ABSTRACT

Title of Document: ASSESSING WETLAND RESTORATION ON

THE DELMARVA PENINSULA USING VEGETATION CHARACTERISTICS

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Directed By: Professor Andrew H. Baldwin, Environmental

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With wetland restoration, post-restoration monitoring is essential for determining developmental trajectories, particularly when comparing to natural reference systems. As part of the Mid-Atlantic Conservation Effects Assessment Project, 15 depressional wetlands on the Delmarva Peninsula of Maryland and Delaware were surveyed for above-ground vegetation and seed bank community composition, annual biomass production, and vegetation carbon content (10 restorations from prior-converted cropland (aged 5-31 years), and 5 natural forested depressions). Within each wetland, hydrologic zones (emergent, transition, upland) were also denoted and sampled. Restored wetlands showed more seed bank community similarity to natural wetlands than above-ground vegetation communities. Restorations also produced more annual herbaceous biomass than natural systems, and lower annual leaf litter biomass. After this period of post-restoration development, restored wetlands do not perform vegetation-related functions identical to their natural counterparts; however, these restorations are performing important vegetation-based functions that require yet more time to truly develop.

ASSESSING WETLAND RESTORATION ON THE DELMARVA PENINSULA USING VEGETATION CHARACTERISTICS

By

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Dedication

This thesis is dedicated to my family: my mother Amy; my father Tom; and my sister Kyra. Through thick and thin, we stand by each other; you always show me love and respect, and there is never a day where I do not think about each one of you. Thank you all for supporting me in everything I do, and for always being there when I need a hand.



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Chapter 1: General Introduction

1.1 Wetland Restoration Historical Efforts

In 1992, the National Research Council defined restoration as "a return of an ecosystem to its conditions prior to disturbance". A majority of wetlands in the Mid-Atlantic region are forested, inland wetlands (Tiner 1987; Tiner and Burke 1996). In 2009, it was reported that 95% of wetlands in the United States were forested, freshwater wetlands (Dahl 2011). An update to this report stated that there are continuing coastal wetland losses throughout the U.S., indicating that inland, forested wetlands will be the areas where most restoration should be concentrated, and thus most monitoring of the post-restoration process is needed (U.S. Fish & Wildlife Service 2013).

The Conservation Effects Assessment Project (CEAP), a USDA study, is striving to provide more detailed assessments of effects and effectiveness of restoration in terms of ecosystem services. There are many components of CEAP, one of which being wetlands. CEAP's mission is to utilize multiple investigator efforts in measuring the efficacy of conservation practices in many ecosystems and geographic regions (Maresch et al. 2008). The Wetland Reserve Program (WRP) and Conservation Reserve Program-Wetland Initiative (CRP) are programs to work with landowners and wetlands on their property, and many of the wetlands monitored by CEAP have been restored under the WRP and CRP directives.

The MIAR-CEAP team has spent the past few years visiting restored and natural wetlands, along with prior-converted croplands that were historically wetlands, each ranging in hydrology in order to better assess the effects and efficacy of wetland

restorations. This survey encompassed 48 wetlands in three categories (natural, restored, and prior-converted cropland) across four states (Maryland, Delaware, Virginia and North Carolina). These results have gone on to support working groups in plant modeling (MIAR-CEAP Plant Working Group) and are also feeding information into the Integrated Landscape Model (ILM), both of which have worked to produce accurate wetland descriptive models.

1.2 Post-Restoration Assessment

1.2.1 Vegetation Ecosystem Services

The ecosystem services provided by wetlands are quantifiable and numerous. On the macro scale, wetlands serve as habitat for many levels of fauna, including amphibians, birds, mammals and fish, as well as on the smaller scale for insect life and benthic communities (Mitsch and Gosselink 2007). Vegetation communities are often diverse, with many native species found. On the micro scale, wetlands are excellent processors of nutrients including those from farm runoff. Reduced decomposition leads to organic matter enrichment in soils, making wetlands the prime real estate for agricultural development that was seen so heavily in previous centuries (Mitsch and Gosselink 2007). The understanding of nutrient processes is increasingly important today, as nutrient retention has many benefits beyond the ecological, even going so far as to become economically viable (Grossman 2012).

1.2.2 Hydrologic Gradients

Hydrology also plays a significant role in all types of wetlands (Mitsch and Gosselink 2007, Nel et al. 2011), but hydrologic gradients can be very pronounced in depressional wetlands in particular (Whigham et al. 2002, Verhoeven et al. 2008, Nilsson

et al. 2012, McLaughlin and Cohen 2013). Many studies looking at wetland hydrology focus on the quality and nutrient availability of the sediment and water, while fewer look at the vegetation composition (Hoelzel and Otte 2003, Patten et al. 2008, Pyzoha et al. 2008, Kirwan and Guntenspergen 2012, Janousek and Mayo 2013). Several studies focus on the differences between wetland hydrologic zones, such as emergent and temporary/transition/wet meadow (Whigham et al. 2002, Koning 2005, Wilson et al. 2013, Klemas 2013); others focus more on comparing the wetland to local upland hydrology (Morley and Calhoun 2009). Literature searches conducted by the author revealed no papers that had included surveys across all of these hydrologic zones, including between different wetland zones as well as the upland buffer, in the context of wetland restoration, pertaining to plants in particular. Upland buffers have been recognized as important in wetland restoration, but perhaps they have not been studied as extensively as is necessary (Mitsch and Gosselink 2007).

1.2.3 Vegetation and Seed Bank Communities

Determining the vegetation communities of restored wetlands is a common metric for assessing restoration effects and efficacy. The comparison of above-ground vegetation composition alone, a common assessment method, is no longer appropriate for assessing the functionality of a young restored wetland, as many other vegetation-related characteristics play important, ecologically functional roles in post-restoration development (Ardon et al. 2010, De Steven and Lowrance 2011, Yepsen 2014, McFarland et al. In Review). It is becoming common to complete surveys that include multiple vegetation characteristics in order to obtain a more comprehensive look at the functions of the wetland. Studies focusing on depressional wetlands have looked in different areas of

the U.S., including Carolina Bays (Schalles and Shure 1989, Busbee et al. 2003, Sharitz 2003, De Steven et al. 2010), Delmarva bays (Whigham et al. 2002), the similar Prairie Pothole depressional basin (Mulhouse and Galatowitsch 2003, Matthews and Spyreas 2010); this approach has even been applied to other ecosystem types as well (grassland: Martin et al. 2005). Whatever the ecosystem, it is important to focus on the restoration pathway that will restore the desired ecosystem function, be it community, productivity, or nutrient cycling (Palmer et al. 1997).

If used appropriately, vegetation community characteristics provide an integrative look at the functional development of restoration of a wetland; this usually means that more than one vegetative component must be utilized, and in more than one sampling year. Above-ground plant communities, if used as a sole measure of assessment, can provide a misleading comparison between restored and natural communities, especially if only sampled once (Whigham et al. 2002, Ervin et al. 2006, Tuxen et al. 2008, Matthews and Spyreas 2010). The restored wetlands need to have time to establish before comparisons can be made, and that may take decades. However, simply because a restored wetland does not look like a natural wetland does not mean that it is not providing substantial ecosystem services (Yepsen et al. 2014, McFarland et al. In Review). By returning to sample the wetland vegetation over a number of years, a more complete understanding of the wetland can be gained, and a timeline of the progression of the restoration will be obtained (Whigham et al. 2002, Mitsch et al. 2012, McFarland et al. In Review). Although the differences in above-ground communities between natural and restored wetlands is well documented, little is known about the seed bank communities in depressional restored wetlands and how they compare with their natural counterparts, particularly when considering within-wetland hydrologic variability.

1.2.4 Biomass and Carbon

Biomass production is a defining characteristic of wetlands, particularly when distinguishing the different types of biomass ecosystems can produce. Natural depressional wetlands on the Atlantic Gulf Coast are mainly comprised of small forested basins, which differ strongly compared to their herb-dominated young restored counterparts both in size (natural bays tend to be larger than restored wetlands) and in vegetation composition. As the restorations age, however, they have shown the capability to develop woody buffers around their emergent wetland areas, mimicking the development of a reference system (McFarland et al. In Review). Commonly, only above-ground herbaceous biomass is studied, which is not sufficient for understanding the full capabilities of these systems; wetlands dominated both by herbaceous and wooded communities are capable of producing annual biomass as herbaceous cover, leaf litter, and below-ground root in growth. These biomasses will also contribute directly to the input of carbon into the soil, and the amount of carbon will depend on both the biomass type and quantity. Age of restoration is likely to affect this as well, potentially driving these inputs to more closely resemble that of natural systems. Although herbaceous biomass dynamics between restored and natural wetlands are well understood, little is known about the carbon input capabilities in depressional restored wetlands, particularly as they age.

1.3 Prior and Current Studies

In a large-scale survey from 2010 and 2012, MIAR CEAP-Wetlands surveyed wetlands for: pollutant/nutrient regulation; greenhouse gas emissions; sediment pollutants; amphibian diversity and habitat; plant community biodiversity and productivity; hydrology

and topography; and application of remote sensing for future monitoring efforts (Lang et al. 2009). In terms of the vegetation community, restored wetlands were found to have higher overall species richness than natural wetlands; restored wetlands had more herbaceous species while natural wetlands had more woody species (Yepsen et al. 2014). Herbaceous biomass production was also higher in restored wetlands, while natural wetlands had higher woody biomass production (McFarland et al. In Review).

Concurrently, a revisitation study was conducted through the Smithsonian Environmental Research Center (SERC). Restored wetlands were originally monitored between 1993 and 1996 for changes in vegetation composition and biomass, as well as other factors (Whigham et al. 2002). In 2011, these wetlands were revisited to re-measure the vegetation characteristics. Herbaceous biomass had significantly increased in the 15 years since the original study, and many wetlands now displayed significant tree growth (Figure 4). This indicates that repeat monitoring provides a more accurate understanding of the progression of wetland development; this coupled with comparison to reference wetlands allows for a more complete look at the vegetation development of restored wetlands.

In 2013, as a new study of the MIAR CEAP-Wetland project, 15 wetlands (10 restored [7 CEAP, 3 SERC] and 5 natural) on the Delmarva Peninsula of Maryland and Delaware were revisited to gather vegetation and soil characteristics measured in tandem in order to assess the relationships of nutrient exchange and conversion of biomass to bulk density more accurately. All data for both vegetation and soil characteristics were not only collected in the same wetlands, but at the same research plots, allowing for direct correlation in analysis. The tight collaboration between these two aspects of the wetland

ecosystems allows for a more accurate representation of the ecosystem services of these wetlands. With tightly linked data between soil and vegetation characteristics, a more comprehensive picture of the wetland can be created. My research comprised the vegetation component of this more intensive survey.

1.4 Goals

My research focused on the post-restoration assessment of restored depressional wetlands compared to local natural reference systems, as well as across wetland-to-upland hydrological gradients (emergent, transition, upland). My goals were to:

- 1) Compare plant community composition between wetland types (natural vs restored) and across a within-wetland hydrologic gradient (emergent, transition, upland) in both above-ground (vegetative) and below-ground (seed bank) communities. This is addressed in chapter 2 by describing plant community composition and structure in each community type (vegetation and seed bank) as well as comparisons between the data sets for an understanding of similarity.
- 2) Compare annual plant biomass production between wetland types (natural vs restored) and across a within-wetland hydrologic gradient (emergent, transition, upland). This is addressed in chapter 3 by describing biomass production of different types (herbaceous, leaf litter, root ingrowth), as well as an assessment of existing woody stems.
- 3) Assessing ability of wetlands to contribute carbon to soil between wetland types (natural vs restored) and across a within-wetland hydrologic gradient (emergent, transition, upland). This is addressed in chapter 3 by comparing carbon quantities

of different plant biomasses, as well as surface soil carbon content in restored and natural wetlands, as well as across restoration age.

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Chapter 2: Above-ground Vegetation and Seed Bank Community

Differences between Natural and Restored Wetlands on the Delmarva

Peninsula

2.1 Abstract

Standing vegetation communities in restored wetlands often differ significantly from local reference systems. Vegetation composition can also vary distinctly across small distances even within one wetland. Seed bank assessment, when compared with a vegetation survey, may provide insight into mechanisms controlling post-restoration ecosystem development. As part of the USDA Mid-Atlantic Conservation Effects Assessment Project, above-ground vegetation and seed bank communities of 15 depressional wetlands were surveyed on the Delmarva Peninsula of Maryland and Delaware (10 restorations from prior-converted cropland, and 5 natural forested depressions). Within each wetland, hydrologic zones (emergent, transition) were sampled and compared to local upland areas. Seed banks showed stronger similarities than above-ground vegetation overall between restored and natural wetlands and across a hydrologic gradient than above-ground vegetation communities. Although above-ground vegetation surveys are useful in evaluating restorations, seed banks provide additional information for assessing restoration trajectory toward reference communities.

2.2 Introduction

As was demonstrated in McFarland et al. (In Review), restoration is an iterative process. To restore a wetland from a previously farmed field and only visit it once in the

post-restoration development is not a sufficient analysis of the ecosystem's development; it is even less informative when that visit occurs only during the first decade post restoration. The development of a restored ecosystem is a lengthy process, taking decades and perhaps even centuries (Kirkman et al. 2000, Ardon et al. 2010, Hefting et al. 2012, Kirkman et al. 2012, Moreno-Mateos 2012). In wetlands, this post-restoration trajectory has been extensively studied both in the short term (De Steven et al. 2007, De Steven and Sharitz 2008, Matthews et al. 2009, Matthews and Spyreas 2010, De Steven et al. 2010) and the long term (Mulhouse and Galatowitsch 2003, De Steven and Lowrance 2011, Zerbe et al. 2013). The benefits to post-restoration visits over a longer time involve developing a better idea of the trajectory of development, which can then be used for determining ecosystem services development. This has been previously accomplished by comparison to a local reference system (Brinson and Rheinhardt 1996, Kurz et al. 2013).

Post-restoration monitoring of ecosystems, particularly wetlands, is a national and international goal (USDA-NRCS 2006). Recent studies focus highly on freshwater wetlands, as they make up 95% of the wetlands in the United States and as such are where much of the need for restoration efforts are required (Dahl et al. 2011, Barendregt and Swarth 2013). Other studies are more focused on the current state of wetlands, as well as their future—this helps in determining post-restoration trajectory development of ecosystem functions and services (Junk et al. 2013). As agricultural fields are commonly used as areas for inland depressional restorations, recent studies also include identifying the potential biodiversity enhancements that these restorations provide as they develop (Hefting et al. 2012). Wetlands are also temporally variable, over short (seasonally) and long term (years or decades) (Deimeke et al. 2013). Studies assessing the post-restoration

development trajectories of depressional wetlands are common both in the United States, as well as globally (Lou et al. 2014).

Previous studies have emphasized the importance of comparing emergent wetland communities to their local surroundings in their ecosystem functional development (Sutton-Grier et al. 2011, Pfeifer-Meister et al. 2012, Spyreas et al. 2012, Carvalho et al. 2013, O'Connell et al. 2013). This typically provides both a more complete comparison of vegetation communities within wetlands, as well as between natural and restored system (Moreno-Mateos and Comin 2010). It is common to complete surveys that include multiple vegetation characteristics, such as vegetation community composition paired with productivity analyses, in order to obtain a more comprehensive look at the functions of the wetland (Schalles and Shure 1989, Palmer et al. 1997, Busbee et al. 2003, Sharitz 2003, Martin et al. 2005). A previous study of emergent plant communities conducted an in-depth survey of the emergent wetland vegetation communities (Yepsen et al. 2014). This created an in depth snapshot of the ponded communities at that time, but did not give insight into vegetation changes across hydrologic gradients from emergent to upland communities.

Using multiple vegetation factors to assess restoration, such as seed bank community and composition and productivity, is superior to assessments based on single measures (Warwick and Brock 2003, Liu et al. 2006, Ma et al. 2012, Beas et al. 2013). Many studies have been conducted looking at the difference between in field vegetation and the seed bank communities, as this provides insight into the vegetation potential for future growing seasons, as well as re-growth after natural disasters (Heaven et al. 2003, Combroux and Bornette 2004, Petersen and Baldwin 2004, Robertson and James 2007, Price et al. 2010, Abella et al. 2013). Analysis of seed bank composition has been suggested for use in

restoration assessment, including in wetland ecosystems, as it is a good indicator of the potential standing community in subsequent growth seasons (Wetzel et al. 2001, Baldwin 2004, La Peyre et al. 2005, Neff and Baldwin 2005, Neff et al. 2008).

While there are many studies that focus on above-ground surveys alone, and others that focus on seed bank surveys only, fewer studies have looked at the relationships between above- and below-ground (seed bank) communities (Abella et al. 2013); fewer still have looked at these relationships in restored and natural wetlands (Neff and Baldwin 2005, Neff et al. 2009). In previous studies, restored wetlands have showed low similarity to natural reference systems in above-ground vegetation (Yepsen et al. 2014) as well as in seed banks (Neff et al. 2009); however, these surveys have not compared between above-ground vegetation and seed bank communities, and so it is unknown if the variability between restored and natural systems is stronger or weaker in vegetation or in seed bank samples. Natural wetlands have been shown to be more established, and their above-ground communities tend to have lower species richness (the total number of different species in the designated research area), lower diversity (species richness appropriated by relative abundance of each species), and higher evenness (how close in numbers each species in an environment are) than their restored counterparts (Yepsen et al. 2014); this is expected in the natural wetlands as well. Studies have also shown similar trends in the seed bank communities in natural as compared to restored wetlands (Ficken and Menges 2013). Other studies have implied the importance of ponding on the emergence of seedlings (Paillisson and Marion 2005, Sorrell et al. 2010), and have shown that areas of high ponding duration significantly influence the resulting above-ground communities seed banks will produce while not as strongly affecting the seed bank communities. In depressional systems, this

ponding regime corresponds to a hydrologic gradient shifting from areas where ponding will occur most of the year (emergent) to areas that are seasonally ponded (transition), and comparing these areas to local upland communities. The effects of ponding in this hydrologic gradient should be similar in these depressional systems as the flooding effects seen in more tidal freshwater systems (Neff et al. 2009).

A survey was conducted between 2010 and 2012, by the USDA Mid-Atlantic region's Conservation Effects Assessment Project (MIAR CEAP-Wetlands), to assess biotic and abiotic aspects of restored inland depressional systems, including soils, vegetation, faunal diversity and hydrologic analyses. This survey was geographically widespread but only represented a snapshot of the functionality and development of these systems. The research in this chapter was conducted to better understand the effect of restoration practice on vegetation and soil characteristics in different hydrological areas of each wetland type, as well as to compare different wetland characteristics such as soil and vegetation within identical research plots, as well as the influence of time (Fenstermacher 2012, Ator et al. 2013, Denver et al. 2014). In order to untangle the chronology of wetland development, some older wetland restorations from a prior study by Whigham et al. (2002) at the Smithsonian Environmental Research Center (SERC) were also included to provide insight into longer restoration trajectories.

The objective of my research was to measure and compare field vegetation composition and seed bank communities between wetland types across a hydrologic gradient. I hypothesized that there would be low similarities between above-ground and seed bank in natural wetlands, and higher similarities in restored wetlands (calculated using Bray-Curtis dissimilarities, analyzed using PermANOVA and represented visually through MDS),

confirming results from previous studies looking at above-ground vegetation (Yepsen et al. 2014) and seed bank surveys (Heaven et al. 2003), as well as including the added component of comparing directly between the two survey types (a more novel approach). I also hypothesized that species richness will be higher in restored wetlands, both in above-ground and seed bank communities (calculated using direct species counts, analyzed using nested ANOVA), confirming previous above-ground vegetation results from this study (Yepsen et al. 2014) as well as previous seed bank richness analyses (Ficken and Menges 2013). Finally, I hypothesized that natural wetlands will have more even above-ground communities (Shannon evenness) (Ficken and Menges 2013).

2.3 Methods

2.3.1 Study Sites

Sites were depressional wetlands located on the Mid-Atlantic Coastal Plain. Twelve sites were selected a sub-selection of the original 48 wetland used in the 2011 CEAP survey, and three sites were added from the study conducted by the SERC (Figure 2.1). All wetlands are on the Delmarva Peninsula, in Delaware and on the Eastern Shore of Maryland. Five sites are natural forested depressions, and ten sites are restored systems on farmlands. CEAP restored wetlands range in age between 5 and 13 years, while SERC wetlands range in age between 21 and 31 years. Restoration methods were mostly conducted by soil excavation, followed by compaction. A few grasses and woody species were planted at certain wetlands to facilitate wetland development.

To select research plots, wetlands were divided into 10 sections with the top sections facing towards north, to create a stratified random plot design (Figure 2.2). Transects were set up in sections 1, 4, and 7 in most wetlands to discourage overlapping

plots and communities; some wetlands required selecting other sections randomly due to variations in wetland restoration design (i.e. berming along one side was not sampled, and all three transects would be selected from the non-bermed side). Wetlands were also divided into emergent, transition, and upland hydrologic zones (zones 1, 2, and 3) based on hydric soil profiles (Figure 2.3). Only zones 1, 2, and 3 were sampled. In each sampling section, a 100-m² circular plot (radius = 5.642m) was set up in each hydrologic zone, creating 3 plots per transect, 9 plots per wetland, and 135 plots across all wetlands (90 restored plots and 45 natural plots).

2.3.2 Vegetation Survey

In August of 2013, vegetation cover was estimated at each 100-m² circular research plot in the 15 wetlands using cover class designations specified by Peet et al. 1998 (Table 2.1). This entailed identifying any green (living) and above-ground species of any functional type; this survey will hereby be referred to as "vegetation". Any species that could not be identified in the field was brought back to the lab and identified using Brown and Brown (1972 and 1984), Gleason and Cronquist (1991 and 1998) and GoBotany (New England Wildflower Society [NEWFS]). Identified plants brought back to lab were pressed, and representative samples were stored in the lab herbarium. Nomenclature for plants was determined using the USDA Plants Database. Vegetation community data was converted from cover classes to midpoint values for easier comparison to seed bank communities.

2.3.3 Seed Bank Analysis

In March of 2013, five 5-cm by 5-cm subsample cores were taken haphazardly within each plot and composited for seed bank analysis (Figure 2.4). Composite samples

were washed through a series of screens (4 mm and 150 µm) to break up large aggregates and to concentrate the seeds in the samples (Ter Heerdt et al. 1996, Thompson et al. 1997, Price et al. 2010). The entire samples were then spread on top of 2.5-cm deep soilless planting media (50% Sunshine Professional Growing Mix LC1, 50% Lambert Canadian Sphagnum Peat Moss; pH 8.4) and grown in the misting room in the greenhouse on campus at UMCP. Samples were monitored regularly, and seedlings were identified and counted as they germinated and (in many cases) produced inflorescences. Plants were allowed to grow between April and November, and the remaining unidentified plants were brought back to the Wetland Ecology lab at University of Maryland at College Park (UMD) and identified to the lowest taxonomic resolution possible, generally species. This survey will hereby be referred to as "seed bank".

2.3.4 Data Analysis

Both vegetation and seed bank communities were relativized to accurately compare species cover in vegetation to seedling counts in seed banks; this was done by dividing cover of each species by the total percent per the research plot in which it occurred for vegetation communities, and dividing seedling counts by the total seedling count of the research plot in which it occurred for seed bank communities. Each community was quantified for species richness (S = total number of species per plot), Shannon-Weaver diversity index ($H' = -\sum[\log(p_i)\cdot p_i]$, where p_i is the importance values for species i, identified as the relative cover of each species (cover of a species divided by sum of cover values for all species in the plot)), and Shannon-Weaver evenness (Shannon evenness index $= J = H'/\ln[S]$, where H'=Shannon-Weiner diversity index and S = number of species in the plot (i.e., species density)). Presence of same species between the two surveys

(vegetation and seed bank) was quantified using a Jaccard's Similarity Index; this is calculated using the equation: $\frac{j}{r} * 100\%$, where j is the number of species in common between the two areas and r is the total number of unique species for each study (unique in vegetation survey plus the unique in seed bank survey), giving a percentage of similarity. Ordinations were calculated using Bray-Curtis dissimilarities, as opposed to Euclidian distances; this was in order to determine dissimilarity in species community composition. Similarity between data sets was analyzed using a Mantel test.

Univariate species composition and seedling germination data were analyzed by analysis of variance (JMP Pro 11, SAS Institute Inc., Cary, NC). Means were compared with Tukey's Honest Significant Difference. Multivariate analyses were performed using PERMANOVA (Plymouth Routines In Multivariate Ecological Research version six, PRIMER-E Ltd., Lutton, UK).

<u>2.3.5 Tables</u>

Table 2.1: Cover classes for vegetation survey (Peet et al. 1998).

Peet Method: Cover	Cover	Cover class
Class Scale	Percentage	midpoint (%)
1	Trace	0.1%
2	0-1%	0.5%
3	1-2%	1.5%
4	2-5%	3.5%
5	5-10%	7.5%
6	10-25%	17.5%
7	25-50%	37.5%
8	50-75%	62.5%
9	75-95%	85%
10	>95%	97.5%

2.3.6 Figures

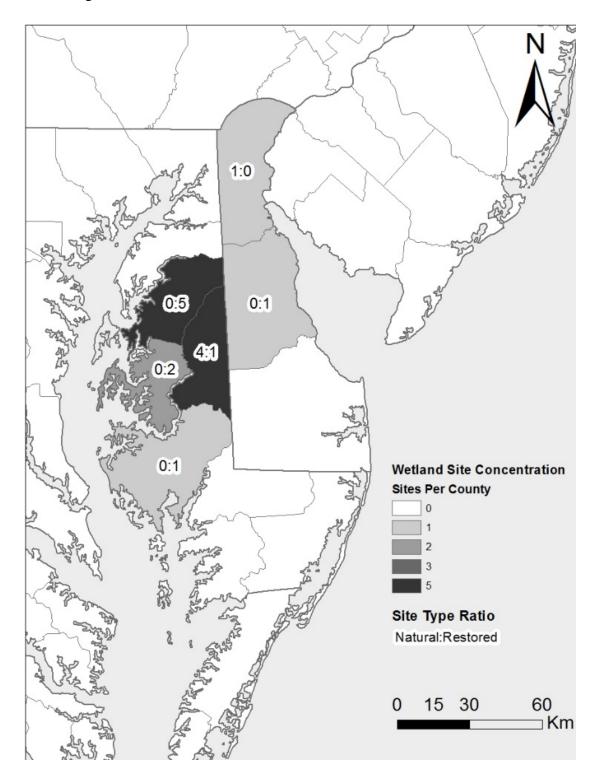


Figure 2.1: Map of site locations. Sites are located on the Delmarva Peninsula (Eastern Shore of Maryland and Delaware). Created by Shelley Devereaux.

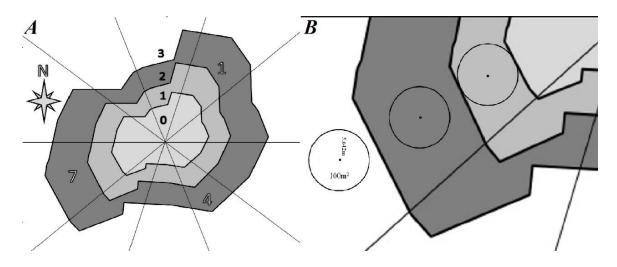


Figure 2.2: Wetland set-up: A) division of entire wetland into sections; B) demonstration of plot design in each hydrologic zone (Area = $100m^2$; radius = 5.642m).

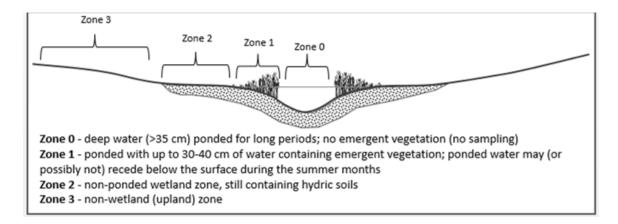


Figure 2.3: Cross-section through a typical depressional wetland, showing the division of hydrologic zones within wetlands and local uplands used in this research. Vegetation studies were conducted within zones 1, 2, and 3 (AKA emergent, transition, and upland, respectively). Data was not collected in zone 0. Reprinted from Palardy 2013, adapted from M. Rabenhorst.

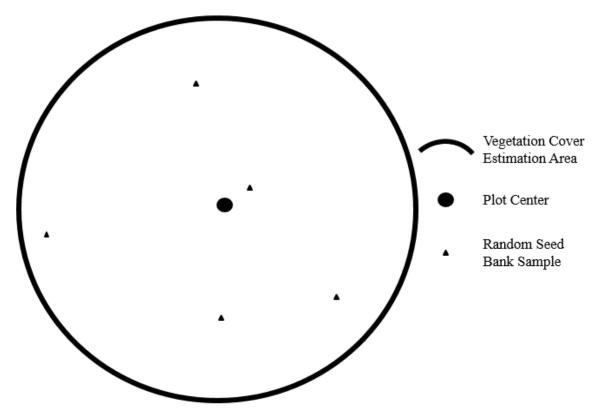


Figure 2.4: Plot layout. Thick outline represents vegetation cover estimate area; small triangles represent haphazardly-sampled seed bank samples.

2.4 Results

2.4.1 Vegetation

Above-ground species richness of plant communities differed significantly both across wetland type and hydrologic zone; restored wetlands had higher species richness than natural wetlands, and there were more species in the transition and upland zones than in the emergent zone in both wetland types (Figure 2.5A; Table 2.2). Shannon-Weaver Diversity in the vegetation communities of restored wetlands was significantly higher than natural wetlands, but only natural wetlands showed a statistical difference between hydrologic zones; the diversity peaked in the transition zone, and was significantly lower in the emergent zone (Figure 2.5C). Vegetation evenness was not significantly different in

vegetation, neither between wetland types nor across hydrologic zones (Figure 2.5E). The effect of hydrologic zone within wetland type (through nested design) was significant in both restored and natural wetlands for species richness, but only in Natural wetlands for Shannon-Weaver diversity; there was no nested effect of hydrologic zone within wetland type on Shannon evenness for natural nor restored wetlands (Figure 2.5, Table 2.2).

2.4.2 Seed Bank

Restored seed bank samples had significantly higher emerging seedling richness than seed banks from Natural wetlands by almost an order of magnitude (Figure 2.5B). Restored seed banks had a significant trend within the three hydrologic zones, with the highest seed bank richness in the two wetland zones (emergent and transition). Seed bank Shannon-Weaver diversity differed significantly between wetland types, with restored systems having higher diversity than natural systems. Diversity did not differ across the hydrologic zones within either wetland type (Figure 2.5D). Evenness was significantly higher in Natural wetlands than in restored wetlands, though the variability in natural systems was also higher (Figure 2.5F). There was no effect of hydrologic zone on Shannon-Weaver evenness within either wetland type. The only significant effect of hydrologic zone within wetland type (through nested design) was in restored wetlands for species richness (Figure 2.5, Table 2.2).

Restored wetlands had significantly higher seedling density than natural wetlands (Table 2.3). Emergent zones had the highest seedling density across both of the wetland types. Transition zones had higher seedling density than upland zones in restored wetlands, while upland zones had higher seedling density than transition zones in natural wetlands. Hydrologic zones did not significantly differ from each other in natural wetlands in terms

of seedling density, but hydrologic zones all significantly differed from each other in restored wetlands (Table 2.3)

2.4.3 Comparison

Natural sites had only a quarter the vegetation richness and half the seed bank richness of restored sites (Figure 2.6). Natural sites also had nearly equal portions of unique species between above-ground vegetation (54%) and seed bank composition (51%), whereas restored sites had more species in vegetation (91%) than in the seed bank (35%). Natural sites shared very few species between seed bank and vegetation measurements (5%; Figure 2.6: C), but restored systems shared significantly more species between seed bank and vegetation surveys (26%; Figure 2.6: D). A higher proportion of species were shared between the two wetland types in the seed bank (39%; Figure 2.6: B) than in vegetation (11%; Figure 2.6: A). Had only an above-ground vegetation survey been conducted (which is the normal approach), 42 species present in natural wetlands would have been missed (46% of all species present in both surveys), whereas only 21 species present in restored wetlands would have been missed (only 8% of all species present in both surveys) (Figure 2.6).

Seed bank composition was significantly dissimilar between wetland types, though vegetation differed more (Table 2.4). Restored wetlands showed stronger dissimilarities within type than natural wetlands (Figure 2.7). Seed banks were also significantly different across the different hydrologic zones sampled, but again not as strongly so as the standing field composition. Seed banks showed slight variation across hydrologic zones within restored wetlands (Pair-wise PERMANOVA, p < 0.1), but no significant differences across hydrology within natural wetland systems (p > 0.5). Vegetation varied across hydrologic

zone both within restored (Pair-wise PERMANOVA, p < 0.05) and natural wetlands (p < 0.05) (Figure 7, Table 2.4).

Vegetation and seed banks had higher similarities in restored systems than in natural systems using Jaccard's similarity index (2-way ANOVA, p < 0.0001) (Figure 2.8). While emergent and transition zones showed high similarities between above- and belowground composition, upland zones showed significantly lower similarity (p < 0.0001). There is no relationship between the two surveys, meaning there is not redundancy between the two data sets (Mantel's test, r = 0.011, p > 0.1).

2.4.4 Tables

Table 2.2: ANOVA results (F ratios) for vegetation and seed bank composition richness, diversity, and evenness between wetland type (natural vs restored) and across the hydrologic gradient (emergent, transition, upland zones). Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = ***; p < 0.001 = ****; p < 0.0001 = ****. In Zone w/in Type, Nat. = Natural wetlands, Rest. = Restored wetlands.

		df	Richness		Diversity		Evenness	
Vegetation	Wetland Type	1, 13	54.39****		11.39***		1.79	
	Hydrologic Zone	2, 26	12.05****		5.56**		1.87	
	Zone w/in Type	2, 44	<u>Nat.</u> 12.21 ****	Rest. 11.53****	Nat. 3.64*	Rest. 2.51	<u>Nat.</u> 1.39	Rest. 0.51
Seed Bank	Wetland Type	1, 13	147.35***		34.72***		22.89****	
	Hydrologic Zone	2, 26	2.82		1.53		0.065	
	Zone w/in Type	2, 44	<u>Nat.</u> 1.17	Rest. 5.26**	<u>Nat.</u> 0.77	Rest. 1.38	<u>Nat.</u> 0.54	Rest. 1.59

Table 2.3: Density of seedlings (expressed as seeds/ m^2) counted in controlled greenhouse growth experiment. These values were calculated using number of germinated seedlings in experimental trays multiplied by the sample surface area of 0.00905 m^2 . Values presented as means \pm 1 standard error. Natural and Restored wetlands differed significantly from each other, as denoted by asterisks; hydrologic zones significantly different where letters are present.

Wetland type/ Hydrologic zone	Seedling Density		
Natural	1479 ± 269****		
Emergent	1864 ± 605		
Transition	1201 ± 220		
Upland	1371 ± 500		
Restored	38639 ± 4364****		
Emergent	64056 ± 9293^{a}		
Transition	40938 ± 6031 ^b		
Upland	$10923 \pm 1909^{\circ}$		

Table 2.4: PerMANOVA results (F ratios) for vegetation and seed bank Bray Curtis dissimilarity between wetland type (natural vs restored) and across the hydrologic gradient (emergent, transition, upland zones). Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = **; p < 0.001 = ***; p < 0.001 = ***.

		df	Bray-Curtis
	Wetland Type	1, 13	5.33***
Vegetation	Hydrologic Zone	2, 26	2.7862***
	Type x Zone	2, 44	2.0594***
	Wetland Type	1, 13	2.563**
Seed Bank	Hydrologic Zone	2, 26	1.6678*
	Type x Zone	2, 44	1.316

2.4.5 Figures

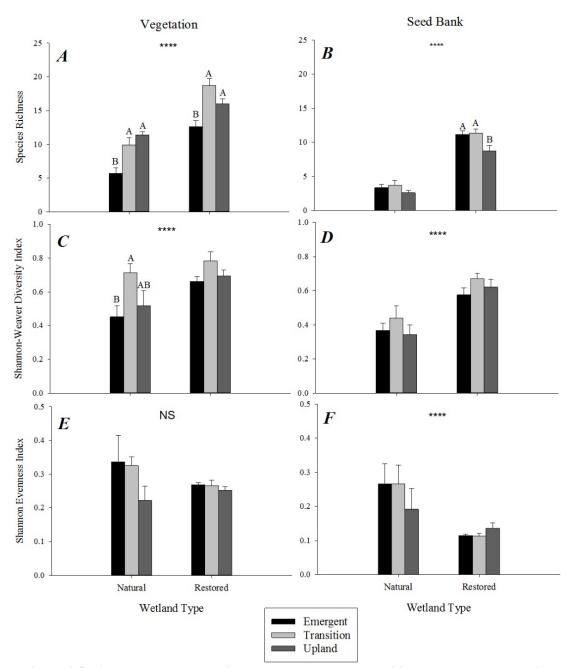


Figure 2.5: Above-ground vegetation and seed bank composition results: mean species richness (Veg-A, SB-B), Shannon-Weaver diversity (Veg-C, SB-D), and Shannon evenness (Veg-E, SB-F) between wetland type (natural vs restored) and across the hydrologic gradient (emergent, transition, upland zones). Error bars represent mean ± 1 S.E. Letters represent significant differences between hydrologic zones within wetland type; asterisks represent differences between wetland types ignoring hydrologic zones (at p < 0.05); NS = no significant differences between natural and restored wetlands; bars without letters indicate no significant differences between hydrologic zones. Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = ***; p < 0.001 = ***; p < 0.0001 = ****.

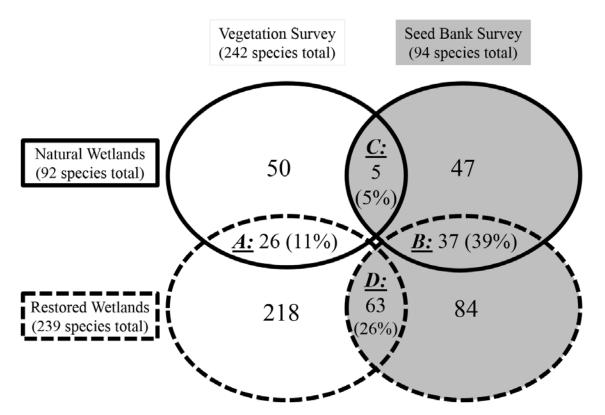


Figure 2.6: Species richness comparisons between wetland types (natural and restored) and vegetation vs. seed bank surveys based on total species counts per category. \underline{A} : species in vegetation surveys that appeared in both natural and restored wetlands; \underline{B} : species in seed bank surveys that appeared in both natural and restored wetlands; \underline{C} : species in natural wetlands that appeared in both vegetation and seed bank surveys; \underline{D} : species in restored wetlands that appeared in both vegetation and seed bank surveys.

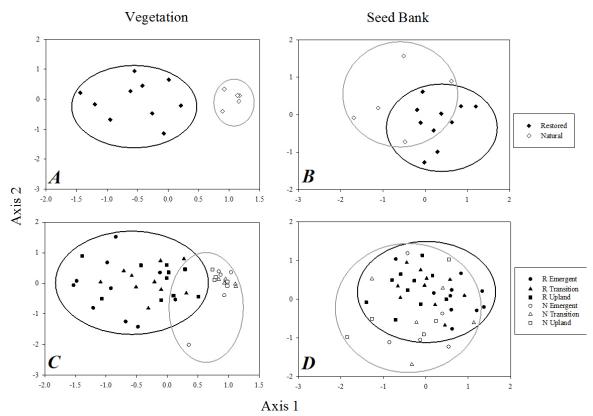


Figure 2.7: Bray Curtis MDS ordinations of PERMANOVA results. A) Vegetation diversity organized by wetland type (p=0.001); B) Seed bank diversity organized by wetland type (p=0.006); C) Vegetation diversity organized by wetland type and hydrologic zone (p=0.001); D) Seed bank diversity organized by wetland type and hydrologic zone (p=0.125). In figures C and D legend, R=Restored and N=Ratural.

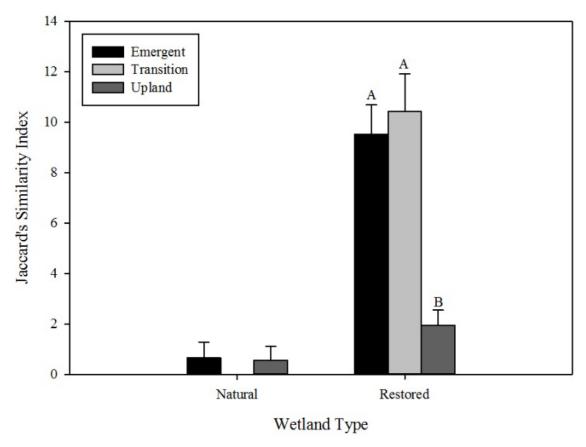


Figure 2.8: Jaccard's Similiarity Index for vegetation and seed bank composition between wetland type (natural vs. restored) and across the hydrologic gradient (emergent, transition, upland zones). Error bars represent mean \pm 1 S.E. Letters represent significant differences between different hydrologic zones within wetland type (at p < 0.05).

2.5 Discussion

This study reveals that seed banks show higher similarities between restored and natural wetlands than did the above-ground vegetation communities. The larger difference in vegetation than seed banks between restored and natural wetlands was most evident in the whole-community Bray-Curtis dissimilarity analyses. This implies that although above-ground community composition may be easier to measure, including a seed bank analysis may reveal greater similarity in overall composition between restored and natural than vegetation. It is also important to note that the sampled hydrologic zone did not appear to drastically affect either the vegetation or seed bank communities. In these depressional

systems, this likely means that the gradient change from wetland to upland is gradual enough so as to be ubiquitous across the two wetland types.

2.5.1 Vegetation

There were distinct trends across hydrologic zones in species richness (Figure 2.5A). As the community shifted from the emergent area of the wetland toward the upland, there were more species. This was visually apparent as well—there were few species in the ponded area in both natural and restored systems. Differences across the emergent hydrologic zones were not as distinctly pronounced, however, as the natural forest system was well developed around the pond. This meant that the species composition varied less from zone to zone. Had only an above-ground survey been conducted, more species would have been missed in the natural sites than the restored sites. This supports previous findings in this study (Yepsen et al. 2014), and elaborates further on the relationships within each wetland type by including the effect of hydrologic gradient suggested by other studies (Hölzel and Otte 2003, Paillison and Marion 2005, Sorrel et al. 2012).

The distinction between natural and restored above-ground vegetation was most pronounced in the Shannon-Weaver diversity index. Natural systems had lowest diversity in the ponded area, and highest diversity in the transition zone. This difference was not significantly different in the restored systems, though a similar trend of low diversity in ponded areas versus high diversity in transition zones can be seen (Figure 2.5C). Many other studies have found that restored wetlands have higher above-ground plant biodiversity than natural systems overall (Mitsch and Wilson 1996, De Steven et al. 2006, Gutrich et al. 2009); however what sets this study apart is the inclusion of hydrologic

gradient effect analysis, generating a better understanding of where these differences originate.

When considering Shannon Evenness across the species counts per sample as well, neither wetland type nor hydrologic zone separated out in a significant trend (Figure 2.5E). Particularly in the restored systems, all hydrologic zones sampled had similar evenness. In terms of ecological importance, this indicates that the different areas of the wetland are comparably diverse. There was not a significant difference between natural and restored systems, either, meaning that the evenness seen in restored systems may be at least partially explained by the movement towards a more stable ecosystem (Matthews and Spyreas 2010). Even though there was higher diversity and richness in restored wetlands (significantly), restored and natural communities have similar species evenness.

These results suggest that while these different wetland areas are functionally different in terms of other characteristics, their plant communities are very comparable. There was a stronger trend of decreasing evenness from emergent to upland zones in the natural systems, which suggests that this is the trend for which restorations should be aiming. Koning (2005) had alluded to hydrologically-driven composition variability, and this study has confirmed this effect for natural and restored depressional systems. Visually, the older restorations have made large strides towards the natural forest-encompassed systems. Forested borders that were not present 15 years prior are now so thick that it is almost impossible to reach the emergent wetland in some areas. Herbaceous plants that had once been present have been replaced by more woody plants. As these younger restorations age, a similar trend is likely to be seen as well.

2.5.2 Seed Bank

Natural and restored systems differed significantly in richness, diversity and evenness; restored systems had higher richness and diversity, while natural systems were more even. This differed from my original hypothesis, as I was anticipating more similar results between the two wetland types in the seed banks. Other studies confirm this result, as seed banks of restored systems often do not show as many of the important species natural wetlands possess after a short post-restoration development (Neff and Baldwin 2005, Neff et al. 2009). This similarity was better expressed in the composition analysis, discussed later, but the community analyses such as richness, diversity and evenness were all very different between the two wetland types. This could be due to decreased emergence of seeds from the seed banks of natural systems, since there are fewer opportunities for seeds to emerge and establish due to the high canopy cover and resulting shade, as well as high levels of propagule production in the restored systems. With so much more herbaceous cover in the restored systems, they may be producing more readily germinating seeds. However, it actually may be due to seeds of woody plants tending to not persist in the seed bank, but rather germinate right away, causing them to not be able to become established due to the persistent canopy cover mentioned earlier (Price et al. 2010). The mechanisms behind seed establishment and community development are critical for understanding more about why these restored and natural wetlands have such different richness and diversity values (Abella et al. 2013).

Methodologically, there are some alterations that might be beneficial to include in future applications of seed bank analysis as a metric for post-restoration monitoring. Since the seeds that will germinate are likely the ones that benefit most from the greenhouse

environment, defining the greenhouse environment to optimize conditions for germination by as many species as possible is important (Abella et al. 2013). This would include water levels within trays, humidity, light availability (intensity and time of day), soil media type, and others as well. While these conditions were monitored to the best of the researcher's ability, conditions should be consistently monitored and optimized to ensure seeds are not missed due to suboptimal conditions. Some seeds have different life strategies (e.g. periods of dormancy, cold stratification, mycorrhizal relationships, pH needs, etc) that might not have been reflected well enough for germination. There were also periods of excessive drying in the greenhouse that may have caused irreparable damage to the seeds as well.

Effect on hydrologic regime on seedling emergence, while certainly important in the germination capability of seeds, was not included as part of this study (Paillisson and Marion 2005, Ficken and Menges 2013). It is clear from the results that the seedlings did not show too significantly different of trends from zone to zone. If the ponding regime is particularly important in the emergence of different communities, then it would be a good manipulative experiment to check how ponding will change this; though this has been studied in tidal systems (Neff et al. 2009), it is less studied in depressional systems where the ponding changes are not as regular or cyclic. While this was a part of the initial methods plan, it became clear early on that greenhouse manipulation of ponding levels for each wetland type and each hydrologic zone would be too cumbersome a method to take on in addition to all other required methods (i.e. would have tripled the greenhouse study, requiring too much manpower to maintain). In the future, a hydrologic manipulation would explain many of the methodological questions this study has raised.

2.5.3 Comparison of Wetland Types and Survey Type Efficacy

When it comes to comparing the overall richness of the two different wetland types, the importance of the seed bank study becomes clear (Figure 2.6). For example, in natural wetlands, the two surveys only had 5 species in common out of a total of 92 species. This is only 5% of the total species of those natural systems, compared to 26% of species shared between surveys in restored systems. This indicates that if only an above-ground survey had been conducted, then almost 50% of unique species in the natural systems would have been missed but only about 30% in the restored systems.

When compared within survey types, the usefulness of seed bank studies becomes even clearer. In the vegetation survey, there were only 11% of species shared between restored and natural wetlands. If only this survey had been done, these systems would have appeared potentially too different even to compare. When looking at the similarity within the seed bank study, restored and natural systems shared almost 40% of species. This makes them much more comparable in terms of composition, and means that the seed bank comparison may be even more useful than the above-ground survey in this respect, a point that others have alluded to previously but never definitively determined prior to this study (Middleton 2003).

The similarity within the restored systems can also be seen when the two surveys are compared using the Jaccard's similarity index (Figure 2.8). While natural systems were not terribly similar between vegetation and seed bank surveys, restored systems showed fairly high similarity. The restored wetlands, though not the bordering uplands, have high similarity between the vegetation and seed bank surveys. Jaccard's similarity index has not been used often in comparing similarities between seed bank surveys and vegetation

surveys, particularly not when considering restored and natural wetlands; where it has been used, the results are clear and defined (Wetzel et al. 2001). Previous studies have relied mostly on ordination such as Principal Component Analysis (Combroux and Bornette 2004) and Detrended Correspondence Analysis (Stroh et al. 2010), which is an inappropriate measurement for this type of data due to using Euclidian distance rather than Sorenson's (Bray-Curtis) dissimilarity; many other studies have neglected to compare the seed bank and vegetation surveys in any noticeable metric (Liu et al. 2005, Peyre et al. 2005), while others ignored the vegetation survey completely, focusing solely on the seed bank analysis and ignoring the important relationship between the two (Heaven et al. 2003, Hoetzel and Otte 2003). Jaccard's similarity index allowed me to identify direct plot-by-plot relationships between the two datasets, and be able to apply those back to the observational factors of interest (wetland type and hydrologic gradient).

The usefulness of the seed bank study is also apparent when doing a composition analysis and ordination (Figure 2.7). In the above ground survey, the natural systems separate distinctly from the restored systems, when analyzed alone as well as with the zones teased out. This indicates that the above-ground survey comparison would not be useful when looking at species composition and dissimilarity. This questions the usefulness of the reference system method of post-restoration monitoring—how can we justify using these systems as references, if they are not similar?

When analyzing the community metrics from the seed bank survey, the reliability of using reference systems becomes apparent again. Though the natural systems separate from the restored systems when analyzed by wetland type, the two types become intermixed when analyzing by type and zone together, supporting findings from the

literature (Andreas et al. 1995). Since these systems are so much more similar within the seed bank, it indicates that including a seed bank should continue to be used for comparison purposes between restored and natural depressional wetlands.

One concern when using these types of analyses is redundancy between the datasets. Can these surveys be compared to one another, or are the data sets too dissimilar? The results of the Mantel test show that these data sets are independent, without a statistically significant relationship between the two datasets. This indicates that the datasets represent two distinct communities within restored and natural wetlands, and each community has an important role to play, and that the importance of the seed bank community should not be ignored by simply assuming that it is a smaller subset of the vegetation community. This has been suggested by others in the past (Neff et al. 2009, Beas et al. 2013), and the confirmation here is important for implementing seed bank analyses in future post-restoration monitoring efforts.

2.5.4 Implications for Wetland Restoration Monitoring

Improvements to the seed bank study can significantly extend the applicability of these data. One argument against implicating these methods to future studies has been the difficulty and time-consuming aspect of the procedure. Greenhouse set up and monitoring of germination takes a lot of time, and the effort required for each seed bank might not seem beneficial enough to continue to use. However, vegetation studies may individually only take a few hours per site, but are only a sample of the community at a single point in time. Thus vegetation must be sampled really twice or three times a year, as well as over multiple years, to get a reasonable assessment of what is there and to describe temporal changes. Seed banks integrate seed accumulation over multiple years, and only requires

the one-time experimental dedication of a few months. Seed bank surveys are laborious in the short term, but represent one long sampling period that does not need to be repeated; a good representative vegetation survey needs to be done multiple times a year for multiple years. As has been discussed, the use of the seed bank study significantly improved this study in particular. Continued development of the methods might provide a way to decrease the effort needed, and increase the accessibility.

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Chapter 3: Restoration Effects on Annual Biomass Production and Plant-Based Carbon Content in Depressional Wetlands on the Delmarva Peninsula

3.1 Abstract

Although wetland restoration has increased in recent decades, little is known about mechanisms controlling carbon accumulation in these newly created ecosystems. Of particular interest is temporal development of annual biomass production and carbon accumulation in surface soils. I compared ten restored and five natural depressional freshwater wetlands on the Delmarva Peninsula (Maryland and Delaware, USA). At each wetland, annual biomass was assessed by measuring above-ground herbaceous biomass, existing woody plant biomass, root ingrowth biomass, and woody plant leaf litter biomass. Additionally, soil samples were collected to a depth of 10 cm. Biomass and soil samples were analyzed for total carbon (C) content. Restored wetlands produced significantly higher mean herbaceous biomass (369.8 g/m²) compared to natural wetlands (99.0 g/m²). In contrast, natural wetlands on average produced more leaf litter than restored sites (444.6 and 149.9 g/m², respectively), as well as more belowground biomass. Restoration age was significantly related to surficial carbon accumulation: older restorations showed less herbaceous carbon input and more leaf litter carbon compared to younger restorations. Although plant communities in restored and natural wetlands differed, annual biomass inputs to soil were similar. Restoration age (5-30 years) did not have a significant effect on restored wetland soil carbon. These findings demonstrate that even relatively young restorations receive inputs of non-woody biomass similar to natural wetlands. More longterm monitoring post-restoration is required to determine if restored wetlands will develop

surface soil carbon stocks comparable to those of their natural counterparts, even after several decades.

3.2 Introduction

Many approaches have been used to quantify wetland restoration functional development. The most common vegetation-based practice is the assessment of plant communities and primary productivity (Schalles and Shure 1989, Palmer et al. 1997, Busbee et al. 2003, Mulhouse and Galatowitsch 2003, Martin et al. 2005, De Steven et al. 2010, Matthews and Spyreas 2010); other methods include measuring nutrient content of the vegetation and soil (Whigham et al. 2002, Güsewell et al. 2003, Jordan et al. 2003, Sharitz et al. 2003, Ehrenfeld and Toth 2008, Ray et al. 2012, Meyers et al. 2013). In recent years, however, it has become apparent that the comparison of vegetation composition and nutrient concentrations is not sufficient to draw overarching conclusions about post-restoration developmental trajectories in a newly restored wetland (Ardon et al. 2010, De Steven and Lowrance 2011, Yepsen et al. 2014). If only using the species and nutrient compositions as the sole indicators of evaluation, a young, herbaceous restored wetland does not resemble a forested natural system.

In the mid-Atlantic coastal plain, particularly on the Delmarva Peninsula of Maryland and Delaware, there are many freshwater wetland systems; farther inland, these are often in the form of depressional basins (Mitsch and Gosselink 2007, Dahl 2011). Often, depressional wetland restoration occurs on abandoned agricultural fields, with the goal of the restorations mimicking local natural systems. In the Mid-Atlantic region of the U.S., natural wetlands are often forested, with high levels of organic soil built up and large amounts of woody biomass (Fenstermacher 2012, McFarland et al. In Review), while the

restorations are mostly dominated by herbaceous vegetation. In order to mimic natural systems, restored wetlands need to have time to establish before comparisons can be made, and that may take decades. Natural and restored sites often don't look like each other; however, simply because a restored wetland does not look like a natural wetland does not mean that it is not providing comparable ecosystem services.

Recently, studies have quantified components of nutrient cycling in the restoration process, even comparing them to natural wetlands. Some studies focus on the ecosystem services provided by newly restored or created systems, such as the removal of nitrogen and other nutrients (Chow et al. 2012, Moore and Hunt 2012, Sims et al. 2012, Passporte et al. 2013, Tsiknia et al. 2013); others focus on post-restoration biogeochemical cycling (Inglett and Inglett 2013); while others still focus on the introduction of organic matter and the subsequent effects on nutrient cycling (Sutton-Grier et al. 2009, Chow et al. 2012). Using nutrient-based ecosystem services assessment as a measurement of restoration functions would assist wetland managers in making clear comparisons between established, natural systems and the younger restored wetlands. Achieving many ecosystem functions similar to those of natural systems may be achievable prior to a century of establishment. Not only may restored sites be delivering ecosystem services comparable to natural sites, but restored wetlands may provide services that the natural systems do not.

One of the newer approaches to assessing wetland ecosystem services is to assess their carbon sequestration capabilities. Many studies report that wetlands are a net carbon sink, meaning they play an important role in the storage and sequestration in the global carbon cycle (Liu et al. 2014, Lunstrum and Chen 2014). Some researchers debate this point,

however, pointing to the production of greenhouse gases, such as methane, that may negate a wetland's net carbon storage (Shvidenko et al. 2000, Lal 2004). One researcher has spent over a decade documenting the variety of ways that soil carbon can affect the global carbon budget by investigating different ecosystems (Lal 2002, Lal 2011), as well as different carbon inputs and levels of soil dynamics such as erosion and direct sequestration (Lal 2003, Lal 2005). Recent studies have also shown that wetlands are net carbon sinks, as well as net ameliorators of greenhouse gas production, even allowing for methane and nitrous oxide emissions (Mitsch et al. 2013, Bridgham et al. 2014). These findings have provided a foundation in carbon developmental dynamics spanning multiple ecosystems and urbanization scales; the findings of post-cultivation carbon development are particularly relevant to wetlands restored on former agricultural fields and their subsequent carbon-based ecosystem functions.

Carbon accumulation has also been studied previously in numerous wetland types across different levels of wetland restoration. Recent studies have shown that restored wetlands provide small but distinct capability to sequester carbon, particularly atmospheric CO₂ (Burden et al. 2013), increasing the importance of this particular ecosystem service. Common techniques for measuring where this carbon is stored include primarily looking at soil to depths of up to 1 meter, combined with carbon stock assessments of the potential sources of carbon and organic matter input, such as the above-ground herbaceous biomass, leaf litter, and existing woody stems (Schoengart et al. 2011, Fernanda Adame et al. 2013). As the global need to better understand an ecosystem's ability to sequester carbon grows, so does the breadth of the body of literature—studies on carbon accumulation and potential storage have been done in wetland ecosystems across the globe, but rarely in the US (Asia:

Flint and Richards 1991; Brazil: Schoengart et al. 2011; Canada: Murphy et al. 2010; England: Burden et al. 2013; Mexican Caribbean: Fernanda Adame et al. 2013). Even with all of this research, however, little work has been done on the comparison not only between restored and natural systems, but again the intra-wetland variations that are potentially responsible (such as hydrologic gradients).

Above-ground biomass is another common metric amongst restoration efforts, though only a few studies look at below ground productivity (Symbula and Day 1988, Jones et al. 1996, Rodgers et al. 2004, Bickford et al. 2012, Luan and Cao 2012). Looking at both the above and below ground biomass in tandem provides a more complete look at the productivity of a wetland; this can be a strong indicator of both ecosystem health and community trajectory (Edwards and Mills 2005, Darby and Turner 2008, Murphy et al. 2010, Eid et al. 2012). This productivity also directly compares to the capability of these wetlands to store and convert carbon, based on the relative annual and perennial inputs, as well as different communities and water quality (Tong et al. 2011). It is important to have a multi-faceted approach to assessing restorations, particularly when assessing ecosystem functions; however, few studies are able to successfully integrate more than one or two measurements. By measuring all of the above vegetation characteristics within wetlands, a more comprehensive picture of the functionality of the restoration becomes clear. Previous research by the authors, incorporating plant composition, biomass, and nutrient concentration dynamics in restored and natural wetlands, has shown that just measuring one of these characteristics at a time is less desirable (McFarland et al. In Review).

Restored depressional wetlands have been shown to have differing levels of productivity than their local natural counterparts—restored wetlands will produce high

amounts of herbaceous biomass, while natural wetlands have established woody communities (DeSteven et al. 2007, Matthews and Spyreas 2010, McFarland et al. In Review). What is less understood is the belowground biomass production capabilities of restored systems as compared to natural systems. Some research has been done investigating root density in a chronosequence of wetland restorations (Rodgers et al. 2004), but this was limited to white cedar wetlands, and could be a result limited to the individual study. Another relatively understudied wetland effect is the correlation of within-wetland hydrologic gradients and their corresponding biomass productions—that is, how is a restored wetland's ability to produce similar amounts of biomass in a seasonally ponded wetland area correlated to a similar area in a natural system (emergent biomass production in restored wetlands as compared to emergent biomass production in natural wetlands, e.g.). Hydrological effects on biomass production have been studied in the past (Cook and Hauer 2007), but not as thoroughly when considering the comparison of restored and natural wetland systems.

The Conservation Effects Assessment Project (CEAP) was created by the U.S. Department of Agriculture (USDA) to assess the effects and effectiveness of conservation practices. The wetland component of CEAP currently involves monitoring studies in seven of their eleven regions across the nation, including the Coastal Plain in the Mid-Atlantic region (MIAR) along the Atlantic Gulf Coast Plain. Natural wetland systems are used as local references for restored wetlands in each region as a benchmark for development (Brinson and Eckles 2011). The MIAR research group in the Mid-Atlantic has conducted multiple surveys of restored depressional wetlands since 2009, including hydrology (Ator et al. 2013; Denver et al. 2014), soils (Fenstermacher 2012, Ator et al. 2014), amphibians,

and vegetation (Yepsen et al. 2014). Assessment and evaluation of restorations in the MIAR surveys has been based on comparisons of restored wetlands and local natural wetlands, which have for many decades had no anthropogenic manipulation into a non-forested state.

The objective of my study was to compare A) total annual biomass production and B) plant-based carbon content between wetland types across a hydrologic gradient, as part of the collective effort of the Mid-Atlantic region's Conservation Effects Assessment Project effort (MIAR CEAP-Wetlands). I hypothesized that: herbaceous aboveground biomass would be greater in restored wetlands (confirming previous findings); tree biomass, including both fallen leaf litter and existing tree trunks, would be greater in natural wetlands (confirming and extrapolating on previous findings, McFarland et al. In Review); root biomass would be higher in restored ecosystems. I also hypothesized that transition zones would have the highest overall plant biomass, followed by the upland zones, and then emergent zones. Finally, I hypothesized that overall annual plant-based carbon input would be highest in natural sites, but older restorations would have plant-based carbon contents similar to natural systems.

3.3 Methods

3.3.1 Study Sites

The study sites and research plots used were the same as the sites used in chapter 2 (section 2.3.1); for maps and site divisions, please refer to figures 2.1 and 2.2 from that chapter (section 2.3.5)

A total of 15 depressional wetlands were selected for study on the Delmarva Peninsula of Maryland and Delaware. The 15 sites divided into ten restorations on farmlands, and five sites in natural forested basins. Restored wetlands ranged in age between 5 and 31 years. Wetlands were divided into hydrologic zones (emergent, transition, and upland, or zones 1, 2, and 3) to better facilitate functionality. In each sampling section, a 100-m² circular plot (radius = 5.642m) was set up in three transects in each hydrologic zone, creating 3 plots per zone, 9 plots per wetland, and 135 total research plots (90 restored and 45 natural).

3.3.2 Above-ground Biomass

Above-ground biomass was sampled for both herbaceous and tree-based peak biomass. In August of 2013, 0.25-m² herbaceous biomass plots were harvested between 0.5 and 1.5 meters away from the installed root bags (two samples total) (Figure 3.1). Vegetation was cut at the soil surface and biomass was weighed in the field with a portable scale. A composited subsample was also weighed in the field and returned to the laboratory where the samples were dried for a minimum of 48 hours at 60°C in a Grieve oven (Model SC 350 forced air drying oven). The moisture content of the subsamples was used to calculate biomass of the samples that were weighed in the field.

Tree biomass was estimated using two methodologies: estimation of diameter at breast height (DBH) for standing woody biomass, and collection of leaf litter biomass. Trees, defined as single stems taller than 1 m and DBH > 2.5 cm, were sampled for purposes of estimating standing biomass in 100 m² circular plots (diameter of 5.462 m). DBH was estimated for each tree present in the plot in cover classes designated by Peet et al. 1998 (Table 3.1). Tree biomass in each 100 m² plot was calculated from the DBH measurements using Jenkins et al. (2004) where Biomass (bm) = $\text{Exp}(\beta_0 + \beta_1 \ln DBH)$, then converted to g/m^2 for comparison across biomass types.

Leaf litter biomass (annual leaf deposition by trees and shrubs only) was estimated in November of 2013 by collecting and compositing two to six 0.25m^2 samples per research plot, depending on percentage of leaf fall cover (Figure 3.1). Leaf fall in inundated plots (plots with >50% water cover) was only collected from dry areas of research plots to avoid premature leaf decomposition. Samples were returned to the laboratory and dried for a minimum of 48 hours at 34°C in an environmental chamber with 12% humidity. Standing woody biomass is reported as g/m^2 for purposes of comparing it with the biomass of herbaceous species.

3.3.3 Below-ground Biomass

In March of 2013, two 5-cm by 30-cm cylindrical Superfine Peat root ingrowth cores were installed at each plot in each of the 15 wetlands (Figure 3.1). Methodology was adapted from Bickford et al. 2012. Root cores were left in ground for 8 months (March—November). In November, root cores were extracted and brought back to the lab, where they were stored at 4°C before processing began in January. Cores were then washed through a sieve to remove peat. Roots were categorized into fine, coarse, and all others in each of the different depths of the root core. Collected roots were then dried for a minimum of 48 hours at 40°C. Biomass values are presented in g/m² for better comparison to the above-ground biomass values. Due to the minimal amount of root matter obtained, there was not enough material present to perform nutrient analyses.

3.3.4 Soil Samples

Concurrently with herbaceous biomass sampling, two 5-cm by 10-cm cylindrical soil cores were taken randomly within each herbaceous plot. Soil samples were composited and returned to the lab, where they were dried at 40°C for a minimum of seven days.

Samples were then ground using a Wiley Mill, and then were analyzed for organic matter content by heating the sample 16 hours at 400C in a muffle furnace (designated as "Loss on Ignition", or "LOI" for the remainder of the manuscript).

3.3.5 Carbon

Plant-based carbon content, as defined by percent carbon concentration multiplied by each biomass value, were calculated using percent carbon content, determined with a CHN elemental analyzer. Percent carbon contents were then applied to biomass amounts for herbaceous and leaf litter biomasses to determine their carbon content. Soil samples, standardized to g/m² for purposes of direct comparison to plant-based values, were also analyzed for percent carbon content with a CHN elemental analyzer. A standard carbon content was applied to the calculated biomass to obtain carbon stocks for the standing woody biomasses, acquired from Thomas and Martin 2012; these values were not directly calculated through elemental analysis.

3.3.6 Statistical Analysis

Univariate biomass data were analyzed by split-plot analysis of variance (JMP Pro 11, SAS Institute Inc., Cary, NC). There were 15 wetlands sampled (10 restored and 5 natural). Hydrologic zone was nested in wetland type, and there were 3 hydrologic zones per wetland, with three replicates per zone; total samples collected was n = 135. Means were compared between hydrologic zones with Tukey's Honest Significant Difference.

<u>3.3.7 Tables</u>

Table 3.1: Cover class and Diameter at Breast Height (DBH) methods for vegetation survey (Peet et al. 1998).

Peet Method:	Tree Diameter at Breast		
DBH Class	Height (DBH)		
A	<1 cm		
В	1-2.5 cm		
C	2.5-5 cm		
D	5-10 cm		
Е	10-15 cm		
F	15-20 cm		
G	20-25 cm		
Н	25-30 cm		
I	30-35 cm		
J	35-40 cm		
Measure	>40 cm		

3.3.8 Figures

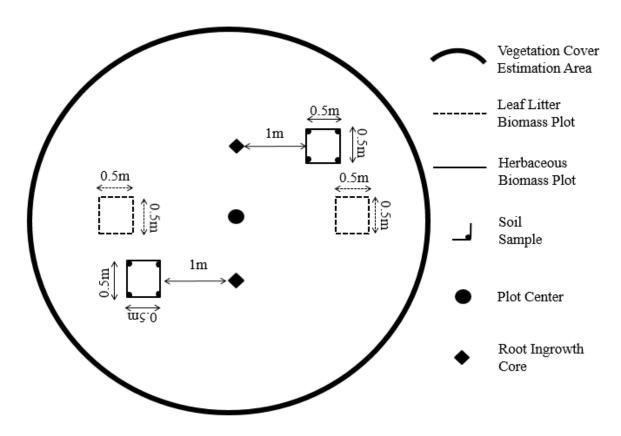


Figure 3.1: Plot layout. Thick outline represents vegetation cover estimate area; diamonds represent root bags; full square represents herbaceous biomass plot; dots in corners of full squares represent soil samples; hashed squares represent random leaf litter collections (two are shown, but up to six were collected).

3.4 Results

3.4.1 Biomass

Restored wetlands had significantly higher annual herbaceous biomass across all hydrologic zones than natural wetlands; neither restored nor natural wetlands showed any zonation trends across the different hydrologic zones (Figure 3.2A, Table 3.2). Natural wetlands contained higher standing woody biomass (Figure 3.2B, Table 3.2) and had greater annual tree leaf litter production (Figure 3.2C, Table 3.2) than restored systems. Trends across hydrologic zones were only present in natural systems in tree biomass. Both standing woody biomass and annual tree leaf litter showed statistically lower biomass in

the emergent zones, and woody biomass also had the highest biomass production in transition zones (Figure 3.2B,C). Annual root growth was not significantly different between restored and natural wetlands, though there was a significant effect of hydrology in the natural wetlands, with the most roots produced in the upland zones (Figure 3.2D, Table 3.2).

3.4.2 Carbon

There was significantly higher organic matter present in the top 10 cm of soil in natural compared to restored systems (Figure 3.3, Table 3.2). Within the natural systems, there was also a distinct trend of increased organic matter through hydrologic zones, with the highest amount in the emergent (ponded) areas and the lowest content in the upland (non-wetland) areas (Figure 3).

Carbon contents differed among all above-ground biomass inputs, as well as carbon stocks within the first 10 centimeters of soil (Figure 3.4). Overall, natural and restored systems had comparable amounts of annually-deposited plant-based carbon; restored systems had more carbon deposited through herbaceous biomass, while natural systems created more tree-based leaf litter than restored systems (Table 3.3). Natural systems also had higher carbon stocks in surface soil (to 10 cm), and natural sites showed a high level of carbon stored in standing woody biomass as well (Table 3.3). No carbon stock varied significantly between the three hydrologic zones in any noticeably distinct way from the overall wetland variability (Figure 3.4).

There was no significant effect of restoration age on annual carbon input (herbaceous and tree-based leaf litter) in the restored wetlands (Figure 3.5, Table 3.3). When wetland type was compared directly, natural sites were not significantly different

from restored sites (Table 3). Different sources contributed accordingly to the overall variability in total carbon content (Figure 3.6). Soil carbon content, to a depth of 10 cm, remained relatively constant with restoration age. Herbaceous carbon input decrease significantly with restoration age. Restorations contributed significantly more leaf litter input with age, and there was a definitive increase in tree presence with restoration age (Figure 3.7, Table 3.3).

<u>3.4.3 Tables</u>

Table 3.2: ANOVA results (F ratios) for biomass and loss on ignition between wetland type (natural vs restored) and across the hydrologic gradient (emergent, transition, upland zones). Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = ***; p < 0.001 = ***; p < 0.0001 = ****.

	Wetland	Hydrologic	Zone x	Туре
	Туре	Zone	Natural	Restored
df	1, 13	2, 26	2, 14	2, 29
Herbaceous Biomass	32.86****	0.053	0.079	0.069
Standing Tree Biomass	49.91****	2.46	3.53*	2.27
Leaf Litter Biomass	84.65****	3.46*	5.13*	2.43
Root Ingrowth	4.89**	1.86	15.46****	1.13
Loss on Ignition	1.56	98.21****	3.96*	0.62

Table 3.3: ANOVA results (F ratios) for wetland type (natural vs restored) and regression F-values and r^2 values across restoration age (restored wetlands only, 5-31 years). Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = **; p < 0.001 = ***; p < 0.0001 = ****.

	Wetland Type	Age (Regressi	on)
	(ANOVA)	F value	\mathbf{r}^2
df	1, 13	2, 14	
Total Carbon	124.13****	2.90	0.032
Soil	387.56****	1.42	0.016
Herbaceous	29.14***	9.89***	0.101
Wood	45.91****	15.64***	0.151
Leaf Litter	105.55****	10.10**	0.103

3.4.4 Figures

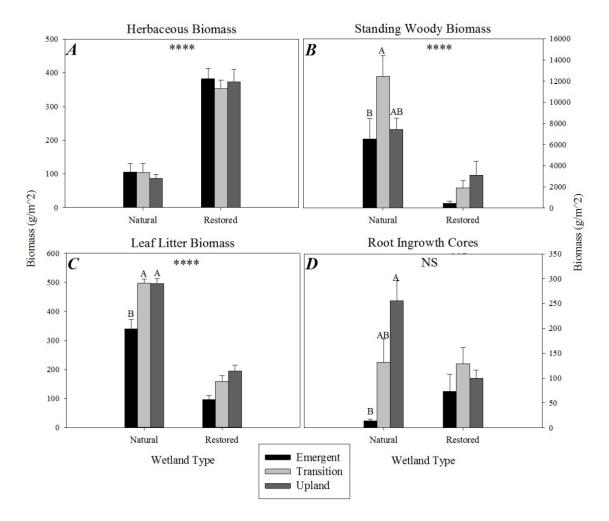


Figure 3.2: Mean biomass measurements (g/m²) between wetland types and across hydrologic zones: A) Herbaceous biomass; B) Existing woody biomass; C) Tree and Shrub eaf litter biomass; D) Root ingrowth core biomass. Error bars represent mean \pm 1 S.E. Letters represent significant differences between hydrologic zones within wetland type; asterisks represent differences between wetland types ignoring hydrologic zones (at p < 0.05); NS = no significant differences between natural and restored wetlands; bars without letters indicate no significant differences between hydrologic zones. Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = **; p < 0.001 = ***; p < 0.001 = ****.

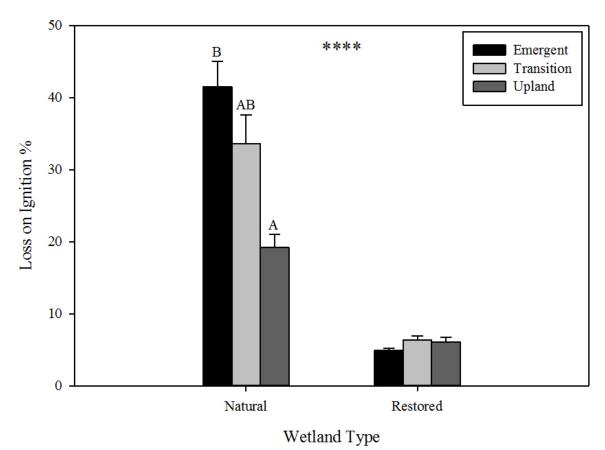


Figure 3.3: Variation in soil organic matter content (based on loss on ignition measurements) between wetland types and across hydrologic zones. Error bars represent mean \pm 1 S.E. Letters represent significant differences between hydrologic zones within wetland type; bars without letters indicate no significant differences between hydrologic zones. Restored sites differed significantly from natural sites. Significance levels are as marked as follows: p < 0.05 = *; p < 0.01 = ***; p < 0.001 = ****; p < 0.0001 = *****.

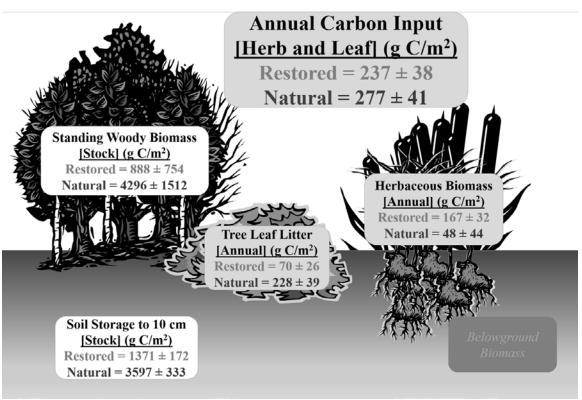


Figure 3.4: Carbon contents of different wetland ecosystem components. Two above-ground biomass types (herbaceous cover, tree leaf litter) combine to make the total annual carbon input; these boxes are denoted in light gray. Two standing stocks of carbon (standing woody biomass and soil carbon storage to a depth of 10 cm) for references to existing carbon contents in wetlands; these boxes are denoted in white. A reference to belowground biomass (root ingrowth) is also included, as it contributes a significant input of carbon to wetland soils; however, the root carbon content at these sites was not analyzed. Values are means \pm 1 standard error.



Figure 3.5: Annual plant-based carbon input for different restoration ages (herbaceous carbon input and tree leaf litter carbon input). Bars to the left of the dotted line represent different total carbon stock values wetland for wetlands of specific ages; bars to the right of the dotted line represent total carbon stock values for all wetlands within each wetland type (Nat = Natural, Rest = Restored), and are provided for total wetland type reference. Error bars are +1 S.E. of the mean.

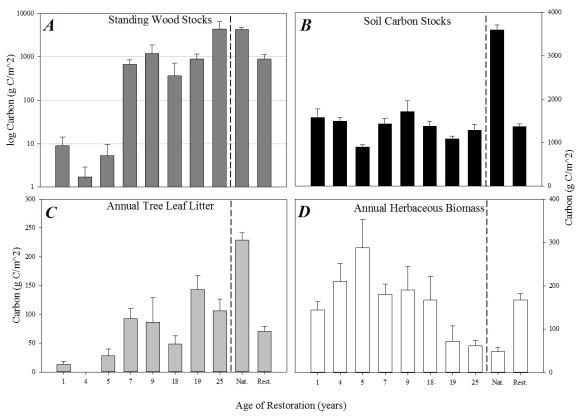


Figure 3.6: Carbon storage for different restoration ages divided by source. A) Log of carbon content for standing woody trunks; B) Soil carbon stocks; C) Annual tree leaf litter carbon input; D) Annual herbaceous biomass carbon input. Figures A and B represent existing, relatively constant stocks of carbon; figures C and D represent annual biomass depositions. Figures A and C both represent tree-based carbon contents. Bars to the left of the dotted line represent different total carbon stock values wetland for wetlands of specific ages; bars to the right of the dotted line represent total carbon stock values for all wetlands within each wetland type (Nat = Natural, Rest = Restored) , and are provided for stock reference.

3.5 Discussion

3.5.1 Biomass

When comparing restored with natural wetland types, the strongest difference is the type of biomass each wetland type produces. The natural depressional wetlands studied here are well established, with distinct borders of woods surrounding the open wetlands. This means that natural systems' annual above-ground biomass production is dedicated to these trees—annually, leaf litter creates a layer of decomposable material, while the trees themselves serve as standing carbon storage. The restored systems, the younger ones in

particular, have not had the time to develop any sort of woody presence, and therefore dedicate themselves to producing a high volume of herbaceous biomass. This supports earlier findings of this study (McFarland et al. In Review), and corroborates findings from other studies (Sharitz 2003, Kirkman et al. 2012). Restored systems require many years of biomass development post restoration in the successional cycle to even be able to produce trees without direct plantings of trees and shrubs around their borders (Sharitz 2003). Even though some of the younger CEAP restorations had had some trees planted around the wetland border (in the transition and upland areas), they still do not have the truly developed woody communities that mimic natural systems [see chapter 2 Discussion, section 2.5.1].

One interesting development this project created that increased its specificity from the original study in 2011 was the addition of a leaf litter analysis. The amount of standing woody biomass has never been comparable to the amount of annual herbaceous production of these systems, simply due to the mechanism of annual turnover (Figure 3.2). However, these natural systems are producing high volumes of leaf litter annually, which is clear by the deciduous tree species composition. When compared directly, the amounts of herbaceous biomass and amounts of leaf litter are inversely related; natural systems have low herbaceous input and high leaf litter input, while restored systems have high herbaceous input and low leaf litter input. The volumes of each biomass are closely proportional, with each wetland type producing a high biomass of between 450 and 550 g/m², and a low input of between 100 and 200 550 g/m² (Figure 3.2). These data corroborate previous findings in Carolina Bays on the Atlantic Gulf Coast (Megonigal et al. 1997: 200-800 g/m² leaf litter, Whigham et al. 2002: 150-400 g/m² herbaceous biomass,

Busbee et al. 2003: 350-550 g/m² leaf litter), but with even more specificity due to the increase in sample size and addition of the effect of restoration.

Annual root ingrowth of these systems was not significantly different between restored and natural systems (Figure 3.2). While the origin of the roots (plant type, e.g.) was not able to be determined, it can be assumed that different plants were producing the differing amounts of root growth in each system; however, these results indicate that even in differing vegetation communities, the overall effect is that plants are producing roots annually at similar rates between the two wetland types. This result is confounded by the significant effect of hydrologic zone in the natural wetlands, however; there was low root production in the emergent areas of natural wetlands, while there was concurrently very high root production in the local upland zones. This does not directly reflect the known high productivity of these systems (Odum 1988, Bickford et al. 2012), and begs more research into the differences in below-ground productivity capabilities of depressional wetlands.

Tidal systems studied thus far in the Mid-Atlantic region have found high annual root ingrowth, some even producing root masses comparable to the above-ground herbaceous biomass sampled (Kirwan and Guntenspergen 2012). Many of these previous root studies were based in tidal systems, however, and as these wetlands are non-tidal inland systems it may have had a significant effect on both the community driven root production as well as the relative need for such dense root mats to be created. Tidal systems create dense root mats, while inland wetlands do not (Darby and Turner 2008, Bickford et al. 2012). The only way to be truly sure about the amount of belowground biomass and potential carbon sources is to also perform a soil coring technique to quantify how much

root mass exists prior to the year's ingrowth (Neill 1992, Symbula and Day 1998). For a better comparison of root production in these systems, a more complete analysis should be performed, which would include the analysis of existing root material as well.

3.5.2 Carbon

The mechanisms of carbon storage are less understood in restored wetlands. Although the goal of restoration is "a return of an ecosystem to its conditions prior to disturbance" (NRC 1992), this functionality depends mainly on local parameters and temporal fluctuation (Burden et al. 2013, Lloyd et al. 2013, Lunstrum and Chen 2014). Studies thus far have been limited to a few wetlands within one ecosystem type. In the hopes of creating a very detailed wetland profile, in order for the data from this study to be more widely applicable to other geographic regions, within-wetland sampling was increased for a more comprehensive study. Some research has been done recently to determine the restorability of carbon storage in restored grass-based ecosystems (Lawrence and Zedler 2013), but begs further research into more complex systems as compared to local reference. Furthermore, previous studies have practically ignored hydrologic effect within depressional wetlands (moving from emergent to transition, then out of the wetland to local upland areas), though hydrology directly influences the ability of wetland ecosystem functionality (Jordan et al. 2003, Ardon et al. 2010, Chague-Goff et al. 2010, McLaughlin and Cohen 2013).

Natural wetlands in this study have distinctly higher carbon stores in their soils than restored systems, even if only measured to a depth of 10 cm. These high carbon stocks were also sampled to 50 cm (C. Palardy and M. Rabenhorst, pers. comm..). When it comes to the restorations, these young systems have not had enough time to create carbon storage

in soil. The main source of SOM in natural systems is potentially coming from breakdown of existing woody biomass (which are not deposited regularly), which these restorations have not yet developed. Consequently, they have not had the years of high annual leaf input the natural systems have had, meaning that most of their input is coming from annual herbaceous deposition. Other studies have focused more on the herbaceous biomass and downed woody stems for sources of annual carbon input (Fernanda Adame et al. 2013), but fewer have focused on the benefits of annual leaf litter inputs.

Another factor these restorations may be experiencing is an elevation, or hydrologic, limit for the accumulation of organic material. Wetlands will not continue to build up organic matter if the soils are at the pond-depth limit for the accumulation of organic material, as any new material deposited annually on the surface will oxidize. This is the elevation above which soils are insufficiently saturated by ponding, preventing anaerobic respiration by decomposers. Roots will add to organic material but there is so much mineral material within the restored soils that they may never reach the carbon storage level of natural sites. If this is the explanation, more care needs to be taken in the restoration process to mimic the natural soils in order to facilitate ability to develop carbon stocks.

When considering the carbon-related benefits natural wetlands are receiving from different biomass sources, it is important to consider how these different biomasses are broken down and contribute to the soil organic matter. One particular study on this topic looked at a series of Detrital Input and Removal Treatments (DIRT), and which involved partitioning different litter inputs (adding or removing leaf litter and decomposing wood) in forests and subsequently analyzing the effects on soil organic matter and microbial

communities (Lajtha et al. 2005). This particular study identified that added woody biomass, in the form of wood or leaf litter, meant that there was a decreased loss of dissolved carbon from the soils. In a subsequent study, the researchers found that after a period of 50 years of litter input manipulation (addition versus removal of litter inputs), there was a distinct increase in bulk density of soils (Lajtha et al. 2014). While these studies were performed in forests and prairies, these natural forested wetlands might perform similarly if subjected to the same experiment types, particularly in the upland and transition edges. This means that, in these young restorations (only aged up to 30 years), they have not had the time to develop significant leaf litter and decomposing wood inputs to the soil, even in the very surface of the soil. In time, perhaps, these recently developed tree borders will begin providing adequate amounts of litter detritus for improving the surficial bulk density of the soil; however, to be sure, it would need to be closely monitored.

3.6 Conclusions

When assessing functionality of these wetland restorations, it is important to consider multiple aspects of their characteristics. Often, visual appearance is used as a measure of vegetation functionality, which leaves these restorations seemingly lacking compared to the established natural systems. By incorporating multiple analyses, including above-ground estimates and combining productivity estimates with carbon sequestration potentials, a better understanding of the relationships between the natural reference system and the early successional restoration has been created. Although the natural and restored wetlands differ tremendously in their vegetation structure and thus their appearance (one is forested, the other marsh-like), surface carbon inputs to soils are similar, indicating similarity of function.

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Chapter 4: General Conclusions

4.1 Post-Restoration Vegetation Monitoring

Measuring secondary vegetation characteristics, as well as conducting a conventional above-ground vegetation survey, is an approach to measure post-restoration development as a function of important features of the plant community. These characteristics, such as biomass production, storage of carbon, and patterns of nutrient availability, are all metrics that are important components of ecosystem functions (Ehrenfeld and Toth 2008, Zhang et al. 2011, Klemas 2013, Raab 2014). A vegetation community survey is the approach most often used in post-restoration development assessment; however, recent studies that have been done thus far on restored wetlands indicate that temporal changes in vegetation following restoration are often not predictable (Whigham et al. 2002, DeSteven et al. 2010). This indicates that reference system based assessment methods (i.e., similarity between plant communities in a restored wetland compared to an appropriate regional reference type) may be limited for a variety of reasons, even though other functional elements of the restoration are deemed to be efficacious (Matthews and Spyreas 2010, De Steven and Lowrance 2011). By measuring these secondary vegetation characteristics in concurrence with an above ground community survey, certain temporal variability can be eliminated to develop a clearer picture of the vegetation's developmental status of the restoration. (Meyer et al. 2013, Zilverberg et al. 2014)

In order to fully utilize one characteristic to get as thorough an assessment as possible, I used multiple vegetation metrics to best understand the differences and dynamics between restored and natural depressional wetlands in the Delmarva Peninsula of Maryland and

Delaware, as well as assessing the within-wetland nested effect of hydrologic gradient. Chapter 2 compared above- and below-ground composition between wetland types and across the hydrologic gradient; the above-ground component focused on a conventional emergent standing vegetation survey, and the below-ground component was comprised of a greenhouse-based seed bank analysis. Chapter 3 focused on assessing differences in biomass types and quantities between wetland types and across the hydrologic gradient; this chapter also looked at carbon inputs in each wetland type from the different above-ground biomasses present in each wetland.

4.2 Major Findings

4.2.1 Chapter 2: Community Composition

The most relevant finding from chapter 2 was that, when comparing restored to natural wetlands seed banks show higher similarity in composition than vegetation communities, particularly when incorporating the effect of within-wetland hydrologic gradient. This shows that in order to get more comprehensive comparisons of full-wetland vegetation communities, adding a seed bank analysis for restoration assessment is essential. However, I would emphasize that this seed bank analysis would be added not as an alternative to a traditional above-ground vegetation survey, and as an additional technique for a more complete understanding of the compositional dynamics within the full wetland community. While the vegetation communities are easy to assess in the moment, the addition of a seed bank provides a better source of comparison between two disparate communities, and can provide insight into other aspects of the wetland's future development as well, such as the likely emerging community and recovery post-disturbance in the two wetland types. Seed banks also integrate vegetation composition

over multiple years (at least for species with persistent seeds), while vegetation surveys are only snapshots of the community at one point in time. Analysis of seed banks will also help predict future vegetation dynamics and resilience to disturbance; thus, seed banks perform as indicators of biodiversity maintenance related ecosystem functions.

4.2.2 Chapter 3: Biomass and Carbon

Restored and natural wetlands showed clear differences in biomass, both in type produced and quantity. Natural systems have more tree biomass (leaf litter, standing wood), while restored systems have more herbaceous biomass. There was only significant root growth in natural wetlands (in the transition and upland zones), and it appears that restored systems not able to produce significant annual root mass. Often, forested wetlands have higher productivity than adjacent upland forests because there is a more permanent source of water and nutrients.

In this study, natural wetlands had significantly more plant-based carbon contents overall, as well as higher carbon stored in the top 10 cm of soil. Restored systems appear to have not had enough time to create carbon storage in soil, as it appears that deposition mainly coming from leaf litter. When looking at the effect of restoration age on carbon accumulation, these trends become clearer. Soil carbon (in the top 10 cm) remains constant with restoration age, and does not get close to the amount of carbon stored in the surface soil of natural wetlands. Biomass carbon value changes with restoration age approach natural values; herbaceous carbon decreases significantly with age, and there is significantly more leaf litter input. There is also a definitive increase in tree presence with restoration age. These results indicate that natural systems are still very different from young restorations, and suggest that restored sites have not yet developed climax vegetation

communities nor carbon storage similar to local natural systems; likely, this is due to not having had enough time to do so yet. In the future, using natural systems as reference should continue be paired with measure of functionality, such as carbon storage and accumulation.

4.3 Implications for Post-Restoration Monitoring Practices

The development of viable plant communities is an essential element of any wetland restoration effort; however, it has not always been clear which metrics should be used to evaluate the functional development and guide future restoration efforts. One approach is to base the assessment on the restoration of plant communities on their similarity to plant communities in natural reference wetlands (e.g., Martin et al. 2005). This approach is based on the notion that species diversity can be used as a metric of ecosystem status as well (Palmer et al. 1997). A second approach is to measure the post-restoration development as a function of other important features of the plant community; such as biomass production, storage of carbon, and patterns of nutrient availability - all metrics that are important components of ecosystems functions (Ehrenfeld and Toth 2008). The first approach is one that is most often used but the relatively small number of studies that have been done thus far on restored wetlands indicate that temporal changes in vegetation following restoration are often not predictable, and the benchmarks for restoration (i.e., similarity between plant communities in a restored wetland compared to an appropriate regional reference type) may be limited for a variety of reasons, even though other functional elements of the restoration are deemed to be progressing along an optimal trajectory (Matthews and Spyreas 2010, De Steven et al. 2010).

I suggest implementing a third, combination approach—development of an ecosystem is not measured by one metric alone, but by the functionality of different metrics all in tandem. This approach is not a new idea (Simenstad et al. 2006, Moreno-Mateos et al. 2012); however, it is often ignored for the sake of saving time or labor. The third approach combines the community comparison approach with the plant features approach: a vegetation survey is conducted, to better understand the community present, and other metrics are measured as well (such as the annual biomass, carbon input, seed bank presence, microbial communities, water level, etc.) to get as close to a complete picture of the ecosystem at that moment in time as possible. Only then can the functional developmental trajectory of the ecosystem be assessed, rather than comparing pieces of restorations to pieces of natural systems, a technique that has been proven to be ineffectual and outdated (Simenstad and Thom 1996, Zedler and Callaway 1999, McFarland et al. In Review).

In these young restored depressional wetlands, the initial goal of the restoration, though not necessarily stated outright, was for restored systems to provide similar levels of key ecosystem functions to their natural counterparts (Lang et al. 2009, Yepsen et al. 2014). In the studies performed thus far by the MIAR-CEAP researchers, results showed that young restorations, while identifiable as wetlands, were not performing identical ecosystems the local natural systems; those functions that the restored systems shared with the natural systems were not being performed at the same level or rate (Ator et al. 2013, Denver et al. 2014, Yepsen et al. 2014). Metthea Yepsen, in her thesis based on an earlier vegetation community study of this project, stated a few important questions set forth to answer with this project: "What are we losing when a restoration doesn't restore a site to a natural state?

Why aren't restored sites being returned to a natural state? Is it even possible to restore natural conditions?" (Yepsen 2012). This project, in its attempt to clarify the vegetation differences and similarities between restored and natural depressional wetlands, made significant headway in understanding the questions posed by Yepsen. Through this project, I have identified that while restored wetlands (after 5-30 years of restoration) do not resemble natural systems superficially (i.e., in their immediately visible above-ground vegetation communities), they will continue to resemble more natural systems as they continue to age and develop. Time, in the end, is the most important component to ecosystem restoration (Mitsch and Wilson 1996).

For restoration managers and other professionals, this added element of time can be daunting, as it means that the results they are aiming for may not be seen for many decades. While there are many things to do in order to speed up the natural restoration process, such as planting of desired species and organic matter amendments to replace lost soil carbon, these are "Band-Aid" treatments that will only cure the problem superficially. Time and monitoring are the only ways to ensure that the goal of mimicking a natural system is reached if the restorations are left to their own devices; anthropogenic influence, such as better understanding of how to design and build wetlands, can help ensure this goal as well.

Functionality is the basis of wetland ecosystem services, and should as such be the basis for how their post-restoration development should be assessed. The functional goals of a restoration should be determined by those who restore the system in the first place—not all wetlands are the same, and the reasons for their restoration will not necessarily be the same as a result. Some wetlands are created as wildlife habitat (e.g. for ducks, frogs, etc.), while others are created to mitigate nutrient flow. In each of these cases, the managers

and monitors of the wetland have a choice to make—how best can the development of this burgeoning ecosystem be assessed? As a natural wetland is an established, functional ecosystem that provides desirable services managers want their wetlands to eventually mimic, the use of a reference system as a benchmark for development is often a paradigm for assessing post-restoration wetland development.

However, who is to say that a perfect mimic of a natural system is the optimal end goal? Mitsch and Gosselink (2007), in an elaboration on earlier research, have emphasized the necessity of restoration for function over form; there is a fine balance between allowing the system to self-design (relying on natural development to create the expected end-goals), and managing the ecosystem to create desired functionality (potentially to the point of overengineering) (NRC 1992, Mitsch and Jørgensen 2004). While the young restorations studied for this project are not identical to their natural counterparts, they are certainly continuing to develop and change. This development could be approaching the preferred goal of mimicking a natural system, or these restorations could be approaching a new steady state, performing ecosystem functions at different rates or levels than natural systems, but perhaps even performing new, beneficial services as well. If we limit ourselves to only seeing one end goal possible, then we close ourselves off to the possibility that multiple outcomes are possible from restoration of an ecosystem. Time will tell what these wetlands are capable of, and human influences can shape their future.

4.4 Conclusions

This study has shown that wetland restoration is a lengthy and dynamic process. In order to get a clear understanding of the relationship between restored and natural systems, multiple facets have to be considered, and they should be monitored over a long period of

time. While young restorations may not mimic natural systems within a decade, as time progresses they continue to develop and become more stable ecosystems. In restoration, the end goal needs to be clear, and perhaps it does not always need to be the creation of a man-made "natural" ecosystem. Perhaps it can be a new breed of ecosystem, with some aspects of natural systems and some that have not yet been discovered.

4.5 References

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Appendix 1: Species List

Species observed at each wetland type and hydrologic zone. Taxonomy and species names according to USDA Plants Data Base from February 2015. Nat = Natural; Rest = Restored. FacWET = wetland indicator status, where: OBL = obligate wetland; FACW = facultative wetland; FAC = facultative; FACU = facultative upland; UPL = upland; TBD = to be determined.

								Se	ed	Ba	nk												
		T	уре		Zone		N	atur	al	R	estore	ed	T	vpe	1 2	Zon	e	N	atur	ral	Re	stor	ed
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3		Rest	1	2	3	1	2	3	1	2	3
Acalypha rhomboidea	FACU		X		X	X					X	X		X	X	X	X				X	X	X
Acer negundo	FAC		X		X						X				<u> </u>								
Acer rubrum	FAC	X	X	X	X	X	X	X	X	X	X	X			<u> </u>								
Achillea millefolium	FACU		X			X						X			<u> </u>								
Agrostis stolonifera	FACW		X		X						X			X		X						X	
Alisma plantago-aquatica	TBD		X	X	X					X	X			X	 	X						X	
Allium vineale	FACU		X		X						X												
Ambrosia artemisiifolia	FACU		X	X	X	X				X	X	X		X	X	X	X				X	X	X
Amerlanchier canadensis	FAC	X				X			X														
Ammannia coccinea	OBL		X	X		X				X		X	X	X	X	X			X		X	X	
Anagallis arvensis	FACU													X		X	X					X	X
Andropogon elliottii	FAC		X		X						X												
Andropogon gerardii	FAC		X		X	X					X	X											
Andropogon virginicus	FAC													X		X						X	
Apocynum cannabinum	FACU		X	X	X	X				X	X	X		X		X						X	
Aralia spinosa	FAC		X			X						X											
Asclepias incarnata	OBL		X		X						X												
Asclepias syriaca	UPL		X		X	X					X	X											

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		$T_{\mathbb{C}}$	уре		Zone		N	atur	al	R	estore	ed	T	vpe	2	Zon	e	No	atur	al	Re	stor	ed
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3
Asimina triloba	FAC		X		X						X												
Asparagus officinalis	FACU		X		X	X					X	X											
Baccharis halimifolia	FAC		X		X	X					X	X											
Betula nigra	FACW		X		X						X												
Bidens aristosa	FACW		X	X	X	X				X	X	X		X	X	X	X				X	X	X
Bidens bidentoides	FACW		X	X	X					X	X			X	X						X		
Bidens bipinnata	FAC		X			X						X											
Bidens coronata	TBD		X		X	X					X	X											
Bidens frondosa	FACW		X	X	X					X	X		X			X			X				
Bidens laevis	OBL		X	X						X													
Bidens tripartita	FACW	X	X	X	X	X	X			X	X	X											
Boehmeria cylindrica	FACW		X	X	X	X				X	X	X		X	X	X					X	X	
Campsis radicans	FAC	X	X	X	X	X		X		X	X	X											
Carex albolutescens	FACU		X	X	X					X	X												
Carex longii	OBL		X	X						X													
Carex lupulina	OBL		X		X						X												
Carex lurida	OBL		X	X	X	X				X	X	X											
Carex vulpinoidea	FACW		X	X	X	X				X	X	X											
Carya glabra	FACW	X		X	X	X	X	X	X														
Carya tormentosa	TBD	X	X	X	X	X	X	X	X			X											
Cephalanthus occidentalis	OBL	X	X	X	X		X			X	X		X	X	X	X			X		X	X	
Chamaecrista fasciculata	FACU		X		X	X					X	X											
Chasmanthium laxum	FACW	X		X	X	X	X	X	X														
Cichorium intybus	FACU		X		X	X					X	X											
Cinna arundinacea	FACW		X		X	X					X	X											

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Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3
Cladium mariscus	OBL		X	X						X													
Clethra alnifolia	FACW	X	X	X	X	X	X	X	X			X	X		X		X	X		X			
Commelina communis	FAC													X	X						X		
Conyza canadensis	TBD		X	X	X	X				X	X	X											
Cornus florida	UPL	X	X			X			X			X											
Cyperus echinatus	FAC		X		X	X					X	X											
Cyperus erythrorhizos	OBL		X		X						X		X	X	X	X	X	X			X	X	X
Cyperus esculentus	FAC		X	X	X					X	X												
Cyperus pseudovegetus	FACW		X	X	X	X				X	X	X		X		X	X					X	X
Cyperus retrorsus	FACU													X		X	X					X	X
Cyperus strigosus	FACW		X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cypripedium acaule	FACU	X		X		X	X		X														
Daucus carota	UPL		X			X						X											
Desmodium paniculatum	FACU		X	X	X	X				X	X	X											
Dichanthelium acuminatum	FAC	X		X			X																
Dichanthelium Leucothrix	TBD		X		X						X		X	X		X	X			X		X	X
Dichanthelium scoparium	FACW		X			X						X											
Dichanthelium sphaerocarpon	FACU		X	X	X	X				X	X	X											
Digitaria filiformis	TBD													X	X						X		
Digitaria ischaemum	UPL		X		X	X					X	X	X	X	X	X	X	X			X	X	X
Digitaria sanguinalis	FACU		X	X	X	X				X	X	X		X	X	X	X				X	X	X
Diodia teres	FACU		X		X	X					X	X		X	X	X	X				X	X	X
Diodia virginiana	FACW		X	X	X	X				X	X	X											
Echinacea purpurea	TBD		X		X	X					X	X											
Echinochloa crus-galli	FACW		X	X	X	X				X	X	X		X	X	X	X				X	X	X

					7	⁷ ege	tati	on								Se	ed	Ba	nk				
		T_{\cdot}	уре		Zone		N	atur	al	R	estore	ed .	$T_{\mathbb{C}}$	уре	2	Zon	e	N	atur	al	Re	estor	ed
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3
Eclipta prostrata	FACW		X	X						X			X	X	X	X	X	X		X	X	X	X
Elaeagnus angustifolia	FACU		X			X						X			ļ						 		
Elaeagnus umbellata	TBD		X			X						X											
Eleocharis engelmannii	FACW		X	X						X			X	X	X	X	X	X			X	X	X
Eleocharis obtusa	OBL		X	X	X					X	X		X	X	X	X	X	X	X	X	X	X	X
Eleocharis quadrangluata	OBL		X	X						X											 		
Eleocharis tuberculosa	OBL		X		X						X												
Elymus virginicus	FAC		X		X	X					X	X			! !						 		
Epilobium coloratum	OBL		X		X						X				į								
Eragrostis hypnoides	OBL												X		! !	X			X		<u> </u>		
Erechtites hieraciifolia	TBD		X		X	X					X	X			ļ .								
Erigeron annuus	FACU		X			X						X			ļ								
Eubotrys racemosa	FACW	X		X	X		X	X							!						<u> </u>		
Euonymus americanus	FAC	X				X			X						!						 		
Eupatorium hyssopifolium	TBD													X	!		X						X
Eupatorium perfoliatum	FACW		X		X						X				!						 		
Eupatorium rotundifolium	FAC		X		X	X					X	X			į						 		
Eupatorium sessilifolium	TBD		X		X	X					X	X			ļ						 		
Euthamia caroliniana	FAC		X			X						X			ļ								
Euthamia graminifolia	FAC		X	X	X	X				X	X	X			ļ						 		
Fagus grandifolia	FACU	X	X			X			X			X											
Fimbristylis annua	FACW		X	X	X	X				X	X	X		X	X	X	X				X	X	X
Fimbristylis autumnalis	OBL		X	X	X					X	X			X		X						X	
Fraxinus nigra	FACW		X	X	X	X				X	X	X											
Fraxinus pennsylvanica	FACW		X		X	X					X	X			ļ								

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		T_{\cdot}	уре		Zone		N	atui	al	R	estore	ed .	T	уре	Ź	Zone	e	N	atur	al	Re	stor	ed
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3
Galactia regularis	TBD		X	X	X	X				X	X	X									 		
Galium tinctorium	FACW		X	X	X					X	X			X		X						X	
Geum vernum	FAC		X		X	X					X	X											
Gratiola aurea	OBL		X	X	X					X	X												
Gratiola neglecta	OBL												X	X	X	X	X		X	X	X	X	X
Gratiola virginiana	OBL		X	X						X			X	X	X	X	X			X	X	X	X
Hedera helix	TBD		X			X						X											
Hemerocallis lilioasphodelus	TBD		X	X	X					X	X										! !		
Hibiscus moscheutos	OBL		X	X	X	X				X	X	X											
Hypericum canadense	FACW		X	X	X					X	X		X	X	X	X			X		X	X	
Hypericum mutilum	FACW		X	X	X	X				X	X	X	X	X	X	X	X	X	X		X	X	X
Ilex opaca	FAC	X	X	X	X	X	X	X	X		X	X									 		
Ipomoea hederacea	FACU		X			X						X		X			X						X
Ipomoea lacunosa	FAC		X	X	X	X				X	X	X		X	X	X	X				X	X	X
Ipomoea purpurea	UPL		X		X	X					X	X											
Juglans nigra	UPL		X			X						X											
Juncus biflorus	TBD		X	X	X					X	X												
Juncus bufonius	FACW		X		X	X					X	X	X	X	X	X	X	X	X	X	X	X	X
Juncus canadensis	OBL		X	X	X	X				X	X	X									!		
Juncus effusus	FACU		X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X
Juncus marginatus	FACW		X	X	X					X	X		X	X	X	X	X	X	X		X	X	X
Juncus repens	OBL												X		X			X] 		
Juncus scirpoides	FACW		X	X	X					X	X												
Juncus secundus	FAC		X	X	X	X				X	X	X] 		
Juncus tenuis	FAC		X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X

					7	ege	tati	on								Se	ed	Ba	nk				
		$T_{\mathbb{C}}$	vpe		Zone		N	atur	al	R	estore	ed	$T_{\mathbb{C}}$	vpe	2	Zone	2	No	atur	al	Re	stor	ed
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3
Juniperus communis	OBL		X		X	X					X	X											
Juniperus virginiana	FACU		X			X						X											
Kosteletzkya virginica	FACW		X	X						X													
Kummerowia striata	FACU		X	X	X	X				X	X	X		X		X	X					X	X
Lactuca canadensis	FACU		X		X	X					X	X											
Lactuca serriola	FAC		X	X	X	X				X	X	X											
Leersia oryzoides	OBL		X	X	X	X				X	X	X	X	X	X	X	X	X			X	X	X
Lemna minor	OBL		X	X	X					X	X												
Lespedeza cuneata	FACU		X	X	X	X				X	X	X		X			X						X
Lindera benzoin	FACW		X			X						X											
Lindernia dubia var. anagallidea	OBL		X	X	X					X	X		X	X	X	X	X	X	X	X	X	X	X
Liquidambar styraciflua	FAC	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X		X		
Liriodendron tulipifera	FACU	X	X	X	X	X	X	X	X			X	X		X		X	X		X			
Lobelia inflata	FAC		X			X						X											
Lonicera japonica	FAC	X	X	X	X	X	X				X	X											
Ludwigia alternifolia	OBL		X	X	X	X				X	X	X	X	X	X	X	X		X	X	X	X	
Ludwigia palustris	OBL		X	X	X					X	X		X	XX	X	X	X	X	X	X	X	X	X
Ludwigia peploides	OBL		X	X						X													
Ludwigia polycarpa	OBL		X	X						X													
Ludwigia repens	OBL		X	X	X					X	X		X	X	X	X	X	X	X	X	X	X	X
Ludwigia sphaerocarpa	OBL												X	X	X			X			X		
Lycopodium obscurum	TBD	X			X	X		X	X														
Lycopus americanus	OBL		X	X	X					X	X			X			X						X
Lycopus virginicus	OBL		X	X	X	X				X	X	X											
Lyonia ligustrina	FACW	X				X			X														

			Seed Bank																				
		$T_{\mathbb{C}}$	уре		Zone		N	atur	al	R	estore	ed .	T	уре	1 2	Zon	e	Natural			Restor		ed
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3
Magnolia virginiana	FACW	X		X	X	X	X	X	X						 								
Maianthemum racemosum	FACU		X			X						X			 								
Malus pumila	TBD		X	X	X	X				X	X	X											
Malus sylvestris	TBD		X			X						X											
Medeola virginiana	TBD	X			X	X		X	X														
Mediago sativa	UPL		X	X		X				X		X			 								
Mentha spicata	FACW		X	X	X					X	X				<u> </u>								
Microstegium vimineum	FAC	X	X		X	X			X		X	X			! !								
Mikania scandens	FACW		X	X	X	X				X	X	X		X		X						X	
Mimulus ringens	OBL		X		X						X												
Mitchella repens	FACU	X			X	X		X	X														
Mollugo verticillata	FAC												X	X	X	X	X	X			X	X	X
Morella cerifera	FAC		X	X	X	X				X	X	X	X	X	X	X	X	X				X	X
Morus rubra	FACU		X		X	X					X	X											
Muhlenbergia asperifolia	FACW		X		X	X					X	X											
Muhlenbergia schreberi	FAC													X	X						X		
Nuttallanthus canadensis	TBD												X	X		X	X		X				X
Nyssa sylvatica	FAC	X	X	X	X	X	X	X	X	X	X	X		X	 	X						X	
Oldenlandia uniflora	FACW													X	X	X	X				X	X	X
Onoclea sensibilis	FACW		X		X	X					X	X			 								
Osmunda regalis	TBD	X			X			X							 								
Oxalis dillenii	FACU		X			X						X	X	X	X	X	X		X	X	X	X	X
Panicum amarum	FAC		X	X	X					X	X												
Panicum dichotomiflorum	FACW												X	X	X	X	X		X	X	X	X	X
Panicum rigidulum	TBD	X	X	X	X	X		X	X	X	X	X											

		Vegetation												Seed Bank											
		Ty	уре		Zone		N	atur	al	R	estore	ed	T	уре	Zone			Natural			Re	stor	ed		
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3		
Panicum verrucosum	FACW												X		X			X							
Panicum virgatum	FAC		X	X	X	X				X	X	X	X			X			X						
Parthenocissus quinquefolia	FACU		X	X	X	X				X	X	X													
Paspalum laeve	FACW		X		X						X														
Photinia pyrifolia	TBD	X		X			X																		
Phragmites australis	FACW		X	X	X	X				X	X	X													
Phytolacca americana	FACU		X			X						X													
Pinus taeda	FAC	X	X	X	X	X			X	X	X	X													
Plantago virginica	FACU												X	X		X	X		X			X	X		
Platanus occidentalis	FACW		X	X	X	X				X	X	X													
Polygonum amphibium	TBD													X	X						X				
Polygonum cespitosum	TBD		X	X	X	X				X	X	X		X	X	X					X	X			
Polygonum glabrum	TBD		X	X						X															
Polygonum hydropiperoides	OBL		X	X	X					X	X			X	X	X					X	X			
Polygonum lapathifolium	OBL		X	X		X				X		X		X		X	X					X	X		
Polygonum pensylvanicum	OBL		X	X	X	X				X	X	X		X	X	X	X				X	X	X		
Polygonum persicaria	OBL		X	X	X					X	X			X	X		X				X		X		
Polygonum punctatum	OBL		X		X						X			X		X						X			
Polygonum sagittatum	OBL		X		X						X														
Polypremum procumbens	FACU		X		X						X		X	X	X	X	X	X	X		X	X	X		
Populus alba	TBD												X				X			X					
Potamodeton diversifolius	OBL		X	X	X	X				X	X	X													
Prunus virginiana	FACU		X			X						X													
Prunus serotina	FACU	X	X			X			X			X	X				X			X					
Pteridium aquilinum	FACU	X		X			X																		

		Vegetation												Seed Bank												
		T_{2}	уре		Zone		N	atur	al	R	estore	ed	T	vpe	2	Zon	e	Natural			Re	stor	ed			
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3			
Quercus alba	FACU	X	X	X	X	X	X	X	X		X	X														
Quercus michauxii	FAC	X		X	X		X	X																		
Quercus phellos	FACW	X	X		X	X		X	X		X	X														
Quercus rubra	FACU	X	X		X	X		X	X			X														
Ranunculus repens	FAC		X	X	X	X				X	X	X														
Ranunculus sardous	FAC													X	X		X				X		X			
Rhexia mariana	FACW		X	X	X	X				X	X	X														
Rhododendron atlanticum	FAC	X		X	X	X	X	X	X																	
Rhododendron viscosum	OBL	X		X	X	X	X	X	X																	
Rhynchospora chalarocephala	OBL		X		X						X															
Rhynchospora macrostachya	OBL		X	X						X																
Robinia pseudiacacia	UPL		X			X						X														
Rorippa palustris	OBL													X	X	X					X	X				
Rosa multiflora	FACU		X	X	X	X				X	X	X														
Rubus argutus	FAC		X	X	X	X				X	X	X														
Rudbeckia hirta	FACU		X		X	X					X	X														
Rumex crispus	FAC		X		X	X					X	X														
Salix nigra	OBL		X	X	X					X	X															
Sassafras albidum	FACU	X			X	X		X	X																	
Schoenoplectus americanus	OBL												X			X			X							
Schoenoplectus pungens	OBL		X	X	X					X	X		X	X	X	X			X		X					
Scirpus cyperinus	OBL		X	X	X					X	X															
Setaria faberi	UPL		X	X	X	X				X	X	X	X	X		X	X		X			X	X			
Setaria pumila	FAC		X	X	X	X				X	X	X		X	X	X	X				X	X	X			
Smilax glauca	FAC	X	X			X			X			X														

		Vegetation												Seed Bank												
		T_{2}	уре		Zone		N	atur	al	R	estore	ed .	$T_{\mathbb{C}}$	уре	2	Zon	e	Natural			Re	stor	ed			
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3			
Smilax rotundifolia	FAC	X	X	X	X	X	X	X	X	X		X			 						 					
Solanum carolinense	FACU		X	X	X	X				X	X	X			<u> </u>						<u> </u>					
Solidago altissima	FACU		X	X	X	X				X	X	X														
Solidago bicolor	FACU		X		X	X					X	X			<u> </u>											
Solidago canadensis	FACU		X		X	X					X	X									 					
Sorghastrum nutans	FACU		X			X						X			 						 !					
Sorghum halepense	FACU	X	X	X	X	X	X			X	X	X														
Spirodela polyrrhiza	OBL		X	X	X					X	X		X	X	X		X			X	X					
Strophostyles helvola	FAC		X		X	X					X	X									 					
Symphoricarpos orbiculatus	FACU		X			X						X									 					
Symphyotrichum lanceolatum	FACW		X		X	X					X	X	X	X		X	X		X	X	 	X	X			
Symphyotrichum ontarionis	FAC													X		X	X				! !	X	X			
Symphyotrichum racemosum	FACW		X		X	X					X	X	X	X	X	X	X			X	X	X	X			
Symphyotrichum subulatum	OBL													X	 	X					 	X				
Taraxacum officinale	FACU		X		X	X					X	X														
Thelypteris palustris	OBL	X			X			X							 						 					
Toxicodendron radicans	FAC	X	X	X	X	X	X	X		X	X	X									 					
Trifolium hybridum	FACU		X		X	X					X	X		X		X						X				
Trifolium repens	FACU		X		X	X					X	X	X	X	X	X		X			X	X				
Trifolium virginicum	TBD	X		X			X																			
Triplasis purpurea	TBD		X			X						X														
Typha angustifolia	OBL		X	X						X					 						 					
Typha latifolia	OBL		X	X						X																
Ulmus americana	FAC		X			X						X														
Ulmus procera	TBD		X	X	X	X				X	X	X														

		Vegetation												Seed Bank												
		T_{\cdot}	уре		Zone		N	atui	al	R	estore	ed	T_{\cdot}	<u> </u>	Zone			atur	al	Re	stor	ed				
Plant Name	FacWET	Nat	Rest	1	2	3	1	2	3	1	2	3	Nat	Rest	1	2	3	1	2	3	1	2	3			
Ulmus rubra	FAC		X		X	X					X	X														
Vaccinium corymbosum	FACW	X		X			X								 											
Vaccinium fuscatum	FACW	X	X	X	X	X	X	X	X			X														
Vaccinium pallidum	TBD	X		X		X	X		X						 											
Verbascum blattaria	FACU		X		X						X			X	X	X	X				X	X	X			
Verbesina occidentalis	FACU		X			X						X			 											
Veronica peregrina	FAC													X	X	X	X				X	X	X			
Viburnum acerifolium	FACU	X				X			X						 											
Viburnum dentatum	FAC		X			X						X									!					
Vitis labrusca	FAC		X	X	X	X				X	X	X			 											
Vitis riparia	FACW		X	X	X	X				X	X	X														
Wolffia columbiana	OBL		X	X	X					X	X															
Woodwardia virginica	OBL	X	X	X	X	X		X	X	X	X															
Xanthium strumarium	FAC		X	X	X	X				X	X	X			 											
Xyris difformis	OBL		X	X	X					X	X			X	X	X	X				X	X	X			
Total Species Cour	nts	50	209	132	174	160	29	29	35	111	155	144	47	83	61	74	60	25	28	22	56	67	54			

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