

ABSTRACT

Dissertation title: EFFECTS OF ANNUAL AND PERENNIAL
COMMUNITY DYNAMICS ON TIDAL FRESHWATER
MARSH ECOSYSTEM FUNCTIONING

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Tidal freshwater marshes are complex systems with many linkages between the physical, chemical, and biological components. Understanding how the community dynamics of a tidal freshwater marsh affect ecosystem processes may be applicable towards restoring properly functioning wetlands that improve the filtration of excess nutrients and toxins, subsequently improving water quality for downstream areas. The first question explored is why annual species exist in a marsh dominated by perennials. Annual species may exist through facilitation or competition with neighboring species, or through relationships with abiotic variables including elevation and seed rain. Through many field and greenhouse studies, I have determined that competition between annual and perennial species may exist, but abiotic factors are driving the vegetative composition of the marsh. Understanding if annual patches move through time is imperative for relating the plant community to ecosystem processes. To explore the temporal community dynamics, I examined the composition of the belowground marsh seed bank and the aboveground vegetation composition for three years. I have learned that the seed bank partially drives the vegetation composition. Furthermore, additional environmental factors may play a role in determining aboveground vegetation composition. I examined differences in the ecosystem processes of denitrification and its influencing variables among communities dominated by annual species, perennial species, and a mixture of the two. No differences in denitrification rates existed among community types; however organic nitrogen, which is driven by vegetation increased with denitrification rates. Communities readily move through space and time and may influence nutrient cycling in tidal freshwater marshes. Therefore, restoration managers should take into consideration species that maximize nitrogen removal and the variables that control their spatial and temporal movement when planning restoration designs and alternatives.

EFFECTS OF ANNUAL AND PERENNIAL COMMUNITY DYNAMICS
ON TIDAL FRESHWATER MARSH ECOSYSTEM FUNCTIONING

by

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DEDICATION

I dedicate my dissertation to my loving family whose support has always given me the courage to go in new and challenging directions; to my network of friends who never doubt my abilities and choices; and to those who work to preserve, restore, and recreate aquatic ecosystems around the world.

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CHAPTER I

INTRODUCTION

Problem Statement

The transfer of nitrogen through our Nation's waterways has greatly increased owing to human activities such as burning of fossil fuels and production of nitrogen fertilizers (Vitousek et al. 1997). Increasing nitrogen availability in the short-term can increase plant productivity and standing biomass (Vitousek and Howarth 1991); however, through time, as nitrogen makes its way through soil substrates to stream and ground water, nitrogen enrichment can reduce biological diversity (Tilman 1987), deplete soil minerals and acidify soils (Likens et al. 1996), and severely alter downstream ecosystems (Nixon et al. 1996). In the Chesapeake Bay, the increase in nitrogen and other nutrients flowing through the watershed have been deemed responsible for large hypoxic areas found in the Bay (Cooper and Brush 1991).

Hypoxic zones are areas of extreme low oxygen and are found in estuaries, oceans, and lakes. These low oxygen areas are formed after excess nitrogen and phosphorus enter the area and trigger large blooms of phytoplankton and zooplankton that consume all of the water's dissolved oxygen as organisms respire. Hypoxic zones can be detrimental to estuarine ecosystems by causing substantial mortality of sessile organisms that cannot escape suboptimal or lethal conditions (Eby et al. 2005), limiting oyster success through increased dinoflagellate toxin production (Brownlee et al. 2005), and impacting habitat quality and growth rates of nekton (Eby et al. 2005). Hypoxic zones also have economic consequences; as shrimp, crab, and fish catches decline catch

per unit effort decreases leading to inadequate salaries for watermen and an increase in the price of seafood for consumers.

A natural way to reduce the risk of hypoxic zones developing in coastal areas is through the process of denitrification. Denitrification, the reduction of nitrate and nitrite in water and sediments to gaseous forms of nitrogen (NO, N₂O, N₂) that are released into the atmosphere, is an integral process for improving water quality. An anaerobic environment with excess nitrate available for reduction and organic matter to fuel microbes is necessary for the process of denitrification to occur. These are characteristics found in tidal freshwater marsh ecosystems; thus, tidal freshwater marshes are ideal locations for denitrification and for improving water quality of coastal systems.

Tidal Freshwater Marshes

Tidal freshwater marshes are an ideal solution to reducing hypoxic areas of coastal regions for several reasons. They are situated in the landscape between pollution sources upstream and hypoxic areas downstream. Tidal freshwater marshes have been called the kidneys of the landscape as they are capable of filtering out and removing a large percent of nutrients that pass through them (Odum 1988). The filtration of nutrients results in tidal freshwater marshes being nitrogen sinks through ecosystem processes such as denitrification.

Tidal freshwater marshes receive tidal activity similarly to salt marshes, but without the influence of salinity, thereby resulting in very diverse and productive plant communities (Parker and Leck 1985). Tidal freshwater marshes support many more annual and perennial species than their brackish and salt marsh counterparts, and the plants are tightly linked to chemical and physical processes in the ecosystem (Whigham

et al. 1978, Simpson et al. 1983). Because plant functional groups, such as annuals and perennials, have different morphological, physiological, and life history characteristics, they may impact ecosystem processes differently. Not only are tidal freshwater marshes productive, diverse, and efficient at improving water quality, they are responsible for many human-valued functions including providing wildlife habitat for a diverse number of terrestrial and aquatic species (Odum et al. 1984), stabilizing water supplies through amelioration of floods and drought, and absorbing impacts from large storms through shoreline stabilization and attenuation of tidal energy (Mitsch and Gosselink 2000).

Despite their many human-valued functions, tidal freshwater marsh area has decreased substantially since colonization of the U.S. and continues to decrease each year. The estimated total tidal freshwater marsh area in the conterminous U.S. is 820,000 ha (Field et al. 1991), with 164,000 ha along the Atlantic Coast and approximately one-half of that in New Jersey and 16,000 ha in Virginia (Odum et al. 1984). Tidal wetlands are predominantly lost owing to the pressures of urbanization. Fifty-two percent of the U.S. population lives within 80 km of the U.S. coast (Southworth 1989). Dahl (1990) estimates that 53% of all wetlands in the conterminous U.S. were lost from the 1780s to 1980s. Coastal wetlands were being lost at an estimated rate of 8,100 ha/yr between 1922 and 1954; however the rate accelerated to 19,000 ha/yr between 1954 and 1970 (Gosselink and Baumann 1980). Even after many federal wetland protection laws were established in the 1970s and 1980s, an additional 1.7% of remaining coastal wetlands were lost by 1990 (Dalh and Johnson 1991), and continue to be lost even today at a rate of 0.1% / yr (Tiner 1998).

Another major factor contributing to the current and potential future loss of tidal freshwater marshes is global warming and sea level rise (Gornitz 1991, Michener et al. 1997). Recent increases in global carbon dioxide concentration due to fossil fuel use and land-use change, and increases in methane and nitrous oxide due to agriculture are largely to blame for recent climate change phenomena (IPCC 2007). A rise in sea level has been linked to global climate change through the widespread melting of snow and ice, and warming of the ocean's temperature (Barth and Titus 1984, Warrick et al. 1993, IPCC 2007). Global sea level has risen at a rate of 3.1 mm/yr from 1993-2003, and is projected to rise between 0.18-0.59 m by the end of the current century based on various emissions scenarios (IPCC 2007). In the Chesapeake Bay, sea level is rising at twice the average global rate (Douglas 1991). Furthermore, the IPCC (2007) states that, "both past and future anthropogenic carbon dioxide emissions will continue to contribute to warming and sea level rise for millennium, due to the timescales required for removal of this gas from the atmosphere." Therefore, a reliable prediction would be that the water level of the Chesapeake Bay may raise a *minimum* of 0.36 m in the next 100 years (IPCC 2007).

In the short-term, climate variability may cause marsh dry-outs (Manabe and Wetherald 1986), where areas of tidal freshwater marshes endure drought conditions and increased salinity, which would cause them to become a source of nitrogen to the landscape instead of a sink (Dowrick et al. 1999, Mulhouse et al. 2005, Brown et al. 2006). However, in the long-term, sea level rise may impose several major changes in tidal freshwater marsh ecosystems. A change in the frequency and duration of water inundation could alter nutrient cycling by affecting the amount of marsh that experiences sedimentation and anoxic conditions, but scientists are unsure of what exact changes will

take place. For example, larger anoxic areas could act as nitrogen sinks by increasing the capacity of a wetland for denitrification in the water column; however, denitrification occurring in the sediment from the coupling of nitrification/denitrification would decrease because aerobic areas required for nitrification would shrink. Also, a rise in sea level could cause anaerobic conditions to shift soil reduction-oxidation reactions, causing phosphorus bound in the sediments to be released into overlying water and transported downstream (Michner et al. 1997). Vegetation may be severely stressed by anoxic soil causing reduced growth rates (Day et al. 1993) and oxygen deficiencies in the roots (DeLaune et al. 1987). Furthermore, rising sea level will increase salinity levels in tidal freshwater marshes, and salt stress will negatively impact the current species composition of a tidal freshwater marsh through osmotic stress, ion imbalance, and nutrient deficiency (Jones 1981).

Because tidal freshwater marshes are mostly located adjacent to highly urbanized areas, the ability to migrate landward as sea level rises and salt water intrudes will be significantly compromised. Human infrastructure, including roads, dikes, and bulkheads will prevent marshes from landward movement and result in the ultimate demise of tidal freshwater marsh ecosystems owing to conversion to salt marsh habitat and complete marsh inundation if sedimentation rates cannot keep up with sea level rise. Therefore, with the increasing pressures of urbanization and sea level rise, the many functions that tidal freshwater marshes provide need to be studied so that these valuable ecosystems can be effectively preserved, restored, and/or recreated. A recent increase in interest of restoring coastal marshes has developed, but little is known about how they function. Understanding the complex interactions among the biological, chemical, and physical

variables in tidal freshwater marshes may assist in their preservation, and their restoration may serve as another potential means of improving water quality in coastal zones and specifically, the Chesapeake Bay.

Research Questions, Hypotheses, and Predictions

The two overarching goals of my dissertation were to 1) explore the processes affecting spatial and temporal patterns of annual and perennial plant communities in freshwater tidal marshes and 2) determine how vegetation patterns affect the ecosystem functioning of tidal freshwater marshes. The project was specifically designed to inform land managers in preparing successful restoration designs for freshwater tidal marshes of the Northeastern United States. A freshwater tidal marsh owned by the National Park Service, Dyke Marsh Preserve, located near Alexandria, Virginia, was used as the natural laboratory for the study. Thus, results are directly applicable to the restoration of this important national park, which lost half of its marsh area between 1930 to 1970 to a sand and gravel mining enterprise. I describe the physical, chemical and biological aspects of Dyke Marsh Preserve in Chapter II. The chapter describing the study site is then followed by several chapters that summarize my detailed investigations of vegetation patterns and processes of the marsh. Specifically, I studied the following questions and associated hypotheses.

1. Why are annual species abundant in some areas of a marsh dominated by perennial plant species?

Freshwater tidal marshes may be invaded by aggressive perennial species such as *Phragmites australis* and *Typha* spp. that decrease the diversity of a marsh (Houlahan and Findlay 2004, Silliman and Bertness 2004, Boers et al. 2007), yet many marshes in the

Eastern United States remain diverse supporting patches of annuals within a perennial species matrix. Annual patches in tidal marshes may form through disturbances (Grime 1977), including ice scour (Belanger and Bedard 1994), wrack-burial (Brewer et al. 1998), and large storms (Nyman et al. 1995). Yet once dominant patches of annual species are formed, they may shift in size and composition owing to the complexity of biological, chemical, and physical interactions in a tidal freshwater marsh. Therefore, my first question focused on the spatial dynamics of annual species in a tidal freshwater system that is a heterogeneous plane of species. I investigated mechanisms that may explain the spatial patterns in Chapters III through VII.

I begin exploring spatial dynamics by examining if sediment levels are fluctuating at Dyke Marsh in Chapter III. The movement of sediments in tidal marshes is well documented, but linking the movement of sediments to the movement of vegetation patches dominated by annual species has not been thoroughly studied. Sedimentation is a function of plant association, distance to tidal inlet, distance to stream, animal activity and elevation (Pasternack et al. 2000). For example, Pasternack et al. (2000) created a quantitative index relating plants to physical and chemical parameters to study marsh geomorphology in a Chesapeake Bay tidal freshwater marsh. They found elevation to impact summer-average sedimentation the most, but plant association and distance from tidal inlet were also significant variables. *I hypothesized that fluctuating sediment level would change local elevation.* If discernable changes can be detected within my three-year study period, they would allow me to draw inferences on whether areas of accretion or erosion are associated with changes in vegetation composition.

After examining changes in sediment level through time and space, I explore spatial dynamics of annual species by studying relationships between elevation of the marsh surface and abundance of annual species at different life history stages in Chapter IV. The vegetative composition of a tidal freshwater marsh is directly affected by gradual elevation differences (Cornu and Sadro 2002), water inundation from the tide (Baldwin et al. 1996), and nutrients available in the soil (Knops et al. 2002). Numerous tidal freshwater marsh studies have found water level to be the primary driver influencing seed germination and seedling survival (Baldwin et al. 1996, Baldwin et al. 2001, Baldwin and Pendleton 2003), vegetative growth (Baldwin et al. 2001, Cornu and Sadro 2002; Baldwin and Pendleton 2003), and species richness (Baldwin et al. 1996; Brewer et al. 1997, Cornu and Sadro 2002). Perennial species can expand vegetatively if conditions are flooded, but annual species' seeds may not germinate in flooded conditions (Baldwin et al. 2001). Flooding during the beginning of the growing season may inhibit successful germination of annual species and cause lower annual species abundance (Baldwin et al. 2001, Cornu and Sadro 2002). *Therefore, I predicted that elevation is associated with changes in abundance of annual species in the seed bank, abundance of annual species seedlings, and/or abundance of mature annual species, and that germination (seed to seedling transition) and survivorship (seedling to mature plant transition) is also influenced by elevation.* Understanding the influence of elevation on life history stages and transitions between stages can have significant management implications by highlighting specific species and elevations that need to be restored to produce a desired diversity of annual and perennial species.

As explored in Chapter IV, annual species may be more sensitive to elevation changes and subsequently water inundation than perennial species (Baldwin et al. 2001). Annual species abundance may also be influenced by the species around them through facilitation, inhibition, and competition. In Chapter V, I explore facilitation of an annual species by a perennial species through oxygenation of the substrate. I focus on *Typha angustifolia* and *Impatiens capensis*, which are two co-occurring dominant species observed in tidal freshwater marshes of the eastern United States. Facilitative relationships, e.g., increased growth via soil oxygenation, are common in plant communities of tidal marshes. However, only a few studies have examined the positive interactions of plant species in wetlands through rhizosphere oxygenation (Schat and Van Beckhoven 1991, Bertness and Hacker 1994, Castellanos et al. 1994, Hacker and Bertness 1995, Callaway and King 1996). *Typha angustifolia* contains aerenchymous tissue similar to that found in past studies with *T. latifolia* (Callaway and King 1996), and is thought to oxygenate the substrate in a similar fashion. *Therefore, I predicted that I. capensis* growth would be reduced and reduction-oxidation (redox) potential would be higher in greenhouse mesocosms containing *T. angustifolia* compared to mesocosms without *T. angustifolia*. I also predicted that extrinsic abiotic factors, such as elevation and tidal fluctuations, introduce oxygen to the root zone of *I. capensis*, allowing the species to thrive even in the absence of *T. angustifolia*.

While Chapter V explores facilitation, Chapter VI studies the possibility that the dominant marsh annual, *I. capensis* competes with four common perennial species for light and soil nutrients. When stress caused by water inundation is reduced, plant interactions can shift from facilitative to competitive (Bertness 1991, Bertness and

Shumway 1993), which often results in a decline in species richness and abundance (Brewer et al. 1997). For example, in a stressful environment with high water level one species may ameliorate anoxic conditions for another species, thereby allowing that species to grow in the stressful environment. If water level is then lowered and stress is reduced, then more ideal growing conditions may cause the two species to shift to a competitive relationship. Plants in tidal freshwater marshes may compete for light (Parker and Leck 1985) and nutrients. *I hypothesized that species that germinate early in the growing season, such as I. capensis, inhibit the success of later germinating species by altering the light supply to the soil surface with their large cotyledons. Therefore, I predicted that the shade from the large cotyledons of early germinating I. capensis, the dominant annual species in Dyke Marsh, would prevent later germinating perennials from emerging and/or becoming established.* I also wanted to see if nutrient uptake and light availability would interact in affecting the germination and establishment of perennial seeds and seedlings. Because *I. capensis* germinates first, it begins taking up nutrients first and may deplete the nutrient pool available for later germinating species. *Specifically, I predicted that I. capensis would have a stronger competitive edge in the low nutrient environment, because in addition to the shading effects, it would deplete the nutrient pool before other species had a chance to germinate.*

Chapter VII is the last chapter dedicated to answering why annual species are abundant in some areas of a marsh dominated by perennial plant species. Whereas the previous chapters focus on environmental factors and interspecific interactions, Chapter VII focuses on the importance of dispersal in contributing to community structure of tidal freshwater marshes. Specifically, I focus Chapter VII on seed rain composition and how

the spatial and temporal variations in seed rain composition may influence annual species distribution in the marsh. The dispersal of seeds through water ways (hydrochory) can be an important driver of community dynamics in wetland ecosystems (Schneider and Sharitz 1988, Cappers 1993, Neff and Baldwin 2005). Hydrochory may result in more diverse wetland communities (Girel and Manneville 1998, Jansson et al. 2005, Leyer 2006) through the introduction of new species (Mitsch et al. 1998), including exotic species (Thomas et al. 2005, Tabacchi et al. 2005, Thomas et al. 2006). *My main objective was to explore the composition and spatial and temporal variations of the seed rain by assessing the density of seeds and species richness available in the surrounding river and shoreline of Dyke Marsh through time.* The results of this study may inform site managers about the seasonal availability of local seed supply, both native and exotic, that may contribute to a restoration project.

2. How do species dominance patterns affect marsh ecosystem processes?

The second question of my dissertation specifically asks if the composition of vegetation influences how much, where, and when the ecosystem process of denitrification occurs in a tidal freshwater marsh. Chapter VIII thoroughly examines this question, as well as explores how other chemical and physical variables may affect denitrification rates.

Aquatic plant communities have the capability to alter denitrification rates (Cornwell et al. 1999) by influencing the environmental conditions necessary for denitrification to occur. When ammonium and nitrate are taken up by plants, the amount of nitrogen available for denitrification declines. Annual species may allocate nitrogen towards fast growth and reproduction, while perennials may allocate nitrogen towards continued growth of rhizomes (Reddy and DeBusk 1987). Therefore, in autumn when

annual species senesce the nitrogen in their tissues is incorporated back into the sediment; however perennial species keep some nitrogen from the substrate when underground structures containing nitrogen do not senesce. Denitrifying microbes use the labile carbon from decomposed vegetation as fuel for the process of denitrification. Annual and perennial species may influence organic matter differently by the amount and quality of biomass that senesces each year. Sedge and grass species tend to have more lignin in their tissues than broad-leaved species, which results in slower decomposition rates and less labile carbon available for denitrifying microbes (Melillo et al. 1982, Hobbie 1996, Hume et al. 2002). Furthermore, an increase in organic matter can indirectly increase denitrification rates by increasing sediment metabolism, which reduces oxygen in the soil and creates anaerobic environments ideal for denitrification. (Cornwell et al. 1999). *Thus, denitrification rates may differ between patches dominated by annual and perennial species owing to the different life history characteristics of annual and perennial species that differ in their effects on pools and fluxes associated with denitrification.*

Besides biotic drivers of denitrification, marsh surface elevation determines the extent and variability of aerobic and anaerobic zones in the substrate owing to daily tidal fluctuations that inundate areas differently depending on marsh surface elevation. The fluctuation of oxygen in the substrate is necessary for the coupling of nitrification and denitrification; the process of nitrification in the aerobic zone produces the nitrate needed for the process of denitrification to take place in the anaerobic zone. *Thus, marsh surface elevation may influence denitrification rates in a tidal freshwater marsh.* If scientists can better understand interactions between influential biological, physical, and chemical variables and the process of denitrification in tidal freshwater marshes, restoration

managers may effectively restore and recreate these ecosystems to maximize denitrification rates, thereby decreasing the amount of excess nitrogen that flows downstream and contributes to hypoxic zones in Chesapeake Bay.

3. Are annual species dominance patterns stable in a marsh dominated by perennials, or do annual patches fluctuate from year to year?

After exploring why annual species exist in a tidal marsh dominated by perennials, their spatial dynamics, and how that influences the important ecosystem process of denitrification, my third dissertation question examines the temporal dynamics of annual species. To better grasp the future of a tidal freshwater marsh and its ecosystem functions, knowing if and why plant community structure shifts through time is imperative. Chapter IX addresses this question through a field study that measured above-ground plant community compositions and belowground seed bank composition, their relationships to each other, and their locations through time.

Seed banks and standing vegetation have been studied in tidal freshwater marshes (Leck and Simpson 1995, Leck 2003, Peterson and Baldwin 2004a); however, whether and how seed banks influence the composition of standing vegetation and how standing vegetation affects the seed bank in space and time is not well understood. Seeds of many tidal freshwater marsh plant species fall to the sediment close to the parent plant (Leck and Simpson 1993) where they may be incorporated into the seed bank or washed away by tidal flushing. Tidal flushing pushes sediments (and hence seed banks) around and plays a role in how seeds are dispersed throughout the marsh, which may decouple the relationship between seed banks and vegetation. Unfortunately, very little data exist on relationships between tidal flushing and seed distribution in tidal marshes. Furthermore,

the channels that flow through and around a tidal marsh offer a direct influx of seeds to the marsh. When the tide level rises, water spills over the channel banks and flows over the marsh surface; then when the tide level recedes, seeds may become trapped by the sediment surface and vegetation similar to how vegetation traps sediment. Elevation tends to increase with distance from tidal channels (Simpson et al. 1983, Odum et al. 1984), and several studies have discovered that annual species prefer higher elevations in tidal freshwater marshes (Baldwin and Mendelssohn, 1998; Leck, 2003, Seabloom and van der Valk, 2003). Some studies have found that wetlands dominated by annual species have high seed bank-vegetation similarity owing to ideal moisture conditions and shelter from existing dense vegetation (Ungar and Woodell 1993, Jutila 2003). *Therefore, I predicted that areas with high similarity between vegetation and seed bank composition will occur farthest from tidal channels; and that higher similarity will be found in plots at higher elevations, because plots with high elevation should support more annual species.* Acquiring a better understanding of seed bank-vegetation relationships may assist management decisions for restoration design regarding whether or not to plant a newly restored or created wetland site. Another use of this information is to link the temporal changes in community composition that are driven by intrinsic (e.g., interspecific interactions) or extrinsic (sea level rise) factors to changes in denitrification rates in tidal freshwater marshes.

4. What effects may future climate change have on relationships between community dynamics and nitrogen dynamics in a tidal freshwater marsh?

The final question is intended to bring all of the learned information from the above questions together to examine how community dynamics and ecosystem functioning in a tidal freshwater marsh may change in the face of future climate change. Chapter X describes a dynamic ecosystem model that was simulated using STELLA software (HPS 1993), and parameterized and calibrated using field data collected from the aforementioned studies. The chapter also describes the climate change scenarios that were developed for the predictive model. A simulation model can be a useful tool to scientists and managers by lending insight into how communities and ecosystems may change in response to disturbances (Odum and Odum 2000). By creating different climate change scenarios, I examined how the disturbance of rising water and increasing temperatures would alter plant community composition, and then how those alterations would change nitrogen dynamics, which would ultimately influence the amount of nutrients that flow downstream into the Chesapeake Bay.

CHAPTER II

SITE DESCRIPTION – DYKE MARSH PRESERVE

Location and Land Use

Dyke Marsh Preserve (DMP) is located approximately one mile south of Alexandria, in Fairfax County, Virginia (Figure 1). The Potomac River borders the marsh to the east and the George Washington Memorial Parkway borders the west. Just to the north of the marsh is the Belle Haven marina and picnic area and to the south is Mount Vernon (Figure 2). DMP is located in the Potomac River watershed, which

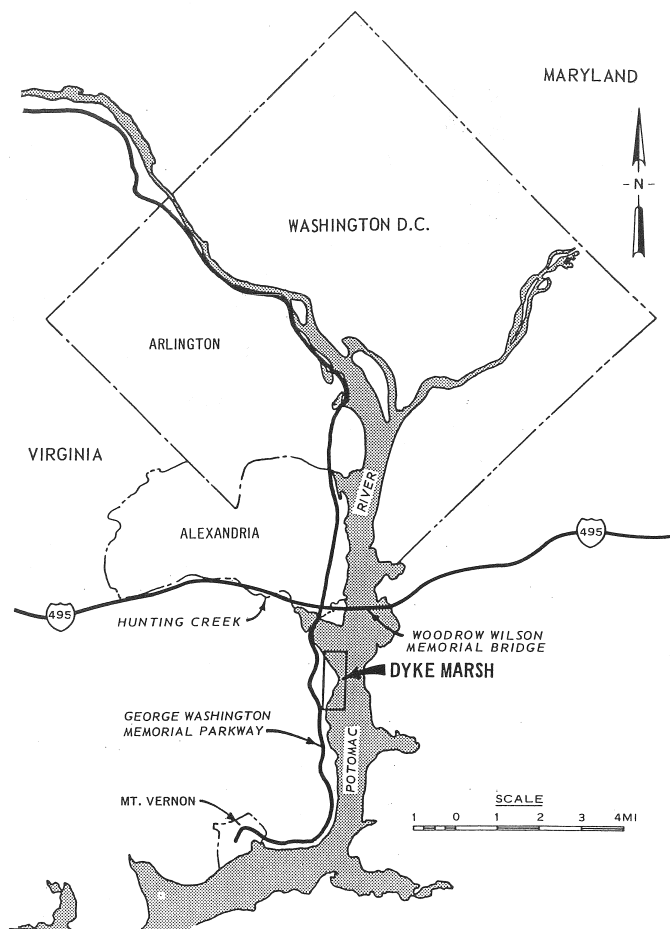


Figure 1. Location of Dyke Marsh Preserve.

encompasses a 14,670 square mile area in 4 different states (Maryland, Pennsylvania, Virginia, and West Virginia) (ICPRB 2004). The Potomac River originates in the mountains of West Virginia and flows 616 km to the Chesapeake Bay. The

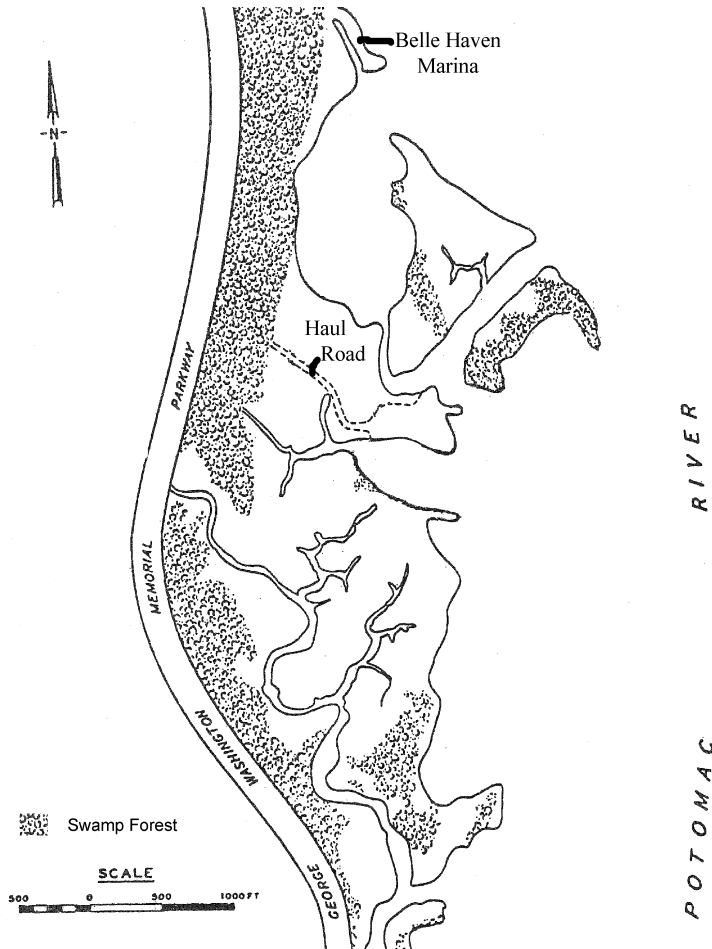


Figure 2. Dyke Marsh Preserve.

watershed is comprised of 14 sub-watersheds, supporting major industries such as agriculture, forestry, fishing, coal mining, chemical production, paper production, and military and government infrastructure (ICPRB 2004). Forests, agriculture, development, and water and wetlands make up the land use of the watershed (Figure 3). The watershed contains 5.35 million people (2000 Census), with 81% in urban areas, 18.6% in rural

areas, and 0.7% on farms. Three-quarters of the watershed's population (3.7 million) live in the Washington D.C. metropolitan area, near Dyke Marsh (ICPRB 2004).

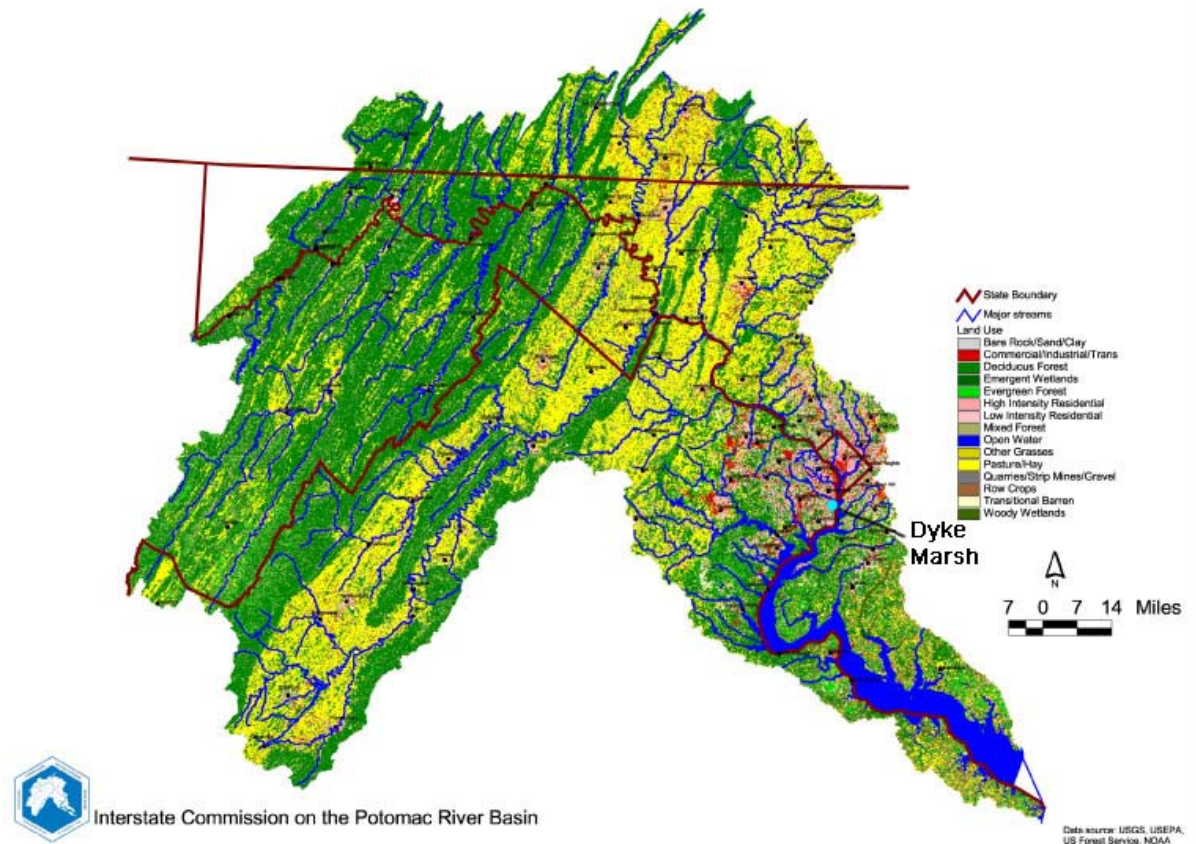


Figure 3. Land use of the Potomac River watershed.

The formation of Dyke Marsh began with Pleistocene deposits 5,000 to 7,000 years ago (NPS 1977). Hunting Creek (Figure 1) enters the Potomac River at Dyke Marsh carrying a large concentration of bedload. The velocity of the stream is reduced as it enters the slower moving Potomac River and deposition occurs. The deposited sediment was composed of fine particles suitable for marsh vegetation (Palermo and Zeigler 1976). In the early 1700s, explorers recorded several Native American villages along the Potomac River (Parsons et al. 1976), whose inhabitants appeared to favor Dyke

Marsh for hunting and fishing (NPS 1977). Hunting Creek (Figure 1) first appeared on a map in 1731 (Parsons et al. 1976). In the early 1800s, one of the first colonial landowners established dikes around emergent marsh habitat to create land for grazing (Palermo and Zeigler 1976, NPS 1977). Shortly after, the area was deemed not suitable for grazing and the area was not maintained. The land was then abandoned, allowing tidal channels to form through breaches in the dikes and an intertidal marsh was reestablished (Palermo and Zeigler 1976, NPS 1977).

Dyke Marsh consisted of 263 ha in the 1930s when Smoot, Sand and Gravel Corporation (SSGC) acquired ownership (Palermo and Zeigler 1976) (Figure 4). By 1940, SSGC began dredging open water areas for sand and gravel found between 16 and 12 m deep (NPS 1977). In the late 1950s, the government and local citizens noticed the ill effects SSGC's activities were having on the environment. In 1959, Public Law 86-41 was enacted stating that the National Park Service (NPS) was to take over ownership of Dyke Marsh, while allowing SSGC to continue to dredge areas of Dyke Marsh. The mandate also stated, "The Secretary shall administer all of the lands described in this bill as...so that fish and wildlife development and their preservation as wetland wildlife habitat shall be paramount...". However, continued dredging and the use of barges and a Haul road (Figure 2) increased environmental degradation of the marsh. Dredging ceased in 1972 when it was realized that no effective management plan for the site existed (NPS 1977). Section 86 of Public Law 93-251 (7 March 1974) was written to empower the Army Corps of Engineers to assist the NPS in planning, designing and implementing the restoration of the historic and ecological values of the marsh. In 1976, the National Park Service took over direct management responsibilities of the remaining 196 ha of



Figure 4. Aerial photographs of Dyke Marsh Preserve and the embayment of Hunting Creek through several decades. On the left is an aerial photo from 1937, the middle is an aerial photo from 1959, and on the right is an orthophoto from 1994.

wetland, of which 200 acres had been dredged (NPS 1977). They began writing an environmental assessment (EA) that was published in 1977. The EA was prepared to assist in the decision-making process concerning appropriate management options for Dyke Marsh (NPS 1977).

Geology

Dyke Marsh is located in the Atlantic Coastal Plain province (NPS 1977, Johnston 2000). The Coastal Plain of Virginia is underlain by stratified deposits of mud, sand, clay and gravel, which lie upon older crystalline rocks (NPS 1977, Johnston 2000). The marsh lies on top of alluvium deposits approximately 15.2 m thick, comprised of sand and gravel with lenticular interlayered units of silt and clay (NPS 1977). The composition of the alluvial deposits reflects the changing conditions of swift moving waters where only heavy materials would fall out, to slack water allowing finer silts and clays to settle (NPS 1977).

Historically, Hunting Creek was a major source of the mineral load to the marsh (NPS 1977). Today, the creek has a reduced impact on Dyke Marsh because its outflow has been severely altered by the George Washington Memorial Parkway, construction of apartments and businesses, and channelization of its course (NPS 1977, Johnston 2000). The increased sediment load was deposited at the creek's confluence with the Potomac, consequently reducing the confluence's size and ability to flood the marsh (NPS 1977, Johnston 2000).

Surface soils of Dyke Marsh are similar to the source materials in the uplands to the west of the marsh, although smaller particle sizes could be derived from materials almost anywhere in the Potomac drainage (NPS 1977). The 1963 Fairfax County Soil

Survey Report suggests that the soils at DMP are Coastal Plain sediments belonging primarily to the Beltsville and Matapeak soil associations (NPS 1977). Tests of the outer dike remnants indicate that they contain no rock internally, or other material foreign to the marsh (NPS 1977). Additionally, cobblestones on the surface of one dike are typical of the nearby Potomac basin (NPS 1977).

Topography

Dyke Marsh is part of the shallow littoral freshwater marsh complex of the Potomac estuary (NPS 1977). The marsh is situated between small hills to the west, and the Potomac estuary (NPS 1977). Most of the emergent marsh lies on a plateau, 1.2 m above mean low tide (MLT), and therefore is not permanently inundated by the area's 1 m tidal range (NPS 1977). The current topographical relief is provided by tidal action carving guts into the marsh plateau. A gradual increase in gradient occurs as one moves west across the marsh into upland areas.

Shoreline sloughing and erosion have become a priority concern of Dyke Marsh. Accelerated shoreline erosion results from the high-energy situation caused by different heights between the marsh edge and the dredged areas immediately offshore (NPS 1977). Maps from the 1800s show spot depth measurements of less than -1.2 m MLT in the Potomac River along DMP (Dick Hammerschlag, personal communication, USGS, September 2004). Because of dredging, the bottom now varies to a maximum of -9.14 m MLT (NPS 1977). Although the deep areas (holes) may be gradually filling by sediment deposition, the natural re-establishment of bottom contours to pre-dredging elevations is estimated to take hundreds of years (NPS 1977). Dredging activity also resulted in the

creation of two islands from the intact marsh, by initiating a direct connection of two major tidal channels (NPS 1977).

Hydrology

Dyke Marsh is situated 17.7 river km downstream from the head of the tidewaters on the Potomac River (Myrick and Leopold 1963). The average annual flow of the tidal Potomac River is $323 \text{ m}^3 \text{ s}^{-1}$, with a mean tidal range of 0.5-0.9 m and a normal 0.91 m flux (Carter et al. 1994). Flow rates upstream on the Potomac average a volume of $312 \text{ m}^3 \text{ s}^{-1}$ and can range from $3.5 \text{ m}^3 \text{ s}^{-1}$ to $14,000 \text{ m}^3 \text{ s}^{-1}$ (NPS 1977). The highest flows occur in March and April after significant upstream snowmelt. The flow effect of the Potomac River on the marsh is usually minimal due to the long distance from the main channel of the river to the marsh, although the entire marsh is within the flood plain of the Potomac (NPS 1977). A hydrologic simulation model designed to enhance ecosystem monitoring and provide information for future restoration projects at Dyke Marsh found that the overall flushing rate per tidal cycle for the main marsh, based on values of mean low and high tide volume was $0.92 \text{ m}^3 \text{ s}^{-1}$ (Harper and Heliotis 1992). The highest velocity was found along Hog Island Gut in the mid-channel ($21\text{-}35 \text{ cm s}^{-1}$), although tidal velocity was not observed to be disruptive to inter-tidal vegetation. Dye tests confirmed high flushing rate per tidal cycle in the marsh. The main marsh is primarily watered from the south by Hog Island Gut, and secondarily from the north by an inlet south of Haul Road. The narrow beach around the northeast corner of the main marsh, at an elevation of 0.85 m, blocked Potomac River waters except when tides exceeded mean highs (Harper and Heliotis 1992).

The remaining remnant dikes, along with two islands, protect the main marsh from downriver flows, although the combined effects of southerly to easterly winds and incoming tides can cause temporary complete inundation of the marsh (NPS 1977). Wind and boat-created waves, as well as scour from major flood events, result in significant water action along the shorelines that erode along steep banks and impacts marsh vegetation (NPS 1977). Large and infrequent storms out of the northeast are hypothesized to control much of the winter dynamics in the marsh. After the Northeastern storms, boats from the marina have been found washed up in the marsh on the north side of the Haul Road (personal communication, Dan Sealy NPS 2004).

Drainage

In DMP, Dyke Marsh Creek and Hog Island Gut drain most of the high lands west of the marsh (Carter et al. 1994), and remnants of Wrecked Recorder Creek drain most of the northern sector of the marsh (NPS 1977). The drainage within Dyke Marsh is controlled by the overall influence of the Potomac River and tidal flows. Minor drainages flow away from the outer edges, through the emergent marsh, and towards the two major tidal creeks (NPS 1977). Tidal channels have different discharge cycles than terrestrial channels, because tidal channels change more rapidly in width and less rapidly in depth than terrestrial channels (Myrick and Leopold 1963). The tidal channels in Dyke Marsh display zero discharge and high discharge twice in every tidal cycle (Myrick and Leopold 1963). In Dyke Marsh, channel discharge varies depending on how flow has shaped the length of channel in question (Myrick and Leopold 1963).

Water Quality

The water quality of Dyke Marsh is dominated by anthropogenic effluent from upstream, which includes high turbidity, excessive nutrients, some heavy metals and toxic chemicals (NPS 1977, Johnston 2000). Turbidity has been critical in the loss of submersed aquatic vegetation, therefore resulting in the sequential loss of dependent species such as diving ducks and fish (NPS 1977, Johnston 2000). Nutrient loads in the marsh have become extreme at times, resulting in exploding surficial blue green algae populations (NPS 1977). Declining algal populations cause bacteria populations to increase; this ultimately results in the loss of fish and other organisms affected by dissolved oxygen deprivation (NPS 1977, Johnston 2000). Data collected from 1962-1971 near the Blue Plains Sewage Treatment Plant (4.0 km upstream), in 1979 from the Potomac River near Dyke Marsh, and in 1985 from the Hunting Creek embayment show a trend of water quality improvement (Johnston 2000). The water quality of the Potomac River near DMP since 1985 is shown in Figure 5.

Climate

The temperate climate of Dyke Marsh is typical of Washington, DC with strong seasonal patterns (NPS 1977). Average annual precipitation is 101.6 cm, of which up to 30.4 cm may be snowfall (Johnston 2000). Summers are warm and humid with a July mean daily maximum of 30°C, and winters are considered mild with a January mean daily minimum of -2°C (Johnston 2000). Wind is an important factor to the marsh. Easterly to southerly winds create surface waves, which break on the marsh's exposed shores. Less frequently, major coastal systems create stronger wave action (NPS 1977) (e.g. Hurricane Isabel in 2003). The northwesterly winds of winter do not threaten the

marsh due to protection by the wooded islands at the north end (NPS 1977). The climatic conditions described above allow for a relatively long growing season of approximately 208 days (Johnston 2000).

Air quality of Dyke Marsh is similar to that along the Potomac River from Washington, DC southward (Wester and Sullivan 1970). The primary pollutant is ozone (Johnston 2000). There is no information relating air pollution episodes to vegetation stress at Dyke Marsh (Johnston 2000).

Vegetation

DMP is composed of three major vegetation communities, the tidal freshwater marsh, the floodplain forest and the swamp forest. The forests vary in height and have better drained zones than the marsh (NPS 1977). For the most part, the floodplain forest has remained a relatively stable community through the marsh's history (Kelso et al. 1993). The emergent marsh community is very diverse compared to other types of coastal marshes. According to Myrick and Leopold (1963), the dominant vegetation of the marsh appeared to be *Typha latifolia*. In the spring of 1992, seven dominant herbaceous species were found: *Peltandra virginica*, *Typha latifolia*, *Impatiens capensis*, *Nuphar lutea*, *Acorus calamus*, *Leersia oryzoides*, and *Scirpus fluviatilis* (Lindholm 1992) (Figure 8). Few trees have been observed in higher areas of the marsh. Scattered individuals of *Fraxinus pennsylvanica* and *Salix nigra* are present (Myrick and Leopold 1963).

Few rare plant species have been found in the emergent marsh. A Natural Heritage Inventory from June 1991 identified *Geum laciniatum*, *Sida hermaphrodita*, and *Carex decomposita* as rare species found in Dyke Marsh (Johnston 2000). *Geum laciniatum* and *S. hermaphrodita* are currently listed as extremely rare, with five or

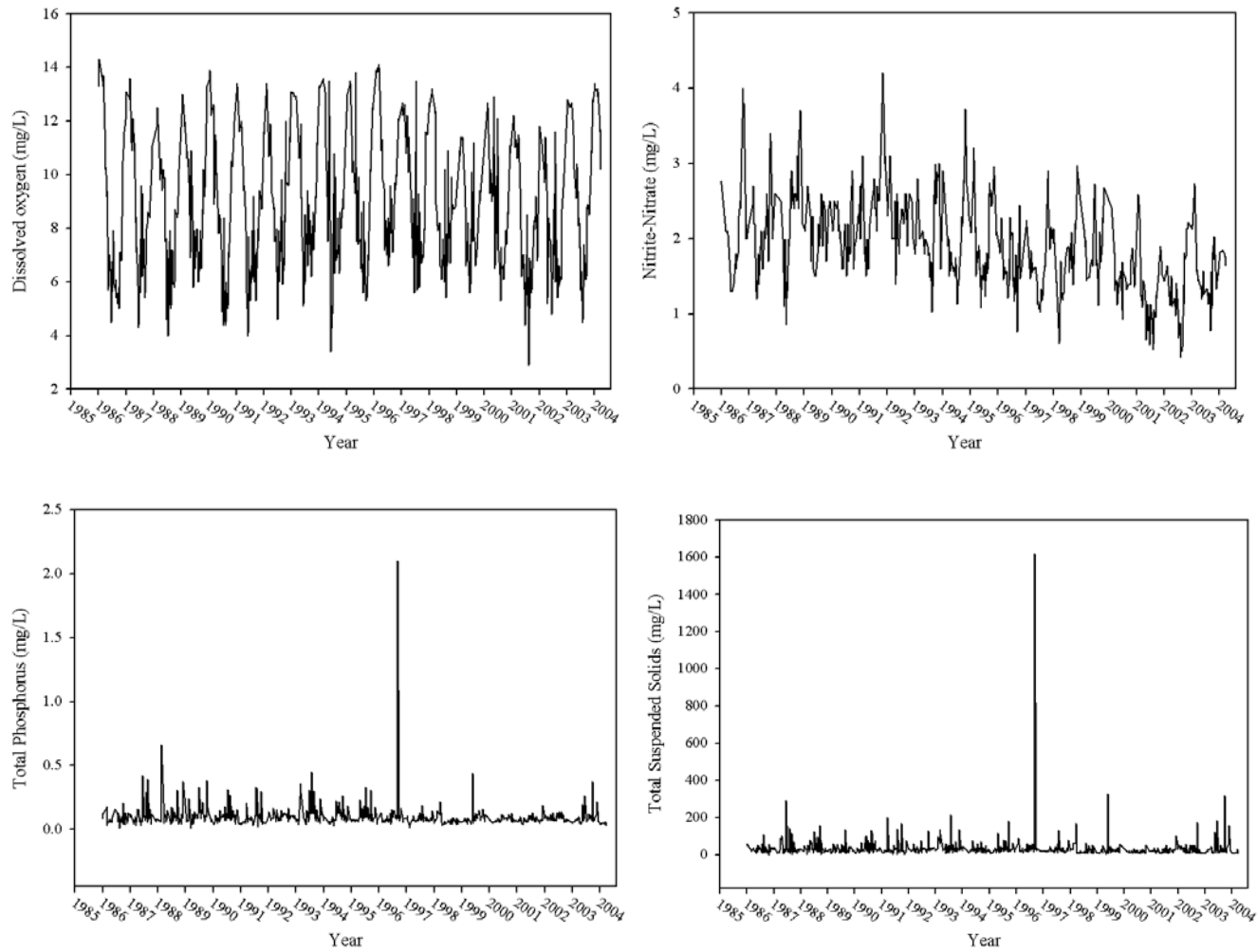


Figure 5. Water quality data sampled on the Potomac River near Dyke Marsh Preserve from 1985 to July 2004 (Chesapeake Bay Program Water Quality Data, <http://www.chesapeakebay.net/data/>, accessed September 2004).

fewer occurrences in Virginia, and *C. decomposita* is listed as very rare with 6-20 occurrences in Virginia (Townsend 2004). Various changes in the marsh vegetation have been observed throughout the years. Most notably, *Plantago cordata* has become extinct in Dyke Marsh. This species is on the Federally Endangered Species List and was historically very common in this area. No records of this species have been found in the marsh since 1918 (Kelso et al. 1993).

Vegetation patterns have also changed in Dyke Marsh. *Nuphar lutea* did not appear in aerial photos from the 1970s. In the 1990s numerous clumps of *N. lutea* were observed in the waterways (Kelso et al. 1993). The increase in *N. lutea* could indicate an increase in sediment deposits in the marsh over the last two decades (Kelso et al. 1993). Exotic and invasive species continue to exist in Dyke Marsh. Two small patches of *Phragmites australis* exist in the marsh. One of the patches has been chemically controlled by the NPS and appears to have decreased in size. Very small amounts of *Lythrum salicaria* have been observed on the edges of the islands and the marsh, and none in the interior of the emergent marsh.

Prior to the 1930s, SAV had a major presence in the marsh and surrounding waters (Carter et al. 1994). Submerged vegetation began to decline in the late 1930s and was not recorded as present in the 1977 Environmental Assessment of Dyke Marsh. SAV began to reappear in the early 1980s and by 1986 the cover of SAV in continuously inundated portions of the marsh was 70-100 percent (Carter et al. 1994). Various reports from before 1996 concluded that SAV is reestablishing in the Potomac River, including Dyke Marsh (Johnston 2000). The dominant species is *Hydrilla verticillata*. Other

species that are present include *Vallisneria americana*, *Najas* spp., and *Ceratophyllum demersum*.

Invertebrates

The exact composition of the benthic community in Dyke Marsh is not known, but reports show the presence of a variety of Annelida, Mollusca, Arthropoda and Hexapoda (Parsons et al. 1976, U.S. Army Corps of Engineers 1988). Species characteristic of polluted waters, such as tubifex worms, leeches and chironomid flies were found in bottom samples from the marsh (U.S. Army Corps of Engineers 1988). A variety of native snails and clams are also common in the marsh. In 1984, the endangered *Lasmigona subviridis* (green floater) and the threatened *Elimia virginica* (Piedmont elimia) were found along the Potomac River near the marsh (Gerberich 1984). The marsh has a healthy population of crayfish, rare amphipods were collected nearby (Uhler 1963). A minimum of 6,000 hexapod species is suggested to exist in DMP (Barrows and Kjar 2003).

Fish

Observations and literature suggest an occurrence of 60 fish species in and/or around Dyke Marsh, including anadromous, catadromous, rare or extirpated, and permanent residents, with the majority of them being predators (Parsons et al. 1976; Jenkins and Burkhead 1994). Several anadromous species use the Potomac River and therefore potentially the Dyke Marsh area. These species include *Alosa pseudoharengus* (alewife), *A. aestivalis* (blueback herring), *A. sapidissima* (American shad), *Morone americana* (white perch), *M. saxatilis* (striped bass), and possibly *Acipenser oxyrinchus* (Atlantic sturgeon) (Jenkins and Burkhead 1994). Dyke Marsh and its surrounding areas

have always been a favored place for fishing. As water quality improves and SAV reappears, fishing for species such as *Micropterus salmoides* (largemouth bass), *Morone saxatilis* (striped bass), *Perca flavescens* (yellow perch) and catfish continues (U.S. Army Corps of Engineers 1988).

Amphibians and Reptiles

A study conducted around Mount Vernon (just south of Dyke Marsh) in 1902 included several herpetological species that have not been found in recent years. Then, species included the marbled salamander, scaly salamander, slimy salamander, newt, swamp tree frog, brown-back lizard, ground snake, ring-necked snake, red-bellied snake and DeKay's snake (Hay 1902).

In 1977 the most common amphibians and reptiles in the emergent marsh were the bullfrog, leopard frog, common snapping turtle, painted turtle and several species of water snakes (NPS 1977). Observations by Walter Bulmer and his students in the emergent marsh of DMP between 1996 and 1999 included 7 species of amphibians, 7 species of turtles, and 7 species of snakes (personal communication, Walter Bulmer, 2004).

Birds

Dyke Marsh is important to many bird species, resident and migratory. Currently, 95 species of birds are associated with the marsh preserve, of which 46 are confirmed breeding species (Cartwright 2004). Additionally, there have been over two hundred species of birds that have been sighted occasionally in the marsh (Gaskill 2000).

Dyke Marsh supports the only known nesting population of *Cistothorus palustris* (marsh wrens) in the upper Potomac tidal zone (Spencer 2000), although there are others nearby on the Anacostia River. *Cistothorus palustris* used to be found all along the marshes of the Potomac, but swiftly disappeared with their habitat. In 1950, 87 singing males were counted in the marsh (Davis 1950), but by 1998 only 31 territories were found (Spencer 2000).

Mammals

Few mammal studies have been conducted in Dyke Marsh. Through those studies, 34 species of mammals, with the majority being insectivores, have been observed (Abott 1976, Parsons et al. 1977, pers. comm., W. Bulmer, 2004). One species that has been severely affected by human activity is the *Ondatra zibethicus* (muskrat). This species historically had large stable populations and now the population has disappeared or is diminishing (Kelso et al 1993). It is thought that the decline of this species is from dredging activities. Dredging dramatically changed the macro-environment and size of the marsh. Environmental changes along with human presence could cause the species to leave or decline (Kelso et al. 1993).

Threatened and Endangered Species

After a thorough investigation of federally listed status of all species found in Dyke Marsh, only three threatened or endangered species were found. The plant species *Plantago cordata*, now extinct in Dyke Marsh, is listed as a candidate species on the federal threatened and endangered species list. Short-nose sturgeon (*Acipenser brevirostrum*), though not sampled at DMP, is listed as endangered on the federal list, which means it is threatened with extinction throughout all or a significant portion of its

range. The final listed species is the bald eagle (*Haliaeetus leucocephalus*). The bald eagle is federally listed as, “threatened, but proposed for delisting”. From communication with the NPS and Friends of Dyke Marsh, other species of concern in DMP include marsh wren (*Cistothorus palustris*), least bittern (*Ixobrychus exilis*), and rails (*Rallus elegans*, *Rallus limicola*, and *Porzana carolina*).

CHAPTER III

SEDIMENT LEVEL CHANGE AT DYKE MARSH

The movement of sediments in tidal marshes is well documented, but linking the movement of sediments to changes in vegetation composition has not been well studied. Sedimentation can be a function of vegetation structure, distance to tidal inlet, distance to tidal streams, animal activity, and elevation (Pasternack et al. 2000). A feedback exists between elevation and sedimentation; while sedimentation is a function of elevation, elevation is a variable that changes through time as a function of sedimentation (Pasternack and Brush 2001). Several studies have found sedimentation rates to decrease with increasing elevation and distance from channels (Letzsch and Frey 1980, Stoddart et al. 1989, Leonard 1997, Pasternack and Brush 1998). Furthermore, Pasternack and Brush (2001) studied tidal freshwater wetlands along Otter Point Creek, MD and found that plant associations (community types) significantly influenced sedimentation. Sedimentation rates varied spatially and temporally within and among habitats before the growing season. However, once vegetation became established, sedimentation decreased predictably across vegetation zones from floating leaf to levee/shrub marsh communities (Pasternack and Brush 2001).

To understand more about how sediment accretion and depletion may affect species dominance patterns, I hypothesized that sediments may be shifting in relation to their proximity to tidal channels, and that this may alter plot community types (annual, perennial, and mixed) by changing local elevation and subsequent water inundation. Because annual species readily colonize new areas through seeds, I predicted that annual species would respond faster than perennial species to changes in sediments. Thus,

shifting sediments should be correlated with greater shifts in the annual species component of tidal freshwater marshes.

Methods

Ten various sized patches of *Impatiens capensis* Meerb., a common annual in tidal freshwater marshes (Simpson *et al.* 1985) and the dominant annual species at Dyke Marsh, were delineated using a Trimble GeoExplorer II unit. Using ArcView, 38, 1-m² plots were blindly placed inside (n=18), outside (n=10), or on the edge (n=10) of the *I. capensis* patches in the summer of 2004 to ensure the study included plots that were initially dominated by annuals, perennials, and a mixture of both annual and perennial species (Figure 6). More plots were placed inside the patches because we were focusing on annual species dynamics and placing them within the context of the whole marsh. Initial elevations were recorded at the center of each plot in July 2004 with a Topcon Precision GPS HiPer Lite Pro (± 2 cm elevation accuracy). PVC poles were placed in the center of each plot and measured from the pole-top to the sediment surface. The poles were used to aid in navigation to each plot, and for measuring sediment level changes. Pole height was measured using a standard tape measure in July 2004, April 2005, July 2005, March 2006, and October 2006. Measuring the height of PVC poles pushed into the marsh may not be the most ideal technique to better understand sediment accretion and depletion. Because the poles were not anchored into the sediment, the annual freezing and thawing of the sediment may shift the pole up, down, or from side to side.

I determined plot distance to nearest tidal channel to explore whether sediments may be shifting in relation to their proximity to tidal channels. Distances from plots to

nearest tidal channel were determined using a digitized channel map and the measure tool in ArcView. A channel map for Dyke Marsh was digitized by referencing a September 2005 QuickBird image and a May 2004 MrSID image (unpublished data, Annette Elmore). To assess the community type of each plot at the beginning and end of the study, I recorded percent cover (Braun-Blanquet 1964) of all species for every plot during peak biomass in August 2004 and 2006.

Analysis of covariance (ANCOVA) along with a Tukey comparison test were performed to test whether the change in sediment level from July 2004 to October 2006 was correlated with community type and plot distance to nearest seed source. Distance was the continuous independent variable, community type (annual, perennial, and mixed) was the categorical independent variable, and change in sediment level was the response variable. To determine if plot community types changed, the community type of each plot in July 2004 when the study began was compared to the community type of the plot in October 2006 when the study ended. If the community type was the same, the plot was labeled “N” and if the community type changed, the plot was labeled “Y”. A one-way ANOVA was then performed to test whether a change in plot community type from 2004 to 2006 was correlated with a change in sediment level. Linear regression was used to determine if a relationship existed between sediment level change and elevation. Distance from plot to nearest tidal channel was square root transformed to conform to normality assumptions. The change in sediment level data was normally distributed and therefore not transformed. Statistical analyses were performed in SAS system version 8.01 for Windows (SAS Institute, Cary, North Carolina, USA). Significance was determined at $\alpha=0.05$.



Figure 6. *Impatiens capensis* patches (hashed) and permanent plots (black dots) studied at Dyke Marsh.

Results

Sediment level change from July 2004 to October 2006 ranged from -7.92 cm to +2.65 cm with a mean of -2.29 cm. Five of the 38 plots increased in sediment level and 33 plots decreased in sediment level from 2004 to 2006. Distance from plot to nearest tidal channel ranged from 0-45.6 m with a mean distance of 13.2 m. All but three of the 38 plots occurred less than 25 m from the nearest tidal channel. Sediment level change was not significant with distance from plot to nearest tidal channel (Figure 7). No relationship existed between sediment level change and community type ($F=1.13$, $p=0.37$). When examining if plots that changed vegetation community from 2004 to 2006 were correlated with a change in sediment level, no relationship was found ($F=0.27$, $p=0.60$). Furthermore, no relationship existed between sediment level change and elevation ($R^2=0.07$, $p=0.12$).

Discussion

Sediment accretes in some areas and erodes in others at Dyke Marsh. The majority of the plots in Dyke Marsh (87%) are losing sediment, while only 13% accreted sediment during the three-year study. Much of the literature discusses how marshes accrete soil and some studies have even explored the sediment movement of tidal freshwater marshes through time (Pasternack and Brush 1998, Orson et al. 1990). While I did not consider possible mechanisms for the accretion or erosion of sediments at Dyke Marsh, I can offer suggestions from past literature of what those mechanisms may be. The majority of the marsh may have lost sediment due to erosion of the marsh system from boater and high wind waves and ice scouring. Furthermore, the absence of large storm events at Dyke Marsh during the three-year study period may explain the lack of

sediment accretion. Many others have found large storm events to substantially contribute to the deposition of sediment in tidal marshes (Harrison and Bloom 1977, Rejmanek et al. 1988, Brush 1989). On the other hand, five of the plots at Dyke Marsh did gain sediment.

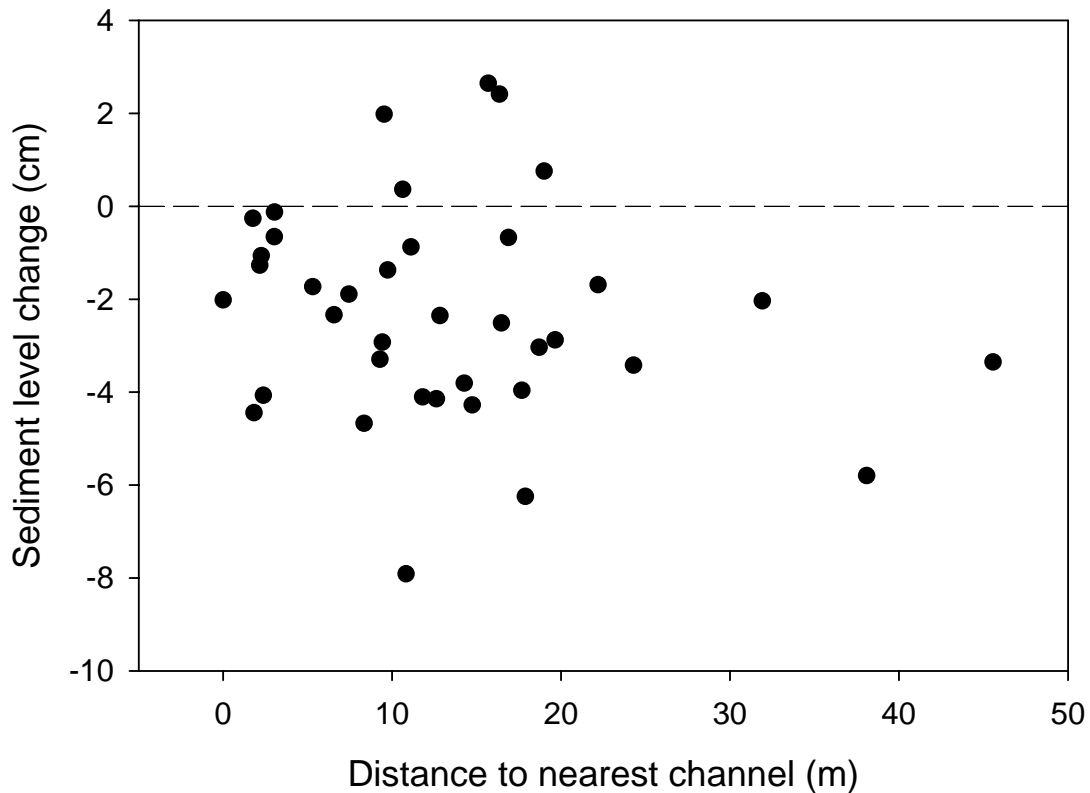


Figure 7. Sediment level change between 2004 and 2006 was not correlated with distance to nearest tidal channel in Dyke Marsh.

The two plots with the greatest sediment accretion were located next to each other near the intersection of a smaller channel into the large channel that flows through Dyke Marsh. The increase in sediment level may have also been from excess sediments entering the small channel from the George Washington Memorial Parkway overpass immediately upstream from these plots. While I am not aware of any studies directly examining the relationship between roads and sedimentation in wetlands, some studies

have discovered that land use change may influence sedimentation in tidal freshwater marshes (Orson et al. 1992, Orson 1996, Hayward et al. 2004, Church et al. 2006).

While sediment level change was not significant with distance to tidal channel, some plots with greater sediment level change were at farther distances from tidal channels. In addition, there was no relationship between elevation and sediment level change. A new and popular method for precisely measuring sediment dynamics in wetlands is the use of SETs or sedimentation-erosion tables (Boumans and Day 1993, Cahoon et al. 1995). I think sediment dynamics in relation to elevation and distance to tidal channel could be studied indepth with these more rigorous techniques (SETs) and more sampling points. Furthermore, the majority of Dyke Marsh suffered a decrease in sediment level. Orson et al. (1990) found rates of sediment accumulation greatest near the tidal channels and lowest accretion rates farthest from tidal channels in an upper Delaware River estuary tidal freshwater marsh. Interestingly, three of the five plots that gained sediment at Dyke Marsh were found near tidal channels.

No relationships were discovered between sediment level change and community type, specifically shifts in the annual species component, or changing plant communities from 2004-2006. The length of the study period was most likely not long enough to capture the influence that sediment level could have on plant communities. However, I still believe that long-term sediment dynamics can change elevations throughout tidal freshwater marshes and subsequently control the amount of water that inundates a given area, thereby influencing the plant species that are able to germinate and grow to maturity.

CHAPTER IV

ANNUAL SPECIES GERMINATION & SURVIVAL ACROSS AN ELEVATIONAL GRADIENT

(At the time of dissertation submission, this chapter is in review for publication with the journal *Wetlands*, titled “Annual species abundance in a tidal freshwater marsh: germination and survival across an elevational gradient” by K.N. Hopfensperger and K.A.M. Engelhardt.)

Tidal freshwater marshes are typically high in species richness and productivity compared to other tidal marshes owing to low salinity stress but high diurnal tidal fluctuations that deliver nutrients. Annual species are an important component of the diversity of these tidal freshwater marshes. Numerous studies have found annual species to dominate the seed bank (Parker and Leck 1985, Leck and Simpson 1995, Leck 1996, 2003) and to dominate mature vegetation cover in tidal freshwater marshes (Whigham and Simpson 1978, Simpson et al. 1983, Odum et al. 1984, Leck and Simpson 1995). Here, we examine germination and seedling survivorship of annual species across an elevational gradient to better understand if elevation limits annual species abundance and species richness at different life history stages. This information has important implications for marsh restoration that targets the development of a mixed annual and perennial marsh.

Wetland plant communities are often distributed in distinct zones that are driven by various abiotic and biotic factors. For example, water inundation (Seabloom et al. 1998, Casanova and Brock 2000, Seabloom and van der Valk 2003, Brose and Tielbörger 2005) and soil moisture (Noe and Zedler 2001) can limit species assemblages to those species that can tolerate the constant or periodic

anaerobic conditions typical of wetland environments. Likewise, salinity determines species distributions across salt, brackish, and freshwater marshes (Baldwin et al. 1996, Baldwin and Mendelssohn 1998, Noe and Zedler 2000). Anaerobic soils and high salinity are both stressful environmental conditions to which wetland species are specifically adapted. For example, perennial species of freshwater marshes, such as *Typha latifolia* L., produce extensive aerenchymous tissue to transport air to the roots (Crawford 1993, Callaway and King 1996). These adaptations are not as highly developed in many annual species, suggesting that annual species should decrease in abundance with greater water inundation. Furthermore, Menge and Sutherland (1976) proposed that biotic factors gain importance as the impact of flooding decreases with elevation. Indeed, previous studies have found an increase in annual species germination with increasing elevation in prairie pothole wetlands (Seabloom et al. 1998), ephemeral agricultural pools (Brose and Tielbörger 2005), salt marshes (Noe and Zedler 2001), and tidal freshwater marshes (Baldwin et al. 1996, Baldwin et al. 2001, Leck, 2003). In a New Jersey tidal freshwater marsh, Leck (1996) found germination success of several common annual species to decrease with increasing water inundation. Several studies have also found mature annual species abundance to increase with elevation in prairie pothole wetlands (Seabloom and van der Valk 2003), riverine wetlands (Hudon 2004), brackish marshes (Baldwin and Mendelssohn 1998), and tidal freshwater marshes (Leck 2003).

While many of the previously mentioned studies examined annual species germination and/or mature vegetation patterns along elevation gradients, the relationship between elevation and the survival of annual species from germination to

maturity has not been investigated. We know that annual species abundance in tidal freshwater marshes tends to increase at higher surface elevations, but this pattern may occur for several reasons, 1) germination of annual species is higher at higher elevations, 2) survival from seedling to adult is higher at higher elevations, 3) fecundity is higher at higher elevations, or 4) dispersal is greater into higher elevations. In this study, we focused on the first two explanations by comparing abundances of annual species seeds, seedlings, and mature vegetation along an elevation gradient in a tidal freshwater marsh near Alexandria, Virginia, to examine the relative roles of germination and survivorship on species abundance patterns of annual species. Elevation and water inundation are tightly linked in this system where inundation at higher elevations is shallower, shorter in duration, and sometimes less frequent. We specifically tested whether changes in marsh elevation is associated with changes in abundance of annual species in the seed bank, abundance of annual species seedlings, or abundance of mature annual species. We then tested whether germination (seed to seedling transition) and survivorship (seedling to mature plant transition) is influenced by elevation. Understanding the influence of elevation on life history stages and transitions can have significant management implications by highlighting specific species and elevations that need to be restored to produce a desired diversity of annual and perennial species.

Methods

Study site

Dyke Marsh Preserve (DMP) is a tidal freshwater marsh on the Potomac River south of Alexandria, Virginia (38°46' N, 77°03' W) and lies on top of alluvium

deposits approximately 15.2 m thick, comprised of sand and gravel with lenticular interlayered units of silt and clay underlain by older crystalline rocks (NPS, 1977). The climate of the region is temperate with July mean daily maximum temperature of 31°C and January mean minimum temperature of -2°C (Johnston 2000). Average annual precipitation is 101.6 cm, of which up to 30.4 cm may be snowfall (Johnston 2000). The average annual flow of the tidal Potomac River is 323 m³s⁻¹, with a mean tidal range of 0.5–0.9 m (Carter et al. 1994).

The vegetation of DMP, including forested wetland and emergent marsh, is characterized by high biodiversity with over 373 species from 93 different families of plants (Xu 1991). The emergent marsh consists primarily of vegetation typical of tidal freshwater marshes along the Atlantic Coast (Simpson et al. 1983, Odum et al. 1984, Leck and Simpson 1995). Vegetation patterns in the marsh can be described as a blanket of perennial species interspersed with various sized patches of dominant annual species.

Data collection

Ten various sized patches of *Impatiens capensis* Meerb., a common annual in tidal freshwater marshes (Simpson *et al.* 1985) and the dominant annual species at Dyke Marsh, were delineated using a Trimble GeoExplorer II unit. Using ArcView, 38, 1-m² plots were blindly placed inside (n=18), outside (n=10), or on the edge (n=10) of the *I. capensis* patches in the summer of 2004 to ensure the study included plots that were initially dominated by annuals, perennials, and a mixture of both annual and perennial species (Figure 6). More plots were placed inside the patches because we were focusing on annual species dynamics and placing them within the

context of the whole marsh. We recorded elevations at the center of each plot in July 2004 with a Topcon Precision GPS HiPer Lite Pro (± 2 cm elevation accuracy). The elevation data were tied to a local benchmark (NAD83 VA North) to georeference plot locations and elevations.

We sampled the seed bank of each plot by taking three soil cores, 10 cm length by 3.81 cm diameter, per plot in March 2006 before germination commenced in the spring. The soil cores were then homogenized and germinated in the greenhouse at two water depths (flooded and saturated) to increase chances of germination for species adapted to different water depths. The seedling emergence technique was used to determine density and species composition of the seed bank samples (Poiani and Johnson 1988, Gross 1990, Baldwin et al. 2001). Samples were spread over vermiculite in black plastic bedding trays (27x53x5 cm) and placed in a greenhouse misting room for germination. Seedlings emerging from each sample were identified as young as possible, and removed from the tray when identified. Seedlings of unknown species were transplanted and allowed to mature for identification.

We counted the number of seedlings for each annual species per plot in April 2006 during peak field seedling density (Parker and Leck 1985, Hopfensperger, pers. obs.). Seedlings in the field were identified through comparisons to known seedlings that were grown in the greenhouse. Number of seedlings per 1-m² plot was estimated using four square, 0.0225 m² subplots per plot. We then counted the number of stems for each annual species in the same subplots during peak standing biomass in late June 2006.

Statistical analyses

Linear regressions tested whether abundance of annual species that germinated in the greenhouse from soil cores, number of seedlings in the field, and abundance of mature stems were correlated with plot elevation. Likewise, a one-way ANOVA tested whether elevation differed among plots dominated by annuals, perennials, or mixed species. A one-way ANOVA was also used to determine if a difference existed between the numbers of annual seeds that germinated in the low versus highly saturated treatments in the greenhouse. Initial number of seedlings in plots can mask a relationship between elevation and mature stems. Thus, analysis of covariance (ANCOVA) tested whether mature stem density was correlated with elevation even when seedling density was accounted for, using elevation as the continuous independent variable, life history (seedling or mature) as the categorical independent variable and density of seedlings or mature stems as the response variable. Pearson correlations tested for relationships among number of seeds germinated in the greenhouse, seedling abundance, and mature stem abundance for all species collectively and individually to determine if constraints exist with life stage transitions. Abundance of annual seedlings and abundance of *I. capensis* seeds and seedlings were square root transformed to conform to normality assumptions. Statistical analyses were performed in SAS system version 8.01 for Windows (SAS Institute, Cary, North Carolina, USA). Significance was determined at $\alpha=0.05$.

Results

Elevations of the plots ranged from 0.17-0.64 m and were significantly higher at plots dominated by mature annual species (0.45 ± 0.02 m) than at plots dominated

by perennial species (0.35 ± 0.03 m) (ANOVA; $F=4.67$, $df=37$, $p=0.016$). Elevation of mixed dominant species plots did not differ from annual or perennial species dominated plots (0.41 ± 0.03 m).

Annual species were found in the seed bank of all 38 plots throughout the marsh. The only annual species found in the seed bank and as seedlings were *Amaranthus cannabinus* (L.), *I. capensis*, and *Bidens laevis* (L.) B.S.P; therefore, this study focuses on these three annual species only. The only other annual species found in the plots as mature plants were *Polygonum* spp., and the only other annual species observed in the marsh (though not in any plots) was *Zizania aquatica* L. *Amaranthus cannabinus* and *I. capensis* germinated from soil cores of over half of the plots (Table 1). *Bidens laevis* was less common in the seed bank (Table 1). More annual species germinated in greenhouse containers with low water inundation (4.50 ± 0.54) versus the highly saturated containers (1.66 ± 0.26) (ANOVA; $F=22.86$, $df=1,74$, $p<0.001$). However, abundance of all annual species germinating collectively from the soil cores was not correlated with plot elevation ($R^2=0.129$, $p=0.976$, $n=38$). Interestingly though, abundance of each individual annual species germinating from the seed bank increased with elevation; *A. cannabinus* ($R^2=0.129$, $p=0.027$, $n=38$) and *I. capensis* ($R^2=0.172$, $p=0.011$, $n=38$). *Bidens laevis* was too rare in the seed bank of the plots to show a relationship with elevation.

Similar to seed bank results, annual species were present as seedlings in all 38 plots, but species identity and abundance differed. *Impatiens capensis* was found in almost all of the plots, *B. laevis* in over half of the plots, and *A. cannabinus* in less than a quarter of the plots (Table 1). Collectively, the abundance of all annual species

seedlings increased with elevation ($R^2=0.385$, $p<0.001$, $n=38$). Species-specific analysis showed that abundance of *I. capensis* ($R^2=0.474$, $p<0.001$, $n=38$) and *B. laevis* ($R^2=0.155$, $p=0.015$, $n=38$) seedlings increased with elevation (Figure 8). *Amaranthus cannabinus* seedlings were too rare to show a relationship between abundance of seedlings and elevation.

Table 1. Annual species counted as germinated seeds in the March seed bank, seedlings in April, and as mature stems in June 2006 in 38 plots at Dyke Marsh Preserve, Virginia, USA.

Species	Mean (# / m ²)	Standard Error	Maximum (# / m ²)	Number of plots found in (out of a possible 38)
MARCH – seed bank				
<i>Amaranthus cannabinus</i>	791	156	3504	26
<i>Bidens laevis</i>	77	28	584	7
<i>Impatiens capensis</i>	868	201	4672	23
APRIL – seedlings				
<i>Amaranthus cannabinus</i>	41	27	1022	8
<i>Bidens laevis</i>	204	53	1555	21
<i>Impatiens capensis</i>	699	91	2244	37
JUNE – mature stems				
<i>Amaranthus cannabinus</i>	4	1	5	2
<i>Bidens laevis</i>	30	10	256	13
<i>Impatiens capensis</i>	281	28	644	36

Impatiens capensis and *B. laevis* were the only two dominant species counted as mature stems, because *A. cannabinus* was found in only two plots (Table 1).

Abundance of mature annual stems increased with elevation ($R^2=0.432$, $p<0.001$, $n=38$) (Figure 9); *I. capensis* stems increased with elevation ($R^2=0.386$, $p<0.001$, $n=38$), whereas *B. laevis* showed no relationship with elevation. Density of seedlings and mature stems were correlated with elevation ($p<0.001$) and with life history ($p<0.001$) (ANCOVA; $F=42.09$, $df=75$, $p<0.001$, $n=38$). No interactions were found between the independent variables.

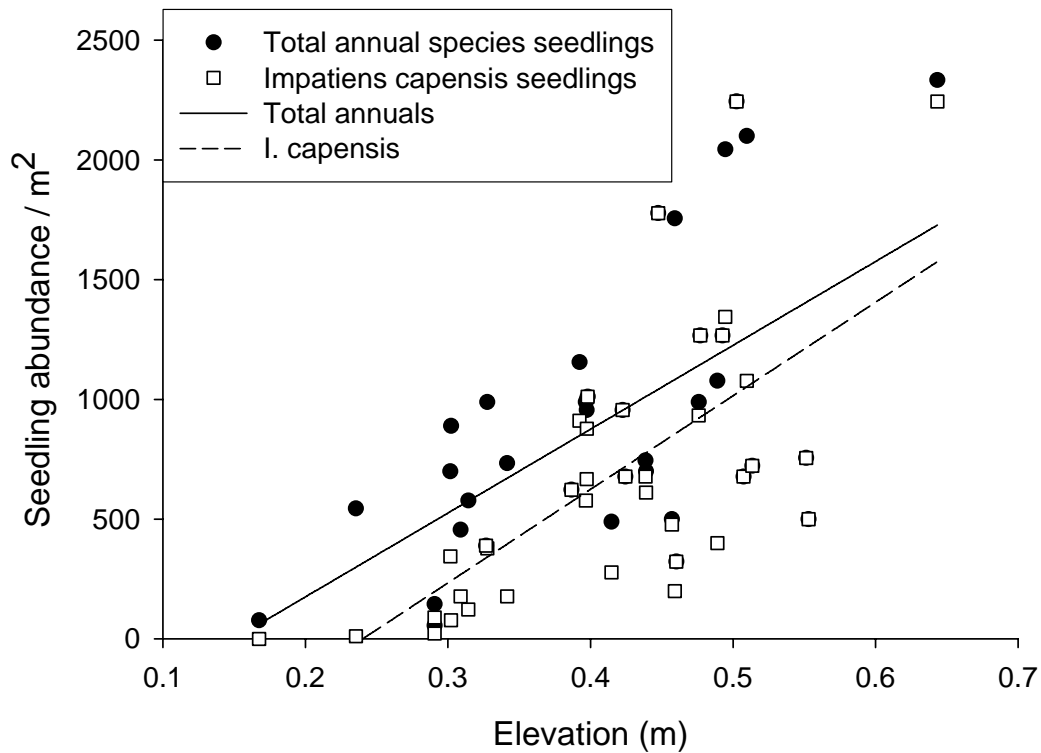


Figure 8. Relationships between seedling abundance of all annual species and *Impatiens capensis* seedling abundance with elevation. $n=38$.

We found several significant correlations between life history stages (transitions) of annual species. When examining annual species collectively, no correlation was found from seed to seedling, but survivorship, the transition from seedling to maturity, produced a strong correlation ($r=0.734$, $p<0.001$). *Impatiens capensis* produced a similar pattern in that the transition from seed to seedling ($r=0.418$, $p=0.010$) was weaker than the transition from seedling to mature stem ($r=0.793$, $p<0.001$). *Bidens laevis* was rare in the seed bank, however the transition from seedling to maturity correlation in the field was strong ($r=0.651$, $p<0.001$).

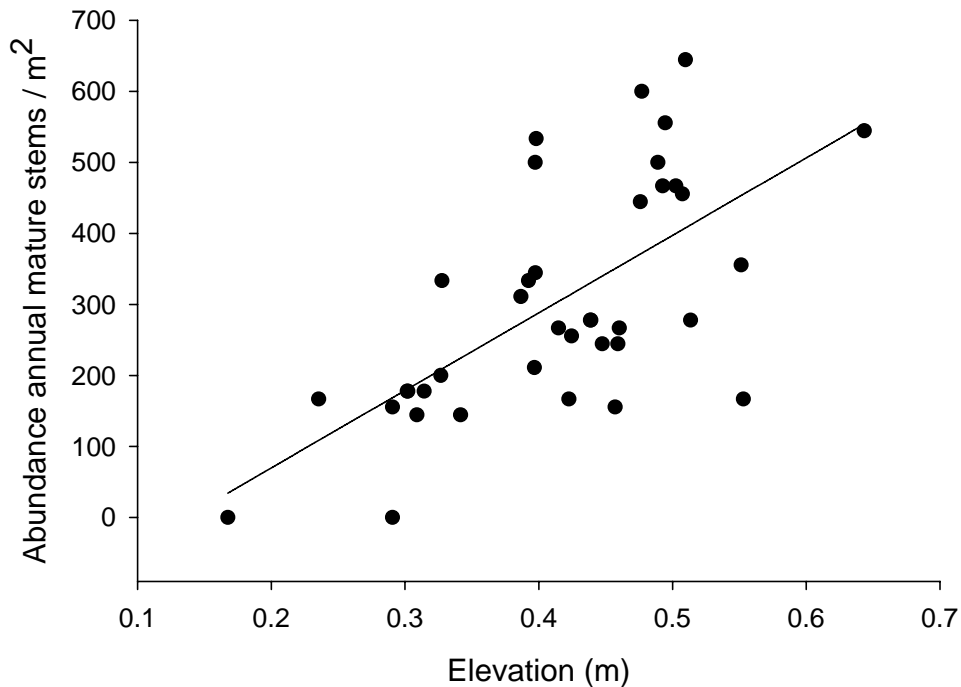


Figure 9. The relationship between mature stem density of all annual species and elevation. $n=38$.

Discussion

The purpose of our study was to identify the importance of marsh surface elevation on three life history stages of annual species, seeds, seedlings, and mature stems, and their life history transitions, germination and survivorship, to identify potential constraints on the abundance and distribution of annual species in a marsh. Seedling and mature stem densities of all annual species collectively increased with elevation, but seed bank density was not correlated with elevation. That elevation was higher inside patches dominated by annuals than outside of the patches solidifies the positive relationship between annual species and elevation. These results concur with other studies that report relationships between wetland surface elevation and seedling density (Bertness and Ellison 1987, Leck 1996, Abernethy and Willby 1999, and

Coops et al. 1999) and mature stem density (Simpson et al. 1983, Baldwin et al. 2001, Cornu and Sadro 2002, Baldwin and Pendleton 2003).

Wetland surface elevation and water inundation may be an important factor in the germination and establishment of annual wetland species because more oxygen is available for seeds to germinate when wetland soils are not constantly saturated (Leck 1996). For example, Leck et al. (1994) found in a greenhouse study that *B. laevis* seeds failed to germinate in hypoxic conditions. Our observation that more annual seeds germinated in the less saturated greenhouse containers supports Leck's findings. Annual species seeds are found in the seed banks of all elevations in Dyke Marsh, but individually, the species' seeds occupy different elevation ranges. *Amaranthus cannabinus* seeds were found in highest densities at mid elevations and were infrequently found at low and high elevations, while *I. capensis* and *B. laevis* seeds were found more commonly at the higher marsh elevations. This may explain why we did not find a relationship between seed density of all species combined and field elevation whereas seed density of individual species and elevation were positively related.

Annual species seedlings increased in abundance in the field with elevation. Given that annual species seeds germinated more readily in lower moisture conditions in greenhouse containers may explain why we found *B. laevis* seedling densities to increase with elevation. Likewise and perhaps for the same reason, the dominant annual of the marsh, *I. capensis*, increased in seed, seedling, and mature stem abundance with elevation; however, elevation was most strongly correlated with *I. capensis* seedling density. In a field experiment, Baldwin et al. (2001) found the

abundance of mature annual species to decrease by more than an order of magnitude with increasing water inundation. As water inundates substrate, oxygen is lost through a series of reduction-oxidation reactions. Therefore, the longer water floods the substrate, the chance of anoxic conditions developing increases, which in turn leaves no oxygen for plant roots to use for respiration.

The abundance and distribution of annual species is ultimately limited by the transition between the seed to the seedling stage (Baldwin et al. 1996, Baldwin et al. 2001, Leck 2003) and the seedling stage to the mature stage. Life history transitions did not limit *I. capensis* presence at Dyke Marsh given that correlations between seed and seedling and between seedling and maturity were strong. Therefore, another factor other than life history transitions may be driving *I. capensis* distribution. Elevation was most strongly related to seedling density. We therefore hypothesize that water inundation during early summer, when *I. capensis* germinating and striving to gain access to the plant canopy, limits *I. capensis* abundance and distribution in Dyke Marsh. The importance of *I. capensis* existing in the local seed bank and germinating is not trivial; however, we think the annual environmental fluctuations that occur during germination and the seedling life stage determine whether or not the species dominates at maturity.

Germination appears to limit *B. laevis* and *A. cannabinus* distribution patterns. *Bidens laevis* was not found in the seed bank of many plots, and seed and seedling abundances were not correlated. We therefore suggest that distribution of *B. laevis* was limited by its abundance in the seed bank and germination rather than its life history transition from seed to seedling. Our data demonstrate that mature *A.*

cannabinus are successful at contributing their seeds to the seed bank, yet germination success seems to be severely limiting its distribution. The positive relationship between *A. cannabinus* seed bank density and elevation may be a simple function of more seeds falling near parent plants that are already present at higher abundances at the higher elevations. In a prairie pothole wetland system, Seabloom et al. (1998) explain a correlation between regeneration and adult niches as a positive feedback loop owing to species germinating at highest rates in the same areas where they are most common as adults. Thus, a strong relationship between number of annual mature stems and germinated seedlings (Figure 10) may be attributed to this “seed shadow” near the parent plant.

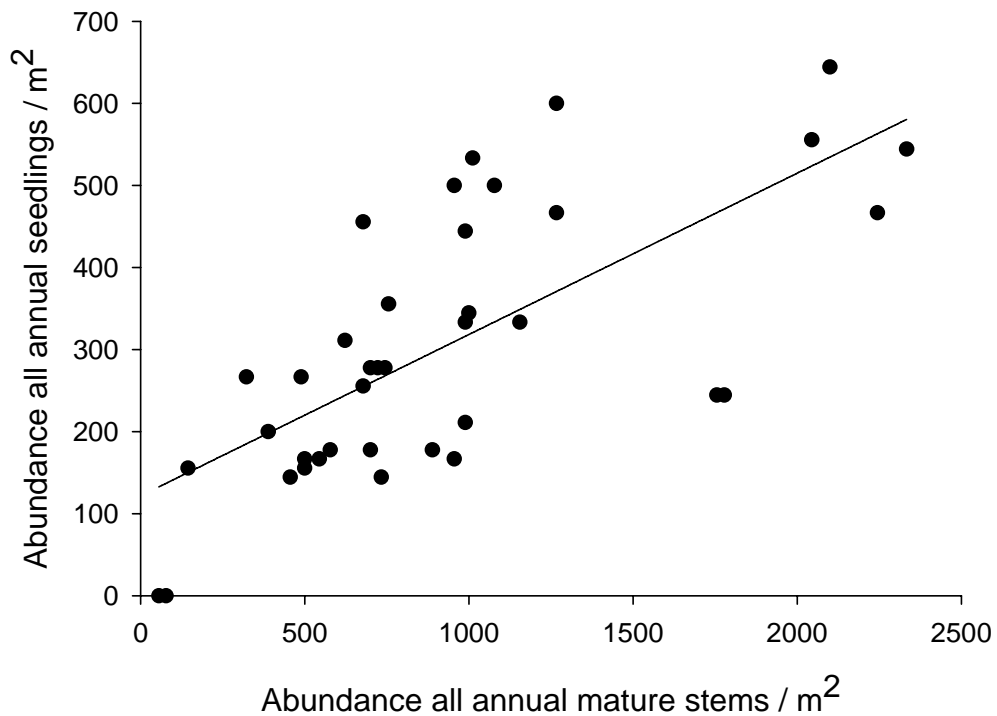


Figure 10. The relationship between seedling abundance and mature stem abundance for all annual species per m². $n=38$.

We do not believe other possible explanations for increased annual species abundance with elevation, including greater fecundity and greater dispersal into higher elevations hold true for tidal freshwater marshes. While we could not find any studies on fecundity of annual species in tidal marshes, Lenssen and de Kroon (2005) found that in stressful environments (i.e. high water inundation) the weaker competitor, *Rumex palustris*, produced more seeds. Producing more seeds at lower elevations may be useful, because regular tidal disturbance at the lower elevations provides for greater opportunity for seed recruitment (Van der Sman et al. 1993; Davis et al. 2000). In addition, Van Zandt et al. (2003) found *Iris hexagona*, a perennial salt marsh species, to increase seed production with the increased stress of salinity. These studies would lead one to predict an increase in annual species at lower elevations owing to greater fecundity; however annual species tend to be more abundant at higher elevations. Thus, fecundity probably does not drive annual species distribution in a tidal freshwater marsh. Greater dispersal of annual species into areas of higher elevation in a tidal freshwater marsh is also not a probable explanation for why more annuals are found at higher elevations. Others have documented finding the greatest number of species nearest to stream channels (i.e. lower elevations) (Leck and Graveline 1979, Leck and Simpson 1993) possibly because water regularly flows over the marsh surface in these areas and seeds from the regional pool may settle out. Furthermore, many seeds of annual marsh species are dispersed via hydrochory (water ways) versus wind or other means (Bakker et al. 1985, Huiskes et al. 1995, Middleton 1995). Therefore, these studies would predict more annual species at lower

elevations, so we do not consider greater dispersal at higher elevations to be a valid explanation for an increase in annuals at higher elevations.

Overall we conclude that germination and survival from seedling to mature plants are both important to annual species distribution in tidal freshwater marshes, but that the importance of either process differs among species. Understanding relationships among species, plant life forms, and environmental gradients is necessary for restorationists to reach their goals. Managers already take elevation gradients into consideration when designing tidal restorations, and knowing relationships between specific plant life forms and physical features may help to ensure a restored system that functions properly with a diverse biotic component. Furthermore, the relationship between annual species distribution and elevation is crucial for managers to understand when faced with rising sea level. Sea level rise will increase the water inundation in tidal freshwater marshes, and therefore decrease the amount of suitable habitat for annual species. Areas of higher elevation will need to be created to ensure continuation of the important annual component of diverse tidal freshwater marshes.

CHAPTER V

FACILITATION DRIVEN ANNUAL SPECIES DOMINANCE

(At the time of dissertation submission, this chapter has been accepted for publication in the journal *Wetlands*, titled “Coexistence of *Typha angustifolia* and *Impatiens capensis* in a tidal freshwater marsh” by K.N. Hopfensperger and K.A.M. Engelhardt.)

Freshwater tidal wetlands are often dominated by perennial species such as *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha* sp. However, some marshes remain diverse and support a mixture of annual, perennial, monocot, and dicot species. Such diversity raises the question, “What are the mechanisms that allow certain species to locally co-occur in tidal freshwater marshes?” One mechanism may be the amelioration of the wetland environment by aerenchymous species that allows other species to survive in an otherwise hostile environment.

Species like *Impatiens capensis* Meerb., may be sensitive to elevation changes (Cornu and Sadro 2002) and subsequently water inundation (Baldwin et al. 2001) because they typically do not produce aerenchyma, the porous tissue that assists in gas transport in plants and is commonly formed in flood-tolerant species.

Aerenchyma allows oxygen and other gases to reach buried portions of a plant, and allows the escape of carbon dioxide and ethylene into the atmosphere (Cronk and Fennessy 2001). Other species, such as *Typha latifolia* L., typically have greater porosity and storage capacity for oxygen than *I. capensis* (Crawford 1993). Strand (2002) found *T. angustifolia* L. to have a high oxygen shoot flow rate compared to 31 other macrophyte species, resulting in leakage of oxygen from roots to the substrate through pressurized ventilation. Furthermore, Matsui and Tsuchiya (2006) discovered

T. angustifolia to increase its root porosity, root mass ratio, and root aerobic respiration capacity in hypoxic conditions. Therefore, it is possible that *T. angustifolia*, found in many tidal freshwater marshes, while aerating its roots and rhizomes, may dispose excess oxygen into the soil for available respiratory uptake by nearby annuals that do not have as much, if any, aerenchymous tissue.

Only a few studies on the positive interactions of plant species in wetlands through rhizosphere oxygenation exist in the literature (Schat and Van Beckhoven 1991, Bertness and Hacker 1994, Castellanos et al. 1994, Hacker and Bertness 1995, Callaway and King 1996). For example, in a salt marsh on the coast of Holland, Schat and Van Beckhoven (1991) found *Plantago coronopus* L. and *Samolus valerandi* L. clumped around the highly aerenchymous *Juncus maritimus* Lam., which greatly enhanced soil oxygenation. Similarly, a montane wetland study found *T. latifolia* to significantly affect the survival of *Salix exigua* Nutt. and *Myosotis laxa* Lehm. due to the ability of *T. latifolia* to aerate the soil near the *S. exigua*'s and *M. laxa*'s roots (Callaway and King 1996). Collectively, these studies show that facilitative interactions among species may affect plant distribution patterns and the success of neighboring species. We do not know, however, whether tidal freshwater marsh species exhibit the same type of interaction.

To explore facilitation of vegetative growth through oxygenation of the substrate in tidal freshwater wetlands, we focus on *T. angustifolia* and *I. capensis*, which are two co-occurring dominant species commonly observed in tidal freshwater marshes of the eastern United States. *Typha angustifolia* contains aerenchymous tissue similar to that found in past studies with *T. latifolia* (Callaway and King 1996),

and is thought to oxygenate the substrate in a similar fashion. To test this "facilitation" hypothesis, we compared *I. capensis* growth and reduction-oxidation (redox) potential in greenhouse mesocosms containing *T. angustifolia* to mesocosms without *T. angustifolia*. Alternatively, we tested whether co-occurrence of the two species is driven predominantly by extrinsic abiotic factors, such as elevation and tidal fluctuations that introduce oxygen to the root zone of *I. capensis*, allowing the species to thrive even in the absence of *T. angustifolia*. We tested the "elevation" hypothesis in the field by measuring marsh surface elevation and determining associations between it and the two species. The complementary "inundation" hypothesis was tested by subjecting replicated greenhouse mesocosms to differing inundation regimes. To rule out competition for sediment pore water nutrients that may mask a facilitative interaction, we monitored pore water nutrients in the greenhouse mesocosms.

Methods

Study Area

Field sampling was conducted in 2004 at Dyke Marsh Preserve (DMP, 38.77° N, 77.05° W), a tidal freshwater marsh on the Potomac River, just south of Alexandria, Virginia. The greenhouse experiment took place in summer 2005 at the University of Maryland Center for Environmental Science, Appalachian Laboratory in Frostburg, Maryland (39.65° N, 78.93° W).

Dyke Marsh Preserve is owned and managed by the National Park Service and is one of the few large tracts of freshwater tidal wetlands remaining on the Potomac River in the Chesapeake Bay Watershed. The Potomac River has an average annual

flow of $323 \text{ m}^3\text{s}^{-1}$ (Carter et al. 1994). Flow rates upstream of the site on the Potomac average a volume of $312 \text{ m}^3\text{s}^{-1}$ and can range from $3.5 \text{ m}^3\text{s}^{-1}$ to $14,000 \text{ m}^3\text{s}^{-1}$ (NPS 1977). The highest flows occur in March and April after significant upstream snowmelt. The flow effect of the Potomac River on the marsh is usually minimal due to the long distance from the main channel of the river to the marsh, although the entire marsh is within the flood plain of the Potomac (NPS 1977). The mixed tidal cycle of the Potomac River at Dyke Marsh during the growing season ranged between 0.6 m below sea level to 0.8 m above sea level in 2004 (Hopfensperger unpublished data). The tide fluctuated on average 0.92 m during a typical day in the growing season.

Dyke Marsh is located in the Coastal Plain of Virginia, which is underlain by stratified deposits of mud, sand, clay and gravel from the ocean, which lie upon older crystalline rocks (NPS 1977, Johnston 2000). The marsh lies on top of alluvium deposits approximately 15-m thick, comprised of sand and gravel with lenticular interlayered units of silt and clay (NPS 1977). Surface soils are hydric, Coastal Plain sediments belonging primarily to the Beltsville and Matapeak soil associations (NPS 1977). June 2006 sediment nitrate-N concentrations from throughout Dyke Marsh ranged from 0-22 mg N/kg, and ammonium-N concentrations ranged from 3-32 mg N/kg. June 2006 overlying water nitrate-N concentrations from throughout Dyke Marsh ranged from 0-0.7 mg N/L, and ammonium-N concentrations ranged from 0.05-0.4 mg N/L (Hopfensperger, unpublished data).

Typha angustifolia and *I. capensis* have been observed growing together year after year throughout Dyke Marsh. Similar patterns are observed in other regional

tidal freshwater marshes (Leck and Simpson 1995). *Impatiens capensis* reproduces through annual seed production. The seeds of *I. capensis* must be cold-stratified before they can germinate. *Impatiens capensis* begins to emerge in late March/ early April in Dyke Marsh. *Typha angustifolia* generally sprouts from belowground vegetative rhizomes in Dyke Marsh, not seed (Hopfensperger, personal observation), and can be found sprouting in late March.

Field Study

We established 9 transects throughout DMP using an orthophoto of the marsh to *a priori* select transect locations that guaranteed the major portions of the marsh and its entire elevation gradient were sampled. Transects were bounded by the Potomac River, a swamp forest, and large tidal channels that could not be traversed on foot. The photo gave us no indication what vegetation should be expected at any given location, ensuring an unbiased sampling. In July 2004, we placed quadrats (1x1m) along the transects at 25 m intervals for a total of 92 samples. We recorded percent cover (Braun-Blanquet 1964) for all species in every quadrat to test whether *T. angustifolia* and *I. capensis* covary in space across the marsh. Marsh elevation was measured in every quadrat using Topcon Precision GPS HiPer Lite Pro with a published accuracy of ± 2 cm (<http://www.topconpositioning.com>) to test for associations between elevation and the two study species. The elevation data was tied to a local benchmark (NAD83 VA North) to georeference plot locations and elevations.

Greenhouse Experiment

In October 2004, we collected mature seeds of *I. capensis* at DMP and stored them in the dark at 4°C. The seeds were planted in March 2005 in the greenhouse and grown to seedling size (15-20 cm) in preparation for the experiment. In March 2005, we filled forty 19-liter (37-cm high by 29-cm diameter), undrained, plastic buckets with a combination of sand, silt, and humus to mimic sediment composition at DMP. Sediment composition of the marsh was previously determined as 77% organic matter and the mineral component was 7% sand, 43% clay, and 50% silt for 15 subsampled 2004 soil cores using soil particle analysis (Gee and Bauder 1986). The mesocosms were saturated with water, spaced evenly and randomly in the greenhouse, and exposed to the same ambient temperature and light. Temperature, monitored 24 hours a day (Micro-Grow Greenhouse Systems, Inc.), ranged between 7 and 31°C during the experiment. We planted half of the mesocosms in May 2005 with mature transplants of *T. angustifolia* (1-1.2 m in height) that were collected from DMP in July 2004 and maintained in the greenhouse over winter. The other half of the mesocosms remained empty as controls. We manipulated water level in half of the planted and half of the control mesocosms by adjusting water level twice daily throughout the entire length of the experiment. Water levels were low (at sediment surface) from 8:00 to 16:00 and high (5-cm above sediment surface) the rest of the time. The other half of the mesocosms were maintained at a constant water depth of 2-cm above sediment surface. We manipulated water level to provide a time each day for roots to undergo oxic conditions at the sediment surface, similar to oxic/anoxic fluctuations in the marsh. The water fluctuations did not simulate the actual tidal

fluctuations at Dyke Marsh, but manipulated the depth of standing water. On average at Dyke Marsh, plots with co-occurring *T. angustifolia* and *I. capensis* are inundated with 5-cm and greater standing water for eight hours per day (Hopfensperger unpublished data). Therefore, we doubled the length of 5-cm inundation time to 16 hours for our experiment to create guaranteed anoxic conditions for redox measurements – an ideal environment for *T. angustifolia* to aerate the rhizosphere. The above treatments were combined in a full-factorial design to result in: (1) *T. angustifolia* with water depth manipulation, (2) *T. angustifolia* without water depth manipulation, (3) no *T. angustifolia* with water depth manipulation, and (4) no *T. angustifolia* without water depth manipulation.

After a 3.5-month establishment and acclimation period, redox readings were taken for 10 consecutive days in June 2005. Soil redox potential, a measure of the oxidation state of the soil environment (Schlesinger 1997), was measured daily between 8:00 and 10:00 in all mesocosms with a redox platinum electrode (Beckman Instruments, USA). Measurements were taken adjacent to the *T. angustifolia* rhizomes at a depth of 2-cm to capture the area of interaction between *T. angustifolia* and *I. capensis* roots. *Impatiens capensis* is shallow-rooted; thus, redox measurements would not have been relevant below 2-cm depth. Redox measurements have been found to be more variable at shallower depths (Yang et al. 2006); however, previous studies of redox measurements at three depths (-5 cm, -1 cm, and +1 cm relative to sediment surface) in a submersed marsh and in mesocosms showed no difference in variability among depths (Engelhardt, unpublished data). Thus, variability of redox

measurements at the shallow sediment depth of our greenhouse experiment was not likely to introduce a Type II error.

Two weeks after the completion of the first phase of the experiment, *I. capensis* seedlings of similar height (20 cm) were added to five of the ten replicates of each of the four treatment combinations. We allowed *I. capensis* plants to establish and acclimate for one month, replaced individuals that died, and then measured redox for 10 days in August 2005. Redox measurements were taken daily as in June 2005. Soil pore water, removed with mini-tension lysimeters (Daiki Corp., Japan) at 2-cm below the soil surface from each replicate on day 6 before water level was drawn down, was analyzed for nitrate-N (automated cadmium reduction method), ammonium-N (phenate method), and orthophosphate (molybdenum blue method) concentrations using flow injection analysis (Lachat QuikChem Automated Flow Injection Analysis System; APHA 1998, USEPA 1999) to test for effects of *T. angustifolia* on nutrients in the experimental units. On day 10, all above- and belowground *I. capensis* was harvested, separated, dried in a 70°C oven until constant weight, and weighed for biomass measurements. The experiment was conducted from March until August when both species emerge and grow in the field. The timeline did not mimic the exact growing season of both species in Dyke Marsh Preserve (*T. angustifolia* = late March-September; *I. capensis* = March-October), but was reasonably close. The length of the experiment was adequate to allow all plants to become established and to grow.

Data Analyses

Pearson's correlations tested for relationships between percent cover of *I. capensis*, *T. angustifolia*, and elevation in the field. Multiple regression tested for a significant association between the two species while accounting for elevation.

A multiple analysis of variance (MANOVA) with least squares means and Tukey comparisons tested whether *T. angustifolia* and/or water depth manipulation (fixed effects) affected *I. capensis* above- and belowground biomass (response variables) in the greenhouse experiment. Similarly, repeated measures multiple analysis of variance tested for treatment effects of *T. angustifolia* and water depth manipulation on redox potential measured repeatedly through time. Fixed effects consisted of species (*I. capensis*, *T. angustifolia*) and water depth manipulation (fluctuating, constant); the random effect was mesocosm; the response variable was redox potential; and the repeated measure was day of the redox readings. Repeated measures analysis of variance also tested for treatment effect of timing (June vs. August) on redox potential to determine if the amount of time *T. angustifolia* was in the mesocosms had an effect. The fixed effect was timing; the random effect was mesocosm; the response variable was redox potential; and the repeated measure was day of redox readings. A 3-way analysis of variance (ANOVA) with least square means and Tukey comparisons were performed to compare redox potential among *I. capensis*, *T. angustifolia*, and water level manipulation treatments. MANOVA was used to test for differences in the concentration of nitrate-N, ammonium-N, and orthophosphate among the species and tide treatments. Least square means with Tukey adjusted post hoc tests were carried out to further clarify differences among

species. Above- and belowground *I. capensis* biomass, nitrate-N, ammonium-N, orthophosphate, and *I. capensis* cover in the field were all log transformed to conform to normality assumptions. Redox potential and *T. angustifolia* cover in the field did not require transformation. Data were analyzed using SAS (SAS Inc. 1985) with significance defined at $\alpha=0.05$.

Results

Elevation of the plots studied in the marsh ranged from 0.17 m to 0.64 m above sea level. When combining elevation and tide level data for each plot, water level fluctuated between 0.64 m of water above the sediment surface for the highest plot and 0.45 m below the sediment surface for the lowest plot. Average *I. capensis* cover was 25-50% and ranged from 0-100%. Average *T. angustifolia* cover was 10-25% and ranged from 0-75%. *Typha angustifolia* and *I. capensis* co-occurred in 57 plots out of 92 plots. *Typha angustifolia* occurred in 72 plots total and in 15 plots without *I. capensis*. *Impatiens capensis* occurred in 63 plots total and in 6 plots without *T. angustifolia*. Cover of *I. capensis* and *T. angustifolia* were positively associated (Figure 11; Pearson correlation; $r=0.393$, $p<0.001$) and cover of *I. capensis* and *T. angustifolia* increased with elevation (Pearson correlation; $r=0.615$ and $r=0.544$ respectively, $p<0.001$ for both species where $N=92$). Multiple regression that tested for an association between *I. capensis* (response variable) and *T. angustifolia* (independent variable) when accounting for elevation (independent variable) was significant ($R^2=0.3693$, $p<0.001$, $N=92$). However, *I. capensis* cover was influenced only by elevation ($p<0.001$), and not by *T. angustifolia* cover ($p=0.4038$).

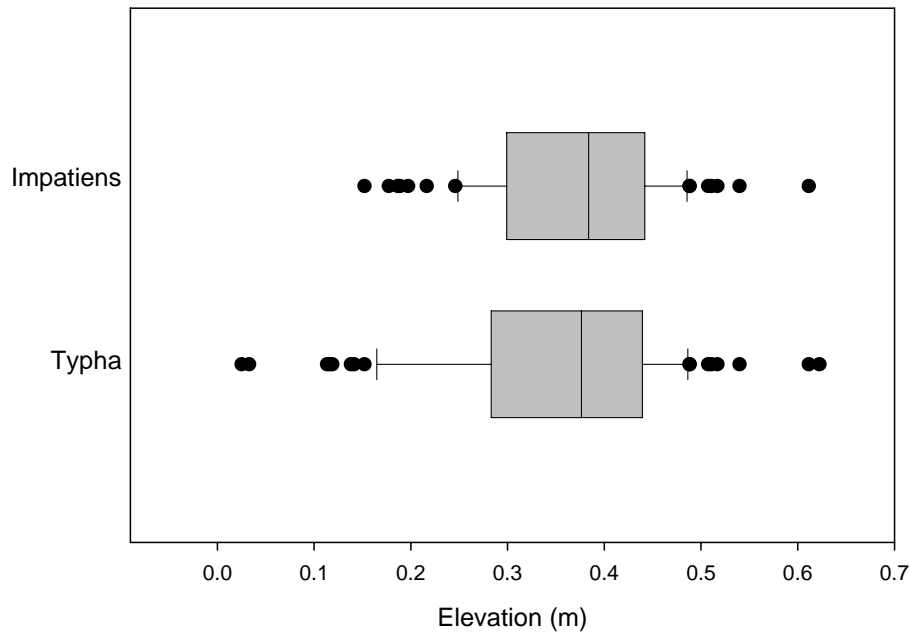


Figure 11. Distribution of *Typha angustifolia* and *Impatiens capensis* along the elevational gradient at Dyke Marsh. The box represents the 25th percentiles around the median line. The whiskers represent the 10th and 90th percentiles, and dots represent the outliers to demonstrate the full elevation range of the species.

Typha angustifolia and water level manipulation did not affect aboveground biomass of *I. capensis* (Table 2; Figure 12) in greenhouse mesocosms. However, belowground biomass of *I. capensis* was significantly lower in the presence of *T. angustifolia* (Table 2) than when *I. capensis* was planted alone (Figure 11). Water fluctuation did not affect belowground biomass of *I. capensis* (Table 2).

Table 2. MANOVA results for treatment effects of *Typha angustifolia* and water level fluctuation on above and belowground *Impatiens capensis* biomass. The level of significance is indicated by * $P < 0.05$.

	Overall Model	<i>T. angustifolia</i>	Water fluctuation
	F _{df,df}	F _{df,df}	F _{df,df}
Aboveground biomass	1.38 _{3,16}	3.67 _{1,16}	0.01 _{1,16}
Belowground biomass	2.87 _{3,16}	5.99 _{1,16} *	1.90 _{1,16}

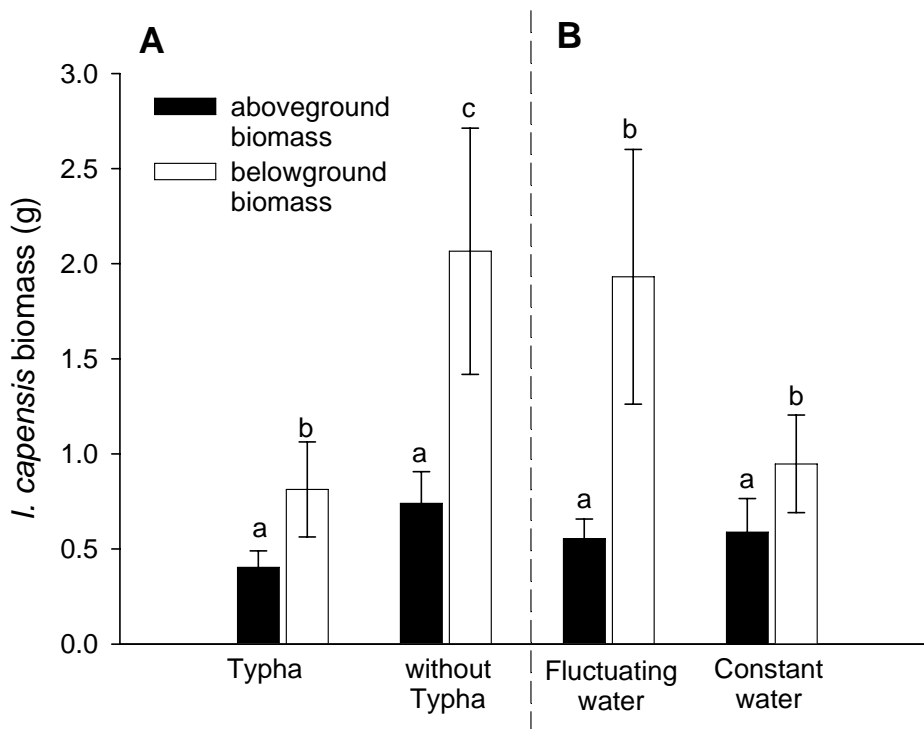


Figure 12. Aboveground and belowground biomass averages of *Impatiens capensis* in treatments A) with and without *Typha angustifolia*, and B) with fluctuating and constant water level. Error bars represent +1 SE. Bars sharing the same letters are not statistically different using Tukey's LSD. Tests were done separately for above- and belowground biomass.

Redox potential averaged across the water level treatment was significantly lower in the presence of *T. angustifolia* in a repeated measures MANOVA (Table 3). The opposite was true for *I. capensis*; redox potentials averaged across the water level treatment were higher in the presence of *I. capensis* (Table 3). Redox potential was higher in mesocosms with water level fluctuation than in the controls with constant water level (Table 3). Furthermore, redox potential was higher in June (mean±SE=119.3±9.3) than in August (mean±SE =75.3±5.5).

Table 3. Repeated measures MANOVA results for treatment effects of *Typha angustifolia*, *Impatiens capensis*, and water level fluctuations on reduction-oxidation potential (redox) in August when both *T. angustifolia* and *I. capensis* were growing in the experimental mesocosms. The controls were absence of *T. angustifolia* or *I. capensis* and constant water level. Redox measurements were repeated once per day between 8:00 and 10:00 for 10 days. The repeated measures effect was not significant. The level of significance of the three independent factors on redox is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Overall Model	Control	Treatment
	F _{df,df}	Mean (± SE)	Mean (± SE)
<i>Typha angustifolia</i> Absence/presence	111.68 _{1,32} ***	145.9 (6.2)	4.5 (5.9)
<i>Impatiens capensis</i> Absence/presence	8.77 _{1,32} **	55.4 (8.1)	95.0 (7.3)
Water level (constant vs. fluctuating)	8.05 _{1,32} **	56.2 (6.2)	94.2 (9.0)

Nitrate levels did not differ among any of the treatments (Table 4). However, lower ammonium and phosphate concentrations were measured in *T. angustifolia* mesocosms than in mesocosms without *T. angustifolia* (Table 5). *Impatiens capensis* and water level fluctuation did not affect nitrate, ammonium, or phosphate concentrations (Table 5). None of the interactions between independent variables were significant.

Table 4. MANOVA results for treatment effects of *Impatiens capensis*, *Typha angustifolia*, and water level fluctuation on soil pore water ammonium-N (NH₄-N), nitrate-N (NO₃-N), and orthophosphate (ortho-P) concentrations. The level of significance is indicated by * $p < 0.05$, *** $p < 0.001$.

	Overall Model	<i>I. capensis</i>	<i>T. angustifolia</i>	Water fluctuation
	F _{df,df}	F _{df,df}	F _{df,df}	F _{df,df}
NH ₄ -N (mg/L)	12.11 _{6,33} ***	2.57 _{1,33}	64.88 _{1,33} ***	1.54 _{1,33}
NO ₃ -N (mg/L)	1.54 _{6,33}	0.93 _{1,33}	3.89 _{1,33}	3.62 _{1,33}
ortho-P (mg/L)	2.62 _{6,33} *	0.09 _{1,33}	13.32 _{1,33} ***	0.56 _{1,33}

Table 5. Mean (± 1 SE) of nitrate-N ($\text{NO}_3\text{-N}$), ammonium-N ($\text{NH}_4\text{-N}$), and orthophosphate (ortho-P) for each *Typha angustifolia* by water level treatment combination. Superscript letters that are the same within a row denote no significant difference between the treatments at $\alpha=0.05$.

	Treatment			
	<i>T. angustifolia</i> w/ water fluctuation	<i>T. angustifolia</i> w/ water constant	no <i>T. angustifolia</i> w/ water fluctuation	no <i>T. angustifolia</i> w/ water constant
$\text{NO}_3\text{-N}$ (mg/L)	0.0001 \pm 0.31 ^a	0.0056 \pm 0.30 ^a	0.0057 \pm 0.26 ^a	0.0256 \pm 0.23 ^a
$\text{NH}_4\text{-N}$ (mg/L)	0.1764 \pm 0.06 ^a	0.4446 \pm 0.05 ^a	3.5531 \pm 0.09 ^b	2.8082 \pm 0.08 ^b
ortho-P (mg/L)	0.0259 \pm 0.01 ^a	0.0211 \pm 0.01 ^a	0.1392 \pm 0.04 ^b	0.1118 \pm 0.03 ^b

Discussion

Community ecologists have long been fascinated by the question of what processes drive species abundance patterns. Such processes include species adaptations to the abiotic environment, species interactions, and stochastic dispersal or disturbance events. Which of these processes dominate community structure varies in space and time, making predictions of which species are likely to persist in a community exceedingly difficult. Tidal freshwater marshes are no exceptions; these marshes are famous for their zonation patterns of species across environmental gradients (Odum et al. 1984, Mitsch and Gosselink 2000, Baldwin et al. 2001) suggesting that adaptations drive their distributions. Within each zone, coexistence may be driven by interspecific interactions, such as facilitation and competition (Bertness and Shumway 1993, Cornu and Sadro 2002). Using complementary field observations and a greenhouse experiment, we tested whether intrinsic biotic interactions or extrinsic abiotic gradients can explain the co-occurrence of *T.*

angustifolia and *I. capensis* in tidal freshwater marsh systems of the eastern United States.

Field observations at Dyke Marsh Preserve showed that an abundance of *I. capensis* and *T. angustifolia* covaried in space at DMP suggesting that *T. angustifolia* could be facilitating the growth of *I. capensis*. However, our greenhouse experiment failed to support the facilitation hypothesis; aboveground biomass of *I. capensis* was not higher in the presence of *T. angustifolia*, and *I. capensis* accumulated substantially less belowground when grown in sympatry with *T. angustifolia* (Figure 13). While we expected *T. angustifolia* to increase the redox potential of sediments, the species actually decreased redox values (Table 3), and this effect became more pronounced during the growing season as plants matured. Redox potential is an indirect measurement of oxygen in the substrate, but several salt marsh studies found it to be a useful and efficient measurement for describing species effects on the ecosystem (Bertness and Hacker 1994, Castellanos et al. 1994, Hacker and Bertness 1995).

At 2-cm rooting depth, which is the relevant depth for studying interactions between *T. angustifolia* and shallow-rooted *I. capensis*, *T. angustifolia* and sediments surrounding the roots were a net oxygen sink rather than a net oxygen source judging from redox values in treatments with plants compared to treatments without plants (Table 3). Thus, *T. angustifolia* was not facilitating the growth of neighboring *I. capensis* through rhizosphere oxygenation at 2-cm rooting depth. Therefore, our results failed to support similar studies done in salt marsh systems. Hacker and Bertness (1995) observed that *Iva frutescens* L. had smaller and thicker leaves with

lower leaf and flower density growing without *Juncus gerardi* Loisel. than growing with it. *Juncus gerardi* was found to maintain high redox potential in the root zone (5-cm depth), allowing *I. frutescens* to experience normal respiration (Hacker and Bertness 1995). Similarly, Castellanos et al. (1994) found *Spartina maritima* (M.A. Curtis) Fern. to facilitate the invasion of *Arthrocnemum perenne* (P. Mill.) Moss by oxygenating the substrate through aerenchymous tissue, thereby increasing *A. perenne* biomass in a salt marsh system. Our results may differ from those mentioned because we focused exclusively on a shallow rooting depth that may not be deep enough for the effects of *T. angustifolia* on redox potentials to be measured. At this shallow depth microbial respiration through decomposition of organic matter may possibly drive redox potentials of the substrate. In a laboratory experiment of estuarine aggregates, Kerner and Edelkraut (1995) found coupling between aerobic and anaerobic processes, where anaerobic net production of DOC significantly enhanced O₂ consumption, which could in turn influence redox potential. Furthermore, Nielsen and Anderson (2003) found the decomposition of mangrove leaves (*Rhizophora apiculata* Blume) to reduce redox potential at the sediment-water interface through increased respiration.

Impatiens capensis belowground biomass decreased in the presence of *T. angustifolia*, and ammonium and phosphate concentrations in sediment pore water were lower in the presence of *T. angustifolia*. These results suggest a competitive relationship between the two species. Results may be interpreted within the context of scale. Our experimental units were small and closed, which allowed *T. angustifolia* to draw down sediment nutrients enough to limit *I. capensis* root growth. Nutrients in

natural systems, on the other hand, are constantly replenished through tidal flushing, and nutrient resources may not be limiting. We did not test for allelopathic extracts, but inhibition of *I. capensis* root growth by *T. angustifolia* through allelopathy may be an alternative mechanism explaining the decrease in *I. capensis* root biomass when grown in sympatry with *T. angustifolia*. Several studies have found the extracts of *Typha* spp. to inhibit the growth of other species (Elakovich and Wooten 1995, Gallardo et al. 1998, Uchida and Tazaki 2005, Leeds et al. 2006). Autotoxicity of *T. latifolia* has been found to suppress seed germination and inhibit seedling growth (McNaughton 1968, Grace 1983, Ervin and Wetzel 2003). Irrespective of the exact mechanism of competition, our data does not lead us to conclude in any way that adult *T. angustifolia* facilitates adult *I. capensis*, which does not rule out the possibility that competition among the two species may mask facilitative interactions, that interactions may be stronger at other life stages, or that *T. angustifolia* facilitates *I. capensis* through other mechanisms besides rhizosphere oxygenation, such as providing firm substrate for *I. capensis* to root on.

Interestingly, water level fluctuations did not affect biomass growth of *I. capensis*, but did increase redox potential. Fluctuating water level may increase redox potential compared to constant water level by introducing more oxygen to the rhizosphere during water level draw downs. Our water manipulations provided oxic conditions at the sediment surface for eight hours per day, which is a substantial amount of time for aeration to occur at the surface, thereby allowing for a change in redox potential and growing conditions compared to treatments with constant standing water. However, *I. capensis* biomass was expected to increase with water

level fluctuations, and this was not observed. Thus, the greenhouse results failed to support the inundation hypothesis; oxygenation of shallow sediments through water level fluctuations does not appear to enhance the growth of *I. capensis* in the absence of *T. angustifolia*.

Typha angustifolia and *I. capensis* showed similar distributions along elevational gradients in the field (Figure 11), and cover of both species increased at higher elevations. Thus, the elevation hypothesis could not be rejected; the positive association between the two species in the field may simply be explained by similar and strong interactions with a dominant environmental gradient. In fact, when accounting for differences in elevation of our study plots, the species-species interaction between *T. angustifolia* and *I. capensis* was reduced. Therefore, elevation, not intrinsic species interactions, may be driving the distribution of *T. angustifolia* and *I. capensis* in DMP. However, elevation is an indirect gradient and may be representative of many different variables such as water inundation or disturbance. Other unmeasured extrinsic factors that may influence the co-occurrence of these two species in a natural system include microtopography (Ervin 2005), sediment trapping (Bruno 2000), and temperature and nutrient variations (Chapin et al. 1979).

The controlled conditions of greenhouse experiments always raises questions about the validity and relevance of results to field conditions. Our study is no exception. For example, the water level treatment in our greenhouse experiment was designed to ensure daily fluctuations in aerobic and anaerobic conditions; however, water level changes in the greenhouse mesocosms (5cm) did not replicate the range in tidal fluctuations observed in the field (0.92 m). Therefore, our result of no change in

I. capensis belowground biomass in response to water level fluctuations may be suspect. However, the greenhouse treatment did show the desired effect of reduced redox potential under flooded conditions. These anaerobic conditions were prolonged as we doubled the amount of time that mesocosms were flooded relative to field plots. Thus, we set the experiment up to find a treatment effect on *I. capensis* growth, yet we did not find one. Another limitation of the greenhouse experiment may be that the duration of the experiment did not mimic the length of the growing season at Dyke Marsh Preserve. Thus, the lack of a treatment effect on *I. capensis* aboveground biomass accumulation may have been the result of a shortened growing season rather than the result of no interactions with *T. angustifolia*. However, we observed significant effects of *T. angustifolia* on belowground *I. capensis* biomass, which may be a more relevant measure of interspecific interactions as *T. angustifolia* decreased sediment nutrients. It is also unlikely that positive or negative interactions between species would need to be endured throughout an entire growing season for interspecific interactions to be observed. Many facilitative and competitive interactions between marsh plants occur during the seedling growth stage (Lenssen et al. 1999, Ervin and Wetzel 2000), such that the effects of these interactions on community structure and biomass accumulation will have run its course once the plants reach maturity.

In conclusion, while the two study species were positively associated in the field and while we had reason to believe that *T. angustifolia* could ameliorate the waterlogged wetland environment through rhizosphere oxygenation, we found no evidence for facilitative interactions. In contrast, we found strong associations with

elevational gradients, suggesting that both species may be equally limited by the saturated soils of tidal freshwater marshes. Numerous tidal freshwater marsh studies have found water level to be the primary driver influencing seed germination and seedling survival (Baldwin et al. 1996, Baldwin et al. 2001, Baldwin and Pendleton 2003), vegetative growth (Baldwin et al. 2001, Cornu and Sadro 2002, Baldwin and Pendleton 2003), and species richness (Baldwin et al. 1996, Brewer et al. 1997, Cornu and Sadro 2002). Furthermore, *I. capensis* may exist in this waterlogged environment without aerenchyma through the production of an adventitious root system at the marsh surface that allows access to air, moisture and nutrients from the water and sediment (Cronk and Fennessy 2001). In fact, burial of these roots under even a thin layer of sediment under saturated conditions appears to decrease chances of survival (Hopfensperger, personal observation). Other physical factors or life history considerations may explain the co-occurrence of these two species in Dyke Marsh Preserve including microtopography or interactions at other life stages of the plants. These interactions need to be considered further to conclusively determine the mechanisms of species interactions between the two dominant wetland species. For now, however, our data leads us to conclude that the physical habitat template of the marsh may be driving the distribution and co-occurrence of the two dominant species more than biotic interactions.

CHAPTER VI

COMPETITION DRIVEN ANNUAL SPECIES DOMINANCE

Competition between annual and perennial species may be one mechanism that explains the distribution and local abundance of annual species in tidal freshwater marshes. Plants in tidal freshwater marshes must compete for light and nutrients (Parker and Leck 1985). Early germinating species, such as the annual species *Impatiens capensis*, may lower the germination rate of species that germinate later by altering the light supply to the soil surface with their large cotyledons. Parker and Leck (1985) examined seed bank compositions in relation to mature vegetation zonation patterns along a stream channel and discovered that the most vigorous seedlings had a competitive advantage over competing species owing to competition for light. Therefore, to fully understand annual species abundance patterns in a tidal freshwater marsh, I hypothesized that species that germinate early in the growing season, such as *I. capensis*, inhibit the success of later germinating species by altering the light supply to the soil surface with their large cotyledons. Therefore, I predicted that the shade from the large cotyledons of early germinating *I. capensis*, the dominant annual species in Dyke Marsh, would prevent later germinating perennials from emerging and/or becoming established.

The stress of water inundation is believed by many to be the main driver in community dynamics of tidal ecosystems (Baldwin et al. 2001, Emery et al. 2001, Huckle et al. 2003, Leck 2003), and when stress is high (e.g. water inundation is high) competition may be diminished (Grime 1977, Tilman 1982, Bertness 1991). In high marsh areas, where stress from water inundation is reduced, resources may interact in

affecting the germination and establishment of perennial seeds and seedlings. Huckle et al. (2003) found when studying salt marsh species that when nutrients were reduced, the species moved away from competition and coexistence occurred. In addition, Emery et al. (2001) found salinity and soil anoxia to drive plant zonation in a salt marsh. Therefore, other factors aside from water inundation (nutrients, salinity, soil oxygen) can also create a stressful environment and influence competition. Because *I. capensis* germinates first, it begins taking up nutrients first and may deplete the nutrient pool available for later germinating species. Specifically, I predicted that *I. capensis* would have a stronger competitive edge in the low nutrient environment, because after taking up nutrients from the initial nutrient pool, there may be little nutrients left available for later germinating species in addition to the shading effects.

Methods

In October 2004, I collected mature seeds of *I. capensis* and *P. virginica* at Dyke Marsh Preserve (see Chapter II for study site description) and stored them in the dark at 4 °C for four months. *Leersia oryzoides*, *T. angustifolia* and *S. fluviatilis* seeds were obtained from Ernst Conservation Seeds, a regional seed supplier. A complete randomized split plot design (Littell et al. 1996) was used to test whether germination and seedling survival of the four perennial species were reduced under the canopy of *I. capensis* seeded at three different densities (Figure 13). Ten replicate whole plots, plastic trays (25 by 52cm by 6cm deep), were set in the greenhouse for each perennial species. Four square (12.7cm wide by 5.7cm deep) plastic containers filled 3.5 cm deep with soil were placed into each whole plot. Miracle Grow© potting soil was

used in five of the whole plot replicates for each perennial species to test for the effects of soil nutrients on germination and establishment of perennial species in the presence and absence of *I. capensis*. Ten perennial seeds were added to all experimental units in May 2005. One experimental unit within each whole plot received ten *I. capensis* seeds (low density) and one received twenty-five *I. capensis* seeds (high density). The other two units within each whole plot stayed *I. capensis* free; however, one of the units was covered in shade cloth to test whether the perennial species was inhibited by light without the added effects of *I. capensis*. The whole plots were spaced evenly and randomly in the greenhouse, and exposed to the same ambient temperature and light. Temperature, monitored 24 hours per day (Micro-Grow Greenhouse Systems, Inc.), ranged between 9 and 35°C during the experiment. Tap water was used for all whole plots in the experiment and depth was monitored and maintained at a constant level daily for all whole plots. Seedlings were counted in July 2005 and the experiment terminated.

Split plot randomized complete block analysis of variance (ANOVA) was performed for each perennial species separately using a 'proc mixed' approach to test for the effects of shading by *I. capensis* on the germination of perennial species. Independent variables included nutrient level, shade, and *I. capensis* density. The dependent variable was the number of perennial seeds that germinated. The ANOVAs were then followed by Least-Squares Means and Tukey tests. The number of germinated *L. oryzoides* seeds was square-root transformed to conform to normality assumptions. Statistical analyses were performed in SAS (version 8.01, SAS Institute, Cary, NC, USA). Significance was determined at $\alpha=0.05$.

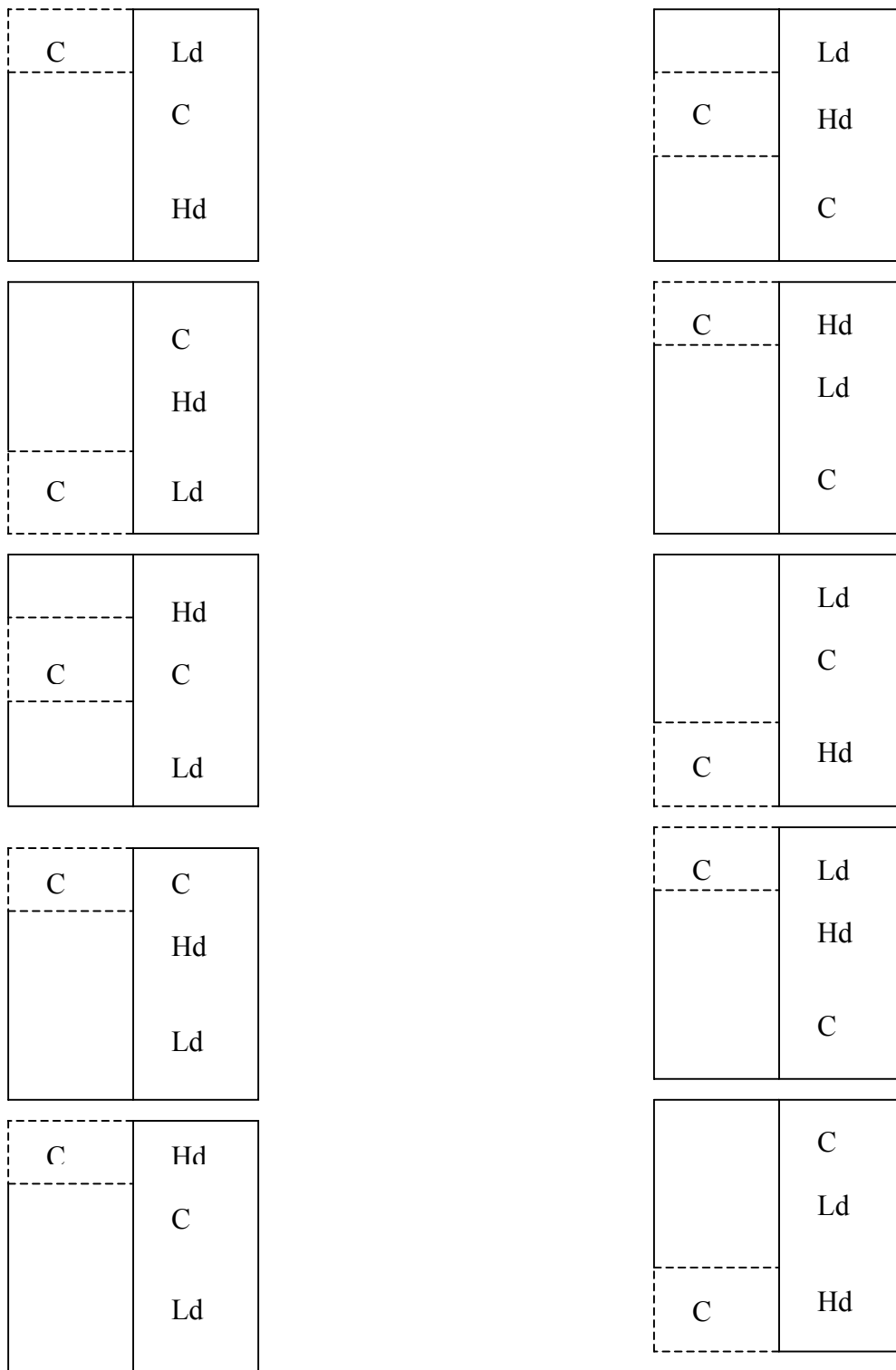


Figure 13. Diagram of experimental set up. Control (C) = 0 *I. capensis* seeds, low density (Ld) = 10 *I. capensis* seeds, and high density (Hd) = 25 *I. capensis* seeds. The dashed lines represent the shaded control. One column of whole plots contained experimental units with high nutrient soil and the other column had soil without added fertilizer. Each of these treatments was replicated for *T. angustifolia*, *L. oryzoides*, *P. virginica*, and *S. fluviatilis*.

Results

The mean number of seeds that germinated among the four perennial species varied greatly (Table 6). Only one *S. fluviatilis* seed germinated in the entire experiment, therefore statistics were not carried out for *S. fluviatilis*. Furthermore, *P. virginica* germinated successfully in all containers; therefore germination was not significantly influenced by *I. capensis* density, shade cloth, or nutrient level.

Table 6. Minimum, maximum, and mean number with 1 standard error of all seeds that germinated in all treatment containers for each perennial species. *Schoenoplectus fluviatilis* is excluded because only one seed germinated.

	Minimum	Maximum	Mean	Standard error
<i>Peltandra virginica</i>	6	10	8.7	0.20
<i>Typha angustifolia</i>	0	10	3.8	0.56
<i>Leersia oryzoides</i>	0	10	2.9	0.44

Typha angustifolia seeds germinated more readily in containers without any *I. capensis* regardless of nutrient levels ($F=3.86$, $p=0.03$; Figure 14). Shade cloth did not influence *T. angustifolia* germination. *Impatiens capensis* density did not influence *L. oryzoides* germination. However, more *L. oryzoides* germinated in high nutrient containers compared to low nutrient containers ($F=14.12$, $p=0.001$; Figure 15). A significant interaction was detected between nutrient level and the shade cloth treatment for *L. oryzoides*. More *L. oryzoides* seeds germinated in high nutrient treatments with or without shade cloth than in low nutrient treatments (differences of least square means; $t=3.83$, $p=0.001$), but within the high nutrient treatment, more *L. oryzoides* seeds germinated with the shade cloth than without (differences of least square means; $t=-2.78$, $p=0.001$).

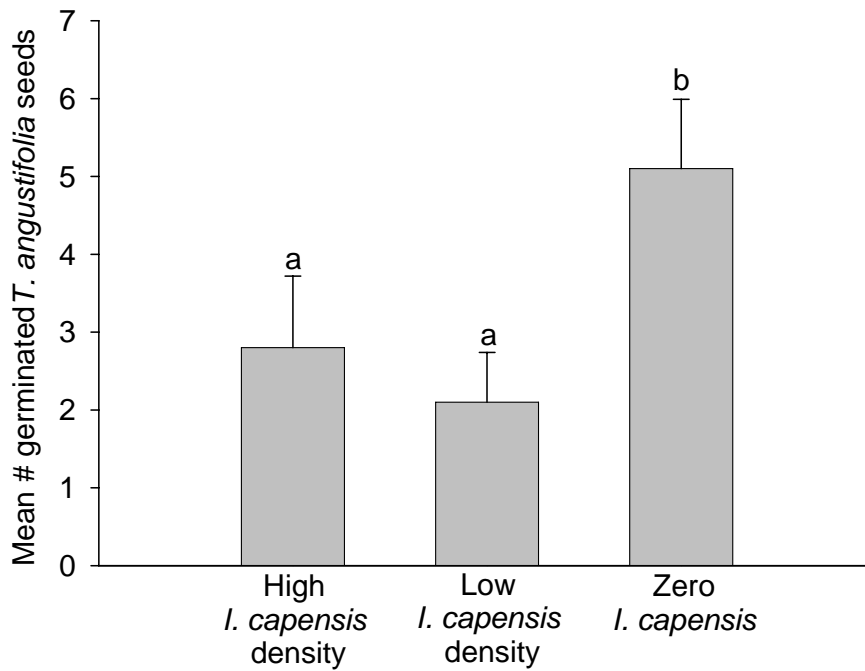


Figure 14. Mean number +1 standard error of *Typha angustifolia* seeds that germinated in high, low, and zero density of *Impatiens capensis*. Differing letters demonstrate significant differences between treatments.

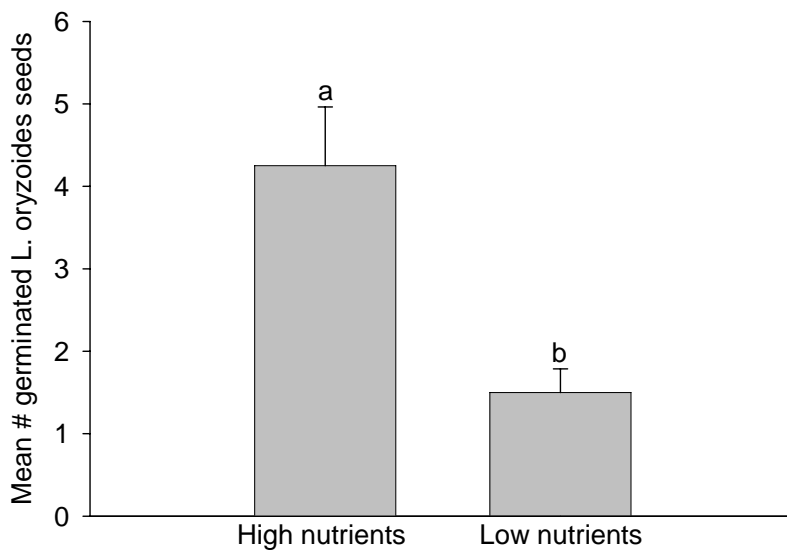


Figure 15. Mean number +1 standard error of *Leersia oryzoides* seeds that germinated in high and low nutrient environments. Differing letters demonstrate significant differences between treatments.

Discussion

Competition for light and nutrients may only explain why annual species dominate some areas at Dyke Marsh in some cases. The greenhouse experiment demonstrated negative effects of *I. capensis* density on *T. angustifolia*. Past studies have shown that *Typha* spp. requires a high light environment for successful germination (Grime et al. 1981, Grace 1983, McIninch and Garbisch 2003). The greater the number of *I. capensis* seedlings with their large shading cotyledons, the more light is intercepted by the *I. capensis*, which decreases the amount of light reaching the soil surface. Thus, *T. angustifolia* seeds germinate in a suboptimal light environment. This also explains why *T. angustifolia* seeds had poor germination rates in the shade cloth treatments and shows that the species compete for light, not for nutrients.

That *T. angustifolia* germination was negatively influenced by high *I. capensis* density may partially explain aboveground vegetation patterns observed at Dyke Marsh. *T. angustifolia* often co-occurs with *I. capensis* in the marsh; yet patches that are dominated by *I. capensis* persist year after year. Therefore, in areas where *I. capensis* forms dense patches in early spring, *T. angustifolia* may not be as prevalent. But, it is the physical gradient of elevation, and subsequent water inundation that ultimately drives the distribution of *I. capensis* (Chapter IV). Thus, elevation appears to drive *I. capensis* distribution, which in turn appears to influence *T. angustifolia* distributions.

Impatiens capensis density did not have a strong influence on *L. oryzoides* germination. That more *L. oryzoides* seeds germinated under the shade cloth than

without it suggests that *L. oryzoides* seeds may prefer a slightly shaded environment for germination. This may explain why *I. capensis* density did not have a direct affect on *L. oryzoides* germination, but may have provided ideal light requirements for germination of *L. oryzoides*.

Peltandra virginica proved very successful in germinating in all treatment combinations. Others have noticed the ability of *P. virginica* to germinate in a variety of conditions (West and Whigham 1975-1976, Leck 1996). Through a series of greenhouse studies, Leck (1996) found *P. virginica* to germinate at all buried depths, when inundated with water, and at a variety of temperatures and soil moisture levels (Leck 1996). Furthermore, in a pilot study examining germination of perennial species at varying water inundation treatments, I found *P. virginica* to readily germinate in low, mid, and high water inundation treatments.

Lastly, *S. fluviatilis* did not germinate in any of the treatment combinations; therefore, the competitive response of this species could not be analyzed. *Schoenoplectus fluviatilis* may not have germinated owing to improper pre-planting care. McIninch and Garbisch (2003) suggest storing seeds in a cold dry environment over winter, which is what was done. However, the seeds used for this experiment were obtained from a seed company and not collected from Dyke Marsh; therefore, I am uncertain of the care the *S. fluviatilis* seeds received previously. *Schoenoplectus fluviatilis* seeds may also be stored in a cold and wet environment, but only for a limited amount of time (McIninch and Garbisch 2003).

In the future, this study could be replicated at the field site. Small raised plots could be established in the marsh with a barrier between the marsh seed bank and the

experimental plot. Seeds of the study species could be planted in spring and the plots consistently monitored and weeded. Such study conducted in the field would provide more realistic field conditions. Furthermore, because we have learned of the strong influence elevation has on marsh vegetation from the previous studies; the study could also be carried out at varying elevations.

CHAPTER VII

SEED RAIN DYNAMICS

(At the time of dissertation submission, this chapter has been accepted with revisions for publication in the journal *Plant Ecology*, titled “Floating seed rain dynamics of a tidal freshwater marsh on the Potomac River, USA” by K.N. Hopfensperger and A.H. Baldwin.)

Wetland species can be distributed by various mechanisms including wind and animals; however, water dispersal, or “hydrochory”, has been found to be the primary method of seed dispersal (Bakker et al. 1985, Huiskes et al. 1995, Middleton 1995). Hydrochory can be an important driver of community structure in wetland ecosystems (Schneider and Sharitz 1988, Cappers 1993, Neff and Baldwin 2005) because it can result in the introduction of new species (Mitsch et al. 1998) and the introduction of exotic species (Thomas et al. 2005, Tabacchi et al. 2005, Thomas et al. 2006) leading to more diverse wetland plant communities (Girel and Manneville 1998, Jansson et al. 2005, Leyer 2006).

Seed dispersal via water may play an integral role in the regeneration of restored wetland systems. Gurnell et al. (2006) investigated the vegetation colonization of a newly created channel in the United Kingdom. Hydrochory was the dominant source of seeds deposited along river banks in the winter. Plants that were recruited from these deposited seeds then acted as a significant local seed source the second year, which created a feedback loop trapping additional propagules and sediment, thereby propelling river bank succession. Huiskes et al. (1995), Wolters et al. (2005), and Gurnell et al. (2006) all found the seasonality of seed dispersal through water ways to strongly influence colonization of newly created wetland areas. During the reestablishment of a salt marsh in Germany, Wolters et al. (2005) found

peak dispersal of salt marsh species in the fall. Lastly, hydrochory (Syphax and Hammerschlag 1995) played a more critical role than dredge material (Baldwin and DeRico 2000) in the revegetation of a tidal freshwater marsh restoration in Washington, D.C.

The successful regeneration of restored wetlands by hydrochory leads to the main objective of our study – to determine if available seed sources are sufficient to recolonize restored or newly created tidal freshwater marsh habitat on a large river in a highly urbanized setting. We investigated this objective by assessing the density of seeds and species richness through time in the adjacent river and the shoreline of our study site. The results of our study may specifically inform site managers about the seasonal availability of local seed supply, both native and exotic, that may contribute to a restoration project. In general, the results of our study provide scientists with a more complete picture of seed dispersal dynamics of tidal freshwater marshes.

Methods

Study Area

Water surface trawl and drift-line sampling took place at Dyke Marsh Preserve (38.77° N, 77.05° W), a tidal freshwater marsh on the Potomac River, just south of Alexandria, Virginia (Figure 16). Throughout the 1940s-1970s, approximately 110 ha of marshland along the outer fringes of Dyke Marsh was dredged for underlying sand and gravel. The federal government was given control of the existing 196 ha of swamp forest and emergent marshland in 1976. We focus on the shoreline of the emergent marsh both on shore and in the water of the Potomac River immediately adjacent to the marsh. At the study site, mixed tides occur daily

with a mean tidal range of 0.5-0.9 m (Carter et al. 1991). Flow rates upstream of the site on the Potomac average a volume of 312 m³/s and can range from 3.5 m³/s to 14,000 m³/s (NPS 1977). The highest flows occur in March and April after significant upstream snowmelt. Two major creeks flow through the marsh study site, Hog Island Gut and Wrecked Recorder Creek. Hydrologic studies conducted on the two channels were completed before significant dredging occurred (Myrick and Leopold 1963). No current hydrologic information exists on the two channels.

The vegetation composition of Dyke Marsh is typical of tidal freshwater marshes on the east coast (Whigham and Simpson 1977; Leck and Simpson 1995; Mitsch and Gosselink 2000), but may differ in seasonal vegetation patterns. Past literature on regional freshwater tidal marshes suggests that biomass production by annual species is lower than perennial species in spring and then exceeds that of perennial species towards the end of the growing season (Whigham 1978). Dyke Marsh is unique in that while the biomass production of annual species increases noticeably throughout the growing season, it never surpasses the amount of perennial biomass production in the marsh (Hopfensperger, personal observation). Dominant annual species in Dyke Marsh include *Impatiens capensis* Meerb., *Amaranthus cannabinus* (L.) Sauer, *Bidens laevis* (L.) B.S.P., and *Polygonum arifolium* L.. Dominant perennial species in the marsh include *Typha angustifolia* L., *Peltandra virginica* (L.) Schott, *Nuphar luteum* (L.) Sm., *Acorus calamus* L., and *Schoenoplectus fluviatilis* (Torr.) M.T. Strong.

Water Surface Trawl Sampling

Water surface trawling took place in fall 2003, and spring, summer, and fall of 2004 and 2005 on the Potomac River near the DMP shoreline for a total of seven sampling events. In October 2003, six 200-m transects were established around the perimeter of the emergent marsh (Figure 16). During each sampling event, three trawls were made along each transect using a modified plankton net with a seed trap that was towed by a motor boat (Neff and Baldwin 2005) to sample the floating seed rain. The net was dragged approximately 0.6 m from the side of the boat, ahead of the wake, at a speed of 2.7-2.9 km/hr. After each of the three trawls on every transect, the seed trap was scraped and rinsed into a plastic bag.

The seedling emergence technique was used to determine density and species composition of the trawl samples (Poiani and Johnson 1988, Gross 1990, Baldwin et al. 2001). Samples were spread over vermiculite in black plastic bedding trays (27x53x5 cm) and placed in a greenhouse misting room for germination. Coarse material including leaves, sticks, and trash was rinsed with water over the tray to remove any seeds and was then discarded. All trays were stored at approximately 4°C over winter to cold stratify any remaining seeds, and then placed back into the greenhouse to continue germination in the spring. Seedlings emerging from each sample were identified as young as possible, and removed from the tray when identified. Seedlings of unknown species were transplanted and allowed to mature for identification.

Drift-line Sampling

The abundance and species richness of seeds was quantified along 920 m of emergent marsh drift-line along the Potomac River. The drift-line area is located along the upper tidal limits of the shore line where coarse organic debris settles (Bakker et al. 2002). Drift-line samples were 10 cm² by 2 cm deep and were taken at 40 random points in March, July, and October of 2005 and March 2006 (Figure 16). Sample points were located by using a random number table ranging from 5 to 75 to determine meters between sampling points; then when we reached a sampling point, we randomly tossed the plot template onto the drift-line to determine the exact sample location. Samples were germinated in the greenhouse using the emergence methods described above and seedlings identified. All plant identifications followed the nomenclature of Gleason & Cronquist (1991).

Data Analyses

Mean, maximum, and standard error of seedling and species density were calculated for greenhouse trays of each transect and each sampling event. Repeated measures analysis of variance (RMANOVA) tested for the effect of sampling event on seedling density of trawl and drift-line samples to determine if seasonality had an effect. The fixed effect was sampling event, the response variable was seedling density, and the repeated measure was transect. Repeated measure ANOVAs were similarly performed to test for the effect of sampling event on species richness for trawl and drift-line data. We calculated area-adjusted seedling density (seedling density / sample surface area; density/m²) for trawl and drift-line samples to standardize units and allow comparison to past regional studies. Drift-line species

richness was log+1 transformed to conform to normality assumptions. Drift-line seedling density, seed trawl seedling density, and seed trawl species richness were square-root transformed to conform to normality assumptions. Data were analyzed using SAS (SAS Inc. 1985) with significance defined at $\alpha=0.05$.

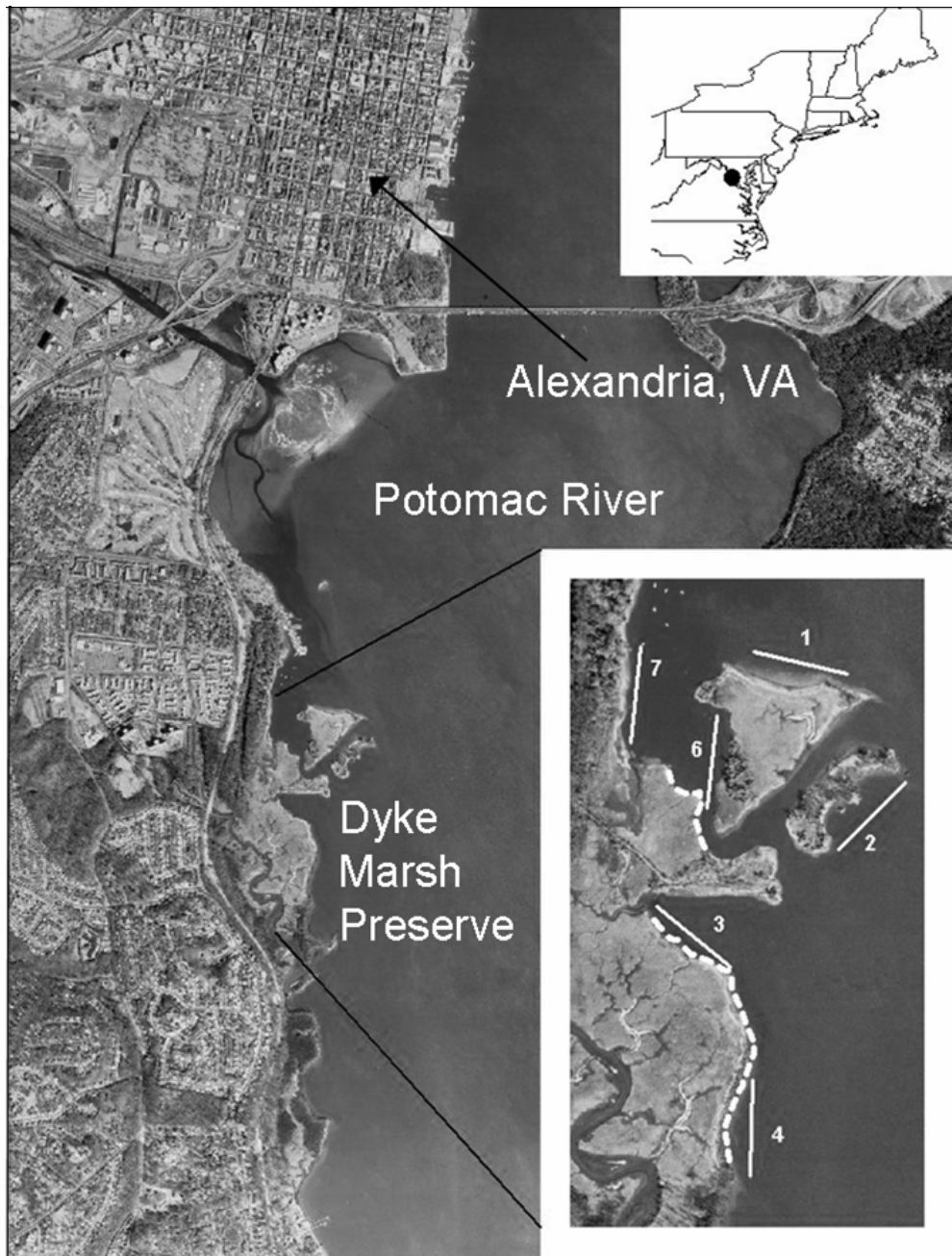


Figure 16. Location of Dyke Marsh Preserve on the Potomac River. Inset includes transect (solid) and drift-line (dashed) sampling locations.

Because of the difference in number of individuals collected between the two sampling methods, and to be able to compare our results to previously published studies, we calculated sample-based rarefaction curves and species richness estimations using EstimateS 5.0.1 (Colwell 1997). The rarefaction curves remove sampling effects and allow for comparisons of species richness when samples contain different numbers of individuals (Colwell & Coddington 1994; Gotelli & Colwell 2001). Using EstimateS, we estimated the total number of species in the sampled seed pool using nonparametric asymptotic species richness estimators to determine if our sampling effort was adequate for both sampling techniques. Chao 1 (Chao 1984) was the first estimator to reach an asymptote for both techniques; therefore we will only discuss the Chao 1 data (Colwell & Coddington 1994). Interestingly, the Chao 2 estimator produced a strong positive bias and grossly overestimated richness at low numbers of individuals.

Non-metric multidimensional scaling (NMS) was performed separately on the species pool from each sampling event for the drift-line and the seed trawl data using PC-ORD (MjM Software Design 2002) to examine similarity of species pools among the sampling events. For both NMS analyses, Sørensen's distance measure was used, along with a supplied starting configuration that was calculated from an initial random configuration, and 15 runs with real data.

Results

A total of 42 species were identified using both the drift-line and seed trawl methods. The number of emerged seedlings was much greater in the drift-line (1,669 seedlings) than in the seed trawl samples (292 seedlings). Dominant species found in

both the drift-line and seed trawl samples were *Amaranthus cannabinus* and *Pilea pumila* (Table 7).

Water Surface Trawling

The seed trawls contained an area-adjusted average of 420 seeds/m² (4.2 million seeds/ hectare) with the lowest sampling event of the study being 0 seeds/m² in August 2005, and the highest being 1370 seeds/m² in October 2004. Rarefaction analysis indicated that species accumulate rapidly with sampling effort and ended with 28 species when sampling 250 individuals (Figure 17a). The species richness estimator Chao 1 leveled off rapidly and estimated 30 species (± 0.56 SE) (Figure 17a). The low standard error, and the fact that the rarefaction analysis ends with a value similar to the Chao 1 estimate demonstrate that our sampling effort was successful in capturing most species within the floating seed pool.

Collectively from all sampling events, the seed trawls produced 30 species. All dominant species in the seed trawls were annuals, including *Impatiens capensis*, *A. cannabinus*, *Bidens laevis*, and *P. pumila* (Table 7). Fall sampling events contained 22 species. Sixteen of the 22 species were only found in the fall, and *I capensis* and *B. laevis* dominated the fall species pool. Ten species were found during spring sampling events, three of which were unique to spring samples, and *P. pumila* dominated the spring species pool. Seven species were sampled during summer sampling events, two of which were only found in summer samples, and *Lycopus amplexans* dominated the species pool in the summer.

Table 7. Number of seeds germinated, all sampling seasons collectively, for each species, from the water surface trawling and drift-line sampling techniques. Superscripts show which season that species was found in: (a)=spring, (b)=summer, and (c)=fall.

Species	# seeds germinated	
	Water Surface Trawling	Drift-line Sampling
<i>Amaranthus cannabinus</i> (L.) Sauer	35 ^{a,b,c}	74 ^{a,c}
<i>Ammania latifolia</i> L.	0	1 ^b
<i>Bidens frondosa</i> L.	2 ^c	6 ^b
<i>Bidens laevis</i> (L.) B.S.P.	32 ^{a,b,c}	4 ^a
<i>Carex grayi</i> Carey	0	3 ^a
<i>Cuscuta gronovii</i> Willd. ex J.A. Schultes	2 ^c	17 ^{a,c}
<i>Echinochloa muricata</i> (Beauv.) Fern.	0	1 ^b
<i>Eclipta prostrata</i> (L.) L.	4 ^c	0
<i>Eleocharis engelmannii</i> (Steud.)	0	2 ^a
<i>Helenium autumnale</i> L.	0	2 ^a
<i>Hibiscus moscheutos</i> L.	2 ^c	0
<i>Hydrilla verticillata</i> (L.f.) Royle	1 ^c	5 ^c
<i>Impatiens capensis</i> Meerb.	67 ^{a,c}	0
<i>Iris sisyrinchium</i> L.	1 ^b	0
<i>Juncus effuses</i> L.	0	4 ^{b,c}
<i>Leersia oryzoides</i> L. (Sw.)	11 ^{a,c}	10 ^{a,c}
<i>Ludwigia palustris</i> L. (Ell.)	2 ^c	134 ^{a,b,c}
<i>Lycopus amplexans</i> Raf.	7 ^{a,b}	0
<i>Microstegium vimineum</i> (Trin.) A. Camus	0	2 ^a
<i>Mikania scandens</i> L. Willd.	0	2 ^a
<i>Najas minor</i> All.	1 ^c	54 ^{a,b,c}
<i>Nuphar lutea</i> (L.) Sm.	1 ^c	1 ^a
<i>Peltandra virginica</i> (L.) Schott	15 ^c	0
<i>Pilea pumila</i> (L.) Gray	62 ^{a,b,c}	39 ^{a,b}
<i>Polygonum pensylvanicum</i> L.	0	1 ^a
<i>Polygonum persicaria</i> L.	1 ^c	4 ^{a,c}
<i>Polygonum punctatum</i> Ell.	2 ^c	1 ^c
<i>Ranunculus cymbalaria</i> Pursh	4 ^{a,c}	0
<i>Rorippa palustris</i> (L.) Bess.	0	2 ^a
<i>Rotala ramosior</i> (L.) Koehne	0	2 ^b
<i>Rumex crispus</i> L.	1 ^b	0
<i>Sagittaria latifolia</i> Willd.	0	3 ^{a,b,c}
<i>Schoenoplectus fluviatilis</i> (Torr.) M.T. Strong	5 ^{b,c}	17 ^{a,b}
<i>Solanum dulcamara</i> L.	2 ^c	0
<i>Typha angustifolia</i> L.	16 ^c	1276 ^{a,b,c}
<i>Zizania aquatica</i> L.	1 ^c	2 ^a
Unknown species	15 ^{a,c}	0

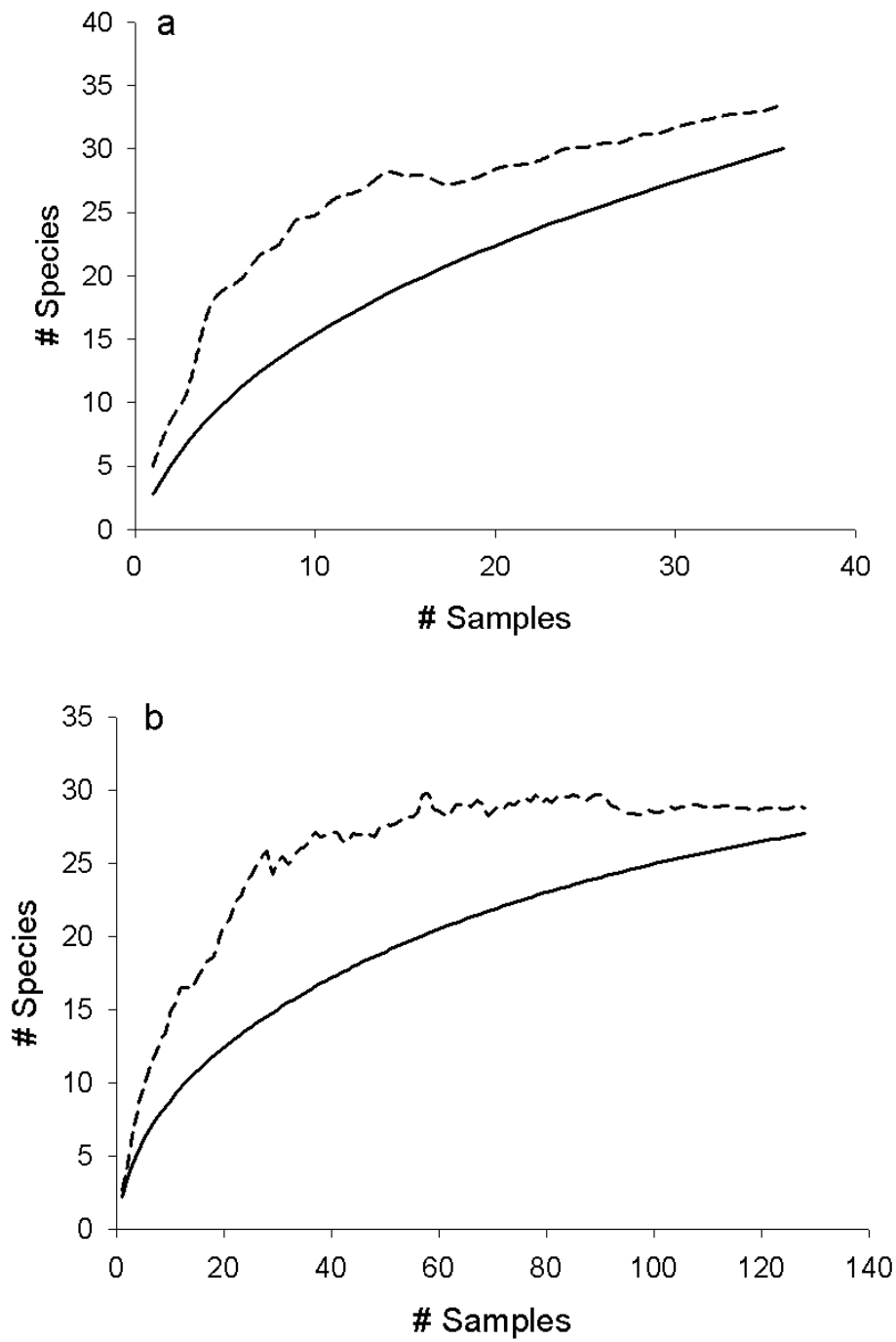


Figure 17. Rarefaction curve (solid line) and mean Chao 1 values (dashed line) for water surface trawls (a) and drift-line (b) sampling at Dyke Marsh Preserve.

The highest number of species and seedlings were found during the fall sampling events, versus spring and summer (RMANOVA overall model for seedling density: $F=15.54$, $df=2, 39$, $p<0.001$, and species richness: $F=17.84$, $df=2, 39$, $p<0.001$; Figure 18). Fall had higher seedling density than spring ($p=0.006$) and summer ($p<0.001$), however spring and summer seedling density did not differ ($p=0.134$). Similarly, fall had higher species richness than spring ($p=0.001$) and summer ($p<0.001$), however spring and summer species richness did not differ ($p=0.268$). Interestingly, the summer 2005 sampling event did not have any seeds germinate at all. A 3-dimensional NMS solution demonstrated slight differences in seed pool composition among the three seasons with a final stress value of 16.4 and cumulative $R^2=0.599$. The stress value is not optimal; however the value does fall within the expected range for ecological community data (Clarke 1993, McCune and Grace 2002).

The seed trawl transects did not differ in seedling density or species richness with all sampling events combined (ANOVA for seedling density: $F=1.82$, $p=0.113$). However, transects containing high seedling density differed among seasons. In spring sampling, transect one had the highest seedlings, followed by transect two and three (ANOVA overall model: $F=6.90$, $p=0.001$; Figure 19). Transects two, three, and seven had the highest seedling density in fall; however no differences existed among the transects in fall (ANOVA $F=0.98$, $p=0.441$) or summer (ANOVA $F=1.13$, $p=0.364$; Figure 19).

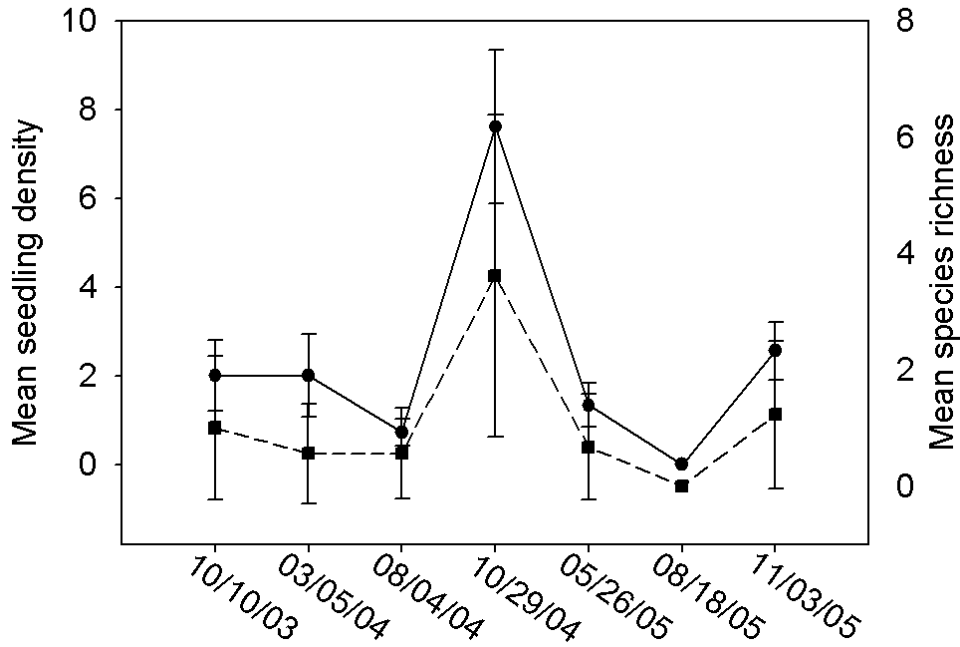


Figure 18. Mean seedling density (solid line, ●) and mean species richness (dashed line, ■) per water surface trawl sampling event at Dyke Marsh Preserve.

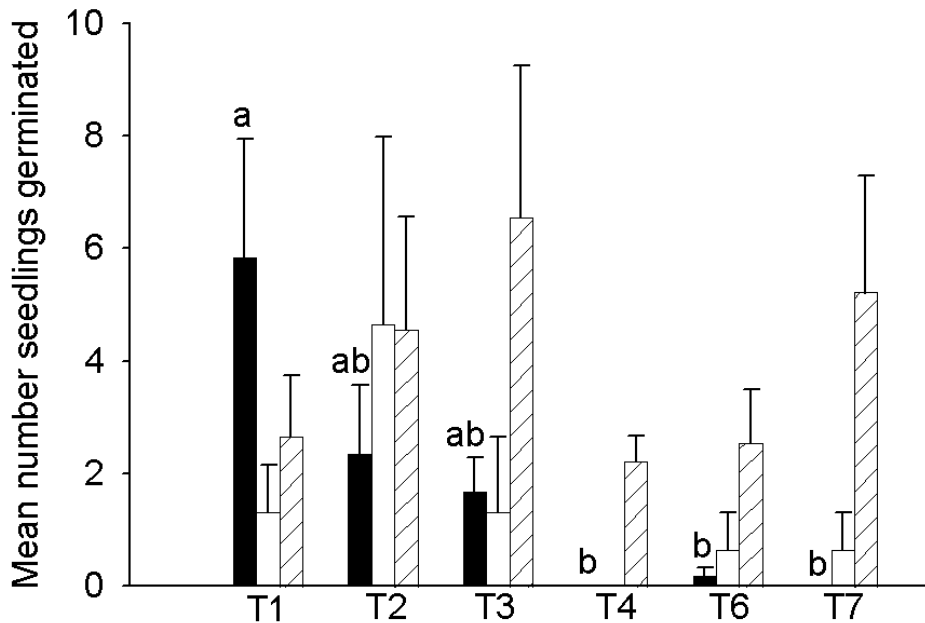


Figure 19. Differences in average seedling density per trawl transect in spring (black), summer (white), and fall (pattern) sampling seasons. Different letters represent significant differences among transects in spring ($\alpha=0.05$). No differences existed between transects in summer and fall.

Drift-line

An area-adjusted average of 10,500 seeds/m² (10.5 million seeds/ hectare) was sampled from the drift-line, with the lowest being 2100 seeds/m² in fall 2005, and the highest being 22,000 seeds/ m² in summer 2005. The drift-line sampling resulted in 27 species from all sampling events. Fourteen of the species found in the drift-line samples were also found in the seed trawl samples. Rarefaction analysis indicated that species accumulate moderately with sampling effort and ended with 26 species when sampling from 1500 individuals (Figure 17b). The species richness estimator Chao 1 leveled off rapidly and estimated 29 species (± 0.19 SE) (Figure 17b). These results demonstrate that we captured most of the species in the drift-line seed pool. While the Chao 1 values are very similar for the floating seed and drift-line communities, the estimates were derived separately from different populations of seeds. The two species pools are comprised of different species, thereby indicating a more species rich ecosystem than suggested by Chao 1 values for each sampling method alone (Table 7).

Dominant species in the drift-line included *Typha angustifolia*, *Ludwigia palustris*, *A. cannabinus*, *Najas* spp., and *P. pumila* (Table 7). Spring sampling events captured 20 species, and 10 of the 20 species were found only in the spring. Eleven species were found in summer samples, 4 of which were unique to summer. The fall drift-line samples contained eleven species, two of which were unique to fall samples. *Typha angustifolia* and *L. palustris* dominated samples from all seasons, and *A. cannabinus* was most prevalent in spring, while *Najas* spp. was found most in fall samples.

In contrast to the seed trawl samples, the highest number of species and seedlings for the drift-line samples were found in spring (RMANOVA overall model for seedling density: $F=9.48$, $p<0.001$, Figure 20; and species richness: $F=10.20$, $p<0.001$). Seedling density was higher in the spring than summer ($p=0.003$) and fall ($p<0.001$); however, summer and fall seed density did not differ ($p=0.463$). Similarly, species richness was also higher in spring than in summer ($p=0.001$) and fall ($p<0.001$), but summer and fall did not differ in species richness ($p=0.5431$). A 3-dimensional NMS solution from the three sampling events demonstrated that spring, summer, and fall differed in seed pool composition by separating out in ordination space. The NMS had a cumulative $R^2=0.322$ and a final stress value of 19.3 (Figure 21).

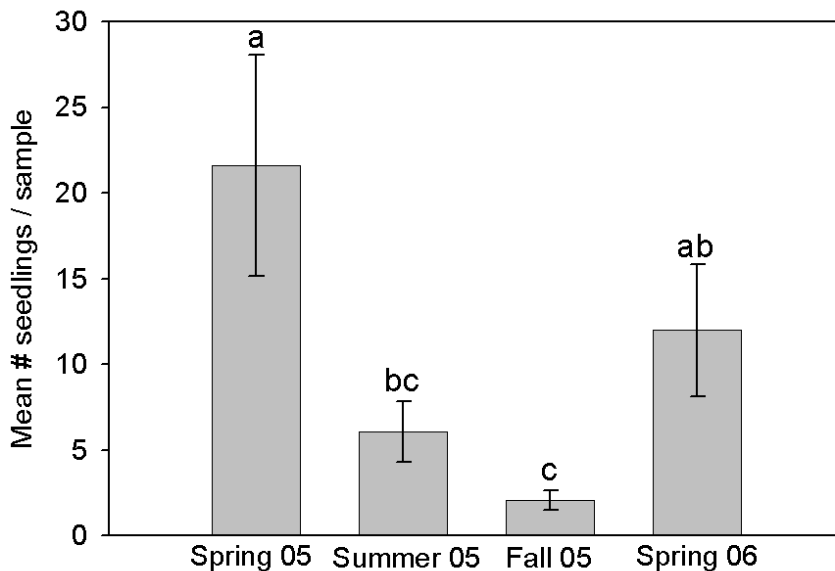


Figure 20. Average number of germinated seedlings from drift-line sampling at Dyke Marsh Preserve.

Discussion

Differences between water trawl and drift-line

Dyke Marsh Preserve receives a low seed supply through hydrochory compared to other regional tidal freshwater marshes. Neff and Baldwin (2005) estimated 104 species in seed trawls. Approximately 37 species were found while sampling 250 individuals at Kingman and Kenilworth marshes on the Anacostia River in Washington, D.C. Kenilworth Marsh is located less than 15 miles from Dyke Marsh Preserve and the Anacostia River flows directly into the Potomac River just upstream of Dyke Marsh. The dramatic differences (30 versus 104 species in the floating seed communities) between the two marshes are intriguing and may be explained by the distance between marsh area and mid-river. The width of the Anacostia River is narrower than the Potomac River, therefore seeds may have a better chance of reaching the river channel and flowing downstream on the Anacostia than on the wider Potomac River. In contrast, we found an extremely high density of seedlings in the DMP drift-line compared to the Kingman Marsh drift-line (10,500 versus 1500 seedlings/ m², respectively). The large difference between seedling density in the drift-lines at Kingman Marsh and Dyke Marsh may be due to 1) a small sample size of the drift-line at Kingman Marsh, and 2) the sampling of drift-lines in non-vegetated areas at Kingman Marsh.

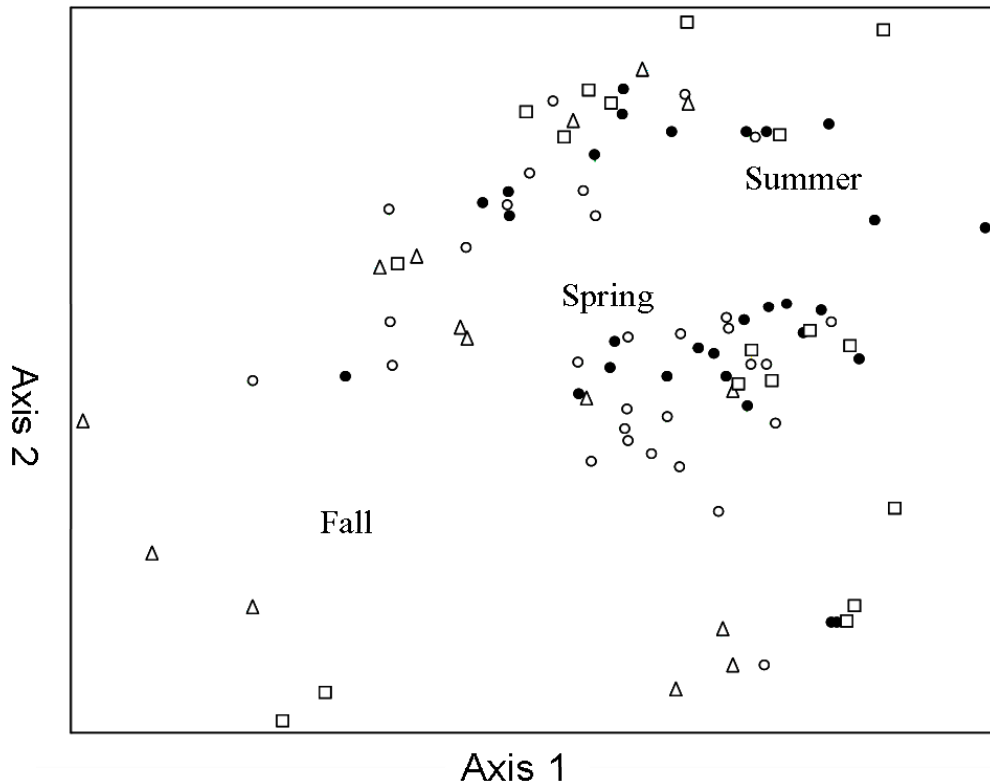


Figure 21. Nonmetric multidimensional scaling ordination of the community composition from each drift-line sampling event. Fall 2005 (Δ) communities separate out from spring 2005 (\circ) and spring 2006 (\bullet) communities, which separate out from summer (\square) communities. Axis 1 $R^2=0.117$; Axis 2 $R^2=0.145$.

Few individuals are required to adequately sample the floating seed pool through our water trawl sampling, and many more individuals are required to adequately sample the drift-line. The difference in the number of seeds found in the water trawl versus the drift-line samples at Dyke Marsh may be explained by several factors. First, some of the seeds found in the drift-line may have been dispersed through wind rather than water. This may explain why several species found in the drift-line were not found in the water trawl samples; however, extensive literature supports the dominant dispersal mechanism of seeds to be hydrochory in aquatic systems (Schneider and Sharitz 1988, Cappers 1993, Bakker et al. 2005). Second, the

drift-line samples are time composited, while the trawl samples are snapshots in time. Furthermore, the trawl samples may miss small, dense seeds such as *Juncus effusus* L., which was found in the drift-line and not the trawls (Table 7). Lastly, all of the water trawl samples were collected on an ebb tide as the water flow may transport local vegetation seeds out of the marsh and into the channels and river, thereby demonstrating that the seed rain of Dyke Marsh may be influenced by the local vegetation.

Spatial Variation

Floating seeds may not disperse miles downstream – the source of water-dispersed seeds may be the local marsh vegetation and not vegetation from areas upstream (Bakker et al. 2002). Even with dramatically lower number of species in the water trawls than marshes on the Anacostia River (30 vs. 104 species), species accumulation curves for Dyke Marsh leveled off much more quickly than curves for the Anacostia (Neff and Baldwin 2005). Reaching an asymptote sooner, may demonstrate that the source pool of species for Dyke Marsh is the existing marsh itself. Furthermore, transects with the highest density of seedlings were located downstream of major tidal creeks outlets. For example, density of seeds was high for transect 3 (Figure 16), which was located immediately downstream to the outlet of Wrecked Recorder Creek. Similarly, transect 2, an area with a high density of seeds, receives all of the water flow off of an island, and transect 7 receives flow from the adjacent swamp forest corridor. Meanwhile, transects 1 and 6 with a low density of seeds are on the upland sides of the island, where the water flows across the island away from them, and transect 4 is a substantial distance downstream from a stream

outlet. The above information stresses the importance of transect location selection for assessing seed sources. Transects should be located immediately downstream of stream outlets and adjacent to land areas with high amounts of runoff.

We suggest that long-distance seed dispersal via water is rare for tidal freshwater marsh ecosystems. Seeds that disperse from a parent plant into the channel network of a tidal freshwater marsh situated on a large river have a low chance of making it to the main channel and dispersing miles downstream. We hypothesize that at Dyke Marsh, seeds are dispersed and float along the outskirts of the marsh until the tide then washes them back into the marsh through the channel network and washes them onshore, as witnessed by our drift-line samples. Neff and Baldwin (2005) found higher densities of floating seeds in trawls adjacent to marshes than in the channel of the Anacostia River; however, they did find Kenilworth Marsh to be a seed source for the very close proximity, newly restored Kingman Marsh. The Anacostia River is much narrower than the Potomac River, so seeds may be transported farther downstream during flood events in the main channel of the Anacostia River than they do in the large channel in the tidal freshwater reaches of the Potomac River.

Temporal Variation

Both the seed trawl and drift-line sampling resulted in seasonal variation of species richness and seedling density. Higher species richness and seedling density were found in the fall water trawls versus spring and summer. Wolters et al. (2005) found a similar pattern in diaspore dispersal in an England tidal salt marsh where the main dispersal of diaspores took place between October and December. High dispersal may occur in the fall owing to the end of peak biomass and plant

senescence. During this time, seeds are being released everywhere – into the air, the water, and the substrate below the parent plant. Many of the seeds find their way to the water, either directly or indirectly through tidal flushing (Bakker et al. 1985, Huiskes et al. 1995). Finally, they are concentrated in the river in the fall.

Contrary to peak richness and density in the water trawls, we found the highest drift-line species richness and seedling density in the spring and summer. High density in the spring is logical with the above pattern of mass seed dispersal in the fall. In autumn, seeds are being dispersed, being flushed towards the channels, and floating in the water. In winter, seeds begin to collect and concentrate in the drift-line. Once in place in the drift-line, seeds cold-stratify, which is a requirement for germination for many tidal freshwater marsh species (Leck and Simpson 1993). This may explain the difference between spring drift-line and trawl densities. Seeds floating in the water over winter and during spring may not be properly cold stratified and therefore do not germinate.

Through our study we have confirmed the importance of hydrochory as a seed dispersal mechanism in tidal freshwater marshes, as well as the importance of using more than one sampling method. However, seed density and species richness surrounding Dyke Marsh was significantly lower than at near-by Kingman and Kenilworth marshes, suggesting that seed dispersal may be a more local phenomenon than was previously thought for tidal freshwater marshes. We suggest that the drift-line of a marsh may provide a more ideal environment for the necessary cold stratification of many marsh species than floating in the water. Therefore, if managers were to restore Dyke Marsh through adjacent marshland creation, hydrochory should

not be depended on as the only mechanism for species colonization. If managers only rely on hydrochory, the drift-line margins of the newly created areas may be colonized, but the interior could remain vulnerable to wind-dispersed invasion by species such as *Typha* spp. and *Phragmites australis* (Cav.) Trin. ex Steud. that could create unwanted homogenous vegetative stands.

CHAPTER VIII

EFFECTS OF SPECIES DOMINANCE PATTERNS ON DENITRIFICATION

(At the time of dissertation submission, this chapter is in preparation for submission to the *Journal of Environmental Quality*, titled “Denitrification dynamics in a tidal freshwater marsh of the Potomac River, USA” by K.N. Hopfensperger, S.S. Kaushal, S.E.G. Findlay, and J.C. Cornwell.)

The transport of nitrogen through streams and rivers draining coastal watersheds has greatly increased due to human activities (Howarth et al. 1996, Vitousek et al. 1997). Increases in nitrogen export from landscapes have been associated with extensive hypoxic areas that can develop in coastal waters such as the Chesapeake Bay (Cooper and Brush 1991, Eby et al. 2005, Kemp et al. 2005). Hypoxic zones can be detrimental to ecosystems by causing substantial mortality of sessile organisms (Eby et al. 2005), limiting oyster success through toxin production (Brownlee et al. 2005), and impacting habitat quality and growth rates of nekton (Eby et al. 2005). Denitrification, the conversion of nitrate and nitrite to gaseous forms of nitrogen (NO , N_2O , N_2), can represent a “natural” way for wetlands to reduce nitrogen loads to coastal waters. Denitrification is performed by anaerobic heterotrophic bacteria that require low oxygen and organic carbon as electron donors.

Tidal freshwater marshes may represent important sinks for nitrogen in the landscape because they are located in areas within the watershed where they can intercept upland sources of nitrate (Odum 1988), and they support environmental conditions, such as low O_2 , reduction-oxidation reactions, and high organic matter inputs, that can promote denitrification. Plant communities composed of species with

different functional traits may be intrinsic drivers of denitrification rates in a tidal freshwater marsh (Cornwell et al. 1999). Functional traits may be related to species' life history traits (Engelhardt 2006), where annual and perennial species may differ in affecting forms and amounts of nitrogen available and providing varying qualities of organic matter (Reddy and DeBusk 1987). High organic matter inputs may increase denitrification rates by indirectly influencing oxygen concentrations in the soil (Cornwell et al. 1999) and providing carbon needed for denitrifier metabolism. Also, plants may differentially oxygenate their rooting zones thereby affecting conditions for denitrification. Because of the different life history characteristics of annual and perennial species, potential effects of marsh vegetation on the extent or location of "hot spots" of denitrification (McClain et al. 2003) in tidal freshwater marshes may need to be considered. Therefore, we hypothesized that organic matter quality of annual species versus perennial species would increase denitrification rates. Furthermore, we hypothesized that the aeration of rooting zones by perennial species, such as *Typha angustifolia*, may increase denitrification rates, but were unsure if quantity of biomass or other variables would counteract the effect of increased oxygen.

In tidal freshwater marshes, the variability of marsh surface elevation and daily tidal fluctuation allow for alterations in oxic and anoxic zones in the substrate. Thus, marsh surface elevation may influence denitrification rates in a tidal freshwater marsh by influencing redox conditions and the coupling of nitrification and denitrification (McManus 1998, Puckett et al. 1993, Khan and Brush 1994, Mitsch and Gosselink 2000).

The objective of our study was to identify patterns in potential drivers of denitrification in a tidal freshwater marsh located in the Chesapeake Bay watershed. Published results of denitrification rates in tidal freshwater marshes are rare (Merrill and Cornwell 2000), possibly because denitrification is difficult to measure and tidal freshwater wetlands are smaller and more fragmented than their coastal marine counterparts (e.g. Kemp et al. 1990, Cornwell et al. 1999, Merrill and Cornwell 2000, Groffman et al. 2006). In addition, considerably more work has been done studying denitrification in marine and estuarine wetlands (e.g. Kemp et al. 1990, Joye et al. 1996, Kana et al. 1998, Addy et al. 2005), although similar underlying mechanisms may be relevant in tidal freshwater systems. Differences between tidal freshwater and salt marshes that may influence denitrification rates include a lack of salinity, higher plant productivity, and higher plant diversity in the freshwater system (Odum 1988, Mitsch and Gosselink 2000). Our specific questions included 1) what are the rates of denitrification in a tidal freshwater marsh; and 2) whether certain environmental factors (elevation, plant community composition, and sediment organic matter quantity and quality) may influence denitrification in the marsh. We quantified denitrification rates using two independent techniques to optimize both quantity and quality of our estimates. The denitrification enzyme activity technique (DEA) measures denitrification potential and tends to underestimate rates from coupled nitrification/denitrification (Groffman et al. 2006), but can be useful because it allows for numerous samples to be analyzed per sampling event (Cornwell et al. 1999). We measured DEA in June and October to verify when denitrification rates are highest in a tidal freshwater marsh. Others have found higher denitrification rates in summer

months than in spring or fall (Joye et al. 1996, Merrill and Cornwell 2000, Greene 2005). Another independent method we used was membrane inlet mass spectrometry technique (MIMS), which can be advantageous because it measures N_2 fluxes in unperturbed sediment cores with high temporal resolution (Kana et al. 1998), does not inhibit coupled nitrification/denitrification, and can provide precise results (Kana et al. 1994).

Methods

Study Area

Dyke Marsh Preserve supports an 80 ha tidal freshwater marsh on the Potomac River, just south of Alexandria, Virginia (38.77° N, 77.05° W). Dyke Marsh is owned by the National Park Service, which took over direct management in 1976 after 81 ha of the marsh had been dredged away for sand and gravel (NPS 1977). Currently, the National Park Service is studying possible restoration scenarios for Dyke Marsh. The climate of the region is temperate with July mean daily maximum temperature of 31°C and January mean minimum temperature of -2°C (Johnston 2000). Average annual precipitation is 101.6 cm, of which up to 30.4 cm may be snowfall (Johnston 2000). Mixed tides at the study site have a mean tidal range of 0.5–0.9 m and a normal 0.91-m fluctuation (Carter et al. 1994). Flow rates upstream of the site on the Potomac average 312 m^3s^{-1} and can range from 3.5 m^3s^{-1} to 14,000 m^3s^{-1} (NPS 1977). The highest flows occur in March and April after significant upstream snowmelt. The flow effect of the Potomac River on the marsh is usually minimal owing to the long distance from the main channel of the river to the marsh, although the entire marsh is within the flood plain of the Potomac River (NPS 1977).

Nitrate concentrations in the Potomac several km below the marsh were high, averaging $1.4 \pm 0.4 \text{ mg L}^{-1}$ (2001-2005 data; Chesapeakebay.net). Dyke Marsh also receives inputs from Cameron Run/Huntington Creek, which is the major drainage for the city of Alexandria and enters the Potomac River directly upriver of the marsh. Hog Island Gut, the major channel that meanders through Dyke Marsh, flows directly into the marsh from the towns of Belle Haven and Belle View under the George Washington Memorial Parkway, and has an average flow of $4.83 \text{ m}^3 \text{ s}^{-1}$ on ebb tides (Harper and Heliotis 1992).

Dyke Marsh is located in the Coastal Plain of Virginia, which is underlain by stratified, oceanic deposits of mud, sand, clay and gravel atop older crystalline rocks (NPS 1977, Johnston 2000). The alluvium deposits covering the marsh are approximately 15 m thick, comprised of sand and gravel with lenticular interlayered units of silt and clay (NPS 1977). The hydric surface soils provide ideal habitat for a diverse plant community typical of Atlantic Coast tidal freshwater marshes (Simpson et al. 1983, Odum et al. 1984, Leck and Simpson 1995). Vegetation in the marsh is comprised of a heterogeneous blanket of perennial species interspersed with various sized patches that are dominated by annual species (Hopfensperger, personal observation).

Vegetation Structure

Thirty-eight, 1 m^2 plots were sampled for community composition by recording percent cover (Braun-Blanquet 1964) of all species for every plot during peak biomass in July 2006. The plots were established throughout Dyke Marsh in the summer of 2004 by first delineating ten patches of *Impatiens capensis* Meerb., a

common annual species in tidal freshwater marshes of the eastern United States (Simpson et al. 1985) and the dominant annual species at Dyke Marsh, using a Trimble GeoExplorer II unit. The 38 plot locations were then placed blindly inside (n=18), outside (n=10), or on the edge (n=10) of all the *I. capensis* patches using ArcView to ensure the study included plots that were initially dominated by annuals, perennials, and a mixture of both annual and perennial species. Species richness was calculated for each plot as the number of total species present in the plot.

Aboveground living plant material of dominant annual species, *I. capensis*, *Bidens laevis* (L.) B.S.P., and *Amaranthus cannabinus* (L.) Sauer, and dominant perennial species, *Typha angustifolia* L., *Schoenoplectus fluviatilis* (Torr.) M.T. Strong, *Peltandra virginica* (L.) Schott, and *Nuphar lutea* (L.) Sm., was analyzed for tissue nitrogen and carbon concentrations in June and October 2006. Leaves from each species were gathered from three different random locations throughout the marsh. Samples were dried at (48 h at 110°C), ground through a 60 mesh screen, and analyzed for total N and C content using a Carlo-Erba CHNS/O analyzer.

Physical and Chemical Environment

Marsh elevation was measured in the center of every plot in July 2004, using a Topcon Precision GPS HiPer Lite Pro with an accuracy of ± 2 cm. The elevation data were tied to a local benchmark (NAD83 VA North) to georeference plot locations and elevations.

Nutrient concentrations of the Potomac River and large and small channels that flow through the marsh were sampled to give us an idea of the amount of nutrients entering and leaving through the marsh system waterways. Water samples

were taken in June and October 2006 from the Potomac River (two sampling locations), two very small channels in the marsh, Hog Island Gut (a large channel), and an unnamed larger channel during flood and ebb tides. Samples were filtered immediately upon return to the laboratory and then analyzed for ammonium-N (phenate method), nitrite-N and nitrate-N (automated cadmium reduction method), organic N (offline digestion method), and total N concentrations using flow injection analysis (Lachat QuikChem Automated Flow Injection Analysis System; APHA 1998, USEPA 1999).

Two sediment cores, 10 cm length by 3.81 cm diameter, were collected from all 38 plots in June and October using a PVC tube. Samples from each plot were homogenized, large roots and rhizomes were removed, and samples were sieved to 2 mm. Samples were dried at 70°C to a constant weight and then pulverized using a jar mill. We analyzed the sediment samples for total carbon and nitrogen with a Carlo-Erba CHNS/O instrument. Organic matter of each sediment core was obtained using the loss on ignition technique (Nelson and Sommers 1996). Available inorganic N (NH_4^+ plus NO_3^-) was extracted with 1 M KCl from all sediment samples. We then analyzed extracts for ammonium-N, nitrite-N, nitrate-N, organic N and total nitrogen using flow injection analysis with a Lachat Instrument 8000 Series.

Denitrification Rates in Sediments

Two independent techniques were used to measure different aspects of denitrification. The denitrification enzyme assay (DEA) technique measures potential rates (Smith and Tiedje 1979) and was used to test hypotheses regarding differences in denitrification rates among community types. The technique allows for numerous

samples to be analyzed at one collection time, but it only measures denitrification potential rather than actual rates. The membrane inlet mass spectrometry (MIMS) technique allows for fewer sites to be analyzed at a time. Potential denitrification rates in the sediments were measured for each plot in June and October 2006. Three sediment cores (10 cm length by 3.81 cm diameter) were taken from all 38 plots in June and October 2006. Samples from each plot were homogenized, large roots were removed by hand, and held at field moisture for all analyses. For the DEA analyses, sediments were amended with KNO_3^- , glucose, chloramphenicol, and acetylene, and incubated under anaerobic conditions for 90 minutes. Gas samples were taken at 30 and 90 minutes, stored in evacuated glass vials, and analyzed for N_2O by electron capture gas chromatography.

Direct flux estimates of denitrification rates in the sediments were measured from two plots dominated by annual species, two plots dominated by perennial species, and two plots with a mixture of species in November 2006 using MIMS (Kana et al. 1994). Samples were taken by hand using 30 cm long by 10 cm inner diameter PVC cores to depths ranging from 15 to 20 cm. Sediment cores with overlying water were sealed at both ends with rubber stoppers. Cores were transported to the laboratory in coolers immediately after collection, placed in a temperature controlled room set at 13.7 °C (the temperature of the water at the field site) submerged in 0.5 μm filtered water collected from Dyke Marsh, and left in the dark with bubblers to equilibrate overnight. After ~15 hours of equilibration, core tubes were sealed with no headspace using polycarbonate lids equipped with o-rings, magnetic stir-bars, and valved sampling ports, and then arranged around a central

magnetic turntable that slowly turned the stir-bars. Cores were incubated in the dark for six hours. Initial aliquots of 30 mL for nutrient analyses and duplicate 7 mL for N₂ and O₂ analyses were drawn from each core and then every 1.5 hours for the duration of the incubation. A blank control core tube without sediment was treated the same as the experimental cores throughout the incubation.

Core water samples for nutrient analyses were filtered with 0.2 µm syringe filters when collected and immediately frozen. Samples were later analyzed for ammonium-N, nitrite-N, nitrate-N, and ortho-phosphate using flow injection analysis with a Lachat Instrument 8000 Series. Samples for N₂ analysis were collected in gas-tight, ground glass stoppered vials, preserved with mercuric chloride and stored underwater at ambient temperature or lower to prevent degassing. Water samples were pumped through a gas permeable silicon membrane under high vacuum to allow dissolved gas molecules from the sample to pass into the attached mass spectrometer. Dissolved gas concentrations for N₂, O₂, and Ar were determined from the intensities of mass spectrometer signals at m / e 28, 32, and 40, respectively. We corrected the data for instrument background and drift, and for difference in gas solubility due to temperature differences between mass spectrometer standards. The blank control core was used to standardize all experimental core fluxes. Changes in dissolved gas concentration ratios with time were used to calculate sediment-water N₂ and O₂ fluxes.

Statistical Analyses

We used linear regression analyses to determine whether annual and/or perennial species cover was related to elevation. We used one-way analysis of

variance (ANOVA) to further test for elevational differences among plots dominated by annual, perennials, or mixed species. The sampled species were grouped into three groups differing in morphology and life history: annual broad-leaf, perennial broad-leaf, and perennial graminoids. Repeated measures ANOVA was used to determine if the response variable C:N varied among plant groups and season (June vs. October). Repeated measure ANOVAs were also used to determine whether the water chemistry (water ammonium-N, nitrite-N, nitrate-N, organic N, and total N), all sediment variables (C:N, organic matter, NH_4^+ , NO_2^- , NO_3^- , organic N, and total N), and DEA rates varied between June and October. One-way ANOVAs determined whether any sediment chemical variables (C:N, organic matter, NH_4^+ , NO_2^- , NO_3^- , organic N, and total N) or DEA and MIMS rates differed among community types (annual, perennial, mixed). Simple linear regressions explored relationships between any of the sediment variables, elevation, and DEA and MIMS rates. Regressions were also used to determine relationships between MIMS rates and the overlying core water nutrients ammonium-N, nitrate-N, and ortho-phosphate. To conform to assumptions of normality, sediment organic matter, ammonium-N, nitrate-N, total N, and DEA rates were square root transformed, and sediment organic N was natural log transformed. All statistical analyses were performed in SAS system for Windows (SAS Institute v8). Significance was determined at $\alpha = 0.05$.

Results

Seventeen species were identified in the aboveground vegetation; dominant species included *I. capensis*, *P. virginica*, *T. angustifolia*, *Polygonum arifolium* L., *B. laevis*, and *N. lutea*. Plot elevations ranged from 0.17-0.64 m above sea level. Annual

species cover increased with elevation ($R^2=0.42$, $p<0.001$), whereas perennial species cover did not. This correlation is corroborated by an ANOVA showing elevation to be higher in plots dominated by annual species than in plots dominated by perennial species ($F=4.67$, $df=37$, $p=0.016$). Tissue C:N ratio was higher in perennial graminoid species than in annual and perennial broad leaf species in both June (ANOVA, $F=13.04$, $df=17$, $p=0.001$) and October ($F=7.23$, $df=17$, $p=0.006$); however the three functional groups did not differ in tissue C:N ratio between seasons (RMANOVA, $F=2.0$, $p=0.168$; Table 8).

Table 8. Tissue C:N concentration means \pm 1 standard error. Perennial graminoids were significantly different from the other two functional groups at $\alpha = 0.05$ ($n=18$). Seasons did not differ within each functional group.

	June	October
Annual broad leaf	14.5 \pm 1.29	15.7 \pm 1.93
Perennial broad leaf	10.9 \pm 0.39	12.5 \pm 0.36
Perennial graminoids	21.7 \pm 2.27*	26.6 \pm 4.32*

Water nitrate-N and organic N had the highest concentrations in the overlying water column at Dyke Marsh in both June and October (Table 9). Water ammonium-N concentration in the water was higher in June than in October (ANOVA, $F=11.95$, $p=0.003$). In contrast, nitrate concentration was much higher in October than in June (ANOVA, $F=9.59$, $p=0.007$).

Table 9. Channel water concentration means \pm 1 standard error. $\alpha = 0.05$; $n=12$.

	June	October	F; df; P-value
NH ₄ -N (mg N/L)	0.17 \pm 0.07	0.06 \pm 0.03	11.95; 1, 23; 0.003
NO ₂ -N (mg N/L)	0.02 \pm 0.004	0.01 \pm 0.002	3.67; 1, 23; 0.07
NO ₃ -N (mg N/L)	0.36 \pm 0.09	0.67 \pm 0.17	9.59; 1, 23; 0.007
Organic N (mg N/L)	0.33 \pm 0.01	0.30 \pm 0.02	1.31; 1, 23; 0.27
Total nitrogen (mg N/L)	0.88 \pm 0.07	1.05 \pm 0.17	3.36; 1, 23; 0.09

Annual, perennial, and mixed community types did not differ in sediment C:N ratio, sediment or organic matter. However, sediment nitrate-N concentrations in June were higher in plots dominated by perennial species than in plots dominated by annual species (ANOVA, $F=3.89$, $p=0.03$; Figure 22). Sediment C and N both increased with elevation in both June and October ($R^2=0.12$, $p=0.03$; Figure 23), as did sediment organic matter in June ($R^2=0.17$, $p=0.01$). Sediment nitrate concentrations also increased with elevation in June ($R^2=0.14$, $p=0.02$; Figure 24); however, none of the other sediment nitrogen variables were related to any of the biotic or physical variables. All measured nitrogen variables were higher in June than in October (Table 10), and sediment organic matter did not differ between seasons.

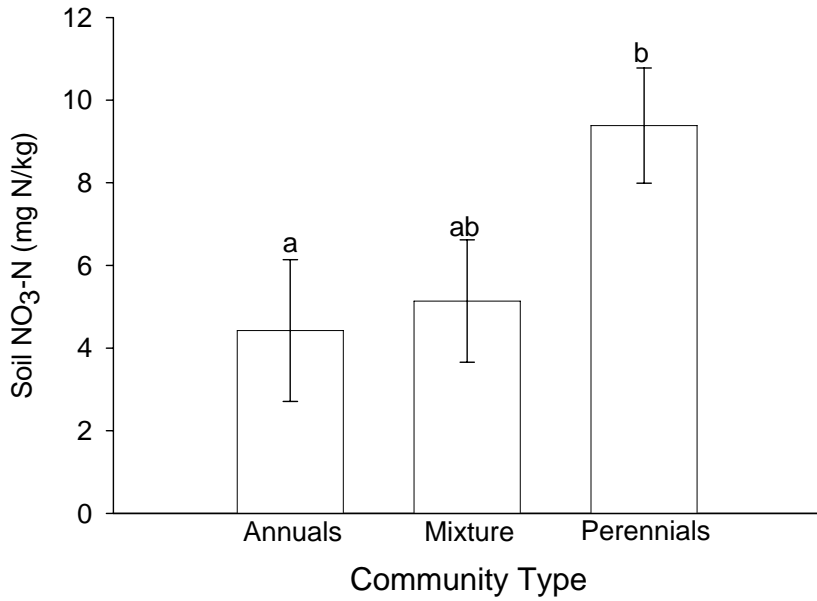


Figure 22. Soil nitrate-N means \pm 1 standard error for each community type (annual, perennial, or a mixture of the two) in Dyke Marsh. Matching letters above the error bars represent no significant difference. $\alpha = 0.05$.

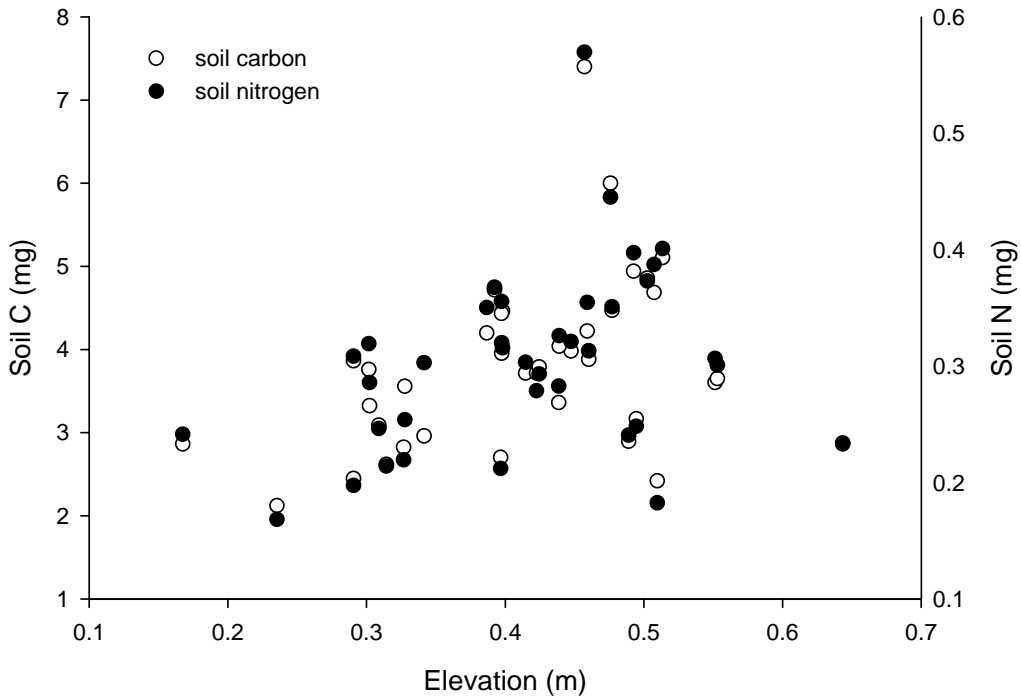


Figure 23. Relationships between soil C and soil N with elevation in June 2006 at Dyke Marsh.

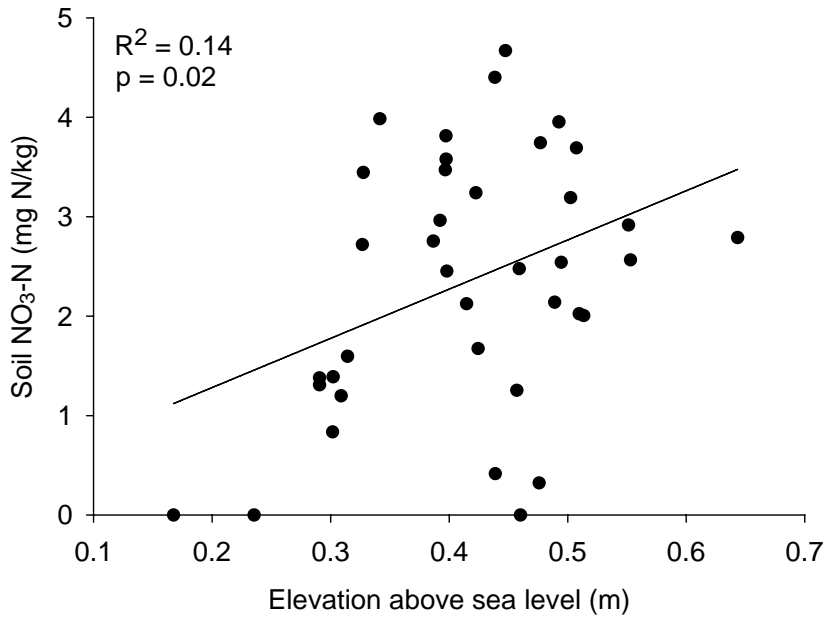


Figure 24. Soil nitrate-N increased significantly with elevation in June 2006 at Dyke Marsh.

Table 10. Nutrient concentrations in extracts of sediments (means \pm 1 standard error). All nutrient concentrations were significantly greater in June than the October (RMANOVA). $\alpha = 0.05$; $n=38$.

	June	October	F; df; P-value
NH ₄ -N (mg N/L)	14.4 \pm 1.2	4.5 \pm 0.4	74.5; 1, 70; <0.001
NO ₃ -N (mg N/L)	7.1 \pm 1.0	0.1 \pm 0.03	92.0; 1, 70; <0.001
Organic N (mg N/kg)	36.2 \pm 3.9	8.3 \pm 0.6	120.9; 1, 70; <0.001
Total nitrogen (mg N/kg)	57.5 \pm 4.6	12.9 \pm 0.7	146.2; 1, 70; <0.001

Potential denitrification rates (DEA) did not vary among community types; however, mean potential denitrification rates were greater in June than in October (RMANOVA, $F=20.06$, $p<0.001$; Figure 25). In June, potential denitrification rates from DEA increased with increasing sediment ammonium-N ($R^2=0.12$, $p=0.04$) and were not related to any other biotic, physical, or chemical variables. In October, potential denitrification rates from DEA increased with total N ($R^2=0.13$, $p=0.03$) but were not related to any other measured variables. Denitrification rates using the MIMS technique were only measured in October and did not differ among community types (ANOVA, $F=0.32$, $p=0.75$; Figure 26). Furthermore, the only relationship we found between denitrification rates obtained from MIMS and any measured biotic, physical, and chemical variables, was with sediment organic N ($R^2=0.72$, $p=0.03$; Figure 27).

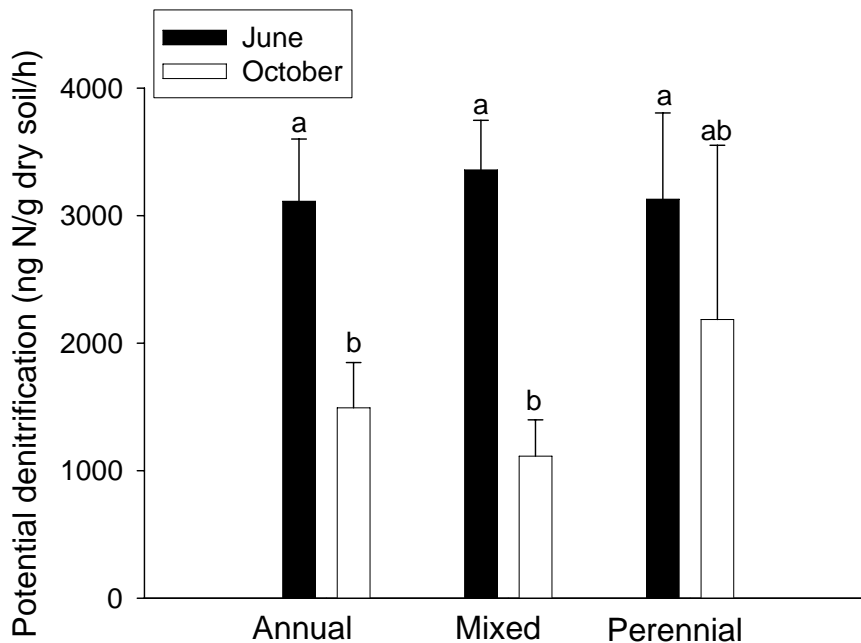


Figure 25. Mean potential denitrification rate measured using DEA with standard error bars for each community type: annual, perennial, or a mixture of the two, in Dyke Marsh. Matching letters above error bars represent no significant difference. $\alpha = 0.05$.

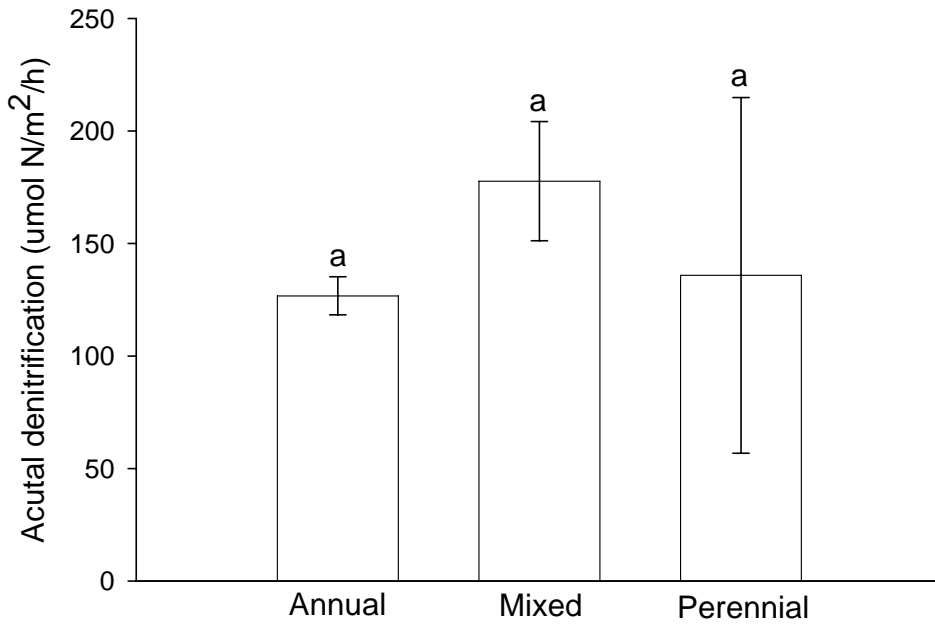


Figure 26. Mean denitrification rate measured using the MIMS technique with standard error bars for each community type: annual, perennial, or a mixture of the two, in Dyke Marsh. Matching letters above the error bars represent no significant difference. $\alpha = 0.05$.

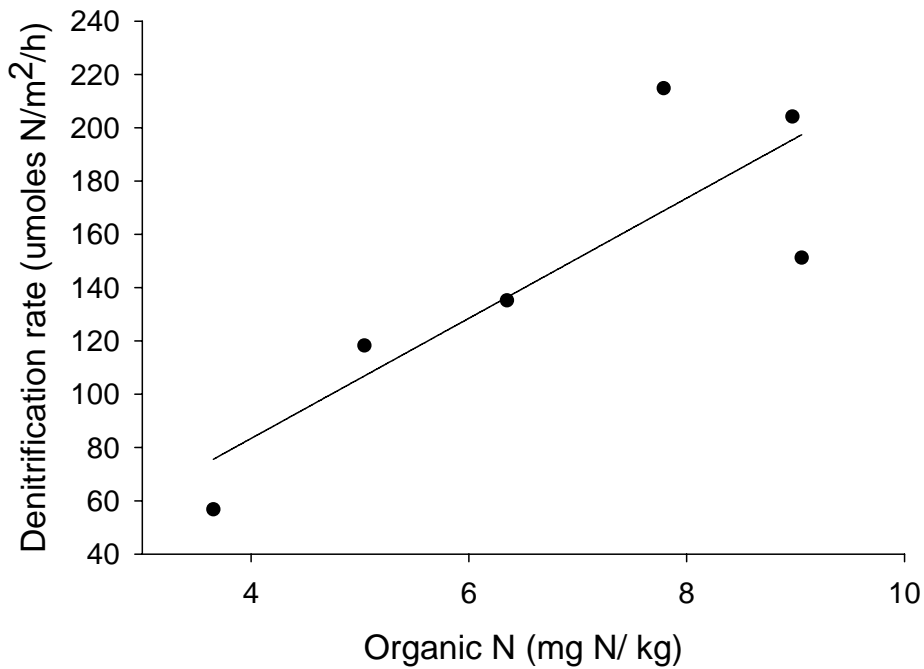


Figure 27. Relationship found between denitrification rates measured using MIMS to sediment organic N during October 2006 at Dyke Marsh.

Comparisons were made between denitrification rates derived from potential rates of N₂O production by DEA and those derived from total N₂ production rates by MIMS in the fall of 2006. A total of six comparisons were made for the six plots where we used both techniques. We found the DEA and MIMS rates to be fairly comparable and within the same order of magnitude for all six plots.

Discussion

Contrary to our original hypothesis, we did not find significant differences in denitrification rates among plant community types. One reason for this finding may be homogenization of soil characteristics throughout the marsh. Chapter IX demonstrates spatial and temporal movement of annual and perennial species through the marsh. Therefore, if species senesce and then change marsh locations, then they could influence soil carbon and organic matter in multiple areas of the marsh even if they are not the current dominant species in a specific area. With species influencing the soil in one location one year and then in a different location the next year, soil characteristics such as carbon and organic matter may become homogenized enough throughout the marsh to not see a difference in denitrification rates among community types.

There are few studies linking plant community composition and denitrification in marshes, although other work has been done on linking wetland plant diversity to other ecosystem functions (e.g. Levin et al. 2001, Brown et al. 2006). Otto et al. (1999) found that non-native plant and native plant communities in tidal freshwater marshes respond differently to nitrogen amendments in biomass production and foliar N content, but potential denitrification rates in sediments still

did not vary. Otto et al. (1999) suggest that microbial biomass and activity may be influenced so strongly by high organic matter levels in the sediments and tidal flushing that community nitrogen dynamics may not lead to marked differences in denitrification rates. This is consistent with results from the present study. Instead we observed a large change in denitrification rates with seasonality suggesting that temperature and/or nitrate availability in sediments were environmental variables that may be very important in influencing rates. Indeed, we found sediment extract nitrate concentrations to be higher in June (0-21.8 mgN/kg) versus October (0-0.23 mgN/kg; Table 10); however we also found plots dominated by perennial species to have higher sediment nitrate than annual and mixed communities. This demonstrates the complex interactions that exist among community structure and ecosystem processes in tidal freshwater marshes.

We did not find a significant relationship between elevation in the marsh and denitrification rates. Other studies of denitrification in wetlands have found denitrification rates to vary with organic matter content and anoxic microsites in sediments (Parkin 1987, Gold et al. 1998, Jacinthe et al. 1998; Findlay et al 2002; Casey et al. 2004). Our study documented relationships between plant community composition and many sediment variables (C, N, organic matter, NO_3) with elevation, demonstrating that variables that influence denitrification do vary with elevation gradients. However, elevation is an indirect gradient and may be representative of many different variables such as water inundation or disturbance. The relationships found may exist owing to the anoxic conditions that are created with the water inundation from the mixed tidal cycles. For example, percent organic matter in the

sediment may increase with increasing elevation in the marsh due to the potential effect of changes in water inundation on decomposition rates (Pfauder and Zimmer 2005, Langhans and Tockner 2006). At higher elevations, there is less overlying water and tidal fluctuations, therefore decomposition rates may be slower (Pfauder and Zimmer 2005) and there may be less leaching of organic nutrients resulting in high amounts of organic matter remaining in the sediment. Pfauder and Zimmer (2005) found intermediate daily inundation to increase microbial respiration, thereby speeding up decomposition rates; and they found higher microbial density under longer inundation times. Lower elevations in the marsh may receive larger inundation with longer residence time resulting in greater litter removal and consequently lower sediment organic content. We speculate the longer duration of standing water at low elevations may inhibit the process of nitrification (Baldwin and Mitchell 2000), potentially resulting in lower sediment nitrate concentrations than at higher elevations where there is more oxygen exchange in the sediment.

Denitrification rates using DEA were significantly higher during the summer at Dyke Marsh than in the fall, which is similar to what other aquatic studies have found (Merrill and Cornwell 2000; Gribsholt et al. 2005; Smith et al. 2006). Seasonal variations may depend on the temperature of the sediment and/or the concentration of dissolved oxygen in the overlying water (Kaplan et al. 1977; Kim et al. 1997; Richardson et al. 2004), or the amount of available nitrate and ammonium (Smith et al. 2006). Gribsholt et al. (2006) found that transformation rates of ammonium were three times higher in spring than in fall in a tidal freshwater marsh. They also discovered shorter inundation durations in fall that may have led to aerobic

conditions, thereby limiting denitrification rates. Our data showed that at Dyke Marsh when nitrate-N levels were high in the sediment (June), denitrification rates were high, and when nitrate-N levels in the sediment were low (October), denitrification rates were low. Therefore, the process of denitrification at Dyke Marsh may be either responsive to nitrogen availability in sediments as it fluctuates from season to season, or conversely denitrification may play a substantial role in influencing the nitrate concentration in sediments, or a combination of both of these scenarios.

Surprisingly, relatively few studies on denitrification have been conducted in tidal freshwater marsh ecosystems; nevertheless results from Dyke Marsh showed similar rates of denitrification (using the DEA method) to these other published studies (Table 11). The June denitrification rates from Dyke Marsh (Virginia) were within the confidence interval of rates from a tidal freshwater marsh in Connecticut (Findlay et al. 2003), and substantially higher than rates from a brackish tidal marsh in New Jersey (Windham and Meyerson 2003). To our knowledge, there have been no published studies of denitrification using the MIMS method in tidal freshwater marshes. Estimates of denitrification rates using MIMS for Dyke Marsh (range=56-214, mean=147 $\mu\text{mol m}^{-2} \text{h}^{-1}$) were similar to those rates from other aquatic ecosystems using the MIMS method. Smith et al. (2006) studied the Iroquois river, which runs through Indiana and Illinois and discovered rates averaging 100 $\mu\text{mol m}^{-2} \text{h}^{-1}$. When investigating denitrification along a salinity gradient, Kana et al. (1998) found rates averaging 125 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in the brackish area of the Choptank River, Maryland.

Table 11. Examples of a few denitrification rates published for tidal freshwater marshes. DEA = denitrification enzyme activity. For comparison, average June rate at Dyke Marsh using DEA was 3924 ng N/g/h.

Citation	Location	Technique	Denitrification Rate
Windham and Meyerson 2003	New Jersey	DEA	1800 ng N/g/h
Findlay et al. 2003	Connecticut	DEA	4928 ng N/g/h
Otto et al. 1999	New York	DEA	15694 ng N/g/h
Gribsholt et al. 2006	Belgium	Isotope pairing method	1000 $\mu\text{mol N/m}^2/\text{h}$
Bowden et al. 1991	Massachusetts	Acetylene block	5.7 $\mu\text{mol N/m}^2/\text{h}$
Verhoeven et al. 2001	Maryland	Acetylene block	83 $\mu\text{g N/m}^2/\text{h}$

Our results from MIMS taken four weeks following the DEA measurements produced comparable results within the same range. A recent study by Bernot et al. (2003), which is one of the few studies to actually compare DEA and MIMS denitrification techniques, found denitrification rate estimates using both techniques were similar in a Texas estuary. Spring and summer measurements of denitrification using MIMS in mainstem Potomac River sediments adjacent to the marsh were considerably lower than those observed in the marsh (49 ± 28 and $63 \pm 34 \mu\text{mol m}^{-2} \text{h}^{-1}$), despite similar nitrate concentrations (Bailey et al. 2006). These data suggest marshes may be a more important nitrogen sink than bottom sediments.

Although we found the two techniques to produce comparable rates between two sampling dates separated by a span of four weeks, there may have been potential errors in estimation associated with each method. Because Dyke Marsh is not N-limited (see Table 10), some of the problems with the DEA method do not exist for our study; however major concerns with the DEA method include inhibition of

nitrification, incomplete inhibition of N_2O reduction, and extracting the sediment cores may have disturbed the samples. Therefore, DEA results may lead to an underestimation, thereby creating an inaccurate picture of denitrification (Groffman et al. 2006). However, the DEA technique may also overestimate denitrification rates because the samples are anoxic and amended with glucose. A concern with the MIMS technique is that it is also performed in a laboratory where natural vertical advection conditions are not replicated and solute transport between surface water and sediment pore water is controlled mainly by diffusion (Mann and Wetzel 2000, Smith et al. 2006). Furthermore, much uncertainty with the MIMS method is created by potentially variable denitrification rates in blanks, resulting in larger errors at the lower range of denitrification rates (Smith et al. 2006).

Coupled nitrification/denitrification may be important in wetland sediments (Patrick and Reddy 1976, Reddy et al. 1989). This process may be particularly influenced by tidal fluctuations and large inputs of organic matter to the sediment in tidal freshwater marshes. Previous work has shown that coupled nitrification/denitrification in sediments of tidal freshwater wetlands may be important during certain seasons (Norwicki et al. 1999, Hamersley and Howes 2005), even though several studies on streams and rivers found nitrate in the overlying water column to influence denitrification rates (e.g. Seitzinger 1988, Kemp and Dodds 2002, Smith et al. 2006, Inwood et al. 2007). We examined the potential of nitrate concentrations in overlying water to influence denitrification rates in the cores from the MIMS technique by periodically measuring changes in nitrate concentrations in overlying water during a 12 hr. incubation of the sediment core. We examined the

difference in nitrate-N concentration of the overlying column water in the MIMS cores before and after the incubation and found only slight decreases in some cores but no decreases in others (Table 12). Because nitrate-N values did not significantly decrease throughout the incubation ($P < 0.05$), it appears that nitrate-N concentrations and availability in overlying water may not be the prime determinant of denitrification in sediments. The denitrification that occurred may have been supported by nitrate availability in sediments and/or the coupling of nitrification and denitrification in the sediment. It is difficult to assess the relative importance of coupled nitrification/denitrification in Dyke Marsh without proper use of ^{15}N labeling techniques that may be useful in quantifying and partitioning nitrification and denitrification in wetland sediments (e.g. Risgaard-Petersen 2003, Hamersley and Howes 2005, Cook et al. 2006).

Table 12. Total denitrification rate for each plot sampled using the MIMS technique in October 2006 for Dyke Marsh. Denitrification rates of the six plots did not vary significantly among vegetation community types. Column water nitrate-N concentrations varied only slightly between the start and end of the core incubations.

Community	Denitrification ($\mu\text{mol}/\text{m}^2/\text{h}$)	Column water $\text{NO}_3\text{-N}$ (mg/L)	
		Initial	Final
Annual	118.26	1.53	1.55
Annual	135.16	1.53	1.52
Mixed	151.21	1.52	1.13
Mixed	204.17	1.47	1.47
Perennial	56.77	1.53	1.51
Perennial	214.85	1.51	1.45

The mean rate of denitrification at Dyke Marsh using the direct flux MIMS technique was $147 \mu\text{mol N/m}^2/\text{h}$ and there were no significant differences in rates from MIMS across community type. When multiplying the denitrification rate by the current area of Dyke Marsh ($809,345 \text{ m}^2$), there may be a nitrogen removal potential of $118,974 \text{ mmol N/h}$ corresponding to a depth of 10 cm, or approximately 14,600 kg of nitrogen over an annual scale assuming no large seasonal variations (however rates may be much higher in spring and summer). If the U.S. National Park Service decides to recreate the marsh area that was lost due to previous decades of dredging (Hopfensperger et al. 2004, Hopfensperger et al. 2007), we estimate that restoring Dyke Marsh to its pre-dredging size of approximately 162 ha would approximately double the potential for mass removal of nitrogen. Therefore, restoring the area of Dyke Marsh through restoration efforts could greatly increase the nitrogen removal potential and may increase water quality flowing through the marsh. This potential nitrogen removal may be important for downstream areas, because the current amount of nitrogen entering Dyke Marsh through marsh channels and the Potomac River in summer and fall can be substantial (Table 9).

Although there is increasing interest in coastal wetlands restoration projects (Boesch 2006, Costanza et al. 2006, Mitsch and Day 2006), managers should potentially consider different options with respect to developing environmental variables (e.g. organic matter, plant communities, and elevation) that have been linked to denitrification. For example, providing labile organic matter through planting new vegetation, using substrate or fill rich in carbon, or adding decomposing vegetation may enhance denitrification rates in restoration projects aimed to expand

tidal freshwater marshes. A previous spatially explicit study comparing distributions of sediment chemical properties (including organic matter) and DEAs in created and restored wetlands to natural wetlands clearly demonstrated that created/restored wetlands are spatially homogenous in respect to denitrification and its related sediment properties versus the heterogeneous natural wetlands (Consanje and Reddy 2004, Bruland et al. 2006). The authors suggest the reduced spatial variability in created and restored wetlands is due to prior land-use and mitigation activities homogenizing sediment properties and that this results in the lack of developing the full range of biogeochemical cycling that occurs in natural wetlands. Elevation may also be important in influencing sediment properties and denitrification rates in Dyke Marsh, even though we only found a relationship between elevation and pore-water nitrate concentration and no relationship between denitrification rate and elevation. Managers may need to consider which topography will result in the most effective zones of nitrogen removal within the hydrologic context of the marsh. If sea level rise is not considered at Dyke Marsh, newly created areas may become permanently inundated through time, resulting in the loss of aerobic fluctuations and nitrification potentially influencing denitrification rates and consequently increasing hypoxic areas in the Chesapeake Bay. Because tidal freshwater marshes have been studied less compared to marine and estuarine wetlands, more work needs to be done on factors influencing rates of denitrification. Tidal freshwater marshes may represent important sinks of nitrogen in the landscape at the land margin interface with coastal ecosystems that may deserve attention from restoration efforts.

CHAPTER IX

SEED BANK AND VEGETATION DYNAMICS THROUGH TIME

(At the time of dissertation submission, this chapter is in preparation for submission to the *Journal of Applied Ecology*, titled “The chicken or the egg? Seed bank and vegetation dynamics in a tidal freshwater marsh” by K.N. Hopfensperger, K.A.M. Engelhardt, and T.R. Lookingbill.)

Vegetation communities are rarely stable; they may change directionally through space and time or they may fluctuate annually around some mean composition. Plant species turnover in tidal freshwater marshes depends on successful recruitment from local and regional species pools and the strength of interactions among the parent vegetation, the seed bank, and properties of the landscape. Thus, when wetland restoration project managers decide on whether to plant native vegetation or allow the system to self-design through natural recruitment from seed, they must understand these feedbacks. Some wetland restoration efforts have had success planting newly created or restored areas was successful (Reinartz and Warne 1993, Mulhouse and Galatowitsch 2003, Mitsch et al. 2005), while others found minimal effects of initial restoration plantings had no advantages (Simenstad and Thom 1996, Campbell et al. 2002, Kellogg and Bridgham 2002). For example, Neff and Baldwin (2005) determined that *Leersia oryzoides* L. (Sw.), a prolific colonizer dispersed via water, did not need to be planted when restoring a marsh on the Anacostia River in Washington, D.C.

Seed banks and standing vegetation have been studied in detail in tidal freshwater marshes (Leck and Simpson 1995, Leck 2003, Peterson and Baldwin 2004a); however, whether and how seed banks influence the composition of standing vegetation and how standing vegetation affects the seed bank in space and time is not

well understood. Most seeds of tidal freshwater marsh species disperse close to the parent plant (Leck and Simpson 1993) where they are incorporated into the seed bank or are washed away by tidal flushing. Leck and Simpson (1994) explored seed bank and vegetation dynamics in a New Jersey, USA, tidal freshwater marsh. They found seedling composition to mirror the species composition of the seed rain, and suggested that future plant distribution patterns cannot be determined solely by examining the distribution and abundance of adult plants. Furthermore, they found the seed bank to be diverse and to be influenced by a combination of seed production, dispersal, and seed persistence. In a later study of a newly created tidal freshwater marsh, Leck (2003) found that the large, persistent seed bank contributed to rapid development of a complete vegetation cover within one year. However, at the end of the four-year study, no spatial or temporal patterns in similarity were discovered between the seed bank and vegetation (Leck 2003). The differing results of the two studies led us to examine annual fluctuations in tidal freshwater marsh plant community composition and the relationship between standing vegetation and seed banks across time and space. The following three hypotheses were tested specifically (Figure 28): 1) Standing vegetation composition remains unchanged through time (pathway 1); 2) Aboveground vegetation composition determines seed bank composition for the following year (pathway 2); and 3) Seed bank composition drives that year's standing vegetation (pathway 3). We further hypothesized that the observed relationships are influenced by vegetation type and landscape structure, in particular distance to and size of nearest tidal channels and elevation.

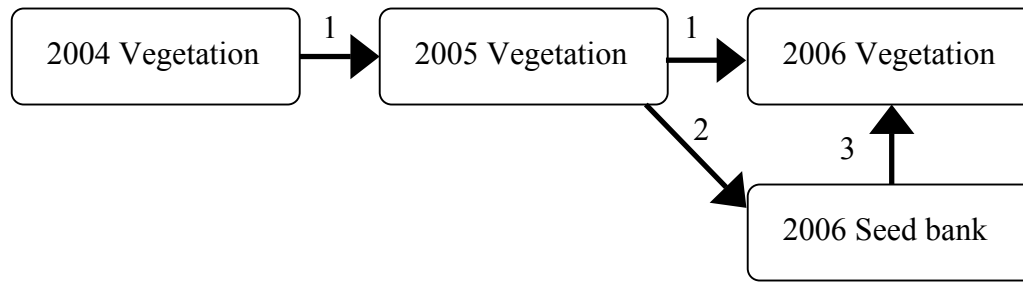


Figure 28. Conceptual flow diagram of pathways studied between the tidal freshwater marsh seed bank and aboveground vegetation.

Annual and perennial species may impact seed bank and vegetation dynamics in tidal freshwater marsh ecosystems differently because annual species rely solely on seeds to persist from year to year whereas perennial species can also reproduce vegetatively. Furthermore, while very little data exists on relationships between tidal flushing and seed distribution in tidal marshes, we hypothesized that areas dominated by annual species, which are characterized by dense stems, would be more efficient at trapping seeds than areas dominated by perennials such as *Peltandra virginica* (L.) Schott and *Nuphar lutea* (L.) Sm. that are typically less dense owing to large leaves. Tidal flushing moves sediments and hence seed banks (Pasternack and Brush 2001), thereby influencing dispersal of seeds and potentially decoupling the relationship between seed banks and vegetation. How much the relationship is decoupled, however, may depend on the structure and density of vegetation. Therefore, we predicted that higher similarity between standing vegetation and seed bank composition would be found in plots dominated by annual species, because annual species may provide more parent seeds and their dense stem structure may trap more sediments and seeds (Jutila 2003). Also, because annual species provide and trap their own seed, which then becomes available to germinate the following year, we

predicted plots dominated by annual species may change community composition the least through time.

Tidal channels offer a direct influx of seeds to the marsh substrate. When the tide level rises, water spills over the channel banks and flows over the marsh surface; when the tide level recedes, seeds from the regional pool may settle out and become trapped by the sediment surface and vegetation, and/or local seeds may be carried away to be deposited elsewhere. Leck and Simpson (1993) and Leck and Graveline (1979) both found the greatest number of species nearest to the stream channel. We hypothesized that the chance of a seed being trapped or carried away with sediment by tidal fluctuations would increase closer to tidal channels. Thus, we predicted that similarity between standing vegetation and seed bank composition would increase with distance from tidal channels. The size of the tidal channels may also influence seed deposition patterns. Larger channels contain a larger volume of water and may carry more sediment and seeds from the region; therefore the potential for immigration and emigration is higher nearer larger channels. On the other hand, smaller channels with smaller discharge may allow for fewer seeds to be deposited and taken away.

Elevation has been found to play a notable role in explaining patterns and processes of tidal freshwater marshes (Simpson et al. 1983, Odum et al. 1984, Mitsch and Gosselink 2000). Elevation tends to increase with distance from tidal channels (Simpson et al. 1983, Odum et al. 1984), and annual species tend to prefer higher elevations in tidal freshwater marshes (Baldwin and Mendelssohn 1998, Leck 2003, Seabloom and van der Valk 2003). Therefore, we predicted that higher similarity

between vegetation and seed bank composition would be found in plots at higher marsh elevations, because plots with high elevation support more annual communities, which we expect to be more stable, and because tidal fluctuations are less likely to carry parent seeds away.

Methods

Study Area

Field sampling was completed from 2004-2006 at Dyke Marsh Preserve (DMP, 38.77° N, 77.05° W), an 80 ha tidal freshwater marsh on the Potomac River, just south of Alexandria, Virginia. The marsh is owned by the National Park Service, which is seeking to recreate parts of the marsh that were lost to sand and gravel dredging in the 1930-1970's. The climate of the region is temperate with July mean daily maximum temperature of 31°C and January mean minimum temperature of -2°C (Johnston 2000). Average annual precipitation is 101.6 cm, of which up to 30.4 cm may be snowfall (Johnston 2000). Mixed tides at the study site have a mean tidal range of 0.5–0.9 m and a normal 0.91-m flux (Carter et al. 1994). Flow rates upstream of the site on the Potomac average 312 m³s⁻¹ and can range from 3.5 m³s⁻¹ to 14,000 m³s⁻¹ (NPS 1977). The highest flows occur in March and April after significant upstream snowmelt. The flow effect of the Potomac River on the marsh is usually minimal owing to the long distance from the main channel of the river to the marsh, although the entire marsh is within the flood plain of the Potomac River (NPS 1977).

Dyke Marsh is located in the Coastal Plain of Virginia, which is underlain by stratified, oceanic deposits of mud, sand, clay and gravel atop older crystalline rocks (NPS 1977, Johnston 2000). The alluvium deposits covering the marsh are

approximately 15 m thick, comprised of sand and gravel with lenticular interlayered units of silt and clay (NPS 1977). The hydric surface soils provide ideal habitat for a diverse plant community typical of Atlantic Coast tidal freshwater marshes (Simpson et al. 1983, Odum et al. 1984, Leck and Simpson 1995). Vegetation in the marsh is comprised of various sized patches of dominant annual species within a heterogeneous mix of perennial species.

Seed Bank and Vegetation Patterns

Ten various sized patches of *Impatiens capensis* Meerb., a common annual in tidal freshwater marshes (Simpson *et al.* 1985) and the dominant annual species at Dyke Marsh, were delineated using a Trimble GeoExplorer II unit. Using ArcView, 38, 1-m² plots were blindly placed inside (n=18), outside (n=10), or on the edge (n=10) of the *I. capensis* patches in the summer of 2004 to ensure the study included plots that were initially dominated by annuals, perennials, and a mixture of both annual and perennial species (Figure 6). More plots were placed inside the patches because in 2004 we were initially focused on annual species dynamics and placing them within the context of the whole marsh. The seed bank of each plot was sampled by taking three soil cores, 10 cm length by 3.81 cm diameter, per plot in March 2006 to determine seed bank composition and species abundance. The seedling emergence technique was then used to determine species composition of the seed bank (Poiani and Johnson 1988, Gross 1990, Baldwin et al. 2001). The soil cores were homogenized and spread over vermiculite in bedding trays and placed in a greenhouse misting room for germination at two water depths (flooded and saturated) to assure that species that prefer low and high water inundation had an opportunity to

germinate. Seedlings emerging from each sample were identified as young as possible and removed from the tray when identified. Seedlings of unknown species were transplanted and allowed to mature before identification. We recorded percent cover (Braun-Blanquet 1964) of all species for every plot during peak biomass in late July/early August 2004, 2005, and 2006 to assess the composition of the standing vegetation of the marsh. Cover was estimated by the same observer each year to minimize observer bias.

Data from all years were classified into discrete species groups (communities) using hierarchical agglomerative clustering with Ward's linkage method and Sørensen's distance measure (PC-ORD; MjM Software Design 2002). The seed bank and vegetation communities were classified together, but separated clearly into discrete groups in the classification analysis.

Sørensen's index of similarity (Sørensen 1948) was used to discern similarities between seed bank and vegetation composition and between vegetation compositions of consecutive years. Sørensen's index of similarity is simple, effective, and widely used to calculate floristic similarity, so results may be readily compared to other studies (Clarke and Warwick 2001, McCune and Grace 2002, Magurran 2004):

$$\text{Sørensen similarity} = 2w/(A+B),$$

where A = the number of species aboveground, B = the number of species belowground, and w = the number of species found aboveground for both years. We also used analysis of similarity (ANOSIM; Primer 5 Version 5.2.9 2002) to statistically compare seed bank and vegetation composition and vegetation compositions of consecutive years. ANOSIM computes a nonparametric test statistic

(R) from the ranked similarities of elements of a similarity matrix. A range of (-1, 1) is possible for R , with 1 representing complete dissimilarity among sampling categories (i.e., all samples collected in one year were more similar to each other than to any of the samples collected in other years). Random permutations of the similarity matrix and recalculation of R determine the significance level.

Community composition was plotted in ordination space using non-metric multidimensional scaling (NMS) to provide a visual and further statistical understanding of similarity of seed bank and standing vegetation compositions through space and time (PC-ORD; MjM Software Design 2002). NMS is a nonparametric technique where the axes are solved simultaneously through iterations and are not ordered. The number of axes chosen influences the final solution and produces various levels of stress. “Stress” in relation to NMS is the departure from monotonicity in the relationship between the original space and the reduced ordination space (McCune and Grace 2002). For all NMS analyses, we used Sørensen’s distance measure and chose the number of axes that minimized the final stress of the solution.

One-way analysis of variance (ANOVA) was used to determine if similarity between the 2006 spring seed bank and 2006 summer vegetation differed among community types. ANOVA was also used to determine if the temporal trends found in the standing vegetation from 2004 through 2006 (e.g. plot remained the same community type, the plot changed one year and then changed back the next, etc.) differed among community types. Chi-square goodness-of-fit test was then used to determine if the number plots representing annual, perennial, or mixed community

types differed within the plots whose standing vegetation remained the same community type from 2004 through 2006. Analyses to determine if the number plots representing annual, perennial, or mixed community types differed within the other temporal trends (e.g. plot changing community type one year and changing back again, or plot changing community in only one year) were not performed due to the low number of plots that represented these other trends. Community type for the ANOVA and Chi-square analyses was determined as the community type that dominated over the three-year sampling period.

Landscape Variables

Distances from each plot to the nearest channel were determined in ArcView using a digitized channel map for Dyke Marsh built from a September 2005 QuickBird image, a May 2004 MrSID image, and field verification data (A.H. Elmore unpublished data). Channels were placed into size classes according to their cross-sectional areas: #1 < 0.05 m²; #2 < 0.40 m²; #3 < 2.0 m²; #4 < 7.5 m²; and #5 > 7.5 m².

Marsh elevation was measured in the center of every plot in July 2004, using a Topcon Precision GPS HiPer Lite Pro with an accuracy of ±2 cm. The elevation data were tied to a local benchmark (NAD83 VA North) to georeference plot locations and elevations.

ANOVAs were used to determine if temporal trend in standing vegetation from 2004 through 2006 changed with elevation or distance to tidal channel. Multiple regression tested whether Sørensen's index of similarity between the seed bank and vegetation for all years combined was related to elevation and distance to channel. Analysis of covariance (ANCOVA) was then used to determine if similarity between

the 2006 seed bank and vegetation was correlated with plot distance to nearest channel even when channel size was accounted for, using distance as the continuous independent variable, channel size as the categorical independent variable, and similarity in species composition between the seed bank and vegetation as the response variable. ANCOVA was also used to determine if similarity between the 2006 seed bank and vegetation was correlated with elevation when community type was accounted for, using elevation as the continuous independent variable, community type as the categorical independent variable, and similarity as the response variable. Community type for statistical analyses using only 2006 vegetation data (ANOVA and ANCOVA) is represented by the classification analysis results for the 2006 vegetation plots. Distance from plot to nearest channel was square root transformed to conform to normality assumptions. Statistical analyses were performed in SAS system for Windows (SAS Institute 2000). Significance was determined at $\alpha = 0.05$.

Results

A total of 25 species were identified in the aboveground vegetation and the seed bank of Dyke Marsh. Twenty-two species germinated from the seed bank; dominant species included *Typha angustifolia* L., *I. capensis*, *Amaranthus cannabinus* (L.) Sauer, and *Cuscuta gronovii* Willd. ex J.A. Schultes. Seventeen species were identified in the aboveground vegetation; dominant species included *I. capensis*, *P. virginica*, *T. angustifolia*, *Polygonum arifolium* L., *Bidens laevis* (L.) B.S.P., and *N. lutea*. Sixteen of the 25 species were present in both the seed bank and the vegetation. Species found in the seed bank, but not in the vegetation included

Ranunculus cymbalaria Pursh, *Ludwigia palustris* L. (Ell.), *Juncus effuses* L., *Mikania scandens* L. Willd., *Carex frankii* Kunth, and *Pulchea foetida* (L.). Species found in the vegetation and not in the seed bank included *Onoclea sensibilis* L., *Acorus calamus* L., and *Zizania aquatica* L. Elevations of the plots ranged from 0.17-0.64 m. Distances from plot to nearest channel ranged from 0-45.6 m. The majority (76%) of plots were closest to channels of size class #2 (<0.40 m²), and no channels of size class #4 (<7.5 m²) were found near any plots.

The cluster analysis resulted in an eight-class solution that reasonably described the seed bank (2006) and vegetation (2004-2006) composition at Dyke Marsh (1.93% chaining; Table 13). We found that a classification with seven or less classes left out important associations, and ten classes were too many and included similar associations. Five of the eight classes represented the standing vegetation communities. Two of the eight vegetation classes were dominated by annuals (classes 3 & 4), one class was dominated by perennials (class 2), and two classes were a mixture of both annual and perennial species (classes 1 & 5). Species that were abundant in multiple classes included *I. capensis*, *T. angustifolia*, and *P. virginica*. Species that were not dominant in the marsh vegetation, but were also present in some of the classes included *Schoenoplectus fluviatilis* (Torr.) M.T. Strong and *L. oryzoides*.

Temporal variability of the aboveground vegetation at Dyke Marsh differed whether examining the marsh as a whole or at the plot level. At the whole marsh scale, vegetation composition essentially did not change from year to year (Table 14).

Species composition was 94% similar between 2004 and 2005 and 100% similar between 2005 and 2006 (Sørensen's similarity index; Table 15).

Table 13. Class descriptions represented in the seed bank and vegetation classification from Dyke Marsh. Classes 1-5 represent the vegetation and classes 6-8 are found only in the seed bank.

Class number	Description
1	<i>P. virginica</i> w/ <i>Leersia oryzoides</i> & annuals
2	<i>T. angustifolia</i> & <i>P. virginica</i> w/ <i>I. capensis</i>
3	<i>I. capensis</i> & <i>P. virginica</i> w/ <i>A. calamus</i> , <i>P. arifolium</i> , <i>B. laevis</i>
4	<i>I. capensis</i> w/ <i>S. fluviatilis</i>
5	<i>I. capensis</i> & <i>N. lutea</i>
6	<i>T. angustifolia</i> w/ <i>I. capensis</i> & <i>A. cannabinus</i>
7	<i>A. cannabinus</i>
8	<i>T. angustifolia</i>

Table 14. The number of plots representative of each community type of standing vegetation for all study years.

	Dominated by annuals	Dominated by perennials	A mixture of annuals and perennials
2004	20	8	10
2005	19	8	11
2006	21	6	11

Table 15. Comparison of species composition at Dyke Marsh Preserve between the standing vegetation in 2004, 2005, and 2006 and the seed bank composition of 2006 using Sørensen's similarity index and then tested by analysis of similarity (*R*, *p*-value). *R* and *p*-values for seed bank-vegetation relationships are global analysis of similarity values; *R* and *p*-values for temporal vegetation relationships are pair-wise analysis of similarity tests.

	Vegetation 2004	Vegetation 2005	Vegetation 2006
Vegetation 2005	94.1 (0.118, 0.001)	--	
Vegetation 2006	94.1 (0.022, 0.010)	100 (0.080, 0.002)	--
Seed bank 2006	--	71.8 (0.557, 0.001)	71.8 (0.562, 0.001)

However, four different temporal trends emerged at the plot scale (Table 16). The most common trend (74% of the plots) was for plots to remain in the same vegetation class from 2004 through 2006 (e.g., plot 5 in Table 16 and Figure 29). Fifty-four percent of the plots that remained in the same vegetation class were dominated by annual species, 18% were dominated by perennial species, and 28% were a mixture of the two (X^2 goodness-of-fit, $p=0.056$). The next most common trend (16% of the plots) was for plots to change class from 2004 to 2005, and then to revert back to the original 2004 class in 2006 (e.g., plot 14 in Figure 29), and 66% of the plots following this trend were dominated by annuals, while 17% of the plots were each dominated by perennials and a mixture of the two (Table 16). Two plots (Plots 17 annual and 27 mixed) changed vegetation class from 2004 to 2005, but then remained in the same class for 2006 (Figure 29). Another two plots (Plots 26 annual and 36 mixed) remained in the same class from 2004 to 2005, but then changed class in 2006 (Figure 29). Overall, of the ten plots that presented temporal trends throughout the study period, six were dominated by annual species, three were a mixture of annuals and perennials, and only one was dominated by perennial species (ANOVA; $F=0.40$, $df=2$, $p=0.68$). No relationships were found between standing vegetation temporal trends and elevation (ANOVA; $F=0.55$, $df=37$, $p=0.65$) or distance to tidal channel (ANOVA; $F=2.26$, $df=37$, $p=0.10$).

Table 16. Aboveground community classes for each plot in 2004, 2005, and 2006. Descriptions of community classes are presented in Table 13. Community types are represented by A= dominated by annuals, M= mixture of annual and perennial, and P= dominated by perennials.

Plot Number	Vegetation 2004	Vegetation 2005	Vegetation 2006	Community Type
1	3	3	3	A
2	3	3	3	A
3	3	3	3	A
4	3	3	3	A
5	3	3	3	A
6	3	3	3	A
7	4	4	4	A
8	2	2	2	P
9	2	2	2	P
10	2	2	2	P
11	1	1	1	M
12	4	2	4	A
13	4	2	4	A
14	5	4	5	M
15	2	2	2	P
16	4	4	4	A
17	2	4	4	A
18	5	5	5	M
19	5	5	5	M
20	5	5	5	M
21	5	5	5	M
22	5	5	5	M
23	2	4	2	P
24	5	5	5	M
25	2	2	2	P
26	4	4	1	A
27	2	5	5	M
28	5	5	5	M
29	4	4	4	A
30	4	5	4	A
31	4	2	4	A
32	4	4	4	A
33	4	4	4	A
34	4	4	4	A
35	4	4	4	A
36	5	5	4	M
37	4	4	4	A
38	4	4	4	A

We found only a weak relationship between the seed bank and the previous year's standing vegetation. Sørensen's similarity index between the 2005 standing vegetation and the 2006 seed bank was 71.8%, which is considered moderately similar using ANOSIM (Table 16). The 2005 vegetation data did not overlap with the 2006 seed bank data in the NMS ordination (Figure 30A). Conversely, an NMS ordination of the 2006 seed bank data and the 2006 aboveground vegetation shows a strong overlap between the two datasets (Figure 30B). Here, the Sørensen's similarity index was also 71.8%; however, ANOSIM results demonstrated slightly higher similarity (Table 15).

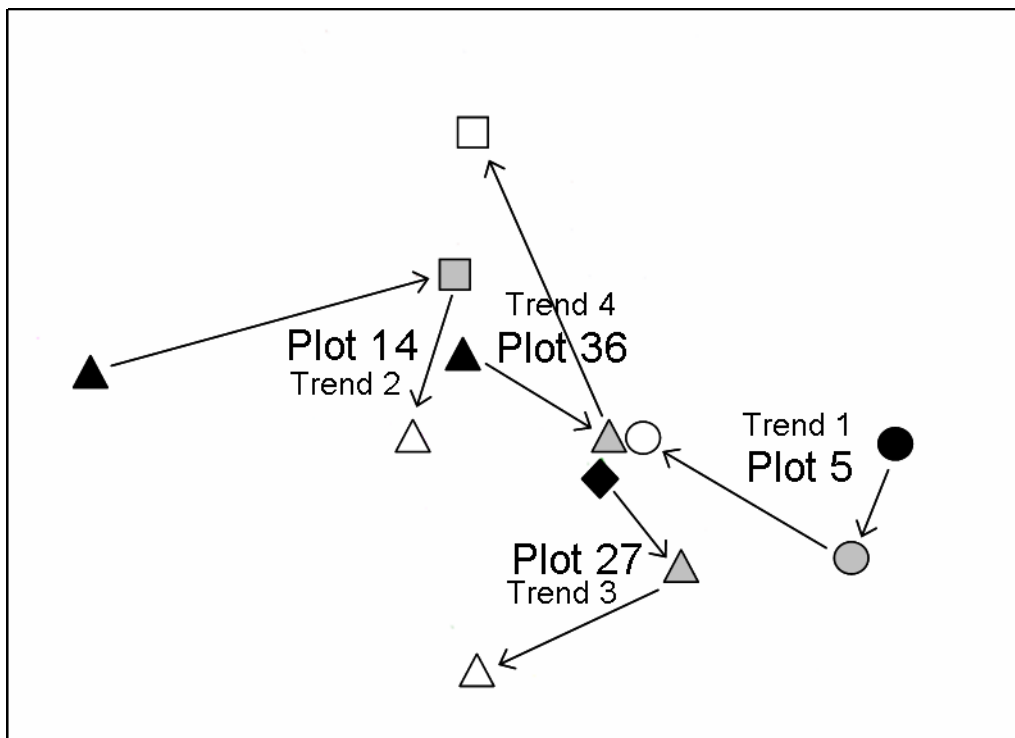


Figure 29. Non-metric multidimensional scaling ordination showing the four trends of spatial and temporal movement in the aboveground vegetation at Dyke Marsh. Arrows represent the movement of one plot from 2004-2006 through ordination space. All black shapes represent 2004, gray shapes represent 2005, and white shapes represent 2006. Vegetation classes are as follows: \diamond = class 2 (*Typha* and *Peltandra* w/ *Impatiens*); \square = class 3 (*I. capensis* and a mixture of species); \circ = class 4 (*I. capensis* w/ *S. fluviatilis*); \triangle = class 5 (*I. capensis* and *N. lutea*).

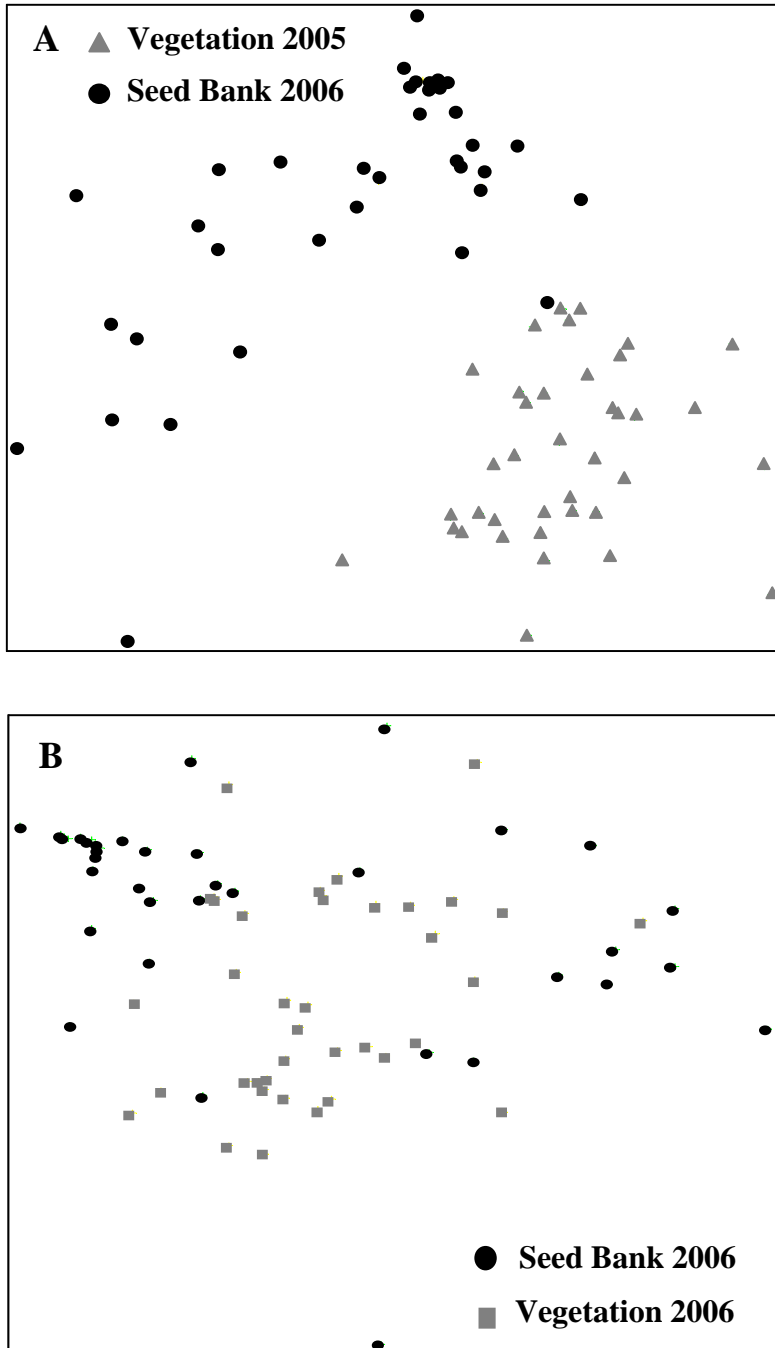


Figure 30. NMS analysis comparing the seed bank composition of 2006 with A) the vegetation composition of 2005 (stress=14.43). The axes with the highest R^2 are represented; axis 1 $R^2=0.280$ and axis 2 $R^2=0.346$. And with B) the vegetation composition of 2006 (stress=13.67). The axes with the highest R^2 are represented; axis 1 $R^2=0.358$ and axis 2 $R^2=0.296$.

Similarity between seed bank and vegetation was significantly greater in plots dominated by annual species than in plots dominated by perennial species or a mixture of the two (ANOVA; $F=3.02$, $df=37$, $p=0.034$). Seed bank and vegetation composition were 48% similar in plots dominated by annual species, while plots dominated by perennials were 34% similar and plots with a mixture of annuals and perennials were 33% similar. However, community type did not influence the significant relationship between similarity and elevation ($p=0.048$; ANCOVA overall model; $F=3.65$, $df=5$, $p=0.010$).

Seed bank and vegetation composition became more similar with increasing elevation (Figure 31) and increasing distance to nearest channel (multiple regression; overall model $R^2=0.208$, $p=0.006$). In contrast, channel size did not influence similarity between seed bank and standing vegetation composition when accounting for the significant influence of distance to tidal channel (ANCOVA overall model; $F=3.03$, $df=3$, $p=0.024$).

Discussion

While vegetation composition of the entire tidal freshwater marsh did not change over the three-year period of the study, we show that 1/4 of the communities sampled at the plot scale changed composition through time while 3/4 did not (pathway 1; Figure 28). Whether community composition fluctuates or not depends on the life history traits of the component species and whether the composition of the soil seed bank and the standing vegetation mimic each other (pathways 2 and 3; Figure 28), which may vary in space across environmental gradients.

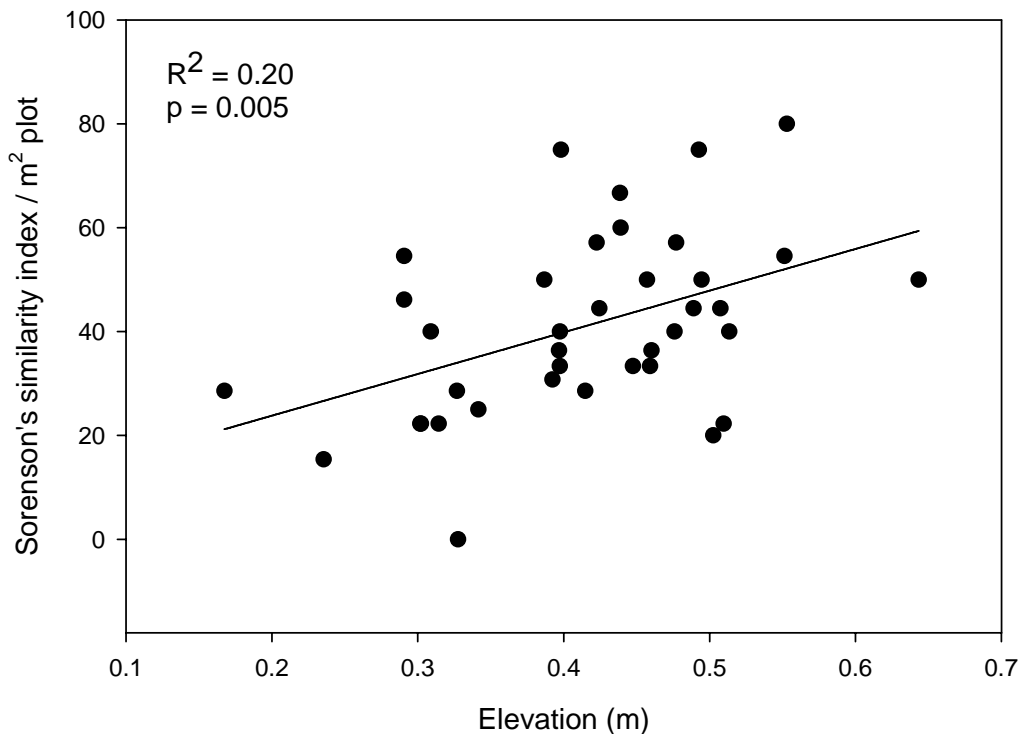


Figure 31. Similarity between seed bank and vegetation composition at each permanent plot increases with elevation at Dyke Marsh ($N = 38$).

We first discuss the observed temporal patterns in community composition of a tidal freshwater marsh. We then examine similarity between seed bank and standing vegetation composition and show how similarity is a function of landscape structure (community type, elevation, distance to and size of channels). Understanding relationships between changing community composition, seed banks, and landscape structure will allow us to inform the effective restoration of tidal freshwater marshes by highlighting the importance of developing spatially explicit restoration and monitoring designs.

Annual species provide more parent seeds and then trap those seeds with their dense stem structure than dominant perennial species that have sparser stem density

such as *P. virginica*. We therefore expected plots dominated by annuals to change community composition the least. In fact, this is what was observed; 75% of the plots that were dominated by annuals in 2004 did not change species composition, whereas only 62.5% of the plots that were dominated by perennial species in 2004 did not change species composition through 2006. Many annual tidal freshwater marsh species produce persistent seed banks (Leck and Simpson 1994), which allow annual species to be reliably recruited each year to the standing vegetation. Data from a separate study showed the 2004 and 2005 seed banks collected in the spring of each year to be highly similar in composition (Hopfensperger, unpublished data), suggesting seed banks are indeed persistent. Leck (2003) studied a newly created tidal freshwater marsh in New Jersey and found that the seed bank contributed to rapid development of complete vegetation cover within one year of marsh creation. After four years, species similarity between the seed bank and vegetation was moderate (Leck 2003), indicating additional colonization from the region. Leck's (2003) study is essential in demonstrating that donor soil and plant transplantation may not be necessary for tidal freshwater marsh creation. However, many other site characteristics such as waterfowl abundance, proximity of invasive species, and proximity of nearby reference sites must be examined before following this suggestion. In the end, even though more than half of the plots that changed community type were dominated by annual species and the annual species seem to be producing reliable seed banks, landscape structure may be playing an important role in determining standing vegetation patterns.

Temporal trends in the standing vegetation are a function of survival and recruitment from the local and regional species pool. Standing vegetation did not strongly influence the following year's seed bank composition (pathway 2), suggesting that sediments and their seeds are well mixed through tidal flushing. The seed bank was sampled in the spring such that sediments had time to shift and mix over the winter months. In contrast, the composition of the seed bank influenced standing vegetation composition (pathway 3), suggesting that species composition in this tidal freshwater marsh is primarily driven by recruitment from regional seed sources. This recruitment is not homogeneous across the entire marsh but depends on landscape structure. Specifically, we found that elevation and distance to nearest channel appear to influence similarity between the seed bank and vegetation of the same year. In contrast, similarity was not affected by channel size and community type (dominated by annuals, perennials, or a mix of the two life histories).

The extensive network of tidal channels scour and deposit sediments and seeds throughout the marsh, thereby creating areas of temporally shifting vegetation where tidal flushing is strong, and areas that are relatively stable where tidal flushing is weak. Areas at higher elevations may rarely be inundated by tides. Thus, seeds do not travel far from the parent plant and may be incorporated into the seed bank without tidal contributions of new seeds. In addition, plots at farther distances from tidal channels are less likely to receive seed inputs from the region because vegetation closer to the channels will have intercepted them. Thus, plots with higher similarities between seed bank and vegetation communities were farthest from tidal channels and at higher elevations. Furthermore, channel size may not have been a factor at Dyke

Marsh, because there was not much variation in the size of channels throughout the marsh; most of the channels found throughout the marsh were the smallest size classes #1 and #2 ($<0.40 \text{ m}^2$).

Our data leads us to believe that while a reliable seed bank is essential for recruitment into the local species pool, local elevations and subsequent hydrologic conditions that exist during germination may dictate the mature standing vegetation community each year in a tidal freshwater marsh. However, elevation is an indirect gradient and may be representative of many different variables such as water inundation or disturbance. The amount of water inundation an area or plot receives from a series of spring storms, a high amount of snowmelt, or drought conditions may influence the composition of the seed bank through scouring and deposition events. In addition, many dominant tidal freshwater marsh species germinate more readily at higher elevations where conditions tend to be drier (Baldwin et al. 2001, Peterson and Baldwin 2004b). Thus, which seeds germinate and are recruited into the species pool will depend on elevation gradients and the environmental conditions experienced each spring. Along with elevation and distance to tidal channels, disturbance from ice scour (Belanger and Bedard 1994), large storms (Nyman et al. 1995), or wrack-burial (Brewer et al. 1998) may play an important role in determining community dynamics (Grime 1977); however these disturbance mechanisms have rarely been studied in tidal freshwater marshes.

Our study provides support for several recommendations on restoring and creating tidal freshwater marsh habitat. First, spatial and temporal marsh vegetation patterns are scale dependent. For example in our study, the same species made up the

composition of the entire marsh ecosystem from year to year, but the abundances and locations of those species shifted annually within parts of the marsh. Therefore, scale must be taken into account when monitoring restoration success. Restoration monitors should inventory vegetation at a smaller scale to obtain data that could be used for understanding spatial and temporal dynamics within the marsh, and then pool that data to study whole marsh temporal vegetation dynamics.

Second, restoration managers may allow for partial self-design where diverse seed banks or seed rain are present. Leaving a site to colonize on its own can greatly reduce the cost of a restoration; however, the method of self-design is not without problems. Even if desired species are present in the seed rain, they may not germinate under the current environmental conditions (Neff 2002). In addition, invasive and exotic species may colonize a site as readily as native species. Few studies are published on the long-term success of leaving a created or restored wetland site unplanted (Zedler and Callaway 1999, NRC 2001). On the other hand, studies that document the outcome of “Fast-forward” (initial planting) restoration methods are few and report conflicting results. Furthermore, many studies may not accurately represent the long-term success of a planted site owing to the short time and small spatial monitoring scales (Mitsch and Wilson 1996). Therefore, we recommend seeding or planting key species that are not in the seed bank, and to be flexible and aware that the vegetation composition may change spatially and temporally.

Third, creating a physical habitat template that allows the establishment, survival and reproduction of a variety of wetland species is key. An extensive network of channels throughout a tidal freshwater marsh is necessary to allow

dispersal of seeds and flow of nutrients to all marsh areas. Syphax and Hammerschlag (1995) found channel creation a successful technique for their tidal freshwater restoration in Washington, D.C. Similarly in a salt marsh restoration in New Jersey, Weishar et al. (2005) found that breaching dikes and allowing high velocity sheet flow across the marsh plain produced braided stream channels throughout the marsh favorable for restoration. In combination with creating a network of tidal channels, a variety of elevations are necessary to ensure successful germination of a variety of species, and therefore, a marsh that supports a diversity of species characteristic of low, mid, and high elevations.

CHAPTER X

LINKING VEGETATION PATTERNS AND NITROGEN DYNAMICS IN A TIDAL FRESHWATER MARSH

Situated at the interface between upland watersheds and coastal estuaries, tidal freshwater marshes are responsible for removing significant amounts of nitrogen from our waterways (Otto et al. 1999, Verhoeven et al. 2001, Findlay et al. 2003, Gribsholt et al. 2006), thereby improving downstream water quality. For example, hypoxic areas that develop in Chesapeake Bay contribute to poor water quality and are detrimental to numerous aquatic organisms (Cooper and Brush 1991, Brownlee et al. 2005, Eby et al. 2005, Kemp et al. 2005). However, tidal freshwater marsh ecosystems may alleviate some of these problems by intercepting polluted water entering an estuary and removing nitrogen through the microbial process of denitrification that is promoted by low O₂, reduction-oxidation reactions, and high organic matter inputs common in these systems (Odum 1988). Tidal fluctuations allow for the development of a thin oxic surface layer of sediment above the generally anaerobic sediments of a tidal freshwater marsh (Mitsch and Gosselink 2000), which allows for the coupling of nitrification and denitrification processes. and the removal of nutrients from the system (Mitsch and Gosselink 2000). Furthermore, the diverse and high productive vegetation community of a tidal freshwater marsh provides an unlimited supply of organic matter to the substrate as fuel for denitrifying microbes (Barko et al. 1991).

Different plant species may indirectly affect the process of denitrification in a variety of ways (Cornwell et al. 1999). Annual and perennial species may alter the amount and form of nitrogen available for denitrification (Reddy and DeBusk 1987). For example, annual plant species may allocate nitrogen towards new growth, which is then fully senesced and returned to the sediment in the fall. In contrast, perennial species may store a portion of nitrogen in belowground structures that do not senesce each year. Annual and perennial species may also influence organic matter differently by the quality and quantity of biomass that senesces each year.

Tidal freshwater marsh systems are on the decline, not only from urbanization, but also from global warming. The fact that temperatures are increasing and sea level is and will continue to rise has now been confirmed and is accepted by policy makers (IPCC 2007). Increasing temperatures are directly linked to rising sea level (IPCC 2007), which can have deleterious effects on tidal freshwater marsh ecosystems. While tidal freshwater marshes were originally created under conditions of slowly rising sea level (Belknap and Kraft 1977, Colquhoun and Brooks 1986, Fletcher et al. 1993), the rate at which sea level is predicted to rise is radically greater than historic rates. In the short-term, climate variability may cause marsh dry-outs (Manabe and Wetherald 1986), where areas of tidal freshwater marshes endure drought conditions and increased salinity, which would cause them to become a source of nitrogen to the landscape instead of a sink (Dowrick et al. 1999, Mulhouse et al. 2005, Brown et al. 2006). However, in the long-term, any marshes that fail to accumulate sediment at the rate of sea level rise will become open bodies of water. In Chesapeake Bay, sea level is expected to rise double the average global rate (Douglas

1991). Therefore, tidal freshwater marsh ecosystems in the Bay watershed have a high chance of being permanently inundated by water, thereby completely removing the important functions that these upriver marshes provide.

Little is known about what effects sea level rise will have on tidal freshwater marsh ecosystem processes, which are driven by the interactions between sea level rise, the physical environment of the marsh, marsh vegetation dynamics, and nutrient cycling. Martin and Reddy (1997) created a spatially-explicit model to evaluate the fate and transport of nitrogen in wetland systems. They discovered that wetland vegetation is integral in the transport of soluble nitrogen, and that wetland species with greater evapotranspiration rates promote greater nitrogen removal (Martin and Reddy 1997). However, while Martin and Reddy's (1997) model examined wetland vegetation and nitrogen, sea level rise was not a component of the model. Rybczyk et al. (1998) and Day et al. (1999) both modeled the effects of sea level rise on wetlands. Rybczyk et al. (1998) focused on simulating the response of elevation, which was linked to primary production, eustatic sea level rise, and several sediment parameters in a Louisiana wetland. They discovered that wetland sediment accretion would not be enough to keep pace with current or predicted rates of rising sea level. Day et al. (1999) used a simulation model to predict the effect of sea level rise on wetland elevation in Venice Lagoon, Italy. They found that several sites would be underwater in the next 100 years with the predicted rise in sea level. However, these specific models did not incorporate vegetation, nutrients, water inundation, and sea level rise together as parameters in one model.

In this paper we explore the potential effects projected sea level rise might have on a tidal freshwater marsh's ability to remove nitrogen. To address this problem we studied the relationships between marsh vegetation and denitrification, which allowed us to project the direct and indirect effects of sea level rise on denitrification. We created a model based on field studies of a tidal freshwater marsh (Chapters VII-IX) for parameterization and calibration. Simulations were run with low and high scenarios of climate change created by the Intergovernmental Panel on Climate Change (IPCC). Our goal was to better understand how an increase in sea level may alter marsh plant communities, and how those vegetation changes may affect denitrification rates, which will ultimately influence the amount of nitrogen that flows downstream into the Chesapeake Bay.

Methods

Site description

Dyke Marsh Preserve is one of the last large tracts of tidal freshwater marsh remaining along the Potomac River, Virginia, USA. The 80 ha marsh is owned by the National Park Service, who is seeking to recreate parts of the marsh that were lost to sand and gravel dredging during the 1930-1970's. The climate of the region is temperate with an annual average temperature range of -2–31°C, and average annual precipitation is 101.6 cm (Johnston 2000). The site experiences mixed tides with a mean tidal range of 0.5–0.9 m and a normal 0.91-m flux (Carter et al. 1994). The hydric surface soils of the marsh provide ideal habitat for a diverse plant community typical of Atlantic Coast tidal freshwater marshes (Simpson et al. 1983, Odum et al. 1984, Leck and Simpson 1995). Vegetation in the marsh is comprised of a

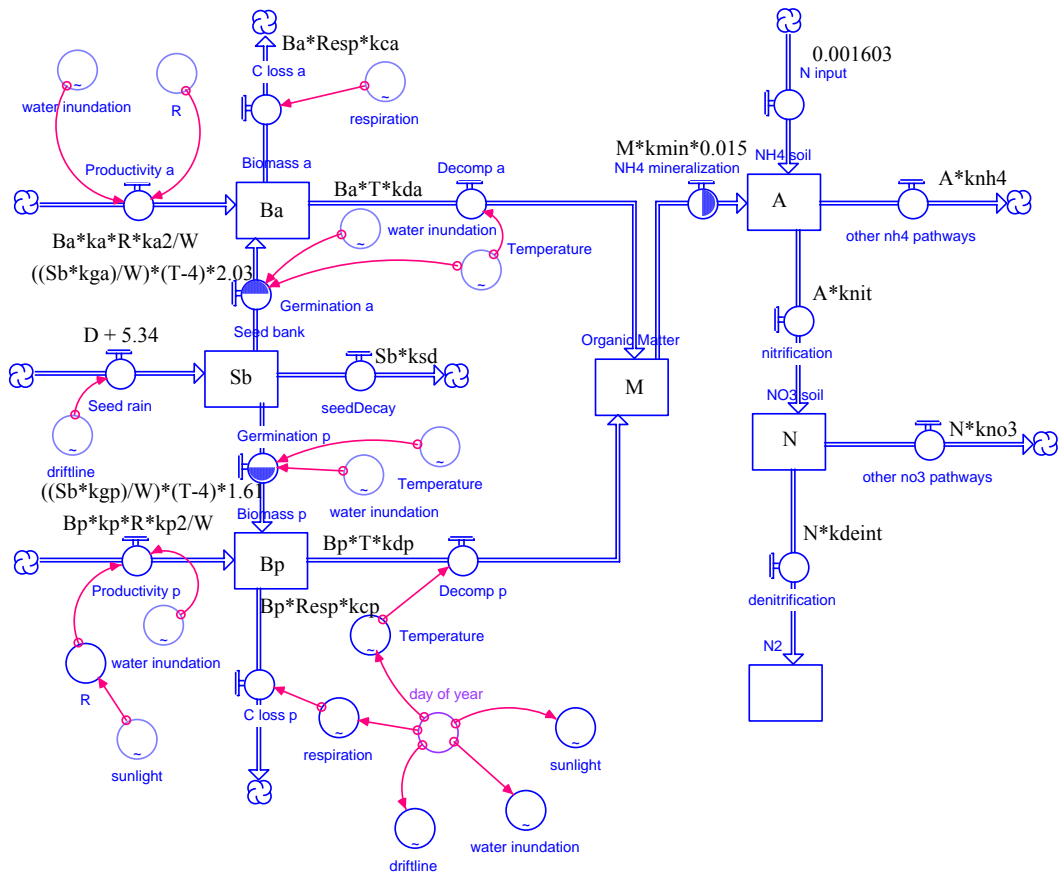
community of a few dominant perennial species interspersed with various sized patches of dominant annual species.

Model boundaries and structure

The model (Figures 32 and 33) represents the emergent marsh area of Dyke Marsh, an open-system with water and nutrients flowing into and out of the system. Nitrogen inputs to the model come from the watershed, and outputs continue on downstream to the Chesapeake Bay. The model uses five forcing functions, temperature, sunlight, respiration, water inundation, and seed rain. Sunlight ($W\ m^{-2}$) data represents solar radiation at the site (Barry and Chorley 1992). Respiration values were obtained from a carbon gas flux study performed on macrophytes in a Virginia tidal freshwater marsh (Neubauer et al. 2000). Water inundation was estimated by averaging the mean daily tide height above sea level for each month of 2005 at Dyke Marsh, and relativizing it to one so there would be no negative values. The seed rain forcing function (Sr) was a summation of the external input from drift-line collections and internally generated from resident plants ($-5.34\ seeds\ m^{-2}\ d^{-1}$) in Dyke Marsh (Figure 33). Drift-line inputs were estimated by using the net change in the number of seeds in the drift-line between each sampling period to estimate the total number of incoming seeds per day. These results were then divided by the total marsh area to get number of seeds per day per m^2 . Our field study (Chapter VII) revealed that drift-line contribution was much smaller than marsh internal seed generation. This agreed with Leck and Simpson's (1993) observation that parent plant contribution to the seed bank was significant in a tidal freshwater marsh. To estimate parent plant contribution to the seed rain, we divided the initial seed bank value of

2924 seeds m^{-2} by our best estimate of seed bank turnover time, which was 1.5 years (547.5 d; =5.34 seeds $\text{m}^{-2} \text{d}^{-1}$).

We programmed the simulation model with STELLA iconographic modeling software (version 7.0.1; High Performance Inc., USA). Numerical simulation used Runge-Kutta 4 integration method with $\Delta t = 1$ day. A list and description of all abbreviations, inputs, flows, and storages programmed into the model are shown in Table 17.



$$\begin{aligned}
 dBa &= Ba*ka*R*ka2/W + (Sb*kga)/W*T-4*2.03 - Ba*Resp*kca - Ba*T*kda \\
 dBp &= Bp*kp*R*kp2/W + (Sb*kpa)/W*T-4*1.61 - Bp*Resp*kcp - Bp*T*kdp \\
 dSb &= D+5.34 - Sb*ksd \\
 dM &= Ba*T*kda + Bp*T*kdp - M*kmin*0.015 \\
 dA &= M*kmin*0.015 + 0.001603 - A*knh4 - A*knit \\
 dN &= A*knit - N*kno3 - N*kdenit
 \end{aligned}$$

Figure 32. STELLA diagram of Marsh Vegetation and Nitrogen model with pathway expressions given in the rate of change equations for state variables. Abbreviations are listed under the column “Variable” in Table 18.

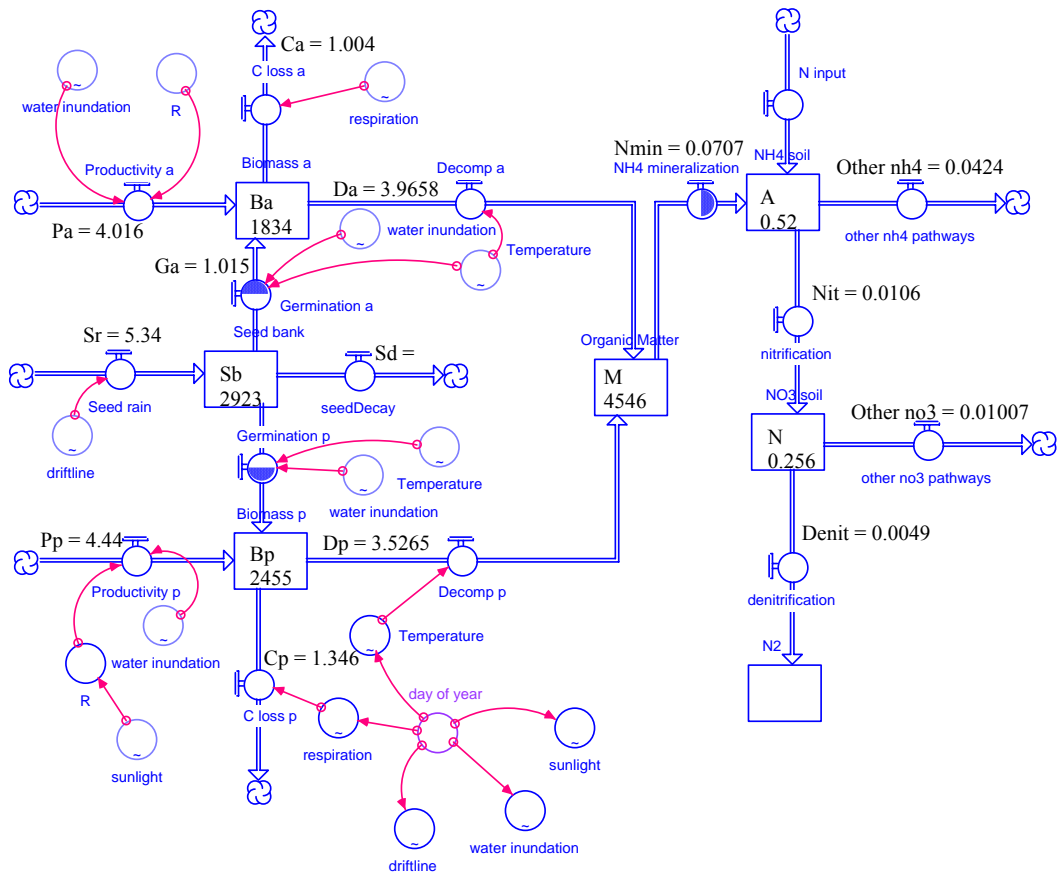


Figure 33. STELLA diagram of Marsh Vegetation and Nitrogen model with definitions and calibration values of flows and storages (*Ba*, annual biomass; *Sb*, seed bank; *Bp*, perennial biomass; *M*, organic matter; *A*, sediment ammonium; *N*, sediment nitrate). Abbreviations listed under the column “Variable” in Table 18.

Table 17. Description of driving energies, stocks, and flow data used to calibrate the Marsh Vegetation and Nitrogen model.

Note	Description	Variable	Equation	Calibration			Reference	
				Value	Unit	k-Value		
Forcing Functions								
	Driftline	D		0.008	seed m ⁻² d ⁻¹		Field data from DMP Estimated using field data from DMP and reference	Hussey & Odum 1992
	N input	Ninput		0.001603	g d ⁻¹			
	Respiration	Resp		0.0053	g C m ⁻² d ⁻¹		Estimated as 20% sunlight	Neubauer et al. 2000
	Reflectance	R		50	W m ⁻² d ⁻¹			
	Sunlight	S		250	W m ⁻² d ⁻¹			Barry and Chorley 1992
	Seed rain	Sr	D+5.34	5.34	seed m ⁻² d ⁻¹		Estimated using field data and reference	Leck and Simpson 1994
	Temperature	T		27.5	°C d ⁻¹		Field data from DMP, averaged by month, and relativized by 1	
	Water inundation	W		1.14	m d ⁻¹			
Flows								
	Seed decay	Sd	Sb*ksd	4.9399	seed m ⁻² d ⁻¹	0.00169	Estimated	
	Productivity annuals	Pa	Ba*ka*R*ka2 / W	4.016	g m ⁻² d ⁻¹	ka=9.32*10 ⁻⁴ ka2=0.0536	Estimated	
	Productivity perennials	Pp	Bp*kp*R*kp2 / W	4.44	g m ⁻² d ⁻¹	kp=9.32*10 ⁻⁴ kp2=0.0442	Estimated	
	Germination annuals	Ga	((Sb*kg _a)/W)* (T-4)*2.03	1.015	g m ⁻² d ⁻¹	8.3*10 ⁻⁶	Estimated using field data from DMP and references	Whigham et al. 1978 Leck and Simpson 1994
	Germination perennials	Gp	((Sb*kg _p)/W)* (T-4)*1.61	0.483	g m ⁻² d ⁻¹	4.98*10 ⁻⁶	Estimated using field data from DMP and references	Whigham et al. 1978 Whigham et al. 1979 Leck and Simpson 1994
	Carbon loss annuals	Ca	Ba*Resp*kca	1.004	g m ⁻² d ⁻¹	0.103	Estimated 20% of Ba	Neubauer et al. 2000
	Carbon loss perennials	Cp	Bp*Resp*kcp	1.346	g m ⁻² d ⁻¹	0.103	Estimated 20% of Bp	Neubauer et al. 2000

Stocks	Decomposition annuals	Da	Ba*T*kda	3.9658	$\text{g m}^{-2} \text{d}^{-1}$	$7.86*10^{-5}$	Estimated 79% of Ba	Mitsch & Gosselink 2000
	Decomposition perennials	Dp	Bp*T *kdp	3.5265	$\text{g m}^{-2} \text{d}^{-1}$	$5.22*10^{-5}$	Estimated 52.4% of Bp	Mitsch & Gosselink 2000
	NH4 mineralization	Nmin	M*kmin	0.0707	$\text{g m}^{-2} \text{d}^{-1}$	$9.34*10^{-4}$	Estimated using field data from DMP and reference	Bowden et al. 1991
	Other NH4 pathways	Other nh4	A*knit	0.0106	$\text{g m}^{-2} \text{d}^{-1}$	0.0815	Estimated using field data from DMP and reference	Bowden et al. 1991
	Nitrification	Nit	A*knh4	0.0424	$\text{g m}^{-2} \text{d}^{-1}$	0.0414	Estimated using field data from DMP and reference	Bowden et al. 1991
	Other NO3 pathways	Other no3	N*kno3	0.01007	$\text{g m}^{-2} \text{d}^{-1}$	0.0393	Estimated using field data from DMP and reference	Bowden et al. 1991
	Denitrification	Denit	N*kdenit	0.0049	$\text{g m}^{-2} \text{d}^{-1}$	0.0191	Averaged field data using DEA	
	Biomass annuals	Ba	Pa + Ga – Ca – Da	1834	g m^{-2}		Estimated using field data from DMP and reference	Whigham et al. 1978
	Seed bank	Sb	Sr – Ga – Gp	2923	seed m^{-2}		Field data from DMP	
	Biomass perennials	Bp	Pp + Gp – Cp – Dp	2455	g m^{-2}		Estimated using field data from DMP and reference	Whigham et al. 1978
	Organic matter	M	Da + Dp – Nmin	4546	g m^{-2}		Field data from DMP	
	NH4 sediment	A	Ninput + Nmin – Nit – other NH4	0.52	g m^{-2}		Field data from DMP	
	NO3 sediment	N	Nit – Denit – other NO3	0.256	g m^{-2}		Field data from DMP	
N2	N2	Denit	0	g m^{-2}		Start model at 0		

State variables

The model state variables included seed bank (Sb), annual biomass (Ba), perennial biomass (Bp), organic matter (M), sediment ammonium (A), sediment nitrate (N). Sb was assumed to represent the number of annual and perennial seeds available for germination per m^2 throughout Dyke Marsh. Ba and Bp represented total above and belowground biomass of annual and perennial species, respectively, throughout the entire emergent marsh. M represented all organic matter (composed of carbon, nitrogen, etc.) in the top 10 cm of sediment per m^2 in Dyke Marsh. A and N represented available inorganic nitrogen concentrations from sediment extracts in the top 10 cm of sediment throughout Dyke Marsh. The nitrogen gas stock (N_2) was included to sum the amount of nitrogen gas produced from denitrification, but did not have an effect on any stocks or processes.

Interactions and pathways

A major outflow pathway for the seed bank was seed decay (Sd). Tidal freshwater marshes have a high rate of seed decay due to the transient nature of many of the annual species seeds (Simpson et al. 1983, Parker and Leck 1985, Simpson et al. 1985).

The other pathway options for seeds to leave the seed bank included germination of annual and perennial species (Figure 32). Germination rate was modeled as the function of Sb , ambient temperature ($T - 4^\circ\text{C}$), and water inundation (Table 17). The temperature term was forced to equal zero during the winter, which is 4°C (the mean winter T) was subtracted from ambient T . This stopped the process of germination during the winter months. Seed germination in tidal freshwater marshes has been tightly linked to elevation and subsequent water inundation (Baldwin et al. 1996, Baldwin et al. 2001,

Leck, 2003). Therefore, we had water inundation inhibit both annual and perennial germination by relating germination to the inverse of inundation (Table 17). Unit conversions were necessary in the annual and perennial germination pathways to convert seeds m^{-2} coming from the seed bank into g biomass m^{-2} for the biomass storages (Table 18). The unit conversions were obtained by calculating grams per stem, calculating the amount of stems per seed, and then multiplying them together to get g biomass per seed.

Sunlight enters the system and is converted into annual and perennial biomass through a series of rate changes. Production rate of biomass was a function of available light (R), biomass standing stock, rate of photosynthesis (light used by the biomass), and the rate of productivity (new biomass created from light through photosynthesis), all divided by water inundation (Figure 32). Similar to germination, water level can also influence biomass production and survival (Phipps 1979) and is therefore also included in the production equations.

Table 18. Values and sources for variables used to calculate the annual and perennial unit conversions from seeds m^{-2} to g biomass m^{-2} for the germination pathways.

Units	Annual	Reference	Perennial	Reference
g biomass $m^{-2} d^{-1}$	5.02	Calibration <i>Ba</i> divided by 365 d	6.73	Calibration <i>Bp</i> divided by 365 d
stem m^{-2}	1.3	Used a ratio calculation between <i>Bidens</i> g m^{-2} and stem m^{-2} , and <i>Impatiens</i> g m^{-2} ^a	2.3	Data for <i>Peltandra</i> reported in Whigham et al. (1978).
g stem ⁻¹	3.86	= 5.02 / 1.3	2.93	= 6.73 / 2.3
m^2 seed ⁻¹ day ⁻¹	1/2.47	900 <i>Impatiens</i> seeds m^{-2} ^b / 365 d	1/4.20	Estimated
stem seed ⁻¹	0.526	= 1.3 * (1/2.47)	0.548	= 2.3 * (1/4.2)
Unit conversion g biomass seed ⁻¹	2.03	= 0.562 * 3.86	1.61	= 0.548 * 2.93

^a Data from Whigham et al. 1978.

^b Data from Leck and Simpson 1994.

Biomass is lost through respiration, herbivory, and decomposition after senescence. We grouped respiration, herbivory, and all other possibilities of biomass loss, aside from decomposition, as carbon loss (Figure 33). Respiration is the dominant pathway of carbon loss in a tidal freshwater marsh (Mitsch and Gosselink 2000). Therefore, carbon loss for annuals and perennials in the model was represented as the product of specific respiration rate, biomass standing stock, and a rate coefficient. Temperature is a dominant factor in controlling decomposition rates in tidal freshwater marsh ecosystems (Odum et al. 1984). Thus, annual and perennial biomass loss through decomposition was represented as the product of biomass, temperature, and a specific decomposition rate.

After annual and perennial biomass decomposed to organic matter, the next step was to convert organic matter to available ammonium in the sediment. We call this pathway ammonium mineralization and it was assumed to be a function of organic matter. A unit conversion was necessary to convert grams of carbon into grams of nitrogen. We also incorporated the amount of organic matter that is organic carbon into the unit conversion. For example, 50% of percent organic matter in tidal freshwater marsh sediment is organic carbon (Mitsch and Gosselink 2000), and the standard C:N is 30:1. Therefore, our unit conversion of organic matter to sediment ammonium was 0.015.

Nitrogen from the watershed enters the system as ammonium and flows into the sediment ammonium stock. To calculate the incoming ammonium to the system, we estimated the amount of incoming water and multiplied it by the ammonium concentration we measured in the water at Dyke Marsh. To do so, we assumed that the amount of water entering the marsh per day is equal to the amount being evapotranspired.

Approximately 0.96 cm of water is evapotranspired per day during the summer in a tidal freshwater marsh (Hussey and Odum 1992). We converted this amount into $L\ d^{-1}$ and then multiplied it by the June 2006 ammonium-N concentration we measured in Hog Island channel that flows through Dyke Marsh to obtain an estimate of ammonium entering the marsh.

We focus on ammonium leaving the sediment through the process of nitrification and group all other processes, uptake by vegetation, ammonium-N immobilization, and anammox, into “other ammonium pathways”. Nitrification was simply assumed to be a function of sediment ammonium, while the flow “other ammonium pathways” was calculated as the product of sediment ammonium and a rate coefficient (Figure 33). Nitrogen enters the sediment nitrate stock only through nitrification, but leaves through denitrification and “other nitrate pathways” which encompassed processes such as nitrate reduction, anammox, uptake by vegetation, and burial. Denitrification and “other nitrate pathways” were functions of sediment nitrate content.

Field data collection

Vegetation. During peak biomass in late July 2006, we recorded percent cover (Braun-Blanquet 1964) of all species for 38, 1 m² plots in Dyke Marsh to assess the composition of the standing vegetation of the marsh. The 1 m² plots were blindly placed inside (n=18), outside (n=10), or on the edge (n=10) of ten various sized patches of *Impatiens capensis* Meerb., the dominant annual species at Dyke Marsh, that were delineated using a Trimble GeoExplorer II unit in July 2004. The ratio of annuals to perennials was calculated for the entire marsh and used in calculations for any model

variable that included an estimate of marsh percent annuals or percent perennials, along with reported literature values.

Tide height. Tide height at Dyke Marsh was measured continuously on the Potomac River and used for the forcing function “water inundation” in the model. A gauge, consisting of a submersible pressure transducer (Druck, CS420-L), and a datalogger (Campbell Scientific, Logan, UT) were installed in May 2004. Surface water level measurements were taken every five minutes and averaged every 15 minutes.

Drift-line. Drift-line data from Dyke Marsh was used for the forcing function “seed rain”. The abundance and species composition of seeds were sampled along 920 m of emergent drift-line along the Potomac River edge of Dyke Marsh. Drift-line samples 10 cm² by 2 cm deep were taken at 40 random points in March, July, and October of 2005 and March 2006. The seedling emergence technique was then used to determine species composition of the seed bank (Poiani and Johnson 1988, Gross 1990, Baldwin et al. 2001). The soil cores were homogenized and spread over vermiculite in bedding trays and placed in a greenhouse misting room for germination at two water depths (flooded and saturated) to assure that species that prefer low and high water inundation had an opportunity to germinate. Seedlings emerging from each sample were identified as young as possible and removed from the tray when identified. Seedlings of unknown species were transplanted and allowed to mature before identification. In November, all trays were refrigerated at 4°C over winter to cold stratify any remaining seeds, and then placed back into the greenhouse to continue germination in the spring.

Seed bank. The seed bank data from Dyke Marsh was used to calculate the seed bank stock calibration value. The seed bank of the 38 plots was sampled by taking three

soil cores, 10 cm length by 3.81 cm diameter, per plot in March 2006 to determine seed bank composition and species abundance. Samples were germinated using the seedling emergence technique described for the drift-line sampling. Samples were spread over vermiculite to germinate in the greenhouse, and seedlings were identified and removed as young as possible.

Soil chemistry. Sediment organic matter, ammonium-N, and nitrate-N were used to calibration nitrogen pathways. Two sediment cores, 10 cm length by 3.81 cm diameter, were sampled from all 38 plots in June 2006 using a PVC tube. Samples from each plot were homogenized, large roots and rhizomes were removed, and samples were sieved to 2 mm. Samples were dried at 70°C to a constant weight and then pulverized using a jar mill. Bulk density of the soil cores was measured as the oven-dry weight of the soil per unit volume (Birkeland 1984). Organic matter of each sediment core was obtained using the loss on ignition technique (Nelson and Sommers 1996). Available inorganic N (NH_4^+ plus NO_3^-) were extracted with 1 M KCl from all sediment samples. We then analyzed all sediment samples for ammonium-N (phenate method) and nitrate-N (automated cadmium reduction method) using flow injection analysis (Lachat QuikChem Automated Flow Injection Analysis System; APHA 1998, USEPA 1999).

Denitrification. Denitrification rates were used to calculate a calibration value for the “denitrification” flow in the model. Potential denitrification rates in the sediment of Dyke Marsh were measured for each plot in June 2006 using denitrification enzyme assays (DEA) (Smith and Tiedje 1979). Three sediment cores (10 cm length by 3.81 cm diameter) were taken from all 38 plots. Samples from each plot were homogenized, large roots were removed by hand, and held at field moisture for all analyses. Sediment

samples were amended with KNO_3^- , glucose, chloramphenicol, and acetylene, and incubated under anaerobic conditions for 90 minutes. Gas samples were taken at 30 and 90 minutes, stored in evacuated glass vials, and analyzed for N_2O by electron capture gas chromatography.

Water nutrients. Ammonium-N concentration in the water at Dyke Marsh was used to estimate the “nitrogen input” flow, which represents nitrogen entering the system. Water samples were taken from Hog Island Gut, a large channel that flows through Dyke Marsh in June 2006. Samples were filtered immediately upon return to the laboratory and then analyzed for ammonium-N with the phenate method, using flow injection analysis.

Model calibration

Values used to calibrate the model are displayed in Figure 33. Table 17 provides a description of the pathways, difference equations, calibration values, units, values of pathway coefficients (i.e., k 's), assumptions, and references used to calibrate the model.

State variables. Seed bank was determined as 2924 seeds m^{-2} for the calibration. Annual biomass used for calibration was obtained by averaging the aboveground biomass (g m^{-2}) reported for *Polygonum* spp., *Zizania aquatica*, and *Bidens* spp., all annual species found in Dyke Marsh, and adding it to the belowground average for *Polygonum* and *Zizania* values provided by Whigham et al. (1978). Perennial biomass was obtained in a similar way using aboveground data on *Nuphar advena*, *Peltandra virginica*, *Scirpus* spp., *Typha* spp., and *Acorus calamus* (all dominant perennial species found in Dyke Marsh) and using belowground data on *N. advena*, *P. virginica*, and *Typha* provided in Whigham et al. (1978). Organic matter of the sediment was represented as the product of average organic matter per m^2 and average sediment bulk density, both obtained from

Dyke Marsh, and then converted to g m^{-2} . Sediment ammonium and nitrate stock concentrations used for model calibration were obtained from analyzed sediment cores from Dyke Marsh that were averaged, multiplied by the bulk density of the sediment, and converted into g m^{-2} .

Pathways (flows). The amount of reflected sunlight was estimated as 20%, leaving 200 W m^{-2} for biomass. We estimated the amount of light available by multiplying 200 W m^{-2} by the respective proportions that annual (42.76%) and perennial (57.24%) species make up of the total biomass. Annual species biomass production was estimated as 80% of the initial standing biomass $\text{m}^{-2} \text{ d}^{-1}$, and perennial species biomass as 66% of the initial standing perennial biomass. Perennial biomass production was slightly lower than annual biomass production because perennial biomass has a longer turnover time than annuals. Germination pathway calibration values were estimated from the literature as $0.5 \text{ seed m}^{-2} \text{ d}^{-1}$ for annuals and $0.3 \text{ seed m}^{-2} \text{ d}^{-1}$ for perennials (Whigham et al. 1978). Values were estimated because no known published results exist for number of germinating seeds $\text{m}^{-2} \text{ d}^{-1}$. Furthermore, we estimated a lower value for perennial species because they also rely on vegetative reproduction, whereas annuals rely solely on reproduction by seeds. Calibration values for annual and perennial carbon loss were estimated by multiplying the total amount of marsh respiration, $2.91 \text{ g m}^{-2} \text{ d}^{-1}$ (Neubauer et al. 2000), by the proportion of annual (42.8%) and perennial (57.2%) species in the marsh. Herbivory was not included in this value because, while marsh mammals can consume large areas of vegetation (Evers et al. 1998), direct herbivory may be small compared to other pathways of carbon loss in tidal freshwater marshes (Odum 1988, Mitsch and Gosselink 2000) and has not been observed in Dyke Marsh (Hopfensperger,

personal observation). We estimated 79% loss of biomass through decomposition for annuals and 52.4% for perennial species; both values that worked best for the model. Mitsch and Gosselink (2000) report 60-90% biomass may become available to the detrital food chain in tidal freshwater marshes.

Nitrogen calibration values for ammonium mineralization, nitrification, other ammonium pathways, and other nitrate pathways were all estimated using values reported by Bowden et al. (1991) to guide us. We related the ammonium mineralization value provided by Bowden et al. (1991) to our measured data for Dyke Marsh and then increased it by 29.7% to account for the increase in our nitrogen input compared to Bowden et al.'s (1991). To account for the fact that aquatic plants preferentially uptake ammonium over nitrate; we estimated the rate of other ammonium pathways to be 73% and the rate of nitrification to be 15% of ammonium mineralization. The rate of other nitrate pathways was then estimated to be 95% of nitrification. The calibration value used for denitrification was obtained from analyzing sediment cores from Dyke Marsh for potential denitrification enzyme activity.

Model verification

Model validation is difficult for our model because an independent data set does not exist for comparing the simulated output data. We created and calibrated our model using data we collected from our field site and from known values in the literature leaving no independent data set to use for validation. Therefore, we verified our model by comparing our simulated data to independent ranges reported in the literature.

The simulated results of the model state variables stayed within logical and published ranges of observed data after 75 years of run time (Table 19). Seed bank model

results fall within other reported seed bank values for tidal freshwater marshes on the Atlantic coast (Parker and Leck 1985, Baldwin and DeRico 1999). Annual and perennial biomass levels produced by the model fall within the range of peak standing biomass values reported in the literature (Whigham et al. 1978, Odum et al. 1984, Mitsch and Gosselink 2000). The annual and perennial carbon loss model pathway results, mostly representative of respiration, fall within the values reported by Neubauer et al. 2000. Organic matter values produced by the model were somewhat lower compared to reported values by Fickbohm and Zhu (2006); however published values in g m^{-2} versus percent organic matter were very difficult to find for tidal freshwater marshes. Our modeled sediment ammonium and nitrate values were comparable to published values for other tidal freshwater marshes (Bowden et al. 1991, Otto et al. 1999, Fickbohm and Zhu 2006).

Table 19. Ranges of simulation results from our model (75 years run time) and published literature for each model state variable.

Description	Variable	Model results		Published range		Reference
		Min	Max	Min	Max	
Seed bank seeds m^{-2}	Sb	2911	2959	1645 2000	3620 12000	Parker & Leck 1985 Baldwin & DeRico 1999
Biomass annual^a g m^{-2}	Ba	1731	1945	1017 1000	1939 3000	Whigham et al. 1978 ^b Odum et al. 1984
Biomass perennial^a g m^{-2}	Bp	2285	2585	1017 1000	1578 3000	Mitsch & Gosselink 2000 Whigham et al. 1978 ^b Odum et al. 1984
Organic matter g m^{-2}	M	4147	4678	780 590	2100 11230	Mitsch & Gosselink 2000 Fickbohm & Zhu 2006
NH4 sediment g m^{-2}	A	0.49	0.55			
mg kg^{-1}		13.54	15.19	10	60	Otto et al. 1999
mg kg^{-1}				4.07	14.72	Fickbohm and Zhu 2006
NO3 sediment g m^{-2}	N	0.35	0.39			
mg kg^{-1}		9.67	10.77	0.04	9.87	Fickbohm and Zhu 2006

^aPublished ranges only include species found at Dyke Marsh.

^bPublished ranges are summations of reported above and belowground biomass.

Sensitivity analyses

We examined the sensitivity of annual and perennial decomposition pathways, ammonium mineralization pathway, sediment ammonium, sediment nitrate, and nitrogen gas stocks to changes in the annual and perennial biomass productivity and external nitrogen loading. To allow time for the model to stabilize, simulations were conducted for ten-year runs. The sensitivity of productivity and nitrogen input parameter flows were reduced by 50% (halving) and increased by 200% (doubling). Varying the input parameters by halving or doubling may not reflect the probable or a possible range of variation for the production and nitrogen input parameters. However, after sensitivity is assessed, highly sensitive parameters can be re-analyzed within a realistic range.

Climate change applications

To simulate the effect of various climate change scenarios on the biomass and nitrogen cycling at Dyke Marsh, we manipulated the forcing functions temperature and water inundation. Our two climate change scenarios are representative “Low” and “High” estimates for temperature warming and sea level rise published by the Intergovernmental Panel on Climate Change (IPCC 2007). Our low scenario consisted of increasing the temperature forcing function by 1.8°C and increasing the water inundation by 0.76 m. Our high scenarios consisted of increasing the temperature forcing function by 4.0°C and increasing water inundation by 1.18 m. The temperature estimates for our scenarios were directly the “best estimates” reported by the IPCC (2007) as the °C at 2090-2099 relative to 1980-1999. Similarly, the IPCC (2007) reported ranges of sea level rise for the same time periods, using the same methods. However, sea level in the Chesapeake Bay is projected to rise at a rate double that of the global rate (Douglas 1991). Therefore, we

obtained the water inundation values for our low and high scenarios by taking the high-end value of the IPCC (2007) range and multiplying it by two to represent the possible rise in sea level in the Chesapeake Bay and subsequent Potomac River.

Results

State variables

The simulation model produces a peak in the seed bank in early spring just before germination takes place (Figure 34). During the 10 year time period of the model, the seed bank ranged from 2910 to 2958 seeds m^{-2} . The model results in annual and perennial biomass peaking in summer, similar to natural conditions found in the field (Figure 34). Annual biomass ranged from 1730 to 1944 $g m^{-2}$ and perennial biomass ranged from 2316 to 2585 $g m^{-2}$.

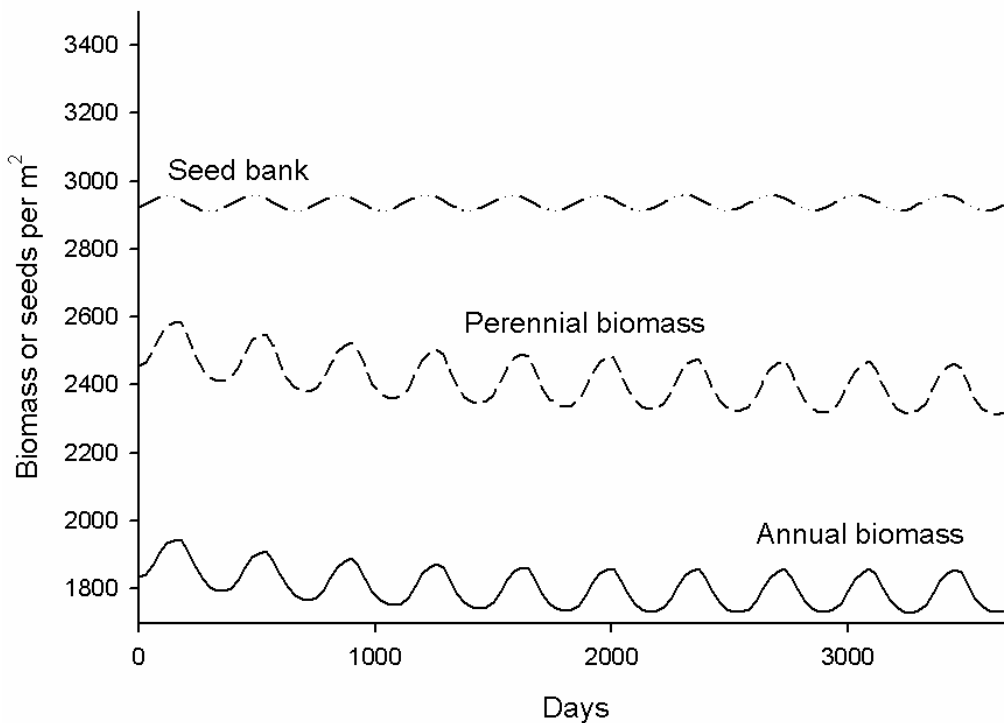


Figure 34. Baseline model simulation data for the seed bank and annual and perennial biomass stocks.

Organic matter, sediment ammonium, and sediment nitrate all peak in the fall during plant senescence (Figure 35). During the model's 10-year run time, organic matter ranges from 4560 to 4678 g m⁻², sediment ammonium ranges from 0.52 to 0.55 g m⁻², and sediment nitrate ranges from 0.35 to 0.39 g m⁻². After 10 years, the marsh removes 25.36 g m⁻² nitrogen through the process of denitrification.

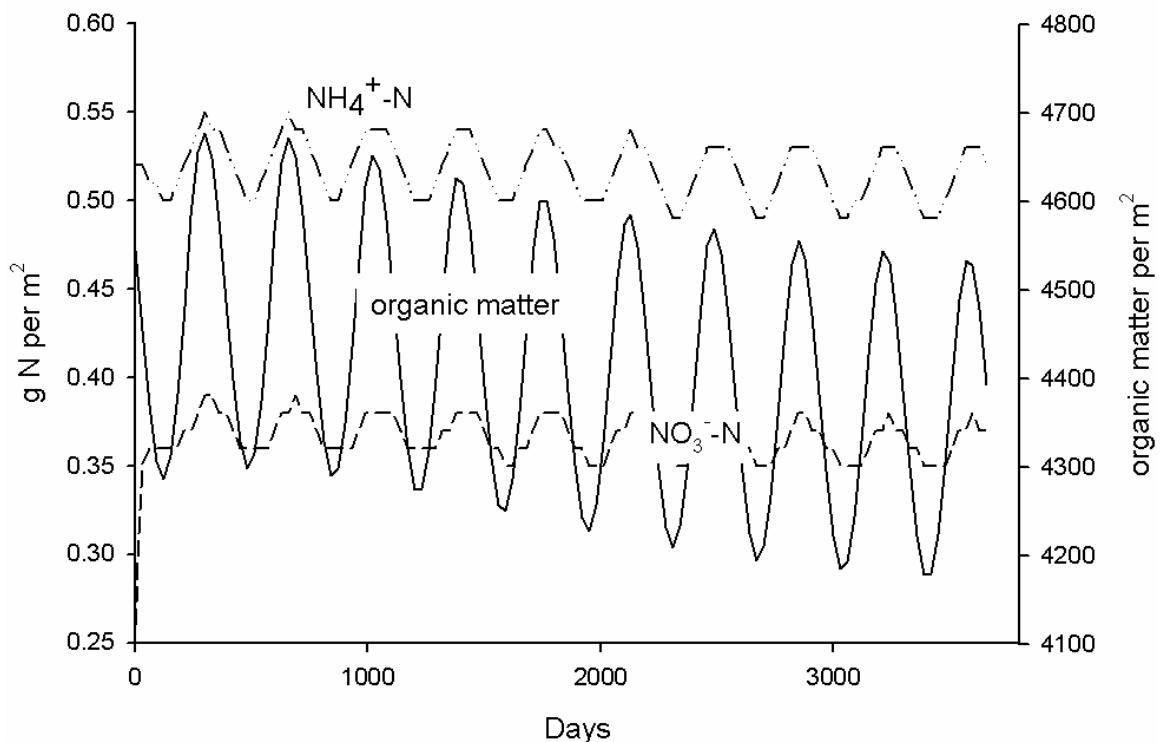


Figure 35. Baseline model simulation data for the organic matter, sediment ammonium, and sediment nitrate stocks.

Sensitivity analyses

Annual and perennial decomposition rates were most sensitive to doubling productivity (Table 20), but only responded mildly to halving productivity, and did not respond at all to changes in nitrogen input to the system. Doubling productivity probably caused the greatest change to decomposition rates, because these rates are driven by a

multiplicative relationship with biomass. Ammonium mineralization was equally sensitive to halving and doubling productivity and was not sensitive to manipulating nitrogen input to the system.

Table 20. Summary of parameter results to model sensitivity analyses.

Description	Parameter	Units	Baseline	Productivity		N input	
				50%	200%	50%	200%
Decomposition annuals	Da	$\text{g m}^{-2} \text{d}^{-1}$	1.88	2.14	3.64	1.88	1.88
Decomposition perennials	Dp	$\text{g m}^{-2} \text{d}^{-1}$	1.66	1.46	3.59	1.66	1.66
NH4 mineralization	Nmin	$\text{g m}^{-2} \text{d}^{-1}$	4.23	2.07	8.38	4.23	4.23
NH4 sediment	A	g m^{-2}	0.53	0.26	1.04	0.52	0.54
NO3 sediment	N	g m^{-2}	0.37	0.19	0.73	0.37	0.38
Nitrogen gas	N2	g m^{-2}	27.63	24.15	42.95	27.28	28.32

Ammonium mineralization responded to changes in biomass production because biomass directly impacted organic matter, which directly influenced the amount of material available for mineralization (Table 20). However, ammonium mineralization was not affected by a change in the nitrogen input to the system because the nitrogen input was only one-seventh of the ammonium mineralization rate, relatively a small fraction of the total. Therefore, doubling only makes the nitrogen input two-sevenths of the ammonium mineralization rate and halving only one-fourteenth. Sediment ammonium and nitrate were both most sensitive to changes in productivity. Halving and doubling productivity produced similar changes to the ammonium and nitrate state variables. However, the ammonium and nitrate variables were slightly sensitive to manipulations of the nitrogen input into the system. Lastly, nitrogen gas was most sensitive to doubling productivity and nitrogen input, and least sensitive to halving the nitrogen input. The sensitivity

analysis is important in demonstrating that major fluctuations in biomass can readily influence the amount of nitrogen that is removed from the marsh.

Scenarios

The simulations revealed that both the low and high climate change scenarios, increasing temperature and water inundation, would greatly influence vegetation and nitrogen dynamics at Dyke Marsh. Annual and perennial species biomass quickly decline and then level-off around 2000 days (6 years). This pattern emerged for both the low and high climate change scenarios (Figure 36).

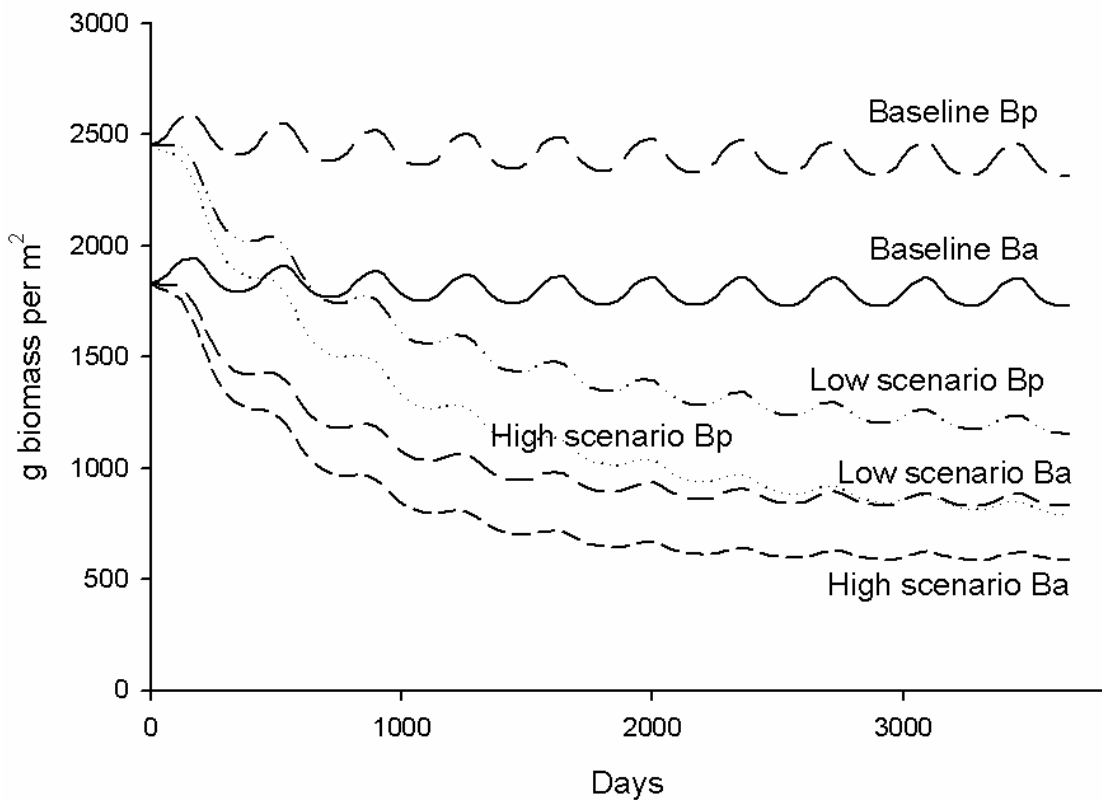


Figure 36. Response of annual and perennial biomass to the low and high climate change scenarios compared to baseline model values. Model run time = 3650 days.

Annual biomass decreased from an initial value of 1834 g m⁻² to 829 g m⁻² in the low change scenario and to 585 g m⁻² in the high change scenario. Perennial biomass

decreased from an initial value of 2455 g m^{-2} to 1110 g m^{-2} in the low change scenario and to 740 g m^{-2} in the high change scenario. A substantial decrease in the biomass of the model led to a subsequent decrease in sediment ammonium and sediment nitrate under both climate scenarios. Sediment ammonium and nitrate have a lag time of approximately 730 days (2 years) before they begin to decline considerably, and then they begin to level-off around 3000 days (~ 9 years) for both climate scenarios (Figure 37).

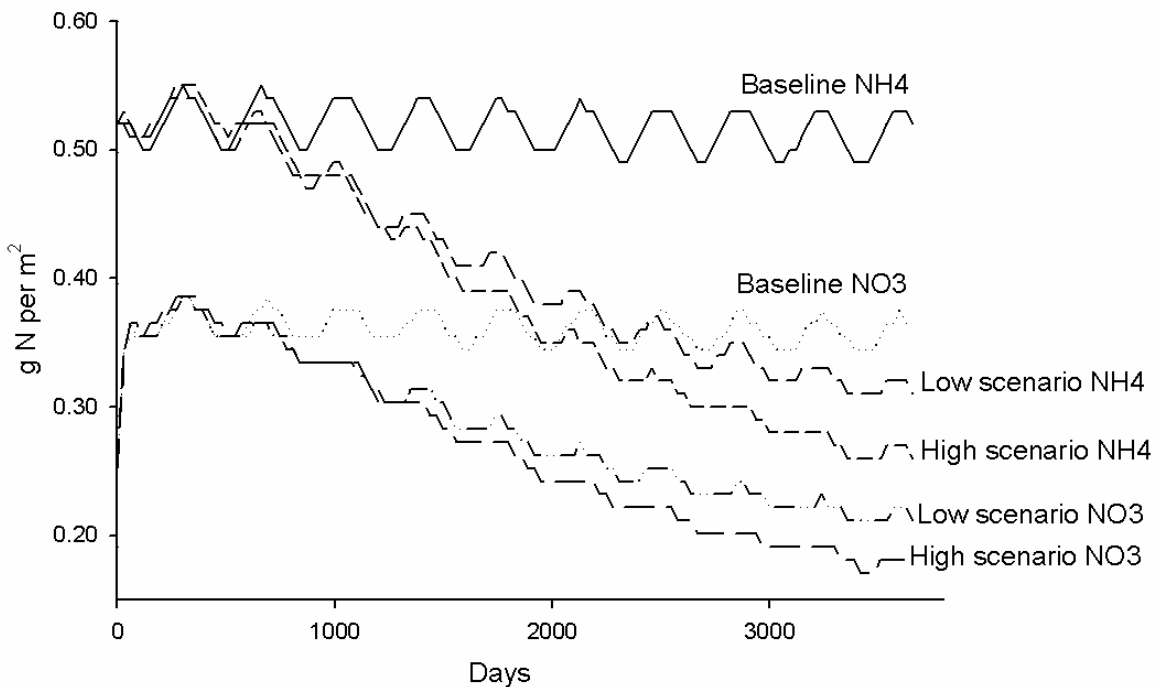


Figure 37. Response of sediment ammonium and nitrate to the low and high climate change scenarios compared to baseline model values. Model run time = 3650 days.

Sediment ammonium declines from 0.52 g m^{-2} to 0.28 g m^{-2} in the low scenario and to 0.23 g m^{-2} in the high scenario. Sediment nitrate declines from 0.26 g m^{-2} to 0.20 g m^{-2} in the low scenario and to 0.16 g m^{-2} in the high change scenario. Both the low and high climate change scenarios caused a decrease in production of nitrogen gas through

denitrification (Figure 38). Nitrogen gas values decreased from 25.36 g m⁻² to 20.39 g m⁻² in the low change scenario and to 19.36 g m⁻² under the high change scenario.

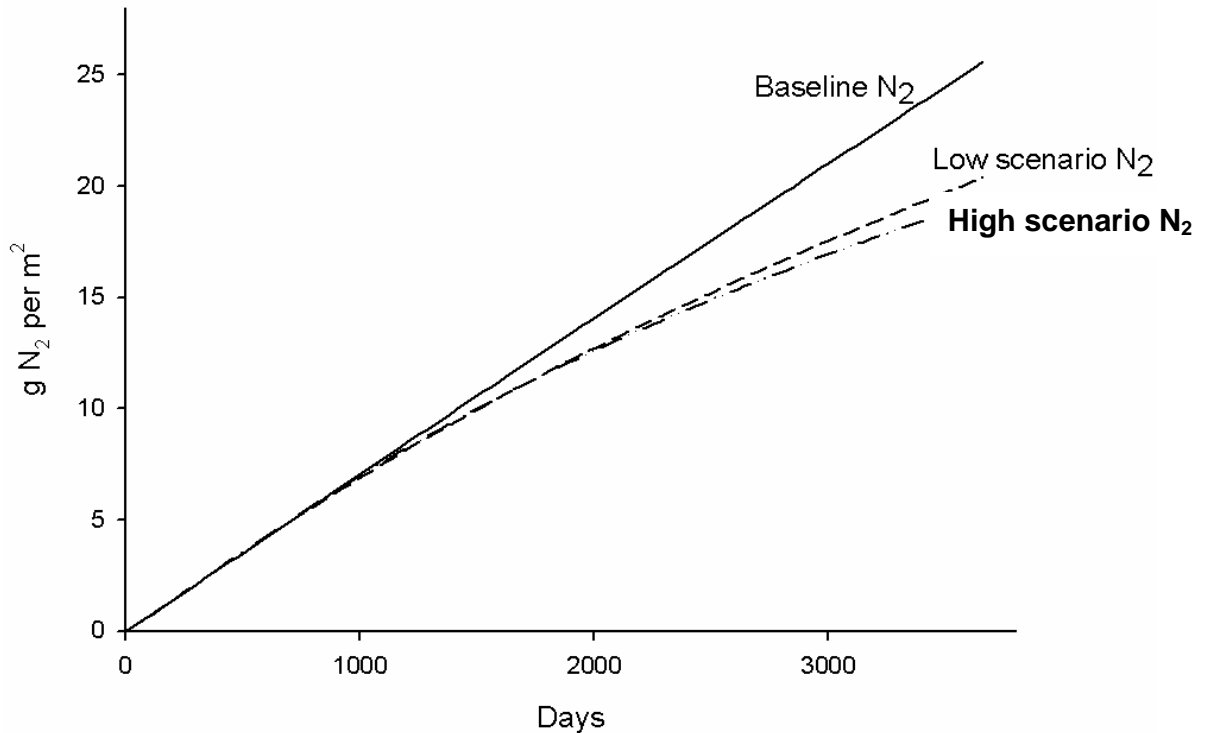


Figure 38. Response of nitrogen gas to the low and high climate change scenarios compared to baseline model values. Model run time = 3650 days.

Discussion

Our model demonstrates that vegetation is linked to and can influence the nitrogen dynamics in a tidal freshwater marsh. We found that biomass changes in response to temperature and water inundation increases influenced sediment ammonium and nitrate levels. Similarly, Martin and Reddy (1997) included vegetation in their model of wetland nitrogen cycling and found it to be an important driver of particulate organic nitrogen in both the aerobic and anaerobic sediment layers. If vegetation is an important driver for wetland ecosystem processes, marsh vegetation needs to be effectively restored

and managed in the face of changing water levels as sea level rise. The climate change scenarios both produced significant losses in annual and perennial biomass and subsequent reduction in nitrogen removal in a tidal freshwater marsh. Rising sea level may inundate a large portion of current low marsh areas, thereby inhibiting germination of emergent marsh species. A lack of emergent vegetation will reduce the amount of organic matter supplied to the sediment and result in a decrease of available nitrogen and nitrogen removal processes. The reduction in nitrogen removal will allow for more nitrogen to flow downstream into Chesapeake Bay and contribute to the growth of hypoxic areas. Furthermore, the model we created is a simplification of all of the intricate linkages and relationships among the biological, chemical, and physical variables in a tidal freshwater marsh. For model simplification, we did not incorporate the relationship between water inundation and nitrogen processes into the model. In a natural system, an increase in sea level may create permanent anaerobic conditions in low marsh areas, resulting in not only a decrease in decomposition, but also a decrease in the important coupling of nitrification/denitrification processes. Without this coupling, denitrification rates and nitrogen removal could be severely reduced.

Tidal marsh managers must consider future sea level rise when recreating and restoring marsh area today. Because most tidal freshwater marshes are located in highly urbanized areas, they do not have the ability to migrate inland with sea level rise, owing to urban constraints such as roads, parking lots, and buildings. Therefore, tidal freshwater marshes should be created with a variety of elevations that may withstand the rise in sea level, substrate that will not readily subside with sea level rise, and vegetation that is not highly sensitive to water inundation.

Our model was intended to be a first step towards examining the intricate linkages between vegetation, nutrients, and sea level rise. Simulation models, such as the one presented here, can be useful for informing scientists and managers of the different relationships among important marsh variables and which variables they should focus future management efforts on with regards to a future rise in sea level. The model has much room for improvement to become a more accurate and useful tool. Model improvements could include: 1) linking forcing functions such as temperature and water inundation to all of the pathways; 2) creating a direct feedback from the nitrogen cycle to the vegetation; and 3) providing more specific nitrogen pathways (separating out “other ammonium and nitrate pathways”). Developing a spatial model could be accomplished by adding different marsh elevation components such as ranges of elevations representing low marsh, mid marsh, and high marsh. Managers could then compare the strengths of different relationships among biological, chemical, and physical variables among different elevation ranges and use that information to determine management strategies for sea level rise. With the improvement of wetland simulation models, and further collection of tidal freshwater marsh data, scientists and managers may become better prepared to handle the changes that sea level rise may impose upon a threatened ecosystem.

CHAPTER XI

CONCLUSION

In an effort to improve our understanding, management decision-making, and restoration of tidal freshwater marshes, I have studied how community dynamics of marsh vegetation influence ecosystem functioning of tidal freshwater marsh ecosystems. Water quality of coastal areas may be greatly improved by using our knowledge of these kidney-like ecosystems to manage them for maximum nitrogen removal. Scientists and managers must also incorporate future trends into the management decisions of today. Global warming *is* occurring and sea level rise *will* happen. The proximity of our few remaining tidal freshwater marshes to densely populated urban areas places the marshes in grave danger of submergence and total disappearance; thereby removing our ideal natural filtration systems completely from our landscapes. A loss of tidal freshwater marshes may result in more polluted waters, more hypoxic areas, less habitat for wildlife, and less commercial fisheries in the Chesapeake Bay.

I attempted to improve our understanding of these ecosystems by asking four main interrelated questions that examined: 1) the spatial dynamics of marsh vegetation; 2) how the spatial community dynamics influence ecosystem processes; 3) the temporal dynamics of marsh vegetation; and 4) how sea level rise may affect interactions between community dynamics and marsh ecosystem processes. The take-home message emerging from my research is that restoration and creation of tidal freshwater marsh systems will be necessary with sea level rise. When managers focus on restoring the vegetation, elevation, or nutrient removal ability of these ecosystems, they must acknowledge and think about how these variables are all inter-related and influence each other.

Spatial Vegetation Dynamics

While vegetation patches, specifically comprised of annual species, are most likely formed in tidal marshes through disturbance processes (Grime 1977), including ice scour (Belanger and Bedard 1994), wrack-burial (Brewer et al. 1998), and large storms (Nyman et al. 1995), my studies focused on mechanisms that allow the patches to persist. Through my various field and greenhouse observations and experimental studies, I have learned that the vegetation of Dyke Marsh is primarily structured by the physical environment including elevation, water inundation (Chapter IV), and sedimentation (Chapter III). Vegetation structure is also partially determined by competition (Chapters V & VI) and seed rain dynamics (Chapter VII). Even though sediment levels were only studied for a short time in Dyke Marsh, my study demonstrated overall sediment depletion. However, a longer study will be needed to discern whether the observed sediment depletion is a short-term phenomenon caused by the absence of large storm events during the study period, or whether the short-term dynamics are symptomatic of longer term trends. Such a study has recently begun at Dyke Marsh by the U.S. Geological Survey. My studies show that germination and mature stem density of annual species is positively correlated with elevation and therefore negatively correlated with frequency and magnitude of water inundation. Similar to other tidal freshwater marsh studies, I found the seeds of the three dominant annual species to occupy the seed bank at different elevation ranges, thus separating in niche space. Therefore, the water inundation that plants are exposed to during germination and seedling life stages appears to be important to annual species distribution, but the degree of importance differs among species.

After several greenhouse studies examining facilitative and competitive interactions between annual and perennial marsh species, I have learned that facilitative relationships may not be a dominant mechanism explaining the coexistence of the studied species, and that competitive interactions may play a minor role in the spatial dynamics of annual species. The facilitation experiment between a dominant annual and perennial species of Dyke Marsh further supported findings that species are positively associated with marsh surface elevation. The competition experiment suggested that dominant annual *Impatiens capensis* and dominant perennial *Typha angustifolia* directly compete for light. *I. capensis* and dominant perennial *Leersia oryzoides* competed only for nutrients in the sediments, whereas *I. capensis* and dominant perennial *Peltandra virginica* did not show any evidence of competition. The lack of strong competitive interactions further supports my thesis that other mechanisms drive spatial dynamics of vegetation at Dyke Marsh.

The last variable I studied that may influence plant spatial dynamics was the seed rain of Dyke Marsh. I found that the marsh received fewer seeds and hence fewer species through hydrochory compared to regional tidal freshwater marshes. However, distinct temporal patterns in seedling density and species richness of the drift-line and water trawls emerged from the data. The timing of restoring or creating a new site should coincide with seed dispersal to maximize the seed rain influence. However, I found low seed and species abundance in the seed rain, and immigration from regional sources probably has a minor impact on the vegetation structure at Dyke Marsh. Therefore, the seed rain should not be depended on for a restoration at Dyke Marsh. The impact of the studied mechanisms on vegetation spatial dynamics is summarized in Table 21.

Table 21. A summary of mechanisms that may be implicated in explaining spatial dynamics of marsh vegetation at the germination and mature life stages. “Yes” represents that the variable plays a role in driving spatial dynamics; “No” represents the variable does not influence spatial dynamics. Bolded letters represent results that are statistically significant. Dashes represent relationships that were not tested.

	Germination	Mature Vegetation
Elevation	YES	YES
Facilitation	--	NO
Competition	YES	YES
Hydrochory	NO	--

Influence of Community Dynamics on Ecosystem Processes

Communities can influence ecosystem processes through the functional traits of the component species. I chose to study denitrification and associated ecosystem variables because denitrification is an important process that allows wetlands to enhance the quality of polluted water. While no significant differences were detected in denitrification rates among community types, nor relationships with elevation, denitrification may still be indirectly influenced by marsh vegetation through plant impacts on the biogeochemistry of the sediments. Plant leaf tissues of three functional groups (broad leaf perennial, broad leaf annual, and graminoid perennial) differed in C:N ratios, thereby contributing different quality of organic matter to the sediment. This was also demonstrated by sediment organic carbon differing among the community types (annual, perennial, and mixed). In addition, denitrification responded to sediment organic nitrogen. Therefore, if community types differ in the quality and quantity of organic nitrogen they contribute to the sediment, they may indirectly influence denitrification rates. Furthermore, denitrification rates varied seasonally just as vegetation does, with

significantly higher rates in June versus October when the majority of vegetation has senesced. If patches of vegetation influence denitrification rates, vegetation maps may be used to locate denitrification “hot spots” – locations where denitrification rates are highest. However, we did not find a direct link between community types and denitrification rates; therefore, other factors such as nitrogen availability in the sediments and tidal flushing may be more important in determining denitrification hot spots. Therefore, more work needs to be done examining relationships between several dominant marsh species and denitrification. If certain species are found to produce greater denitrification rates than others, then marsh managers can plant and/or manage for these species to maximize nitrogen removal from the ecosystem. Relationships found between the biological, chemical, and physical variables in this study are summarized in Table 22.

Table 22. Summary of relationships between biological, physical, and chemical variables at Dyke Marsh. Dashes represent no significant relationship, and “+” represent a positive relationship between the variables with the respective variables. Abbreviations are as follows: A=annual species, P=perennial species, n.a.=not applicable, OM=organic matter, Org N=organic nitrogen, TN=total nitrogen.

	<i>Biological</i>		<i>Chemical (sediment)</i>				
	Tissue C:N	OM	C:N	NH ₄ ⁺	NO ₃ ⁻	Org N	TN
<i>Biological</i>							
Community Type	P>A	—	—	—	A>P	—	—
<i>Physical</i>							
Elevation	n.a.	+	+	—	+	—	—

Temporal Vegetation Dynamics

The study of seed bank and vegetation changes through time has led to a more confident understanding of the mechanisms driving temporal dynamics of vegetation at

Dyke Marsh. I found community composition of the standing vegetation to change at the plot level owing to a thriving seed bank and local elevation. Similarity in community composition between seed bank and standing vegetation increased with elevation and distance to nearest channel; however channel size and community type (dominated by perennial or annual species) did not influence similarity. Seed banks at plots farthest from channels and at high elevations were comprised mostly of the parent plant species. I conclude that because there was not complete similarity between seed bank and vegetation communities of the same year, other drivers such as local elevations and hydrologic conditions may play a role in determining the standing vegetation community each year in a tidal freshwater marsh. Vegetation communities may be more variable and less predictable near channels and at lower elevations where tidal flushing of propagules in and out of an area occurs more readily. Relationships among seed bank, vegetation, elevation, and hydrologic variables are summarized in Table 23.

Table 23. Summary of correlations among vegetation and seed bank communities, and relationships between similarity and environmental variables. “Y” represents a correlation between the two variables. The larger and bolder the “Y” is, the stronger the correlation was. A dash represents no significant relationship found, and upward arrows represent a significant increase in both variables.

	Vegetation 2004	Vegetation 2005	Vegetation 2006	Similarity
Vegetation 2005	Y			
Vegetation 2006	Y	Y		
Seed bank 2006		Y	Y	
Elevation				↑
Distance to channel				↑
Channel size				—

Effect of Climate Change on Marsh Interactions

The simulation model I created to examine how climate change may influence the interactions between community vegetation dynamics and the nitrogen cycle demonstrated a distinct linkage between the two in the face of global warming and sea level rise. The model demonstrated that a change in biomass indirectly influenced sediment ammonium and nitrate levels. Furthermore, climate change scenarios produced significant losses in biomass and a reduction in nitrogen removal in a tidal freshwater marsh. I highly recommend that managers of tidal freshwater marsh ecosystems begin incorporating the threat of sea level rise into their management plans immediately. We know sea level rise will occur; we are beginning to understand the effect sea level rise may have on tidal freshwater marsh ecosystems; therefore we must begin to protect these systems from widespread devastation today through effective restoration.

Restoration Recommendations

- Understanding relationships between vegetation and environmental gradients is necessary for restoration practitioners to create a functioning tidal freshwater marsh. Knowing relationships between specific plant life forms and physical and chemical variables may help to ensure a functioning restored system with a diverse biotic component. (Chapter IV)
- Seed density and species richness in the waters surrounding Dyke Marsh was significantly lower than at near-by Kingman and Kenilworth marshes. Thus, my results suggest that seed dispersal may be a more local phenomenon than was previously thought for tidal freshwater marshes within the region. Therefore, if managers were to restore Dyke Marsh through adjacent marshland creation,

hydrochory should *not* be depended on as the only mechanism for species colonization. If managers only rely on hydrochory, the drift-line margins of the newly created areas may be colonized, but the interior could remain vulnerable to wind-dispersed invasion by exotic species that create unwanted homogenous vegetative stands. (Chapter VII)

- Restoration managers may allow for partial self-design where seed banks are present and/or an abundant and species rich seed rain exists. However, even if desired species are present in the seed rain, there is a chance they may not germinate under the current environmental conditions, and invasive and exotic species may colonize a site as readily as native species. Therefore, we recommend seeding or planting key species that are not in the seed bank, and to be flexible and aware that the vegetation composition may change spatially and temporally. We found few readily abundant species in the seed bank; they included *I. capensis*, *A. cannabinus*, and *T. angustifolia*. Species abundant in the seed trawls included *L. oryzoides*, *I. capensis*, *B. laevis*, *A. cannabinus*, and *P. pumila*. Therefore, I believe the only species not to plant include *I. capensis*, *A. cannabinus*, and *T. angustifolia*; however *I. capensis* and *A. cannabinus* are annuals and if they do not emerge in the first year or two, they will not be present in the marsh to disperse new seeds. (Chapter IX)
- Managers should consider creating an extensive network of small channels throughout a tidal freshwater marsh to allow for dispersal of seeds and flow of nutrients and sediments to all marsh areas. (Chapter IX)
- Managers could consider different options to provide sufficient organic matter for denitrification in a newly created or restored site: 1) Immediately plant a newly

created area so that biomass is introduced to the substrate the first year; 2) Use a substrate or fill material that already contains labile organic matter for denitrification.

(Chapter VIII)

- I found spatial and temporal marsh vegetation patterns to be scale dependent. Therefore, scale must be taken into account when monitoring restoration success. Restoration monitors should inventory vegetation at a smaller scale to obtain data that could be used for understanding spatial and temporal dynamics within the marsh, and then pool that data to monitor species extinction and addition to the system. (Chapter IX)
- Elevation is a very important variable in tidal freshwater marsh ecosystems. A variety of elevations (low, mid, and high marsh) are necessary in a tidal freshwater marsh to ensure successful germination of a variety of species, specifically annuals. Elevation may also be important in influencing soil properties and denitrification rates in Dyke Marsh. Managers may need to consider how topography will result in the most effective zones of nitrogen removal within the hydrologic context of the marsh. (Chapters VIII and IX)
- As sea level rises, elevation is probably the most crucial variable that drives community composition and ecosystem functioning. Areas of higher elevation will need to be created to ensure survival and reproduction of annual species and to ensure the maintenance of diversity in tidal freshwater marshes. Furthermore, marsh topography should be designed in a way that will not readily subside with sea level rise, and create areas that will allow for the coupling of nitrification and

denitrification. Lastly, vegetation that is not highly sensitive to water inundation should be planted. (Chapters IV, VIII, and X)

Future Directions

Through the various field and greenhouse studies I completed, I have learned that there are several gaps in our knowledge of tidal freshwater marshes and many topics that could be expanded on. The following is a list of topics that I think would be useful to gather more information on for the management and restoration of tidal freshwater marsh ecosystems.

- Knowledge of sediment dynamics in tidal freshwater marshes, including the use of sediment-erosion tables, would be beneficial to thoroughly understand long-term accretion and depletion.
- In situ facilitation and competition experiments with co-occurring dominant annual and perennial species would help to better understand if either of these mechanisms drives species distributions in tidal freshwater marshes.
- Information on the relationships between tidal flushing and seed distribution in tidal marshes. A more thorough understanding of how varying characteristics of tidal channels influence seed distribution throughout a marsh would be useful when deciding whether and where to plant a newly restored or created tidal freshwater marsh.
- More information on other nitrogen removal pathways is needed for tidal freshwater marshes. In addition to microbial denitrification, dissimilatory nitrate reduction to ammonium (DNRA), anaerobic ammonium oxidation (anammox),

and denitrification coupled to sulfur oxidation may also play a role in nitrate removal, but we have no idea how large of a role.

- Because tidal freshwater marshes have been studied less compared to marine and estuarine wetlands, more work needs to be done on factors influencing rates of microbial denitrification.
- A further understanding of the end product of microbial denitrification is needed in tidal freshwater marshes. Denitrification may produce N_2 or N_2O , which is a harmful greenhouse gas; therefore, knowing what is being produced and if different variables can change the end product would be useful for improving air quality.
- Improvements to the developed simulation model would be useful for future scenario examinations. More detail such as incorporating feedbacks, more nitrogen pathways, and forcing function links could be added. Developing a spatial model with different marsh elevations could also be very useful when studying impacts of rising sea level.

REFERENCES

- Abbott, J.M. 1976. Wildlife recorded at Dyke Marsh, east Fairfax County, Virginia--mostly in the period 1946-1976. Friends of Dyke Marsh, Alexandria, VA.
- Abernathy, V.J. and N.J. Willby. 1999. Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. *Plant Ecology* 140:177-190.
- Addy, K., A. Gold, B. Nowicki, J. McKenna, M. Stolt, and P. Groffman. 2005. Denitrification capacity in a subterranean estuary below a Rhode Island fringing Salt Marsh. *Estuaries* 28:896-908.
- American Public Health Association (APHA). 1998. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, DC.
- Bailey, E.M., M. Owens, W.R. Boynton, et al. 2006. Sediment phosphorus flux: pH interactions in the tidal freshwater Potomac River estuary. Final report prepared for the Interstate Commission on the Potomac River Basin. Technical Report Series No.TS-505-06-CBL of the University of Maryland Center for Environmental Science.
- Bakker J.P., M. Dijkstra, and P.T. Russchen. 1985. Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. *New Phytology* 101:291-308.
- Bakker J.P., P. Esselink, K.S. Dijkema, et al. 2002. Restoration of salt marshes in the Netherlands. *Hydrobiologia* 478:29-51.
- Baldwin A.H. and E.F. DeRico. 2000. The seed bank of a restored tidal freshwater marsh in Washington, D.C. *Urban Ecosystems* 3:5-20.
- Baldwin, A.H., M.S. Egnotovitch, and E. Clarke. 2001. Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. *Wetlands* 21:519-531.
- Baldwin, A.H., K.L. McKee, and I.A. Mendelssohn. 1996. The influence of vegetation, salinity and inundation on seed banks of oligohaline coastal marshes. *American Journal of Botany* 83:470-479.
- Baldwin, A.H. and I.A. Mendelssohn. 1998. Effects of salinity and water level on coastal marshes: an experimental test of disturbance as a catalyst for vegetation change. *Aquatic Botany* 61:255-268.
- Baldwin A.H. and F.N. Pendleton. 2003. Interactive effects of animal disturbance and elevation on vegetation of a tidal freshwater marsh. *Estuaries* 26:905-915.

- Baldwin, D.S. and A.M. Mitchell. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: A synthesis. *Regulated Rivers-Research and Management* 16:457-467.
- Barko, J.W., D. Gunnison, and S.R. Carpenter. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. *Aquatic Botany* 41:41-65.
- Barrows, E.M. and D.S. Kjar. 2003. Biodiversity Database of the Washington, D.C. Area. Website. <http://biodiversity.georgetown.edu>. Accessed 12 March 2004.
- Barry, R.G. and R.J. Chorley. 1992. *Atmosphere, weather, and climate*. Sixth edition. Routledge, London, UK.
- Barth, M. and J. Titus. 1984. *Greenhouse effect and sea level rise*. Van Norstrand Reinhold, New York, NY, USA.
- Belanger, L. and J. Bedard. 1994. Role of ice scouring and goose grubbing in marsh plant-dynamics. *Journal of Ecology* 82:437-445.
- Belknap, D.F. and J.C. Kraft. 1977. Holocene relative sea level changes and coastal stratigraphic units on the northwest flank of the Baltimore Canyon Trough geosyncline. *Journal of Sedimentary Petrology* 47:610-629.
- Bernot, M.J., W.K. Dodds, W.S. Gardner, et al. 2003. Comparing denitrification estimates for a Texas estuary by using acetylene inhibition and membrane inlet mass spectrometry. *Applied and Environmental Microbiology* 69:5950-5956.
- Bertness M.D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125-137.
- Bertness, M.D. and A.M. Ellison. 1987. Determinants of pattern in a New England salt marsh community. *Ecological Monographs* 57:129-147.
- Bertness M.D. and S.D. Hacker. 1994. Physical stress and positive associations among marsh plants. *The American Naturalist* 144:363-372.
- Bertness M.D. and S.W. Shumway. 1993. Competition and facilitation in marsh plants. *The American Naturalist* 142:718-724.
- Birkeland, P.W. 1984. *Soils and Geomorphology*: Oxford University Press, New York, p. 14-15.
- Boers, A.M., R.L.D. Veltman, and J.B. Zedler. 2007. *Typha x glauca* dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering* 29:232-244.

- Boesch, D.F. 2006. Scientific requirements for ecosystem-based management in the restoration of Chesapeake Bay and Coastal Louisiana. *Ecological Engineering* 26:6-26.
- Boumans, R.M.J. and J.W. Day, Jr. 1993. High precision measurements of sediment elevation in shallow coastal areas using a sedimentation-erosion table. *Estuaries* 16:375-380.
- Bowden, W.B., C.J. Vörösmarty, J.T. Morris, et al. 1991. Transport and processing of nitrogen in a tidal freshwater wetland. *Water Resources Research* 27:389-408.
- Braun-Blanquet, J. 1964. *Pflanzensoziologie*. Springer-Verlag, New York, NY, USA.
- Brewer J.S., J.M. Levine, and M.D. Bertness. 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. *Oikos* 80:333-341.
- Brewer, J.S., J.M. Levine, and M.D. Bertness. 1998. Interactive effects of elevation and burial with wrack on plant community structure in some Rhode Island salt marshes. *Journal of Ecology* 86:125-136.
- Brose, U. and K. Tielbörger. 2005. Subtle differences in environmental stress along flooding gradient affect the importance of inter-specific competition in an annual plant community. *Plant Ecology* 178:51-59.
- Brown, C.E., S.R. Pezeshki, and R.D. DeLaune. 2006. The effects of salinity and soil drying on nutrient uptake and growth of *Spartina alterniflora* in a simulated tidal system. *Environmental and Experimental Botany* 58:140-148.
- Brown, C.J., B. Blossey, J.C. Maerz, and S.J. Joule. 2006. Invasive plant and experimental venue affect tadpole performance. *Biological Invasions* 8:327-338.
- Brownlee, E.F., S.G. Sellner, and K.G. Sellner. 2005. *Prorocentrum minimum* blooms: potential impacts on dissolved oxygen and Chesapeake Bay oyster settlement and growth. *Harmful Algae* 4:593-602.
- Bruland, G.L., C.J. Richardson and S.C. Whalen. 2006. Spatial variability of denitrification potential and related soil properties in created, restored, and paired natural wetlands. *Wetlands* 26:1042-1056.
- Bruno, J.F. 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology* 81:1179-1192.
- Brush, G.R. 1989. Rates and patterns of estuarine sediment accumulation. *Limnology and Oceanography* 34:1235-1246.

- Cahoon, D.R., D.J. Reed, and J.W. Day, Jr. 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology* 128:1-9.
- Callaway, R.M. and L. King. 1996. Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* 77:1189-1195.
- Campbell, D.A., C.A. Cole, and R.P. Brooks. 2002. A comparison of created and natural wetlands in Pennsylvania, USA. *Wetlands Ecology and Management* 10:41-49.
- Cappers, R.T.J. 1993. Seed dispersal by water: a contribution to the interpretation of seed assemblages. *Vegetation History Archaeobotany* 2:173-186.
- Carter, V., N.B. Rybicki, J.M. Landwehr, and M. Turtora. 1994. Role of weather and water quality in population dynamics of submersed macrophytes in the tidal Potomac River. *Estuaries* 17:417-426.
- Cartwright, L. 2004. Breeding Bird Survey for Dyke Marsh Preserve. Unpublished data.
- Casanova, M.T. and M.A. Brock. 2000. How do depth, duration, and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology* 147:237-250.
- Casey, R.E., M.D. Taylor, and S. J. Klaine. 2004. Localization of denitrification activity in macropores of a riparian wetlands. *Soil Biology and Biochemistry* 36:563-569.
- Castellanos E.M., M.E. Figueroa, and A.J. Davy. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* 82:239-248.
- Chao, A. 1994. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11:265-270.
- Chapin, III F.S., K. Van Cleve, and M.C. Chapin. 1979. Soil temperature and nutrient cycling in the tussock growth form of temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. *Journal of Ecology* 67:169-189.
- Church, T.M., C.K. Sommerfield, D.J. Velinsky. 2006. Marsh sediments as records of sedimentation, eutrophication and metal pollution in the urban Delaware Estuary. *Marine Chemistry* 102:72-95.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.

- Clarke, K.R. and R.M. Warwick. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* 216:265-278.
- Colquhoun, D.J. and M.J. Brooks. 1986. New evidence from the southeastern U.S. for eustatic components in the Late Holocene sea levels. *Geoarchaeology: An International Journal* 1:275-291.
- Colwell, R.K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. Version 5. User Guide and Application. <http://viceroy.eeb.uconn.edu/estimates>. Cited 4 Dec 2006.
- Colwell R.K. and J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London* 345:101-118.
- Cook, P.L.M., F. Wenzhofer, S. Rysgaard, et al. 2006. Quantification of denitrification in permeable sediments: insights from a two-dimensional simulation analysis and experimental data. *Limnology and Oceanography-Methods* 4:294-307.
- Cooper, S.R. and G.S. Brush. 1991. Long-term history of Chesapeake Bay anoxia. *Science* 254:992-996.
- Coops, H., N. Geilen, and G. van der Velde. 1999. Helophyte zonation in two regulated estuarine areas in the Netherlands: vegetation analysis and relationships with hydrological factors. *Estuaries* 22:657-668.
- Cornu, C.E. and S. Sadro. 2002. Physical and functional responses to experimental marsh surface elevation manipulation in Coos Bay's South slough. *Restoration Ecology* 10:474-486.
- Cornwell, J.C., W.M. Kemp, and T.M. Kana. 1999. Denitrification in coastal ecosystems: methods, environmental controls, and ecosystem level controls, a review. *Aquatic Ecology* 33:41-54.
- Corstanje, R. and K.R. Reddy. 2004. Response of biogeochemical indicators to a drawdown and subsequent reflood. *Journal of Environmental Quality* 33:2357-2366.
- Costanza, R., W.J. Mitsch, and J.W. Day. 2006. A new vision for New Orleans and the Mississippi delta: applying ecological economics and ecological engineering. *Frontiers in Ecology and the Environment* 4:465-472.
- Crawford, R.M.M. 1993. Root survival in flooded soils. Pages 257-283. *In: A. Gore (ed.) Mires: swamp, bog, fen and moor, Ecosystems of the world, Vol. 4A.* Elsevier Science, Amsterdam, The Netherlands.

- Cronk, J.K. and M.S. Fennessy. 2001. *Wetland Plants: Biology and Ecology*. Lewis Publishers, New York, NY, USA.
- Dahl, T.E. 1990. Wetlands losses in the United States, 1780s to 1980s. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. 21 pp.
- Dahl, T.E. and C.E. Johnson. 1991. Wetlands status and trends in the conterminous United States mid-1970s to mid-1980s. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C. 28 pp.
- Davis, E.G. 1950. Birds of the season. *Atlantic Naturalist* 6:24-25.
- Davis, M.A., J.P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88:528-534.
- Day, J.W., W.H. Conner, R. Costanza, G.P. Kemp, and I.A. Mendelson. 1993. Impacts of sea level rise on coastal systems with special emphasis on the Mississippi River deltaic plain. Pages 276-296. *In*: R.A. Warrick, E.M. Barrow, and T.M.L. Wigley (eds.) *Climate and sea level change: observations, projections and implications*. Cambridge University Press, Cambridge, England.
- De Laune, R.D., S.R. Pezeshki, and W.H. Patrick, Jr. 1987. Response of coastal plants to increase in submergence and salinity. *Journal of Coastal Research* 3:535-546.
- Douglas, B.C. 1991. Global sea-level rise. *Journal of Geophysical Research-Oceans* 96:6981-6992.
- Dowrick, D.J., S. Hughes, C. Freeman, et al. 1999. Nitrous oxide emissions from a gully mire in mid-Wales, UK, under simulated summer drought. *Biogeochemistry* 44:151-162.
- Eby, L.A., L.B. Crowder, C.M. McClellan, C.H. Peterson and M.J. Powers. 2005. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Marine Ecology-Progress Series* 291:249-261.
- Elakovich, S. D. and J. W. Wooten. 1995. Allelopathic, herbaceous, vascular hydrophytes. Pages 58-73. *In*: K.M. Inderjit, M. Dakshini, and F.A. Einhellig (eds.) *Allelopathy: Organisms, Processes, and Applications*. American Chemical Society, Washington, D.C., USA.
- Emery, N.C., P.J. Ewanchuk, and M.D. Bertness. 2001. Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology* 82:2471-2485.
- Engelhardt, K.A.M. 2006. Relating effect and response traits in submersed aquatic macrophytes. *Ecological Applications* 16:1808-1820.

- Ervin, G.N. and R.G. Wetzel. 2000. Allelochemical autotoxicity in the emergent wetland macrophyte *Juncus effusus* (Juncaceae). *American Journal of Botany* 87:853-860.
- Ervin, G.N. and R.G. Wetzel. 2003. An ecological perspective of allelochemical interference in land-water interface communities. *Plant and Soil* 256:13-28.
- Evers, D.E., C.E. Sasser, J.G. Gosselink, D.A. Fuller, and J.M. Visser. 1998. The impact of vertebrate herbivores on wetland vegetation in Atchafalaya Bay, Louisiana. *Estuaries* 21:1-13.
- Fickbohm, S.S. and W.X. Zhu. 2006. Exotic purple loosestrife invasion of native cattail freshwater wetlands: effects on organic matter distribution and soil nitrogen cycling. *Applied Soil Ecology* 32:123-131.
- Field, D.W., A.J. Reyer, P.V. Genovese, and B.D. Shearer. 1991. Coastal wetlands of the United States. National Oceanic and Atmospheric Administration and U.S. Fish and Wildlife Service, Washington, D.C. 59 pp.
- Findlay, S.E.G., S. Dye, and K.A. Kuehn. 2002. Microbial growth and nitrogen retention in litter of *Phragmites australis* compared to *Typha angustifolia*. *Wetlands* 22:616-625.
- Findlay, S., P. Groffman and S. Dye. 2003. Effects of *Phragmites australis* removal on marsh nutrient cycling. *Wetlands Ecology and Management* 11:157-165.
- Fletcher, C.H., J.E. Pizzuto, J. Suku, and J.E. van Pelt. 1993. Sea-level rise acceleration and the drowning of the Delaware Bay coast at 1.8 ka. *Geology* 21:121-124.
- Gallardo, M.T., B.B. Martin, and D.F. Martin. 1998. An annotated bibliography of allelopathic properties of cattails, *Typha* spp. *Florida Science* 61:52-58.
- Gaskill, K. 2000. Updated birds of Dyke Marsh checklist. Original from the National Park Service in 1993; updated in 2000.
- Gee, G.W. and J.W. Bauder. 1986. Particle-size Analysis. Pages 383-411. *In:* A.L. Page (ed.) *Methods of Soil Analysis, Part 1, Physical and Mineralogical Methods*, second edition. American Society of Agronomy, Madison, WI, USA.
- Gerberich, A.G. 1984. The endangered and threatened freshwater mollusks of Maryland. Pages 245-266. *In:* A.W. Norden, D.C. Forester, and G.H. Fenwick (eds) *Threatened and endangered plants and animals of Maryland*. Natural Heritage Program, Special Publication 84-I, Maryland Department of Natural Resources.
- Girel, J. and O. Manneville. 1998. Present species richness of plant communities in alpine stream corridors in relation to historical river management. *Biological Conservation* 85:21-33.

- Gleason, H.A. and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada, second edition. The New York Botanical Garden, New York, NY, USA.
- Gold, A.J., P.A. Jacinthe, P.M. Groffman, W.R. Wright and R.H. Puffer. 1998. Patchiness in groundwater nitrate removal in a riparian forest. *Journal of Environmental Quality* 27:146-155.
- Gornitz, V. 1991. Global coastal hazards from future sea level rise, palaeogeography, palaeoclimatology, palaeoecology. *Global and Planetary Change Section* 89:379-398.
- Gosselink, J.G. and R.H. Baumann. 1980. Wetland inventories: wetland loss along the United States coast. *Zeitschrift für Geomorphologie N.F. Suppl. Bd. 34*:173-187.
- Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecological Letters* 4:379-391.
- Grace, J.B. 1983. Autotoxic inhibition of seed germination by *Typha latifolia*: an evaluation. *Oecologia* 59:366-369.
- Greene, S.E. 2005. Nutrient removal by tidal fresh and oligohaline marshes in a Chesapeake Bay tributary. M.S. Thesis, University of Maryland.
- Gribsholt, B., H.T.S. Boschker, E. Struyf, et al. 2005. Nitrogen processing in a tidal freshwater marsh: A whole-ecosystem ¹⁵N labeling study. *Limnology and Oceanography* 50:1945-1959.
- Gribsholt, B., E. Struyf, A. Tramper, et al. 2006. Ammonium transformation in a nitrogen-rich tidal freshwater marsh. *Biogeochemistry* 80:289-298.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169-1194.
- Grime, J.P., G. Mason, A.V. Curtis, et al. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69:1017-1059.
- Groffman, P.M., M.A. Altabet, J. K. Böhlke, et al. 2006. Methods for measuring denitrification: diverse approaches to a difficult problem. *Ecological Applications* 16:2091-2122.
- Gross, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology* 78:1079-1093.

- Gurnell, A.M., I.P. Morrissey, A.J. Boitsidis, et al. 2006. Initial adjustments within a new river channel: interactions between fluvial processes colonizing vegetation, and bank profile development. *Environmental Management* 38:580-596.
- Hacker, S.D. and M.D. Bertness. 1995. Morphological and physiological consequences of a positive plant interaction. *Ecology* 76:2165-2175.
- Hamersley, M.R. and B.L. Howes. 2005. Coupled nitrification-denitrification measured in situ in a *Spartina alterniflora* marsh with a (NH₄⁺)-N-15 tracer. *Marine Ecology-Progress Series* 299:123-135.
- Hay, W.P. 1902. A list of batrachians and reptiles of the District of Columbia. *Proceedings of the Biological Society of Washington* 15:121-145.
- Harper, J.D. and F.D. Heliotis. 1992. Dyke Marsh Hydrologic Model. George Mason University, Fairfax, VA.
- Harrison, E.Z. and A.L. Bloom. 1977. Sedimentation rates on tidal marshes in Connecticut. *Journal of Sedimentary Petrology* 47:1484-1490.
- Hayward, B.W., H.R. Grenfell, and K. Nicholson. 2004. Foraminiferal record of human impact on intertidal estuarine environments in New Zealand's largest city. *Marine Micropaleontology* 53:37-66.
- Hilderbrand, R.H., A.C. Watts, and A.M. Randle. 2005. The myths of restoration ecology. *Ecology and Society* 10:19.
<http://www.ecologyandsociety.org/vol10/iss1/art19>. Accessed 12 March 2007.
- Hobbie, S.E. 1996. Temperature and plant species control over litter It should be recognized that the plants used in these decomposition in Alaskan tundra. *Ecological Monographs* 66:503-522.
- Hopfensperger, K.N., K.A.M. Engelhardt, and S.W. Seagle. 2004. Should we restore Dyke Marsh? A management dilemma facing George Washington Memorial Parkway. Handbook for National Park Service GWMP Workshop, November 4, 2004, 105 pp. <http://www.al.umces.edu/DMP/workbook.htm>. Accessed 25 April 2007.
- Hopfensperger, K.N., K.A.M. Engelhardt, and S.W. Seagle. 2007. Ecological feasibility studies in restoration decision-making. *Environmental Management* 39:843-852.
- Houlahan, J.E. and C.S. Findlay. 2004. Effect of invasive plant species on temperate wetland plant diversity. *Conservation Biology* 18:1132-1138.

- Howarth, R.W., G. Billen, D. Swaney, et al. 1996. Regional nitrogen budgets and riverine N&P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. *Biogeochemistry* 35:75-139.
- HPS. 1993. Stella II: Technical documentation. High Performance Systems, Inc., 45 Lyme Road, Hanover, NH, USA.
- Huckle, J.M., R.H. Marrs, and J.A. Potter. 2002. Interspecific and intraspecific interactions between salt marsh plants: integrating the effects of environmental factors and density on plant performance. *Oikos* 96:307-319.
- Hudon, C. 2004. Shift in wetland plant composition and biomass following low-level episodes in the St. Lawrence River: looking into the future. *Canadian Journal of Fisheries and Aquatic Sciences* 61:603-617.
- Huiskes, A.H.L., B.P. Koutstaal, P.M.J. Herman, et al. 1995. Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology* 83:559-567.
- Hume, N.P., M.S. Fleming, and A.J. Horne. 2002. Denitrification potential and carbon quality of four aquatic plants in wetland microcosms. *Soil Science Society of America Journal* 66:1706-1712.
- Hussey, B.H. and W.E. Odum. 1992. Evapotranspiration in tidal marshes. *Estuaries* 15:59-67.
- Intergovernmental Panel on Climate Change (IPCC). 2007. Climate change 2007: the physical basis. Summary for Policymakers. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. <http://www.ipcc.ch/> Accessed 22 March 2007.
- Interstate Commission on the Potomac River Basin (ICPRB). 2004. <http://www.potomacriver.org>. Accessed 5 September 2004.
- Inwood, S.E., J.L. Tank, and M.J. Bernot. 2007. Factors controlling sediment denitrification in Midwestern streams of varying land-use. *Microbial Ecology* 53:247-258.
- Jacinto, P.A., P.M. Groffman, A.J. Gold and A. Mosier. 1998. Patchiness in microbial nitrogen transformations in groundwater in a riparian forest. *Journal of Environmental Quality* 27:156-164.
- Jansson, R., U. Zinko, D.M. Merritt, et al. 2005. Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *Journal of Ecology* 93:1094-1103.

- Jenkins, R.E. and N.M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, MD.
- Johnston, D.W. 2000. The Dyke Marsh Preserve ecosystem. *Virginia Journal of Science* 51:223-271.
- Jones, R.G. 1981. Salt tolerance. Pages 271-292. *In*: C.B. Johnson (ed.) *Physiological processes limiting plant productivity*. Butterworths, London, England.
- Joye, S.B., S.V. Smith, J.T. Hollibaugh, and H.W. Paerl. 1996. Estimating denitrification rates in estuarine sediments: a comparison of stoichiometric and acetylene based methods. *Biogeochemistry* 33:197-215.
- Jutila, H.M. 2003. Germination in Baltic coastal wetland meadows: similarities and differences between vegetation and seed bank. *Plant Ecology* 166:275-293.
- Kana, T.M., C. Darkangelo, M.D. Hunt, J.B. Oldham, G.E. Bennett, and J.C. Cornwell. 1994. Membrane inlet mass spectrometer for rapid high-precision determination of N₂, O₂, and Ar in environmental water samples. *Analytical Chemistry* 66:4166-4170.
- Kana, T.M., M.B. Sullivan, J.C. Cornwell, and K.M. Groszkowski. 1998. Denitrification in estuarine sediments determined by membrane inlet mass spectrometry. *Limnology and Oceanography* 43:334-339.
- Kaplan, A., J. Gale, and A. Poljakoff-Mayber. 1977. Effect of oxygen and carbon dioxide concentrations on gross dark CO₂ fixation and dark respiration in *Bryophyllum daigremontianum*. *Australian Journal of Plant Physiology* 4:745-752.
- Keddy, P.A. 1989. Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. *Canadian Journal of Botany* 67:708-716.
- Kellogg, C.H. and S.D. Bridgham. 2002. Colonization during early succession of restored freshwater marshes. *Canadian Journal of Botany* 80:176-185.
- Kelso, D., Z. Xu, G. Marcella, and L.K. Thomas, Jr. 1993. A historical delineation of the Dyke Marsh vegetation. Report to the National Park Service.
- Kemp, M.J., and W.K. Dodds. 2002. Comparison of nitrification and denitrification in prairie and agriculturally influenced streams. *Ecological Applications* 12:998-1009.
- Kemp, W.M., W.R. Boynton, J.E. Adolf, et al. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology-Progress Series* 303:1-29.

- Kemp, W.M., P. Sampou, J. Caffrey, and M. Mayer. 1990. Ammonium recycling versus denitrification in Chesapeake Bay sediments. *Limnology and Oceanography* 35:1545-1563.
- Kerner, M. and F. Edelkraut. 1995. Decomposition of organic matter in aggregated seston from the Elbe estuary – redox dependency and production of low molecular weight DOC compounds. *Marine Ecology Progress Series* 123:281-293.
- Khan, H. and G.S. Brush. 1994. Nutrient and metal accumulation in a freshwater tidal marsh. *Estuaries* 17:345-360.
- Kim, D.H., O. Matsuda, and T. Yamamoto. 1997. Nitrification, denitrification and nitrate reduction rates in the sediment of Hiroshima Bay. *Japanese Journal of Oceanography* 53:317-324.
- Knops, J.M.H., K.L. Bradley, and D.A. Wedin. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters* 5:454-466.
- Langhans, S.D. and K. Tockner. 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia* 147:501-509.
- Leck, M.A. 1996. Germination of macrophytes from a Delaware River tidal freshwater wetland. *Bulletin of the Torrey Botanical Club* 123:48-67.
- Leck, M.A. 2003. Seed-bank and vegetation development in a created tidal freshwater wetland on the Delaware River, Trenton, New Jersey, USA. *Wetlands* 23:310-343.
- Leck, M.A., C.C. Baskin, and J.M. Baskin. 1994. Germination ecology of *Bidens laevis* (Asteraceae) from a tidal freshwater wetland. *Bulletin of the Torrey Botanical Club* 121:230-239.
- Leck, M.A. and K.J. Graveline. 1979. Seed bank of a freshwater tidal marsh. *American Journal of Botany* 66:1006-1015.
- Leck, M.A. and R.L. Simpson. 1993. Seeds and seedlings of the Hamilton Marshes, a Delaware River tidal freshwater wetland. *Proceedings of the Academy of National Science Philadelphia* 144:267-281.
- Leck, M.A. and R.L. Simpson. 1994. Tidal freshwater wetland zonation: seed and seedling dynamics. *Aquatic Botany* 47:61-75.
- Leck, M.A. and R.L. Simpson. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *American Journal of Botany* 82:1547-1557.

- Leeds, J.A., S. Newman, and S. M. Smith. 2006. Factors affecting seed germination of *Eleocharis cellulose* and *Rhynchospora tracyi* from the northern Everglades. *Wetlands* 26:368-375.
- Lenssen, J.P.M. and H. de Kroon. 2005. Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. *Journal of Ecology* 93:138-147.
- Lenssen, J., F. Menting, W. van der Putten, and K. Blom. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos* 86:523-534.
- Leonard, L.A. 1997. Controls of sediment transport and deposition in an incised mainland marsh basin, southeastern North Carolina. *Wetlands* 17:263-274.
- Levin, L.A., D.F. Boesch, A. Covich et al. 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4:430-451.
- Letzsch, W.S. and R.W. Frey. 1980. Deposition and erosion in a Holocene salt marsh, Sapelo Island, Georgia. *Journal of Sedimentary Petrology* 50:529-542.
- Leyer, I. 2006. Dispersal, diversity and distribution patterns in pioneer vegetation: the role of river floodplain connectivity. *Journal of Vegetation Science* 17:407-416.
- Likens, G.E., F.H. Bormann, N.M. Johnson, D.W. Fisher, and R.S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed ecosystem. *Ecological Monographs* 40:23-47.
- Lindholm, D.A. 1992. 1992 Dyke Marsh herbaceous plant study. George Mason University, Fairfax, VA, USA.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models, SAS Institute Inc., Cary, NC, USA.
- Manabe, S. and R.T. Wetherald. 1986. Reduction in summer soil wetness induced by an increase in atmospheric carbon-dioxide. *Science* 232:626-628.
- Magurran, A.E. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK.
- Mann, C.J. and R.G. Wetzel. 2000. Hydrology of an impounded lotic wetland – subsurface hydrology. *Wetlands* 20:33-47.
- Martin, J.F. and K.R. Reddy. 1997. Interaction and spatial distribution of wetland nitrogen processes. *Ecological Modelling* 105:1-21.

- Matsui, T. and T. Tsuchiya. 2006. Root aerobic respiration and growth characteristics of three *Typha* species in response to hypoxia. *Ecological Research* 21:470-475.
- McClain, M.E., E.W. Boyer, C.L. Dent, et al. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301-312.
- McCune, B. and J.B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.
- McIninch, S.M. and E.W. Garbisch. 2003. Propagation of wetland plants: herbaceous plants, shrubs, and trees. Environmental Concern, Inc., St. Michaels, MD, USA.
- McManus, J. 1998. Temporal and spatial variations in estuarine sedimentation. *Estuaries* 21:622-634.
- McNaughton, S.J. 1968. Autotoxic feedback in relation to germination and seedling growth in *Typha latifolia*. *Ecology* 49:367-369.
- Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621-626.
- Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *American Naturalist* 110:351-369.
- Merrill J.Z. and J.C. Cornwell. 2000. The role of oligohaline marshes in estuarine nutrient cycling. Pages 425-441. *In*: M.P. Weinstein and D.A. Kreeger (eds.) *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Michener, W.K., E.R. Blood, K.L. Bildstein, et al. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7:770-801.
- Middleton, B.A. 1995. Sampling devices for the measurement of seed rain and hydrochory in rivers. *Bulletin of the Torrey Botanical Society* 122:152-155.
- Mitsch, W.J. and J.W. Day. 2006. Restoration of wetlands in the Mississippi-Ohio-Missouri (MOM) River Basin: experience and needed research. *Ecological Engineering* 26:55-69.
- Mitsch, W. J. and J. G. Gosselink. 2000. *Wetlands*. Third edition. John Wiley, New York, NY, USA.
- Mitsch, W.J. and R.F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. *Ecological Applications* 6:77-83.

- Mitsch, W.J., X. Wu, R.W. Nairn, et al. 1998. Creating and restoring wetlands – a whole-ecosystem experiment in self-design. *Bioscience* 48:1019-1030.
- Mitsch, W.J., L. Zhang, C.J. Anderson, et al. 2005. Creating riverine wetlands: ecological succession, nutrient retention, and pulsing effects. *Ecological Engineering* 25:510-527.
- Mulhouse, J.M. and S.M. Galatowitsch. 2003. Revegetation of prairie pothole wetlands in the mid-continental US: twelve years post-reflooding. *Plant Ecology* 169:143-159.
- Mulhouse, J.M., L.E. Burbage, and R.R. Sharitz. 2005. Seed bank-vegetation relationships in herbaceous Carolina bays: responses to climatic variability. *Wetlands* 25:738-747.
- Myrick, R.M. and L.B. Leopold. 1963. Hydraulic geometry of a small tidal estuary. U.S. Geological Survey Professional Paper 442-B. U.S. Government Printing Office, Washington, DC.
- National Park Service (NPS). 1977. Environmental Assessment of Dyke Marsh. National Capital Region, National Park Service, U.S. Department of Interior.
- National Research Council (NRC). 2001. Compensating for wetland losses under the Clean Water Act. National Academy Press, Washington DC.
- Neff, K.P. 2002. Plant colonization and vegetation change in a restored tidal freshwater wetland in Washington, D.C. MS thesis, University of Maryland.
- Neff, K.P. and A.H. Baldwin. 2005. Seed dispersal into wetlands: techniques and results for a restored tidal freshwater marsh. *Wetlands* 25:392-404.
- Nelson, D.W. and L.E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pages 961-1010. *In* D.L. Sparks, A.L. Page, P.A. Helmke, R.H. Loeppert, et al. (eds). *Methods of Soil Analysis, Part 3, Chemical Methods*. Soil Science Society of America Book Series, Madison, WI, USA.
- Neubauer, S.C., W.D. Miller, and I.C. Anderson. 2000. Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study. *Marine Ecology-Progress Series* 199:13-30.
- Nielsen T. and F. O. Andersen. 2003. Phosphorus dynamics during decomposition of mangrove (*Rhizophora apiculata*) leaves in sediments. *Journal of Experimental Marine Biology and Ecology* 293:73-88.

- Nixon, S.W., J.W. Ammerman, L.P. Atkinson, et al. 1996. The fate of nitrogen and phosphorus at the land-sea margin of the North Atlantic Ocean. *Biogeochemistry* 35:141-180.
- Noe, G.B., and J.B. Zedler. 2000. Differential effects of four abiotic factors on the germination of salt marsh annuals. *American Journal of Botany* 87:1679-1692.
- Noe, G.B., and J.B. Zedler. 2001. Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. *Journal of Vegetation Science* 12:61-74.
- Norwicki, B.L., E. Requentina, D. VanKeuren, and J. Portnoy. 1999. The role of sediment denitrification in reducing groundwater-derived nitrate inputs to Nauset Marsh estuary, Cape Cod, Massachusetts. *Estuaries* 22:245-259.
- Nyman, J.A., C.R. Crozier, and R.D. Delaune. 1995. Roles and patterns of hurricane sedimentation in an estuarine marsh landscape. *Estuarine Coastal and Shelf Science* 40:665-679.
- Odum, H.T. and E.C. Odum. 2000. *Modeling for all scales: An introduction to system simulation*. Academic Press, San Diego, CA, USA.
- Odum, W.E., T.J. Smith III, J.K. Hoover, and C.C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States East Coast: a community profile. U.S. Fish and Wildlife Service Report FWS/OBS-83/17.
- Odum W.E. 1988. Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics* 19:147-176.
- Orson, R.A. 1996. Some applications of paleoecology to the management of tidal marshes. *Estuaries* 19:238-246.
- Orson, R.A., R.L. Simpson, and R.E. Good. 1990. Rates of sediment accumulation in a tidal freshwater marsh. *Journal of Sedimentary Petrology* 60: 859-869.
- Orson, R.A., R.L. Simpson, and R.E. Good. 1992. The paleoecological development of a late Holocene, tidal freshwater marsh of the upper Delaware River estuary. *Estuaries* 15:130-146.
- Otto, S., P. Groffman, S.E.G. Findlay, and A.E. Arreola. 1999. Invasive plant species and microbial processes in a tidal freshwater marsh. *Journal of Environmental Quality* 28:1252-1257.
- Palermo, M.R. and T.W. Zeigler. 1976. Feasibility study for Dyke Marsh demonstration area Potomac River, Virginia. U.S. Army Engineer Waterways Experiment Station Technical Report D-76-6.

- Parker, V.T. and M.A. Leck. 1985. Relationships of seed banks to plant distribution patterns in a freshwater tidal wetland. *American Journal of Botany* 72:161-174.
- Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. *Soil Science Society of America Journal* 51:1194-1199.
- Parsons, Brinckerhoff, Zuade, and Douglas. 1976. Final Dogue-Little Hunting-Belle Haven Environmental Baseline Evaluation. Task Order 10.6. Fairfax County, Virginia.
- Pasternack G.B. and G.S. Brush. 1998. Sediment cycles in a river-mouth tidal freshwater marsh. *Estuaries* 21:407-415.
- Pasternack G.B. and G.S. Brush. 2001. Seasonal variations in sedimentation and organic content in five plant associations on a Chesapeake Bay tidal freshwater delta. *Estuarine Coastal and Shelf Science* 53: 93-106.
- Pasternack G.B., W.B. Hilgartner, and G.S. Brush. 2000. Biogeomorphology of an upper Chesapeake Bay river-mouth tidal freshwater marsh. *Wetlands* 20:520-537.
- Patrick, W.H. and K.R. Reddy. 1976. Nitrification-denitrification reactions in flooded soils and water bottoms – dependence on oxygen-supply and ammonium diffusion. *Journal of Environmental Quality* 5:469-472.
- Peterson, J.E. and A.H. Baldwin. 2004a. Variation in wetland seed banks across a tidal freshwater landscape. *American Journal of Botany* 91:1251-1259.
- Peterson, J.E. and A.H. Baldwin. 2004b. Seedling emergence from seed banks of tidal freshwater wetlands: response to inundation and sedimentation. *Aquatic Botany* 78:243-254.
- Pfaunder, A. and M. Zimmer. 2005. Intermediate tidal stress promotes the detritivore-mediated decomposition of *Spartina* litter. *European Journal of Soil Biology* 41:135-141.
- Phipps, R.L. 1979. Simulation of wetlands forest vegetation dynamics. *Ecological Modelling* 7:257-288.
- Poiani, K.A. and W.C. Johnson. 1988. Evaluation of the emergence method in estimating seed bank composition of prairie wetlands. *Aquatic Botany* 32:91-97.
- Puckett, L.J., M.D. Woodside, B. Libby, and M.R. Schening. 1993. Sinks for trace metals, nutrients, and sediments in wetlands of the Chickahominy River near Richmond, Virginia. *Wetlands* 13:105-114.

- Reddy, K.R. and W.F. DeBusk. 1987. Nutrient storage capabilities of aquatic and wetland plants. Pages 337-357. *In*: K.R. Reddy and W.H. Smith (eds) Aquatic plants for water treatment. Magnolia Publishing, Orlando, FL, USA.
- Reddy, K.R., W.H. Patrick, and C.W. Lindau. 1989. Nitrification-denitrification at the plant root-sediment interface in wetlands. *Limnology and Oceanography* 34:1004-1013.
- Reinartz, J.A. and E.L. Warne. 1993. Development of vegetation in small created wetlands in southeast Wisconsin. *Wetlands* 13:153-164.
- Rejmanek, M., C.E. Sasser, and G.W. Peterson. 1988. Hurricane-induced sediment deposition in a Gulf coast marsh. *Estuarine Coastal Shelf Science* 27:217-222.
- Richardson, W.B., E.A. Strauss, E.M. Monroe, et al. 2004. Denitrification in the upper Mississippi River: rates, controls, and contributions to nitrate flux. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1102-1112.
- Risgaard-Petersen, N. 2003. Coupled nitrification-denitrification in autotrophic and heterotrophic estuarine sediments: on the influence of benthic microalgae. *Limnology and Oceanography* 48:93-105.
- Rybczyk, J.M., J.C. Callaway, and J.W. Day. 1998. A relative elevation model for a subsiding coastal forested wetland receiving wastewater effluent. *Ecological Modelling* 112:23-44.
- SAS Institute Inc. 1985. SAS User's Guide: Statistics, Version 5. SAS Institute Inc. Cary, NC, USA.
- Schat H. and K. Van Beckhoven. 1991. Water as a stress factor in the coastal dune system. Pages 76–89. *In*: J. Rozema and J. A. C. Verkleij (eds.) *Ecological Responses to Environmental Stresses*. Kluwer Academic, Dordrecht, The Netherlands.
- Schlesinger, W.H. 1997. *Biogeochemistry: an analysis of global change*, second edition. Academic Press, San Diego, CA, USA.
- Schneider, R.L. and R.R. Sharitz. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* 69:1055-1063.
- Seabloom, E.W., A.G. van der Valk, and K.A. Moloney. 1998. The role of water depth and soil temperature in determining initial composition of prairie wetland coenoclines. *Plant Ecology* 138:203-216.
- Seabloom, E.W. and A.G. van der Valk. 2003. The development of vegetative zonation patterns in restored prairie pothole wetlands. *Journal of Applied Ecology* 40:92-100.

- Seitzinger, S.P. 1988. Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. *Limnology and Oceanography* 33:702-724.
- 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.
- Simenstad, C.A. and R.M. Thom. 1996. Functional equivalency trajectories of the restored Gog-Le-Hi-Te estuarine wetland. *Ecological Applications* 6:38-56.
- Simpson, R.L., R.E. Good, M.A. Leck, and D.F. Whigham. 1983. The ecology of freshwater tidal wetlands. *BioScience* 33:255-259.
- Simpson, R.L., M.A. Leck, and V.T. Parker. 1985. The comparative ecology of *Impatiens capensis* Meerb. (Balsaminaceae) in Central New Jersey. *Bulletin of the Torrey Botanical Club* 112:295-311.
- Smith, L.K., M.A. Voytek, J.K. Böhlke, and J.W. Harvey. 2006. Denitrification in nitrate-rich streams: application of N₂:Ar and 15N-tracer methods in intact cores. *Ecological Applications* 16:2191-2207.
- Smith, M.S. and J.M. Tiedje. 1979. Phases of denitrification following oxygen depletion in soil. *Soil Biology and Biochemistry* 11:262-267.
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter* 5:1-34.
- Southworth, A.D. 1989. Conserving southeastern coastal wetlands. Pages 223-257. *In* W.J. Chandler (ed.) *Audubon wildlife report 1989/1990*. Academic Press, New York, NY, USA.
- Spencer, S.C. 2000. Population abundance and habitat requirements of the marsh wren (*Cistothorus palustris*) at Dyke Marsh National Wildlife Preserve. M.S. Thesis. George Mason University, Fairfax, VA.
- Stoddart, D.R., D.J. Reed, and J.R. French. 1989. Understanding salt-marsh accretion, Scolt Head Island, Norfolk, England. *Estuaries* 12:228-236.
- Syphax, S.W. and R.S. Hammerschlag. 1995. The reconstruction of Kenilworth Marsh – the last tidal marsh in Washington, D.C. *Park Science* 15:16-19.
- Tabacchi, E., A.M. Planty-Tabacchi, L. Roques, et al. 2005. Seed inputs in riparian zones: implications for plant invasion. *River Resources and Applications* 21:299-313.

- Thomas, J.R., D.J. Gibson, and B.A. Middleton. 2005. Water dispersal of vegetative bulbils of the invasive exotic *Dioscorea oppositifolia* L. in southern Illinois. *Journal of the Torrey Botanical Society* 132:187-196.
- Thomas, J.R., B.A. Middleton, and D.J. Gibson. 2006. A landscape perspective of the stream corridor invasion and habitat characteristics of an exotic (*Dioscorea oppositifolia*) in a pristine watershed in Illinois. *Biological Invasions* 8:1103-1113.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ, USA.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189-214.
- Tiner, R.W. 1998. *In search of swampland: a wetland source book and field guide*. Rutgers University Press, New Brunswick, NJ, USA.
- Townsend, J.F. 2004. *Natural Heritage Resources of Virginia: Rare Plants*. Natural Heritage Technical Report 04-06. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia. Unpublished report. April 2004.
- Uchida, T. and F. Tazaki. 2005. New methods and allelopathic considerations of riparian buffer zones using *Phragmites australis* (Cav.) Trin. *Ecological Engineering* 24:559-569.
- Uhler, F.M. 1963. *Plants and animals noted in Dyke Marsh and adjacent waters along the tidal Potomac River, Fairfax County, Virginia, with suggestions regarding development for aquatic wildlife in that area*. 26 October and 19 November 1963.
- Ungar, I.A. and S.R.J. Woodell. 1993. Similarity of seed banks to aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower Peninsula, South Wales. *International Journal of Plant Sciences* 15:746-749.
- U.S. Army Corps of Engineers. 1988. *Final Report. Potomac River dredged material placement site study*. Baltimore District.
- U.S. Environmental Protection Agency (USEPA). 1999. *Methods and guidance for analysis of water*. EPA 821-C-99-004. Office of Water, Office of Science and Technology, USEPA, Washington, DC.
- Van der Sman, A.J.M., N. Joosten, and C.W.P.M. Blom. 1993. Flooding regimes and life history characteristics of short-lived species in river forelands. *Journal of Ecology* 81:121-130.

- Van Zandt, P.A., M.A. Tobler, E. Mouton, K.H. Hasenstein, and S. Mopper. 2003. Positive and negative consequences of salinity stress for the growth and reproduction of the clonal plant, *Iris hexagona*. *Journal of Ecology* 91:837-846.
- Verhoeven, J.T.A., D.F. Whigham, R. van Logtestijn, and J. O'Neill. 2001. A comparative study of nitrogen and phosphorus cycling in tidal and non-tidal riverine wetlands. *Wetlands* 21:210-222.
- Vitousek, P.M., J.D. Aber, R.W. Howarth, et al. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737-750.
- Vitousek, P.M. and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13:87-115.
- Vretare Strand, V. 2002. The influence of ventilation systems on water depth penetration of emergent macrophytes. *Freshwater Biology* 47:1097-1105.
- Warrick, R.A., E.M. Barrow, and T.M.L. Wigley (eds). 1993. *Climate and sea level change: observations, projections and implications*. Cambridge University Press, Cambridge, England.
- Weishar, L.L., J.M. Teal, and R. Hinkle. 2005. Designing large-scale restoration for Delaware Bay. *Ecological Engineering* 25:231-239.
- West, D. and D.F. Whigham. 1975-1976. Seed germination of arrow arum (*Peltandra virginica* L.). *Bartonia* 44: 44-49.
- Wester, H.V. and M. Sullivan. 1970. 1970 episode of air pollution damage to vegetation in Washington, D.C. area. Office of the Chief Scientist Annual Report, 1970, National Park Service, Washington, DC.
- Whigham, D.F. 1978. Relationship between aboveground and belowground biomass of freshwater tidal wetland macrophytes. *Aquatic Botany* 5:355-364.
- Whigham, D.F., J. McCormick, R.E. Good, and R.L. Simpson. 1978. Biomass and primary production in freshwater tidal wetlands of the middle Atlantic Coast. *In*: R.E. Good, D.F. Whigham, and R.L. Simpson (eds.) *Freshwater wetlands: ecological processes and management potential*. Academic Press, Inc., New York, NY, USA.
- Whigham, D.F. and R.L. Simpson. 1978. The relationship between aboveground and belowground biomass of freshwater tidal wetland macrophytes. *Aquatic Botany* 5:355-364.
- Whigham, D.F., R.L. Simpson, and M.A. Leck. 1979. The distribution of seeds, seedlings, and established plants of Arrow Arum (*Peltandra virginica* (L.) Kunth) in a freshwater tidal wetland. *Bulletin of the Torrey Botanic Club* 106:193-199.

- Windham, L. and L.A. Meyerson. 2003. Effects of common reed (*Phragmites australis*) expansions on nitrogen dynamics of tidal marshes of northeastern US. *Estuaries* 26:452-464.
- Wolters, M., A. Garbutt, and J.P. Bakker. 2005. Plant colonization after managed realignment: the relative importance of diaspore dispersal. *Journal of Applied Ecology* 42:770-777.
- Xu, Z. 1991. Final report on inventories of plant species and communities in Dyke Marsh, Alexandria, Virginia. George Mason University, Fairfax, VA.
- Yang, J., Y.M. Hu, and R.C. Bu. 2006. Microscale spatial variability of redox potential in surface soil. *Soil Science* 171:747-753.
- Zedler, J.B. and J.C. Callaway. 1999. Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology* 7:69-73.