were identified in DE and NJ (Table 1). Although the number of introduced populations found along these rivers was not recorded, introduced *P. australis* was clearly more common (R. E. Meadows, pers. obs.) and many of the native populations had introduced *P. australis* growing nearby or immediately adjacent to them.

MARYLAND AND VIRGINIA. Native *Phragmites australis* populations were found along all rivers surveyed in MD with the exception of the Sassafras River. Only two native populations were found along the Chester River. Introduced *P. australis* was common along both of these rivers. Similarly, the main stem of the Wicomico River was also dominated by introduced *P. australis*, with only two native populations found in the drainage, both located along Wicomico Creek (Table 1).

The distribution of native *Phragmites australis* along the Choptank River can be divided into two zones which are separated by the Route 331 bridge which crosses the river just west of Tanyard, MD. Downstream of the bridge, populations were dominated by introduced *P. australis* (99.8% of total estimated area) and only two native ones were identified, both of which were being overgrown by introduced populations. Upstream of the bridge, native and introduced populations occupied approximately the same amount of area (21.9 vs. 21.4 ha, respectively) but more introduced populations were found. The

Table 1. Major rivers and tributaries surveyed, distance traveled along the main channel, and the number and estimated size of *Phragmites australis* populations. More detailed locations of each population are available from the authors. NA = data not collected.

State & County	River Drainage	Km covered	No. Native populations	Estimated Native area (ha)*	No. Introduced populations	Estimated Introduced area (ha)*
MD						
Cecil/Kent	Sassafras River	12.4	0	0.0	NA	NA
Kent/Queen Anne	Chester River	19.1	2	0.6	NA	NA
Talbot/Caroline	Choptank River	35.5	36	16.9	323	52.0
Talbot/Caroline	Tuckahoe Creek	17.6	30	5.1	7	0.9
Dorchester/Wicomico	Nanticoke	14.7	36	7.7	50	4.2
Dorchester	Marshyhope Creek	9.9	3	0.2	0	0.0
Wicomico	Wicomico River	14.8	0	0.0	87	12.9
Wicomico/Somerset	Wicomico Creek	11.7	2	0.1	35	4.6
Somerset/Worcester	Pocomoke River	13.4	22	14.1	117	22.3
VA						
Accomac	Pitt's Creek	11.1	7	0.3	64	5.7
DE						
New Castle	Christina River	14.6	0	0.0	NA	NA
New Castle	Appoquinimink River	10.1	12	1.0	NA	NA
New Castle	Drawyer's Creek	7.6	2	<0.1	NA	NA
New Castle	Blackbird Creek	14.6	1	<0.1	NA	NA
New Castle/Kent	Smyrna River	12.0	3	0.4	NA	NA
Kent	Leipsic River	15.6	0	0.0	NA	NA
Kent	St. Jones River	12.5	1	0.1	NA	NA
Kent	Murderkill River	6.7	3	0.1	NA	NA
Sussex	Love Creek	3.0	1	<0.1	NA	NA
Sussex	Indian River	5.1	0	0.0	NA	NA
NJ						
Salem	Salem River	15.9	0	0.0	NA	NA
Salem	Alloway Creek	15.1	0	0.0	NA	NA
Salem	Hope Creek	7.3	0	0.0	NA	NA
Salem/Cumberland	Stow Creek	14.9	0	0.0	NA	NA
Cumberland	Cohansey River	28.1	1	<0.1	NA	NA
Cumberland	Maurice River	18.9	0	0.0	NA	NA
	Manomuskin Creek	7.5	0	0.0	NA	NA
	Menantico Creek	5.7	0	0.0	NA	NA

* area in hectares should be interpreted as minimum area occupied due to the survey method used.

majority of introduced populations were small in size (≤0.1 ha) and had moderate to dense stem density. Many of the native populations in the same areas were also small in size but had sparse to moderate stem density. However, there were several dense native populations that were at least 2.5 ha in size. Along the Tuckahoe River, native populations were more common than introduced ones (16 vs. 7 populations).

Along the Nanticoke River more marsh habitat was occupied by native *Phragmites australis* than by introduced although more introduced populations were found (Table 1). As along the Choptank, the majority of introduced populations were small in size and had moderate to dense stem density, while native populations typically had lower stem density and could be found in larger population sizes. The Marshyhope tributary had no introduced *P. australis* along the 9.9 km of river we surveyed.

Native *Phragmites australis* along the Pocomoke drainage was typically found up side creeks (96% of native populations) rather than along the main stem of the river where nearly all populations were introduced. While the majority of native populations were small in area and had low culm density, several very large native populations were found which were dense and extended across the marsh plain to the upland edge of the marsh. In fact, the largest *P. australis* population found across all rivers was a native one in the Pocomoke

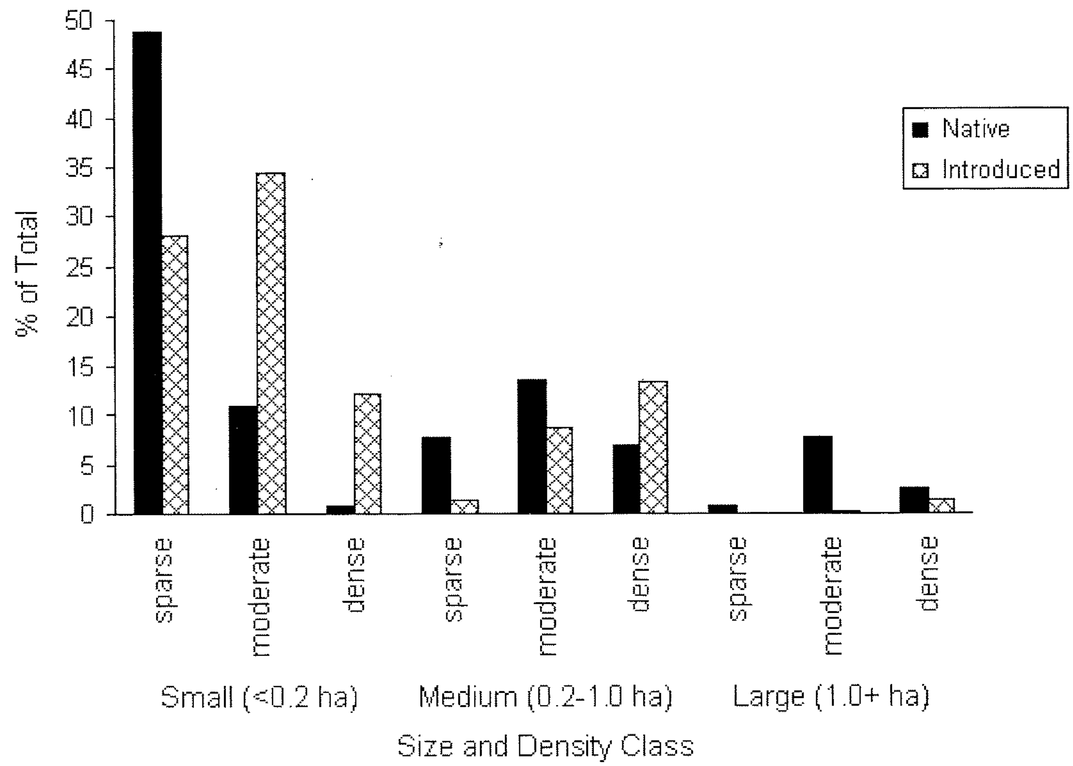

FIG. 2. Proportion of native and introduced *Phragmites australis* populations, indicated as percent of all populations within a subspecies, found in each of three size and three density classes along the Choptank, Nanticoke, Wicomico, and Pocomoke Rivers in MD. Density classes are as follows: sparse = < 10 stems m^{-2}; moderate = 10-50 stems m^{-2}; dense = > 50 stems m^{-2}.

drainage which we estimated to occupy 4 ha. Several native populations were also found along the VA portion of Pitt's Creek.

GENETIC ANALYSIS. The native or introduced status of all 41 populations sampled was determined using genetic tests and all were confirmed to have been correctly identified in the field based on morphology alone. Four different native *Phragmites australis* haplotypes were identified, F, Z, AB, and AC, with haplotype F being the most common. All 11 native samples from DE and NJ were haplotype F, as were 10 of 14 native samples from the Choptank, Nanticoke, and Pocomoke rivers in MD. Haplotype Z was found along the Wicomico River, and two novel haplotypes, AB and AC (GenBank Accession No. AY714215, AY714216), were found in the Choptank river drainage.

Discussion. Although it has largely disappeared elsewhere on the Atlantic coast (Saltonstall 2003a), native *P. australis* clearly persists in freshwater and oligohaline marshes across the Delmarva Peninsula. Particularly along the upper Choptank and Nanticoke rivers in MD, native *P. australis* remains common and several large well established and apparently older populations were found.

Across our survey area, native *Phragmites australis* was most common in habitats with apparently low salinity although native *P. australis* was found historically along the borders of brackish marshes along the Atlantic Coast (Saltonstall 2002) and other known extant native populations in New England are in salt marsh communities. Recent greenhouse trials comparing performance of native and introduced *P. australis* grown from rhizomes collected along the Appoquinimink River (DE) found that the native plants had greater than 50 percent mortality at a salinity of 5‰ while introduced *P. australis* showed a reduction in growth but no increased mortality at this salinity (Vasquez et al. 2005). While

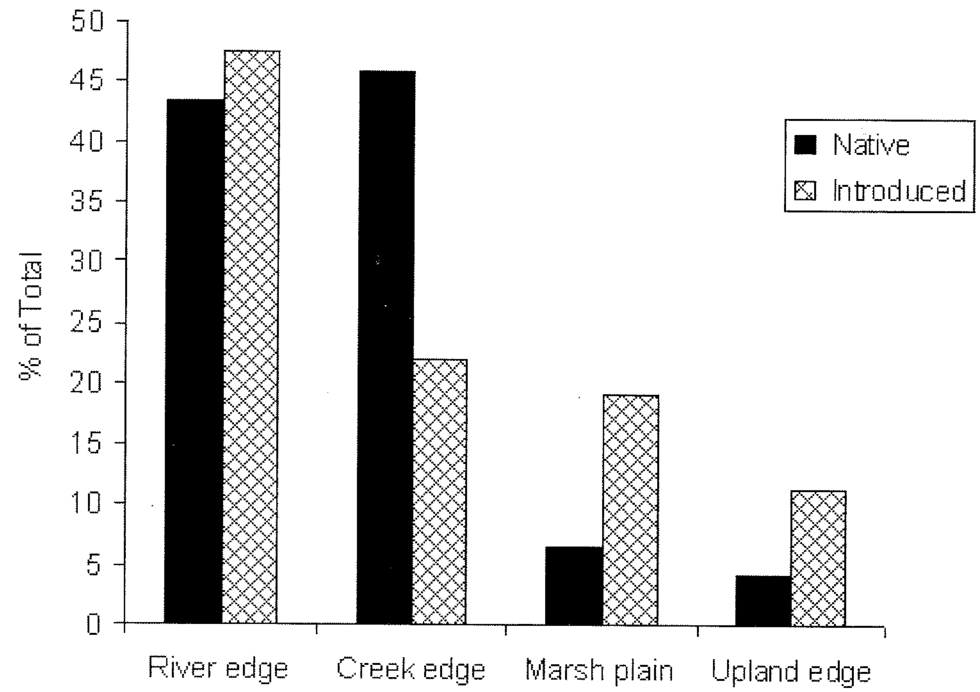

FIG. 3. Proportion of native and introduced *Phragmites australis* populations, indicated as percent of all populations within a subspecies, found at different positions within the marsh complex along the Choptank, Nanticoke, Wicomico, and Pocomoke Rivers in MD.

further research is needed, it appears that salinity may be one factor controlling the distribution of native *P. australis* in the mid-Atlantic region today.

GENETIC DIVERSITY OF NATIVE *P. AUSTRALIS*. Haplotype F is the most common form of native *Phragmites australis* found today in this region. Previous studies have also identified it along the Rappahannock River in VA, a tributary of Chesapeake Bay on its western shore. Historically this haplotype ranged from the mid-Atlantic north to New England and was common throughout the Atlantic coast (Saltonstall 2002) but no other populations are known today north of NJ.

Three other closely related haplotypes (Z, AB and AC) were also identified among the native populations sampled in this study, indicating that the haplotype diversity of native *Phragmites australis* in the mid-Atlantic region remains high. Haplotype AB was found on the Tuckahoe River in MD and has also been identified on Block Island, RI (Saltonstall unpub. data) suggesting that this haplotype may have had a more extensive distribution historically.

Of the 161 native populations we identified using morphological features, 27 were verified using genetic analysis and all 27 proved to be correctly identified. It thus appears that the morphological characters used in our field survey are reliable for distinguishing native and introduced *P. australis* populations in the mid-Atlantic region.

TRENDS IN THE DISTRIBUTION OF *PHRAGMITES AUSTRALIS*. Why is native *P. australis* still common on the eastern shore of MD but quite rare in DE and southern NJ, while introduced *P. australis* does not dominate the oligohaline marshes of MD but is very common in DE and NJ? The answer here could be related to the long history and extent of human impact in the two regions and the extent of associated habitat disturbance and opportunities for *P. australis* dispersal (Saltonstall 2003a). In 1900, the eastern shores of MD and VA had a population density of 18 persons/km^2 while DE had 37 persons/km^2. Over the next century, Delaware's population quadrupled while that of the remainder of the peninsula doubled (156 persons/km^2 in DE vs 36 persons/km^2 for the MD and VA eastern shore; U.S. Census Bureau 2000). While it is not known exactly where or when non-native Eurasian *P. australis* was introduced to North America, *P. australis* was documented growing on ballast grounds in Philadelphia, PA in the 1870's (Burk 1877) and an herbarium specimen collected in 1877 in Camden, NJ (J. C. Martindale, US-908070) has been shown to be of introduced origin (Saltonstall 2002). Thus it is possible that propagules of introduced *P. australis* were colonizing marshes in DE and southern NJ in the late 1800's, particularly on disturbed sites, and may have outcompeted any native *P. australis* that was present. The earliest confirmed specimen of introduced *P. australis* from the Chesapeake Bay region was collected in 1905 (A. S. Hitchcock, US-908065) from Chesapeake Beach, MD, which is on the western shore of the Bay (Saltonstall 2002). The human population density of the MD eastern shore is much lower than the western shore and development has lagged behind. Studies using aerial photography have documented the establishment of introduced *P. australis* along the Choptank River in recent decades. Rice et al. (2000) found that while *P. australis* could not be detected at King's Creek marsh in the 1930's, by 1972 it was found and it spread rapidly throughout the site in the 1980's and 1990's. Our observations clearly identify these newly established populations as introduced *P. australis*. Although it was present in the Bay watershed, introduced *P. australis* may not have established and become common along the eastern shore of MD until more recently due to geographic isolation. The high frequency of introduced populations, often growing immediately adjacent to native *P. australis*, also suggests that a steady flow of propagules is entering and establishing in these systems and they are likely to become the dominant plants in many marshes if they are allowed to continue to expand (Rice et al. 2000).

Conclusions. The presence of native *Phragmites australis* across the MD watersheds surveyed here is unique today along the Atlantic Coast, where it has largely disappeared elsewhere. Given this, perhaps native *P. australis* can be thought of as an indicator of marshes with a low intensity of human impact. However, pressures of increased urbanization loom today and the arrival of introduced *P. australis* in these systems poses a threat to the diversity of the marshes. We see an opportunity here to try to maintain these native communities since introduced *P. australis* has only recently begun to colonize oligohaline marshes of some rivers and native vegetation still flourishes. Based on patterns of growth elsewhere along the Atlantic coast, including DE and southern NJ, it is likely that introduced populations will soon dominate these systems if allowed to continue spreading and likely impact not only the diversity of vegetation but also use by wildlife of these marshes. Where preservation of native biodiversity, including native *P. australis*, is a goal, early control of introduced *P. australis* may allow for successful maintenance of native freshwater marsh communities in these mid-Atlantic watersheds.

Literature Cited

Bart, D. and J. M. Hartman. 2003. The role of large rhizome dispersal and low salinity windows in the establishment of common reed, *Phragmites australis*, in salt marshes: New links to human activities. Estuaries 26: 436–443.

Bertness, M. D., P. J. Ewanchuk, and B. R. Silliman. 2002. Anthropogenic modification of New England salt marsh landscapes. Proc. Nat. Acad. Sci. USA 99: 1395–1398.

Blossey, B. 2002. *Phragmites*: common reed. Morphological differences between native and introduced genotypes. Retrieved June 20, 2004 from Cornell University, Department of Natural Resources, <http://www.invasiveplants.net/invasiveplants/phragmites/morphology.asp>

Burk, I. 1877. List of plants recently collected on ship's ballast in the neighborhood of Philadelphia. Proc. Acad. Nat. Sci. Phil. 29: 105–109.

Chesapeake Bay Program. 2004. Watershed Profiles. Retrieved July 20, 2004. <www.chesapeakebay.net>

Haslam, S. M. 1972. Biological Flora of the British Isles: *Phragmites communis* Trin. J. Ecol. 60: 585–610.

Kraft, J. C. 1971. Sedimentary facies patterns and geologic history of a Holocene marine transgression. Geol. Soc. Amer. Bull. 82: 2131–2158.

Maryland Department of Natural Resources. 2004. Eyes on the Bay: Recent Water and Habitat Conditions in Maryland's Chesapeake Bay and Coastal Bays. Retrieved July 23, 2004. <http://mddnr.chesapeakebay.net/eyesonthebay/index.cfm>

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

Minchinton, T. E. and M. D. Bertness. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. Ecol. Applic. 13: 1400–1416.

NIERING, W. A., R. S. WARREN, AND C. G. WEYMOUTH. 1977. Our dynamic tidal marshes: Vegetation changes as revealed by peat analysis. Connecticut Arboretum Bulletin 12: 22.

ODUM, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. Ann. Rev. Ecol. Syst. 19: 147–176.

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

RICE, D., J. ROOTH, AND J. C. STEVENSON. 2000. Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. Wetlands 20: 280–299.

SALTONSTALL, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proc. Nat. Acad. Sci. USA 99: 2445–2449.

SALTONSTALL, K. 2003a. Genetic variation among North American Populations of *Phragmites australis*: implications for management. Estuaries 26: 444–451.

SALTONSTALL, K. 2003b. Microsatellite variation within and among North American lineages of *Phragmites australis*. Mol. Ecol. 12: 1689–1702.

SALTONSTALL, K. 2003c. A rapid method for identifying the origin of North American *Phragmites* populations using RFLP analysis. Wetlands 23: 1043–1047.

SALTONSTALL, K., P. M. PETERSON, AND R. J. SORENG. 2004. Recognition of *Phragmites australis* subsp. *americanus* (Poaceae: Arundinaceae) in North America: Evidence from morphological and genetic analyses. SIDA 21: 683–692.

U. S. CENSUS BUREAU. State Quickfacts. Retrieved July 20, 2004. <http://www.census.gov/>

VASQUEZ, E. A., E. P. GLENN, J. J. BROWN, G. R. GUNTENSPERGEN, AND S. C. NELSON. 2005. Salt tolerance underlies the cryptic invasion of North American salt marshes by an introduced haplotype of the common reed *Phragmites australis* (Poaceae). Mar. Ecol. Prog. Ser. 298: 1–8.

WAKSMAN, S. A., H. SCHULHOFF, C. A. HICKMAN, T. C. CORDON, AND S. C. STEVENS. 1943. Bulletin 55 - Part B. The peats of New Jersey and their utilization. Department of conservation and development, State of New Jersey along with New Jersey Agricultural Experiment Station, Rutgers University, Trenton, NJ.