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Impacts of *Phragmites australis* Management on Wetland Plant Community Recovery, Seedbank Composition, and the Physical Environment in the Chesapeake Bay

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IMPACTS OF *PHRAGMITES AUSTRALIS* MANAGEMENT ON WETLAND PLANT
COMMUNITY RECOVERY, SEEDBANK COMPOSITION, AND THE PHYSICAL
ENVIRONMENT IN THE CHESAPEAKE BAY

by

Eric L. G. Hazelton

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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2018

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ABSTRACT

Impacts of *Phragmites australis* Management on Wetland Plant Community
Recovery, Seedbank Composition, and the Physical
Environment in the Chesapeake Bay

by

Eric L. G. Hazelton, Doctor of Philosophy

Utah State University, 2018

Major Professor: Karin Kettenring, Ph.D.
Department: Watershed Sciences

Among the most impactful non-native species in North America is *Phragmites australis* (*Phragmites*), a large-scale clonal grass that colonizes disturbed areas and capitalizes on anthropogenic alterations to the nutrient regime in wetlands. *Phragmites*' dense monocultures crowd out native plants and alter habitat for native fauna.

We conducted a large-scale, long-term study of the effects of *Phragmites* removal on the Chesapeake Bay, looking at the impact of *Phragmites* invasions and management on fauna, composition of *Phragmites*, environment, and subsequent plant community recovery.

We used herbicide to remove *Phragmites* from plots in sub-estuaries while leaving associated *Phragmites* plots intact. We then compared the plant community composition in the recovering *Phragmites*, the intact *Phragmites* (control), and the

reference wetlands from before treatment, through three years of treatment, and one year after treatment.

Analysis of the seedbank in treatment sub-estuaries demonstrated no removal effect on the composition, indicating ample seedbank below *Phragmites* monocultures to facilitate revegetation, as well as substantial presence of *Phragmites* in the seedbank of native wetlands. Within each sub-estuary, there was little variation among treatment types, implying: 1. The seedbanks mix on the tide rather through canopy composition; 2. If uninvaded wetlands undergo disturbances, there are ample *Phragmites* propagules to initiate an invasion.

We found that the plant communities that emerged with *Phragmites* removal did not resemble the species assemblages in the reference wetlands, though they did tend to have larger native species composition than the control plots. Given longer treatment, some of these communities could potentially succeed to the reference state.

Removal plots in other sub-estuaries had *Phragmites* return even with continued spraying. The sub-estuaries that had more uninvaded wetlands adjacent to the *Phragmites* tended to recover more closely to the reference state than those with large *Phragmites* monocultures. An analysis of the conservation value of each removal site showed that removal restored the wetlands closer to the reference condition.

This data calls for caution. The prolific and resilient *Phragmites* may require diverse treatments, such as mowing, grazing, and burning, or active revegetation. If spraying *Phragmites* is the only option, our results suggest that herbicide treatment must continue *in perpetuity*.

PUBLIC ABSTRACT

Impacts of *Phragmites australis* Management on Wetland Plant Community
Recovery, Seedbank Composition, and the Physical
Environment in the Chesapeake Bay

Eric L. G. Hazelton

Biological invasions have adverse economic, cultural, and ecological effects worldwide. Among the most impactful in North America is the invasion of *Phragmites australis* (*Phragmites*), a large-scale clonal grass that rapidly colonizes wetlands. *Phragmites* crowds out native plants and alters habitat for native fauna. In doing so, *Phragmites* also alters human access to water resources and has adverse economic effects, including decreasing property value, inhibiting recreational use, and limiting populations of game species.

The efforts described in this dissertation are a component of a large, multidisciplinary effort to better understand the anthropogenic stressors to Chesapeake Bay, Maryland, at the land/water interface. Utah State University worked in collaboration with the Smithsonian Environmental Research Center and other academic and public organizations to address this problem from multiple directions. The diverse and extensive studies ranged from aquatic and avian faunal composition and submerged aquatic vegetation to our work on the invasive wetland grass, *Phragmites*.

Having assessed the existing literature and its shortcomings, we conducted a large-scale, long-term study of the effects of *Phragmites* removal on the Bay. By removing *Phragmites* from plots in select sub-estuaries of Chesapeake Bay through

herbicide spraying, leaving associated plots intact, and comparing both with native wetland conditions, we sought to better understand herbicidal management of *Phragmites* and the potential for wetland plant community recovery. Although sprayings decreased the relative cover, stem diameters, and stem densities of *Phragmites*, we found that herbicide treatment alone was not adequate to restore native plant communities or significantly affect seedbank composition. Our results demonstrate the resilience of *Phragmites* and call for a diverse range of control measures, including mowing, grazing, burning to expose the seedbank to germination, and—if economics allow—active revegetation to establish the desired plant community composition.

This dissertation provides beneficial data for those who seek to manage *Phragmites* in wetland plant communities, but there is much work still to be done. The literature review, seedbank study, and community analysis included in this volume are components of a larger research program on *Phragmites* management. Future studies should, in particular, investigate revegetation and nutrient amelioration as means to recover pre-invasion vegetation.

DEDICATION

This effort is dedicated to my wife and partner in crime,
Sarah Hazelton. Without her support, love, and patience,
none of this would have been possible.

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than I could have imagined and I hope she reaps a karmic reward. Evan Pool is the greatest lab tech I could dream of. I love you all; you have all enhanced my science and enchanted my life.

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Eric L. G. Hazelton

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CHAPTER I

INTRODUCTION

INTRODUCTION

Invasive species are currently one of the greatest threats to native ecosystems worldwide and their impacts are becoming an increasingly detrimental component of climate change (Mack *et al.* 2000). Invasive plants infest over one hundred million acres of land in the U.S. alone (Meyerson *et al.* 2009) and wetlands are more prone to invasion than other ecosystems as they are sinks for nutrients and other disturbances (Zedler and Kerchner 2004) and propagules (Leck 1989). Wetlands provide cultural, economic, and ecological services (Palmer 2009) and invasive species can decrease their value and function (D'Antonio and Meyerson 2002).

Physical disturbance and nutrient addition facilitate plant invasions by altering competitive balances or creating microsites that allow for establishment of non-native species (McGlone *et al.* 2011; Alpert *et al.* 2000; Harper 1977). In the absence of disturbance, established communities tend to be more resistant to invasions (Kettenring *et al.* 2015; McGlone *et al.* 2011) than disturbed ones. The establishment of resistant native plant assemblages is a critical objective following removal of invasive plants (Kettenring and Reinhardt Adams 2011; Reid *et al.* 2009; Bakker and Wilson 2004; Byun *et al.* 2012). However, in many cases, plant invaders can alter an ecosystem, creating an alternative stable state that prevents pre-invasion plant communities from reestablishing once the invader is removed (Suding *et al.* 2004; Hacker and Dethier 2008). These legacy effects can manifest as invasive propagules in the seedbank, disturbances, or alterations

in the physical environment (changes in nutrient, chemical, hydrologic, or light regimes), all of which can prevent recovering plant assemblages to return to a pre-invaded state (D'Antonio and Meyerson 2002).

Over the past five decades, an invasive European lineage of *Phragmites australis* (Common reed, Poaceae, Trin. Ex Steud.; henceforth *Phragmites*) has rapidly expanded its range into North American wetlands (Saltonstall 2002; Chambers *et al.* 1999; Marks *et al.* 1994). *Phragmites* is an ecological engineer; it alters the hydrology (Windham and Lathrop 1999), sedimentation (Rooth *et al.* 2003), and nutrient availability (Windham and Meyerson 2003) of wetlands, potentially resulting in up to a five-fold decrease in species diversity by out-competing native vegetation and altering habitat (Bertness *et al.* 2002).

The recent expansion of *Phragmites* has been connected to anthropogenic land-use practices that disturb wetlands and increase nutrient availability (King *et al.* 2007; Silliman and Bertness 2004; Chambers *et al.* 2008; Burdick and Konisky 2003; Bart *et al.* 2006). There is research on aspects of *Phragmites* growth and reproduction on an organismal scale that can guide research into the landscape-scale factors that facilitate invasions. *Phragmites* seeds are most prone to establish on denuded, non-inundated substrates (Ekstam *et al.* 1999; Kettenring *et al.* 2015). Once germinated and under enhanced nutrient conditions, *Phragmites* seedlings can undergo “explosive growth” that allows the seedling to establish (Saltonstall and Stevenson 2007). Established genets benefit from clonal integration for nutrient partitioning and to escape physiological stresses related to salinity, drought, or anoxia (Amsberry *et al.* 2000). However, the site-specific impact on restoration outcomes is a major knowledge gap, and managing the factors that promote invasions on a landscape scale is elusive.

Historically, *Phragmites* was thought to spread primarily by clonal growth (Haslam 1972). Recently, researchers found that sexual reproduction is more prevalent in its spread than previously thought and new patches are likely colonized by seed (McCormick *et al.* 2010a,b; Kettenring *et al.* 2010, 2011). Human disturbances, as occur in more developed watersheds, allow for germination microsites (per Harper 1977). Reproduction from seed increases genetic diversity in *Phragmites* populations (McCormick *et al.* 2010a,b; Kettenring *et al.* 2010, 2011), and nutrient runoff increases seed production (Kettenring *et al.* 2011). As genetic diversity increases, *Phragmites* stands produce more viable seeds, which in turn increases local levels of *Phragmites* genetic diversity in a positive feedback loop (Kettenring *et al.* 2011; see discussion in Hazelton *et al.* 2014).

While *Phragmites* does have documented adverse impacts to certain ecosystem services (decreases biodiversity: Bertness *et al.* 2002; waterfowl habitat: Cross and Flemming 1989, cultural perception: Kiviat 2006), it provides a suite of services as a tradeoff (fish habitat: Meyerson *et al.* 2010; bird habitat: Kiviat 2013; Cultural importance: Kiviat 2013; other factors detailed below). In the Anthropocene, ecosystem services should be considered within a context of potential climate change potential benefits of *Phragmites* may eventually outweigh the costs (Gedan *et al.* 2011; Hershner and Havens 2008; Weinstein *et al.* 2003; Ludwig). *Phragmites* accretes sediment and peat at a rate that stabilizes shorelines against sea level rise (Rooth *et al.* 2003). The reed has a higher capacity for nutrient sequestration than native vegetation (Mozdzer and Megonigal 2012). Under elevated nitrogen conditions *Phragmites* is more efficient at carbon sequestration than surrounding vegetation (Martina *et al.* 2016), however carbon

capture likely depends on biogeochemical conditions and stand age, as *Phragmites* can increase methane emissions by oxidizing the deep substrate (Mueller *et al.* 2016; Bernal *et al.* 2017). The tradeoffs in ecosystem services between native plant assemblages and *Phragmites* invasion are often a matter of cultural perception, or management objectives.

Efforts to control *Phragmites* can have unintended consequences. *Phragmites* removal is likely to create the disturbed conditions thought to promote seedling establishment by the reed as its seeds can recolonize areas denuded by *Phragmites* removal. The system-wide impacts of control methods such as herbicide use are unclear (Hazelton *et al.* 2014), as is the efficacy of these methods in returning vegetation to a pre-invaded state and what measures are needed post removal. Studies reporting the composition of plant communities that establish when *Phragmites* is removed are rare (Hazelton *et al.* 2014) and studies on invasive plants seldom report more than two years of post-removal data (Kettenring and Reinhardt Adams 2011), leaving little insight into plant community recovery. If the goal of management efforts is to restore pre-invasion plant assemblages (rare community types, or critical habitat), removing *Phragmites* will not likely achieve this outcome without additional measures (revegetation, managing propagule sources, hydrological restoration, *etc.*). If managers intend to remove *Phragmites*, and are not concerned with restoring specific plant species assemblages, much less effort is likely required. The outcome of *Phragmites* removal is likely site specific and depends on the specific management objectives for each individual wetland. Since these management decisions are nuanced, they should be weighed on a case by case basis (see reviews: Hazelton *et al.* 2014; Gedan *et al.* 2011; Ludwig *et al.* 2003; Hershner and Havens 2008).

While there is corroborating research into the biotic and abiotic conditions that contribute to *Phragmites* establishment, few studies have looked at the implementation of environmental changes on a scale that is adequate to manage invasions. Further, as is common with plant invasion studies, there is little information of site conditions pre-invasion (Barney *et al* 2013; Blossey 1999). Comparisons to non-invaded reference sites or experimentally facilitated invasions can offer insight toward the process of invasions (Kettenring *et al.* 2015). Only by identifying the site-specific physical conditions associated with disturbance (nutrients, salinity, hydrology, *etc.*) that promote, or result from, *Phragmites* invasion, can we minimize unintended consequences of control efforts; restore habitat, increase management efficacy, and work toward preventing future invasions.

My doctoral research addressed several of these knowledge gaps by tracking plant communities and environmental changes in wetland areas that had *Phragmites* removed compared to nearby areas of native vegetation and untreated areas where *Phragmites* was not removed. In order to address the knowledge gaps surrounding *Phragmites* invasion and management, we conducted a large-scale study that monitors numerous components of the invasion and recovery. The major component of my doctoral research is a large-scale manipulation that examines the interplay of nutrients, disturbance, and sexual reproduction on the management of *Phragmites* across the Chesapeake Bay in collaboration with colleagues at the Smithsonian Environmental Research Center (SERC), Utah State University (USU), and several other institutions.

Initially, we conducted a pilot study to determine the role of disturbance on *Phragmites* establishment, and found that upon successful recruitment, the plant will

survive regardless of disturbance regime. Germination was much less reliable, and was dependent on a window of opportunity with favorable tides and weather (Kettenring *et al* 2015). We found that if a seedling survived the initial environmental filters, it was highly likely to grow to reproductive stage and further the invasion.

We then investigated the role of stand age in *Phragmites* invasions in an effort to prioritize management efforts. We documented the plant communities under long-established and recent *Phragmites* stands. We looked at how stand age impacted the plant communities, herbivory rates, and the clonal diversity of stands and found that only clonal diversity changed with time (Hazelton *et al* 2015). Once *Phragmites* was established, it rapidly formed a climax community, and time since invasion did not alter any other factors.

Our overall goal was to investigate the ecology and management of *Phragmites* invasion from as many aspects as possible. Building on the two initial studies, we established a large-scale *Phragmites* removal experiment across Chesapeake Bay to elucidate the impact of *Phragmites* invasion on Chesapeake Bay tidal wetlands, and to document the effect of *Phragmites* removal on both the invader and the estuary. As a team, we documented the molecular ecology, community ecology, edaphic conditions, watershed land-use, and how herbicide treatments affect *Phragmites*' vigor, the physical wetland environment, and the recovery of native vegetation. In order to compare invaded and native wetlands, we asked these questions in an experiment that removed *Phragmites* by herbicide in 8 Chesapeake Bay subestuaries, each with 3 treatments: *Phragmites* removed, *Phragmites* intact as an experimental control, and native reference communities. In each subestuary, we documented: *Phragmites* vigor, plant community

composition and changes, herbivory, flowering and reproductive potential, seedbank composition and potential for passive restoration, and the effect of removal on nutrients, salinity, and tidal inundation. Additionally, we investigated the impact of *Phragmites* removal on the invader's clonal richness, but these results will be presented in forthcoming reports.

In this volume, I present 3 chapters (in addition to the introduction and conclusion) that address our knowledge gaps surrounding *Phragmites* invasions. First is a comprehensive review of *Phragmites* management in the United States. The review helped prioritize our experimental objectives and design. We documented a lack of studies that report plant community recovery, a short duration of studies, and a literature focus on herbicide rather than other management techniques. While reviewing the literature, we were also able to develop a conceptual model of *Phragmites* establishment that describes the role of anthropogenic land-use (driver of change in nutrients and disturbance) on *Phragmites*' growth and reproduction (Hazelton *et al* 2014). Our review of *Phragmites* management was included in a special *Phragmites* edition of Annals of Botany Plants.

The second chapter addresses the capacity for wetlands to recover from *Phragmites* removal using passive revegetation, relying on the existing seedbank to recruit native plants (Hazelton *et al.* in review). We found diverse native seedbanks under the native reference sites and also under *Phragmites* monocultures. In our study wetlands, the seedbanks mix on the tides, are fairly well homogenized, and are independent of the above ground vegetation. There is a large variability in seedbank composition between watersheds, and some variation within a subestuary. The variation is not related to the

existing vegetation composition. While there are diverse seedbanks under invaded sites, if managers desire specific species compositions, active revegetation will still be necessary, a finding that parallels findings in other systems (McGlone *et al.* 2011; Bakker and Wilson 2004). This chapter is in revision at Estuaries and Coasts.

The third chapter included in this dissertation encompasses our findings on the community composition, invader's vigor, and environmental changes that result from *Phragmites* removal. Our major conclusions are that herbicide application impacts *Phragmites*' vigor, but the impact decreases with subsequent treatments. In most cases, native vegetation can recover, however the plant community associations do not resemble those of the reference community. Some of the study sites reverted back to the invaded state of a *Phragmites* monoculture, and more research is needed to identify the factors that lead to reinvasion. The physical environment was altered by herbicide treatment as well. In some cases, removing *Phragmites* lead to an increase in nutrient concentrations, but this trend was not universal across subestuaries. Future work should look into microbial activity associated with *Phragmites* decomposition to determine when herbicide might adversely impact the wetland. When the role of *Phragmites* in accreting marsh substrate is considered, there are situations where the invasive monoculture likely provides greater ecosystem services than the potential conditions following removal.

CONCLUSIONS

The research presented here will further the science of wetland management and improve our knowledge of the ecology of biological invasions. *Phragmites* is an elegant model species for studying the ecology of biological invasions (see Meyerson *et al.*

2016), especially keystone invaders that form stable states. Large-scale manipulations, such as our *Phragmites* removal project in the Chesapeake Bay, provide important opportunities to elucidate the biological and environmental factors that promote invasion across multiple watersheds with varying physical conditions. Human alteration of wetlands is known to facilitate invasion by *Phragmites* and our study will help guide future management decisions and site choice for management and restoration. Current control practices are necessarily aggressive and may have unintended consequences on wetland environments, possibly even promoting further invasion and maintaining *Phragmites*' genetic diversity and its ability to produce abundant viable seed. My research results will hopefully assist managers identify wetlands that are most likely to benefit from restoration by determining the physical conditions and land-use patterns that are associated with invasion and recovery on the Atlantic Coast and across North America.

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CHAPTER II

PHRAGMITES AUSTRALIS MANAGEMENT IN THE UNITED STATES: 40 YEARS
OF METHODS AND OUTCOMES**ABSTRACT**

We reviewed the literature on *Phragmites* management in North America in an effort to synthesize our understanding of management efforts, identify gaps in knowledge and improve efficacy of management. Additionally, we assessed recent ecological findings concerning *Phragmites* mechanisms of invasion and integrate these findings into our recommendations for more effective management. Our overall goal is to examine whether or not current management approaches can be improved and whether they promote reestablishment of native plant communities. We found: (1) little information on community-level recovery of vegetation following removal of *Phragmites*; and (2) most management approaches focus on the removal of *Phragmites* from individual stands or groups of stands over a relatively small area. With a few exceptions, recovery studies did not monitor vegetation for substantial durations, thus limiting adequate evaluation of the recovery trajectory. We also found that none of the recovery studies were conducted in a landscape context, even though it is now well documented that land-use patterns on adjacent habitats influence the structure and function of wetlands, including the expansion of *Phragmites*. We suggest that *Phragmites* management needs to shift to watershed scale efforts in coastal regions, or larger management units inland. In addition, management efforts should focus on restoring native plant communities, rather than simply eradicating *Phragmites* stands. Wetlands and watersheds should be prioritized to

identify ecosystems that would benefit most from *Phragmites* management and those where the negative impact of management would be minimal.

KEYWORDS

Common reed; Ecological restoration; Herbicide; Invasive plant; Invasive species;

Management; *Phragmites australis*; Watershed restoration

INTRODUCTION

Wetlands are landscape sinks for nutrients and propagules, making them especially vulnerable to plant invasions as they are downstream from most disturbances (Zedler and Kercher 2004). One such invader, a Eurasian lineage of the common reed, *Phragmites australis* (hereafter referred to as *Phragmites*), is increasingly dominant in wetlands across North America (Marks et al 1994; Saltonstall 2003; Chambers et al 1999; Kettenring et al 2012 this special issue. *Phragmites* invasions are often associated with decreases in plant biodiversity (Bertness and Ewanchuk 2002; Chambers *et al.* 1999; Keller 2000), declines in habitat quality for fish and wildlife (Chambers *et al.* 2012; Fell *et al.* 2006; Fell *et al.* 2003; Gratton and Denno 2006), disruptions to biogeochemical cycles (Meyerson *et al.* 1999; Meyerson et al 2000; Findlay *et al.* 2003) and other ecosystem services (but see Kiviat 2013 and Kettenring *et al.* 2012 in this volume, which highlight *Phragmites* benefit to wildlife or lack/weaknesses of data on actual impacts). *Phragmites* invasion is becoming an increasingly large management concern in a variety of systems: tidal marshes along the Atlantic Coast (Bertness *et al.* 2002; Chambers *et al.* 1999; Warren *et al.* 2001); the Great Lakes (Carlson *et al.* 2009; Tulbure *et al.* 2007; Uzarski *et al.* 2009; Wilcox 2013); inland brackish wetlands of the Great Basin (Kettenring and Mock 2012); and the Gulf Coast (Kettenring *et al.* 2012 in this special edition).

Phragmites is a clonal, rhizomatous grass with a cosmopolitan distribution (Haslam 1972). Several genetic lineages, including some native lineages, are present in North America (Saltonstall 2002; Saltonstall 2003; Meyerson *et al.* 2012, in this special edition; Lambertini *et al.* 2012a; Lambertini *et al.* 2012b, in this special edition).

However, the invasion by the Eurasian genetic lineage in wetlands across North America has been striking due to its rapid spread, abundance, and impacts. Eurasian *Phragmites*' dominance at the landscape scale has been attributed to anthropogenic factors, including hydrologic alteration, increased nutrients, and global change (Brisson *et al.* 2008; Silliman and Bertness 2004; Minchinton 2002a; Bart *et al.* 2006; King *et al.* 2007; Burdick and Konisky 2003; Mozdzer and Megonigal 2012; Mozdzer *et al.* 2010; Mozdzer *et al.* 2013 in this special edition; Kettenring *et al.* 2011). Since the turn of the 20th century, non-native *Phragmites* in North America has been associated with denuded soil and anthropogenic disturbance (Taylor 1938) but natural disturbances also produce favorable conditions for *Phragmites* establishment (Minchinton and Bertness 2003; Baldwin *et al.* 2010). *Phragmites* thrives in freshwater and brackish wetlands (Meyerson *et al.* 2000; Wilcox *et al.* 2003), and is expanding in managed systems like highway ditches (Lelong *et al.* 2007; Jodoin *et al.* 2008) and constructed wetlands (Havens *et al.* 2003).

Phragmites management strategies typically focus on the use of a limited number of techniques (described later) applied to individual patches or groups of patches. To critically and effectively evaluate restoration after an invasive species has been removed, data need to be collected to assess the initial wetland state, monitor the system through treatment (to inform adaptive management), and monitor for multiple years after treatment (see discussion in Blossey 1999). However, studies on the management of invasive plants (not just those investigating *Phragmites*) rarely report data beyond the response of the invader (reviewed in Reid *et al.* 2009) and monitoring for treatment effectiveness seldom lasts more than two years (reviewed in Kettenring and Reinhardt

Adams 2011). A lack of long-term monitoring is likely due to: (1) the cultural mindset of land management agencies; and (2) financial considerations and logistical constraints. *Phragmites* management in the US has been occurring for over 35 years (Marks *et al.* 1994; Riemer 1976). Yet, while monitoring appears prohibitively expensive for specific projects, land managers spent over \$4.6 million per year on *Phragmites* management across North America over a five-year period (Martin and Blossey 2013), with no published data to justify the effectiveness of these management efforts to restore native plant communities. Given that eradication of *Phragmites* is rare, and is not likely without many years of follow up treatments (Warren *et al.* 2002; Kettenring *et al.* 2012; Lombard *et al.* 2012; Getsinger *et al.* 2006), monitoring of treatment effectiveness should be an essential component of any management program.

Here we review current strategies for *Phragmites* management in North America and identify factors that have the potential to transform future management. We begin with a literature review that addresses two central questions: (1) Are current management practices successful? and (2) do current *Phragmites* management practices allow for the restoration of native species assemblages? We address these questions by building upon earlier comprehensive reviews of *Phragmites* management (Kiviat 2006; Marks *et al.* 1994) in light of recent findings on the relationships among *Phragmites* invasion, land use, and reproductive strategies within and among *Phragmites* patches. We also present a conceptual model of *Phragmites* invasion that integrates recent research findings. We argue that *Phragmites* management is best approached from a holistic perspective that integrates nutrient and disturbance management at landscape scales while addressing modes of reproduction and spread.

REVIEW OF EXISTING CONTROL MEASURES

Methods

We reviewed the available literature on *Phragmites* management in the United States to determine: (1) which practices have been tested, (2) where deficiencies in our knowledge exist, and (3) what is known about recovery of native communities following attempts to eradicate *Phragmites*. We queried Google Scholar® and ISI Web of Science® for the technical and grey literature on *Phragmites* removal. We used the key words “*Phragmites* removal” and “*Phragmites* management” for all available dates. Articles, reports, and theses from North America were included in our review (34 in total), along with reference to conclusions from previous reviews of the same topics. Only field studies that are applicable to management actions were included; meso- and microcosm studies are omitted. While our review focuses on non-native *Phragmites* in North America, they are presented in context with findings from other parts of the world. We did not consider *Phragmites* removal by hydrologic restoration in our quantitative review as that topic has recently been evaluated (Chambers *et al.* 2012), however, this approach is dealt with contextually when tied to another management method.

Results and Discussion

The most common response variables measured in our review were *Phragmites*-only metrics or functional vegetation (vegetation type, diversity, etc) (21/34 studies; Fig. 2.3). Several studies (5) quantified plant species composition following *Phragmites* management, although none performed any analysis that compared plant community composition. Additionally, only one study (Moore *et al.* 2012) compared recovering

vegetation to reference sites, which is often critical in restoration and management (Neckles *et al.* 2002). Notably, two studies reported seed bank changes in response to *Phragmites* management and recorded ample seedbank for passive revegetation. Most studies (14) reported a single year of data and only five report >5 years of follow up data, the most notable of which was a study that reported a 20 year follow up observation (Fig. 2.1). The most commonly tested management technique was the use of herbicides (Fig. 2.2). Twenty-seven of the 34 studies reported results of the use of herbicides alone or in combination with other methods. A combination of cutting or mowing *Phragmites*, often in combination with flooding or herbicide use was studied in 15 instances (Fig. 2.2).

Our review focused on four main categories of methods for controlling *Phragmites*: mechanical, chemical, biological, and novel methods. Here we review these methods to discuss their effectiveness and to highlight research needs.

Mechanical Control: Mechanical control is perhaps the first human reaction to remove an unwanted plant, and the methods vary in efficacy and degree of effort. It is largely achieved with mechanical mowing or cutting with hand tools, hand-pulling, crushing, excavation of entire plants, burning, or cutting often followed by covering the area with soil or plastic.

Mowing and Cutting: For a perennial rhizomatous grass, mowing does little to reduce its dominance. Mowing actually stimulated shoot production and resulted in increased density of *Phragmites* shoots (but decreased shoot height and biomass) in both non-tidal (Asaeda *et al.* 2006; Derr 2008a; Gusewell *et al.* 1998; Gusewell 2003) and tidal wetlands (Warren *et al.* 2001).

Variable results following cutting were likely due to a combination of phenology, abiotic conditions, and patch size. Impacts from cutting vary relative to the phenology of the plant, due to shoot/rhizome interactions, as reserves are mobilized and stored differently according to season (Weisner and Graneli 1989; Asaeda *et al.* 2006 and references therein). For example cutting in June showed significant impacts to aboveground and rhizome biomass the following growing season, whereas cutting in July showed no significant impacts compared to controls (Asaeda *et al.* 2006) and open wetlands to pelagic flushing (Uzarski *et al.* 2009). External environmental factors (*e.g.*, temperature and salinity) can influence success; cutting just before the flooding season has been reported to improve control (Marks *et al.* 1994; Kiviat 2006). Some researchers report cutting treatments are less effective when soils are sandy or aerated (Weisner and Graneli 1989). One primitive approach broke shoots and removed them by hand (several shoots were held tight and broken below the waterline as the bases were kicked) along shorelines of five fresh water ponds (Smith 2005). High water levels in all ponds resulted in broken/crushed shoots remaining underwater for an extended period and mortality ranged from 41 to 99% after one year (Smith 2005).

On a large scale, hand cutting will largely be ineffective due to time and resources, but may be an important strategy of rapid response efforts. Overall, simply cutting will be ineffective in eliminating *Phragmites*, but with proper timing, cutting may help reduce dominance (through depletion of underground reserves) and control expansion.

The most effective means of *Phragmites* mechanical control is a combination of cutting or mowing (usually in the spring) and covering stubble with plastic (for one

growing season). However, there are limitations to this application; it is usually applied to small areas, as it is labor-intensive (Boone *et al.* 1988; Kiviat 2006; Marks *et al.* 1994; Dawson and Hallows 1983; Willcox 2013). In one removal experiment, *Phragmites* shoot density averaged 0.1/m² beneath the plastic compared to 20.7/m² in plots without plastic (Burdick *et al.* 2010). Thus, unless cutting is combined with plastic sheeting or herbicide, mowing alone will have little effect on *Phragmites* management other than containment.

Burning: Burning of *Phragmites* provides an alternative mechanism for physical removal, similar to mowing, but burning has not been effective unless coupled with either hydrological restoration or herbicide application (Marks *et al.* 1994). Burning alone has produced variable results and even stimulated *Phragmites* growth and stand development (van der Toorn and Mook 1982, Cross and Flemming 1989; Graneli 1989, Thompson and Shay 1985).

Cutting and burning appear to enhance control efforts if used as secondary treatments. For example, mechanical control efforts improved significantly following either herbicide use (Carlson *et al.* 2009) or the reintroduction of flood waters in tidal wetlands (Teal and Peterson 2005; Getsinger *et al.* 2006; Hellings and Gallagher; 1992). In some instances, burning to remove standing dead biomass in winter was found to enhance control following restoration of tidal exchange (Sun *et al.* 2007). Burning aboveground shoots (or other methods like cutting or crushing) followed by flooding can be used to cut off the oxygen flow to the rhizomes (Rolletschek *et al.* 2000; Weisner and Graneli 1989).

Removal or mulching of aboveground material following cutting has been recommended (Marks *et al.* 1994; Kiviat 2006), even though removal and disposal

involves more effort to prevent recolonization from rhizomes. Burning removes the dead thatch and aids in the regeneration of native plants (Ailstock *et al.* 2001) – typically a primary goal where managers wish to control *Phragmites*. Removal by either mechanism also increases light availability that warms exposed soils. Such conditions enhance germination and recruitment of native plants from seed banks, which is critical for wetland recovery (Farnsworth and Meyerson 1999; Ailstock *et al.* 2001; Carlson *et al.* 2009; Marks *et al.* 1994; Kiviat 2006).

Excavation: Excavation provides complete *Phragmites* control, and is likely the only landscape-scale option for mechanical removal, but requires disproportionately greater costs in both time and resources. Land managers have successfully restored *Phragmites*-dominated dredge spoil sites to highly valued salt marshes in New England (Moore *et al.* 2009). In such cases, excavation to elevations at or below mean high water (*i.e.*, coupling removal with restoration of hydrology) results in daily tidal flooding, increased salinity and sulfide, and resulted in restoration of native plant communities and associated faunal species in Connecticut and New Hampshire (Moore *et al.* 2009).

Chemical Control

Herbicide: Herbicides are currently the primary tool used by land managers to control or eliminate *Phragmites* in North America (94% in a recent national survey; Martin 2011; and 97% in Utah alone, Kettenring *et al.* 2012). There are several application methods and two main herbicide active ingredients (glyphosate and imazapyr) that have been used with varying levels of success (see recent herbicide comparison by Cheshier *et al.* 2012). Perhaps one of the greatest challenges in understanding the efficacy of herbicides on

Phragmites management is the lack of data on the long-term impacts of herbicide application on *Phragmites* and non-target species (Fig. 2.1 and 2.3). In addition, few studies have specifically addressed different application rates and/or application time (Mozdzer *et al.* 2008, Derr 2008b, Back and Holomuzki 2008; Back *et al.* 2012) (Cheshier *et al.* 2012)). The majority of the data that we found were not reported in peer-reviewed publications but in technical reports and bulletins in the “grey literature” which are rarely readily available. We divide information on the use of herbicides into (1) herbicide types and their effects on ecosystem recovery, and (2) a comparison of herbicide efficacy and potential effects on non-target vegetation.

Glyphosate: The most commonly used herbicides contain the active ingredient glyphosate; this is likely attributed to the fact that glyphosate herbicides were the only EPA approved herbicides for application in aquatic environments until 2003. Common trade names approved for aquatic application of glyphosate to control *Phragmites* include Rodeo™, GlyPro™, and Aqua Neat™. As a broad-spectrum systemic herbicide, glyphosate is non-selective and will also kill non-target plants including woody and herbaceous plants. According to the Rodeo™ label, glyphosate is taken up through the plant epidermis and subsequently moves into the root system through the vascular tissue. In the plant, it interferes with amino acid synthesis specifically found in plants and microorganisms. Degradation of glyphosate is reported to occur through microbial pathways in less than seven days; however, greenhouse studies have reported persistence of glyphosate or glyphosate-related products for up to 79 days (Meyerson *et al.* 1997), suggesting that any subsequent replanting should occur several weeks after replanting dates given by the label instructions, due to potential negative effects on non-target native

plants. A surfactant must be added to aid in foliar uptake and reported toxicity in fauna has been attributed to surfactants in the various formulations (Tu *et al.* 2001), and not the herbicide itself.

Historically, glyphosate was applied at the end of the growing season (per label instructions) when plants were translocating resources to belowground rhizomes. Due to the extremely long growing season of non-native *Phragmites* (League *et al.* 2006; Farnsworth and Meyerson 2003), it was possible to apply glyphosate after native plant senescence with minimal effect on native vegetation. Two recent studies have found that, contrary to label instructions, earlier application of glyphosate (June *vs.* September), is more effective at controlling *Phragmites* (Mozdzer *et al.* 2008; Derr 2008b). However, earlier application also has the potential to negatively impact native plants (Mozdzer *et al.* 2008), which is often at odds with management goals.

The use of glyphosate-containing herbicides usually requires multiple applications over successive years to be effective. Unfortunately, no published studies exist that have evaluated how many applications of glyphosate are necessary for complete *Phragmites* control. We speculate the effectiveness of any herbicide is likely related to the amount of belowground reserves, abiotic conditions, and applicator error. However, there is an urgent need to understand the appropriate control application methods to reduce excess herbicides from entering wetland systems (see concentrations tested in Fig. 2.4).

Imazapyr: The active ingredient imazapyr was approved in 2003 by the US EPA for application in wetland habitats labeled as HabitatTM, EagreTM, and EcoImazapyrTM. Since then, land managers have been using this herbicide (Marris 2005; Clarke 2006) to control *Phragmites*. According to the label, imazapyr works by a mechanism targeting broad-

chained plant specific amino acids in meristematic regions, and is translocated belowground to kill rhizomes. Unlike glyphosate, imazapyr is taken up by the plants' leaves as well as its roots. In solution, Imazapyr is broken down through photodegradation with an average half-life of two days. However, in soils where UV breakdown does not occur, microbial breakdown of imazapyr is the primary mechanism of degradation with half-lives ranging from one month to over four years (Tu *et al.* 2001) with soil moisture, soil depth, pH, and temperature affecting the rates of microbial degradation (Vizantinopoulos and Lolos 1994). Toxicity is described as low to birds and mammals; however non-ionic surfactants may have detrimental effects on invertebrates (Tu *et al.* 2001).

Controlled comparative studies have found that imazapyr is more effective than glyphosate in controlling *Phragmites* (Mozdzer *et al.* 2008, Derr 2008b; Getsinger *et al.* 2006, Kay 1995), but not without serious negative consequences to native plants including recolonization following the death of *Phragmites* (Mozdzer *et al.* 2008). The only studies that reported glyphosate exhibiting a greater impact on *Phragmites* under field conditions were two that used higher concentrations than recommended by the manufacturer (30% in study *vs.* <6% recommended) and were not comparable to the rate of imazapyr used (5%) (Back and Holomuzki 2008; Back *et al.* 2012) (Fig. 2.4). Other studies have demonstrated that there is no need to use glyphosate in concentrations higher than those listed on the product label (Cheshier *et al.* 2012), and label instructions should not be exceeded due to potential negative consequences on flora and fauna. Land managers have noted that wetlands are slower to recover when imazapyr is used when compared to glyphosate herbicides (Mozdzer *et al.* 2008), which may be attributed to

greater persistence in the soil. Given the potential for non-selective root uptake of imazapyr by all plants, the presence of imazapyr or imazapyr-residues may be affect seed banks of native plants. Research is critically needed to understand if imazapyr has negative impacts on the seed bank, or if the delayed recovery can be attributed to persistence of the herbicide in the soils impairing growth of seedlings.

Landscape-scale Phragmites Control Programs using Herbicides: Few have investigated or attempted to control *Phragmites* at the landscape level, and even fewer have made the results available to the scientific community. Perhaps one of the largest restoration projects occurred on the Delaware River as part of the Public Service Electric and Gas restoration. Several papers (Teal and Peterson 2005; Kimble and Able 2007; Turner and Warren 2003; Gratton and Denno 2005; URS 2005) were published midway through the restoration process, reporting on the management approach, but the final results assessing if the management objectives to restore vegetatively diverse, functioning wetlands were achieved have never been published as a peer reviewed study.

In Virginia, USA, land managers have established one of the most thorough management and coordination programs that we are aware of by combining efforts with private, state, and federal stakeholders (Myers *et al.* 2009). Partnering with numerous public and private entities, state staff targeted priority conservation areas (the coastal habitats of Virginia around Chesapeake Bay) to reduce the cover and rate of *Phragmites* spread. These efforts spanned six years and often included an initial aerial application that was followed by ground-based applications in subsequent years to control any re-sprouting. Most of the sites that were treated were surveyed by helicopter in 2004 and 2008. Given that the treatments and surveys were coordinated at the landscape level

(Myers et al 2009) the effort enabled land managers to share resources, resulting in one of the few examples of landscape scale management and control.

The coordinated work in Virginia (Myers *et al* 2009) revealed several patterns, which provided insights for future management. In treated areas, land managers were able to reduce *Phragmites* abundance by 34% from 706 acres to 468 acres. However, where aerial control was not applied, there was a 22% increase in *Phragmites* abundance from 657 to 805 acres. Cumulatively over a four-year period, *Phragmites* abundance was only reduced by 4% total since management focused primarily on large stands (>5 acres). However, during this same period, the small (<0.25 ac) and medium (>0.25 and < 5.0 acres) size class populations increased in abundance by 22% and 87%, respectively, accounting for almost all the gains in habitat from controlling the large stands. These findings suggest that targeting large stands may not be appropriate for controlling *Phragmites* at the landscape level. Instead, priority should be given to small patches that are likely to expand in the future and may contribute to future expansion by sexual reproduction (Myers et al. 2009), which is an approach supported in general recommendations for invasive species control (Moody and Mack 1998).

Regardless of the herbicide used, one-time applications are never 100% effective (Kettenring and Reinhardt Adams 2011). In order for a control and restoration program to be successful, land managers must commit to multi-year applications (*e.g.*, Lombard *et al.* 2012, Warren *et al.* 2001; Riemer 1976; Cheshier *et al.* 2012; Kay 1995) in addition to a long-term commitment from land managers and stakeholders (Teal and Peterson 2005).

Biological Control

Plant Competition: Plant competition by native plants can alter the restoration trajectory. Unmanaged areas where *Phragmites* has been controlled effectively, but not replanted with native species, are often reinvaded by *Phragmites* immediately either by seeds or regrowth from rhizomes that were not killed. The importance of *Phragmites* seed banks in reinvasion varies. Earlier studies reported that *Phragmites* was not present in the seed bank (Van der Valk and Davis 1979; Baldwin and DeRico 1999; Wilson *et al.* 1993), however, more recent studies have found ample *Phragmites* seed in the seed bank (Smith and Kadlec 1983; Leck 2003; Welling *et al.* 1988a; Welling *et al.* 1988b; Baldwin *et al.* 2010). As a grass, *Phragmites* seeds do not remain viable in the seed bank for very long. Where germination of *Phragmites* seeds has been reported, the density of the germinated seeds can be almost as high as the number of viable seeds produced (~ 700 seeds / m², Baldwin *et al.* 2010). If this scenario is typical, it suggests that revegetation of areas from which *Phragmites* has been killed should be planted or seeded with native plants as soon as possible, under the theory that native plants will competitively exclude *Phragmites* seedlings (Farnsworth and Meyerson 1999; Wang *et al.* 2006; Carlson *et al.* 2009; Byun *et al.* 2013). Field experiments in tidal marshes have shown that native plants, though smaller, can slow the recolonization of *Phragmites* seedlings (Minchinton 2002b; Minchinton and Bertness 2003) and reduce the success of resprouting from rhizomes (Amsberry *et al.* 2000; Konisky and Burdick 2004; Wang *et al.* 2006; Peter and Burdick 2010).

Greater species richness in resident plant communities may reduce the ability of *Phragmites* to colonize and expand. A wetland with intact vegetation will have fewer

opportunities for *Phragmites* colonization (Kennedy *et al.* 2002). The potential of native species to successfully compete with *Phragmites* was demonstrated in a field experiment in which one or four native species were planted with *Phragmites* shoots that were grown from rhizomes. Plots with greater species richness had the most dramatic effects, reducing *Phragmites* shoot density >50%, biomass >90%, and survival >65% compared with unplanted controls (Peter and Burdick 2010). A Canadian competition study evaluated plant functional diversity as a factor in *Phragmites* competition. Byun *et al.* (2013) found that biotic resistance in plant communities increased by niche preemption (native plants germinated before *Phragmites* seeds), and niche partitioning (functional diversity). These two experiments demonstrate the importance of plant communities and post-control revegetation in resisting *Phragmites* invasion.

Accelerated development or succession provides an alternative management strategy. This strategy can be successful where the vegetation of forested wetlands or upland edges of wetlands has been disturbed and replaced by *Phragmites*. Here, removal could be coupled with planting trees and shrubs to shade out *Phragmites* (Kiviat 2006; Geoff Wilson Northeast Wetland Restoration *pers. comm.*). A survey of *Phragmites* invasion of 15 created tidal wetlands found *Phragmites* stands decreased cover where shrub/scrub habitat developed (Havens *et al.* 2003). This approach may prevent *Phragmites* reestablishment over the long term, or may allow only scattered *Phragmites* plants to survive.

Native seed banks are critical for successful revegetation after *Phragmites* removal. The literature is full of conflicting results, but overall, wetlands tend to have diverse persistent seed banks (Leck 2003; Leck and Leck 2005; Leck and Simpson 1995;

Ungar 2001) and seed bank studies have not resulted in any clear relationship between the diversity of species in the seed bank and *Phragmites* invasion. In a Great Lakes study, Carlson *et al.* (2009) found that the diversity of vegetation after *Phragmites* removal depended upon the diversity of the native seed bank. It has also been shown that a diverse native seed bank can persist in monocultures of *Phragmites* (Baldwin *et al.* 2010). In fact, the diversity of herbaceous species in the seed bank has been found to be greater in stands dominated by *Phragmites* compared to surrounding areas dominated by native vegetation (Minchinton *et al.* 2006). Minchinton and colleagues concluded that the high cover of *Phragmites* and the thick litter layer inhibited the germination of non-*Phragmites* seeds in the seed bank. In a tidal freshwater system, Ailstock *et al.* (2001) found that the seed bank under *Phragmites* and after *Phragmites* removal both had a high diversity of species. These authors concluded that the type of *Phragmites* management will alter the seed bank, with herbicide-burn treatments having a different seed bank species composition compared to herbicide alone which impacts the outcome of passive revegetation. Hallinger and Shisler (2009) reported successful recolonization of native vegetation from the seed bank alone (with minor reseeded) in a New Jersey salt marsh following *Phragmites* removal. In New England, greater plant diversity was found in treated areas compared to both invaded and uninvaded controls (Moore *et al.* 2012). These studies indicate that the seed bank can play an important role in any wetland restoration effort following *Phragmites* removal.

Herbivory: Grazing has long been used to manage *Phragmites* stands, primarily in Europe (Marks *et al.* 1994), yet there are very few empirical studies evaluating grazing in North America (reviewed in Kiviat 2006). Tesauro and Ehrenfeld (2007) used grazing to

manage *Phragmites* and other invasive species in a New Jersey wetland and found the method beneficial to plant species diversity and animal habitat, but the study lacked replication. Brundage (2010) showed that in Maryland, goats can significantly decrease *Phragmites* density, height and biomass while concurrently increasing species diversity in grazed plots. Around the Great Salt Lake in Utah, several agencies use grazing to manage *Phragmites*, primarily using cattle (49% of surveyed land managers in Kettenring *et al.* 2012). Although there are no formal monitoring data available, wetlands in Utah that receive high-intensity, short duration grazing appear to respond best, with *Distichlis spicata* replacing *Phragmites* after three years of grazing rotation (Rich Hansen, Utah Department of Wildlife Resources, *pers. comm.*), and increases in shorebirds and waterfowl as well (Chad Cranney, Utah Department of Wildlife Resources, *pers. comm.*). In contrast, a study that tested goat grazing in New Jersey marshes in low densities (approximately 1 goat per acre) found that goats preferentially ate all vegetation except *Phragmites*, only consuming *Phragmites* when all other options were exhausted (Teal and Peterson 2005; John Teal, J.M. Teal Associates, *pers. comm.*; URS 2005). Forced grazing in small plots, where grazing mammals do not have an alternative food source, can be successful in controlling *Phragmites* if applied appropriately (Silliman *et al.* In review). However, there are obvious tradeoffs associated with high-intensity grazing, such as soil compaction, trampling, and/or nutrient enrichment that may prevent it from being a suitable method in many areas. Diverse communities of natural herbivores also help suppress *Phragmites* expansion. Small mammals appear to decrease establishment of *Phragmites* in lower salinity tidal marshes (Gedan *et al.* 2009). Muskrats graze *Phragmites* in freshwater systems in the western United States (EH *pers. obs.*) and

brackish wetlands (TM, pers. obs.) indicating that natural herbivory will influence species assemblages in wetlands that contain *Phragmites*. Natural grazing by small mammals may be fostered in brackish marshes by providing muskrat platforms and enhancing habitat for natural herbivores (see Kiviat 2006). Other natural herbivores seem deterred by *Phragmites* (*Litorina irrorata*; Hendricks et al. 2011). There is little information on how either natural herbivory or targeted grazing allow for the reassembly of native plant communities.

Classical Biocontrol Organisms: Biocontrol organisms are currently highly prioritized by land management agencies as a low-cost management strategy alternative. Traditional biocontrol agents are insect herbivores found in the invasive plant's native range that can have strong impacts on its growth and reproduction (Tscharntke 1999, Van Driesche *et al.* 2010). Planned introductions of invertebrates are often controversial as there is a potential for unintended effects to non-target organisms or even across trophic levels (Thomas and Reid 2007), with only 27% of studies reporting complete success in eliminating invasive plants (Van Driesche *et al.* 2010). A recent survey of land managers found that 91% would release biocontrol organisms for *Phragmites*, indicating that there is a strong desire for new techniques to control this grass (Martin 2011). Some land managers expressly prohibit the use of biocontrols due to the potential for unintended impacts and the risks to non-target organisms (Tu *et al.* 2001). The search for a biocontrol for *Phragmites* in North America has been going on for over a decade (Tscharntke 1999; Tewksbury *et al.* 2002; Haefliger *et al.* 2005; Blossey 2003), and several potential insect biocontrols have been identified and are currently undergoing

host-specificity testing with potential releases in 2-3 years from time of writing (B. Blossey, Cornell University, pers. comm.).

In the native range of Eurasian *Phragmites*, there are several dozen invertebrate herbivores in reed stands (Tscharntke 1999) and many of the natural enemies are also found in North America (see Tewksbury *et al.* 2002 for a comprehensive review). Indeed, *Phragmites* herbivores are still being discovered in North America (Eichiner *et al.* 2011). Several herbivores prefer native conspecific *Phragmites* to the non-native lineage (Lambert *et al.* 2007), findings that are troubling given the potential impacts on the widely distributed native *Phragmites* in North America. The herbivores currently present in North America are not considered effective at controlling the spread of the invasive form of *Phragmites*, though some can prevent flowering (*e.g.* *Lipara* spp., Lambert *et al.* 2007). An ongoing study in the Chesapeake Bay has found stem infection rates by insects of over 50% (Hazelton *et al.* in review), yet the degree of impact on competitive dominance and reproductive output is yet to be studied.

Novel Methods in *Phragmites* Management

Several new management methods are currently in development, ranging from hydrologic restoration to alteration of rhizosphere conditions, novel molecular tools, and fungal pathogens. Multiple research groups are investigating pathogens as potential biocontrols. A group at Cornell University is looking at oomycetes as a potential *Phragmites* management tool (Nelson 2009). Shearer and Harms (2012) attempted to isolate fungal pathogens that will preferentially attack non-native *Phragmites* in North America. In a converse approach, another group is looking for species specific fungicide

that could eliminate beneficial fungal endophytes in *Phragmites* and decrease performance (USGS Great Lakes Science Center 2012). Gene silencing techniques are in development with a goal of identifying knock out genes associated with *Phragmites* growth and photosynthesis (USGS Great Lakes Science Center 2012).

In tidal wetlands, restoring hydrology often results in increased porewater sulfide shifting the competitive advantage to native vegetation over *Phragmites* (Moore *et al.* 2012; Chambers *et al.* 2003; Warren *et al.* 2001). High concentrations of sulfide impede nutrient uptake (Chambers *et al.* 1997) and also decrease *Phragmites* growth (Howes *et al.* 2005). Observations of lower sulfide levels in tidal marsh soils with *Phragmites* stands suggest that high sulfide levels may limit *Phragmites* distribution (Chambers *et al.* 1997, 2002). Seeds, seedlings and cuttings can tolerate sulfide concentrations of up to approximately 1.5 mM sulfide (reviewed in Chambers *et al.* 2003), but mature culms were able to survive consistent sulfide levels of 1.5mM (Howes *et al.* 2005). These findings suggest that mature stands with clonal connections may be tolerant of high sulfide concentrations. Therefore, hydrologic control might work best following mechanical actions to eliminate aboveground portions of mature shoots, preventing *Phragmites* from oxygenating the rhizosphere.

Other invasive grasses have been successfully managed by nitrogen control including *Bromus tectorum* (Vasquez *et al.* 2008; Kulmatiski and Beard 2006) and *Phalaris arundinacea* (Ianone *et al.* 2008). Vasquez *et al.* (2008) found that more holistic management practices consisting of controlled grazing, microbial change (through carbon amendment), and native planting helped control nitrogen and make sites less invasible by *Bromus tectorum* in semi-arid systems. In other systems, addition of sawdust to promote

microbial nitrogen immobilization, combined with planting diverse plant assemblages allowed native species to recover following management for *Phalaris arundinacea* (Ianone *et al.* 2008). Sawdust addition impacts non-native grasses more than non-native and native forbs and native grasses (Alpert and Maron 2000). Sugar amendment decreased success of multiple invasive plants greater than adding activated charcoal (Mitchell and Bakker 2011). Even carbon amendment will likely require watershed-scale restoration to permanently decrease plant-available nitrogen (Perry *et al.* 2010) and future studies will need to determine the efficacy of such approaches on *Phragmites*.

Based on this review, we see the need for more research that investigates comprehensive, landscape-scale, integrative management strategies. There is a clear bias in the literature to herbicide use and mowing or cutting, which is reflected in recent surveys of land managers (Kettenring *et al.* 2012; Martin and Blossey 2013). These methods may be effective on a site-by-site basis, but they do not address the factors that contribute to *Phragmites* invasion. Whether the management goal is to eliminate *Phragmites* or merely reduce its dominance, control measures will be more successful if linked with establishment of native plants to occupy the site and periodic monitoring to identify, mark and treat invasive plants. Regardless of control method and initial success of native plants, non-native *Phragmites* will recolonize in most cases (unless salinities are high, as in Sun *et al.* 2007) and will be difficult to eliminate from invaded wetlands (Farnsworth and Meyerson 1999; Warren *et al.* 2001).

INTEGRATING RECENT INSIGHTS ABOUT *PHRAGMITES* ECOLOGY INTO MANAGEMENT: A CONCEPTUAL MODEL

Plant invasions, including that of *Phragmites*, are triggered by both intrinsic and extrinsic factors and are typically interactions between nutrients, disturbance, and propagule pressure (Colautti *et al.* 2006). Intrinsic factors are aspects of a species' biology that drive its establishment and spread. Extrinsic factors include anthropogenic disturbances, nutrient enrichment and herbivory. We developed a conceptual model of *Phragmites* spread that is driven by interactions between intrinsic and extrinsic factors (Fig. 2.5). This model can be used to guide future efforts to manage *Phragmites*. The model is comprised of four intrinsic components that positively affect spread: (1) seed quantity; (2) seed viability; (3) germination and recruitment; and (4) genet diversity. In our model, germination and recruitment are central to increasing genet diversity (outcrossing potential). Increased genet diversity through outcrossing potential leads to an increase in seed viability (McCormick *et al.* 2010a, b; Kettenring *et al.* 2010, 2011). Increases in seed quantity or seed viability will result in higher recruitment rates (new clonally diverse *Phragmites* stands), feeding the cycle. Stand age is an intrinsic factor that slows this feedback loop. Three extrinsic factors are nutrients, disturbances, and herbivory; the first two of which positively impact spread while herbivory has a negative effect through reductions in seed production. Nutrients and physical disturbance also fuel the cycle by increasing seed quantity and recruitment (nutrients), and creating microsites for germination (disturbance). We describe each of these components in greater detail below.

Phragmites invasions were long thought to originate primarily from vegetative propagules (*e.g.* rhizomes) on the upland edge of wetlands (Bart *et al.* 2006), despite the fact that *Phragmites* is capable of sexual reproduction and spread from seed. Seed is dispersed by wind or birds (Soons 2006; Haslam 1969) and new molecular evidence has made it increasingly clear that seeds, rather than vegetative propagules, are the primary means of reproduction for colonization by *Phragmites* (Brisson 2008; Belzile *et al.* 2009; Kettenring *et al.* 2010, 2011; Baldwin *et al.* 2010; McCormick *et al.* 2010a, b; Campbell 2007; Kirk *et al.* 2011; Kettenring and Mock 2012).

Viable seed production in *Phragmites* is driven by outcrossing potential, a phenomenon that is enhanced in polyclonal patches (Kettenring *et al.* 2010, 2011). Viable seeds will lead to the production of new clones, thereby increasing outcrossing potential in a positive feedback that is further enhanced by the presence of disturbances and nutrients (Kettenring *et al.* 2010, 2011; McCormick *et al.* 2010a, b). In particular, inflorescence size and seed quantity increase with elevated nutrients (Kettenring *et al.* 2011), and *Phragmites* in watersheds with a greater degree of anthropogenic development produce more seed than those with less human impact (Kettenring and Whigham 2009; King *et al.* 2007; McCormick *et al.* 2010a; Baldwin *et al.* 2010; Kettenring *et al.* 2010). *Phragmites* seedlings then can exhibit “explosive growth” in response to elevated nutrients (Saltonstall and Stevenson 2007).

Phragmites is a disturbance specialist and its seeds require light and large diurnal temperature fluctuation to break dormancy; conditions typically found on bare, non-inundated soils (Ekstam *et al.* 1999; Ekstam and Foresby 1999; Armstrong 1999). Bare soils can be the result of anthropogenic or natural events such as burial by wrack

(Minchinton 2002a; Minchinton *et al.* 2003; Minchinton and Bertness 2003), a water level drawdown (Smith and Kadlec 1983; Whyte *et al.* 2008; Welling *et al.* 1988a; Welling *et al.* 1988b; Tulbure and Johnston 2010; Galinato and VanDerValk 1986; Tulbure *et al.* 2007; Wilcox 2012), or removal of litter and vegetation by wave action (Baldwin *et al.* 2010). Specific conditions for seed germination are found in the upper edge of wetlands where there is ample oxygen (Wijte and Gallagher 1996a) and salinities are typically low (Wijte and Gallagher 1996; Greenwood and MacFarlane 2006). Then the plant expands primarily through vegetative means via rhizome or stolon extension (Bart *et al.* 2006; Amsberry *et al.* 2000). Although susceptible to flooding during early stages, seedling tolerance to flooding increases with age (Mauchamp *et al.* 2001, Wijte and Gallagher 1996b; Baldwin *et al.* 2010; also see review in Engloner 2010; Weisner and Graneli 1989; Clevering 1999).

Clonal diversity decreases with stand age (Koppitz and Kuhl 2000; Koppitz *et al.* 1997; Curn *et al.* 2007; Krivackova-Sucha *et al.* 2007), potentially decreasing future sexual reproduction by decreasing outcrossing potential. Thus, older stands may decrease in management priority as their clonal diversity decreases. Hyper-adapted clones will be able to prevent seeding establishment by shading the underlying substrate. The outcome of these interactions is that a single clone may eventually competitively exclude other clones, potentially decreasing future sexual reproduction by decreasing outcrossing potential. Many of the oldest stands in Chesapeake Bay appear to have decreased their rate of spread (Rice *et al.* 2000), perhaps as a wetland reaches carrying capacity.

In addition to stand age effects on sexual reproduction, several obligate *Phragmites* endophagous herbivores eliminate *Phragmites* apical dominance, thus

destroying flowering potential on attacked culms (*e.g.*, *Lipara* spp., *Giraudiella* spp., *Calamomyia* spp., *Lasioptera* spp., *Tetramesa* spp. in Tschardt 1999; Lambert *et al.* 2007; Tewksbury *et al.* 2002). While the total impact of herbivory on seed production at the stand or population level is not clear, rates of attack can reach levels likely to decrease seed production substantially (often >50% of stems attacked, Lambert *et al.* 2007; >90% Hazelton *et al.* *in review*).

Watershed-scale changes in land use resulting from development, and associated increases in disturbances and the availability of limiting nutrients such as nitrogen, contribute to *Phragmites* invasion (King *et al.* 2007; Silliman and Bertness 2004; Bertness *et al.* 2002). *Phragmites* presence is linked to development at or near the shoreline (Bertness *et al.* 2002, King *et al.* 2007). The absence or disruption of forested buffers at the upland-wetland-estuarine ecotone edge have been shown to result in expansion of *Phragmites* in New England (Silliman and Bertness 2004; Burdick and Konisky 2003) and the Chesapeake Bay (King *et al.* 2007, Chambers *et al.* 2008). Greater wave energy and watershed-scale nutrient loading interact to increase sexual reproduction and clonal diversity in *Phragmites* stands (Baldwin *et al.* 2010; Kettenring *et al.* 2011). Once wetlands within nutrient enriched watersheds have been invaded, *Phragmites* can spread rapidly through sexual reproduction and the subsequent dispersal of seeds (Kettenring *et al.* 2011; McCormick *et al.* 2010a). Anthropogenic vectors (highways and boat transport) promote the transport and expansion of *Phragmites* between watersheds and across the landscape (Lelong *et al.* 2007; Jodoin *et al.* 2008; Kettenring *et al.* 2012, in this special edition).

Our model of *Phragmites* spread and reproduction is consistent with observations in other species, where increasing nutrient availability and physical disturbance make ecosystems more susceptible to invasion (Alpert *et al.* 2000, Richardson and Pysek 2012). In order to truly manage *Phragmites*, we will need to work at the watershed scale to make sites less able to be invaded through nutrient management and decreased anthropogenic disturbance (Alpert *et al.* 2000) and create conditions that do not favor seed production. Nitrogen management may become the most effective means to control *Phragmites* in the future (Kettenring *et al.* 2011), especially with climate change and increasing CO₂ (Mozdzer and Megonigal 2012). Efforts at the watershed scale to promote “restoration to ensure resilience” (Suding 2011) are needed to combat spread from seed. In addition, addressing sexual reproduction as part of management efforts will be critical (Kettenring *et al.* 2011), especially given that the common practice to control *Phragmites* in the fall with glyphosate often occurs after seeds have been produced (Marks *et al.* 1999, Kettenring *et al.* 2011).

CONCLUSIONS

Critiques of *Phragmites* management are not new, and some authors have called for revaluation of *Phragmites* and the tradeoffs associated with management. Several authors have demonstrated that non-native *Phragmites* provides valuable ecosystem services, especially in the context of increasing anthropogenic stressors and climate change. The services include providing resilient vegetation (Ludwig *et al.* 2003), accretion rates that can keep pace with sea level rise (Rooth *et al.* 2003), habitat quality (Meyerson *et al.* 2007), nutrient removal (Mozdzer *et al.* 2010), and other ecosystem

services (Hershner and Havens 2008; Rooth and Windham 2000; Kiviat 2006; Kiviat 2012 in this special edition. The potential ecosystem services provided by *Phragmites* must be weighed against the desired management outcomes (such as waterfowl management Cross and Flemming 1989) associated with *Phragmites* removal. Since we still know little about the composition of vegetation communities after *Phragmites* is removed, we should weigh the costs of management heavily against the assumed benefits. *Phragmites* management has a great economic cost (Martin and Blossey 2013) and can be met with public backlash due to use of herbicide and other cultural perceptions (Teal and Peterson 2005). It is unlikely that a single strategy will work at all sites; and all management actions should be conducted in a case-specific manner with considerations for the likelihood of success and the costs of management in each watershed.

Managers may decide certain landscapes have been altered too far from a natural state to successfully control *Phragmites* and have reached an alternate stable state that includes non-native *Phragmites* monocultures. Choosing to restore sites that are less degraded and facilitating native plant communities are critical steps toward successful management of invasive plants (Reid *et al.* 2009). Research and land managers should focus on identifying and restoring sites that are likely to recover and remain *Phragmites* free (sensu: Ailstock *et al.* 2001; Reid *et al.* 2009). Restoration efforts may not succeed at all unless they are conducted at the watershed scale in order to address the initial cause (or source) of the invasion (Palmer 2009). Based on our model of *Phragmites* invasion, sites that are in low nutrient watersheds where physical anthropogenic disturbances are unlikely should resist invasion (also see discussion in Kettenring *et al.* 2001). Large-scale

comparative studies that manage *Phragmites* across multiple watersheds will help us determine the factors that contribute to success and failure in *Phragmites* restoration efforts (*sensu* Suding 2011). Once established, *Phragmites* is difficult to remove; preventing invasion may be more efficient than control. *Phragmites* control programs that focus on protection of non-invaded wetlands through prioritization will likely be more successful than those aiming to reduce or eliminate *Phragmites* in heavily invaded watersheds.

The actual outcomes of *Phragmites* removal are still largely unclear. In perhaps the most comprehensive study to date, Ailstock *et al.* (2001) recommended site-specific management with clearly defined restoration objectives. Restoration and management efforts that remove an invasive species often do not result in colonization by desirable native species (Suding 2011; Kettenring and Reinhardt Adams 2011). Changes are temporary and do not necessarily lead to habitat improvement. We advocate increased research into the outcomes of *Phragmites* management, the efficacy of management strategies, and preplanning to assess which sites to manage (*i.e.*, tradeoffs between management efforts and potential gains). Research can be used to guide landscape scale multi-year removals that are structured to allow monitoring and adaptive responses to address challenges and meet management outcomes. Programs should also consider possible underlying causes for *Phragmites* invasion (shoreline buffers to prevent disturbance from development and excess nutrient inputs) and broadening partnerships between ecologists, managers, and policy makers (*sensu* Suding 2011) to manage *Phragmites* in a more holistic manner.

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FIGURES

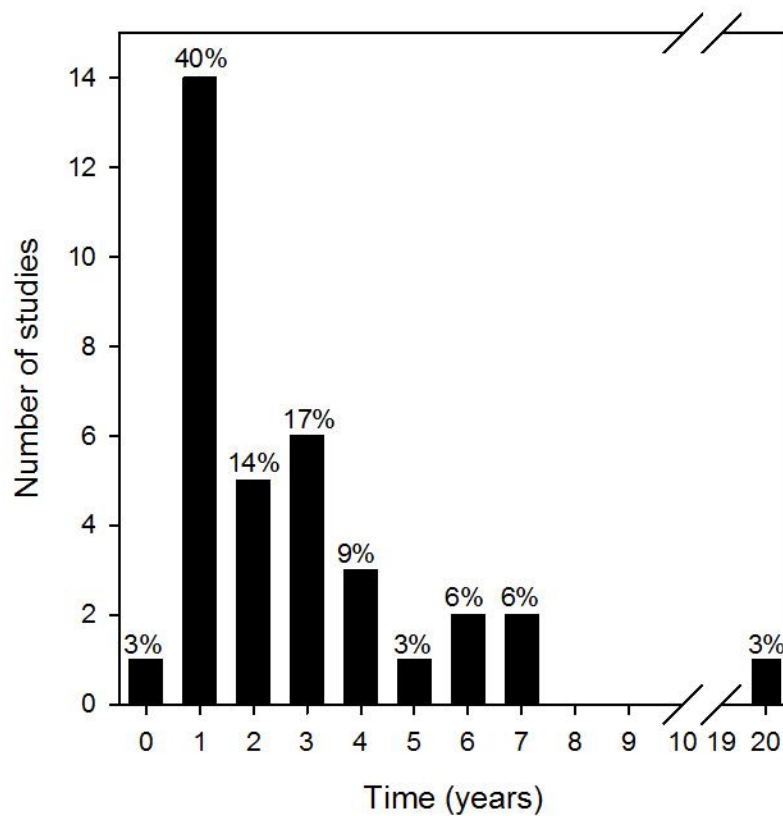


Figure 2.1. Duration of studies included in review. One study conducted a single survey and is denoted with the time=0 bar.

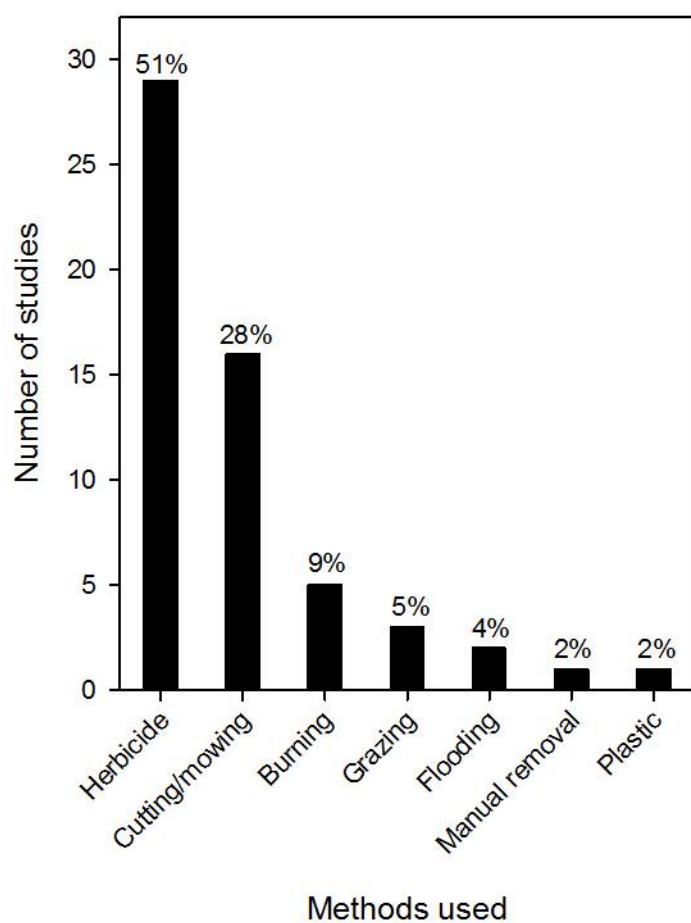


Figure 2.2. Management methods used in reviewed articles. Methods used in combination are counted individually.

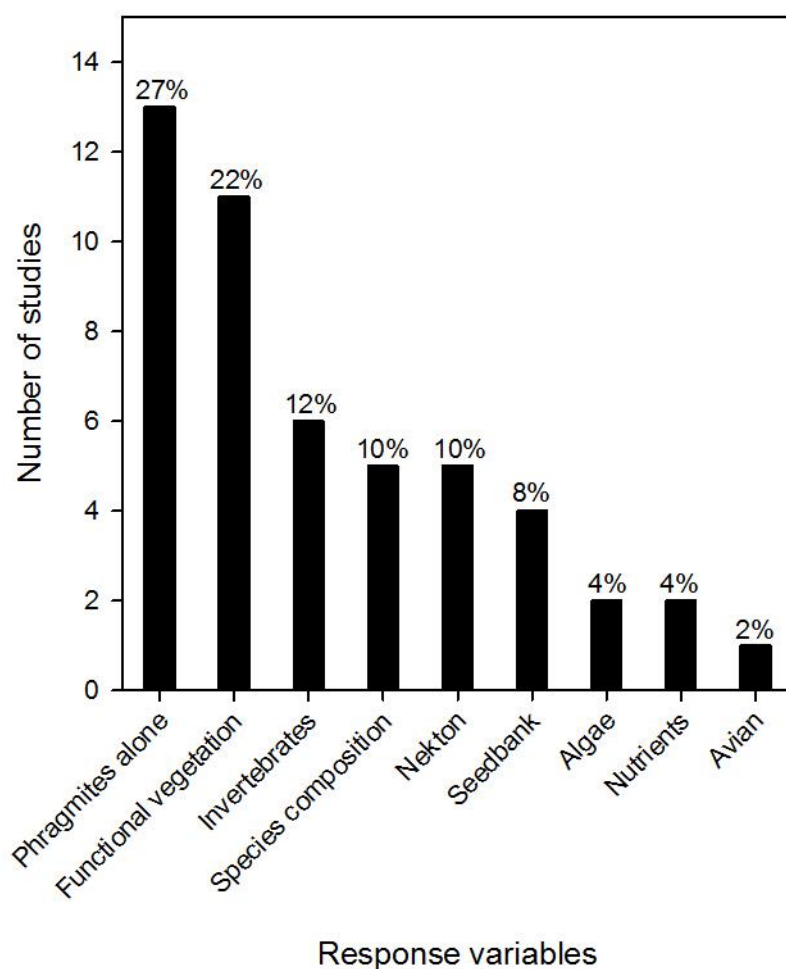


Figure 2.3. Response variables measured in reviewed studies. Functional vegetation represents only diversity, functional groups, or species of interest, but not plant communities. Seedbank represents studies where germination trials were conducted.

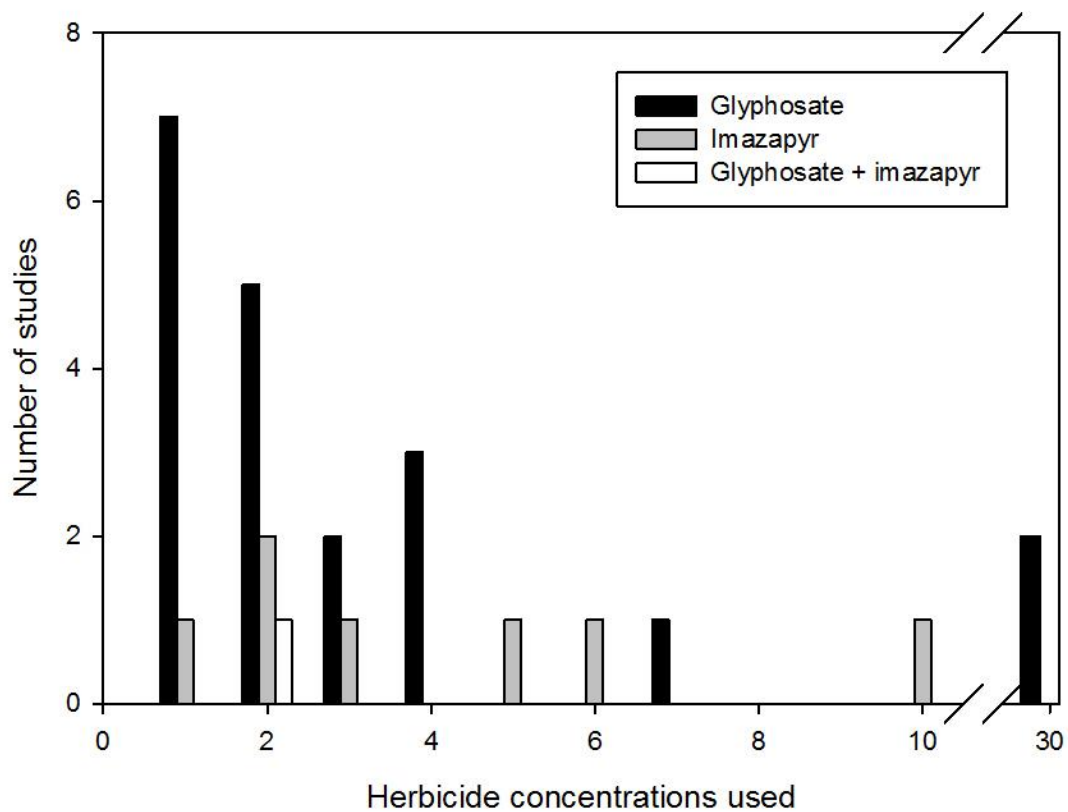


Figure 2.4. Herbicide concentrations (as percent solution of active ingredient in water) used by herbicide removal studies.

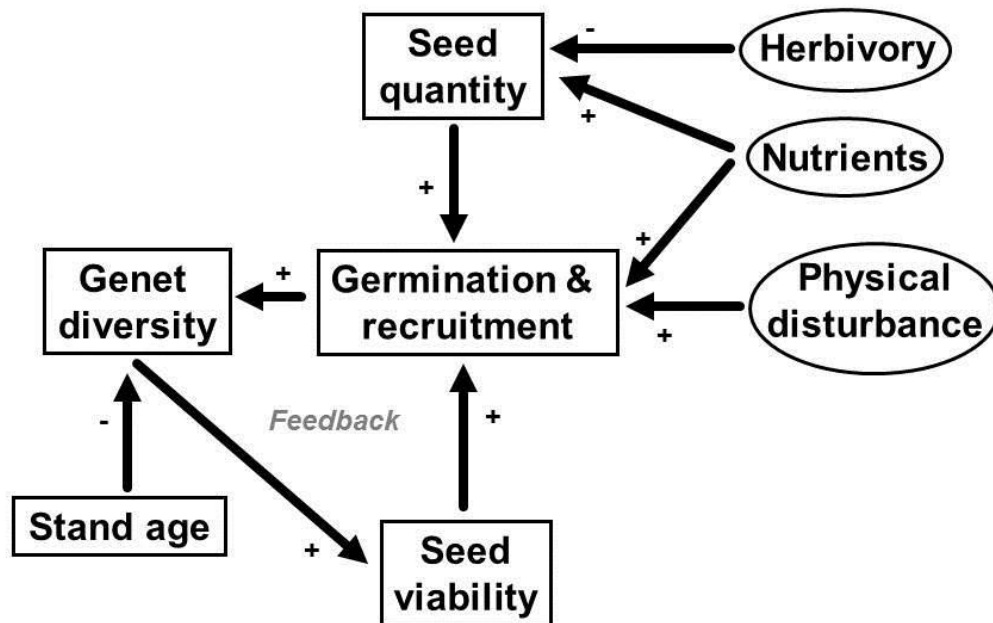


Figure 2.5. Conceptual model of *Phragmites* spread. Intrinsic factors are shown in boxes; extrinsic factors are in ovals. Genet diversity has a positive effect on viable seed production due to increased out-crossing potential. There is a positive feedback between the intrinsic factors affecting sexual reproduction and spread that are further enhanced by physical disturbances and nutrients.

CHAPTER III

SPATIAL AND TEMPORAL VARIATION IN BRACKISH WETLAND
SEEDBANKS: IMPLICATIONS FOR WETLAND RESTORATION FOLLOWING
PHRAGMITES CONTROL

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ABSTRACT

Chesapeake Bay tidal wetlands are experiencing a broad scale and aggressive invasion by the non-native, clonal grass *Phragmites australis*. The grass is often managed with herbicides in efforts to restore native plant communities and wildlife habitat. Management efforts, however, can act as a disturbance resulting in increased light availability, potentially fostering reinvasion from soil seedbanks. If native vegetation establishes quickly from seedbanks, the site should have greater resiliency against invasion, while disturbed sites are rapidly colonized by *P. australis*. We surveyed the soil seedbank of three vegetation cover types in five Chesapeake Bay subestuaries: areas where *P. australis* had been removed, where *P. australis* was left intact, and with native, reference vegetation. We determined the total germination, the proportion of the seedbank that was attributable to invasive species, the richness, the functional diversity,

and the overall composition of the seedbanks in each of the cover types (*i.e.* blocks).

After two years of herbicide treatment in the *P. australis* removal blocks, vegetation cover did impact the total germination or the proportion of invasive species in the seedbank. We also found that seedbank functional composition in tidal brackish wetlands was not influenced by vegetation cover type in most cases. Instead, blocks within a subestuary had similar seedbank functional composition across the years and are composed of diverse functional groups. Based on these findings, we conclude that plant community recovery following *P. australis* removal is not seed-limited and any lack of native vegetation recruitment is likely the result of yet-to-be-determined abiotic factors. These diverse seedbanks could lead to resilient wetland communities that should resist invasions. However, due to the prevalence of undesirable species in the seedbank passive revegetation following invasive plant removal may result in their re-establishment. We also found high enough levels of variation within our subestuaries, and even among plots to warrant analyzing each as a separate case study. The need for active revegetation will need to be assessed on a case-by-case basis to ensure restoration goals are achieved.

KEYWORDS

Invasive plant removal, seedbank, estuary, Chesapeake Bay, *Phragmites*, revegetation

INTRODUCTION

Biological invasions are an increasingly detrimental component of global change, and have the capacity to impact species diversity and a wide range of ecosystem functions and services (Mack *et al.* 2000). Wetlands can be especially vulnerable to invasions and their impacts as wetlands are often downstream of the sources of nutrients, disturbances, and propagules that contribute to invasions (Zedler and Kercher 2005). Tidal wetlands experience additional pressure from invasive species because they receive pollutants and propagules from both the estuaries and the upland watersheds to which they are connected (Leck 1989). Given the large cultural, economic, and ecological value of wetlands (Palmer 2009), mitigating the impacts of invasive species in these systems is critical to maintaining the functions and services they provide (D'Antonio and Meyerson 2002).

Following invasive species removal, facilitating rapid recruitment of native species to recover ecosystem structure and function can, ideally, result in a system that resembles the native reference state. Revegetation is often crucial to establishing plant associations that are resilient and resistant to future or recurring invasions (Kettenring and Reinhart-Adams 2011; Palmer 2009). However, active revegetation, the practice of seeding or planting target species, can be prohibitively expensive (Hallinger and Shisler 2009). Rather than take on the expense, many managers instead follow more passive restoration methods that rely on an existing persistent seedbanks. In addition to being less costly, passive revegetation from the seedbank is often preferred, because it fosters the reestablishment of local species composition and genetic stock (Mitsch and Wilson 1996; William and Jorgenson 2003; Van der Valk and Pederson 1989).

Passive revegetation is particularly beneficial in tidal systems (Leck 2003; Huiskes *et al.* 1995; reviewed in Bakker *et al.* 1996), where water is the predominant vector for propagule transport (Neff *et al.* 2005), and tidal mixing and sorting can contribute to diverse species assemblages (Leck 1989). However, there are tradeoffs associated with passive revegetation. In order to establish a community that is resistant to future invasion, there must be enough propagules to establish viable populations, and they must be from a sufficiently functionally diverse set of species. The greater the functional diversity of revegetation in both growth form (woody, graminoid, forb) and life history (annual, perennial), the more resistant the recovered wetland is likely to be to invasion (Gioria *et al.* 2014; Byun *et al.* 2013; Peter and Burdick 2010) by filling any niche that a future invader would exploit during colonization (“ecological redundancy” Suding 2011). When seedbanks are the primary mode of revegetation, the abundance and composition of the seedbank should be evaluated prior to management actions (Ficken and Menges 2013; Frieswyk and Zedler 2006), for it is possible that there are insufficient seeds to reestablish desired vegetation (Le Peyre *et al.* 2005; Wetzel *et al.* 2001) and/or the proportion of undesirable or weedy species is too high to support revegetation goals.

In this study, we were particularly interested in the potential of Chesapeake Bay brackish tidal wetlands to form resilient (i.e. functionally diverse) native plant communities following the removal of invasive *Phragmites australis* (Poaceae, Trin. Ex. Steud.; here forth *Phragmites*). *Phragmites* has lineages that are native to most regions of North America, but is a management concern due to the rapid range expansion of an invasive Eurasian lineage that forms dense monocultures in wetlands across the continent (Kettenring *et al.* 2012; Saltonstall 2002; Chambers *et al.* 1999). While *Phragmites* is

actively managed across the United States, many management practitioners and land managers do not have the resources to actively revegetate on the scale of their management efforts, potentially leaving denuded wetland soils that are susceptible to new or repeat invasions (Hazelton *et al.* 2014).

Here, we evaluated the capacity of wetlands in five Chesapeake Bay subestuaries to recover from *Phragmites* invasion and subsequent removal through passive revegetation. We sampled soil seedbanks in five subestuaries in three vegetation cover types where: *Phragmites* was removed, *Phragmites* was left intact, and in native reference vegetation. Our four primary questions were:

1. Do vegetation cover type and *Phragmites* removal impact the total seedbank density, species richness, and *Phragmites* emergence?
2. Does vegetation cover type impact seedbank composition?
3. Does removing invasive *Phragmites* by herbicide impact the seedbank composition?
4. Is there enough functional diversity in the seedbank to justify passive revegetation?

METHODS

Sampling

We sampled the seedbank in brackish tidal wetlands in five Chesapeake Bay subestuaries: Nanjemoy, Patapsco, Severn, St Leonard, and Wicomico Rivers (Fig. 3.1) for three years (2011-2013). All subestuaries are located in Maryland, United States. In each subestuary we utilized a block design with three vegetation cover types (*i.e.* blocks):

1) *Phragmites* was removed by herbicide (“Removal”), 2) *Phragmites* was left intact (“Control”), and 3) a native reference (“Reference”). The herbicide removal blocks were sprayed with a 3% glyphosate solution by helicopter in October 2011, with follow-up hand spraying in October 2012. Seedbank samples consisted of five soil cores (5.08 cm diameter by 3 cm deep) collected from five 1m² quadrats (homogenized within each quadrat) along three permanent transects within each block (N=15 per block). Samples from 2012 and 2013 were collected in permanent quadrats, while 2011 samples were collected randomly along transects.

Site descriptions

The Nanjemoy River is a tributary of the Potomac River in southern Maryland (Fig. 3.1). The watershed is predominately forested, which is associated with decreased *Phragmites* invasion in Chesapeake Bay (King *et al.* 2007; Sciance *et al.* 2016). The sampling blocks are adjacent to each other, though the *Phragmites* removal and control blocks are separated by a short dike.

The Patapsco River is in the northern end of Chesapeake Bay and the watershed encompasses the city of Baltimore (Fig. 3.1). The watershed is largely developed (King *et al.* 2007) and the subestuary is subject to urban runoff and associated water quality issues, including sewage spills (Sellner *et al.*, 2001). Our sites were pocket marshes on Marley Creek that form where streams enter the greater Patapsco subestuary. Each block was in a physically separate wetland, all located within a 1.2km stretch of river, but connected by the current of the Patapsco.

The Severn River is another developed watershed according to King *et al.* (2007) that enters the Chesapeake Bay at Annapolis. All three blocks were located along a single 0.5 km long marsh shoreline that is broken up by a large dike and pier between *Phragmites* removal and control blocks and a stream that separates the removal from the reference block.

The St Leonard River is in a forested watershed (King *et al.* 2007) that drains into the Patuxent River (Fig. 3.1). This subestuary has less *Phragmites* cover than the others, though the invasion is spreading rapidly (MM and EH pers. obs.). Native wetlands in this system tend to have low species diversity, and are largely comprised of *Spartina alterniflora* and *Acnida cannabina* (as described in McCormick and Sommes 1982).

The Wicomico, a tributary of the Potomac River in southwestern Maryland (Fig. 3.1), is the largest subestuary in the study. The watershed is predominately forested (King *et al.* 2007). The blocks are located along 0.75km of a continuous fringing marsh that covers nearly 8 km of shoreline. The Wicomico wetland site had more fetch (distance wind can travel over water) than any other in the study, and has relatively low cover of *Phragmites* in the subestuary.

Sample treatment

Soil cores were collected annually, in March while the vegetation was dormant, and kept in dark storage at 4°C until September. Each autumn, the samples were visually checked to remove rhizomes and spread thinly in aluminum tins (one per sample) on top of 200mL of Sunshine Mix #3 in a glasshouse at Utah State University (41.757925 Lat, -111.813078 Lon; 1,412 m elevation, Logan UT, USA). Blank samples containing only

500mL of substrate, but no collected sample, were randomly interspersed among the samples to record fallout from local seed sources. Seedbank composition was determined by the emergence method (Baldwin *et al.* 2001; Poiani and Johnson 1988) under ambient greenhouse light with supplemental light from 1000w high-pressure sodium lighting to maintain a 16/8hr light/dark cycle. Samples were drip irrigated 3 times per day to maintain moist conditions with 400mL of a 20% Hoagland's solution per cycle. Samples were germinated on a 10/27C diurnal temperature fluctuation for 6 months (when germination had slowed to <1 seedling per week) each year. Plants were destructively harvested as soon as they reached an identifiable size. Voucher specimens for each species were grown to flower for deposition in the Intermountain Herbarium at Utah State University. Some genera were grouped together due to an inability to grow each specimen to flower (*Typha* spp., *Cyperus* spp., *Carex* spp.). The blank samples contained high densities of *Oxalis* spp. and the species was removed from all analyses. *Eleocharis parvula* was omitted from analyses since it was impossible to determine whether plants grew from seeds or remnant rhizomes due to its small rhizome size.

Data analysis

To determine the impact of treatment block on total germination, species richness, and *Phragmites* germination we compared the means for each treatment within subestuaries (question 1). These analyses were conducted in JMP (SAS Institute) as a one-way ANOVA comparing mean *Phragmites* germination and total germination across treatment blocks, with quadrat as the unit of replication nested within block.

To analyze community composition (questions 2 and 3), we conducted multivariate data analyses, including perMANOVA and nonparametric multidimensional scaling (NMDS), which can be particularly informative in seedbank studies (Gioria and Osborne 2009). Rare species in each subestuary (present in <5% of samples) were omitted from the community analysis for the subestuary where they were rare (per Legendre and Legendre 2012). Subsequently, samples that did not contain any common species (all zeroes) were removed prior to NMDS and perMANOVA. Multivariate analyses were conducted in Primer® package (<http://www.primer-e.com/>)

We developed regression models to compare plant functional group composition between treatment blocks (questions 3 and 4). Seedbank species were classified by (1) functional groups: graminoids, forbs (including ferns), and woody species; and (2) guild: native annual (NA), native perennial (NP), introduced perennial (IP) (per Kettenring and Galatowitsch 2011); invasive annuals were removed from analysis as they were rare and skewed the interpretation of more common groups. The generalized linear mixed model we developed predicted total germination of plant functional groups and plant guilds within each sample as a function of the predictor variable block (herbicide treated *Phragmites*, intact *Phragmites*, native reference). Invasive annuals were rare (present in <5% of samples) and removed from analysis, as they skewed the interpretation of more common guilds. Species that could not be determined as native or introduced (*Typha* spp., *Acorus* spp.) at the seedling stage were classified as introduced to give a conservative estimate of native diversity (classification according to USDA Plants Database (USDA-NRCS, 2015)). Unlike in the multivariate analyses, rare species were included in the regression analysis, while. Germination counts for each species or genus

were relativized to per m². Linear regression analysis was conducted in SAS using proc GLIMMIX, specifying a negative binomial distribution to account for zero-skewed data (SAS Institute).

Preliminary analyses determined that the differences in seedbanks between subestuaries were profound enough that including subestuary as a factor overshadowed the effect of treatment. Final multivariate and linear regression analyses were conducted separately for each subestuary and each is presented as a separate case study below.

RESULTS

Nanjemoy

Total *Phragmites* germination was a small fraction of the species composition, and only significantly different between the reference and the two *Phragmites* blocks in Years 1 and 2 (Table 3.1; Fig. 3.2A), while total germination of all species across functional types and guilds was highest in the reference block in all years. Species richness was highest in the reference block in Years 1 and 3, but not in Year 2 (Fig. 3.3). Richness was higher in the control than the removal in Years 2 and 3, and the latter block did not seem to have an herbicide effect on richness (Fig. 3.3A).

Table 3.1. *Phragmites* Germination Responses. Results from a one-way ANOVA of treatment effect on total *Phragmites* emergence for all wetlands in all three years ($\alpha=0.05$).

	Year 1		Year 2		Year 3		
	F	P	F	P	F	P	
Nanjemoy	1.75	0.1860	1.58	0.2178	1.57	0.2194	
Patapsco	6.47	0.0035	2.21	0.1226	0.31	0.7360	
Severn	4.65	0.0150	13.49	<0.0001	5.57	0.0072	
St Leonard	11.70	<0.0001	7.55	0.0015	2.94	0.0614	
Wicomico	3.14	0.0537	1.05	0.3589	1.00	0.3765	

In Year 1, prior to herbicide treatment, the seedbank in the native reference wetland differed from the *Phragmites* removal and control blocks, yet there was overlap in seedbank composition between all three blocks (Table 3.2; Fig. 3.4A). In Years 2 and 3, following herbicide treatments, the seedbank in the reference block remained somewhat distinct, and there was little differentiation between the removal and control blocks (Table 3.3; Fig. 3.4B and 3.4C). Pairwise perMANOVA results showed that seedbanks in control and reference blocks were marginally not significantly different ($\alpha = 0.05$) during Year 1, but were significantly different during subsequent years. Meanwhile, the intact control block and the herbicide-treated removal block initially differed significantly but converged following herbicide treatments. During all years of the study, seedbank composition was significantly different between reference wetlands and herbicide-treated blocks (Table 3.2).

Table 3.2. Nonmetric Multidimensional Scaling (NMDS) and perMANOVA Scores for Species Composition. All five study systems are represented for each year. The P(perm) value is indicating the presence of significant differences ($\alpha=0.05$) in seedbank composition and emergence between all three plot types (Control: *Phragmites* intact; Removal: *Phragmites* removed after year 1; Native: native reference plot) within each wetland for each year. The stress values are for the corresponding NMDS graphs in Figure 1.

	Year 1			Year 2			Year 3		
	Pseudo-F	P(perm)	Stress	Pseudo-F	P(perm)	Stress	Pseudo-F	P(perm)	Stress
Nanjemo	3.89	0.001	0.19	2.32	0.002	0.17	1.82	0.023	0.17
Patapsco	8.05	0.001	0.13	6.00	0.001	0.12	4.23	0.001	0.09
Severn	7.74	0.001	0.13	9.79	0.001	0.11	6.53	0.001	0.10
St Leonard	11.00	0.001	0.08	10.74	0.001	0.10	7.64	0.001	0.06
Wicomico	2.03	0.013	0.20	0.51	0.912	0.10	1.30	0.193	0.08

Table 3.3. Pairwise perMANOVA scores for each Treatment. The seedbank species composition for each wetland and year are presented in a pairwise manner to elucidate differences ($\alpha=0.05$) between treatments within each wetland and year. Treatments are: “C” control with *Phragmites* intact; “R” removal plots where herbicide was applied after year 1; “N” native reference plots.

	Year 1		Year 2		Year 3		
	T	P (perm)	T	P (perm)	T	P (perm)	
Nanjemo							
C x N	1.40	0.069	1.65	0.001	1.48	0.025	
C x R	2.29	0.001	0.95	0.497	0.62	0.941	
N x R	2.15	0.001	1.83	0.001	1.69	0.003	
	Year 1		Year 2		Year 3		
Patapsco	T	P (perm)	T	P (perm)	T	P (perm)	
C x N	2.72	0.001	1.74	0.030	1.28	0.030	
C x R	2.02	0.001	2.38	0.001	2.38	0.001	
N x R	3.49	0.001	2.99	0.001	2.99	0.001	
	Year 1		Year 2		Year 3		
Severn	T	P (perm)	T	P (perm)	T	P (perm)	
C x N	2.33	0.001	2.48	0.001	1.55	0.022	
C x R	2.60	0.001	2.73	0.001	2.74	0.001	
N x R	3.37	0.001	4.17	0.001	3.32	0.001	

Table 3.3 (cont.)

	Year 1		Year 2		Year 3		
St Leonard	T	P (perm)	T	P (perm)	T	P (perm)	
C x N	1.27	0.189	4.24	0.001	3.68	0.001	
C x R	3.93	0.001	1.71	0.018	1.14	0.252	
N x R	4.80	0.001	3.60	0.001	3.20	0.001	
	Year 1		Year 2		Year 3		
Wicomico	T	P (perm)	T	P (perm)	T	P (perm)	
C x N	1.45	0.024	0.86	0.654	1.18	0.210	
C x R	1.29	0.123	0.71	0.835	1.26	0.129	
N x R	1.49	0.026	0.51	0.944	0.97	0.467	

The functional vegetation types (forb, graminoid, and woody) showed similar compositional trends (no significant block effects across years) in the Nanjemoy blocks during all three years of the study: increasing germination over time, especially among forbs and graminoids (Fig. 3.5A,B,C). Germination responses of woody plant species were low in all years, however, germination decreased over time. There was no significant block effect on functional vegetation emergence in any year (Fig. 3.5A,B,C).

The seedbank plant guild (native annual, native perennial, and introduced perennial) germination did not show consistent trends over time. In the *Phragmites* control and removal blocks, native annual guild emergence was greater than native perennial in Year 1, while they were equal in the native reference block. In Year 2, the *Phragmites* removal block plant guild composition resembled the pre-treatment (Year 1) pattern, while in the control and reference blocks native annual germination was marginally higher than native perennial and both exceeded germination of introduced perennials. The only significant difference in emergence between blocks was in Year 3,

when the removal block had significantly lower introduced perennial germination than the reference block (Fig. 3.6C).

Patapsco

Total germination was significantly different between the blocks in Years 1 and 2, but not 3 (Table 3.4). The pattern of total emergence was driven by significantly higher germination in the native reference block (, Fig. 3.2B). *Phragmites* emergence was significantly lower in the reference block than the *Phragmites* removal and control blocks in Year 1 (Fig. 3.2B) and there were no significant differences in *Phragmites* germination in Years 2 or 3 (Table 3.1). Species richness was highest in the native reference block, and all blocks showed the lowest richness in Year 3 (Fig. 3.3).

Table 3.4. Total Germination. All five wetlands are presented to determine treatment effect (*Phragmites* removed after year 1; *Phragmites* monoculture intact; native reference plot) impacted total emergence. Results show one-way ANOVA of treatment within the river for each year ($\alpha=0.05$).

	Year 1		Year 2		Year 3		
	F	P	F	P	F	P	
Nanjemoy	7.79	0.0013	5.03	0.0110	7.59	0.0014	
Patapsco	7.13	0.0020	3.73	0.0324	1.52	0.2306	
Severn	5.13	0.0101	2.08	0.1385	4.16	0.0225	
St Leonard	0.30	0.7401	1.35	0.2705	2.47	0.0942	
Wicomico	4.02	0.0253	0.15	0.8602	0.25	0.7797	

In Year 1, the seedbanks of all three blocks in the Patapsco subestuary differed from each other (Fig. 3.2D), but the native reference block was more similar to the *Phragmites* removal block than either were to the *Phragmites* control block (Table 3.2; Fig. 3.4D). Following the first herbicide treatment, the seedbank of the *Phragmites*

removal block differed from the control and reference block so much that there was no overlap between blocks (Fig. 3.2E). The native reference clustered with the *Phragmites* control block (Table 3.2; Fig. 3.4E). In the second year after herbicide application (Year 3), there was more overlap between all three treatments (Table 3.2; Fig. 3.4F). All pairwise comparisons of seedbank composition between blocks were significantly different in each of the 3 years (Table 3.3).

Prior to spraying, the seedbank functional groups showed similar patterns in the two *Phragmites*-dominated blocks: forbs were more prevalent than graminoids, which, in turn germinated more than woody species. The native reference block had fewer graminoids germinate relative to the forbs and woody vegetation. This overall pattern of emergence continued in Year 2 (Fig. 3.5D,E,F). Woody vegetation emergence was significantly higher in the reference block in Years 1 and 3, which was the only significant effect of block on functional vegetation (Fig. 3.5D,E,F). Within the native reference block, woody plant germination was higher than graminoid, but not forb germination in all three years. In all treatments forb germination was exceptionally high in Year 3. Overall, graminoid germination was low in all three treatments for each year. In the removal and reference blocks, forb emergence increased by an order of magnitude between Years 1 and 2, while forb emergence did not increase in the controls until Year 3 (Fig. 3.5D,E,F). *Typha* spp., and *Pluchea odorata* were the dominant forbs across all blocks.

Introduced perennial germination was the distinguishing feature of the functional guild analysis of the Patapsco subestuary. In Year 1, introduced perennial species dominated the *Phragmites* removal block. The native reference had higher germination of

native perennials than any other guild, though introduced perennial germination was high as well (Fig. 3.6D). In Year 2, after spraying, the removal block had similar plant guild responses in the control block (Fig. 3.6E). The control and reference blocks both had high emergence of introduced perennial, which was significantly different from the removal block in Years 2 and 3. The removal had highest germination of native annuals in Year 3, while the reference block had a high germination rate of native perennials (Fig. 3.6F). The introduced perennial guild increases paralleled the forbs pattern seen in the function analysis and was driven by the prevalence of *Typha* spp. The elevated presence of native perennials in the reference site was likely due to the relatively high germination of woody species *Iva frutescens*, *Baccharis halmifolia*, and *Hibiscus moscheutos*.

Severn

Phragmites germination was significantly higher in the removal block in years 2 and 3 and negligible in the reference block in all years (Table 3.1). Total germination was significantly different between the blocks in Years 1 and 3, with the removal block having the lowest emergence (Table 3.4; Fig. 3.2C). Species richness was not significantly different in Year 1, yet richness precipitously decreased in the removal block in Years 2 and 3 (Fig. 3.3C).

In the Severn River, the three blocks clustered individually with minimal overlap, indicating different initial seedbank compositions (Fig. 3.4). Following the initial herbicide treatment, those differences became more pronounced (Fig. 3.4G,H,I). By Year 3, the block from which *Phragmites* had been removed had a more distinct seedbank, as seen in the distance between clusters, from intact control and native reference blocks

(Fig. 3.4I). The three blocks were significantly different from each other in all pairwise comparisons over all three years (Table 3.3).

During Year 1, the functional groups in the removal block resembled the native reference more than the *Phragmites* control in that both seedbanks are dominated by forbs. The reference block initially had higher woody emergence and lower graminoid emergence than the two *Phragmites* dominated blocks (Fig. 3.5G). In Years 2 and 3, forb germination in the control and reference blocks was significantly greater than in the removal; during that period the removal block significantly higher graminoid emergence (Fig. 3.5H,I).

Prior to spraying, all three blocks had high numbers of seeds germinating in the native perennial and introduced perennial guilds. Native annual emergence was significantly higher in removal and reference blocks than the *Phragmites* control block. In Year 2, germination rates of guilds flipped dramatically with native annual germination highest in the control block, followed by the reference, while absent in the removal. All three blocks had high to moderate introduced perennial germination in Year 3. The control and reference blocks had significantly higher rates of native annual germination than the removal (Fig. 3.6G,H,I). The prominence of introduced perennial in seedbank composition in all years and blocks was driven by two species: *Phragmites* and *Typha* spp. The native annual guild, prevalent in alternating blocks over the study, was largely comprised of *P. odorata*. The forb functional group was also likely dominated by *P. odorata* as well. The less common native perennial guild was comprised mostly of *Spartina patens* and *Schoenoplectus robustus*.

St Leonard

Total emergence was not significantly different between blocks in any of the three years (Table 3.4; Fig. 3.2D). *Phragmites* germination was significantly lower in the native reference block in all years (Table 3.1; Fig. 3.2D). Species richness was lowest in the reference block in all years, and highest in the removal block after herbicide application (Fig. 3.3D).

Prior to herbicide treatment, the native reference seedbank in the St Leonard samples was distinct from either of the *Phragmites* dominated sites and exhibited a spatially uniform distribution of seeds within the block, as seen in the tight NMDS plot clustering (Fig. 3.4J). The control and herbicide-treated *Phragmites* block seedbanks were similar, but neither were as spatially uniform as the native reference block (Fig. 3.4J). Following the first spraying treatment, the seedbank at the native reference block remained distinct from the *Phragmites* block. The *Phragmites* removal and control block seedbanks remained similar, but not as evenly as prior to herbicide application (Fig. 3.4K). By Year 3, the *Phragmites* removal and control blocks developed similar and homogeneous seedbanks (Fig. 3.4L). The distinctness of the native reference block, which moved farther from the *Phragmites* control and removal plots in each year, was validated by perMANOVA results; which showed that the reference marsh was significantly different from the *Phragmites*-removal marsh each year (Table 3.3).

Examining the functional group diversity within seedbanks, the native reference block was heavily dominated by forb emergence during the entire study. The most common forb in the reference seedbank was *A. cannabina*. In the reference block, graminoid and woody emergence were negligible in all years, and the graminoid

germination was significantly different than the other blocks in each year (Fig. 3.5J,K,L). In *Phragmites* removal and control blocks, Year 2 graminoid emergence was higher than forb emergence, a shift from other years.

The dominance of *A. cannabina* in the reference marsh was reflected in the species richness and plant guild assembly as well: native annual were the most prevalent group. In all years, the control and removal seedbanks were significantly different and comprised primarily of introduced perennial and native perennial (Fig. 3.6J,K,L). Common native perennial species in this marsh included *Schoeplectus robustus*, and *Eupatorium altissima*. The control and removal blocks both had increased emergence of both perennial guilds in Years 2 and 3 (Fig. 3.6J,K,L).

Wicomico

The total germination and *Phragmites* germination were both significantly different across blocks in Year 1 (Fig. 3.2E) and *Phragmites* was a comparably minor component of the total seedbank composition relative to the other subestuaries. The total germination rate was lowest in the control block in Years 1 and 3, which also had the highest *Phragmites* emergence (Fig. 3.2E). Species richness was not different between the blocks (Fig. 3.3E), which was reflected in the other metrics.

The seedbanks of the blocks in the Wicomico subestuary were similar prior to herbicide application, as indicated by the significant overlap in the NMDS plots (Fig. 3.4M). Differences between *Phragmites*-removal and control treatments emerge by Year 3, though there was still similarities between blocks (Fig. 3.4N,M,O). The reference block was significantly different from control and removal blocks in Year 1, according to

perMANOVA results, but there were no significant differences between blocks during in subsequent years (Table 3.2).

In the initial, pre-spraying sampling, the three blocks showed very similar patterns in emergence between the functional groups. In all three blocks over all three years, forbs dominated the seedbank, followed by graminoids, while woody vegetation was a minor component (Fig. 3.5M,N,O). This pattern persists in Year 2, with the exception of greater graminoid germination in the control block, while the reference and removal blocks remained similar to Year 1. The only significant difference in functional vegetation between blocks was between the control and removal blocks in Year 3. Despite being low relative to forb germination, there was greater graminoid emergence in the Wicomico than other subestuaries. The graminoids were dominated by *Schoenoplectus robustus*, *Schoenoplectus acutus*, and *Spartina cynosuroides*.

As with the functional types, in Year 1 the Wicomico seedbanks had similar plant guild patterns across all blocks (Fig. 3.6 M,N,O). The only change in Year 2 was increased emergence of native perennial species from the control block. During Year 3 native annual germination rebounded to Year 1 levels. None of the guilds were significantly different between blocks in any year (Fig. 3.6M,N,O). Across all blocks and years, the native perennial guild is a prominent component of the seedbank composition. The most prevalent forbs (the dominant functional group) in the Wicomico were the native annual species *P. odorata*, and *A. cannabina*. Common native perennial species included the graminoids mentioned above as well as the native species *Lythrum lineare*, and *Polygonum punctatum*; and the introduced species *Typha* spp., and *Polygonum hydropiperoides*.

DISCUSSION

Other studies on the impact of *Phragmites* presence and removal on seedbanks determined that diverse native seedbanks remain under *Phragmites* monocultures (Baldwin *et al.* 2010; Ailstock *et al.* 2001; Hallinger and Shisler 2009), but germination was often limited by the dense canopy (Minchinton *et al.* 2006). In our study, we examined five Chesapeake Bay subestuaries that were widely distributed across the bay. The subestuaries' seedbank compositions were not comparable, and examining them in the same statistical model would have missed signal from the *Phragmites* treatments and preclude answering our research questions. We considered them as five separate case studies so we could determine the within-subestuary factors that impacted seedbank composition. We set out to answer 4 major research questions: 1. Do vegetation type and *Phragmites* removal impact the total seedbank density, species richness, and *Phragmites* emergence? 2. Does vegetation cover type impact seedbank composition? 3. Does removing invasive *Phragmites* by herbicide impact the seedbank composition? 4. Since functional diversity could lead to a more resilient wetland, is there enough functional diversity in the seedbank to justify passive revegetation? We will discuss the implications of that finding for each of our questions below, and present site characteristics that explain our interpretation.

The effects of herbicide and vegetation type on seedbank density and emergence (question #1) We were concerned about whether the blocks had sufficient seedbank density and richness to result in an effective revegetation. In Year 1, prior to herbicide application, only the Nanjemoy and Wicomico did not display a significant difference between the blocks (removal, control, or reference) on *Phragmites* germination (Table

3.1). Additionally, in these two subestuaries, *Phragmites* was a much lower component of seedbank composition (several orders of magnitude lower) than in the other subestuaries. In the other subestuaries, the block effect was primarily the result of significantly lower *Phragmites* emergence in the native reference blocks than in the control or removal (Fig. 3.5). In subsequent years, the Severn and St Leonard were the only subestuaries that showed a significant block effect on *Phragmites* emergence following treatment (Table 3.1; Fig. 3.5C,D). In the other subestuaries, the lack of significant differences in *Phragmites* germination was the result of decreased emergence in all blocks, and was likely not the result of the herbicide treatment. In Chesapeake Bay, *Phragmites* spread and colonization are predominately the result of seed transport (McCormick *et al.* 2010a; McCormick *et al.* 2010b; Kettenring *et al.* 2011), so the prevalence of viable *Phragmites* seeds in seedbanks following removal would likely work against revegetation and restoration efforts. *Phragmites* was a major component of the overall seedbank composition only in the Severn and St Leonard, and was a small fraction of the total density in the other subestuaries (Fig. 3.5).

Total germination was significantly different between blocks in all subestuaries except the St Leonard in Year 1 (Table 3.4). In most cases, the germination rate was higher in the native reference block than in either of the *Phragmites*-dominated blocks. The exceptions were in the Severn control block in Year 2, the Wicomico control block in Year 2, and the St Leonard control block in Year 2. In Year 2, only the Nanjemoy and Patapsco had significant differences among blocks in total germination, and they were similarly driven by higher germination in the native block (Table 3.4; Fig. 3.5A,B). The same pattern was seen by Year 3 in the Severn and Nanjemoy. However, all other

emergence rates were not significantly different by block and there was no evidence that herbicide treatment impacted total germination in any of the subestuaries (Table 3.4). In fact, several of the subestuaries demonstrated higher total germination rates across blocks in Year 2 than either of the other years (Fig. 3.5).

Species richness did not seem to be impacted by herbicide treatment, but was frequently greater in the native blocks. Contrary to prior conclusions that species richness decreases under plant invasions (Gioria *et al.* 2014), only the Patapsco had consistently higher richness values in the native than other blocks (Fig. 3.6B). In the other subestuaries, richness varied with time and was similar in the control and reference blocks. In the Severn removal block, species richness decreased each year following spraying, which is a potential herbicide effect in that system. Across all of the subestuaries studied, only the St Leonard had consistently lower species richness in the native reference block than in either of the other two. While counterintuitive, the low richness values were likely related to the vegetation composition in the St Leonard native block, which, as described above, was a community of two species *S. alterniflora* and *A. cannabina*.

Relationships between seedbank composition and vegetation cover types (question #2) Wetland seedbanks can be highly variable even at small spatial scales and under the same vegetation types (Huiskes *et al.* 1995). In fact, our multivariate analyses showed that there was a large variation in seedbank composition between blocks, even before we applied herbicide to the removal (Fig. 3.2; Table 3.2 and 3.3). Since two blocks in each subestuary were *Phragmites* monocultures prior to spraying, we did not anticipate finding significant differences in the seedbank. We found significant differences in the seedbank

composition of all five subestuaries in Year 1, so we cannot conclude that the seedbank composition is related to differences in the aboveground vegetation composition of our research blocks. Rather, we found a variation across the subestuary that could be the result of the unique physical conditions of each block and subestuary.

It is likely that the spatial variation in seedbanks prior to treatment was broad enough to account for the differences between the control and removal plots, which were both *Phragmites* monocultures prior to herbicide treatment, in several of the subestuaries (Fig. 3.2). Site history and prior disturbance can alter tidal flow across wetlands and change seed dispersal patterns. In the Nanjemoy, the two *Phragmites* dominated plots were separated by a historic road that could alter how the seeds mixed on the tides, and created large spatial variability in seedbanks. The Patapsco blocks were in discontinuous “pocket wetlands” where the mixing of local seed sources was likely only during larger tidal events. The isolated nature of the blocks was visible in the Year 1 NMDS plot (Fig. 3.2D), which showed strong discrimination of all blocks prior to herbicide treatment. The pretreatment seedbank composition in the Severn River showed variation between the *Phragmites* monocultures as well (Fig. 3.2G). Here too, there were physical characteristics that could alter how tides flood the blocks, a large dike and pier separate the two *Phragmites* blocks from each other. Since the seedbanks show strong dissimilarity within the blocks (Fig. 3.2G,H,I), we believe that the physical structure and topography of the wetland had more impact on seedbank composition than the cover type. Even a small pier, like the one of the St Leonard River that separates the control and removal blocks, could explain the significant differences in seedbank composition between *Phragmites* monocultures (Table 3.2). The control and removal blocks on the

Wicomico are the only ones in the study that did not have a significant pairwise difference in the seedbank composition, although the overall perMANOVA was significant (Table 3.2 and 3.3). The Wicomico subestuary site was a large continuous wetland with the most fetch of any in the study. The fetch may contribute to mixing the seedbank and has been found to impact seedbank composition elsewhere (Baldwin *et al.* 2010).

Seedbank density and diversity can also vary across tidal wetlands at the landscape (subestuary) scale (Elsey-Quirk and Leck 2015; Pederson and Baldwin 2004). In tidal systems, seed transport is dictated by tide flow more than wind or seed rain and variation of the wetland surface can alter how seeds are dispersed (Hopfensperger *et al.* 2009; Huiskes *et al.* 1995). Within the subestuary, physical factors such as fetch can impact seedbank composition between sites and some down-wind areas will receive heavier propagule loads (Baldwin *et al.* 2010). On a smaller scale, seeds sort based on size in tidal systems (Leck 1989). In individual wetlands, fragmentation and debris can also alter the seedbanks (Soomes 2012; Hopfensperger *et al.* 2009). In tidal salt marshes, seedbank composition will discriminate between discrete salinity zones, where the seeds are most likely to survive to establishment (Unger 2001). Spatial and temporal variation in tidal systems made interpretation of results especially complex (Hopfensperger *et al.* 2009; Leck 1989). It is also conceivable that dense vegetation, such as *Phragmites* monocultures, could promote flocculation of seeds. Given all of the impacts of tide and topography on seedbank composition, we believe that the physical characteristics of a wetland impact the species composition more than local seed rain or cover vegetation.

The impact of Phragmites removal on seedbank composition (question #3) We

found enough natural variability in tidal wetland seedbanks to necessitate site-specific answers. In two of our sites, the Patapsco and the Severn, seedbanks in the removal blocks were less similar to the control and reference blocks in Years 2 and 3 than prior to spraying. In both of these cases, the NMDS plots (Fig. 3.2E,F and Fig. 3.2H,I respectively) showed greater distance between the removal blocks and the other blocks over the three study years. In these two subestuaries, the removal seedbank was less similar to the reference and control than the latter were to each other. It appears that removing *Phragmites* may result in a novel state in some cases, and not a convergence on the native reference state, nor a return to the composition of a *Phragmites*-dominated wetland. In a perplexing example, the Nanjemoy exhibited a significant difference between the removal and control block seedbanks in Year 1, but not during Years 2 and 3 (Table 3.3). The convergence of the control and removal seedbank composition in the Nanjemoy after herbicide application was perplexing, especially because the composition of the reference block was still significantly different from the other two. It is unclear whether the changes in composition could be attributed to the herbicide treatment, or if there was another factor affecting seedbank composition. The divergent change in seedbank composition toward a novel state in the Patapsco and Severn River subestuaries appeared to be a result of herbicide application.

Seedbank composition in the St Leonard was similarly nuanced following herbicide application. In Year 2, there were significant differences between all three blocks, while in Year 3, the differences between the removal and control diminished (Fig. 2K,L). It is not clear whether the intermittent differences were the result of herbicide

treatment or attributable to temporal variation. Temporal variation seems to be the driving factor changing the Wicomico's seedbank composition, more so than the herbicide treatment. In Years 2 and 3, the seedbanks in all three blocks converged to be statistically indistinguishable from one another (Fig. 3.2N,O; Table 3.2; Table 3.3). The convergence of seedbank composition in the Nanjemoy and St Leonard was unexpected.

Seedbank composition frequently varies at several temporal scales. On the longest scale, seedbanks change with time from a disturbance or invasion as the persistent native seedbank exhausts itself and undesirable propagules accumulate (Van der Valk and Pederson 1989). Conversely, following restoration, the native seedbank will accumulate with time until it is a viable propagation source (Neff and Baldwin 2005). Episodic or stochastic flooding events can change composition from year to year (Leck 1989). Even within a year, the seedbank composition will vary by season to a degree that management efforts can be timed with desired germination (Morazia-Luna and Zedler 2007). It is likely that three of the subestuaries' seedbanks were undergoing temporal variation in seedbank composition as documented by other studies, and more research on *Phragmites* invasion is justified to determine the site specific factors driving the variation we documented.

Functional diversity in seedbanks: implications for restoration (question #4)

Functional diversity (Byun *et al.* 2013; Gioria *et al.* 2014) and "ecological redundancy" (Suding 2011) contribute to the resilience of a wetland and the system's ability to resist invasion. We sought to determine if the functional diversity in the seedbanks could justify passive revegetation. We approached this question from two angles: diversity in structural form (the functional types: forb, graminoid, woody) and diversity in life history

(guild: annual, perennial, differentiated by native or introduced status). The functional compositions of the seedbanks vary greatly between subestuaries, yet are comparably consistent between blocks in a subestuary. Stability of functional composition over the study area and duration was notably different from the seedbank species composition, which varied with time and space. For each year, the relative contribution of forbs, graminoids, and woody vegetation showed minimal block effects. While the relative contribution of a functional type can vary by year, there was much less variation by block (Fig. 3.3). We observed some exceptions, such as the significant graminoid emergence in the St Leonard removal and control blocks that was nearly absent from the reference block (Fig. 3.2J,K,L). Similarly, woody vegetation in the Patapsco was a significantly greater component of the seedbank in the reference block than the removal and control blocks, but only in Years 1 and 3 (Fig. 3.3D,E,F).

The relative contribution of the three guilds to seedbank composition was more varied than the functional groups (Fig. 3.4). Each subestuary had some introduced perennial seedbank component in all blocks, which was understandable since all blocks either contain, or were in close proximity to, *Phragmites*. The St Leonard had the lowest relative germination of introduced perennials and the highest native annual component in the native reference block, which was significantly different than the *Phragmites* dominated blocks in Years 1 and 3. The removal block in the Severn, on the other hand, had significantly lower germination of native annuals in Years 2 and 3, which may be one of the few impacts of herbicide on the seedbank guilds. In the Patapsco, the reference block and control block had significantly higher emergence rates of the introduced perennial guild than in the removal block (Fig. 3.4E,F). High introduced perennial

germination is likely due two factors: the presence of *Phragmites* in the control block and the prevalence of *Acorus* spp. and *Typha* spp. in the reference block.

Woody species were a very minor component of all of the seedbanks in all of the subestuaries. While low emergence of woody vegetation is well documented in wetland seedbanks (Leck 1989), we were surprised, since they are a major component of the above ground vegetation (unpublished data). The woody species *Iva frusctescens*, *Baccharis halmifolia*, *Hibiscus moscheutos*, and *Kostyletskia virginica* were often the dominant cover in Chesapeake Bay brackish wetlands (McCormick and Somes 1982 and unpublished tidal wetland maps associated with the report). Across years, the St Leonard control had a higher woody component than the other Chesapeake Bay wetlands studied, which is more an artifact of the forested upland border than woody wetland species. Predictably, native annual forbs were a consistent component to the seedbank and were dominated in all sites by *Pluchea odorata*, and *A. cannabina*. In the third year, there was potentially a mast year of *Symphotrichum subulatum*, which appeared in large numbers in the seedbank (Fig. 3.4). Graminoids were the dominant the native perennials, particularly *Spartina patens*, *S. alterniflora*, *Schoenoplectus acutus*, and *Panicum virginica*.

Taken together, it is evident that there were functionally diverse seedbanks under each of the vegetation types and in each block within the subestuaries. Subestuaries like the Nanjemoy, which had higher germination rates of native and annual perennials, in principal should have had a higher likelihood of vegetation recovering from passive revegetation. The native block of the Nanjemoy marsh had a very high diversity of both forbs and graminoids, with >100 total species detected in the seedbank or vegetation (EH unpublished findings).

Restoration potential

In wetland management and restoration, the seedbank composition can offer insight into the potential-for and process-of wetland recovery (Van der Valk and Pederson 1996; Brown 1998; Neff *et al.* 2009). However, as is the case with the current and other studies, seedbank composition does not always predict the above ground vegetation (Brown 1998; Gioria and Pysek 2016; Gioria *et al.* 2014; Hopfensperger *et al.* 2009; Hopfensperger 2007). The theory of self-designed wetlands appeals to many restoration practitioners because of potential to maintain local vegetation compositions and genetic stocks and keep costs low (Leck 2003; Van der Valk and Pederson 1989; Mitsch and Wilson 1996). Despite benefits of passive revegetation, it may not be appropriate in many *Phragmites*-invaded wetlands because of low recovery potential in the seedbanks of old invasions where native species in persistent seeds have been replaced by undesirable species propagules (Wilcok 2012; Frieswyk and Zedler 2006; Van der Valk and Pederson 1989; Bakker *et al.* 1998). Seedbank density and richness decrease in sites that are dominated by invasive plants, which diminish the wetland's recovery potential. A low functional diversity in the potential species composition is particularly common in coastal and riparian restorations (Gioria *et al.* 2014). Additionally, the species that emerge first from any seedbank can be weedy, undesirable, or non-native species, thus restorations relying on soil seedbanks for revegetation should exercise caution (Ficken and Menges 2013; Frieswyk and Zedler 2006). Finally, restored above-ground vegetation does not always reflect the full seedbank composition due to environmental filters that impact germination and recruitment (Gioria and Pysek 2016; Brown 1998; “environmental sieve” Van der Valk 1981). Our results showed that in most

cases there was a functionally diverse seedbank both under *Phragmites* monocultures, and where the invasive vegetation was removed. Wetland restorations where the persistent seedbank has become exhausted require more active revegetation methods (Bakker *et al.* 2010; Morzaia-Luna and Zedler 2007), but even where seedbanks persist the environmental pressure created by flooding, shading, and other limitations on emergence may preclude reliance on self-design.

Tidal wetland seedbanks may not relate to aboveground vegetation, primarily due to the environmental sieve (Van der Valk 1981). Seeds may not settle in a microsite that had the appropriate conditions to break dormancy, or environmental conditions may not fit the conditions required by the seedling to establish and grow. Since germination can limit recruitment, seedbank composition can reflect potential for a site to recover, but may not be predictive of the vegetation composition (reviewed in Gioria and Pysek 2016; see also Brown 1998). Further, the seedbank methods may alter the results. Counting emergence alone only gives an estimate of the seedbank, and relies on germination conditions in the study to yield results (Abella *et al.* 2013). With these caveats in mind, we did find that seedbanks under *Phragmites* invasions in Chesapeake Bay were functionally diverse and highly variable over time and space.

In a recent study of freshwater wetlands, restored wetlands had higher richness and density than natural (McFarland 2016). Also, seedbanks were more similar between restored and natural sites than above ground vegetation was between sites. Though not presented here, cursory analysis of our aboveground vegetation indicated that only the dominant species resembles the seedbank composition; the less common species differed greatly between the plant community and the emerging seedbank (unpublished). In our

study, the Nanjemoy had similar emergence between the control and removal for two years, while differing from the native, although not completely mixed (Table 3.3). The Wicomico showed a high level of similarity between the blocks in Years 2 and 3 as well (Table 3.2). In all other cases, there were highly significant differences between all pair-wise perMANOVA comparisons of blocks within the subestuaries. It is possible that with increased study duration, seedbank composition could converge upon the composition of above ground vegetation, but that was beyond the scope of this study.

Generally, the native reference blocks had higher overall germination, more native plants in the seedbank, and fewer invasive plants emerging. This finding emphasizes the need for intact native wetlands in the vicinity of management efforts. Without the native propagule source, passive revegetation will be unlikely. Species richness often declines under invaded canopies, and the subsequent loss of richness decreases the recovery potential of the invaded site (Gioria *et al.* 2014). We had similar findings in some of the subestuaries, but not consistently (Fig. 3.6). The richness values varied with time, and in the case of the St Leonard, the native block had a very low species richness that coincided with the reference community (Fig. 3.5D). Invaded sites typically had higher counts of invasive propagules than native, while in many cases native vegetation had higher overall emergence. This major finding was in agreement with a review of seedbanks and invasions by Gioria *et al.* (2014).

The best mixing of seedbanks and largest recovery potential were found in the Nanjemoy and Wicomico. Both of these subestuaries had a single wetland dominated shoreline and nearby areas that had intact, diverse native wetland vegetation. They also had the lowest concentration of *Phragmites* along the shorelines, while the developed

subestuaries (Severn, Rhode, and Patapsco; per King *et al.* 2007), had *Phragmites* as the dominant shoreline vegetation. We were not able to determine the longevity of individual species' seeds, but they can vary greatly. The individual species should contribute differently to the persistent seedbank. The physical structure of the wetland surface and the location within the subestuary (regarding fetch and connectivity) likely allowed for the diverse functionality of seedbank species. These two subestuaries had the lowest rates of *Phragmites* emergence in the study, which was contrary to previous studies that found a positive relationship between *Phragmites* propagules and fetch (Baldwin *et al.* 2010). In our findings, it appears that fetch can contribute to homogenizing the seedbank and allow for more native propagules under a canopy of invaders.

The Patapsco lacked sufficient native propagules to rely on passive revegetation, which was likely due to the lack of connectivity to a native propagule source. The Severn seedbank had introduced perennials as a larger proportion of the seedbank than most of the other subestuaries and would likely revert back to an invaded state. The lack of native perennial and graminoid emergence in the St Leonard was likely due to low seed production in *S. alterniflora*, the dominant perennial in the reference block. Without ample propagule production, the removal block in this subestuary is likely to be reinvaded before native vegetation could become established. The Patapsco and Severn both formed novel states in seedbank composition, which might eventually develop into a stable wetland state, but the prevalence of introduced perennial in both systems indicated that any novel state would unlikely be comprised of native vegetation. Overall, the subestuaries with the most mixing among blocks seemed to have the largest proportion of

native propagules in the seedbanks, and the greatest likelihood to establish native plant communities following herbicide treatment.

CONCLUSIONS

Our finding that there were functionally diverse native seedbanks under *Phragmites* monocultures that persisted after removal has important implications for managers who do not have the ability or budget to actively revegetate after *Phragmites* removal (*sensu* Hallinger and Shisler 2009). Specifically, this functional diversity was critical to creating a plant community that was resistant to preventing future *Phragmites* invasion (Byun *et al.* 2013); by filling as many niches as possible, managers can build resilient plant communities that are more likely to resist invasions. In some subestuaries, a functionally diverse seedbank under *Phragmites* monocultures could serve as a propagule source for passive revegetation within the context of self-design (*sensu* Mitsch and Wilson 1996). This self-design potential is particularly true in subestuaries that have high cover of native wetland communities and where *Phragmites* germination was lower. Additionally, site connectivity played a strong role in the evenness of seedbank composition. Based on these observations, we offer managers a strong caveat: there are numerous invasive propagules in each vegetation type, and a wetland will vary in its capacity to recruit native vegetation. Site selection is critical for passive revegetation, and it should only be considered as a single component to an adaptive framework that involves continuous monitoring and method adjustments.

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FIGURES

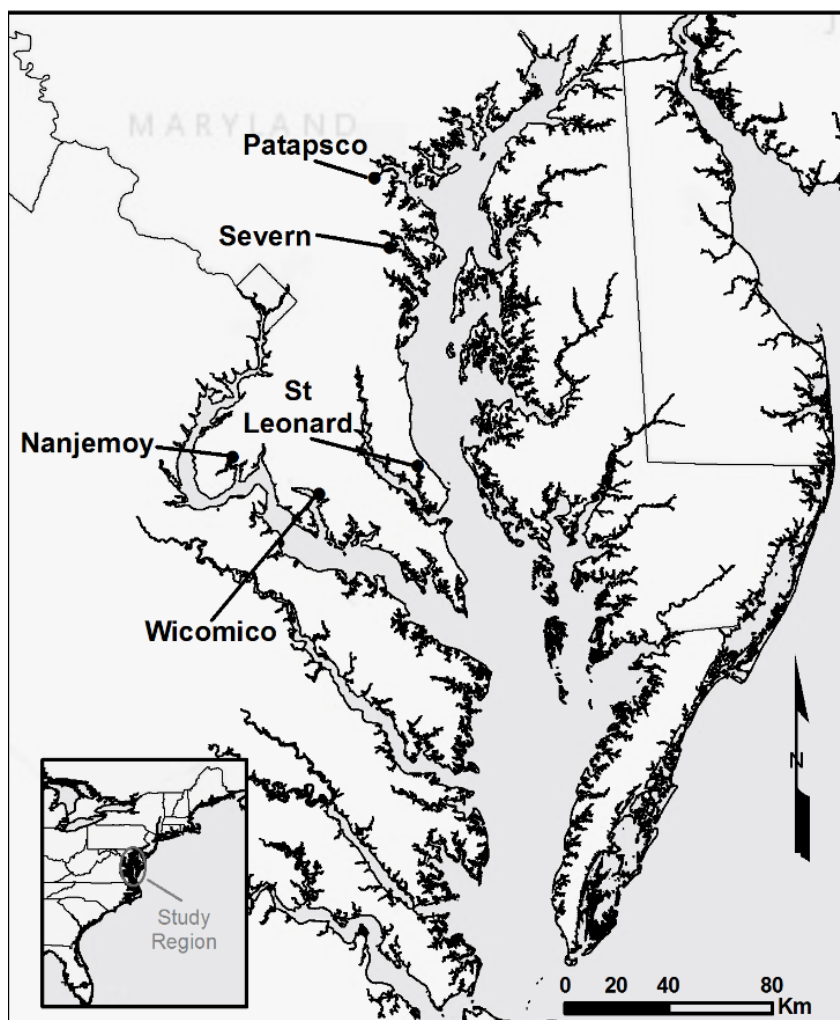


Figure 3.1. Map of sampling sites on the Western Shore of Chesapeake Bay.

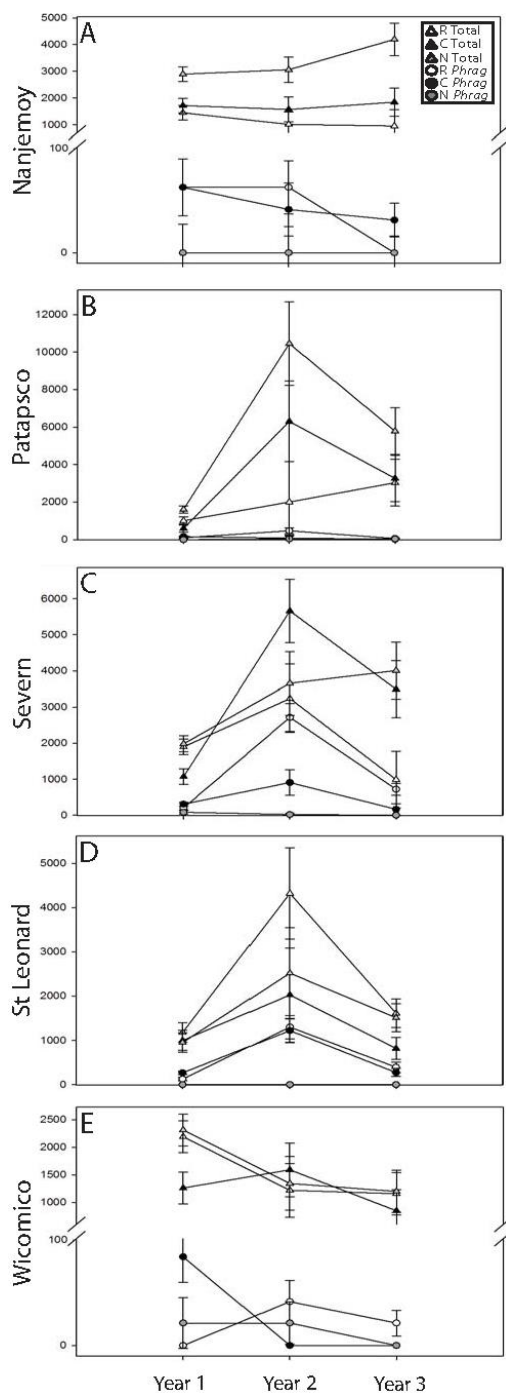


Figure 3.2. Nonmetric Multidimensional Scaling (NMDS) graphs for seedbank composition in all five study wetlands, for each of the three years. Year 1 is prior to herbicide treatment, while Years 2 and 3 are after continued herbicide application. As shown in the legend, circles are for “R”, the *Phragmites* removal plots (with long-dashed line); X indicates that the sample was in a “C” control plot with *Phragmites* left intact (short-dashed lines). The triangle symbol is for samples collected in the “N” native reference plot (solid lines). Details on the NMDS scores and perMANOVA can be found in Table 3.2.

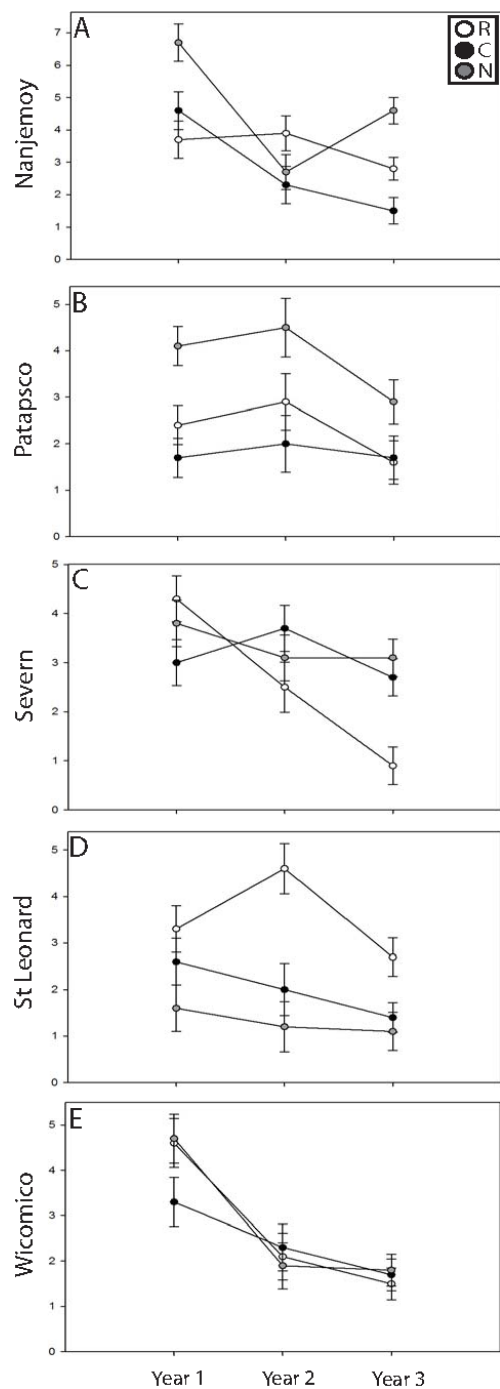


Figure 3.3. Proportional Germination of *Phragmites* and Total Emergence. The five study subestuaries are depicted for both total germination (seedbank density, “Total “ in legend) of all species and, the germination rates of *Phragmites* (“*Phrag*” in legend) relative to blocks. Values on the Y axis are total emergence expressed as m^2 , ± 1 se.

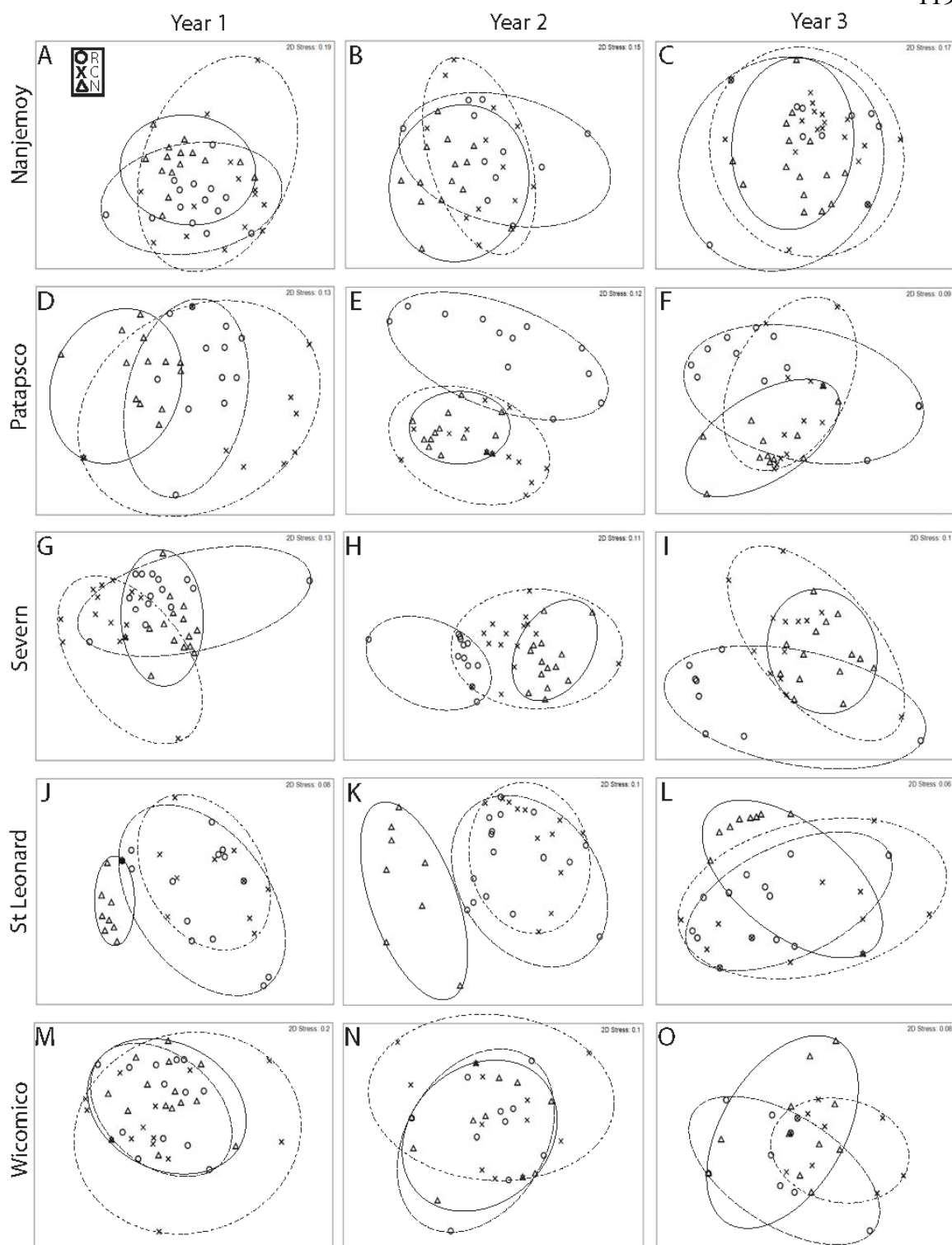


Figure 3.4. Impact of *Phragmites* Removal on Species Richness. Mean species richness across the five subestuaries over time and cover type (“C” control, “R” removal, “N” native). Values on the Y axis are total emergence expressed as per m², +/-1se.

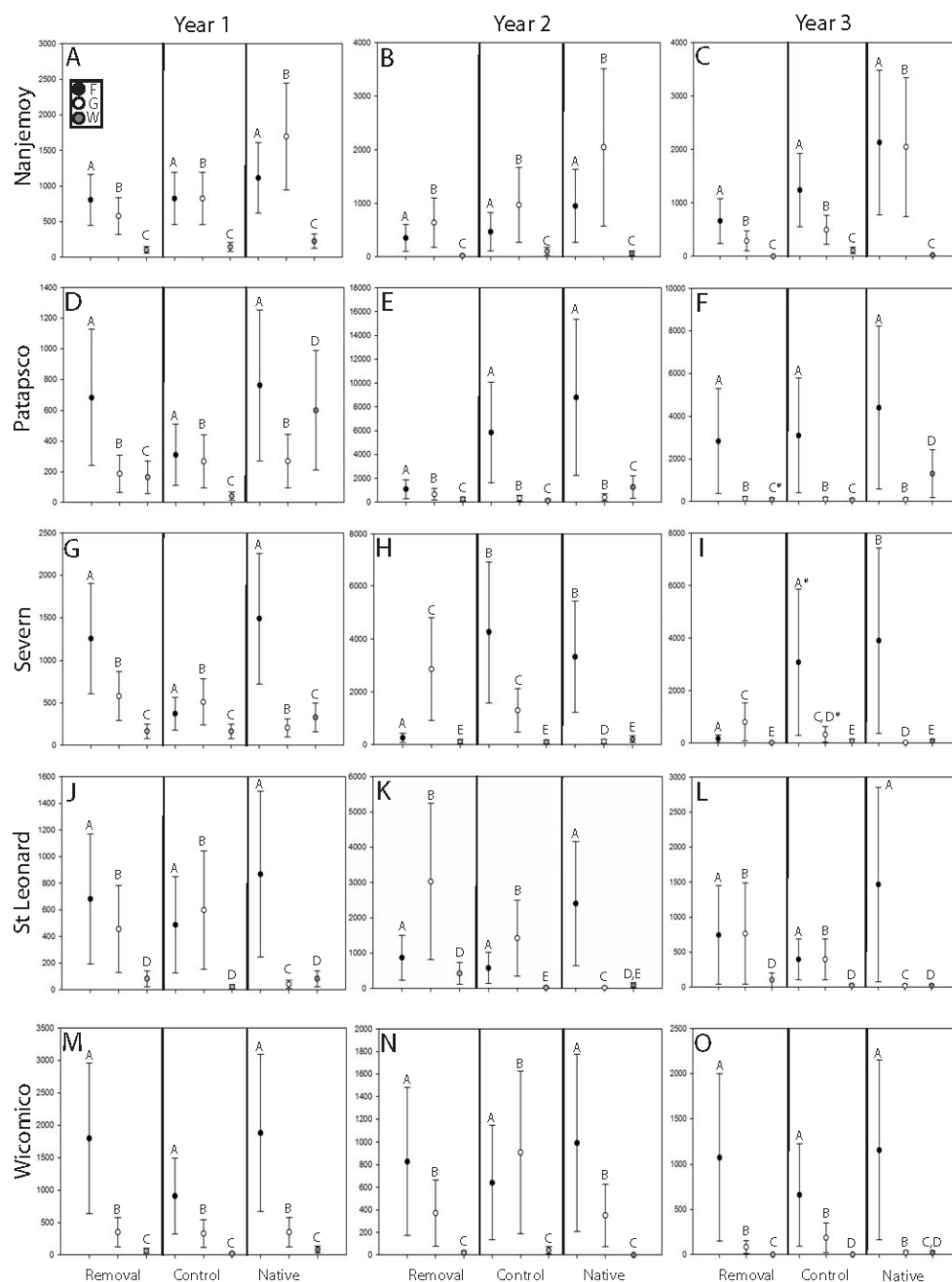


Figure 3.5. Functional Analysis of Germination Rates. The germination rates of “F” forbs, “G” graminoids, and woody “W” are shown on the Y axis and expressed as counts per m² \pm 1se. All five surveyed wetlands are shown, with the germination result for each of the three years. Year 1 is prior to herbicide application. Each sub-figure is divided by plot treatment: Removal where *Phragmites* was treated with glyphosate after Year 1; Control is an intact *Phragmites* monoculture; Native is the native reference plot. Letters above error bars indicate significant differences of each functional type between treatments ($\alpha=0.05$), they do not indicate differences between the functional types. Differences marked with an * are marginally non-significant ($\alpha=0.07$).

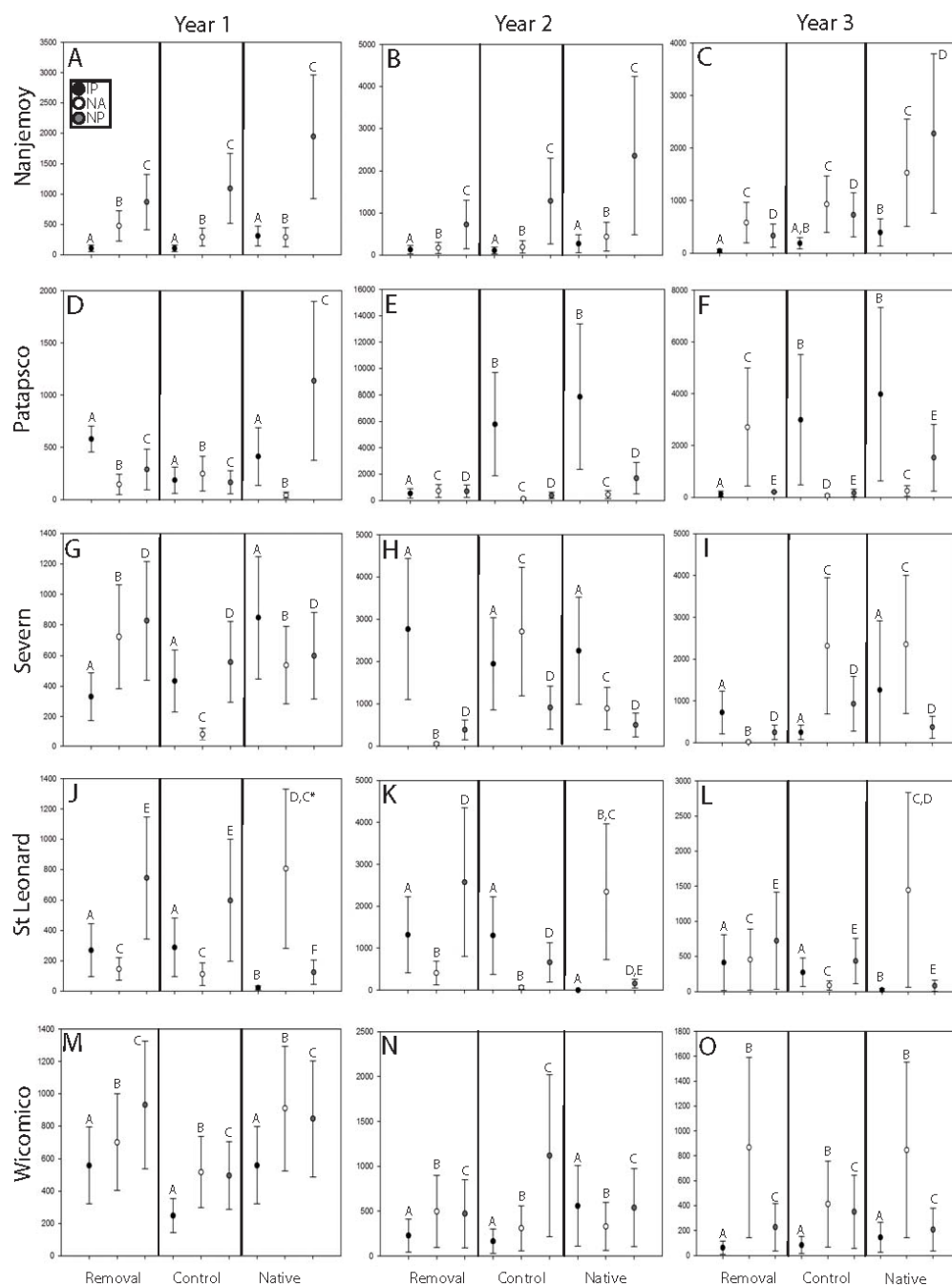


Figure 3.6. Guild Analysis of Life History and Native vs Invasive Germination Rates. All five study subestuaries are represented for each of the three years of the study. Year 1 is prior to herbicide treatment, while the “Removal” plots were sprayed in Years 2 and 3. The Control is an intact *Phragmites* monoculture, and the Native is a native reference wetland. The Y axis displays the emergence of seedlings expressed as number of germinations per $m^2 \pm 1$ se. significance level is $\alpha=0.05$, marked with an * are marginally non-significant ($\alpha>0.05$, <0.07). The three guilds are: “IP” invasive perennials, “NA” native annuals, and “NP” native perennials. Invasive annuals were not present in sufficient numbers to analyze.

CHAPTER IV

LARGE-SCALE INVASIVE PLANT REMOVAL IN CHESAPEAKE BAY TIDAL
WETLANDS: IMPACTS TO PLANT COMMUNITIES, INVADER'S VIGOR, AND
THE PHYSICAL ENVIRONMENT

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Melissa K. McCormick, Dennis F. Whigham

ABSTRACT

We removed invasive *Phragmites australis* (henceforth *Phragmites*) from wetlands in eight subestuaries of Chesapeake Bay to determine if herbicide treatments allow for the recovery of native wetland plant communities. We monitored the vegetation composition, nutrient availability, and *Phragmites* vigor from pre-spraying in August 2011, during herbicide treatments (fall 2011-2014, sampling in subsequent August), and an additional monitoring year (2015). Each subestuary had a plot where *Phragmites* was removed, a plot where *Phragmites* was left intact, and a native reference plot. Herbicide impacted *Phragmites*' vigor (density, cover, stem diameters, flowering), but the effect diminished with each subsequent treatment. Ordinations demonstrated that the plant community response varied by subestuary, with some forming distinct assemblages from both the *Phragmites* intact and native reference plots, and others returning to the invaded state. Overall, the mean coefficient of conservatism increased in treated plots relative to the control, indicating that removal does improve wetland quality. Nutrients and tidal inundation were related to herbicide treatment, but in site specific responses. Our findings

emphasize the need for invasive plant studies that cover large geographic areas, as the responses to removal vary widely between subestuaries.

KEYWORDS

Phragmites, invasive plant, herbicide, estuary, Chesapeake Bay

INTRODUCTION

Removing an invasive plant will not necessarily result in the re-establishment of desirable native plant communities. Nonetheless, the re-establishment of native plant communities that resemble the pre-invasion state is a frequent goal of land managers. Many invasive species are ecosystem engineers that can irreversibly alter the invaded environment to a degree that it will not recover to the initial, pre-invasion state (Hacker and Dethier 2008). The invader, however, may leave behind legacy effects such as seedbanks, altered nutrient and chemical states, and disturbance that often prove difficult to restore the desired community (D'Antonio and Meyerson 2002). Management actions and invasive plant removal can act as a disturbance in itself, facilitating the establishment of new weedy species rather than the desired habitat.

Legacy effects can be difficult to overcome, and practitioners often need to rely on careful site selection for restoration candidates to ensure restoration goals are met. Restoration efforts are best spent on high quality sites (e.g., less disturbed, lower anthropogenic nutrient loads, more native vegetation in landscape), as they are most likely to recover to a native state (Suding 2011, Strayer *et al* 2006). Legacy effects of invaders are particularly pronounced when the invasive plant is altering the hydrologic, salinity, or nutrient regime of the invaded system, at times leading to undesirable (potentially transitional) species assemblages rather than reverting to the pre-invaded vegetation state (Corbin and D'Antonio (2012). How the specific ecology of an invasive plant species and the site history of the pre-invasion plant community interact to impact native plant recovery after management requires managers to consider a range of acceptable recovery outcomes (Hildebrand et al. 2005; White and Walker 1997) and the

role of the practitioner is to guide trajectories of recovery toward these multiple endpoints (Weinstein et al 2013).

Potentially influencing the plant community pre-invasion, the site history can impact the current community composition and the biotic resistance of a wetland. The individual influence of watershed-level or site-specific scale factors can impact nutrient, sediment, hydrologic, and biotic regimes of a wetland (Prasse *et al.* ; Weinstein et al 2012). While legacy effects are the result of ecosystem engineers, site history has an emphasis on anthropogenic influence (King et al 2007; Chambers et al 2008). Palmer (2009) points out that the effect of local management and restoration impacts can be swamped by regional influences and that beneficial actions in a larger, degraded system may be lost to regional processes, which argues further for choosing restoration sites that are in watersheds with a greater likelihood of recovery.

Site selection for invasive plant removal is potentially more critical in wetlands than uplands due to their propensity to disturbance and nutrient loading (Suding 2011; Zedler and Kercher 2004). One wetland invader, *Phragmites australis* (Poaceae, Trin x Steud.; henceforth *Phragmites*) is a focus of management efforts across its introduced range in North America (Hazelton et al 2014). *Phragmites* is native to every continent except Antarctica, including North America. In the past four decades, *Phragmites* has rapidly and aggressively increased its North American range, often forming dense monocultures that compete out any native vegetation (Chambers *et al* 1999). The rapid expansion is the result of a cryptic invasion of a Eurasian *Phragmites* lineage (Chambers *et al* 1999; Saltonstall 2002), in combination with changing anthropogenic land use processes that favor the invader (Sciance *et al* 2016; Bertness *et al* 2002; King *et al* 2007;

Chambers *et al.* 2008; Burdick and Konisky 2003). In an ever expanding range, *Phragmites* is often the primary management focus among wetland practitioners (Kettenring *et al* 2012; Martin and Blossey 2013; Marks *et al* 1994).

Invasive species management and restoration studies tend to be too short in duration to establish long term predictions (Kettenring and Reinhardt Adams 2011), and this is particularly true in the *Phragmites* literature (Hazelton *et al* 2014). Eradication of *Phragmites* is rare, and even more so without many years of follow-up treatments (Warren *et al.* 2002; Getsinger *et al.*2006; Lombard *et al.* 2006). Invasive plant management studies of too short in duration are likely to suffer from a Type I error, in that they may conclude that the treatment was effective even though the invader may rebound rapidly in subsequent years or after monitoring ceases (see discussion in Kettenring and Reinhart Adams 2011; Hazelton et al 2014). Additionally, removing an invasive plant is a disturbance, and therefore the process of invader removal may ultimately facilitate future invasions. Finally, native plant recovery will likely undergo successional changes over multiple growing seasons and multiple years of monitoring are often necessary to determine the efficacy of management efforts on invasive plants (Blossey 1999; Kettenring and Reinhardt Adams 2011).

Further, to date, there are no *Phragmites* management studies that conducted community scale analyses on recovering vegetation, or studies that report comparison to an uninvaded reference site are rare (Hazelton *et al* 2014). While expectation of a linear transition from the invaded state to the historic state ignores legacy effects of the invader, and novel stable states are a potential outcome (Suding *et al* 04), the reference site gives us a baseline to determine the relative impact of restoration and management actions

(Neckles *et al* 2002; White and Walker). Acknowledging the value of reference sites, the non-linear nature of succession following restoration or management of an invasive species may not allow the re-establishment of an historic state. Palmer (2009) makes a case for acknowledging multiple desirable outcomes in wetland restoration and guiding trajectories toward these outcomes and focusing on the most likely result based on variations in time, space, and ecological gradients.

To determine how site selection and the physical environment impact plant community recovery following invasive plant removal, we conducted a large scale removal study of invasive *Phragmites*. We established long term monitoring plots in eight Chesapeake Bay subestuaries and removed *Phragmites* from a section of each to elucidate the impact of *Phragmites* on native vegetation, and the capacity for native plant communities to recover once *Phragmites* is removed. In order to address these goals, facilitate management, and increase the efficacy of restoration efforts, we asked the following questions:

1. Does herbicide treatment impact the vigor of *Phragmites*?
2. Do native plant communities return once *Phragmites* is removed?
3. How does *Phragmites* removal impact the physical environment in the wetlands?
4. Does *Phragmites* removal improve the conservation value of wetlands, and does the recovered wetland have as high a conservation value as the native reference wetland?

METHODS

Sampling

We established long-term transects in plots located in eight Chesapeake Bay subestuaries. In each subestuary, we had three treatments: Control (C) with *Phragmites* left intact; Removal (R) where *Phragmites* was treated with herbicide for 3 consecutive years; Native reference (N) which was on an uninvaded wetland in each subestuary. Prior to herbicide treatments, we located permanent sampling locations along 3 transects per plot, with 5 quadrats per transect (N=15 per treatment in each subestuary). In the fall of 2011, we sprayed the R sites with a 3% glyphosate solution by helicopter. We followed up with additional glyphosate spray treatments (Aqua Neat; <http://www.nufarm.com/USTO/Aquaneat>) in October 2012 and 2013 using the same formula, dispersed by backpack sprayers (approximately 20-24 L per 0.4 hectare along with a surfactant, Cide-Kick http://www.sepro.com/documents/CideKick_Label.pdf, and a marking dye Hi-Light <http://bettervm.basf.us/products/label-and-msds/>, both according to label specifications). In order to determine the efficacy of herbicide treatment in removing *Phragmites* and allowing the recovery of native vegetation, we recorded (detailed below) the plant community change, *Phragmites* vigor, and the abiotic environment. Samples were collected at consistent locations through the duration of the study. We began sampling in August of 2011 prior to herbicide application, continued each August through 2014 (after the final fall-2013 treatment) following herbicide application the previous autumn. We added an additional plant community sampling event in August of 2015 to monitor change after the treatments ended.

Site Descriptions

The eight subestuaries cover multiple tidal and salinity gradients in the Bay, as well as 3 distinct watershed-scale land-use types (according to King *et al* 2007): agricultural, developed, and forested. The watershed-scale land-use impacts the extent and intensity of *Phragmites* invasions, as it impacts the amount of anthropogenic disturbance in the subestuary, primarily in the form of physical disturbance and altered nutrient cycling (Sciance *et al.* 2016; King *et al* 2007; Chambers *et al* 2008; Burdick and Konisky 2003; Bertness *et al* 2002). The subestuaries we studied are: agricultural -- Tred Avon, and Wye; forested -- Nanjemoy, Wicomico, and St Leonard; developed -- Rhode, Severn, Patapsco (Fig. 4.1).

Vegetation

We sampled the vegetation cover in permanent quadrats (5 per transect, three transects per plot) using visual estimates of percent cover on a Braun-Blanquet scale. We sampled at the end of the growing season each summer from 2011 (prior to herbicide treatment) through 2015 (one year after the final herbicide treatment in fall 2013 for sampling in summer 2014). We used nonmetric multidimensional scaling (NMDS) to visualize differences in treatments and time on the plant composition, and compared treatment effects with perMANOVA in Primer+ (www.primer-e.com; Anderson *et al.* 2008). Initially, we conducted an NMDS on all non-relativized data from the R and N plots for all subestuaries collectively for each year in Primer6 (25 iterations). We omitted the *Phragmites* control plots, as the high cover rates of a single species prevented us from detecting the effect of herbicide treatment or from comparing the R and N plots. To

decrease bias caused by rare species, we removed any species that were present in fewer than 100 plots across the entire study from our NMDS analysis (N=13; per Legendre and Legendre 1998). To accompany the NMDS results, we conducted a perMANOVA in Primer+ to determine if there are significant ($\alpha < 0.05$) differences between the vegetation types. To determine the relative contribution of species to the dissimilarity of treatments across subestuaries (but within each year), we conducted a similarity percentages analysis (SIMPER) in Primer+ using Bray-Curtis distances.

Subsequent ordinations compared plant composition within each subestuary, as the subestuaries varied too much from each other to allow detection of a treatment effect. Within each subestuary, we conducted NMDS in Primer6 on non-relativized data, with rare species removed (present in <10% of samples), and 25 iterations. Additionally, we used the NMDS coordinates for each quadrat/year to determine the centroids of the point clouds. We plotted the centroids as vectors to visualize the state transitions of the vegetation for the three treatments each year (modified from Davies *et al* 2012). *Nota bene*: The strongest NMDS correlations are with *Phragmites* specific abiotic variables (standing dead, litter), which we removed from the ordination, as they are not independent of *Phragmites* cover. We did keep nutrients, salinity, and inundation (all explained below) in the NMDS analyses.

In addition to our multivariate analyses, we compared the effect of treatment on the mean coefficient of conservatism (CC; per Lopez and Fennessy 2002) of the species present in each plot. The CC (or Floristic Quality Assessment Index, FQAI) is an effective means of determining wetland quality, as most high CC plants are found in intact, higher quality wetlands (Chamberlain and Ingram 2012). We obtained the CC for

each species observed in the study from the Mid-Atlantic Wetlands Working Group (www.mawwg.psu.edu/tools). This approach allows us to determine the conservation value of vegetation that returns following herbicide treatment, relative to the native reference wetlands. All invasive species, for instance have a CC of 0, while *Spartina alterniflora* has a CC of 7. We took the mean CC for all species present in a quadrat in order to control for differences in species richness (Miller and Wardrop 2006), and to determine the impact of treatment and time on floristic quality.

Herbicide Effects on *Phragmites* Growth, Flowering, and Herbivory

We investigated the impact of herbicide treatment across sites with a meta-analysis of subestuaries to determine effect sizes of the herbicide treatment on mean *Phragmites* cover of the N and R plots. Effect sizes were calculated as the natural log ratio of treatment/control, weighted by number of subestuaries ($k=8$), and analyzed in a random effects model using the metafor package in R version 3.3.3 (Viechtbauer 2010; Rinella and James 2010). We conducted additional meta-analyses on the effect size of herbicide on native cover (N and R plots) and CC (N and R plots).

Phragmites vigor was measured in two stages each season. First, we sampled stem densities, *Phragmites* cover (Braun-Blanquet), and the diameters of a stem in each of the four corners of our 1m² permanent quadrats during our annual vegetation surveys. The combination of these response variables allows consistent comparisons between *Phragmites* cover (current year and standing dead) and the understory vegetation. Stem diameters give a strong estimate of below ground vigor, as grasses do not undergo secondary thickening once a ramet emerges (Haslam 1972).

During the second sampling stage, in the autumn (2011-2014) we sampled the *Phragmites* R and intact-C plots for flowering and herbivory. We counted stems in 0.25m² quadrats inside the permanent quadrats, and recorded attacks by endophagous herbivores and flowering for each stem. We recorded herbivory of endophages, as they can cause the loss of flowering on a given ramet (Tewksbury *et al* 2002; Tschardtke 1999). Since reproduction by seed is the primary means of spread for Chesapeake Bay *Phragmites* (McCormick *et al.* 2010; Kettenring *et al* 2011), the loss of flowering heads could impact the invasion. We identified insect herbivores to guild and focused on the damage caused by species within the Dipteran genre: *Lasioptera*, *Giraudiella*, *Calamomyia*, and *Lipara*. There was also evidence of herbivory from the Hymenopteran *Tetramesa* spp. Species within each of these genera are *Phragmites* obligates and can prevent flowering in the attacked ramet (Tewksbury *et al* 2002). The majority of damage was done by *Lipara* spp. that form galls at the apical meristem of a ramet and eliminate the potential to flower (Tewksbury *et al* 2002; Lambert *et al* 2007; Allen *et al* 2016). *Lipara* spp. are recognizable by the galls they form, or by the creation of a “flag leaf” that results from damage done to the meristem (Blossey *et al* 2002). We only counted ramets as “attacked” if there was a visible gall, flag leaf, exit hole, or obvious frass, as these are most likely to lead to the loss of flowering in the ramet.

Abiotic Environment

We determined the season-long plant available NH₄⁺ and PO₄⁻ by burying mixed anion and cation exchange resins (Binkley and Matson 1983) each June, and retrieved them in August for 2011-2014. The resins were contained in nylon pouches and buried

adjacent to each of the permanent vegetation quadrats. Ion exchange resins have been used effectively in salt marshes (Hazelton *et al* 2010; Theodose and Roths 1999) at higher salinities than are present in our subestuaries. We eluted the resins with 1N KCl each winter. Phosphate was determined using a colorimetric test (per Eaton *et al* 1995). Ammonium concentration was determined on an API Autoanalyzer and converted to ppm per resin mass eluted. We recorded salinities in each quadrat, but the data were highly variable in each plot and did not indicate an interaction with the plant cover due to short term temporal variability and are not presented.

In the fall of 2015, we measured tidal inundation, as a proxy for wetland height, in each quadrat to determine if *Phragmites* removal impacts substrate height. Not part of the initial study design, we added inundation at the end of our sampling years and were limited to a single year of data. We used wooden dowels coated in a combination of a water soluble dye and water soluble glue. Dowels were left in place for a complete tide cycle, and inundation was determined as the distance from the wetland surface to the line where the tides removed the dye solution.

Data Analysis

All variables that are not included in the multivariate ordination and perMANOVA (such as vigor, and abiotic variables) were analyzed as one way ANOVA if year was not a factor (tide height), or as a two-way ANOVA (treatment, year, treatment x year) in JMP (SAS Institute, www.sas.com). Nutrient data were Log(10) transformed to meet the assumptions of ANOVA. On two way models, we conducted post hoc Tukey HSD tests to determine the strength of pair-wise interactions ($\alpha < 0.05$).

RESULTS

Plant Community

In 2011, prior to herbicide application, the cover types discriminated completely from each other across all subestuaries (Fig. 4.2; 2D stress 0.16) which was primarily the result of *Phragmites* contribution to the R plots (98%). Following herbicide application, in the 2012 field season, the plots show much more similarity in plant composition as is evident by increasing overlap between the R and N plots. While there is still some discrimination between cover types in subsequent years, the overlap continues to increase with continuing herbicide treatments (2013-2014). Once herbicide treatments ceased, the overlap between the cover types remained in 2015. Following herbicide application, we recorded 2d stress ≥ 0.20 for all years (Fig. 4.2), which is considered to be approaching results from random data (Legendre and Legendre 1998). While there is substantial overlap in plant composition, there was a significant difference between the cover types for all years ($P(\text{perm}) < 0.001$ for all years). The average dissimilarity between treatments was $>90\%$ for each year of the study. In the R plots, *Phragmites* contributed most to this result in each year (98% in 2011, with a minimum of 61% in 2014). Across all years in the N plots, *Spartina alterniflora* and *Spartina patens* represented the largest contribution to dissimilarity between treatments, and comprised $>50\%$ of the contribution to similarity in the N plots for each year according to SIMPER. In our meta-analysis of the impact of herbicide on native cover, across treatments (N and R), we found a significant effect size only in 2014 and 2015 with native cover increasing after the lag time (Fig. 4.2; Table 4.1).

Within each individual subestuary, our NMDS results (Fig. 4.3 and 4.4; ordination stresses are reported on figures) show overlap between the C and R plots for each subestuary prior to herbicide treatment. The dissimilarity between the R and C plots increased with herbicide treatment in most cases. The pairwise perMANOVA indicated that there were significant differences between the *Phragmites* (C and R) plots compared to the native reference vegetation prior to treatments in all plots. Interestingly, some rivers (Severn, Wicomico, and Wye Rivers) showed significant vegetation compositions between the two *Phragmites* plots even prior to herbicide application, indicating that there is variation in the minor vegetation composition under *Phragmites* monoculture canopies across a subestuary (Table 4.1), which is likely a result of variability across the surface of the wetlands.

Table 4.1. Pairwise perMANOVA results for vegetation composition between treatments for each year. Pairwise results are listed for interactions between (R)emoval, (C)ontrol, and (N)ative reference treatments for each year x subestuary.

NAN	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	5.07	0.001	0.45	0.770	5.04	0.001
2012	3.02	0.001	3.03	0.007	4.68	0.001
2013	3.19	0.001	4.95	0.001	4.55	0.001
2014	4.46	0.001	6.40	0.001	6.14	0.001
2015	3.95	0.001	4.22	0.001	5.61	0.001
PAT	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	4.10	0.001	1.65	0.067	5.14	0.001
2012	3.46	0.001	3.78	0.001	1.35	0.108
2013	3.89	0.001	4.63	0.001	2.40	0.001
2014	4.61	0.001	3.66	0.001	2.89	0.001
2015	3.54	0.001	2.11	0.021	2.46	0.001

Table 4.1 (cont.)

RHO	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	4.42	0.001	0.93	0.538	4.69	0.001
2012	2.68	0.001	4.63	0.001	4.68	0.001
2013	3.61	0.001	2.36	0.006	3.69	0.001
2014	2.41	0.001	1.75	0.007	3.91	0.001
2015	2.70	0.001	1.56	0.029	4.60	0.001
SEV	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	6.73	0.001	1.99	0.026	5.14	0.001
2012	1.74	0.013	13.71	0.001	5.21	0.001
2013	3.10	0.001	3.92	0.001	5.06	0.001
2014	2.17	0.001	7.28	0.001	5.97	0.001
2015	3.72	0.001	3.90	0.001	5.03	0.001
STL	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	22.13	0.001	1.09	0.467	21.89	0.001
2012	8.75	0.001	6.45	0.001	12.76	0.001
2013	11.27	0.001	5.09	0.001	15.46	0.001
2014	8.83	0.001	4.94	0.001	20.17	0.001
2015	9.19	0.001	4.74	0.001	19.63	0.001
TRD	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	6.96	0.001	0.99	0.474	9.33	0.001
2012	5.86	0.001	1.24	0.196	9.33	0.001
2013	7.90	0.001	4.60	0.001	10.14	0.001
2014	6.65	0.001	3.09	0.001	11.63	0.001
2015	5.37	0.001	1.45	0.078	8.65	0.001
WIC	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	8.72	0.001	1.92	0.017	7.44	0.001
2012	4.65	0.001	7.74	0.001	7.69	0.001
2013	3.98	0.001	3.39	0.001	8.02	0.001
2014	3.28	0.001	5.65	0.001	8.65	0.001
2015	2.12	0.001	4.75	0.001	6.83	0.001
WYE	R, N		R, C		N, C	
	t	P(perm)	t	P(perm)	t	P(perm)
2011	5.76	0.001	2.16	0.001	7.00	0.001
2012	3.28	0.001	2.90	0.002	5.06	0.001
2013	3.86	0.001	3.56	0.001	6.79	0.001
2014	4.31	0.001	3.93	0.001	7.36	0.001
2015	4.19	0.001	2.82	0.001	7.83	0.001

The trajectories of change in the NMDS centroids show that in every case, the R plots originate close to the C plots prior to herbicide treatment, even in the sites that had significant perMANOVA differences prior to herbicide. In the Rhode, St Leonard, Tred Avon, and Wye Rivers, once herbicide treatments ceased, the vectors converge back toward the original, prior to spraying state (Fig. 4.5). The remaining five subestuaries showed trajectories that remain in what appears to be a state that does not resemble the reference plots (per Suding *et al* 2004), which is reflected in the community change trajectories (Fig. 4.5). It is likely that native reference communities will not reestablish in some subestuaries through passive restoration.

In all cases but one (Tred Avon, Fig. 4.6), the mean CC of the R plot increased relative to the C plot. In the Patapsco and Rhode Rivers, by the end of monitoring, the CC of R plots was not significantly different from the N plots, while in the Nanjemoy, the CC increased early on in the study, but decreased in 2015 (Fig. 4.6). The meta-analysis of removal effect size revealed a significant within all years (R and N plots) effect size for the impact on herbicide on CC was significant result for all years, with CC increasing with time and treatment (non-significant based on 95% CI; Fig. 4.4; Table 4.2).

***Phragmites* Vigor**

In our meta-analysis of effect sizes of herbicide application on *Phragmites* cover, prior to herbicide application, there was no significant effect between the R and C plots across the subestuaries. In each year post-herbicide application, there was a significant treatment effect on *Phragmites* cover when all subestuaries were analyzed together.

Phragmites cover was significantly lower in the R plots than in C plots (Table 4.2). The

magnitude of treatment effects was significantly different from prespraying in 2011 to subsequent years. Although it appears that treatment effect decreases from 2012 to 2015, the results are not significant (95% CI overlaps; Fig. 4.7).

Table 4.2. Effect size of herbicide application on *Phragmites* percent cover. P value indicates significant treatment effect across watersheds for each year.

Year	t	df	p
2011	0.18	7	0.873
2012	0.77	7	0.0001
2013	0.45	7	0.0001
2014	0.51	7	0.0001
2015	0.35	7	0.005

Generally, herbicide treatment impacted the stem densities in the R plots across the study. Stem densities decreased in each subestuary following the initial herbicide treatment. Interestingly, stem densities in the C plots showed annual variation in the absence of herbicide; however, the decrease was significantly different from the R in each case excepting the Nanjemoy in 2012. Even in this case, the densities showed strong differences by the second year of treatments. In each of the subestuaries, the stem density increased between 2014 and 2015, as soon as the plants were no longer treated by herbicides. Once the herbicide treatment cease, stem density increased at the Patapsco River to such a degree that the R plot had higher densities than the C plot. Cover of *Phragmites* follows similar trends to the stem densities. In the R plots, the cover dropped with herbicide application (Fig. 4.8). In each subestuary, the percent cover of live *Phragmites* rebounded while spraying treatments were still underway, which is reflected in the size effect meta-analysis (Fig. 4.7).

Herbicide treatment resulted in a decrease in the mean stem diameter in the R plots in all of the subestuaries except the Rhode and Wye Rivers, which did not have a significant interaction (year x treatment) effect though there were significant treatment and year effects on stem diameter (Table 4.3). Four of the eight subestuaries (Nanjemoy, Patapsco, St Leonard, Tred Avon) did not have significant differences in stem diameter prior to spraying in 2011, or after spraying ceased prior to collecting 2015 data (Table 4.3), demonstrating that glyphosate application decreases plant vigor after one application. However, the plants were able to recover to the pretreatment diameters as soon as herbicide application stopped. Our data from the Wicomico River followed a similar pattern; however, lower stem diameters in the C plot yielded a significant difference in only 2012 after the first treatment. In the Rhode River, none of the sampling times had a significant treatment effect and we did not get as thorough a die back, as is evident in the cover and densities (Fig. 4.8). Pretreatment, stem diameters in the Severn were significantly different between plots, with the R having nearly twice the mean diameter of the C. Herbicide treatment decreased the diameters in the R plot significantly in 2012, however, a lack of vigor in the C stand meant that there were no significant differences in 2013. The treatment had a large, significant effect on the Severn R plot in 2014, and then in 2015, the two plots showed the same converging trend seen in most of the other subestuaries (Table 4.4). Diameters in the R plot were significantly lower than the C plot at all sampling times in the Wye River (Table 4.4) which could be related to variations in the physical environments (*i.e.* substrate height) of the plots. Much like with cover and density, the stem diameters (with minor exceptions) showed a rapid decrease in

genets' vigor with the initial herbicide application, then *Phragmites* rapidly recovered once the treatments end.

Table 4.3. Treatment effect on *Phragmites* basal stem diameters. Results of a two-way ANOVA are reported with F-scores and P-values for factors treatment and year, and the interaction between the two factors.

	diameters	
NAN	F	P
Treatment	66.48	<0.001
Year	16.28	<0.001
Treatment x Year	2.91	0.024
PAT	F	P
Treatment	62.48	<0.001
Year	12.12	<0.001
Treatment x Year	8.34	<0.001
RHO	F	P
Treatment	5.61	0.019
Year	10.87	<0.001
Treatment x Year	0.66	0.618
SEV	F	P
Treatment	2.43	0.121
Year	14.61	<0.001
Treatment x Year	21.91	<0.001
STL	F	P
Treatment	46.96	<0.001
Year	10.82	<0.001
Treatment x Year	3.28	0.013
TRD	F	P
Treatment	34.80	<0.001
Year	15.03	<0.001
Treatment x Year	10.61	<0.001
WIC	F	P
Treatment	10.48	0.002
Year	20.49	<0.001
Treatment x Year	6.20	<0.001
WYE	F	P
Treatment	136.24	<0.001
Year	12.78	<0.001
Treatment x Year	0.84	0.50

Table 4.4. Pair-wise comparison of treatment on *Phragmites* basal stem diameters in the (R)emoval and (C)ontrol plots are depicted with significance determined by Tukey's HSD ($\alpha < 0.05$).

NAN	C		R		HSD
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	8.23	0.46	7.48	0.46	N
2012	6.56	0.40	3.15	0.46	Y
2013	7.00	0.46	4.02	0.51	Y
2014	6.42	0.46	3.00	0.63	Y
2015	7.95	0.47	5.80	0.56	N
PAT	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	8.54	0.46	8.39	0.46	N
2012	8.13	0.46	2.55	0.80	Y
2013	8.25	0.46	3.69	0.89	Y
2014	7.33	0.46	3.45	0.73	Y
2015	7.24	0.46	6.11	0.68	N
RHO	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	6.39	0.40	5.83	0.40	N
2012	5.51	0.40	5.43	0.46	N
2013	4.63	0.40	3.75	0.50	N
2014	4.37	0.40	3.05	0.44	N
2015	5.28	0.40	4.98	0.40	N
SEV	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	5.98	0.46	10.20	0.46	Y
2012	6.80	0.46	3.88	0.50	Y
2013	6.57	0.46	4.97	0.46	N
2014	6.40	0.46	3.27	0.52	Y
2015	6.05	0.46	7.14	0.46	N
STL	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	8.45	0.56	8.02	0.56	N
2012	6.45	0.45	3.85	0.56	Y
2013	8.92	0.56	4.94	0.56	Y
2014	8.3	0.56	4.90	0.59	Y
2015	8.70	0.56	7.18	0.56	N

Table 4.4 (cont.)

TRD	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	5.42	0.26	5.51	0.26	N
2012	5.17	0.26	3.63	0.26	Y
2013	4.58	0.26	3.32	0.26	Y
2014	4.83	0.26	2.22	0.28	Y
2015	4.18	0.26	4.58	0.28	N
WIC	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	5.62	0.31	6.27	0.31	N
2012	5.28	0.31	2.95	0.38	Y
2013	3.98	0.31	3.71	0.35	N
2014	3.78	0.31	2.20	0.46	N
2015	4.37	0.31	4.28	0.43	N
WYE	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	8.82	0.44	5.52	0.44	Y
2012	7.27	0.44	3.77	0.45	Y
2013	5.73	0.44	3.33	0.49	Y
2014	6.18	0.44	2.40	0.54	Y
2015	7.82	0.44	3.88	0.47	Y

To accurately determine the impact of herbicide on flowering rates, we needed to look at the indirect effect of insect attack on *Phragmites* stems. Insect attack rates varied between years and subestuaries, reaching up to 97% (Table 4.5). The Patapsco River had a significant difference in the density of ramets with herbivore damage between plots prior to herbicide application, and every consecutive year. After the initial spraying treatment, attack rates were lower in the R plots in all of the subestuaries, though not all of the differences are significant (Table 4.5). The St Leonard and Rhode Rivers did not have any significant differences in attack rate (we do not have 2014 data for the Rhode River due to storms) but the data still exhibited the trend of R plots having lower attack rates. In each case that there was a significant interaction between treatment and

herbivory rates (except for 2011 on the Patapsco), the R plot had lower attack rates than C.

Table 4.5. The impact of herbicide on *Phragmites* insect attack rates in the (R)emoval and (C)ontrol plots are depicted with significance determined by Tukey's HSD ($\alpha < 0.05$).

NAN	C		R		HSD
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.44	0.16	0.42	0.16	N
2012	0.43	0.14	0.08	0.16	N
2013	0.68	0.16	0.03	0.16	N
2014	0.97	0.16	0.09	0.16	Y
PAT	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.50	0.06	0.22	0.06	Y
2012	0.56	0.06	0.03	0.06	Y
2013	0.75	0.06	0.01	0.06	Y
2014	0.64	0.06	0.00	0.06	Y
RHO	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.21	0.05	0.30	0.05	N
2012	0.25	0.05	0.08	0.05	N
2013	0.22	0.05	0.09	0.05	N
2014	ND	ND	ND	ND	--
SEV	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.25	0.05	0.34	0.05	N
2012	0.28	0.05	0.09	0.05	N
2013	0.42	0.05	0.39	0.05	N
2014	0.37	0.05	0.10	0.05	Y
STL	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.66	0.07	0.45	0.07	N
2012	0.38	0.06	0.14	0.07	N
2013	0.62	0.07	0.44	0.07	N
2014	0.43	0.07	0.24	0.07	N
TRD	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.47	0.05	0.36	0.05	N
2012	0.36	0.05	0.11	0.05	Y
2013	0.44	0.05	0.09	0.05	Y
2014	0.48	0.05	0.25	0.05	N

Table 4.5 (cont.)

WIC	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.32	0.06	0.33	0.06	N
2012	0.41	0.06	0.10	0.06	Y
2013	0.43	0.06	0.26	0.06	N
2014	0.39	0.06	0.07	0.06	Y
WYE	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.54	0.06	0.33	0.06	N
2012	0.30	0.06	0.20	0.06	N
2013	0.60	0.06	0.15	0.06	Y
2014	0.60	0.06	0.00	0.06	Y

To determine the impact of herbicide on the reproductive potential of a genet or stand, we recorded flowering rates only on unattacked stems, avoiding the indirect effect of herbivory on flower production. There are significant differences in flowering rate prior to herbicide application in the Wicomico and Wye Rivers, while flowering in the remaining subestuaries decreased with herbicide application. Also, similar to the herbivory data, the largest differences in treatment effect occur after 1-2 years of herbicide application (Table 4.6). In the pre-spray year, 2011, there were high flowering rates across all study sites (Table 4.6) with no herbivory effect in 2011 or 2012. In 2013, the treatment effects become apparent, though they are only significant in the Wicomico, Tred Avon, Severn, and Nanjemoy Rivers. Even when not statistically significant, flowering rates in the remaining subestuaries varied by an order of magnitude. By 2014, there were significant differences between C and R plots in all subestuaries (2014 data missing for the Rhode River).

Table 4.6. The impact of herbicide application on *Phragmites* flowering rates (on stems with no herbivore damage) in the (R)emoval and (C)ontrol plots are depicted with significance determined by Tukey's HSD ($\alpha < 0.05$).

NAN	C		R		HSD
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.48	0.06	0.53	0.06	N
2012	0.03	0.05	0.03	0.06	N
2013	0.32	0.06	0.00	0.06	Y
2014	0.49	0.06	0.03	0.06	Y
PAT	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.31	0.07	0.52	0.07	N
2012	0.05	0.07	0.00	0.07	N
2013	0.20	0.07	0.01	0.07	N
2014	0.46	0.07	0.03	0.07	Y
RHO	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.28	0.04	0.45	0.04	N
2012	0.03	0.04	0.00	0.04	N
2013	0.12	0.04	0.01	0.04	N
2014	ND	ND	ND	ND	--
SEV	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.51	0.05	0.42	0.05	N
2012	0.01	0.05	0.01	0.05	N
2013	0.60	0.05	0.07	0.05	Y
2014	0.72	0.05	0.02	0.05	Y
STL	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.44	0.06	0.21	0.06	N
2012	0.04	0.05	0.02	0.06	N
2013	0.61	0.06	0.05	0.06	Y
2014	0.66	0.06	0.04	0.06	Y
TRD	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.64	0.06	0.45	0.06	N
2012	0.03	0.06	0.01	0.06	N
2013	0.78	0.06	0.03	0.06	Y
2014	0.50	0.06	0.01	0.06	Y

Table 4.6 (cont.)

WIC	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.43	0.05	0.20	0.05	Y
2012	0.04	0.05	0.00	0.05	N
2013	0.42	0.05	0.11	0.05	Y
2014	0.43	0.05	0.00	0.05	Y
WYE	C		R		
	Mean	SE	Mean	SE	$\alpha < 0.05$
2011	0.36	0.06	0.67	0.06	Y
2012	0.05	0.06	0.02	0.07	N
2013	0.28	0.06	0.04	0.06	N
2014	0.42	0.06	0.00	0.06	Y

Like the insect attack rates, it appears that there is a lag of at least one growing season between the application of herbicide and the effects becoming evident on the plant. The lag in response to herbicide is in sharp contrast to the other vigor variables (density, diameter, cover) that showed a large initial effect, then the *Phragmites* began to recover.

Abiotic Environment

In the Nanjemoy subestuary; the C plot consistently had the lowest pore water NH_4^+ , while it increased in the R plot to a point where it surpassed the N reference values and has a significant treatment x year interaction effect (Fig. 4.9, Table 4.7, means in Table 4.8). We did not find a treatment x year effect in the Patapsco, Severn, Wicomico, and Wye and their pore water NH_4^+ levels follow largely parallel trends of annual variation. There was more variation in the Wicomico and Wye Rivers' nutrient levels and they both have significant year and treatment effects. The Patapsco and Severn Rivers had less annual variation than the others, and did not have a significant year effect between treatments. The NH_4^+ concentration in Rhode River samples were counter to our

expectations; the C plot had the highest level or was no different than the R plot. In the St Leonard and Tred Avon Rivers, the R values did not deviate much from the C values, while the N plot was higher than the other treatments during some sampling periods, but overlapped in other years (Fig. 4.9). As with the NH_4^+ analysis, only the Nanjemoy River had a clear pattern between nutrients and vegetation type.

Table 4.7. The impact of herbicide application on pore water ammonium and phosphate in intact and treated *Phragmites*. Results of two-way ANOVAs are shown with F-score and P-value.

	Ammonium		Phosphate	
NAN	F	P	F	P
Treatment	15.40	<0.001	4.65	0.011
Year	0.71	0.547	5.21	0.002
Treatment x Year	3.47	0.003	8.13	<0.001
PAT	F	P	F	P
Treatment	1.22	0.299	4.65	0.011
Year	9.20	<0.001	9.20	<0.001
Treatment x Year	1.00	0.430	8.13	<0.001
RHO	F	P	F	P
Treatment	18.30	<0.001	2.50	0.085
Year	12.16	<0.001	10.95	<0.001
Treatment x Year	1.87	0.088	0.82	0.556
SEV	F	P	F	P
Treatment	0.14	0.870	0.70	0.497
Year	27.50	<0.001	1.84	0.141
Treatment x Year	0.48	0.820	0.25	0.960
STL	F	P	F	P
Treatment	0.91	0.403	3.06	0.050
Year	9.55	<0.001	2.15	0.096
Treatment x Year	2.81	0.013	2.47	0.026
TRD	F	P	F	P
Treatment	14.72	<0.001	12.98	<0.001
Year	27.69	<0.001	10.44	<0.001
Treatment x Year	4.06	<0.001	2.03	0.064
WIC	F	P	F	P
Treatment	10.26	<0.001	1.54	0.218
Year	4.66	0.004	12.29	<0.001
Treatment x Year	0.97	0.449	0.54	0.777

Table 4.7 (cont.)

WYE	F	P	F	P
Treatment	10.01	<0.001	10.60	<0.001
Year	6.15	<0.001	2.71	0.047
Treatment x Year	1.25	0.283	1.94	0.077

Table 4.8. Mean season-long pore-water NH_4^+ for each site.. Results are expressed as μg NH_4^+ per g of dry resin. The three treatments are shown: experimental (C)ontrol; *Phragmites* (R)emoval; and (N)ative reference.

	C		N		R	
2011	mean	se	mean	se	mean	se
NAN	22.7	8.7	195.7	43.1	69.3	9.7
PAT	100.5	19.4	157.6	65.2	56.8	23.8
RHO	149.0	30.7	175.1	57.5	40.2	9.0
SEV	117.6	15.1	127.7	14.7	152.4	18.2
STL	64.6	11.6	63.4	24.4	89.1	21.7
TRD	56.4	9.2	158.9	24.7	49.9	9.8
WIC	46.5	17.4	132.5	29.1	42.8	14.1
WYE	47.1	11.5	223.3	46.2	59.4	10.3
	C		N		R	
2012	mean	se	mean	se	mean	se
NAN	52.7	9.7	68.8	7.2	73.3	8.9
PAT	52.6	7.4	68.2	6.8	91.6	15.9
RHO	226.3	51.2	205.6	107.6	108.4	39.3
SEV	48.0	7.6	58.1	6.7	66.9	14.5
STL	81.8	18.5	230.5	47.6	78.2	13.6
TRD	88.7	19.5	115.9	27.6	136.8	36.2
WIC	62.6	14.3	115.2	20.1	358.9	281.4
WYE	50.5	9.0	82.6	11.2	64.0	7.4
	C		N		R	
2013	mean	se	mean	se	mean	se
NAN	35.7	17.9	48.5	8.3	293.5	78.0
PAT	33.2	8.7	74.2	47.3	36.4	9.0
RHO	49.2	6.6	33.8	4.7	39.7	9.2
SEV	34.5	4.7	25.9	3.5	30.6	5.0
STL	33.9	9.2	34.7	7.0	54.0	7.8
TRD	16.5	1.7	24.9	4.7	25.3	7.4
WIC	28.6	5.4	45.0	8.6	34.9	5.0
WYE	56.7	32.2	44.3	10.4	38.6	16.1

Table 4.8 (cont.)

	C		N		R	
2014	mean	se	mean	se	mean	se
NAN	188.5	85.1	256.1	162.2	388.5	171.1
PAT	33.1	9.5	80.9	37.8	58.4	37.3
RHO	154.8	23.8	173.6	26.9	83.6	23.2
SEV	69.374	14.6	74.2	15.19	89.1	24.4
STL	142.7	56.8	93.6	22.4	120.4	36.0
TRD	43.0	14.3	135.1	18.1	46.5	17.3
WIC	52.8	17.8	149.7	34.1	107.9	26.8
WYE	128.1	69.5	147.5	39.83	31.2	6.6

Three subestuaries did not have a significant treatment x year interaction effect on PO_4^- : Rhode, Severn, and Wicomico. In these rivers, the three treatments largely parallel each other and have little discernable pattern between treatments (Fig. 4.10; Table 4.7; means in Table 4.9). The Patapsco River pore water PO_4^- is highest in the R plot, even prior to herbicide treatment. The C and R parallel each other in annual variations, while the N remains comparatively constant across years (Fig. 4.10). In the Tred Avon, PO_4^- was generally highest in the N plot, except for 2012, when the R plot PO_4^- elevated, before dropping off in the two subsequent years. The remaining two subestuaries, the Wye and St Leonard had the highest PO_4^- concentrations in the C plot, which is contrary to our predictions (Fig. 4.10; Table 4.7; means in Table 4.9).

Table 4.9. Mean season-long pore-water PO_4^- for each site. Results are expressed as $\mu\text{g PO}_4^-$ per g of dry resin. The three treatments are shown: experimental (C)ontrol; *Phragmites* (R)emoval; and (N)ative reference.

	C		N		R	
2011	mean	se	mean	se	mean	se
NAN	5.0	1.0	0.9	0.5	0.2	0.1
PAT	1.0	0.2	1.0	0.6	2.5	0.5
RHO	0.3	0.1	1.9	1.3	1.0	0.3
SEV	0.6	0.4	0.2	0.1	0.6	0.3
STL	4.2	3.1	4.0	0.9	1.0	0.5
TRD	1.0	0.3	3.0	0.8	1.4	0.3
WIC	1.1	0.2	1.7	0.5	1.9	0.5
WYE	3.0	0.7	1.2	0.5	0.7	0.1
	C		N		R	
2012	mean	se	mean	se	mean	se
NAN	1.1	0.4	0.4	0.1	0.4	0.1
PAT	0.6	0.1	1.5	0.4	1.5	0.5
RHO	0.4	0.1	1.4	0.9	0.5	0.2
SEV	0.3	0.1	0.3	0.1	0.4	0.1
STL	5.1	4.5	0.3	0.0	0.5	0.2
TRD	1.3	0.3	3.2	1.0	8.0	3.7
WIC	0.8	0.2	0.8	0.3	3.0	2.0
WYE	1.6	0.3	2.2	0.7	1.4	0.3
	C		N		R	
2013	mean	se	mean	se	mean	se
NAN	1.9	0.7	0.7	0.1	8.9	2.9
PAT	1.5	0.3	1.6	0.2	2.5	0.5
RHO	0.5	0.1	0.5	0.1	0.8	0.2
SEV	0.5	0.1	0.5	0.1	0.6	0.1
STL	13.5	7.7	0.5	0.1	1.3	0.6
TRD	0.9	0.2	8.0	4.4	4.5	3.0
WIC	1.0	0.3	0.7	0.3	1.1	0.4
WYE	10.3	5.7	2.5	1.1	2.4	0.4
	C		N		R	
2014	mean	se	mean	se	mean	se
NAN	0.8	0.2	5.2	3.5	13.8	7.5
PAT	0.9	0.5	3.1	1.3	2.1	0.9
RHO	0.0	0.0	0.1	0.0	0.0	0.0
SEV	0.4	0.2	0.6	0.2	0.7	0.2
STL	17.2	13.9	1.0	0.3	1.4	0.5
TRD	0.3	0.1	1.4	0.4	0.5	0.2
WIC	0.4	0.1	0.1	0.0	0.1	0.0
WYE	13.5	7.3	0.8	0.3	2.0	0.9

We recorded the tidal inundation of each quadrat to determine if treatment impacts the relative height of the wetland surface.. Inundation was most similar across plots in the Nanjemoy River ($P = 0.54$, Table 4.10), which was surprising since the R plot in the Nanjemoy was showing signs of erosion and peat loss (EH pers obs). The Rhode River had a marginally non-significant treatment effect on tide height ($P=0.06$). In the Patapsco, the R plot had the highest tides of all treatments, while in the Rhode, the R plot was less inundated than the other two treatments. The C and R plots are similar in the Severn River, while the N experienced substantially less inundation (Table 10). The 4 remaining subestuaries all showed a significant treatment effect on tide height; however, the pattern between treatments is not consistent throughout (Table 4.10). In the St Leonard, the R and N were similar in tide height, and depth of water flooding was significantly lower in the C plot, which could indicate that the R treatment is converging on the physical conditions of the N reference. The Tred Avon had the highest tides in the R plot (Table 4.10), which could be an indication of peat loss. The Wicomico River had the least inundation in the N plot, followed by the C, then R. The largest treatment effect is in the Wye River (Table 4.10), with tide heights in the R plot much lower than the C and N.

Table 4.10. Tidal inundation in plots with *Phragmites* intact (C) as an experimental control, *Phragmites* removed by herbicide (R), and native reference vegetation (N)

	C		R		N			
	mean	se	mean	se	mean	se	F	P
NAN	13.71	3.55	19.03	3.43	17.80	3.43	0.63	0.538
PAT	7.67	2.54	12.73	2.54	5.37	2.54	2.20	0.124
RHO	10.43	1.40	5.67*	1.40	8.90	1.40	3.00	0.060
SEV	10.57	1.38	10.97	1.38	7.07	1.38	2.42	0.101
STL	8.75*	1.88	18.80	1.82	19.87	1.82	10.85	<0.001
TRD	5.00	1.64	10.37*	1.64	3.43	1.64	4.92	0.012
WIC	14.10	2.07	18.23	2.07	8.57*	2.07	5.49	0.008
WYE	21.19	3.33	6.20*	3.33	22.03	3.33	7.15	0.002

DISCUSSION

Phragmites dominated wetlands provide a number of beneficial ecosystem services, such as storm protection, nutrient sequestration, wetland accretion, water quality improvements, among others (reviewed in Kiviat 2013). Yet there are a number of tradeoffs for other ecosystem services, such as loss of overall biodiversity (Silliman and Bertness 2004), habitat loss for native fauna (Dibble and Meyerson 2016), and potentially decreased carbon storage and increased evapotranspiration (Mozdzer and Megonigal 2013). As seen in our community responses, removing *Phragmites* does not necessarily result in the recovery of native communities. This conclusion is reflected in a meta-analysis of faunal recovery following *Phragmites* removal that determined that results will vary based on location, desired species' recovery, and site history (Dibble *et al.* 2013). Management efforts incur economic and ecological costs. We hope to aid practitioners in maximizing the ecological benefits of restoration and invasive species management. We address this in the broader concepts of: adaptive management, tradeoffs, site choice and desired outcomes.

Adaptive management

A careful consideration of management objectives and an adaptive management framework can help managers avoid unintended consequences or loss of services that can accompany invasive plant removal. The true costs of an invasion are difficult to quantify and therefore an objective assessment of the tradeoffs associated with management can be troublesome to attain (Barney *et al* 2013). Most studies on invasive plant management are too short to come to meaningful conclusions, as plant communities often take multiple years to assemble (Kettenring and Reinhardt Adams 2011), and this short coming is especially true in the *Phragmites* literature (Hazelton *et al* 2014). Short studies and a lack of monitoring can further hide the costs of management actions. In our study, we saw major vegetation changes in the fifth year, where some sites underwent an increase in native plant recruitment, while *Phragmites* recolonized others (Fig. 4.3). If we were making management recommendations based on preliminary conclusions, we would not have an appropriate assessment of our impacts to the vegetation or the wetland environment. Our meta-analysis of herbicide efficacy on *Phragmites* cover revealed a trend of diminishing returns with repeated herbicide use; a pattern that resembles *Phragmites* management studies in other regions of North America where *Phragmites* cover reduces most in the first year following herbicide application followed by an increase in cover under continuous herbicide application (Cranney 2016).

We have two potential explanations for the observations of diminishing returns (cover increases even with continued herbicide application) in *Phragmites* management. The first is that less vigorous clones, or those that are more susceptible to glyphosate are removed initially. If this is the case, the remaining clones may benefit from decreased

intraspecific competition. The second scenario is that the herbicide effect is largest on all plant species in the first year and the effect decreases with subsequent applications, as is seen in our meta-analysis of native vegetation cover in R sites. As for the resistant genotypes, we have molecular evidence that the recovery of *Phragmites* cover in R plots is not from recruitment from seed. The clones that return are spreading vegetatively from genets that were already present and detected in each plot (Hazelton and McCormick, unpublished findings) rather than rapidly evolving resistance to glyphosate. The persistent genotypes likely had a lower susceptibility to glyphosate prior to our application. These two scenarios are not mutually exclusive and both warrant further inquiry.

Tradeoffs

Not all invasions should be managed. Plant invasions can leave a lasting legacy on a site that can hinder the establishment of pre-invasion plant communities (Corbin and D'Antonio 2012, Strayer *et al* 2006). Site selection can be critical to successful management and restoration efforts, and efforts should focus on less degraded sites that have a greater likelihood of recovery (Reid *et al* 2009). As seen in our study sites, the outcome of management actions is site specific and a beneficial action in one area may lead to adverse outcomes in another (Hacker and Dethier 2008). The two sites that had the best overall recovery in our study, the Wicomico and Nanjemoy rivers (based on the number of variables observed that converge upon the R vegetation state) have two anecdotal similarities: both wetlands have relatively smaller stands of *Phragmites* that are surrounded by intact, diverse native wetlands (see model in Figure 4.3). Both of these

sites are “forested” in land-use (King et al). More work is needed to determine if there is an actual land-use effect. Smaller invasions with intact native vegetation are a priority, as are sites with access and capacity for long term monitoring and repeated management efforts. Site history and invader legacy both come into play in this case. The smaller *Phragmites* stands may indicate a more recent invasion, potentially due to higher levels of invasion resistance (Levine et al), although it could also be related to distribution of the invader. If the invasion is more recent in these subestuaries, site history may play a role in resistance, more so, the shorter residency of the invader would diminish legacy effects upon removal. Both scenarios emphasize the need for careful site selection in restoration and management (discussed in Reid et al).

Previous studies reported higher standing nitrogen stocks in *Phragmites* than native wetland vegetation (Windham and Meyerson 2003) and it is more efficient at sequestering nutrients than most co-occurring species (Windham and Ehrenfeld 2003). There are lower levels of pore water NH_4^+ under *Phragmites* canopies relative to native vegetation, and when *Phragmites* is removed, NH_4^+ reenters the system as the biomass decomposes (Alldred et al 2016; Meyerson et al 1999; Findlay et al. 2002). Removing *Phragmites* released sequestered PO_4^- into the pore water in one study (Meyerson et al. 1999), but not in others (Findlay et al 2002). *Phragmites* removal can release nutrients back into the pore water and can adversely impact water quality (Alldred and Findlay 2016; Meyerson et al 1999; Findlay et al 2002). The tradeoffs of nutrient sequestration by *Phragmites* should be considered prior to management actions. We saw an increase in nutrients with *Phragmites* R in some, but not all, of our subestuaries and the factors driving the differences are still unclear. The differences in nutrient responses reinforce

the need for invasive plant studies to cover multiple sites and a large geographic area (Kueffer *et al* 2013).

An additional consideration in site choice is the tradeoffs between ecological services provided by the invader, those provided by the native community, and the risks of management (impacts to non-target species, inadequate restorations of native systems, cultural perception, economic costs). *Phragmites* is exceptional at accreting wetland surface height by building below ground biomass, producing persistent litter and biomass, and by trapping sediments (Rooth and Stevenson 2000). In coastal areas that are subject to increasing sea level rise (SLR), plants that can rapidly accrete substrate serve numerous ecosystem services from storm protection to shoreline stabilization. Several authors have discussed the potential importance of *Phragmites* to the coastal zone if SLR outpaces the accretion rates of native vegetation (Rooth and Stevenson 2000; Kiviat 2013).

Site choice and target outcomes

Reference sites can allow for clear targets of management actions (Neckles *et al* 2002), however, the legacy effects of an invasion may have altered the environment in ways that prohibit transition to the original state (Palmer 2009). The formation of plant assemblages that may not resemble the original states, but are less degraded than the invaded system, should be looked at as a potentially acceptable outcome if the new state is in line with management objectives (Suding *et al* 2004; Seastedt *et al* 2008). Following *Phragmites* removal, half of our sites formed assemblages that did not converge upon the reference state, while in all of our sites the N and R were significantly different in

perMANOVA. Typically, the trajectory of change is not the reverse of the trajectory of the invasion (Suding 2011). We could easily see this pattern with the change trajectories in our sites, where the R plots deviated from the C state, but did not converge on the species composition of the N plots, but formed a new (potentially transitional) state once *Phragmites* was removed.

Two subestuaries appeared to establish plant assemblages that were on a trajectory toward the native reference, and two more appear to be on trajectories toward a to-be-determined state. The remaining four sites appear likely to revert to the invaded state without further management. It is likely that these sites were either too degraded to support native vegetation, which may be a legacy effect of the invader, or there may be unknown site history effects that prevent the establishment of native vegetation (sensu Strayer et al). It may be the case that more aggressive management (longer duration of management and monitoring, physical restoration of the wetland environment, revegetation) would alter the physical conditions enough to facilitate native plant communities in these wetlands.

None of our sites recovered to the reference state, though they did all improve in quality, as reflected in the CC results, relative to the original *Phragmites* monoculture. In nearly all of our sites, herbicide application increased the mean CC in the R plots. We modelled the dominant plant species cover across all subestuaries and conducted a meta-analysis of the CC (Table 4.11) and determined that, as a whole, the wetlands increased presence of desirable species, but this decreased with time. Additionally, across all sites, the vegetation quality began to decrease once herbicide application ceased. Looking at the overarching patterns of plant composition, *Phragmites* management efforts do not

eliminate the reed from wetlands, however, the CC does increase. Depending on management objectives (facilitate native species, specific habitat type, increase biodiversity), this could be considered a positive outcome.

Our herbicide treatments did impact *Phragmites* vigor (cover, diameter, flowering) successfully, although the invader recovered even with continued treatments. The reversion of four sites to the invaded state emphasizes the need for an adaptive framework and long term monitoring in all restoration and management projects (*sensu* La Peyre *et al.* 2001). Projects that have multiple target outcomes (perhaps with varying desirability) should be more likely to succeed (Weinstein *et al* 2013; Palmer 2009, Suding *et al* 2004; Suding 2011). Plant invasions change the physical environment (Seastedt *et al* 2004), and recovery is not likely to simply reverse the process of invasion (Suding 2011). Invasive plant removal will likewise change the wetland environment, perhaps in adverse ways. Practitioners and researchers should carefully choose their targets to increase the likelihood of success. With appropriate site selection, and an adaptive framework with multiple acceptable outcomes, invaders can be managed while minimizing adverse and unintended outcomes.

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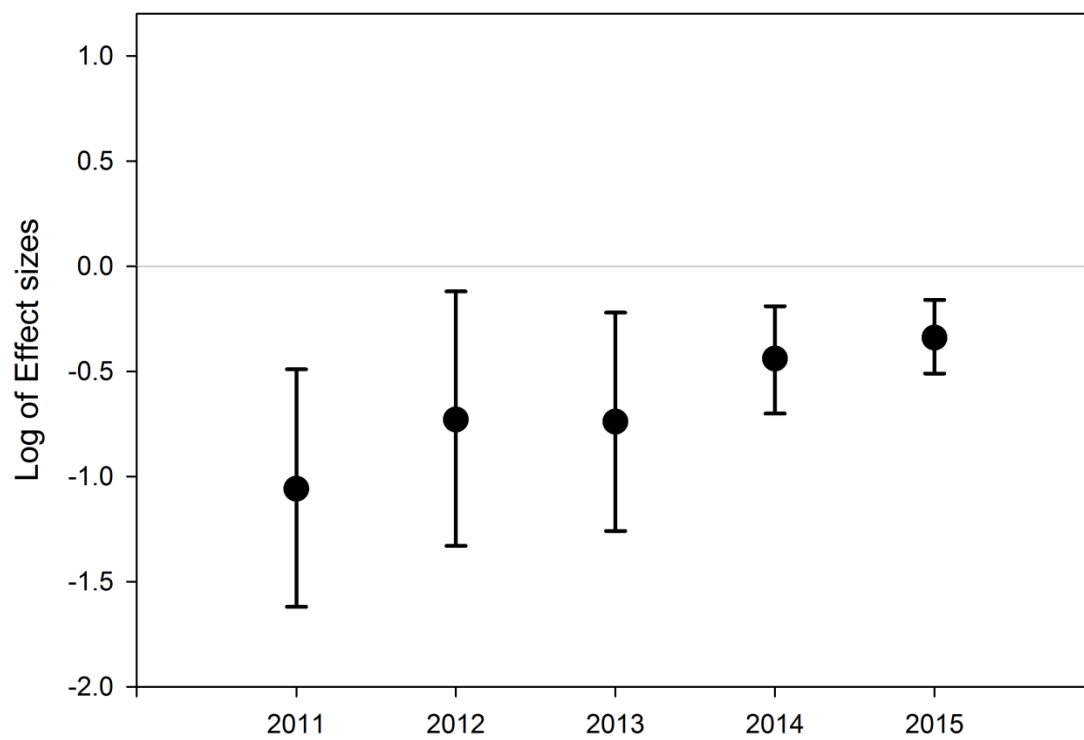
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FIGURES**Figure 4.1.** Effect Size CC

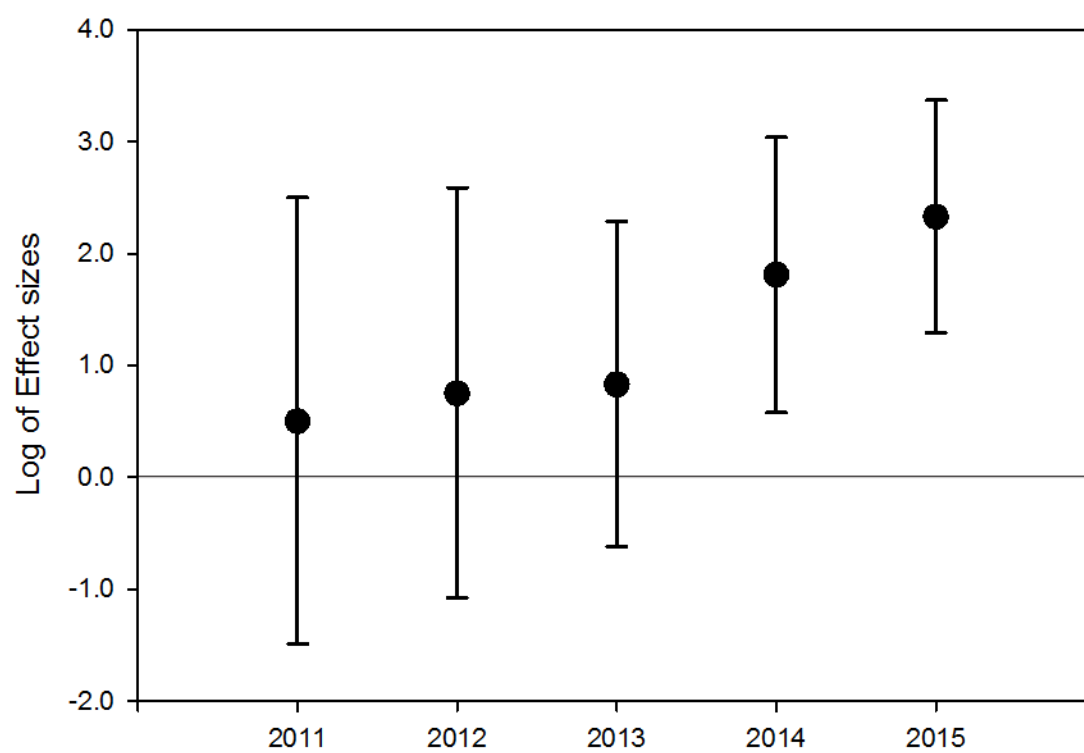


Figure 4.2. Effect Size Native Cover

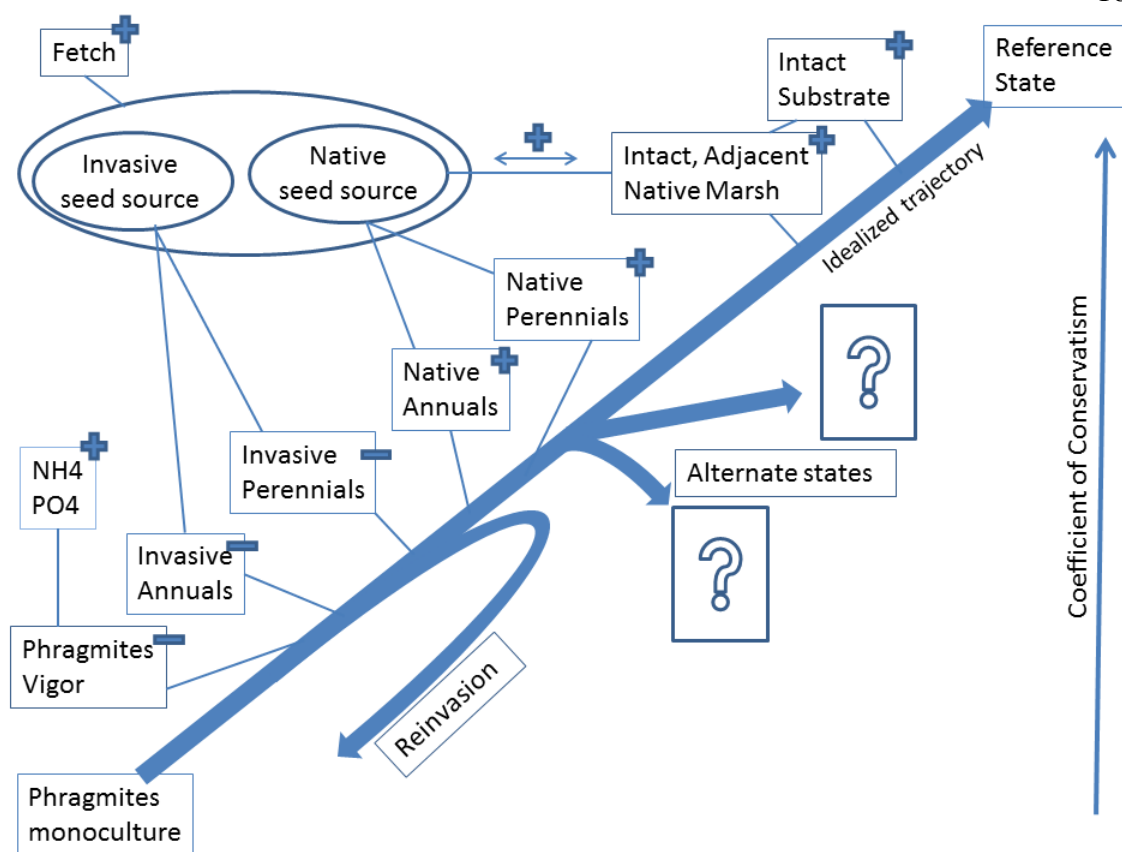


Figure 4.3. Conceptual Model.

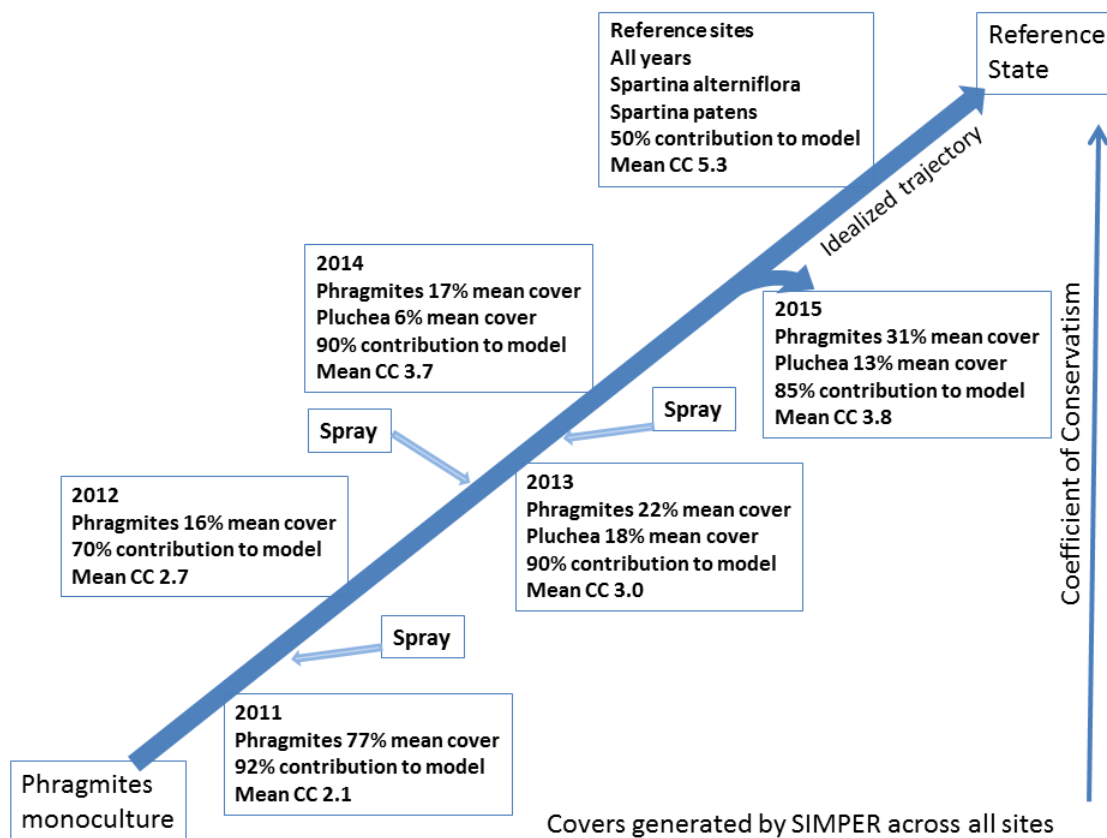


Figure 4.4. Model of Herbicide on CC of our Plots

CHAPTER V

FINAL THOUGHTS ON *PHRAGMITES* REMOVAL AND PLANT COMMUNITY
RECOVERY

In collaboration with Utah State University and the Smithsonian Environmental Research Center, I participated in a large-scale removal study of the invasive grass *Phragmites australis* (*Phragmites*) on Chesapeake Bay. We investigated the ecology of an invasion from multiple perspectives, biological, temporal, and spatial scales. By removing *Phragmites* from wetlands in 8 Chesapeake Bay subestuaries, we were able to investigate the role of land use on invasions and recovery. While no clear patterns emerged, we did document site-specific responses to management efforts.

Native plant communities did not recover in any of our study sites. Some sites reverted to their invaded state, while others formed novel states. It is evident that herbicide treatment alone is insufficient to restore native plant communities. Future studies should investigate revegetation and nutrient amelioration in efforts to recover the pre-invasion vegetation.

Herbicide application did significantly impact *Phragmites* in most cases. The relative cover, stem diameters, and stem densities all decreased with herbicide application. The effect was most evident in the first year following application, and diminished with subsequent treatments. Flowering rate and herbivory also decreased with herbicide treatment, indicating that glyphosate has a substantial impact to the invading grass.

Removing *Phragmites* impacted the nutrient regime in several of our study subestuaries. In some cases ammonium increased as the invader decomposed. This phenomenon was not as universal as anticipated, indicating that there are other processes at play in addition to the capacity for *Phragmites* to sequester nutrients and how the nutrients are released when herbicide is applied.

The results reported here are a major component to an ongoing research program into many facets of the *Phragmites* invasion. We are in process of developing new monitoring methods to streamline management evaluations. As part of a Smithsonian Predoctoral Fellowship, I am developing allometric models of *Phragmites* in 18 Chesapeake Bay subestuaries that looks at habitat heterogeneity and diversity of insect herbivores. I am working to standardize methods for determining nutrient concentrations in brackish wetlands using ion exchange resins. With the Marine Ecology Lab at SERC, we are comparing vegetation composition of Chesapeake brackish marshes to nekton and fish composition adjacent to the wetland shelf.

The largest data sets that are not present in this dissertation are the molecular results generated in collaboration with Dr. McCormick at SERC. The analyses were not complete in time for inclusion. Forthcoming analyses include how herbicide treatment and subsequent reinvasion impact clonal diversity in *Phragmites* wetlands; and how clonal diversity interacts with structural heterogeneity and herbivory. These data will represent a strong contribution to basic and applied ecology of plant invasions.

There is much work yet to be done. The literature review, seedbank study, and community analysis included in this volume are components of a larger research program. Hopefully they will offer a strong contribution to the field. I look forward to

continuing this multifaceted research program and hope that our studies impact research beyond wetland management and restoration.

APPENDICES

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CURRICULUM VITAE

Eric L. G. Hazelton

Education:

Doctor of Ecology (Pending)	2010-2018
<i>Utah State University</i>	<i>Logan, UT</i>
Master of Science in Biology	2004-2007
<i>University of Southern Maine</i>	<i>Portland, ME</i>
Certificate in Applied Geographic Information Systems	2004-2007
<i>University of Southern Maine</i>	<i>Portland, ME</i>
Bachelor of Science in Biology/Ecology with High Honors	1997-2001
<i>Marlboro College</i>	<i>Marlboro, VT</i>

Work History:**Industry Experience:**

Research Ecologist	Aug 2017-Present
<i>US Army Corps of Engineers ERDC-CRREL RS/GIS CX</i>	<i>Hanover, NH</i>
Work in Wetland Research Group.	

Co-Founder/Vice President	Aug 2008-2010
<i>Hazelton Ecological Associates, Inc.</i>	<i>Portland, ME & Athens, GA</i>
S-Corp founded with Peter Hazelton Ph.D. (UGA, Warnell School of Forestry) that focuses on the ecology of invasive organisms in stream, estuarine and terrestrial systems. Corporation closed when enrolled in PhD program.	

Salt Marsh Integrity Technician/ Conference Coordinator	May 2008-May 2010
<i>Rachel Carson National Wildlife Refuge - USFWS</i>	<i>Wells, ME</i>
Recorded biotic and abiotic characteristics of Maine salt marshes for nationwide project.. Coordinated regional workshop on <i>Phragmites</i> control for land managers and researchers.	

Invasive Species Consultant	June 2008-May 2009
<i>Gulf of Maine Research Institute</i>	<i>Portland, ME</i>
Designed and conducted field work on invasion and successional dynamics of <i>Phragmites australis</i> and associated herbivores for GMRI and the ME DOT in a newly-restored salt marsh system. Developed protocols for high-resolution marsh elevation monitoring and ongoing <i>Phragmites</i> control.	

Research Technician	Summer 2007-May 2008
<i>Cornell University</i>	<i>Ithaca, New York</i>
Worked in the Blossey Lab at Cornell comparing ecology and physiology of native and introduced <i>Phragmites australis</i> haplotypes. Conducted spatial analyses of plant distribution and compared plant-herbivore interactions from North America and Europe.	

Research Associate	Summer 2007-Present
<i>Partnership for Environmental Technology Education/NEMO</i>	<i>South Portland, ME</i>

Modeled and mapped impervious surfaces for outreach and municipal planning with Maine Non-Point-Source Education for Municipal Officials (NEMO).

Product Transfer/Improvement Scientist II

2003-2004

Binax Inc.

Portland, ME

Tested and improved immunochromatographic medical diagnostics for malaria and respiratory illnesses. Participated in the FDA submission of 2 major market products.

Teaching Experience:

Botany Instructor

Summer 2018-

-National Conservation Training Center

Sheperdstown, WV

Teaching Assistant

Spring 2012

-Utah State University

Logan, UT

Guest Lecturer

Spring 2011-Fall 2011

-Utah State University

Logan, UT

Visiting Faculty

Fall 2009

-University of New England

Biddeford, ME

ScienceCorps Teaching Fellow (NSF GK-12)

2006-2007

-University of Southern Maine

Portland, ME

Curriculum Developer

2006-2007

-Foundation for Blood Research

Scarborough, ME

Teaching Assistant

Fall 2005-Spring 2006

-University of Southern Maine

Portland, ME

Guest Lecturer

Fall 2005, Fall 2007

-University of Southern Maine

Portland, ME

Adjunct Faculty

Fall 2004

-Southern Maine Community College

South Portland, ME

Students Mentored:

Matthew Sievers

2010-2011

Smithsonian Environmental Research Center, with Melissa McCormick.

Final Project: Effect of Patch Age on the Clonal Diversity of an Invasive Marsh Grass. Project published in Wetlands.

Jared Stapp

2012

Smithsonian Environmental Research Center, with Melissa McCormick.

Final Project: Shoreline Hardening in Chesapeake Bay and its effects on Genetic Diversity of Adjacent, Invasive *Phragmites australis*

Konnon Smith

2013-15

Utah State University, with Karin Kettenring.

Senior Project: Seed viability in native and introduced lineages of *Phragmites australis*.

Evan Christopher Pool

2014-15

Utah State University, with Karin Kettenring.

Capstone project: *Phragmites australis* allometry methods for monitoring.

Melissa Tarasiewicz

2018

USACE ERDC-U participant, with Gabrielle David

Develop phone survey with subject matter experts in vegetation performance standards for wetland mitigation.

Research Experience:

Impacts of *Phragmites australis* Removal on

Clonal and Species Diversity

2010-Present

Utah State University & Smithsonian Environmental Research Center Chesapeake Bay

Doctoral research under Karin Kettenring in collaboration with Dennis Whigham.

Genetic Diversity of Native/Introduced

***Phragmites australis* Stands**

2008-Present

Bowdoin College & Hazelton Ecological Associates

Coastal Maine

Collaboration with Vladimir Douhovnikoff of Bowdoin College to determine genet diversity in *P. australis* stands.

Natural Hybrids of Native/Introduced *Phragmites australis*

2008-2010

University of Rhode Island & Hazelton Ecological Associate

New England

Collaboration with Laura Meyerson at URI looking for natural *P. australis* hybrids.

Herbivore Distribution and Effects on *Phragmites australis*

2006-Present

Cornell University & Hazelton Ecological Associates

Ithaca, NY and Portland, ME

Analyzing data from long term surveys on herbivory in native and introduced *P. australis*. Generating GIS databases of herbivore distribution, and the distribution of native and introduced *P. australis*.

Nitrogen Metabolism in Salt Marsh Grasses

2004-2007

University of Southern Maine

Portland, ME

Work compared leaf and root glutamine synthetase partitioning between *Spartina* species, and between native and introduced *Phragmites australis* subspecies.

Rare Plant Volunteer work

2001-2003

New England Wildflower Society

Mount Mansfield, VT

Worked as a climbing specialist for New England Plant Conservation Program (an NEWFS program) to assist rare plant surveys on the cliffs of Smuggler's Notch, Mount Mansfield, VT

Plant Community Classification and Vegetation Mapping

2000-2002

UVM Environmental Program & Marlboro College

Mount Mansfield, VT

Established a community classification and vegetation map of alpine plant associations, using plant community ordination and supervised classification of color-infrared aerial photography.

Publications:

Peer Reviewed Articles:

- Rohal CB, Cranney C, Hazelton ELG, Kettenring KM. In Review. Invasive *Phragmites australis* control outcomes and native plant recovery are context dependent. Ecological Applications
- Rohal CB, Kettenring KM, Sims K, Hazelton ELG, Ma Z. 2018. Surveying managers to inform a regionally relevant invasive *Phragmites australis* research program. Journal of Environmental Management
- Hazelton ELG, Downard R, Kettenring KM, McCormick MK, Whigham DF. 2017. Spatial and Temporal Variation in Brackish Wetland Seedbanks: Implications for Wetland Restoration Following *Phragmites* Control. Estuaries and Coasts.
- Eller F, Skálová H, Caplan JS, Bhattarai GP, Burger MK, Cronin JT, Guo W-Y, Guo X, Hazelton ELG, Kettenring KM, Lambertini C, McCormick MK, Meyerson LA, Mozdzer TJ, Pyšek P, Sorrell BK, Whigham DF, Brix H. 2017. “Cosmopolitan species as ecophysiological models for responses to global change: the common reed *Phragmites australis*.” Frontiers in Plant Science.
- McCormick MK, Whigham DF, Stapp JR, Hazelton ELG, McFarland EK, Kettenring KM. In review. Shoreline Modification Affects Recruitment of Invasive *Phragmites australis*. Estuaries and Coasts.
- Sciance B, Patrick CJ, Weller DE, Williams MN, McCormick M, Hazelton ELG. 2016. Local and regional landscape factors associated with the invasion of Chesapeake Bay marshes by the common reed *Phragmites australis*. Biological Invasions 18(9): 2661-77.
- Douhovnikoff V, Taylor SH, Hazelton ELG, Smith C, O’Brien J. 2016. Maximal stomatal conductance to water and plasticity in stomatal traits differ between native and invasive introduced lineages of *Phragmites australis* in North America. AoB Plants. aobpla.plw006
- Hazelton ELG, McCormick MK., Sievers MF, Kettenring KM, Whigham DF. 2015. Stand Age is Associated with Genet Diversity, but not Community Structure or Insect Herbivory, in Chesapeake Bay *Phragmites australis*.” Wetlands dx.doi.org/10.1007/s13157-015-0678-7
- Kettenring KM, Whigham DF, Hazelton ELG, Gallagher SK, Baron HM. 2015. “Biotic resistance, disturbance, and mode of colonization impact the invasion of a widespread, introduced wetland grass.” Ecological Applications 25(2): 466-80 dx.doi.org/10.1890/14-0434.1
- Douhovnikoff V, Hazelton ELG. 2014. Clonal growth: Invasion or stability? A comparative study of clonal architecture and diversity in native and introduced lineages of *Phragmites australis* (Poaceae). American Journal of Botany 101(9).
- Hazelton ELG, Mozdzer TJ, Burdick DM, Kettenring KM, Whigham DF. 2014. “*Phragmites australis* Management in the United States: 40 Years of Methods and Outcomes.” Annals of Botany Plants 6:plu001; doi:10.1093/aobpla/plu001
- Mozdzer TJ, Brisson J, Hazelton ELG. 2013. “Physiological Ecology and Global Change Responses of North American Native and Eurasian Introduced *Phragmites australis* Lineages.” Annals of Botany Plants doi: 10.1093/aobpla/plu048 – Awarded Editor’s Choice Designation

- Hazelton ELG, Knight TJ, Theodose TA. 2010. "Glutamine Synthetase Partitioning in Native and Introduced Salt Marsh Grasses" Marine Ecology Progress Series 414:57-64.
- Perkins N, Hazelton ELG, Allan W, Erickson J. 2010. "Place-Based Education and Geographic Information Systems: Enhancing the Spatial Awareness of Middle School Students in Maine." Journal of Geography 109(45):213-8.

Theses:

- Hazelton ELG. 2017. "Impacts of *Phragmites australis* Management on Wetland Plant Community Recovery, Seedbank Composition, and the Physical Environment in the Chesapeake Bay." Dissertation for PhD in Ecology from the Ecology Center and Department of Watershed Sciences, Utah State University.
- Hazelton ELG. 2007. "Partitioning of Glutamine Synthetase in Native and Invasive Salt Marsh Grasses." Thesis for Master's of Science in Biology at University of Southern Maine.
- Hazelton E. 2001. "An Analysis of Cold-Shock in Thermally Variable Environments: Stress-Proteins in Alpine Plants" Plan of Concentration Paper 1, Thesis for Bachelor's of Science in Biology at Marlboro College.
- Hazelton E. 2001. "Plant Communities of the Alpine Zone of Mount Mansfield, Vermont" Plan of Concentration Paper 2, Thesis for Bachelor's of Science in Biology at Marlboro College.

Reports and Extension Documents:

- Kettenring, KM, Cranney C, Hazelton ELG. 2016. Mapping wetland vegetation in the Great Salt Lake Ecosystem. Final report to the Utah Division of Water Quality.
- Kettenring, K.M., C.B. Rohal, C. Cranney, and E.L.G. Hazelton. 2015. Assessing approaches to manage *Phragmites* in Utah wetlands. Final report to the Utah Division of Wildlife Resources, Division of Wildlife Resources. 10 pp.
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- Kettenring KM, Long AL, Rohal CB, Cranney C, and Hazelton ELG. 2014. Assessing approaches to manage *Phragmites* in the Great Salt Lake watershed. Final report to UDNR FFSP
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- Rupp L, Whitesides R, Kettenring K, Hazelton E. 2014. *Phragmites* Control at the Urban/Rural Interface.
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- Kettenring KM, Garvie K, Hazelton ELG, Hough-Snee, N, and Ma Z. 2012. "*Phragmites* invasion and control in the Great Salt Lake watershed: 2012 land manager survey." Final report to UDNR FFSP, Part II.
- Hazelton ELG. 2009. Recommendations for Controlling *Phragmites australis* in a Newly Restored Salt Marsh. Final report to GMRI and MEDOT for Sherman Marsh
- Gilpatrick T, Hazelton EL, and Paradis R. 2002. "Phytosociological Investigations and Mapping of the Alpine Region of Mount Mansfield, Vermont." Vermont Monitoring Cooperative Annual Bulletin.

Invited Presentations and Symposia Organized:

- Hazelton ELG, Kettenring KM, Cranney C, Whigham DF. 2016. "Invasion of the Clones: *Phragmites* Invasion in North America." Invited webinar delivered to the Association of State Wetland Managers.
- Hazelton ELG, Whigham DF. 2015. *Phragmites*: Invasion of the Clones. Or, How I learned to Stop Worrying and Love *Phragmites*. Invited talk for Anne Arundel County Watershed Protection and Restoration Program
- Mozdzer TJ, Hazelton ELG, Whigham DF, Meyerson L, Saltonstall K, Lambertini C, Brix H, Cronin J. 2015. "*Phragmites australis* –A model organism for understanding genetic- to ecosystem–level responses in a rapidly changing world" Symposium (4 sessions) at SWS 2015, Providence RI.
- Hazelton ELG, Kettenring KM, Mozdzer TM, Whigham DF. 2014. "*Phragmites australis* Management in the United States: a case study, and a review of recent findings and current practice." Invited Webinar. Great Lakes *Phragmites* Collaborative. September 2014.
- Hazelton ELG, Whigham DF. 2014. "Fairhaven *Phragmites*: Invasion of the Clones. How I Learned to Stop Worrying and Love *Phragmites*." Invited talk hosted by Advocates for Herring Bay. Fairhaven, MD. August 2014.
- Kornis M, Hazelton ELG, Lellis Dibble K, Breitburg D, Whigham D. 2014. Special Session. "Interactions between Non-Native Flora and Native Fauna in Submerged, Wetland, and Riparian Systems." JASM. Portland OR. May 2014.
- Hazelton ELG, Mozdzer TM, Burdick, D, McCormick M, Kettenring, KM, Whigham DF. 2013. "Evaluating *Phragmites* management in watersheds with differing land uses" Invited Symposium to Society of Wetland Scientists.
- Hazelton ELG, Kettenring KM. 2013. "*Phragmites australis* in the Intermountain West" Invited talk Idaho Weed Conference, Boise ID
- Kettenring KM, Hazelton ELG, McCormick M, Whigham D, Sievers M. 2012. "Dispersal and establishment of *Phragmites australis* in Chesapeake Bay tidal wetlands and impacts on plant species diversity." Symposium at SWS and INTECOL, Orlando, FL.

- Whigham DF, Hazelton ELG, Mozdzer TJ, Kettenring KM, McCormick MK, and Baldwin AH. 2011. "*Phragmites australis* – A European and North American Comparison." Symposium organized for SWS, July 2011, Prague, CZ.
- Hazelton ELG, Burdick DM, Mozdzer TJ. 2011. "The Current State of *Phragmites australis* Management in the United States." Invited symposium talk at SWS, July 2011, Prague, CZ.
- Mozdzer TJ, Megonigal JP, Brisson J, Hazelton ELG. 2011. "Physiological Ecology and Global Change Responses of North American Native and Eurasian Introduced *Phragmites australis* Lineages." Invited symposium talk at SWS, July 2011, Prague, CZ.
- Hazelton ELG. 2011. "Impacts and Control of *Phragmites* in the Chesapeake Bay: Interactions between Environment, Land-Use, Restoration and Genetics." Invited seminar for the Department of Watershed Sciences, Utah State University, Logan, UT.
- Hazelton E. 2008. "Invasion of the Clones: Native and Introduced *Phragmites australis*" Invited Seminar for Southern Maine Community College Seminar Series, South Portland, ME.

Contributed Talks and Posters:

***Denotes presenter**

- Hazelton ELG, McCormick MK, Brooks H, McFarland E, Kettenring KM, Whigham DF. 2018. Interactions between Clonal Richness and Herbicide Efficacy in a Clonal Wetland Invader. Accepted to 12th Clonal Plant Symposium, Brunswick, ME.
- Rohal, CB*, Kettenring KM, Hazelton ELG. 2017. Five years of *Phragmites* management at multiple scales: Plant community outcomes on Great Salt Lake. Society of Wetland Scientists annual meeting, San Juan, Puerto Rico.
- Rohal CB*, Cranney C, Kettenring KM, Hazelton ELG. 2016. "Phragmites management at multiple spatial and temporal scales: treatment comparisons on the Great Salt Lake." SWS, Corpus Christi TX June 2016
- Hazelton ELG*, Kettenring KM, Downard R, Whigham DF. 2015. "Tidal *Phragmites* marshes have diverse native seed banks. What is limiting recruitment after the invader is removed?" SWS, Providence RI, June 2015.
- Hazelton ELG, Long EL, Rohal CB, Cranney C, Kettenring KM, Whigham DF*, McCormick M. 2015. "Phragmites landscape processes and restoration" SWS, Providence RI, June 2015.
- Kettenring KM*, Mock KE, Hazelton ELG, Rohal CB. 2015. "Patterns of *Phragmites* clonal diversity across space, time, and management regimes." SWS, Providence RI, June 2015.
- Rohal CB*, Cranney C*, Kettenring KM, Hazelton ELG. 2015. "Phragmites Management at Multiple Scales: Method Comparisons on the Great Salt Lake" SWS, Providence RI, June 2015.
- Whigham, DF*, Kettenring KM, Rohal CB, Cranney C, Hazelton ELG, McCormick MK. 2015. *Phragmites* landscape processes and restoration. SWS, Providence RI, June 2015.

- Pool E*, Hazelton ELG, Kettenring KM. 2015. A Novel Method to Monitor the Efficacy of *Phragmites* Management. Poster USU, Logan UT.
- Rohal C, Kettenring KM, Hazelton ELG. 2015. Effective Control of Small, Dense *Phragmites australis* Patches in Great Salt Lake Wetlands.
- Whigham DF*, Hazelton ELG, McCormick MK, Kettenring KM. 2015. *Phragmites* Invasion in Chesapeake Bay-Causes, Consequences, and Invasion. Mid Atlantic Chapter Society for Ecological Restoration in Newark, DE. March 2015.
- Whigham DF*, Hazelton ELG, McCormick M, Kettenring KM. 2014. "A landscape-scale approach to management of a major invasive species, *Phragmites australis*, in Chesapeake Bay tidal wetlands." Restore America's Estuaries, Washington, D.C.
- Douhovnikof V*, Hazelton ELG. 2014. "Phragmites clonal growth: invasion or stability?" Poster at ESA, Sacramento CA, August 2014.
- Hazelton ELG*, Kettenring KM, McFarland E, McCormick M, Whigham D. 2014. "*Phragmites* removal results in a novel state that does not resemble native plant communities." JASM, Portland, OR. May 2014.
- Kornis M*, Hazelton ELG, Breitburg D, Whigham D. 2014. "Linking predator/prey interactions in coastal fish communities to habitat heterogeneity of native and invasive intertidal marshes" JASM, Portland OR. May 2014.
- Kettenring KM*, Long LE, Rohal C, Cranney C, Hazelton ELG, Mock K. 2014. "Restoration of *Phragmites*-dominated wetlands of the Great Salt Lake." JASM. Portland OR. May 2014.
- Rohal CB*, Kettenring KM, Hazelton ELG. 2014. "Effective Control of Small, Dense *Phragmites australis* Patches in Great Salt Lake Wetlands." JASM Portland OR. May 2014.
- Hazelton E*, Kettenring K, McCormick, McFarland L, Jordan T, Whigham D. 2013. "The Role of Land Use in Recovery from *Phragmites* Removal." CERF, San Diego. Sept 2013.
- Rohal CB*, Kettenring KM, Hazelton ELG. 2013. "Controlling *Phragmites australis* in Great Salt Lake wetlands." EPA Region 8 wetland workshop, Salt Lake City, UT & 5th World Conference on Ecological Restoration, Madison, WI.
- Kettenring KM*, McKee M, Zaman B, Cranney C, Rohal CB, Hazelton ELG, Mock KM. 2013. "Deciphering and managing the invasion of *Phragmites* in Great Salt Lake wetlands." Universities Council on Water Resources, Lake Tahoe, CA.
- Kettenring KM*, Cranney C, Long AL, Rohal CB, Hazelton ELG, Mock KE. 2013. Ecology Informing Restoration and Restoration Informing Ecology: Invasion Mechanisms and Control of *Phragmites australis* in Great Salt Lake Wetlands. ESA.
- Kettenring K*, Cranney C, Hazelton ELG, Long LA, Mock K, Rohal CB. 2013. "Reciprocal Relationships Between Science and Restoration: *Phragmites Australis* Invasion Mechanisms, Control, and Post-Control Revegetation." SWS Duluth MN, May 2014.
- Hazelton ELG*, McCormick M., Sievers M, Kettenring KM, Whigham DF. 2013. "Are *Phragmites* Invasions Dynamic Through Time?" Society of Wetland Scientists Duluth MN

- Douhovnikof V*, Hazelton ELG. 2013. "Reproductive dynamics and clonal structure in native and invasive subspecies of *Phragmites australis*" ESA 2013, Minneapolis, MN.
- Kettenring KM*, Cranney C, Long AL, Rohal CB, Marty J, Hazelton ELG, and Mock KE. 2013. Reciprocal relationships between ecology and restoration: *Phragmites australis* invasion mechanisms, control, and post-control revegetation. ESA 2013, Minneapolis, MN.
- Rohal CB*, Kettenring KM, Hazelton ELG. 2012. "What are effective treatments for controlling small patches of *Phragmites australis* in Great Salt Lake Wetlands?" Aquatic Plant Management Society . Salt Lake City UT.
- Kettenring KM*, Hazelton ELG, Gallagher S, Baron H, McCormick M, Sievers M, Whigham D. 2012. "*Phragmites australis* invasion into disturbances in Chesapeake Bay Wetlands: Dispersal, colonization, fitness, and restoration" SWS and INTECOL, Orlando, FL. June, 2012.
- Whigham DF*, McCormick MK, Kettenring KM, Hazelton ELG, Wardrop DH, Baldwin A.H. 2011. "The spread of *Phragmites australis* in Chesapeake Bay – is it the perfect storm?" CERF. Daytona Beach, FL
- Whigham D*, Kettenring KM, McCormick MK, Hazelton ELG, Sievers M, Baldwin A. 2011. "Common Reed (*Phragmites australis*) invasion into Chesapeake Bay tidal wetlands – ecological issues and consequences." Seminar. West Virginia University. Davis College of Agriculture.
- Hazelton ELG*, Kettenring KM, Whigham D, McCormick M, Sievers M. 2011. "Large-Scale *Phragmites* Removal in the Chesapeake Bay: On-Going Research on the role of Land-Use and Genetic Diversity on Marsh Recovery" Presented at 7th Workshop of *Phragmites* Research Group, October 2011, Montreal, QE.
- Hazelton ELG*, Douhovnikoff V. 2011. "Clonal Diversity in Native and Introduced *Phragmites australis*" SWS, July 2011, Prague, CZ.
- Clannon L*, Hazelton ELG.* 2009. "Impervious Surface Analysis for Select Urban Impaired Watersheds in Maine" Presented at 2009 Maine Water Conference, Portland, ME.
- Adamowicz SC*, Guntenspergen G, Neckles H, Laskowski H, Taylor J, Hazelton E. 2008. "USFWS Salt Marsh Integrity Assessment" Presented at: Engaging Science in the Practice of Ecosystem-Based Management. Hosted by: Wells NERR, Rachel Carson NWR, and University of New England Center for Sustainable Communities, Wells, ME.
- Hazelton ELG*, Blossey B. 2008. "Native *Phragmites australis* Distribution in the Northeastern United States" New England Estuarine Research Society, Great Bay, NH.
- Hazelton ELG*, Theodose TA, Knight TJ, Blossey B. 2007. "Comparative Physiological Ecology of Native and Introduced *Phragmites australis*: Previous and Proposed Work to Identify Traits Associated with Invasions." *Phragmites australis* Workshop, Cornell University, Ithaca, NY.
- Hazelton ELG*, Knight TJ, Theodose TA. 2007. "Partitioning of Glutamine Synthetase in *Spartina* Grasses." New England Estuarine Research Society, Boothbay Harbor, ME. Winner of Ketchum Award for Best Graduate Presentation.

- Hazelton ELG*, Gilpatrick T, Paradis R. 2007. "Environmental Factors Contributing to Vascular Plant Distribution in the Vermont Alpine." Poster for Spring 2007 Northeast Alpine Research and Stewardship Gathering, Bar Harbor, ME.
- Hazelton ELG*, Perkins N. 2007. "Place-Based Education and Geographic Information Systems: Enhancing the Spatial Awareness of Middle School Students in Maine." Poster for Thinking Matters Conference, University of Southern Maine, Portland, ME.
- Letendre J*, Frankel S, Hamel M, Walker J, Jamison J, Moulton K, Roths J, Curtis A, Hazelton E, Bemis A, Dayton A, Fletcher G, Duboise SM. 2007. "Frameworks for Sustained Microbiological Inquiry in Rural Pre-college Science Classrooms: Experiences of the Maine ScienceCorps GK-12 Fellowship Program." Poster for American Society for Microbiology Conference for Undergraduate Educators, Buffalo, NY and ASM General Meeting, Toronto, CA, May 2007.

Certifications:

American Mountain Guides Association Certified Top-Rope Instructor
Wilderness First Responder (due for recertification)
Wilderness First Aid (current)

Memberships:

Society of Wetland Scientists
Coastal and Estuarine Research Federation
Association of State Wetland Managers

Academic Honors and Grants:

Utah State University Office of Research and Graduate Studies Scholarship:

Awarded to support completion of *Phragmites* project and dissertation in 2016. (\$5,000).

Smithsonian Institution PreDoctoral Fellowship (x2):

Awarded to support molecular research on *Phragmites* spring of 2013 and again in 2014. 6 month fellowship x2 (\$16,500 & \$21,000).

Garden Club of America Coastal Wetland Scholarship:

Awarded to support molecular research on *Phragmites* in spring of 2014. (\$5,000).

Utah State University Office of Research and Graduate Studies Graduate Student Travel Award (x2):

Awarded to support travel to Joint Aquatic Science Meeting in 2014 (\$300), and SWS in 2015 (\$300).

Delta Waterfowl Graduate Student Support (x2):

Awarded to support research on *Phragmites* restoration research on Chesapeake Bay in spring 2012 (\$5,000) and in spring 2013 (\$5,000).

Society of Wetland Scientists Student Research Grant:

Awarded to support doctoral research on *Phragmites* restoration in spring 2012 (\$1,000).

Utah State University Ecology Center Research Fund (x2):

Awarded to support graduate research on *Phragmites* genetic diversity in 2011 (\$4,000) and 2015 (\$4,000).

Utah State University Ecology Center Travel Grant (x3):

Awarded for abstract submitted to 2011 7th Annual *Phragmites* Workshop, Montreal, QE, Oct. 2011 (\$800), *Phragmites* Symposium at 2011 SWS International meeting in Prague, CZ., Jul. 2011 (\$800), and SWS 2015 (\$400).

Utah State University Graduate Student Senate Research Grant:

2010 (\$1,000).

Ketchum Prize for Best Graduate Student Presentation:

Awarded at the Spring 2007 meeting of the New England Estuarine Research Society (NEERS).

NEERS Travel Award:

Awarded for abstract submitted to Spring 2007 NEERS meeting. (\$500)

ScienceCorps Fellowship:

NSF GK-12 Fellowship to support research for exemplary graduate students in Biology and Applied Medical Sciences at the University of Southern Maine, June 2006. (\$30,000)

Professional Service:

- Member of Advisory Committee, Great Lakes *Phragmites* Collaborative
- Reviewer for Wetlands, Aquatic Botany, Environmental Research, Restoration Ecology, CLEAN, Hydrobiologia, PLoS ONE, Revista Biologia Tropica, Invasive Plant Science and Management, Ecological Engineering, Acta Physiologiae Plantarum, Ecology and Evolution, Ecosphere, Biological Invasions, International Journal of Phytoremediation, Plant Biosystems, Annals of Botany: Plants.
- Co-Chair for symposium “*Phragmites australis* –A model organism for understanding genetic-to ecosystem–level responses in a rapidly changing world” at 2015 SWS meeting in Providence, RI
- Co-Chair for special session “Impacts of non-native flora on native fauna” at 2014 JASM meeting in Portland, OR
- Co-Chair for *Phragmites australis* Symposium at 2011 SWS International Meeting in Prague, CZ.
- Member USU Ecology Center Seminar Speaker Committee. 2010-2011.
- Organized and lead *Phragmites australis* Identification Workshops. Intermountain Herbarium USU. Fall 2012.
- USNPS Exotic Plant Management Team volunteer fact sheet author. Summer 2012.
- Coordinated USFWS R5 *Phragmites australis* workshop. 2010.

Media and Outreach:

-***Phragmites* Symposium 2015** featured in GREATecology blog.

Greatecology.com/Phragmites-101

-**Hazelton et al. 2015** featured in SERC Shorelines blog. sercblog.si.edu/?p=6232

-**Hazelton *et al.* 2015** featured in Stewards of Water blog.

<http://www.stewardsofwater.com/blog/2015/8/17/researchers-look-at-phragmites-history>

-**Hazelton *et al.* 2014** featured in AoB Plants blog, and promoted at ESA 2014.

aobblog.com/2014/03/phragmites-australis-management-united-states-40-years-methods-outcomes/

-**Featured in Smithsonian Institution Office of Fellowships and Internships “SI-Q”** outreach video “Do Straws Grow in the Wild?”

www.smithsonianofi.com/blog/2013/12/30/its-itchy/

-**Mozdzer *et al.* 2013** featured in AoB Plants Blog, and chosen as Editor’s Choice article

[aobblog.com/2013/12/physiological-ecology-functional-traits-north-american-native-
eurasian-introduced-phragmites-australis-lineages/](http://aobblog.com/2013/12/physiological-ecology-functional-traits-north-american-native-eurasian-introduced-phragmites-australis-lineages/)

-**Mozdzer *et al.* 2013** highlighted by Maryland SeaGrant for outreach.

Internet Presence:

-Researchgate: www.researchgate.net/profile/Eric_Hazelton

-ORCID: orcid.org/0000-0002-1205-8096

-Academia.edu: usu.academia.edu/EricHazelton

-Twitter: @marshninja

-Researcher ID: www.researcherid.com/rid/D-6599-2014