College of Humanities and Sciences
Virginia Commonwealth University

This is to certify that the thesis prepared by Jeremy D. Fennell entitled *Phragmites australis* patch characteristics in relation to watershed landcover patterns on the Eastern Shore of Virginia, has been approved by his committee as satisfactory completion of the thesis requirement for the degree of Master of Science.

Dr. Donald R. Young, Associate Chair, Department of Biology

Dr. Edward R. Crawford, Department of Biology

Dr. D'Arcy Mays, Chair, Department of Statistical Sciences and Operations Research

Dr. Leonard A. Smock, Chair, Department of Biology

Dr. Robert D. Holsworth, Dean, College of Humanities and Sciences

Dr. F. Douglas Boudinot, Dean, School of Graduate Studies

Date of acceptance

PHRAGMITES AUSTRALIS PATCH CHRACTERISTICS IN RELATION TO WATERSHED LANDCOVER PATTERNS ON THE EASTERN SHORE OF VIRGINIA

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

JEREMY D. FENNELL

B.A., Warren Wilson College, 2002
M.S., Virginia Commonwealth University, 2007

Director: Dr. Donald R. Young
Professor
Department of Biology

Virginia Commonwealth University
Richmond, VA
May 2007

Acknowledgements

I would first like to thank my thesis advisor, Dr. Donald R. Young for steering me in the right direction during my research and imparting many wise life lessons along the way. I also want to thank The Nature Conservancy, Virginia Coast Reserve, and especially Eastern Shore private landowners for the permission to sample on their properties. Financial support was obtained from the National Science Foundation and a Virginia Commonwealth University Graduate Teaching Assistantship. Thanks also to my thesis committee, Dr. Leonard Smock, Dr. Edward Crawford, and Dr. D'Arcy Mays for their helpful contributions to my thesis. I am also thankful for my field assistants, Brian Goodyear and especially Trevor Frost, who both worked long, mucky, sweltering wetland hours with me. Lastly, I am grateful for my wife and family who helped me through graduate school.

Table of Contents

List of Tables

List of Figures

Abstract

PHRAGMITES AUSTRALIS PATCH CHARACTERISTICS IN RELATION TO WATERSHED LANDCOVER PATTERNS ON THE EASTERN SHORE OF VIRGINIA

Jeremy D. Fennell, Master of Science

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

Virginia Commonwealth University, 2007

Thesis Director, Dr. Donald R. Young, Department of Biology

Phragmites australis is a perennial grass presently invading many intertidal and freshwater wetlands throughout much of the Atlantic Coast of North America. The spread of *Phragmites* into coastal wetlands is in part determined by available freshwater and nutrients, especially nitrogen, within the watershed where *Phragmites* populations occur. The Eastern Shore of Virginia is an intensive agricultural area, and watershed landcover may play a major role in *Phragmites* invasion. Forty-five *Phragmites* patches were sampled in eight VA Eastern Shore mainland watersheds and on a barrier island. Regardless of watershed landcover characteristics, there was little variation in *Phragmites australis* patch characteristics along the oceanside of the entire Eastern Shore of Virginia. *Phragmites* is a generalist with broad environmental tolerances. Thus, successful management and eradication plans may have broad scale application for this invasive grass.

CHAPTER 1 Thesis Introduction

Phragmites australis (Cav.) Trin. ex Steud. (the Common Reed), hereto after *Phragmites*, is a wetland grass found in a variety of intertidal and freshwater wetlands of the Atlantic Coast (Chambers et al. 1999, Bart et al. 2006). Although *Phragmites* rhizomes have been identified in soil cores dating back 4000 years in New England (Niering et al. 1977, Orson 1999), a non-native haplotype M has invaded many areas in the Northeast, Great Lakes, and mid-Atlantic coastal wetlands in the last century (Saltonstall 2002, Welch et al. 2006). Haplotype M is presently the most widely distributed haplotype in North America, but is native to Europe and continental Asia. Haplotype M has also shown up at one site in New Zealand, but it is unclear whether it is native (Saltonstall 2002). The native haplotype F has existed on the Delmarva Peninsula for sometime. It is not considered invasive, and has been displaced by haplotype M. Presently, the only confirmed coastal patches of haplotype F are in Allen, MD (Chesapeake Bay area) and Chance, VA (Rappahannock River) (Saltonstall 2002, Vasquez et al. 2005). Haplotype M is distinguished from F by its aggressive growth habit and wider salt tolerance (Saltonstall 2002, League et al. 2006). As expected, a survey based on morphometric characteristics identified only haplotype M in *Phragmites* populations on the Eastern Shore of Virginia (Crawford 2005, *unpublished data*).

Wetlands are linkages in the landscape, and effectively intercept water and associated materials transported from watersheds (Kercher and Zedler 2004). This positioning enables *Phragmites* populations to benefit from nutrient loading and increased freshwater inputs resulting from impervious surfaces such as roads (Bertness et al. 2002, Silliman and Bertness 2004). Land-use activities in a watershed should affect *Phragmites* patch stability as well as the susceptibility of new coastal areas to *Phragmites* invasion.

Phragmites establishment and expansion is well documented (Amesburry et al. 2000, Bart and Hartman 2000, 2002, 2003, Bart et al. 2006). Gaps created by anthropogenic disturbance, such as development, and natural events, such as floods, give *Phragmites* the opportunity to displace native vegetation (Ailstock 2001, Burdick et al. 2001). Seed viability is low, so *Phragmites* colonization typically initiates from emerging rhizome segments buried at the well-drained upland and marsh interface (Whijte and Gallagher 1996, Bart and Hartman 2000). *Phragmites* populations then expand by vegetative propagation into soil with higher edaphic stress (Bart and Hartman 2002), at rates reaching 10 m yr^{-1} (Ailstock 2001). *Phragmites* also has the ability to grow densely (300 stems m^{-2}) in mature stands (Ailstock 2001), and often emerges in the spring before most native species (Meyerson et al. 2000). Once established and expanding, *Phragmites* successfully blocks out sunlight for native species, which normally shifts a diverse wetland community into a *Phragmites* monotype (Minchinton et al. 2006). Also, *Phragmites* litter can exceed 30 cm at one time, further inhibiting native species (Ailstock 2001).

Edaphic stress and flooding are the main limiting factors for *Phragmites* in the coastal environment. After rhizomes emerge and clonally spread down into the mesohaline marsh (5-18 ppt), a zone exists where the invasion halts, usually close to the mean high water mark (Meyerson et al. 2000). *Phragmites* is thus inhibited by anoxia, salinity, and sulfides that exist at elevations with regular tidal flushing (Chambers et al. 1999). Coastal storms can put additional stress on *Phragmites* populations, but most patches tolerate the disturbance, if infrequent.

Salinity is a known stressor of many coastal plant species. *Phragmites* height and stem density is restrained at soil salinities of >18 ppt (Wijte and Gallagher 1996, Meyerson et al. 2000). *Phragmites* is especially sensitive to salinity when new rhizomes attempt to establish, and salinity can interact with factors such as temperature to inhibit seed germination (Gorai et al. 2006). Bart and Hartman (2002) found that even in soils where *Phragmites* clones had invaded, rhizomes could not emerge in the same areas if soil salinity and anoxia were high. Pore water sulfides also restrict *Phragmites* by causing stunted growth, bud death, and blockage of gas pathways (Chambers et al. 1998, Hotes et al. 2005).

Phragmites morphology and physiology may ameliorate the effects of these environmental constraints. In the coastal marsh landscape, *Phragmites* is commonly found around freshwater seeps or locations where deep roots (>80 cm) can access groundwater (Burdick and Konisky 2003). Deep roots are especially effective if there is altered soil drainage, such as a ditch, dredge spoil pile, or tidal barrier, all of which can increase freshwater inflows and/or limit tidal flushing (Bart and Hartman 2000, Burdick et al. 2001, Maheu-Giroux and de Blois 2005, 2007). Also, *Phragmites* has Venturi-enhanced pressurized gas flow. Atmospheric oxygen is forced from the stems into the rhizome network where it flows to clones in more poorly-drained soils (Armstrong et al. 1992, Vretare and Weisner 2000). The increased oxygen is then pushed out into the rhizosphere around the clone, and reduced soil conditions due to anoxia are improved locally (Armstrong et al. 1992).

Despite these adaptations, salinity and sulfides inhibit ammonium (NH_4^+) uptake by *Phragmites*. Ammonium is the major form of N in anoxic coastal marsh soils, as it is the reduced form of nitrate (NO_3^-) (Mendelssohn 1979). Significant decreases in NH_4^+ uptake occur at pore water levels of >20 ppt salinity (Chambers et al. 1998). This decreased uptake results from the sodium ions (Na^+) competing with NH_4^+ for binding sites on the rhizome (Lissner and Schierup 1997, Meyerson et al. 2000), and associated sulfides damaging other plant functions (Chambers 1997). Thus, it is important to account for salinity when gathering pore water NH_4^+ data.

Increased N may give *Phragmites* an advantage over many Atlantic Coast competitors (e.g. *Typha spp.* and *Spartina spp.*). *Phragmites* generally has a higher aboveground and belowground biomass (Windham 2001), standing stock N, and contributes more energy stores aboveground when increased N is available (Meyerson et al. 2000, Minchinton and Bertness 2003). Also, *Phragmites* tolerates high N loading, and is widely used in constructed wetlands in Asia, Europe, and even some locations in America for municipal and agricultural wastewater treatment (Mitsch and Gosselink 2000, Southichak et al. 2006). Hardej and Ozimeka (2002) concluded that aboveground biomass, leaf area index, specific leaf area, stem density, and shoot diameter were all higher in *Phragmites* populations treated with N-rich sewage as opposed to natural populations.

Also, even though eutrophication in Europe and Asia may contribute to *Phragmites* decline, N additions above field conditions do not inhibit NH_4^+ uptake (Romero et al. 1999).

Phragmites responds to N enrichment in natural settings as well. Minchinton and Bertness (2003) found that stem density, height, and aboveground biomass all increased as N was added in a monotypic *Phragmites* stand. Fertilization studies have also concluded that increased pore water NH_4^+ stimulates growth (Rickey and Anderson 2004). Additionally, growing stems and deeper litter, stimulated by N inputs, can reduce osmotic stress by providing increased soil shading. This results in less soil evaporation, and reduces soil salinity throughout the growing season (Burdick et al. 2001).

Although several studies have focused on *Phragmites* effects on marsh N cycling (Meyerson et al. 2000), few have linked *Phragmites* invasion to increased N and freshwater inputs resulting from coastal development (Bertness et al. 2002, Silliman and Bertness 2004). Nitrogen loading from coastal watersheds via groundwater, surface water, and atmospheric inputs cause marine ecosystems, in part, to be the most eutrified (Valiela et al. 1997). Also, percent cropland per watershed area has been related to N loading in the Chesapeake Bay (Jordan et al. 1997).

Along the southern portion of the Delmarva Peninsula, watersheds of the Eastern Shore, VA have a few pockets of development and associated N loading from wastewater. However, the highest potential for N loading in Eastern Shore watersheds is agriculture. A popular crop, the N-fixing soybean, can effectively increase pore water NH_4^+ in

Phragmites patches (Stanhope 2003). Also, fertilizer application and animal waste increase N supplies in the soils surrounding agricultural areas (Pierzynski et al. 2000).

All Eastern Shore watersheds differ in landcover characteristics, which may explain variation in nitrogen and growth parameters of *Phragmites* patches (Porter 2005, *unpublished data*). Watersheds with a higher percentage of cropland, development, grassland, and bare soil could confer the best conditions for *Phragmites* because of increased N input and/or decreased retention of N (Pierzynski et al. 2000). Measurements of soil salinity, sulfides, and tissue chlorides could also decrease based on watersheds with a higher potential for freshwater inputs (ie. high percent of bare soil). Watersheds with a higher percent of forest and wetlands may have a greater potential to sequester N and freshwater, and wetlands situated above the *Phragmites* patches could transform N into forms unavailable to *Phragmites* such as N_2 (Mitsch and Gosselink 2000). Watersheds with a large percent of forest and wetland may have less vigorous *Phragmites* populations, and are thus not as susceptible to invasion. A large percent of wetland landcover may be the least favorable for invasion if the majority of the wetlands are not invaded by *Phragmites* (Mitsch and Gosselink 2000).

No studies to date have directly addressed the issue of *Phragmites* patch characteristics and landcover type in Atlantic coastal watersheds. While *Phragmites* invasion ecology is well studied at the organismal level, further research must scale-up to make conclusions about the abundance and distribution of *Phragmites* populations throughout the coastal landscape. Variation in nitrogen and growth measurements in *Phragmites* patches should reflect patterns in land-use across Eastern Shore watersheds.

Beyond the Eastern Shore, coastal watersheds with a high potential for N loading and increased freshwater inflows should be the most vulnerable to *Phragmites* expansion. The objectives of this study are to determine if differences among watershed landcover on the VA Eastern Shore are related to nitrogen and growth parameters associated with *Phragmites.*

The following manuscript describes my thesis research on *Phragmites* expansion on the Eastern Shore of Virginia landscape. The manuscript has been written in the form required by the journal Wetlands.

CHAPTER 2

Phragmites australis patch characteristics in relation to watershed landcover patterns on the Eastern Shore of Virginia

Jeremy D. Fennell, Donald R. Young, and Edward R. Crawford[1]

Department of Biology
Virginia Commonwealth University
Richmond, VA 23284

---

[1] Address correspondence to D. R. Young
Email: dyoung@vcu.edu

ABSTRACT: *Phragmites australis* is a perennial grass presently invading many intertidal and freshwater wetlands throughout much of the Atlantic Coast of North America. The spread of *Phragmites* into coastal wetlands is in part determined by available freshwater and nutrients, especially nitrogen, within the watershed where *Phragmites* populations occur. The Eastern Shore of Virginia is an intensive agricultural area, and watershed landcover may play a major role in *Phragmites* invasion. Forty-five *Phragmites* patches were sampled in eight VA Eastern Shore mainland watersheds and on a barrier island. Regardless of watershed landcover characteristics, there was little variation in *Phragmites australis* patch characteristics along the oceanside of the entire Eastern Shore of Virginia. *Phragmites* is a generalist with broad environmental tolerances. Thus, successful management and eradication plans may have broad scale application for this invasive grass.

INTRODUCTION

Over the past century Atlantic coastal landscapes have changed drastically. Among the causes of change are anthropogenic disturbances such as land clearing, altered hydrology, eutrophication, and sedimentation, all of which can play a key role in the propagation and dispersal of many invasive plant species (Kercher and Zedler 2004, Bart et al. 2006). Development pressures are expected to remain steady throughout this century for much of the east coast of North America, and invasive species could alter coastal wetland biotic function, aesthetics, and recreational potential (Crooks 2002, Ehrenfeld 2003). It is therefore critical to look at coastal wetlands from new perspectives, especially at the landscape-level, in order to discern which factors are driving invasions.

One of the most persistent U.S. coastal invasives is *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), hereto after *Phragmites* (Marks et al. 1994). *Phragmites* is a perennial wetland grass found in a variety of intertidal and freshwater habitats of the Atlantic Coast (Chambers et al. 1999). *Phragmites* is also cosmopolitan, with large populations on every continent except Antarctica (Vasquez et al. 2005). Although *Phragmites* is native to the Atlantic coast of North America (Niering et al. 1977, Orson 1999), an aggressive Eurasian genotype is presently spreading throughout much of the Chesapeake Bay and Eastern Shore of Virginia as well as other coastal areas including the Great Lakes region (Saltonstall 2002, Thompson 2003, Welch et al. 2006). This invasive genotype may have wider salt tolerance and a more aggressive growth habit than the native counterpart and, therefore, maybe able to exploit its habitat more effectively (Saltonstall 2002, Vasquez et al. 2005, League et al. 2006).

Gaps created by anthropogenic disturbance and natural events enable *Phragmites* to displace native species (Marks et al. 1994, Burdick and Konisky 2003). Seed viability is low, so colonization typically starts from rhizomes (Whijte and Gallagher 1996, Bart and Hartman 2000, Bart et al. 2006). *Phragmites* populations then expand by vegetative propagation throughout the coastal landscape often into areas with higher edaphic stress, especially salinity and sulfides (Chambers 1997, Bart and Hartman 2002). Once established, *Phragmites* successfully blocks out sunlight for native species, and a diverse wetland community becomes a *Phragmites* monoculture (Marks et al. 1994, Minchinton et al. 2006).

At the landscape-level, *Phragmites* invasions move in linear patterns along creek beds or roadways, from the marsh-upland interface into the interior marsh, or in seemingly random directions from a central location (Windham 2001, Maheu-Giroux and de Blois 2005, 2007, Bart et al. 2006). These invasion patterns in coastal areas could be dictated by the availability of freshwater and nutrients within a given watershed along the invasion route (Burdick and Konisky 2003). Commercial agriculture, which is highly-dependent on fertilizer, or those practices which increase impervious surfaces and associated freshwater runoff may enhance *Phragmites* invasion (Pierzynski et al. 2000). Thus, it is important to consider the watershed landcover characteristics within a landscape invaded by *Phragmites*. For example, the Eastern Shore of Virginia is an intensive agricultural area, and with associated fertilizer application, there is an increased potential for enhanced soil fertility for *Phragmites* patches, especially in the form of NH_4^+ (Jordan et al. 1997, Pierzynski et al. 2000). Additionally, N loading from coastal watersheds via groundwater, surface water, and atmospheric inputs cause marine ecosystems, in part, to be more eutrified than many terrestrial habitats (Valiela et al. 1997).

Only a few studies have linked *Phragmites* invasion with coastal development, where vegetation clearing stimulates *Phragmites* growth by increasing freshwater and nutrient inputs (Bertness et al. 2002, Minchinton and Bertness 2003, Silliman and Bertness 2004). Landscape patterns of *Phragmites* invasions are not well understood.

Invasion routes such as in roadside or agricultural ditches can act as corridors for *Phragmites* to rapidly spread throughout a watershed along drainages and waterways (Maheu-Giroux and deBlois 2005, 2007). Agriculture and other landcovers that stimulate freshwater and nutrient infiltration into the soil could enhance *Phragmites* expansion. *Phragmites* expansion may become unmanageable on the Eastern Shore of Virginia if underlying causes and invasion patterns are not understood and managed on a landscape-scale. No studies to date have directly addressed *Phragmites* patch characteristics and landcover types in Atlantic coastal landscapes. The objectives of our study were: 1) to discern if *Phragmites* environmental and patch characteristics differed among watersheds on the Eastern Shore of Virginia 2) to quantify relationships among watershed landcover characteristics 3) and to identify the driving factors behind variation in *Phragmites* patches among watersheds. Connections established among watershed landcover and *Phragmites* patch characteristics could serve to predict the type of coastal watersheds where *Phragmites* will spread more aggressively or appear for the first time.

METHODS

Study site

Sampling was conducted on the Eastern Shore, Virginia, which represents the southern portion of the Delmarva Peninsula. The Eastern Shore of VA is approximately 100 km long, 5-20 km wide, and has a maximum elevation 12-15 m above sea level (Stanhope 2003). Elevation peaks in the middle of the peninsula and water flows into the Chesapeake Bay to the west and Atlantic Ocean to the east (Stanhope 2003). Soils are classified as predominately sandy with a high potential of water and nutrient infiltration. The water table is shallow (3-30 m), and is underlain by the Columbia aquifer from U.S. Route 13 east to the Atlantic Ocean (Gallagher et al. 2001). The Eastern Shore has a relatively low-density of development, and is still primarily agricultural. Wheat, soybean, corn, and tomatoes are the most important crops (Stanhope 2003). *Phragmites* populations are common from the northern to southern most extent of the Eastern Shore (VA DCR 2004).

Eight watersheds were delineated on the Eastern Shore ocean side: Assawoman, Gargathy, Metompkin, Wachapreague, Quinby, Machipongo, Sand Shoal, and Smith from north to south. Geographic Information System (GIS) analyses from the University of Virginia (Porter 2005, *unpublished data*) provided the geographical boundaries of the watersheds and their subwatersheds, but also percent and area of each landcover type in the watershed (Figure 1). The landcover types used were: developed, cropland, upland forest including scrub/shrub, palustrine forest, and estuarine emergent wetland. *Phragmites* populations existed primarily in estuarine emergent wetlands and palustrine forest landcovers.

Phragmites populations

Eastern Shore *Phragmites* patches were located via aerial and ground surveys, and their sizes were calculated and put into a GIS shapefile (VA DCR 2004). This information, provided by the Virginia Department of Conservation and Recreation, helped locate potential study sites. *Phragmites* patches on the Eastern Shore occurred in a variety of locations including down slope of agricultural fields, along tidal creeks, in roadside ditches, and in seemingly isolated forested areas in freshwater drainages. Based on rapid patch expansion observed in aerial photographs, the lack of confirmed haplotype F patches near the study site (Saltonstall 2002), and morphometric characteristics of existing patches (Crawford 2005, unpublished data), all *Phragmites* patches were considered to be the invasive haplotype M.

Patches were sampled during the 2006 growing season. Five patches of *Phragmites* were selected in each of the eight mainland watersheds. Sampled patches were located within tidal creeks or in other drainage types, which facilitated freshwater inflow into the *Phragmites* patches. Another five patches were sampled on Hog Island, which is a barrier island located approximately 8 km offshore of the VA Eastern Shore. Hog Island was selected as a reference because it was undeveloped and assumed to have trace anthropogenically-derived surface or groundwater N inputs.

Soil chlorides, a known limiting factor in *Phragmites* growth and expansion (Fogli et al. 2002), were measured by collecting three soil samples on all dates from each site. Samples were removed from the soil with a hand auger to a depth of 20 cm, and ≈ 200 g was placed in a soil bag. Samples were dried at 105°C for 48 h, and 40 g sub-samples were analyzed for salinity. A 1:5 ratio mixture (weight/volume) of soil to deionized water, with 5 M $NaNO_3$ to extract chloride ions, was created. Salinity of each sample was determined with a chloride specific ion electrode (9617-B, Orion, Boston, MA). From the same soil samples pH was analyzed to assess variation among watersheds. A 1:1 soil to deionized water mixture (w/v) was made. After sitting 30 minutes, pH from the mixtures was determined with a pH electrode (HI 9025, Hanna, Woonsocket, RI).

Tissue chlorides were measured at peak biomass to discern if chlorides present in the tissues related to the amount of soil chlorides found at the site, and if tissue chlorides also limited *Phragmites* growth. A portion of stem and leaf tissue was subsampled from dried aboveground biomass samples. The tissues were ground up in a Wiley mill (#23863, Thomas Scientific, Markam, ON) and measured using hot water extraction (Young et al. 1994). Approximately 0.4 g of ground leaf material was put in a 50 mL tube with 25 mL deionized water. The tubes were placed in a boiling water bath for 1 h, cooled, and the samples were filtered into 50 mL volumetric flasks and brought to volume. Chloride levels were determined by a chloride specific ion electrode (9617-B, Orion, Boston, MA) and ionic buffer as described above.

Pore water was examined for ammonium (NH_4^+), which represents available N in reduced coastal soils (Mendelssohn 1979). NH_4^+ concentrations were determined using standard colormetric procedures (Bart and Hartman 2002). Pore water at each patch was extracted by coring three holes and allowing them to fill with pore water. Approximately 18 mL of pore water was then extracted using a plastic tube attached to hand pump and placed into a 20 mL HDPE sealable bottles, put immediately on ice, and frozen in the lab at -15°C. Samples were thawed for 3 h before analysis. An indophenol reagent mixture fixed the samples and they were then kept in the dark for 1 h to allow color to develop. Absorbance was measured with a Perkin-Elmer Lambda Spectrophotometer set to 640 nm. Percent nitrogen in the stems and leaves was also determined for selected watersheds by grinding up 2-5 g of tissue placed into Perkin-Elmer CHNS/O 2400 Analyzer.

Variation among *Phragmites* populations could indicate variation in edaphic conditions, and thus a number of growth and environmental measurements were taken at least once during the growing season. The *Phragmites* growing season is characterized by three distinct periods: late spring (mid-exponential growth), mid-summer (peak growth), and late-summer (peak biomass). Sampling was conducted in each of the three growth periods to ascertain not only variability among watersheds, but also variation throughout the growing season. The location of each patch was determined via handheld Trimble GeoExplorer CE Series GPS unit.

At peak biomass, three 0.5 m^2 plots were established in the middle of each stand, where a number of growth measurements were taken. Within each plot, the height of the tallest stem and stem density were measured. Aboveground stems were then cut at the ground from a subplot of 0.25 m^2 to assess aboveground biomass (g dry weight m^{-2}). The sample was placed in a drying oven at 80 ^{o}C for 5 days and then weighed. With the aboveground samples, internode length was measured for 3 stems per site. At peak growth, litter depth (soil surface to the top of the litter) was determined, which is an indication of both the productivity of a particular *Phragmites* patch and its potential to inhibit competing seedlings by blocking out sunlight.

Statistics

One-Factor ANOVA and Bonferroni Post-Hoc testing determined significant differences in the edaphic and plant parameters among watersheds. Simple linear and multiple regression quantified relationships among plant growth parameters, tissue chlorides, and the other environmental parameters. Principal components analysis (PCA) identified the most important gradients causing variation in watersheds (McCune and Grace 2002). The variables of watershed size (ha) and watershed landcover types (ha), including developed, cropland, forested/shrub, palustrine forest, and estuarine emergent wetland, were reduced to a substantially smaller dimensional space by finding a best fit line that passed through the center of the watershed data. Canonical correspondence analysis (CCA) compared *Phragmites* growth parameters (aboveground biomass, height, stem density, litter depth, and internode length) to patch environmental variables (soil chlorides, soil pH, and pore water NH_4^+) to find important environmental drivers. A second CCA compared the same *Phragmites* growth parameters to the watershed landcover characteristics. Statistical analyses were conducted using SPSS 14.0 (SPSS, Inc. 2005) and PC-ORD, Version 4 (MjM Software Design 1999).

RESULTS

Phragmites patches sampled for this study were representative of the size distribution of *Phragmites* patches for the entire Eastern Shore (Figure 2). Sampled patches were found in a wide-range of edaphic conditions and locations along the Eastern Shore of Virginia. Non-tidal habitats including roadside ditches, ponds, riparian buffers, landfills, and along overpasses were invaded by *Phragmites*, as well as tidal estuarine marshes and creeks. However, despite *Phragmites* occurrence in every watershed and on many of the Virginia barrier islands including Hog Island (VA DCR

2004), with the exception of patch size, *Phragmites* patch characteristics in this study were nearly uniform along the Eastern Shore landscape.

Environmental factors

Each environmental and growth parameter measured significantly differed ($P < 0.05$) among watersheds. *Phragmites* soil chlorides varied ($P<0.001$, df=8,126, F=7.68); with the highest concentration at Gargathy watershed, 1226 $\pm$ 177 ppm (Figure 3). Tissue chlorides were significantly different ($P=0.007$, df=8,126, F=2.8) as well, Wachapreague was the highest, 48 $\pm$ 3 ppm (Figure 3). Pore water ammonium (NH_4^+) varied among watersheds ($P=0.001$, df=8,126, F=3.78), and was greatest in Quinby, 30 $\pm$ 4 µM (Figure 3). *Phragmites* stem and leaf tissues contained 1.72-10.39% N, though statistics were not run on the preliminary C:N analysis,. Soil pH was stable among watersheds (5.5-6.2 pH), except Hog Island, pH 8.3 $\pm$ 1.6 ($P<0.001$, df = 8,126, F=35.98).

In order to understand relationships among mainland watersheds, landcover characteristics were ordinated (Table 1, Figure 4). PCA axis 1 explained 67% of the variation in the watersheds, while PCA axis 2 explained 24% (Figure 4). Linear regression showed that watershed size was linked to the variation in watersheds, with size explaining 66% of the variation in the PCA axis 1 ($P=0.014$, df=1,6, F=11.6). Watersheds with the lowest and highest landcover (% of watershed) were as follows: developed area was 2% of Sand Shoal to 7% of Quinby, cropland was 21% of Machipongo to 44% of Smith, forested area was 27% of Gargathy to 50% of

Machipongo, and estuarine emergent wetlands represented 1% of Smith to 4% of Assawoman. Machipongo was the largest watershed and Quinby was the smallest.

Patch characteristics

Patch growth parameters also varied along the Eastern Shore watersheds. Height significantly differed ($P<0.001$, df=8,126, F=4.99), as did aboveground biomass ($P=0.002$, df=8,126, F=3.36) among watersheds (Figure 5). Yet, the significant differences were limited to two or three of the nine watersheds. *Phragmites* lowest height and biomass were, 2.7 ± 0.1 m and 747.7 ± 47.4 g m^{-2} respectively, at Wachapreague, whereas Assawoman had the greatest height and aboveground biomass (3.6 ± 0.1 m and 1414.9 ± 193.3 g m^{-2} , respectively) (Figure 5). Average height and biomass across all watersheds was 3.2 ± 0.1 and 1182.3 ± 116.1, respectively. Litter depth at Quinby was significantly higher compared to other watersheds ($P<0.001$, df=8,126, F=5.09), at 12 ± 2 cm (Figure 5). For the other eight watersheds, the litter depth varied from 2 to 6 cm. Stem density and internode length were also significantly different among watersheds ($P<0.001$, df=8,126, F=7.59, $P=0.02$, df 8,126, F=2.39, respectively), although differences were limited to three watersheds. Hog Island had the highest stem density 149.2 ± 6.4 m^2 and internode length was highest at Quinby, 13.3 ± 1.6 cm (Figure 5**).** Average stem density and internode length for all watersheds was 28.6 ± 1.4 and 12.0 ± 2.8, respectively.

Environmental influence on *Phragmites* populations

Phragmites patch growth characteristics were explained in some cases by the environmental parameters among all watersheds. Soil pH explained more variation in stem density and height than the other environmental variables, but NH_4^+ also explained litter depth (Table 2). Not every regression was statistically significant, indicating that many complex interacting factors determined variation in the *Phragmites* patches. A multiple regression was run to discern which factors were causing the variation in aboveground biomass. The resulting regression equation was:

$$\text{Aboveground biomass} = 448.5 + 7.1*\text{stem density} + 253.7*\text{height} - 106.7*\text{Soil pH} - 0.1*\text{Soil Chlorides} - 4.7*\text{Tissue Chlorides}.$$

with $R^2=0.398$, $P<0.001$, df 5,129, F=17.04.

Canonical correspondence analysis (CCA) explained a substantial proportion of the variation in *Phragmites* growth parameters with the environmental variables. CCA axis 1 explained 46% of the variance, and CCA axis 2 explained 16%. NH_4^+ was the major environmental factor for Quinby watershed (Figure 6). CCA related watershed characteristics to growth parameters as well, with 69% of the variation explained in CCA Axis 1 and 16% in Axis 2. Important landcovers were percent developed in the direction of the Quinby watershed and percent estuarine emergent wetland for Gargathy (Figure 7).

DISCUSSION

An aggressive genotype of *Phragmites australis* is invading many Atlantic coastal marshes in North America (Saltonstall 2002, Bart et al. 2006). *Phragmites* ability to exploit vegetation gaps, withstand harsh edaphic conditions, and rapidly grow and exclude native species such as *Spartina spp.*, make its presence problematic on the Eastern Shore of Virginia (Meyerson et al. 2000). Several plant species presently invade Atlantic coastal wetlands (Bertness et al. 2002), but few have the competitive exclusion capabilities of *Phragmites* (Farnsworth and Meyerson 2003). Large-scale studies, such as ours, are therefore necessary to find patterns that help explain the *Phragmites* invasion.

Salinity is a major stressor of coastal *Phragmites* populations (Chambers 1997, Burdick and Konisky 2003). However, at our sample sites soil chlorides were well within *Phragmites* salt tolerance (Meyerson et al. 2000). All Eastern Shore mainland patches sampled existed in freshwater or oligohaline estuarine marshes at 0 ppt-5 ppt salinity, rather than in mesohaline marshes (5 -18 ppt), where *Phragmites* also routinely occurs on the Atlantic Coast (Chambers et al. 1999, Mitsch and Gosselink 2000). This indicates that growth was not inhibited because of insufficient freshwater or drainage (Wijte and Gallagher 1996, Burdick et al. 2001). It is not until 18 ppt salinity that *Phragmites* is significantly hindered, with the most sensitive time during rhizome establishment (Wijte and Gallagher 1996, Chambers et al. 1999, Meyerson et al. 2000, Bart and Hartman 2002, 2003).

Chlorides, which are indicative of soil salinity (Chambers et al. 1998), explained some variation in growth parameters, especially aboveground biomass and stem density among Eastern Shore watersheds. For instance, Assawoman and Hog Island had relatively low soil and tissue chlorides, and higher aboveground biomass, stem density, and height over the other watersheds, whereas Metompkin and Wachapreague had relatively high soil and tissue chlorides and nearly the lowest growth measurements in all categories. Our data further support studies that found stunted growth, interrupted cellular function and nutrient uptake, and mortality of *Phragmites* associated with high soil chlorides and sulfides (Bart and Hartman 2000, Bart et al. 2006).

Eastern Shore *Phragmites* populations sampled were not significantly hindered by salinity, and thus nutrients were absorbed efficiently (Chambers 1997, Mendelssohn et al. 1979). Increased nitrogen (N) can give *Phragmites* an advantage over many Atlantic Coast competitors (e.g. *Typha spp.* and *Spartina spp.*). *Phragmites* generally has a higher aboveground and belowground biomass, standing stock N, and contributes more energy stores aboveground when increased N is available (Meyerson et al. 2000, Windham 2001, Minchinton and Bertness 2003). Although NH_4^+ did not adequately explain all of the growth parameters in simple linear regression, CCA showed that pore water NH_4^+ was the important factor in organizing *Phragmites* patches in the Quinby watershed. Furthermore, %N in tissues ranged from 1.72-10.39 %, and while not all watersheds were sampled, preliminary evidence showed that N was stored in the stems and leaves. This indicated the NH_4^+ was absorbed by the plants, and therefore the competitive effects of Na+ ions on root binding sites was not a factor (Chambers 1997).

Regression analysis for aboveground biomass indicated that many factors explained patch characteristics. Also, despite little variation among most watersheds, growth parameters themselves could be used to explain the variation in biomass. The CCA organized *Phragmites* populations in the watersheds by NH_4^+, but at the landscape-scale more field seasons are needed to assess variation in measurements over time. Additionally, our study did not address such characteristics as nitrogen inputs into soils adjacent to *Phragmites* patches, especially in agricultural fields. More thorough data on immediately surrounding landcover and soil characteristics may be needed to uncover patterns in growth parameters among sites. The CCA, which ordinated watershed landcover to growth parameters, revealed that developed and estuarine emergent landcovers separated the watersheds. This in part showed that *Phragmites* growth was strong in watersheds with ample estuarine habitat for it to grow. Also, landcover data effectively separated watersheds in our PCA. However, the landcover data may have been at too large a scale to directly relate to *Phragmites* growth characteristics among and within sites.

Phragmites is a generalist whose rapid expansion into many intertidal and freshwater coastal wetlands is driven by anthropogenic and natural disturbances (Chambers et al. 1999, Bart et al. 2006). Despite differences in landcover classes and several environmental factors among the Eastern Shore of Virginia watersheds, there was relatively little variation among *Phragmites* patch characteristics. This may indicate that *Phragmites* maintains a broad tolerance across the range of environmental conditions sampled or that on a smaller scale the established patches occur in favorable sites within each watershed. For example, *Phragmites* populations sampled in this study were on earthen mounds built to resist storm surge for waterfront properties and farmland. The increased elevation not only enhanced drainage and decreased the chance for salt infiltration, but also the creation of the mounds removed vegetation (Burdick et al. 2001, Burdick and Konisky 2003). The similarity in patch characteristics across the Eastern Shore landscape may indicate that successful

Phragmites management plans developed at the local or small scale may have broad applications for use in coastal environments.

ACKNOWLEDGEMENTS

We would like to thank The Nature Conservancy, Virginia Coast Reserve, Virginia Department of Game and Inland Fisheries, Virginia Department of Transportation, and several generous Eastern Shore private landowners who allowed us to access sites on their property. Thanks also to our field assistants, Brian Goodyear and especially Trevor Frost, whose help was invaluable, and also Ellen Young, Julie Naumann, Steven Brantley, and Spencer Bissett for their lab and statistical help. Financial support was obtained from the National Science Foundation and a Virginia Commonwealth University Graduate Assistantship.

Literature Cited

Bart, D. and J.M. Hartman. 2000. Environmental determinants of *Phragmites australis* expansion in a NJ salt marsh: an experimental approach. Oikos 89: 59-69.

Bart, D. and J.M. Hartman. 2002. Environmental constraints on early establishment of *Phragmites australis* in salt marshes. Wetlands 22: 201-213.

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.

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

Bertness M.D., P.J. Ewanchuk, and B.R. Silliman. 2002. Anthropogenic modification of New England salt marsh landscapes. Proceedings of the National Academy of Sciences 99: 1395-98.

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

Burdick, D.M. and R.A. Konisky. 2003. Determinants of expansion for *Phragmites australis*, common reed, in natural and impacted coastal marshes. Estuaries 26:407-41

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

Chambers, R.M., T.J. Mozdzer, J.C. Ambrose. 1998. Effects of salinity and sulfide on the distribution of *Phragmites australis* and *Spartina alterniflora* in a tidal marsh. Aquatic Botany 62:161-169.

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

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97: 153–166.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6: 503-523.

Farnsworth, E.J. and L.A. Meyerson. 2003. Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. Wetlands 23: 750-762.

Fogli, S., R. Marchesini, R. Gerdol. 2002. Reed (*Phragmites australis*) decline in a brackish wetland in Italy. Marine Environmental Research 53: 465-479.

Gallagher J., J.W. Wynn, W.G. Reay, R. Robinson. 2001. A GIS analysis of submarine groundwater discharge on the Eastern Shore of VA. First International Conference on Saltwater Intrusion and Coastal Aquifers, Essnonia, Morrocco. April 23-25, 2001.

Gorai, M., A.M. Vadel, M. Neffati. 2006. Seed germination characteristics of *Phragmites communis*: effects of temperature and salinity. Belgian Journal of Botany 139: 76-86.

Jordan, T.E., D.L. Correll, D.E. Weller. 1997. Effects of agriculture on discharges of nutrients from Coastal Plain watersheds of the Chesapeake Bay. Journal of Environmental Quality 26: 836-848.

Kercher, S.M. and J.B. Zedler. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23: 431-425.

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

Maheu-Giroux, M. and S. de Blois. 2005. Mapping the invasive species *Phragmites australis* in linear wetland corridors. Aquatic Botany 83: 310-320.

Maheu-Giroux, M. and S. de Blois. 2007. Landscape ecology of *Phragmites australis* invasion in networks of linear wetlands. Landscape Ecology 22: 285-301.

Marks, M., B. Lapin, and J. Randall. 1994. Phragmites australis (*P. communis*): threats, management and monitoring. Natural Areas Journal 14:285-29.

McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. MJM Software Design. Gleneden Beach, OR. 304 pp.

Mendelssohn, I.A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. Ecology 60: 574-584.

Meyerson, LA. K. Saltonstall, L. Windham, E. Kiviat, S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetland Ecology and 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. Ecological Applications 13: 883-897.

Minchinton, T.E., J.C. Simpson, and M.D. Bertness. 2006. Mechanisms of exclusion of native coastal marsh plants by an invasive grass. Journal of Ecology 94: 342-354.

Mitsch, W.J. and J.G. Gosselink. 2000. *Wetlands*. (3rd Ed.) JW Wiley. NY, NY. 920 pp.

MjM Software Design. 1999. PC-ORD. Version 4. Multivariate Analysis of Ecological Data. Gleneden, OR.

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 22:1-12.

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

Pierzynski, G.M., J.M. Sims, G.F. Vance. 2000. *Soil and Environmental Quality*. (2nd ed.) CRC. Boca Raton, FL. 440 pp.

Porter, J. 2005. *Unpublished data.* Department of Environmental Sciences. University of Virginia. Charlottesville, VA.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proceedings of the National Academy of Sciences 99: 2445-2449.

Silliman, B.R., and M.D. Bertness. 2004. Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. Conservation Biology 18:1424-1434.

Southichak, B., K. Nakano, M. Nomura, N. Chiba, O. Nishimura. 2006. *Phragmites australis*: a novel biosorbent for the removal of heavy metals from aqueous solution. Water Research 40: 2295-2302.

SPSS, Inc. 2005. Statistical Package for Social Sciences (SPSS) for Windows version 14.0. Chicago, Il.

Stanhope, JW. 2003. Relationships between watershed characteristics and base flow nutrient discharges to the Eastern Shore coastal lagoons, Virginia. MS Thesis. College of William and Mary.

Thompson, JA. 2003. Common reed (Phragmites australis) in the Chesapeake Bay: A Draft Bay-wide Management Plan. USFWS *Phragmites* Working Group.

Valiela, I., G. Collins, J. Kremer, K. Lajtha, M. Geist, M. Seely, J. Brawley, C.H. Sham. 1997. Nitrogen loading from coastal watersheds to receiving estuaries: new method and application. Ecological Applications 7: 358-380.

Vasquez, EA, E.P. Glenn, J.J. Brown, G.R. Guntenspergen, and S.G. Nelson. 2005. Salt tolerance underlies the cryptic invasion of North American salt marshes by an introduced haplotype of the common reed *Phragmites australis* (Poaceae). Marine Ecology Progress Series 208:1-8.

Virginia Department of Conservation and Recreation, Division of Natural Heritage. 2004. Distribution and Abundance of Common Reed, *Phragmites australis*, on the Eastern Shore Seaside of Virginia-Year 2. GIS shape files derived Technical Report #04-15. 29 pp.

Vretare, V. and S.E. Weisner, 2000. Influence of pressurized ventilation on performance of an emergent macrophyte (*Phragmites australis)*. Journal of Ecology 88: 978-987.

Welch, B.A., C.B. Davis, and R.J. Gates. 2006. Dominant environmental factors in wetland plant communities invaded by *Phragmites australis* in East Harbor, Ohio, USA. Wetlands Ecology and Management 14: 511-525.

Wijte, A. and Gallagher, JL. 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. 2001. Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish tidal marshes of New Jersey, USA. Wetlands 21: 179-188.

Young, D.R., D.L. Erickson, S.W. Semones. 1994. Salinity and the small-scale distribution of three barrier island shrubs. Canadian Journal of Botany 72: 1365-1372.

Table 1. Important Eastern Shore mainland watershed characteristics. Lancover categories were synthesized from Porter (2005, unpublished data). Units are hectares (ha).

Watershed	Developed	Cropland	Upland Forest /Shrub	Palustrine Forest	Estuarine Emergent Wetland
Assawoman	79.3	1179.0	1172.4	62.7	150.2
Gargathy	10.1	763	516.0	20.1	99.1
Metompkin	170.5	2496.9	2241.6	84.3	130.6
Wachapreague	148.4	1727.5	2283.8	64.9	26.3
Quinby	36.8	173.5	154.6	6.7	7.6
Machipongo	323.1	2162.1	5031.5	218.9	145.9
Sand Shoal	97.7	2027.2	1913.4	75.8	29.5
Smith	95.9	838.5	581.7	14.5	10.2

Table 2. Relationships between *Phragmites* patch and environmental variables according to the ANOVA of the regression. Data are F ratios, (*) P<0.05, (**) P<0.001.

Parameter	Aboveground Biomass	Stem Density	Litter Depth	Internode Length	Height	Tissue Chlorides
Soil Chl.	8.32*	5.27*	0.25	2.74	3.43	5.7*
NH_4^+	<0.01	0.12	8.5**	0.01	<0.01	0.08
Soil pH	1.18	20.51**	0.57	0.07	14.86**	3.46

FIGURE LEGENDS

Figure 1. Eastern Shore of Virginia with *Phragmites* patches, sites (green triangles), and major Seaside watersheds shown, from Porter (unpublished data 2005).

Figure 2. Distribution of *Phragmites* patch sizes (ha) on the seaside of Eastern Shore including the VA barrier islands, and our study sites, whose distribution were representative in size of all *Phragmites* patches (VA DCR 2004).

Figure 3. Important environmental factors effecting *Phragmites* patch growth and distribution. Bars are watershed means ± 1 SE. Watersheds with unlike letters were significantly different according to the Bonferonni multiple comparisons test.

Figure 4. Principal components analysis (PCA) of watershed landcover types: developed, cropland, upland forest/shrub, palustrine forest, and estuarine emergent wetland.

Figure 5. *Phragmites* patch characteristics among the eight Eastern Shore mainland watersheds and Hog Island during the 2006 growing season. Bars are watershed means with errors ± 1 SE. Different letters represent variation among the watershed populations according to Bonferonni multiple comparison test ($P<0.05$). Note that internode length (cm) significantly differed among watersheds.

Figure 6. Canonical correspondence analysis (CCA) relating *Phragmites* environmental parameters (pH, NH_4^+, soil chlorides) to patch characteristics.

Figure 7. Canonical correspondence analysis (CCA) relating *Phragmites* patch characteristics to percent watershed that was each landcover including: cropland, developed, estuarine emergent wetland, forested/shrub.

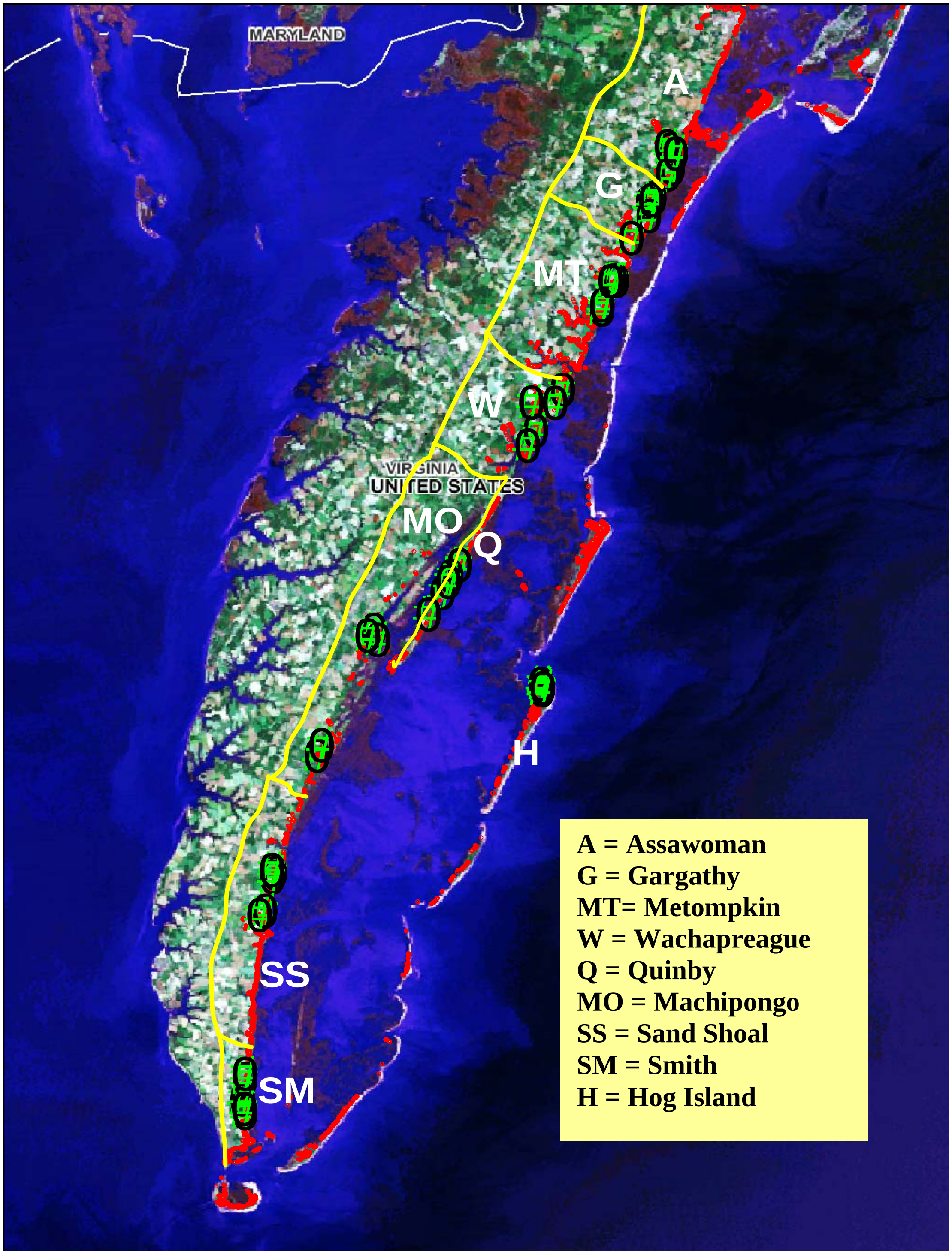
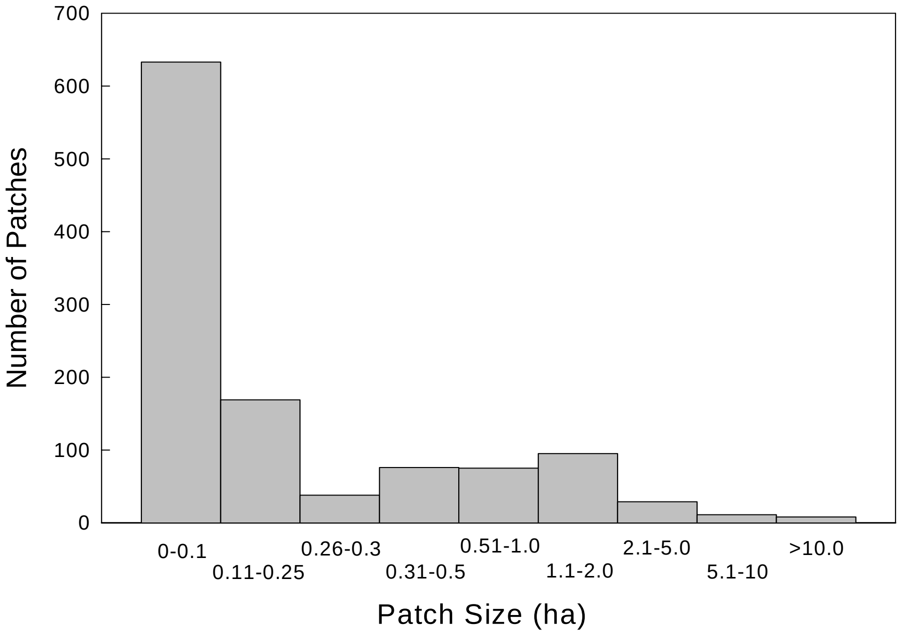

MARYLAND
A
G
MT
W
VIRGINIA
UNITED STATES
MO
Q
H
SS
SM
A = Assawoman
G = Gargathy
MT= Metompkin
W = Wachapreague
Q = Quinby
MO = Machipongo
SS = Sand Shoal
SM = Smith
H = Hog Island

Figure 1


700
600
500
400
300
200
100
0
Number of Patches
0-0.1
0.11-0.25
0.26-0.3
0.31-0.5
0.51-1.0
1.1-2.0
2.1-5.0
5.1-10
>10.0
Patch Size (ha)

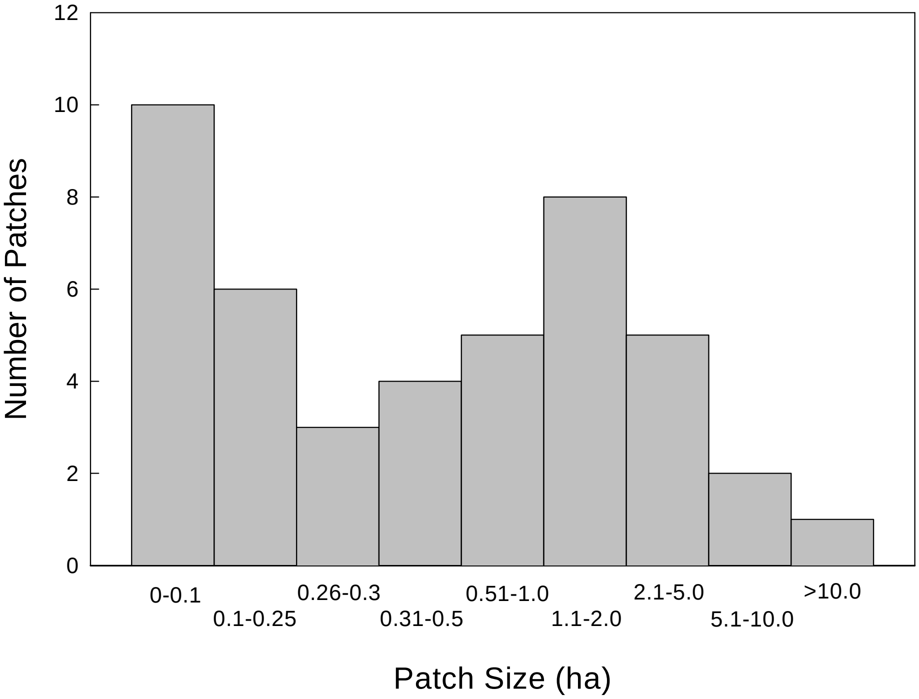

12
10
8
6
4
2
0
Number of Patches
0-0.1
0.1-0.25
0.26-0.3
0.31-0.5
0.51-1.0
1.1-2.0
2.1-5.0
5.1-10.0
>10.0
Patch Size (ha)

Figure 2

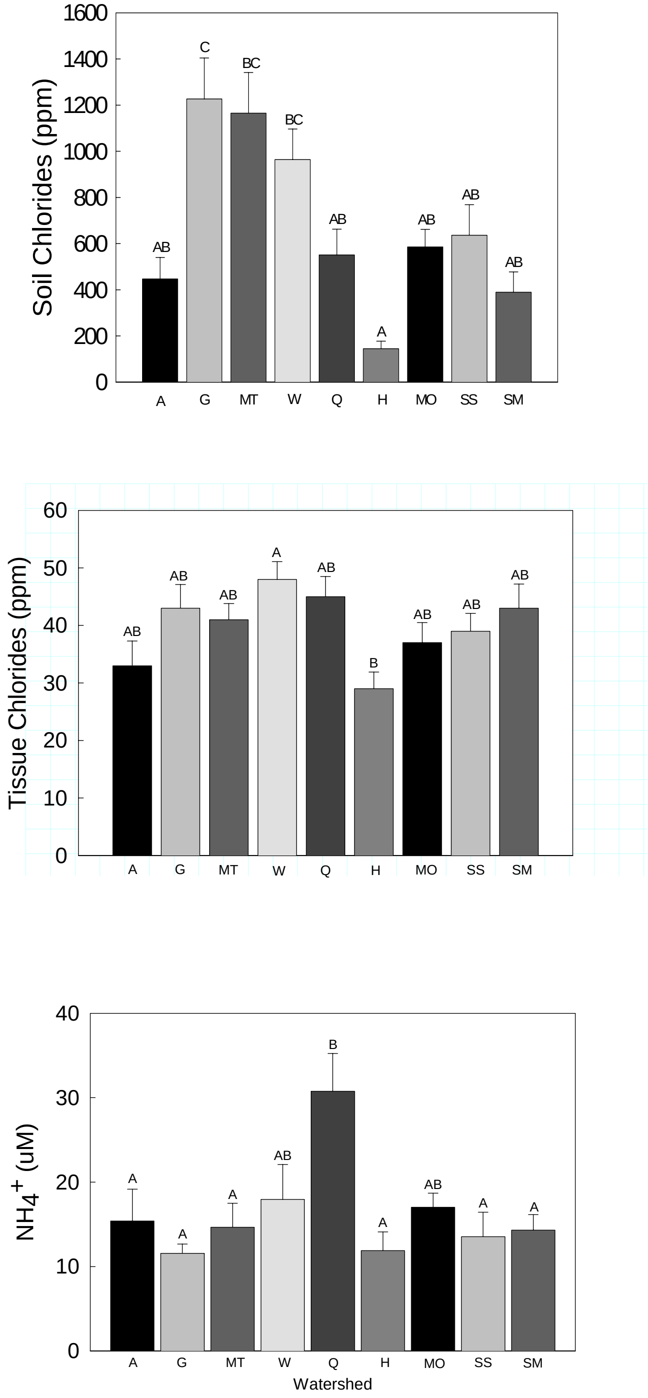

Soil Chlorides (ppm)
0
200
400
600
800
1000
1200
1400
1600
AB
C
BC
BC
AB
A
AB
AB
AB
A
G
MT
W
Q
H
MO
SS
SM
Tissue Chlorides (ppm)
0
10
20
30
40
50
60
AB
AB
AB
A
AB
B
AB
AB
AB
A
G
MT
W
Q
H
MO
SS
SM
NH_4^+ (uM)
0
10
20
30
40
A
A
A
AB
B
A
AB
A
A
A
G
MT
W
Q
H
MO
SS
SM
Watershed

Figure 3

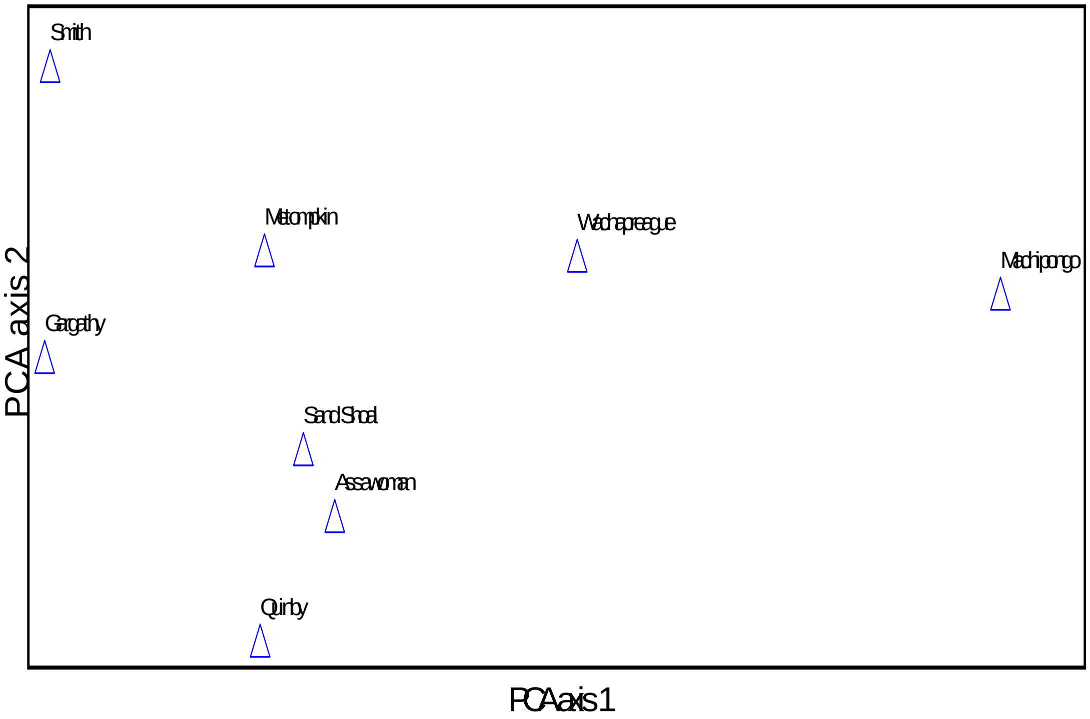

Smith
Metompkin
Wachapreague
Machipongo
Gargathy
Sand Shoal
Assawoman
Quinby
PCA axis 2
PCA axis 1

Figure 4

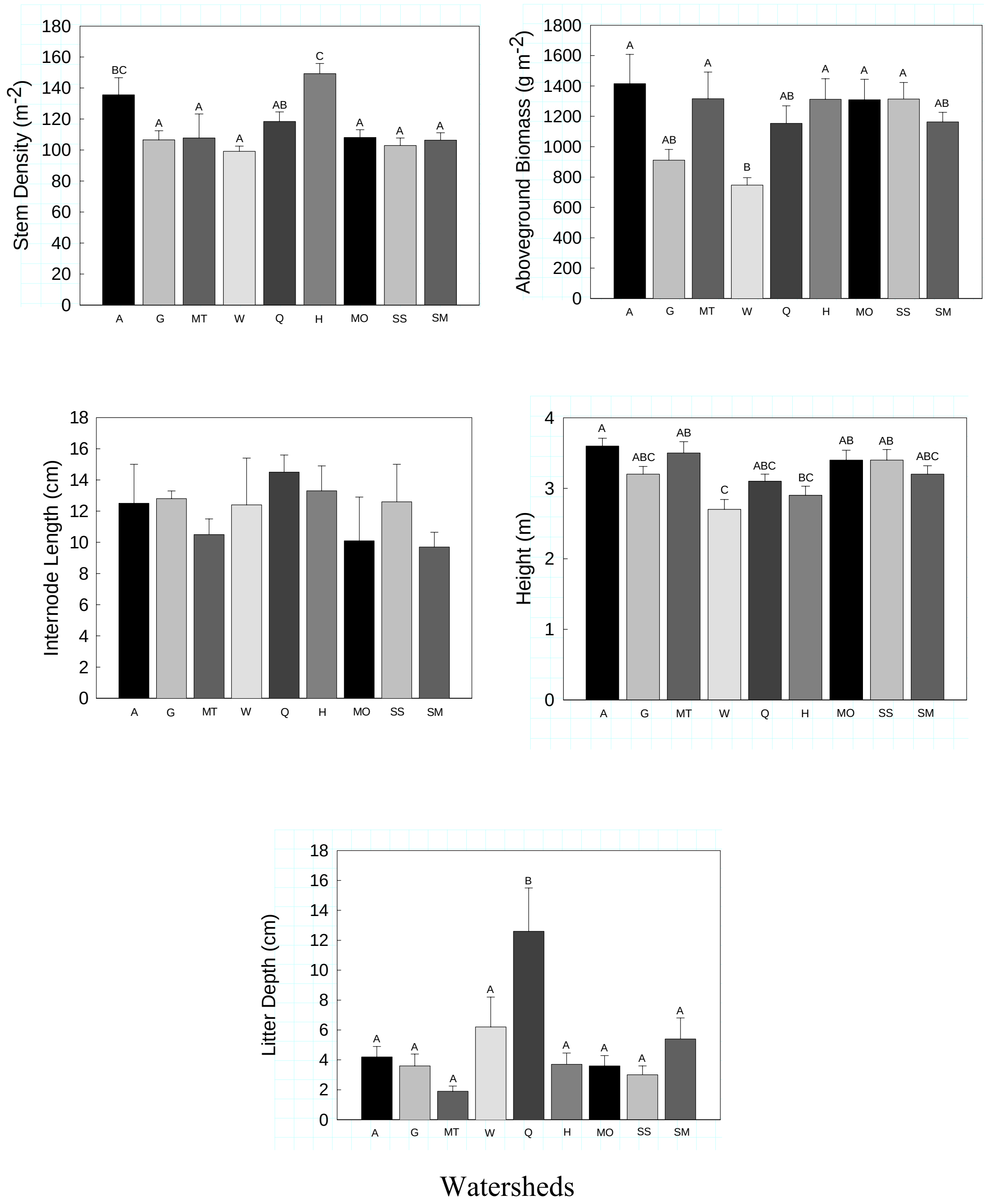

Stem Density (m^{-2})
0
20
40
60
80
100
120
140
160
180
BC
A
A
A
AB
C
A
A
A
A
G
MT
W
Q
H
MO
SS
SM
Aboveground Biomass (g m^{-2})
0
200
400
600
800
1000
1200
1400
1600
1800
A
AB
A
B
AB
A
A
A
AB
Internode Length (cm)
0
2
4
6
8
10
12
14
16
18
Height (m)
0
1
2
3
4
A
ABC
AB
C
ABC
BC
AB
AB
ABC
Litter Depth (cm)
0
2
4
6
8
10
12
14
16
18
A
A
A
A
B
A
A
A
A
Watersheds

Figure 5

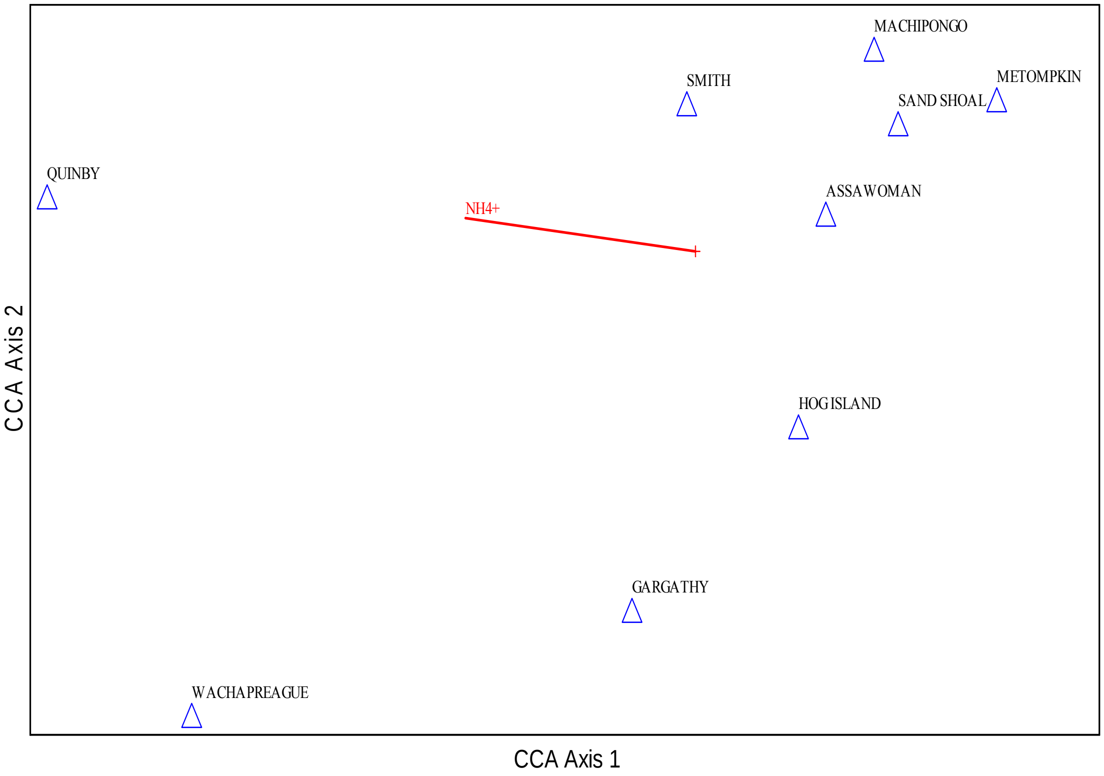

MACHIPONGO
SMITH
METOMPKIN
SAND SHOAL
QUINBY
ASSAWOMAN
NH4+
HOG ISLAND
GARGATHY
WACHAPREAGUE
CCA Axis 2
CCA Axis 1

Figure 6

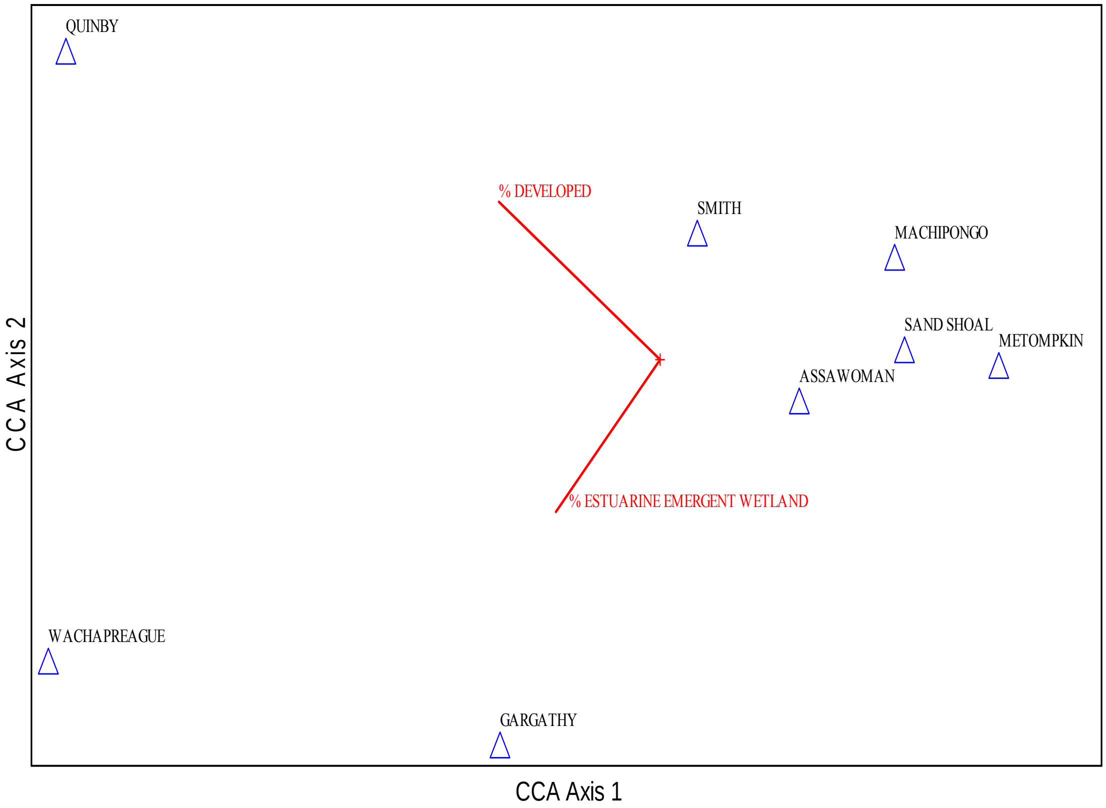

QUINBY
% DEVELOPED
SMITH
MACHIPONGO
SAND SHOAL
METOMPKIN
ASSAWOMAN
% ESTUARINE EMERGENT WETLAND
WACHAPREAGUE
GARGATHY
CCA Axis 1
CCA Axis 2

Figure 7

Literature Cited

Ailstock, MS. 2001. Adaptive Strategies of Common Reed *Phragmites australis*. Environmental Center Anne Arundel Community College.

Amesberry, L., M.A. Baker, P. Ewanchuck, and M.D. Bertness. 2000. Clonal integration and the expansion of *Phragmites australis*. Ecological Applications 10:1110-1118.

Armstrong, J., W. Armstrong, P. M. Beckett. 1992. *Phragmites australis:* Venturi- and humidity-induced pressure flows enhance rhizome aeration and rhizosphere oxidation. New Phytologist 120: 197-207.

Bart, D. and J. M. Hartman. 2000. Environmental determinants of *Phragmites australis* expansion in a NJ salt marsh: an experimental approach. Oikos 89: 59-69.

Bart, D. and J. M. Hartman. 2002. Environmental constraints on early establishment of *Phragmites australis* in salt marshes. Wetlands 22: 201-213.

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.

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

Bertness M.D., P.J. Ewanchuk, and B.R. Silliman. 2002. Anthropogenic modification of New England salt marsh landscapes. Proceedings of the National Academy of Sciences 99: 1395-98.

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

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

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

Chambers, R.M., T.J. Mozdzer, J.C. Ambrose. 1998. Effects of salinity and sulfide on the distribution of *Phragmites australis* and *Spartina alterniflora* in a tidal marsh. Aquatic Botany 62:161-169.

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

Crawford, E.R. 2005. *Unpublished data.* Department of Biology. Virginia Commonwealth University. Richmond, VA.

Gorai, M., A.M. Vadel, M. Neffati. 2006. Seed germination characteristics of *Phragmites communis*: effects of temperature and salinity. Belgian Journal of Botany 139: 76-86.

Hardej, M. and T. Ozimeka. 2002. The effect of sewage sludge flooding on growth and morphometric parameters of *Phragmites australis* (Cav.) Trin. Ex. Steudel. Ecological Engineering 19:343-350.

Hotes, S., E.B. Adema, A.P. Grootjans, T. Inoue, P. Poschlod. 2005. Reed die-back related to increase sulfide concentration in a coastal mire in eastern Hokkaido, Japan. Wetland Ecology and Management 13: 83-91.

Jordan, T.E., D.L. Correll, D.E. Weller. 1997. Effects of agriculture on discharges of nutrients from Coastal Plain watersheds of the Chesapeake Bay. Journal of Environmental Quality 26: 836-848.

Kercher, S.M. and J.B. Zedler. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23: 431-425.

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

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

Maheu-Giroux, M. and S. de Blois. 2005. Mapping the invasive species *Phragmites australis* in linear wetland corridors. Aquatic Botany 83: 310-320.

Maheu-Giroux, M. and S. de Blois. 2007. Landscape ecology of *Phragmites australis* invasion in networks of linear wetlands. Landscape Ecology 22: 285-301.

Mendelssohn, I.A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. Ecology 60: 574-584.

Meyerson, L.A., K. Saltonstall, L. Windham, E. Kiviat, S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetland Ecology and 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. Ecological Applications 13: 883-897.

Minchinton, T.E., J.C. Simpson, and M.D. Bertness. 2006. Mechanisms of exclusion of native coastal marsh plants by an invasive grass. Journal of Ecology 94: 342-354.

Mitsch, W.J. and J.G. Gosselink. 2000. *Wetlands*. (3rd Ed.). Wiley. NY. 920 pp.

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 22:1-12.

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

Pierzynski, G.M., J.M. Sims, G.F. Vance. 2000. *Soil and Environmental Quality*. (2nd ed.) CRC. Boca Raton, FL. 440 pp.

Porter, J. 2005. *Unpublished data.* Department of Environmental Sciences, University of Virginia. Charlottesville, VA.

Rickey, M.A., and R.C. Anderson. 2004. Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata.* Journal of Applied Ecology 41: 888-896.

Romero, J.A., H. Brix, H.A. Comin. 1999. Interactive effects of N and P on growth, nutrient allocation and NH4 uptake kinetics by *Phragmites australis.* Aquatic Botany 64:369-380.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proceedings of the National Academy of Sciences 99: 2445-2449.

Silliman, B.R., and M.D. Bertness. 2004. Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. Conservation Biology18:1424-1434.

Southichak, B., K. Nakano, M. Nomura, N. Chiba, O. Nishimura. 2006. *Phragmites australis*: a novel biosorbent for the removal of heavy metals from aqueous solution. Water Research 40: 2295-2302.

Stanhope, J.W. 2003. Relationships between watershed characteristics and base flow nutrient discharges to the Eastern Shore coastal lagoons, Virginia. MS Thesis, College of William and Mary. 168 pp.

Valiela, I., G. Collins, J. Kremer, K. Lajtha, M. Geist, M. Seely, J. Brawley, C.H. Sham. 1997. Nitrogen loading from coastal watersheds to receiving estuaries: new method and application. Ecological Applications 7: 358-380.

Vasquez, EA, E.P. Glenn, J.J. Brown, G.R. Gunterspergen, and S.G. Nelson. 2005. Salt tolerance underlies the cryptic invasion of North American salt marshes by an introduced haplotype of the common reed *Phragmites australis* (Poaceae). Marine Ecology Progress Series 208: 1-8.

Vretare, V. and S.E. Weisner. 2000. Influence of pressurized ventilation on performance of an emergent macrophyte (*Phragmites australis)*. Journal of Ecology 88: 978-987.

Welch, B.A., C.B. Davis, and R.J. Gates. 2006. Dominant environmental factors in wetland plant communities invaded by *Phragmites australis* in East Harbor, Ohio, USA. Wetland Ecology and Management 14: 511-525.

Wijte, A. and J.L.Gallagher. 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. 2001. Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in Brackish tidal marshes of New Jersey, USA. Wetlands 21: 179-188.

Appendix A. *Phragmites* study sites sampled along the Eastern Shore of Virginia, USA. Coordinates represent latitude and longitude of patch.

Assawoman	37.8432	-75.5181
	37.8431	-75.5182
	37.8459	-75.5237
	37.8323	-75.5217
	37.8282	-75.5263
Gargathy	37.7982	-75.5452
	37.8113	-75.5398
	37.8096	-75.5423
	37.8077	-75.5455
	37.7828	-75.5621
Metompkin	37.7518	-75.5772
	37.7519	-75.5826
	37.7523	-75.5795
	37.7311	-75.5918
	37.7345	-75.5911
Wachapreague	37.6736	-75.6308
	37.6644	-75.6381
	37.6657	-75.6587
	37.6448	-75.6567
	37.6343	-75.6645
Quinby	37.5488	-75.7306
	37.5409	-75.7387
	37.5369	-75.7413
	37.5291	-75.7471
	37.5138	-75.7604
Machipongo	37.5039	-75.8094
	37.5006	-75.8151
	37.4969	-75.8060
	37.4217	-75.8613
	37.4142	-75.8657
Sand Shoal	37.3292	-75.9088
	37.3315	-75.9109
	37.3262	-75.9108
	37.3019	-75.9192
	37.2988	-75.9241

Appendix A. continued

Smith	37.1790	-75.9450
	37.1638	-75.9482
	37.1569	-75.9471
	37.1539	-75.9466
	37.1550	-75.9502
Hog Island	37.4582	-75.6654
	37.4573	-75.6642
	37.4557	-75.6641
	37.4548	-75.6639
	37.4535	-75.6645

VITA

Jeremy D. Fennell was born December 27, 1979 in Durham County, North Carolina. He graduated salutatorian from Hillside High School in Durham, North Carolina in 1998. He received his Bachelor of the Arts in Environmental Studies concentrating in Conservation Biology from Warren Wilson College, North Carolina in 2002. In the interim between his undergraduate and graduate career, he hiked the entire Appalachian Trail southbound with his lovely future wife Ginger from June to November 2003. He also worked as a carpenter, backcountry ranger, and landscape designer. His need to work in the environmental field compelled him to pursue his M.S., and his curiosity about the natural world will hopefully continue in the future. He has accepted a job effective immediately following his graduation with the Virginia Department of Environmental Quality as a Virginia Water Protection Compliance Inspector in Roanoke, VA.