DEVELOPMENT OF FORESTED WETLAND ECOLOGICAL FUNCTIONS
IN A HYDROLOGICALLY CONTROLLED FIELD EXPERIMENT IN
VIRGINIA, USA

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Doctor of Philosophy

By

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To all the citizen scientists who made this project possible.
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ACRONYMS AND ABBREVIATIONS

AGB Leafless woody aboveground biomass
AGR Absolute growth rate
AMB Ambient Cell
BEM Biomass estimation model
BGB Coarse root (>2mm) belowground biomass
BR Bare root
CD Crown diameter (cm)
CMS Compensatory wetland mitigation sites
CSAG Stem cross-sectional area at groundline (cm²)
CWA Clean Water Act
dbh Diameter at breast height
EPS Ecological performance standards
ESD Equivalent stem cross-sectional diameter at groundline (cm)
FHW Forested headwater wetland
FLD Flooded Cell
GAL 1-gallon container
H Height (cm)
PRI Primary successional species group
r:s Root to shoot ratio
RGR Relative growth rate
SAT Saturated Cell
SEC Secondary successional species group
TB Tubeling
USACE United States Army Corps of Engineers
USEPA United States Environmental Protection Agency
VADEQ Virginia Department of Environmental Quality
ABSTRACT

Forested headwater wetlands provide numerous ecosystem functions and services and are often disturbed, impacted, or destroyed due to their position in the landscape. This has led to many successful and unsuccessful attempts to restore these important ecosystems. Returning trees to these restored ecosystems has proven to be particularly challenging. To increase successful forested headwater wetland restoration, this dissertation recommends tree species and stocktypes that could be planted to return lost ecosystem structure and ecological functions. This dissertation focuses on a created experimental system that investigates the responses of seven species of native wetland trees planted using three stocktypes in three distinct hydrologic conditions (normal rainfall, constantly saturated root zone, and flooded above the root crown). This dissertation has been divided into six chapters to facilitate investigation of several research questions.

The first chapter provides an in-depth literature review of forested wetland restoration, highlighting wetland regulations, factors influencing planted trees and the various responses that will be measured in the subsequent chapters. The second chapter investigates survival and morphological development five years following planting and provides recommendations for planting based on these responses.

The third chapter in this dissertation develops a biomass estimation model that relates total biomass to stem morphology based on destructive harvests. The model is then used to determine the biomass accumulated of all living trees after six years allowing for a robust evaluation of each species and stocktypes’ response to the hydrologic treatments. Building upon the model developed in chapter three, the fourth chapter calculates biomass accumulation rates which provide greater insight to how these species develop and change through time.

The fifth chapter investigates the regulatory context for wetland compensatory mitigation standards in Virginia and provides an additional ecological performance standard for evaluating compensatory mitigation site success. This performance standard is based on stem morphology and provides a robust method for evaluating the ecological functioning of compensatory mitigation sites. Finally the sixth chapter provides a brief economic analysis that examines the return on investment for each species and stocktype used in the study and provides overarching conclusions based on the preceding chapters.

The combination of these chapters provides an in-depth analysis of the responses of these planted trees to the experimental hydrologic conditions from the time of planting through six years of growth. These analyses yielded practical and regulatory recommendations that can enhance forested wetland restoration.
DEVELOPMENT OF FORESTED WETLAND ECOLOGICAL FUNCTIONS

IN A HYDROLOGICALLY CONTROLLED FIELD EXPERIMENT IN

VIRGINIA, USA
CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW
There are a wide variety of scientific and legal definitions used to determine which areas of the landscape qualify as a wetland; however, most encompass three general components: 1) presence of water at the surface or within the root zone, 2) unique soil conditions, 3) unique plants, animals, fungi, and bacteria that are adapted to the presence of water (Mitsch and Gosselink 2007). Within Virginia, there are a large number of ecosystems that fall under this general definition, from salt marshes in the coastal plain to bogs and fens in the Blue Ridge Mountains. Each type of wetland has unique physical, chemical, and biological properties often referred to as the ecosystem structure. Additionally, each type of wetland performs unique physical, chemical and biological processes. The processes that take place within an ecosystem are referred to as ecosystem functions and those functions (or combinations of functions) that are of value to humans are referred to as ecosystem services. An important group of wetlands in Virginia are forested headwater wetlands that are valued for their unique landscape position, large amount of area, and associated ecosystem structure, functions and services.

**Forested Headwater Wetlands**

Forested headwater wetlands (FHW) are located in the upper reaches of non-tidal freshwater streams where average annual stream flow is less than 5 ft$^3$/second (33 CFR Section 330.2 (d)). The primary hydrologic inputs are groundwater, overland flow, and precipitation (Brinson et al. 1995, Noble et al. 2011). Several authors define headwater wetlands as those surrounding 1st and 2nd order streams (smallest streams in the landscape) using the Strahler method (Rheinhardt et al. 1998, Rheinhardt et al. 2009,
Noble et al. 2011, Rheinhardt et al. 2012). In the United States there are approximately 3,821,375 km of 1st and 2nd order streams representing approximately 73% of the total length of all streams and rivers (Leopold et al. 1964, Brinson 1993) suggesting potential for a large amount of FHW area. In Virginia, analysis of National Wetland Inventory aerial maps revealed that there are approximately 156,795 ha of vegetated non-tidal headwater wetlands surrounding 1st order streams with an addition 51,835 ha surrounding 2nd order streams (Hershner et al. 2003). These headwater wetlands represent approximately 43% of the 485,623 ha of vegetated wetlands in Virginia (Hershner et al. 2003). Consequently, several authors have investigated various biotic and abiotic characteristics of headwater wetlands in Virginia and the surrounding states (Glascock and Ware 1979, Parsons and Ware 1982, Rheinhardt et al. 1998, Rheinhardt et al. 2000, Brinson et al. 2006, Rheinhardt et al. 2009, Rheinhardt et al. 2012, 2012a).

As the name implies, FHW vegetative structure is dominated by trees and tree biomass accounts for the majority (>96%) of living vegetative biomass (Rheinhardt et al. 2012). The species of trees found in FHW varies by physiographic province, successional stage, hydrologic and soil conditions and site history (fire, logging, etc.). Glascock and Ware (1979) investigated forest composition along small streams in the coastal plain of Virginia that had high water tables and experienced temporary irregular flooding. They concluded that the stands were not virgin stands but secondary growth based on the size of stumps found. The species that ranked within the top three species in at least one stand based on relative importance values (calculated using dominance and density) listed in descending order were Acer rubrum (red maple), Fraxinus pennsylvanica (green ash), Liquidambar styraciflua (sweetgum), Carpinus caroliniana (American hornbeam),
Ulmus americana (American elm), Quercus phellos (willow oak), Quercus michauxii (swamp chestnut oak), Taxodium distichum (bald cypress), Quercus nigra (water oak), Liriodendron tulipifera (tuliptree), Nyssa sylvatica (blackgum), Fagus grandifolia (American beech), Ilex opaca (American holly), Betula nigra (river birch), Pinus taeda (loblolly pine), and Quercus pagoda (cherrybark oak).

Parsons and Ware (1982) investigated soil and vegetation of coastal plain swamps along small stream bottoms including 13 of the same sites investigated by Glascock and Ware (1979). The purpose of their study was to measure additional environmental parameters to determine what factors were influencing the distribution of tree species. While they found similar species as Glascock and Ware (1979), Parsons and Ware (1982) concluded that soil chemistry and soil moisture were the most important factors influencing the distribution of tree species. Sites with higher soil moisture content were dominated by F. pennsylvanica, A. rubrum and U. americana. Drier sites were dominated by C. caroliniana, L. styraciflua, and Q. phellos.

Rheinhardt et al. (1998) investigated the geomorphic setting and vegetation of low order streams within the inner coastal plain of North Carolina in order to provide guidance for permit decisions, restoration efforts, and judging success of restoration attempts. The authors of this paper defined 1st and 2nd order streams as headwater systems. The most important species in the headwater systems of this study were Nyssa biflora (swamp tupelo), A. rubrum, L. styraciflua, and L. tulipifera. They also found that headwater systems had smaller drainage basins, narrower floodplains, steeper floodplain gradients, steeper stream gradients, smaller channel cross-sectional areas, narrower
channel widths, higher graminoid cover and lower phosphorus concentrations than midreach (stream order 3 and 4) systems.

Rheinhardt et al. (2000) described the vegetation of headwater wetlands in the inner coastal plain of Maryland and Virginia with the purpose of developing the hydrogeomorphic (HGM) functional assessment model for wetland on 1st to 3rd order streams. The most abundant canopy trees were A. rubrum, L. styraciflua, Fraxinus spp., N. biflora, L. tulipifera, Ulmus rubra (slippery elm), and U. americana. The density of canopy trees ranged from 318 to 683 stems/ha. Quercus spp. had lower importance values in this study than Parsons and Ware (1982) and the authors suggest that this may have been due to preferential logging of stands or damming by beavers. The sapling stratum (juveniles of potential canopy trees) was dominated by L. styraciflua and A. rubrum. The density of saplings ranged from 0 to 3,111 stems/ha. The dominant subcanopy (shrubs and trees restricted to the understory at maturity) species were C. caroliniana, Lindera benzoin (northern spicebush) and I. opaca. The density of subcanopy species ranged from 254 to 7,747 stems/ha.

Rheinhardt et al. (2009) investigated forest structure and composition in 219 sites from three physiographic provinces (Coastal Plain, Piedmont, and Ridge & Valley) in the Delaware River, Chesapeake Bay, and Albemarle/Pamlico Sound drainage basins. They focused on low order riparian ecosystems (1st to 4th order streams) and defined headwater as 1st to 2nd order streams. The goal was to outline strategies for restoring structure and function to low-order riparian zone forests. To determine forest biomass, three-dimension structure and successional status stand basal area (BA) was used. Early successional systems were defined as BA ≤ 20 m²/ha and mid successional was 20 ≤ BA < 30 m²/ha.
while late successional was defined as $BA \geq 30 \text{ m}^2/\text{ha}$. The dominant species within the late successional stands of the Piedmont region were $A. \text{rubrum}$, $L. \text{tulipifera}$, and $Quercus \text{rubra}$ (northern red oak). They conclude that $Quercus$ spp. may have declined because of fire suppression and that planting $Quercus$ spp. and other heavy mast species might facilitate restoration to a more historically accurate composition represented by late successional stands that provide many habitat and biogeochemical functions.

**Wetland Functions and Services**

Wetland functions are generally defined as processes that occur in wetlands (Hruby 1999) and vary based on wetland type, hydrologic and geomorphic conditions (Brinson 1993), landscape position, season and many other factors. Wetland ecosystem functions fall into three general categories: hydrological, biogeochemical, and habitat and food web support (National Research Council (NRC) 1995). Hydrologic functions include short-term and long-term surface water storage, storage of subsurface water, moderation of groundwater flow or discharge, dissipation of energy, and maintenance of high water tables (NRC 1995, Smith et al. 1995). Biogeochemical functions include transformation, cycling, and storage of elements, retention and storage of dissolved substances and particulates, accumulation of peat, export of organic carbon and accumulation of inorganic sediments (NRC 1995, Smith et al. 1995). The functions related to habitat and food web support include maintenance of characteristic plant and animal communities (composition, abundance and age structure) and maintenance of characteristic energy flow (NRC 1995, Smith et al. 1995).
Principal ecological functions provided by FHW are retention of sediments (Hupp et al. 1993), transformation, cycling and retention of elements (carbon, nitrogen, phosphorus, etc.) (Craft and Casey 2000, Noble et al. 2011), primary and secondary productivity, water storage, groundwater recharge, as well as plant and animal habitat (Morley 2008). Examples of services provided by FHW that are of value to humans include but are not limited to flood mitigation (intercept storm runoff, store floodwater), water quality enhancement (denitrification, nitrogen and phosphorus retention), timber production, vegetation harvests, animal products (pelts, food), aesthetics (recreational hunting), maintenance of biodiversity (rare and threatened species), aquifer recharge, and air quality enhancement (carbon sequestration) (NRC 1995, Mitsch and Gosselink 2007).

The occurrence and rates of these processes within FHW are dependent upon hydrologic and geomorphic conditions as well as nutrient and sediment inputs from surrounding ecosystems (Brinson et al. 1981). Trees, being a major component of FHW, also play an important role in many of the ecosystem functions and services provided by FHW. Trees are often the dominant source of primary production (Rheinhardt et al. 2012) and they heavily contribute to the cycling of elements. Trees in FWH also provide habitat for plants, animals, fungi, and microbial communities. Living and shed bark, wood, roots, flowers, fruits, seeds, leaves and sap are consumed by a number of different organisms including, insects, mammals and birds. Leaf litter and fallen dead wood also provide nutrients for fungus and other microorganisms in the detrital food web. Trees provide shelter from weather and predators in the form of tree cavities, leaf litter and fallen dead wood. Shade provided by trees surrounding streams, estuaries or rivers can reduce air and water temperature enhancing habitat for aquatic organisms. Trees also provide space for
organisms to live, including insects living under and in the bark, birds and mammals building nests in cavities and branches, caterpillars and other insects building nests in the crown, and lichen, moss and fungi living on the bark.

Wetlands ecosystem services (those functions or combinations of functions that are valued by humans) include storing flood waters (Brinson 1993a), enhancing water quality (Sather and Smith 1984), retaining nutrients (Fisher and Acreman 2004), providing wildlife corridors and habitat amenities (Balcombe et al. 2005, Shaw and Fredine 1956), providing erosion control along streams (Silberhorn 1994), providing intrinsic values such as recreation opportunities (Mitsch and Gosselink 2000, Office of Technology Assessment (OTA) 1984), and trapping waterborne sediments that help protect and restore sensitive aquatic ecosystems such as the Chesapeake Bay (USGS 1999). In addition to the value of these wetlands to society, they also play an important role in the integrity of downstream ecosystems.

Downstream Connections

The functions and services provided by FHW influence the functioning and integrity of ecosystems downstream mainly through alteration of water quality and export of organic matter. In Virginia, these ecosystems include streams, rivers, and estuaries including the Chesapeake Bay.

Headwater wetlands can enhance water quality through nutrient uptake and retention, denitrification, and sediment trapping. Nutrient uptake and retention prevent nutrients from entering the water column and are important in reducing eutrophication of the Chesapeake Bay and surrounding estuaries (Lowrance et al. 1997). Through primary
production, nutrients are assimilated into vegetative biomass, preventing those nutrients from being transported downstream (Dosskey et al. 2010). Trees are important to this process because they provide long term storage of nutrients in woody tissue and short term storage in leaves. Headwater wetlands play an important role in reducing eutrophication because they are often located within agricultural landscapes that can have increased nutrient loads. Freeman et al. (2007) found that alteration of headwater systems for agricultural purposes can increase downstream eutrophication and coastal hypoxia.

Chemical processes, such as denitrification, that take place in wetland soil can also enhance water quality. Denitrification can enhance water quality because denitrifying bacteria convert nitrate to the nitrogen gases (NO, N₂O and N₂), which are released to the atmosphere (Seitzinger 1988, Paul 2007). Denitrifying bacteria utilize NO₃⁻ rather than oxygen as the terminal electron acceptor; therefore, this process usually takes place when oxygen concentrations are reduced, such as in wetland soils. Hefting et al. (2005) found that rates of denitrification accounted for greater nitrogen removal than plant uptake in wetter forested riparian sites. Trees can enhance denitrification because their roots provide heterogeneous environments and energy (root exudates) for denitrifying microbes (Groffman et al. 1996). In addition, tree biomass may contribute to the organic carbon needed for denitrification. Through denitrification, water quality may be enhanced because nitrogen, which drives eutrophication in estuaries and coastal water, can be removed from the water prior to entering stream systems.

Water quality can also be enhanced through the trapping of sediment in FHW. Excess sediment in stream systems can degrade the condition and functioning of downstream systems by increasing turbidity, altering plant and animal habitats and
increasing sediment bound nutrients and pollutants. Trees help trap sediment because their large stems and roots slow the flow of surface and ground water, which leads to sediment trapping; they also stabilize existing soil (Dosskey et al. 2010). Additionally, leaf litter from trees slows the overland flow of water increasing sediment retention.

Forested headwater wetlands also influence the functioning of downstream systems through the export of organic matter. These systems can provide a substantial proportion of the total organic matter found within a stream (Dosskey and Bertsch 1994) and can contribute significantly higher concentrations of organic carbon when compared to upland watersheds (Mulholland and Kuenzler 1979). This suggests that organic matter produced in FHW influences the functioning of the detrital food webs found in adjacent streams. Large tree debris increases channel bed roughness, which can slow stream velocity, increase stability and provide habitat for microbes and animals (Harmon et al. 1986, Hilderbrand et al. 1997).

Overall, the ecosystem functions and services performed by FHW are justification for the protection, preservation and restoration of these important ecosystems. However, prior to changes in wetland regulations, a large amount of FHW were lost.

**Wetland Loss**

Between the 1780’s and 1980’s, prior to most wetland regulations, approximately 53% of the estimated 89,435,000 ha of wetlands was lost in the lower 48 states. During the same time period, Virginia lost approximately 42% of the estimated 748,263 ha of wetlands present in the 1780’s (Dahl 1990). Most of the wetlands lost in Virginia have been forested wetlands, which are the most abundant wetland type in Virginia (Tiner and
Finn 1986, USGS 1999). Losses were mainly due to drainage activities associated with agriculture and forestry practices, construction of reservoirs and urban/suburban development (Dahl and Johnson 1991, Tiner and Finn 1986). Additionally, Brinson et al. (1981a) estimated that over 70% of U.S. riparian forests have been lost since pre-settlement time.

**Wetland Regulations and Protection**

With the realization of the importance of wetlands, impacts to these ecosystems are currently regulated by the Clean Water Act (CWA) (33 U.S.C. 1344). The Federal Water Pollution Control Act (1948) was the first major law designed to reduce water pollution and was later amended and renamed the CWA in 1977. Wetland impacts are specifically regulated under Section 404 of the CWA which authorized the USACE under the direction of the United States Environmental Protection Agency (USEPA) to issue permits regulating the discharge of dredged or fill material into “waters of the United States”, which includes wetlands (40 CFR Part 230.1). These permits are now used for any activity that may impact wetlands.

**Mitigation Sequence**

In order to permit wetland impacts while maintaining the physical, biological and chemical integrity of the waters of the United States (the overall goal of the CWA) and fulfilling the 1988 policy goal of ‘No Net Loss’, these regulations now require that impacts to wetlands follow a mitigation sequence. The mitigation sequence was first defined in the 1978 Council on Environmental Quality (CEQ) National Environmental
Policy Act clarification and includes avoidance, minimization and compensation for impacts to wetlands. After the impact has been found to be unavoidable and is minimized, there are four methods of compensating for wetland impacts: 1) restoration of converted wetlands, 2) creation of new wetlands, 3) enhancement of existing wetlands, 4) preservation of existing wetlands (listed in descending priority (33 CFR PART 332, USACE and USEPA 2008). On March 31, 2008, the USACE and USEPA released the “Final Rule” for Compensatory Mitigation and announced the new priority of methods for satisfying mitigation requirements (in order of decreasing priority) as 1) purchasing credits from mitigation banks, 2) payment to an in-lieu-fee program, and 3) permittee-responsible compensatory mitigation (USACE and USEPA 2008).

Development activities in wetlands in Virginia are regulated by the USACE through Section 404 of the Clean Water Act, the Virginia Department of Environmental Quality (VADEQ), through the Virginia Water Protection Permit program and Section 401 of the Clean Water Act; and the Virginia Marine Resources Commission and local Wetland Boards through the Virginia Tidal Wetlands Act of 1972. All permits are reviewed by the USEPA, U.S. Fish and Wildlife Service, Virginia Department of Game and Inland Fisheries, the Virginia Department of Conservation and Recreation, Virginia Department of Historic Resources, the Virginia Marine Resources Commission and any other interested and affected agencies. There are exemptions for certain development activities (e.g. normal farming, silvicultural and ranching activities) that are specified in Section 404(f)(1).
Compensatory Mitigation Ecological Performance Standards

The overall goals of compensatory mitigation sites (CMS) are to replace the structure and ecosystem functions and services that were lost during the permitted impact (33 CFR PART 332). The current legislative-mandated method for determining if a CMS is developing into the desired wetland type and is providing the expected ecological functions is through meeting project specific ecological performance standards (EPS) (aka: success criteria, success standards or release criteria) (33 CFR PART 332.5, USACE and USEPA 2008). Performance standards for all CMSs are required to be clear, objective, verifiable, based on the best available science and able to be assessed in a practicable manner (33 CFR PART 332.5, USACE and USEPA 2008).

Ecological performance standards are developed on a project by project basis (USACE and USEPA 2008). While EPSs vary across USACE districts, the majority are based on soil, vegetation, and hydrologic indicators from the 1987 Federal Delineation Manual (Environmental Laboratory 1987) and subsequent editions (Breaux and Serefiddin 1999, Streever 1999, Matthews and Endress 2008, USACE 2008). Additional EPSs may include survival of planted stock, specific density (or cover) of herbaceous or woody plants, and limiting exotic and nuisance plants (Breaux and Serefiddin 1999, Streever 1999, Matthews and Endress 2008, USACE 2008). Virginia has established hydrologic, vegetation, and soil EPSs for use in CMSs (USACE Norfolk District and the VADEQ 2004, VADEQ 2010). The majority of the Virginia’s EPSs are based on the 1987 Federal Delineation Manual (Environmental Laboratory 1987) and subsequent editions.
Virginia has currently implemented a woody height growth EPS for mitigation banks in particular; however, few projects have implemented this performance standard (Mike Rolband, personal communication). Virginia is among few states to have established a tree growth EPS (Streever 1999, Environmental Law Institute 2004). This may be due to limited information on growth rates of planted trees in created or restored wetlands (Denton 1990, Niswander and Mitsch 1995, Gamble and Mitsch 2006, Pennington and Walters 2006, Henderson et al 2009). In order to ensure that EPSs are being fulfilled for CMS, monitoring and compliance reports are required. The current monitoring period in Virginia for CMS is to monitor for 6 years over a 10 year period (typically years 1, 2, 3, 6, 7, and 10) (USACE Norfolk District and VADEQ 2004).

Most EPSs are structural measurements of the vegetative community and/or physical environment (see above, Wilson and Mitsch 1996) and are not direct measurements of wetland functions or services (Mitsch and Wilson 1996, Streever 1999, NRC 2001). Additionally, many performance standards are not adequate indicators of wetland functions or services (Kentula et al. 1992). Cole (2002) suggested that measurement of herbaceous cover (a common performance standard) may not serve as an accurate indicator of the replacement of wetland functions. Therefore, meeting site specific performance standards does not guarantee that wetland functions and services are being replaced (the overall goal of compensatory mitigation) (Matthews and Endress 2008). Streever (1999) stated comparisons between performance standards and the ability of CMSs to replace lost functions are lacking. Several authors have attempted to develop performance standards that are more closely linked with ecosystem functions and services (Atkinson et al. 1993, Bedford 1996, Brinson 1996, Brinson et al. 1996, Breaux
and Serefiddin 1999, Environmental Law Institute 2004, Faber-Langendoen et al. 2006; 2008, DeBerry and Perry 2015). However, forested CMSs still lack woody EPSs that quantify or are directly associated with ecosystem functions and services.

**Wetland Restoration**

Wetlands are restored for a variety of reasons in addition to restoration as part of the mitigation sequence. These reasons include but are not limited to, failed agriculture (or other failed land use), timber production, following timber harvest, recreation, reclamation of disturbed habitat, re-establishment of bird habitat (Ducks Unlimited), and/or agricultural easements (Agricultural Conservation Easement Program). Additionally, there are several state and federal goals (Chesapeake 2000 Agreement) that seek to increase the amount of wetland area through restoration.

Ecosystem restoration is an applied science that focuses on “the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed” (Society for Ecological Restoration International Science & Policy Working Group 2004). The goals of wetland restoration are to return lost ecosystem structure, functions and services to the landscape (Cairns Jr. 2000) and for the restored ecosystem to be self-sustaining, resilient, and have connections to other ecosystems.

**Assessment of Wetland Restoration**

There are many methods used to determine if restored wetlands are meeting these general goals, and methods can differ based on the underlying reason for restoration. For CMS, restoration success has been partitioned into regulatory and ecological success
(Wilson and Mitsch 1996, Kentula 2000). Successfully fulfilling regulatory obligations does not guarantee successful functional wetland replacement and vice versa. For wetlands restored for reasons other than compensatory mitigation, restoration success has been evaluated using many different methods.

Several studies have found that CMSs are not meeting regulatory obligations. A study completed by the United States Government Accountability Office (USGAO) (2005) found that the USACE had failed to receive monitoring reports from 86% of the surveyed permittee-responsible compensatory mitigation sites, 30% of the surveyed mitigation bank sites, and 17% of the surveyed in-lieu-fee mitigation programs. A national study completed by the National Research Council (NRC) (2001) found that approximately 50% of surveyed CMSs failed to meet prescribed performance standards and concluded that “the goal of no net loss of wetlands is not being met for wetland functions by the mitigation program.” Several regional studies have also suggested that forested CMS did not meet their prescribed vegetation performance standards (Brown and Veneman 2001, Cole and Shafer 2002, Matthews and Endress 2008, Tischew et al. 2010).

Multiple regional and local studies have found that wetlands restored for a variety of purposes are not ecologically successful and several studies have suggested that wetland structure, functions and services are not developing in restored forested wetlands (Atkinson and Cairns Jr. 2001, Brown and Veneman 2001, Cole et al. 2001, Sudol and Ambrose 2002, Atkinson et al. 2005, Hoeltje and Cole 2007, Atkinson et al. 2010, Moreno-Mateos et al. 2012, Stefanik and Mitsch 2012). Important to the present investigation, numerous studies have found that tree density and tree growth were
significantly lower for restored sites as compared to conditions prior to conversion or nearby mature forested wetlands (Brown and Veneman 2001, NRC 2001, Cole and Shafer 2002, Morgan and Roberts 2003, Sharitz et al. 2006, Matthews and Endress 2008).

Tree Establishment in Restored Wetlands

Establishing trees in restored wetlands can be accomplished through natural colonization and/or through tree planting. Tree establishment is often the most difficult task in forested wetland restoration (Matthews and Endress 2008) and results from inadequate natural colonization or through poor survival of planted trees (Robb 2002, Morgan and Roberts 2003, Spieles 2005). At restoration sites where natural regeneration is likely to be unsuccessful, trees are often planted.

Natural Colonization

Colonization of trees into a restoration site can be perceived as the process of tree species immigration and local extinction of individuals that takes place over time (MacArthur and Wilson 1967). Noon (1996) called changes in woody composition over time in created wetlands the process of primary succession while van der Valk (1981) called changes in restored wetlands secondary succession.

In Virginia, the most common early colonizing (pioneer) tree species into old-fields, timbered forested wetlands, and restored/created wetlands are *L. styraciflua*, *A. rubrum*, *F. pennsylvanica*, *Platanus occidentalis* (American sycamore), *Pinus taeda* (loblolly pine), *Salix nigra* (black willow), and *Nyssa aquatica* (water tupelo) (McQuilkin 1940, Monette and Ware 1983, Spencer et al. 2001, Atkinson et al. 2005, Hudson 2010).
These early colonizing species have characteristics that allow them to survive and grow in the environmental conditions present in early successional ecosystems, including, high acclimation potential, broad physiological responses, and increased growth rates (Bazzaz 1979). Additionally, the majority of these species seeds are wind dispersed (*N. aquatica* is dispersed by animals and water) which increases their ability to colonize into early successional ecosystems.

Tree species that arrive later in these ecosystems are typically *Quercus* sp., *Carya* sp. (hickory), *F. grandifolia*, *Pinus* sp., and *L. tulipifera*, which are often the dominant species in mesophytic and southern mixed forest regions of Virginia (Dyer 2006). The composition and abundance of trees that will colonize these ecosystems are dependent upon surrounding seed source composition and density as well as the biotic and abiotic conditions that are present within a given ecosystem (De Steven 1991, Gill and Marks 1991, Myster and Pickett 1993, Hudson 2010, Casanova and Brock 2000, Keddy 1992). The dominant factors that influence colonizing tree density are composition and distance to seed source, size of the adjacent forest, hydrology, and the size (basal area, height) of trees in the adjacent forest (Hudson 2010). Colonization by pioneer tree species from adjacent forests should be considered during restoration design and preparation.

Inadequate natural colonization can result from a total lack of seed source, insufficient amount of seeds of appropriate species in the existing seed bank, or lack of seeds actively being supplied by nearby trees. Additionally, abiotic (hydrology, soil conditions, etc.) and biotic (seed predation, competition, etc.) site conditions can limit natural colonization.
Planting

In addition to colonization of trees from surrounding seed sources, trees can be established at restoration sites through planting trees (seeds, seedlings, saplings) obtained from nurseries or transplanted from other wetland areas (Havens 2004). Selecting the appropriate species and planting stock and using correct planting techniques helps to ensure survival and growth of the planted stock. The first decision when selecting planting stock is whether to use seeds or seedlings/saplings. Whether using seeds or seedlings the source or provenance of planting material can be important (Gardiner et al. 2002). Planting material should come from locations that are within the same cold hardiness zone or ecoregion so that they have some tolerance to the local conditions (Dey et al. 2008).

Direct Seeding

One method of establishing trees in restoration sites is through the planting of tree seeds, often called direct seeding. Direct seeding is often less expensive than planting nursery grown seedlings (Bullard 1992) and can be used to establish any tree species, but efforts mainly focus on Pinus spp., Quercus spp. or Carya spp. (Harmer and Ker 1995, Dey et al. 2008). Most methods of direct seedling come from restoration of bottomland hardwoods for timber production. Direct seeding may be useful on sites that are large in size or far away from seed sources (McKevlin 1992). Clewell and Lea (1989) recommended planting acorns as opposed to broadcast seeding.

Williams et al. (1999) investigated the differences in survival of direct seeded versus containerized and bare root Quercus texana (Nuttall oak) seedlings planted on old-
fields. Results from this study showed that containerized seedlings had greater survival than bare root seedlings in areas with high water tables or flooding, suggesting that direct seeding may not be an appropriate choice for most wetland restoration sites due to the stressful hydrologic conditions.

*Nursery Stocktypes and Production Techniques*

There are numerous woody stocktypes available for afforestation or reforestation projects, including wetland restoration, carbon sequestration projects, various silvicultural and forestry projects, wildlife preserves or other conservation reserve programs. The tree nursery industry in the United States and Canada utilizes many different production techniques to produce a wide variety of woody stocktypes. The overall effects of the various production methods are to alter the above and belowground morphology and physiology of the nursery stock (Chavasse 1980). The goal of altering these characteristics of seedlings is to produce a cost-effective nursery stock that will successfully survive and grow following outplanting.

There are various descriptions used in the nursery industry to describe the size, age, and how the stock was produced, that are not uniformly applied throughout the nursery industry. This can lead to confusion when purchasing nursery stock and difficulty in evaluating stocktypes from a scientific perspective. There have been several attempts to standardize and describe the terminology of nursery stock including the American Nursery & Landscape Association (2004), the USDA Forest Service (Landis 1990, Landis et al. 2010) and the British Columbia Ministry of Forests (1998) Provincial Seedling Stock Type Selection and Ordering Guidelines (Scagel et al. 1998). In 1984 the
Nursery Technology Cooperative at Oregon State University and the USDA Forest Service produced the Forest Nursery Manual: Production of Bareroot Seedlings, which described methods used for bare root seedling production (Duryea and Landis 1984).

Common descriptions of woody nursery stock available for outplanting include cuttings (whips, live stakes), bare root seedlings, tubelings, plugs, containers (many sizes), and balled and burlapped. These descriptive names can be used to describe the age, size, and production technique used, all of which are not uniform throughout the nursery industry. Therefore, when assessing the outplanting success of stock type it is important to focus on the individual morphology and physiology of the seedlings that resulted from the unique production techniques (Pinto 2011b). In general bare root seedlings range in age from one to three years old and are typically planted without soil surrounding the roots. Tubelings are typically similar in age to bare root seedlings; however, they are often planted with soil surrounding the roots and are grown in various shaped (square, round) small containers. Many seedlings are grown in larger containers ranging from 3.8 L to 94.6 L. Containerized seedlings can be grown to various ages and sizes and are often planted with the soil intact around the root system, which allows for planting later in the season. The Virginia Department of Forestry (2012) offers one- two- and three-year old bare root seedlings sold directly from the seedbed and specialty packs (sets of different species that achieve a common goal, e.g. wildlife seedling pack).

Nursery production techniques and conditions that influence the morphology and physiology of woody planting stock include; nursery location (local climate and weather), container size, style and density (or lack thereof), fertilization timing, amount, type (or lack thereof), lifting and storage times and conditions, root and/or shoot pruning, use of
pesticides (fungicides, herbicides etc.), irrigation techniques and amounts (flood pre conditioning (Anderson and Pezeshki 2001), mycorrhizal inoculation (application time and type), application of growth regulators, propagation methods (seeds, clones, tissue culture, grafting), seed source, genetics, size, stratification time, germination period (light, moisture), sowing season, potting soil type (nutrient/OM concentration), amount of soil used, sterilization technique, light intensity and photoperiod, unintended stress, grading/culling techniques, hardening off methods, seedbed conditions, growing time, and overall input costs.

These nursery production techniques and conditions influence the morphological characteristics of seedlings including; stem height, root collar diameter, seedling stem volume, stem mass ratio, root to shoot ratio, aboveground biomass, number of branches, branch diameter, leaf area, leaf mass ratio, foliar color, bud length and amount, disease prevalence, root shape (length, area), root size (mass, volume), root mass ratio, root fibrosity, and the amount of first order lateral roots.

These nursery techniques also influence the physiological characteristics of seedlings including; water use efficiency, plant moisture stress, cold hardiness and heat tolerance, nutrient concentrations and allocation, foliar nitrogen concentrations, vigor (Oregon State University Vigor Test), $\text{CO}_2$ assimilation rates, leaf respiration rates, stem respiration rates, transpiration rates, chlorophyll concentrations, root growth potential (RGP), electrolyte leakage, root carbohydrate concentrations, stem and root moisture content and root respiration rates.

There have been many investigations into how nursery techniques and conditions influence the morphology and physiology of woody seedlings. Duryea and Landis’
(1984) collection of papers on bare root production focused on how nursery design and production techniques influence many characteristics of bare root seedlings. They collected data from 21 nurseries in the northwest U.S. and Canada and interviewed 250 individuals to produce the manual. Brissette et al. (1991) investigated how container nursery techniques such as seed quality, sowing techniques, growing medium moisture, and seedling nutrition affect shoot and root morphology of southern *Pinus* spp.. They concluded that containerized nursery stock provided a viable alternative when bare root stock is not expected to perform well. Chavasse (1980) reviewed factors that affected the seedling during production, including shelter (greenhouses), soil, irrigation, seed treatments, weed control, insects, disease, spacing, conditioning, and lifting techniques. He concluded that the ability of *Pinus radiata* (Monterey pine) to grow well after planting depended more on nursery treatment than on size or any easily measurable morphological characteristic. Duryea and McClain (1984) investigated how irrigation, fertilization, and conditioning at the nursery influence the seedling physiology, including frost hardiness, mineral nutrition, and carbohydrate reserves. Jackson et al. (2012) investigated the effect of nursery fertilization and shelter (greenhouse vs. outdoor) on several morphological and physiological responses of *Pinus palustris* (longleaf pine) seedling and determined an optimal fertilization regiment. Alm and Schantz-Hansen (1974) found that very small containers (14.3 mm diameter) restrict tree root growth of *Pinus banksiana* (jack pine) and *Pinus resinosa* (red pine), while South and Mitchell (2005) developed a “root bound index” to evaluate the effect of restricted root growth in containers. Results suggest that containers produced restricted root growth that resulted in decreased survival following outplanting.
Mycorrhizal Inoculations

The effect of mycorrhizal-root relationships on water absorption has not been completely determined (Pallardy 2008). Dixon et al. (1984) investigated the effect of mycorrhizal inoculation on containerized and bare root *Quercus velutina* (black oak) seedlings. After two years the inoculated container grown seedlings had greater shoot length, root collar diameter, and leaf area compared to the bare root stocktype. Burkett et al. (2005) found that container grown *Q. texana* seedlings inoculated with vegetative mycelia had greater survival than non-inoculated seedlings in flooded conditions. However, additional studies are needed to determine if this nursery production technique provides added benefit when planting trees into restored wetlands.

Alternative Stocktypes

In addition to the common stocktypes available, several tree nurseries have developed specialized stocktypes by using particular production methods. One such stocktype is the Root Production Method (RPM®) that was patented by Forrest Keeling Nursery (Lovelace 1998). According to the Forrest Keeling website, RPM uses “superior seed stock, air-root pruning, special nutrition and soil and proper timing to produce the best plant stock on the market today.” Specifically, Root Production Methods collect seed propagules within 161 km of the planned planting site, grade for quality, and then start selected seeds in 4 cm of composted rice hull, *Pinus* spp. bark and sand. The compost is prepared in a 4:4:2 ratio to create 35-40% porosity, and amended with slow release fertilizers (Grossman et al. 2003). This combination promotes air pruning of the tap root,
and increased production of lateral roots (Shaw et al. 2003, Dey et al. 2004). One to two months after emergence, seedlings are transplanted into individual, bottomless containers 10 cm deep to continue air root pruning of the tap root. Seedlings are then graded based on height, stem diameter, and root development, with only individuals in the top 50% selected (Grossman et al. 2003). As seedlings continue to develop, they undergo a series of transplantings to larger containers and are acclimated to outdoor environments. Containers continue to be shallow and bottomless to encourage air pruning of the tap root.

Research showed after two growing seasons in the nursery, RPM produced *Quercus alba* (white oak) seedlings had basal stem diameters greater than 2.0 cm and heights exceeding 1.5 m, a significant improvement over conventionally produced seedlings (Dey et al. 2004). Root dry weights and root volumes for the same RPM seedlings averaged 101-117 g and 222-252 ml, compared to 18 g in weight and 26-33 ml in volume for conventionally grown bare-root seedlings, also indicating a significant improvement in growth (Dey et al. 2004). Research showed these trends are typical of RPM grown trees (Grossman et al. 2003, Shaw et al. 2003). Because of the potential to improve sapling development, naturally slow growing species, such as *Quercus palustris* (pin oak), *Quercus bicolor* (swamp white oak), *Quercus macrocarpa* (bur oak), are often the subject of RPM treatments (Dey et al. 2004).

Research comparing the field growth of RPM and conventionally produced *Q. alba* seedlings indicated that early rapid shoot growth and acorn mass are significantly greater and occur earlier in RPM produced trees (Grossman et al. 2003). Research also showed that in forest restoration projects, first-year survival was significantly higher and
basal diameter was significantly greater in RPM produced seedlings than in bare-root seedlings (Shaw et al. 2003). Tree height was also greater in RPM grown trees; however, data analysis showed this difference to not be significant (Shaw et al. 2003).

Other studies have shown that survival rates can also be lower for RPM planting stock compared to convention stock types (Henderson et al. 2009). Therefore, additional research is needed to determine if this production technique provides added benefits following outplanting into restored wetlands for a variety of species.

Evaluating Planted Tree Survival and Growth

There are many methods and measurements used to determine how individuals or groups of planted trees respond following outplanting. Common measurements following outplanting include (but are not limited to); survival rates, morphology (height, root collar diameter, crown morphology, leaf area, number of branches, etc.), above and belowground biomass (and allocation patterns), growth rates (morphological or biomass), transplant shock duration, photosynthetic rates, respiration rates, transpiration rates, stomatal conductance, and tissue nutrient concentrations. The sampling methods, measurements, calculations, and statistics used should reflect the underlying research question. The methods used to assess planted trees in this study focus on survival, morphology, biomass, and growth rates.

Survival

One of the most common response variables measured following outplanting is survival. Survival is relatively easy to determine; however, statistically it is a difficult
measure to analyze since it is a binomial response (dead vs. alive), except when analyzed at the stand level (e.g. trees per acre). Survival analysis is a particular branch of statistics that encompasses a variety of methods for survival or similar binomial events. Instead of focusing on the binomial response, many of these methods focus on analyzing “time to event data” (Allison 2010). For planted trees this represents the time between when the tree was planted and when the tree died. This information and statistical methods can be utilized to determine the effect of a given treatment (stocktype, nursery production method, morphological or physiological characteristic) on the survival time of planted trees. The Cox Proportional Hazards Model is one of the most highly cited survival analyses (Cox 1972). The Cox model does not require choosing a particular probability distribution to represent the survival times, can incorporate time-dependent covariates, permits stratification, accommodates both discrete and continuous measurements, and integrates censoring effectively (Allison 2010). These factors make it an appropriate choice for modeling survival times of planted saplings (Burgman 1994, Clarke 2002, Hastwell and Facelli 2003, Frey et al. 2007).

**Morphology**

There are numerous morphological measurements that can be used to evaluate trees following planting, including but not limited to stem (trunk) diameter or area (at groundline or breast height), overall height, number of branches, branch diameter, branch length, crown diameter, area or cover, leaf area, leaf mass, root length, root density, total volume, and total mass. Growth of each of these parameters can be used to quantify development. While many of these morphological parameters are related, each gives
unique information about planted tree responses following outplanting. The morphological factors that are of interest for this study include stem diameter at groundline, height and crown diameter.

**Biomass**

Production and accumulation (storage) of plant biomass is an important ecosystem function that will develop in successfully restored forested wetlands. Therefore, it is an appropriate response for evaluating planted trees. In early successional created and restored forested wetlands the majority of plant biomass is produced by herbaceous vegetation (Atkinson et al. 2005, DeBerry and Perry 2012). However, as restored forested wetlands develop, the production and accumulation of biomass shifts to perennial woody vegetation (shrubs, trees, and woody vines) (DeBerry and Perry 2012), where biomass can remain long-term in the boles, stems, and roots. Therefore, the intended outcome of the restoration process of FHW is that the majority of biomass accumulated will be produced by long lived species, particularly trees.

Quantifying standing biomass and production of planted trees is important in understanding the development of ecosystem structure and functions in restored FHW. Additionally, accurate quantification of tree biomass is an important step in understanding carbon dynamics across a range of forested ecosystems (including wetlands) as they play a large, but yet uncertain, role in the global carbon cycle (Temesgen et al. 2015).

The most common method used to estimate the standing biomass of an individual tree is the use of mathematical relationships between biomass and one or more
morphological woody vegetation characteristic, such as stem diameter and/or height (e.g. Jenkins et al. 2003). This method is commonly referred to as dimensional analysis (Whittaker and Woodwell 1968). Dimensional analysis relies on consistency in the correlations between the changes in relative dimensions of parts of an organism with changes in overall size, referred to as allometry (Gayon 2000, Stevens 2009). While allometric relationships are “not confined to any form of mathematical expression” (Gould 1966), the mathematical relationships describing the allometry of various characteristics of many organisms (including trees) often conform to power laws (Niklas, 2004, Stevens 2009). One focus of this study is developing equations that relate total tree biomass and morphological characteristics. These models will be referred to as biomass estimation models (BEM), but have also been referred to as allometric equations by others (Silesi 2014).

When constructing BEMs for saplings and trees, biomass often only refers to aboveground dry woody material but can refer to “green” (wet) weight and can include leaves, buds, flowers, and roots depending on the goal of the research. The tree dimension variable most often used as a predictor of biomass is diameter at breast height (dbh). The most common height above the soil surface (breast height) where stem diameter is measured is 1.37 m (in United States) but may vary for other countries. When relating biomass to dbh, BEMs can take many forms (see Picard et al. 2015 for examples); however, the most commonly used form is the following power law equation and/or equivalent natural logarithmic transformation of this equation.
\[ Y = aX^b + \varepsilon \quad \text{(Eq. 1)} \]

\( Y = \) biomass (response or dependent variable)

\( a = \) model estimated parameter (normalization or proportionality constant or intercept or allometric constant)

\( X = \) tree dimension variable, dbh (predictor or independent variable)

\( b = \) model estimated parameter ((allometric) scaling coefficient or exponent)

\( \varepsilon = \) error term (random normally distributed additive error term with constant variance)

This model form or equivalent natural logarithmic transformations have been found to provide an accurate representation of the relationship between aboveground biomass and dbh across a wide range of tree sizes from around the world (Whittaker and Woodwell 1968, Tefler 1969, Tritton and Hornbeck 1982, Ter-Mikaelian and Korzukhin 1997, Jenkins et al. 2003, Xiao and Ceulemans 2004, Chojnacky et al. 2014). However, for trees smaller than 1.37 m that lack dbh (seedlings or saplings), very few BEMs have been constructed (Tefler 1969, Roussopoulos and Loomis 1979, Smith and Brand 1983, Williams and McClanahan 1984, Wagner and Ter-Mikaelian 1999, Geudens et al. 2004, Henry et al. 2011). These studies successfully related biomass to other stem measurements, including root collar diameter (stem cross-sectional diameter at groundline), stem diameter just above root collar swelling, and diameter at 15 cm above the root collar.

Development of BEMs for seedlings and saplings is valuable because they can be a major component of understory (Gemborys 1974) and canopy gaps (Ehrenfeld 1980) of mature forests and can be significant components of the vegetative structure in early
successional stages of many ecosystems, including abandoned agricultural fields (Monette and Ware 1983) and recently restored wetlands (Hudson 2010). Additionally, BEMs for seedlings and saplings allow a more inclusive investigation of planted tree development.

Growth

Growth is generally defined as an irreversible change in a measurable quantity (Hunt 1990, Jørgensen et al. 2000). While this definition is simple, there are a multitude of methods designed to describe growth. Common measurable quantities can include size, form, or number (Hunt 1982). These measurable quantities can be applied to a vast range of living and non-living systems from individual bacterium to human populations and from crystals all the way to the entire universe. For the purpose of this paper, growth will focus on groups of planted sapling’s increase in total biomass.

Plant growth analysis has produced many useful methods for describing growth that were developed by researchers from many different backgrounds and schools of thought (Evans 1972, Pommerening and Muszt 2016). These researchers developed methods to address questions specific to their fields, but through time particular methods proved more valuable than others and general trends became apparent. Increases in plant mass through time (referred to as cumulative growth) tends to follow the same general sigmoidal pattern that is found elsewhere in nature (Weiner and Thomas 2001, Pommerening and Muszt 2016). Plants start with little to no detectable increases in mass, then mass increases rapidly. As plants reach maturity, the increase in mass slows (reaches an asymptote) and finally ceases (Hunt 1990). This pattern of growth remains
similar for many types of plants; however, the magnitude and symmetry of the curve can change substantially. Additionally, recent studies have suggested that biomass (or carbon) accumulation of trees may not reach an asymptote (Muller-Landau et al. 2006, Sillett et al. 2010, Stephenson et al. 2014). This study focuses on sapling growth, when biomass is rapidly increasing.

From this general sigmoidal pattern, two biomass growth rates can be determined. The first is termed absolute growth rate (AGR) and is defined as the change in mass over a given time interval (e.g. kg/day). Following the above sigmoidal pattern example, AGR will increase rapidly, peak, rapidly decline, and then slowly taper off. While AGR yields important information, it presents challenges when comparing growth of individuals of different starting masses (Hunt 1982, Hunt 1990, Rees et al. 2010, Pommerening et al. 2016), which is the focus of this study.

Relative growth rate (RGR) can be used to compare individuals of different sizes when calculated correctly (Rose et al. 2009). Relative growth rate is defined as the rate of increase in mass per unit mass per unit of time (g/g/day) or growth per unit mass. Relative growth rate is referred to as an ‘efficiency index’ because it measures the efficiency of plant material to produce new material (Blackman 1919). It is often compared to the rate of compound interest earned on capital in the financial world (Blackman 1919, Hunt 1990). Relative growth rates of trees decline through time as trees grow larger (ontogenetic drift) because of self-shading, increased allocation to structural (non-photosynthetic) components, declines in leaf area ratio, and reduced nutrient availability (Evans 1972, Hunt 1982, South 1995, Rees et al. 2010, Paine et al. 2012, Philipson et al. 2012). Therefore, comparisons of RGR among species or experimental
treatments must account for differences in mass because high values of RGR can occur because plants are either smaller in size or because they are growing faster (Turnbull et al. 2008, Rees et al. 2010, Turnbull et al. 2012).

Tree growth can be positively or negatively influenced by hydrologic conditions depending on the species (Kozlowski 1984). However, there are very few studies that measure total biomass (above and belowground) and calculate AGR and RGR for individual seedlings or saplings grown across a hydrologic gradient (Mitsch and Ewel 1979, Farmer, Jr. 1980, Tang and Kozlowski 1982a,b, Megonigal and Day 1992). Several studies have investigated morphological growth (basal area, stem diameter, tree rings, height, leaf mass, etc.) of trees grown in different hydrologic regimes (Malecki et al. 1983, Mitsch and Rust 1984, Keeland et al. 1997, Kabrick et al. 2005, Anderson and Mitsch 2008, McCurry et al. 2010, Rodríguez-González et al. 2010, Kabrick et al. 2012, Smith et al. 2013). However, a large proportion of these studies fail to account for trees that have a small stem dbh or are not tall enough to have a dbh entirely (Das 2012). Overall, growth rates provide detailed information about how planted trees are responding.

Factors Affecting Tree Survival and Growth

The factors that influence planted tree survival and growth can be divided into three groups based on when they occur relative to outplanting (before, during, after). Outplanting is the act of planting trees or seeds into the ground. There are many factors that will influence the survival and growth of planted trees, including (but not limited to) planting technique, planting density, timing of planting (weather, air and soil temperature), site characteristics, competition/facilitation, browsing/herbivory, soil bulk
density, soil nutrient content, hydrology, site preparation techniques (ripping, ripping, tilling, burning etc.) and stochastic events (pests, diseases, hurricanes, floods, etc.). In addition to these factors, the selection of species and stocktypes is important to the establishment and growth of trees.

The survival and growth of planted trees and the factors that affect these processes change through time. For example, during the first years after planting tree seedlings are most sensitive to environmental factors and most subject to mortality (McLeod and McPherson 1973, Alm and Schantz-Hansen 1974). Mortality becomes important again later in time, following canopy closure, when self-thinning can occur.

**Prior to Outplanting**

Prior to outplanting several factors can greatly influence the survival and growth of trees planted into restored wetland sites, including species selection, planting material selection, and handling and transport of planting material.

**Species selection**

One of the most important decisions made prior to outplanting is which species will be used. Tree species selected to be planted should be those that are found naturally in nearby wetland ecosystems that have conditions (biotic, abiotic, climate, etc.) similar to the restoration site (Nyland 2007). This is especially important for wetland restoration sites having stressful hydrologic conditions. Tree species have unique traits and adaptations that allow for survival and growth in particular environmental conditions. *B. nigra, P. occidentalis, S. nigra*, and *T. distichum* have been shown to be well adapted to
the conditions in recently created wetlands (Spencer et al. 2001, DeBerry and Perry, 2012). An adaptation of these species is that they colonize during dry periods, but can withstand prolonged saturation and inundation following establishment. Some hardwood species (*Quercus* spp. and *Carya* spp.) are planted following wetland creation; however, these species tend to naturally occur later in forest development (Spencer et al. 2001).

Several authors have investigated the survival and growth of various tree species planted in environmental conditions similar to those present in recently restored wetlands. McLeod (2000) began a series of experiments in 1990 that focused on 24 tree species for restoration in bottomland hardwood forests in South Carolina. McLeod et al. (2006) provided a ten year review of the series of experiments. The experimental trials focused on fertilizer, initial morphology, stocktype, tree shelters, root pruning, competition control and *S. nigra* control on the survival and growth of various tree species and stocktypes. Results from this study suggested that woody species should be matched to the hydrologic conditions (due to elevation differences). *Taxodium distichum* and *N. aquatic* were found to be the most flood tolerant species. *F. pennsylvanica, Carya aquatic* (water hickory) and *Quercus lyrata* (overcup oak) were found to be moderately flood tolerant, while *Q. michauxii, Q. texana,* and *Q. phellos* were found to survive better in higher elevations. Stanturf et al. (2004) similarly suggested that matching species to site hydrology is a key factor for success in afforestation of bottomland hardwood forests. Farmer (1980) compared first year growth of six deciduous species grown in nursery conditions and found significant difference between the early successional species (*L. tulipifera* and *Pinus serotina* (pond pine)) and late successional species (*Q. rubra, Quercus montana* (chestnut oak)), *Q. alba,* and *Quercus ilicifolia* (bear oak)) with regard
to dry weight, leaf growth rate and net assimilation rate. The early successional species had higher growth rates, net assimilation rates and high investment in leaf area.

The selection of species is of greater importance than stocktype selection. The selection of species can influence the stocktype selection, as not all stocktypes are commercially produced for all species. Both species and stocktype need to be matched to site biotic and abiotic conditions as well as local climate conditions (Nyland 2007).

Selection of Planting Material

Following the selection of species, the selection of planting material is an important factor that can greatly influence the survival and growth of planted trees (Nyland 2007). Many studies have focused on the appropriate stocktype to ensure survival and growth of planted trees for many different environmental conditions; however, few have investigated how stocktype influences survival and growth in conditions similar to restored wetlands.

Burdett et al. (1984) investigated differences in root growth capacity, height growth, and needle length between container grown (336 mL container) and bare root (2 or 3 year olds) *Picea glauca* (white spruce) seedlings. Container grown seedlings had greater root growth capacity, height growth and needle length compared to bare root seedlings.

Grossnickle and Blake (1987) examined the water relations and root growth of *P. banksiana* and *Picea mariana* (black spruce) container and bare root seedlings during the first season following outplanting on a boreal cut-over site. Bare root seedlings of both species had greater resistance to water-flow through the soil-plant-atmosphere continuum.
early in the growing season. However, this trend did not persist through the growing season. At the end of the growing season both stocktypes had similar new root growth.

Denton (1990) investigated the effect of stocktype on the growth of *T. distichum* in a restored forested compensatory mitigation site in Florida. The results suggest that in order to obtain 33% canopy closure the initial costs could be reduced by planting smaller trees (1-gallon container) at ~2500 stems/ha as opposed to planting 7-gallon trees at ~1000 stems/ha.

A large scale long term study by McLeod (2000) found that bare root seedlings had similar survival to more expensive containerized seedlings of *F. pennsylvanica*, *N. aquatica*, and *T. distichum* when planted in a thermally impacted bottomland hardwood forest.

South et al. (2005) investigated the effect of several containers and bare root seedlings on the survival and growth of *P. palustris* outplanted on old-fields and cutover sites. The results suggest that containerized seedlings had 20% better survival than bare root seedlings having similar root-collar diameters. Mesh-covered plugs had lower field performance compared to the three hardwall containers and styroblock containers. Low root growth potential and high root bound index were correlated with low survival.

A meta-analysis of 122 trials comparing survival between bare root and containerized stock planted across a variety of upland sites found that containerized stock had greater survival than bare root stock in 60.7% of the trials (Grossnickle and El-Kassaby 2015). Pinto et al. (2011a) found that increasing the size of containers for *Pinus ponderosa* (ponderosa pine) increased total height and basal area following outplanting at a mesic site.
Overall, the response of planted trees to stocktype selection is highly variable and dependent upon the species and environmental conditions. How the stocktype is handled prior to outplanting can also influence survival and growth.

**Handling and Transport of Planting Material**

The final factor to be considered prior to outplanting and once the planting stock is selected is the handling and transport of seeds or seedlings to the restoration site. The stocktype selection will determine the appropriate handing techniques used. For example, bare root seedlings should be kept moist the entire time prior to outplanting and should avoid high temperatures that can cause desiccation. Inappropriate handling of planting stock can greatly reduce the potential for survival and growth following outplanting (McKay 1997).

**During Outplanting**

During outplanting the methods used and their successful implementation can influence the survival and growth of trees planted in restored wetlands. The factors that can influence survival and growth include the timing of planting, density and arrangement of planting, and the actual placement of trees in the ground. The optimal time to plant trees and other woody vegetation in the Mid-Atlantic region of the US is fall or early spring. By avoiding planting during winter or summer, trees are able to become established prior to high or low (freezing) temperatures or fluctuations in water levels. Deciduous trees are planted during dormancy to reduce water loss due to evapotranspiration (Landis et al. 2010).
Planting Methods

The actual planting of seedlings into the ground is important for their survival and growth. Incorrectly planting seedlings, too deep, too shallow or leaving a pocket of air around the roots can negatively affect survival and growth (Landis et al. 2010).

Planting Arrangement

The density and arrangement of planting is important to ensure appropriate density in the future and to avoid unnecessary woody competition. A number of studies have focused on how initial planting of economically important trees influences the final timbered product. Smith and Strub (1991) found that increasing initial planting density (from 4.6 x 4.6m to 1.8 x 1.8 m spacing) of southern Pinus spp. (P. taeda and Pinus elliottii (slash pine)) had a negative effect on size, value of the final product, as well as the cost of harvesting and cultural treatments.

The USACE Norfolk District and VADEQ (2004) makes several recommendations as to initial planting densities to establish forests. First they recommend considering recruitment from surrounding areas when the site is narrow, whether the site is exposed to flood waters bearing seeds, whether the original soils and hydrology are not significantly altered, or if a seedbank is present. When direct seeding Quercus spp., they recommend planting 2471-3707 acorns/ha. A 35% germination rate would result in 300-500 seedlings/ha. They recommend planting bare root seedlings at a density of 272-741 stems/ha when colonization from surrounding seed sources is
expected and suggest that lower planting densities of containerized saplings could be used since containerized saplings have higher survival rates.

Few studies have investigated the influence of initial planting density on survival and growth of planted trees. Bullock and Burkhart (2005) investigated the influence of planting density (757 to 6,727 trees/ha) on *P. taeda* stem diameter and found that of the 23.2% of sampled plots exhibiting spatial dependencies, 73.1% showed negative correlations. This suggests that increases in stem density lead to smaller diameter *P. taeda*.

Several authors have suggested planting late successional species (*Quercus* spp., *Carya* spp.) under planted or naturally colonizing pioneer (early successional) tree species to increase the survival and growth of the late successional species (Clewell and Lea 1989). The underlying idea is that the establishment of early pioneer tree species, often called nurse species, can create favorable conditions for the establishment of later successional species. The favorable environmental conditions provided by the nurse species are shade, moderate temperature, moderate moisture extremes, reduction of competing herbaceous vegetation, organic matter added to the soil, decreased soil compaction in the rooting zone, fixed atmospheric nitrogen, increased vertical structural complexity, increased forest diversity, possible reduced costs (Clewell and Lea 1989, Dulohery et al. 2000, Dey et al. 2010).

Dulohery et al. (2000) investigated the effects of a *S. nigra* overstory on planted seedlings of *F. pennsylvanica, T. distichum, N. aquatica, and Q. michauxii*. During the first 2 years the *S. nigra* overstory provided minor growth enhancements; however, by age 5 there was no effect on seedling heights. McLeod et al. (2001) investigated the
response of container grown *Q. lyrata*, *T. distichum*, and *C. aquatica* seedlings to several treatments involving *S. nigra* overstory. Results suggested that after three years survival was not influenced by the *S. nigra* overstory. The heights of *C. aquatica* and *Q. lyrata* were not affected by the *S. nigra* overstory. Twedt (2006) found that when *Quercus* spp. plantings were supplemented with fast growing early successional trees the species diversity, stem density, and maximum tree height were increased. Stanturf et al. (2009) interplanted *Q. texana* with *Populus deltoides* (eastern cottonwood) and found that it did not facilitate the development of the *Q. texana* seedlings.

Dey et al. (2010) provided a summary of many new techniques for afforestation of old-field bottomland forests, including interplanting later successional species (*Quercus* spp.) with early successional species (*P. deltoides*) to mimic natural succession. Overall, the *Q. texana* were able to survive and grow successfully under the canopy of the *P. deltoides* and should be able to replace the *P. deltoides* following harvest.

**Following Outplanting**

Following outplanting there are many factors that can influence survival and growth of planted trees in restored wetlands, including site physical, chemical and biological characteristics, herbaceous and woody competition, browsing/herbivory, and stochastic events (storms, drought, etc.). During the first years after planting tree seedlings are most sensitive to environmental factors and most subject to mortality (McLeod and McPherson 1973, Alm and Schantz-Hansen 1974).

The environmental characteristics of restored wetlands are influenced by prior land use and site preparation techniques (ripping, tilling, burning, fertilizing, etc.). Poor
survival and growth of planted trees can result from unfavorable site conditions, including inappropriate hydrology, low soil organic material content, low soil nutrients, high soil bulk density, and increased rock fragments (Stolt et al. 2000, Campbell et al. 2002, Brueland and Richardson 2004, Bergshneider 2005, Daniels et al. 2005, Bailey et al. 2007, Nyland 2007).

Hydrology

In natural and restored wetlands, low oxygen soil conditions associated with long hydroperiods are among the greatest stressors on wetland vegetation (Mitsch and Gosselink 2007), including planted trees. Saturated or flooded soil conditions lead to the removal of plant available oxygen from the soil pore space (Brady and Weil 2002). This leads to a lack of aerobic respiration in roots, which decreases the energy available for trees to maintain functions of existing tissues (Hale and Orcutt 1987), and many trees exhibit reduced growth when flooding exceeds a few weeks during the growing season (Kozlowski 1984). Kozlowski (1984) provided an in depth review of the effects of flooding on tree seed germination, seedling establishment, shoot growth, cambial growth, root growth, biomass changes, morphological changes, and mortality. Several studies have investigated the effect of hydrology on tree survival, growth, morphology, and physiology following outplanting.

Megonigal and Day (1992) investigated the biomass production, carbon allocation to roots and shoots, and root-system morphology of T. distichum seedlings in response to continuous and periodic flooding in large watertight enclosures. After three growing seasons, there was no significant difference in total biomass between the two treatments.
However, saplings in the continuously flooded treatment had lower root-to-shoot ratios, shallower roots, lower belowground production, and higher aboveground production than those in the periodically flooded treatment. The authors concluded that the saplings in the continuously flooded treatment invested fewer resources belowground because of the abundant water and dissolved nutrients available in the rooting zone.

Niswander and Mitsch (1995) planted 10 tree species in a created wetland along a hydrologic gradient and found that trees located in the shallow water zone were either dead or severely stressed, trees in the wet meadow were healthy, and the trees in the extreme upland were the largest and had the densest foliage.

Perry et al. (1996) investigated survival and growth of planted trees in a created forested wetland in Maryland and found that the canopy diameter increased over two years but the height decreased and that mortality was lower than other created forested wetlands. These results suggest that dieback and re-sprouting are common in created wetlands and low mortality may have resulted from less hydrologic stress.

Burkett et al. (2005) investigated the effect of flooding (two elevations) on Q. texana bare root seedlings, seedlings grown in cones, and seedlings inoculated with vegetative mycelia planted into Sharkey clay soil. The overall results were that in the lower elevation the mycorrhizal inoculated container seedlings had increased survival; however, at both elevations the bare root seedlings had greater height after five years.

In created perched wetlands, Pennington and Walters (2006) found that the survival and growth of planted trees was increased when trees were planted in transitional zones between the created wetland and upland. These transitional zones were
characterized by lower soil saturation, higher soil redox potential, and distinct herbaceous vegetation.

Dickinson (2007) investigated the influence of soil amendments and microtopography in a created tidal freshwater swamp on various vegetation parameters, including planted tree morphological responses. The results from this study suggested that *T. distichum* tubelings planted in soil pits (increased water stress) had increased height, root collar diameter, and buttressing compared to those grown at higher elevations. Those grown at higher elevations had increased roots of greater length. *T. distichum* is a unique tree because of its ability to survive and grow under very stressful hydrologic conditions where other trees may not.

McCurry et al. (2010) investigated the effect of early season flooding on *Q. lyrata, Q. texana* and *Quercus phellos* (willow oak) seedlings and found *Q. lyrata* to have the highest flood tolerance followed by *Q. texana* and finally *Q. phellos*.

**Soil Physical and Chemical Characteristics**

Several studies have investigated the effect of soil chemical and physical characteristics on the survival and growth of planted trees. Soil compaction leads to increases in bulk density, runoff, and erosion, breakdown of soil aggregates, and decreasing porosity, aeration and infiltration (Brady and Weil 2002). Soil compaction is particularly important at CMS because construction methods typically increase soil compaction (Galatowitsch and van der Valk 1996, Whittecar and Daniels 1999, Campbell et al. 2002, Bruland and Richardson 2005, Daniels and Whittecar 2011). Many studies have found that compacted soil reduces the survival and aboveground and belowground
growth of planted trees (Albery et al. 1984, Kozlowski 1999, Siegel-Issem et al. 2005) In particular, soil compaction reduces water and mineral absorption in woody plants and limits the ability of roots to penetrate the soil (Kozlowski 1999). Several authors have suggested that reducing soil compaction in restored wetlands will improve the survival and growth of planted trees as well as the overall functioning of the restored wetland (Daniels and Whittecar 2011). The Piedmont region of Virginia is characterized by clayey soils that typically have higher bulk densities than other soil textures and lower soil organic matter. These soils are often exposed during construction.

Soil organic matter (SOM) content and/or soil carbon content is often low in restored wetlands when compared to natural wetlands (Bishel-Machung et al. 1996, Galatowitsch and van der Valk 1996, Shaffer and Ernst 1999, Whittecar and Daniels 1999, Stolt et al. 2000, Campbell et al. 2002). Low SOM has been shown to contribute to poor survival and growth of planted trees in restored wetlands (Bergshneider 2005, Daniels et al. 2005, Bruland and Richardson 2006). However, several studies have found that standing crop biomass does not increase when SOM is added (Cole et. 2001, Anderson and Cowell 2004, Bailey et al. 2007).

Bailey et al. (2007) investigated the effect of organic matter loading rates and elevation in a created wetland on several vegetation responses, including the growth of planted B. nigra and Q. palustris. Results from this study suggest that the early growth of planted trees responded to both SOM loading rates and hydrology related to elevation. In the lower elevations (increased water stress) the tree growth rates were stunted.

Planted tree survival and growth is affected by presence and abundance of soil nutrients. Stolt et al. (2000) found that plant growth may be limited in restored wetlands
because of low levels of nitrogen. In a greenhouse experiment investigating the effect of flooding and soil nutrients on *T. distichum* and *N. aquatica* growth, Effler and Goyer (2006) found that flooding in combination with low soil nutrients reduced growth, while flooding in combination with fertilization lead to similar growth of trees grown without flooding or fertilization.

Overall, poor soil conditions can reduce the survival and growth of planted trees and can have compounding negative effects when other environmental stressors are present.

*Competition*

The spatial location of herbaceous vegetation and other trees in relation to planted trees can lead to competition for light, water, nutrients, CO$_2$, O$_2$, and space. Competition between planted trees and herbaceous vegetation has been found to negatively affect tree survival, growth, morphology and physiology following outplanting. Species and stocktypes may respond differently to herbaceous and woody competition.

There are several theories that can be used to describe competitive interactions among plant species and how these processes lead to observed plant community structure (MacArthur & Wilson 1967, Grime 2002, Tilman 1988, Taylor et al. 1990, Grace 1990). These theories have been instrumental in determining the appropriate methods for assessing competition among plants.

Gjerstad et al. (1984) reviewed the literature available at the time and found several studies that suggested herbaceous competition control leads to increased survival and growth of planted tree seedlings. Britt et al. (1991) investigated herbaceous control
around *P. taeda* and found that during the first two years following outplanting the trees with low herbaceous competition had significantly greater root collar diameter relative growth rate and net assimilation rate. Morris et al. (1993) found that competition for water was the dominant factor in reducing the growth of *P. taeda* that was planted among several species of herbaceous competitors. Davis et al. (1998) suggested that any factor that reduces soil water content is likely to increase competition intensity. Davies et al. (1999) investigated the effect of herbaceous competition along a water-light-nitrogen gradient and found that seedling survival of *Q. macrocarpa* and *Quercus ellipsoidalis* (northern pin oak) was significantly greater when herbaceous vegetation was removed in the wetter shaded plots. Schweitzer et al. (1999) found that weed control (fabric mat and chemical) increased survival of bare root *Q. texana*, *F. pennsylvanica*, and *Diospyros virginiana* (common persimmon).

Twedt and Wilson (2002) found that physical weed barriers increased the survival of *P. deltoides* and *P. occidentalis*, while chemical weed control adversely impacted *P. occidentalis* survival. Groninger et al. (2004) found that the removal of herbaceous competition using herbicide increased the height and diameter growth of planted *F. pennsylvanica* in a bottomland hardwood site. In created wetlands, Pennington and Walters (2006) suggested targeting transitional vegetation zones (between the created wetland and upland) for tree planting to increase survival and growth. These zones were identifiable by vegetation and had characteristics that increase tree performance. Gardiner et al. (2007) found that herbaceous competitions reduced the survival of *Q. texana* by 8%, height growth by 69%, and root collar diameter by 61% after 2 years compared to trees grown without competition. Pinto et al. (2012) investigated the effect of moisture
stress caused by vegetative competition on three stocktypes of *P. ponderosa*. The results suggest that small stocktypes had low survival when exposed to low moisture conditions caused by herbaceous competition, while larger stock had somewhat improved survival. They concluded that appropriate moisture is critical for survival and that herbaceous vegetation competes substantially for moisture.

Overall, herbaceous competition can lead to decreases in survival and growth of planted trees, but certain methods of herbaceous vegetation control can also reduce survival and growth.

*Herbivory and Browsing*

Survival and growth of planted trees can be significantly decreased by herbivory (Myster and McCarthy 1989, Stange and Shea 1998, Conner et al. 2000, Sweeney et al. 2002). Many methods have been employed to reduce both herbivory and/or herbaceous competition around planted trees including; tree tubes, tree shelters, weed mats, herbicide, site fencing, trapping and hunting, chemical deterrents, attracting predators and removing herbivore cover. These methods have been used in many forest reestablishment projects with mixed levels of success (Myster and McCarthy 1989, Stange and Shea 1998, Schweitzer et al. 1999, Conner et al. 2000, McLeod 2000, Sweeney et al. 2002, Taylor et al. 2004). Often these methods reduce herbaceous competition and/or herbivory, but can lead to other deleterious effects.
Stochastic Events

While some of the factors that influence survival and growth of planted trees can be selected for and controlled, stochastic events, by their nature, cannot. Storms, wind, flooding (Day 1987), drought (Davis and Trettin 2006) and pathogens (insects, fungus, bacteria, viruses) can severely impact planted trees. Restoration plans should always include monitoring of planted material to ensure that planted trees are surviving and growing.

Study Species


The tree species planted in this study include *B. nigra, L. styraciflua, P. occidentalis, S. nigra, Q. bicolor, Q. palustris*, and *Q. phellos*. These species and some of their characteristics are introduced below. The Atlantic and Gulf Coastal Plain wetland indicator status is also included for each species (Lichvar et al. 2012, Lichvar 2013).

*Betula nigra* L.

*Betula nigra* (river birch) (FACW) is a deciduous tree 25 m to 30 m in height, with a stem diameter of 50 cm to 150 cm. *B. nigra* commonly features multiple trunks,
with highly variable, dark gray or brown, scaly bark which sometimes exfoliates in papery sheets. Leaves are alternate, serrated ovals that range from 4 cm to 8 cm in length and 3 cm to 6 cm in length. *Betula nigra* is native to the eastern United States and ranges from New Hampshire south to northern Florida and west to southern Minnesota and eastern Texas. *Betula nigra* is most often found growing in riparian zones, floodplains, wetlands and other habitats featuring moist alluvial soils (Radford et al. 1968, Grimm 1983).

*Betula nigra* seeds are consumed by a number of bird species (*Bonasa umbellus* (ruffed grouse) and *Meleagris gallopavo* (wild turkey)), leaves and twigs are consumed by *Odocoileus virginianus* (white-tailed deer) and host the fungus *Gloeosporium betularum* (Anthracnose leaf blight), and *Phoradendron serotinum* (Christmas mistletoe) colonizes branches (Burns and Honkala 1990, Sullivan 1993, Van Dersal 1938, Horst 2001). European hornets (*Vespa crabro*) were observed removing bark and consuming sap in this study consistent with findings from Santamour and Greene (1986). The damage also attracted a variety of other insects (hornets, bees, flies and beetles). Witch-Hazel bud gall aphid (*Hamamelistes spinosus*) over winter on river birch and feed on young leaves, bronze birch borer (*Agrilus anxius*) feed on vascular tissue, and many caterpillars (including tent caterpillars) feed on and reproduce in branches and foliage (Johnson and Lyon 1988, Adkins et al. 2012). Immature larvae of the birch leafminer (*Fenusa pusilla*) feed between the leaf surface (Latimer and Close 2014). *Acrobasis betulivorella* (species of snout moths) larvae feed on immature terminal leaves of *B. nigra* (Johnson and Lyon 1988).
*Liquidambar styraciflua* L.

*Liquidambar styraciflua* (sweetgum) (FAC) is a deciduous tree ranging from 20 m to 35 m in height, with trunk diameters reaching 2 m. Bark is light brown and deeply fissured with scaly ridges. Leaves range from 7 cm to 19 cm in length and resemble *A. rubrum* leaves with five pointed lobes, except they are alternate rather than opposite. Leaves are dark green and highly glossy, turning orange and red in autumn. In the United States, *L. styraciflua* is a common, southern hardwood and ranges from southern New York south to central Florida and west to Missouri. *Liquidambar styraciflua* is also found in Mexico, Central America, and South America (Radford et al. 1968, Grimm 1983).

*Liquidambar styraciflua* seeds are eaten by birds (*Colinus virginianus* (northern bobwhite), *M. gallopavo* (wild turkey) and several quail), *Sciurus carolinensis* (eastern gray squirrel), and *Tamias striatus* (eastern chipmunk) (Martin et al. 1951, Burns and Honkala 1990, Coladonato 1992, Van Dersal 1938). The small branches and buds are consumed by *O. virginianus* (white-tailed deer) (Harlow et al. 1975, Coladonato 1992) and the bark and cambium are eaten by *Castor canadensis* (North American Beaver) (Martin et al. 1951, Silberhorn 1992). Dead sweetgum trunks (snags) are used by a variety of birds as nesting, perching and foraging areas (Dickson et al. 1983). Many fungi, bacteria, and other parasites use *L. styraciflua* as a host and many insects and beetles feed on and live in leaves and bark of living and decaying trees (Johnson and Lyon 1988, Burns and Honkala 1990). Additionally *Meloidogyne* sp. (nematode) feed on the roots (Horst 2001). The treehopper (*Stictocephala militaris*) lives on sweetgum for its entire life cycle (Ebel and Kormanik 1966).
**Platanus occidentalis L.**

*Platanus occidentalis* (American sycamore) (FACW) is a large tree 30 m to 40 m in height and 1.5 m to 2 m in trunk diameter. The bark of the trunk and larger limbs is highly rigid and flakes off as branches grow, leaving the surface a mottled mixture of white, gray and brown. Leaves are alternate with three to five lobes, bright green on top and paler on the underside. In the fall, they turn brown and wither. *Platanus occidentalis* ranges from Maine, south to Texas, and as far west as Nebraska. The tree is typically found growing in riparian and wetland soils, but also appears in fairly most, upland soils (Radford et al. 1968, Grimm 1983).

Seeds of *P. occidentalis* are eaten by *Haemorhous purpureus*, (purple finch), and *Spinus tristis* (American goldfinch), *Pecile* spp. (chickadees), *Junco hyemalis* (dark-eyed junco), *Anas platyrhynchos* (mallard), *Ondatra zibethicus* (muskrat), *Castro canadensis* (North American Beaver) and *Sciurus carolinensis* (eastern gray squirrel) (Van Dersal 1938, Martin et al. 1951, Sullivan 1994). *P. occidentalis* is of low value as food for *O. virginianus* (white-tailed deer) and *Meleagris gallopavo* (wild turkey) (Sullivan 1994, Allen and Kennedy 1989). *P. occidentalis* often develop hollow trunks as they grow, which can provide shelter for waterfowl and the largest cavities can be used by *Ursus americanus* (American black bear) (Allen and Kennedy 1989, Sullivan 1994). Cavities can also be used by *Strix varia* (Barred owl), *Megascops asio* (Eastern screech-owl), and *Myiarchus crinitius* (great crested flycatcher) (Hardin and Evans 1977, Allen 1987, Sullivan 1994). *Aix sponsa* (wood duck) uses *P. occidentalis* for nesting (Dugger and

**Salix nigra** Marshall

*Salix nigra* (black willow) (OBL) is the largest North American species in the genus *Salix*, growing between 10 m to 30 m in height and 50 cm to 80 cm in trunk diameter, with very dark, brown bark that becomes increasingly fissured with age. Young shoots grow quickly and are light green or brown in color. The species’ leaves are simple and alternate, growing 5 cm to 15 cm in length and 0.5 cm to 2 cm in width. Leaves are lighter on the bottom with a serrated edge. *Salix nigra* is native to eastern North America, ranging from southern Ontario, south to Florida, and west to Minnesota. *Salix nigra* is typically found in wetlands, riparian areas, and other poorly drained sites with alluvial soils (Radford et al. 1968, Grimm 1983).

*Salix nigra* provides habitat to a wide array of organisms. *Sphyrapicus varius* (yellow-bellied sapsucker) pecks holes in bark to feed on the sap (Burns and Honkala 1990, Tesky 1992). The fungus *Pollaccia saliciperda* lives exclusively on members of the Salicaceae family including *S. nigra* (Burns and Honkala 1990, Row and Geyer 2010). Mistletoes (*Phoradendron* spp.) colonize *S. nigra* branches (Burns and Honkala 1990). *O. virginianus* (white-tailed deer), *Cercus canadensis* (elk), *Castro canadensis* (North American beaver) and other rabbits and rodents eat the twigs, leaves and buds (Van Dersal 1938, Martin et al. 1951, Tesky 1992, Row and Geyer 2010). They flower early in spring and are one of the first plants to provide nectar for bees and other insects (Row and Geyer 2010). The larvae of *Limenitis archippus* (viceroy) and *Limenitis*
arthemis (red-spotted purple) among others live on *S. nigra* (Row and Geyer 2010). Numerous caterpillars, moths, sawflys, nematodes, beetles, weevils and borers feed and live on *S. nigra* (Johnson and Lyon 1988, Burns and Honkala 1990, Horst 2001, Row and Geyer 2010).

**Quercus bicolor** Willd.

*Quercus bicolor* (swamp white oak) (FACW) is a small; 20 m to 25 m in height and 50 cm to 70 cm in trunk diameter. The bark is dark gray, scaly and flat-ridged, often resembling that of *Q. alba*. Leaves are lobed with five to seven lobes on each side, ranging from 12 cm to 18 cm in length and 7 cm to 11 cm in width. *Quercus bicolor* is found from southern Maine, south to South Carolina, and west to Minnesota. It typically grows in forested wetlands, riparian zones, or other poorly drained soils (Radford et al. 1968, Grimm 1983).

Acorns of *Q. bicolor* are eaten by squirrels, mice, *O. virginianus* (white-tailed deer), *Castro canadensis* (North American beaver), and *Ursus americanus* (American black bear), other rodents and a variety of birds (Nixon et al. 1970, Burns and Honkala 1990, Snyder 1992, Nesom 2009).

**Quercus palustris** Münchh.

*Quercus palustris* (pin oak) (FACW) is a smaller member of the Lobatae (red oak) section of the *Quercus* family. The species grows 18 m to 22 m in height and 50 cm to 70 cm in trunk diameter with grayish-brown bark that features broad, shallow fissures. The tree has a distinctive branching pattern highlighted by drooping lower branches,
horizontal middle branches, and ascending upper branches. Leaves are lobed with five to
seven lobes with bristles at the tip, and range from 5 cm to 16 cm in length and 5 cm to
12 cm in width. Young trees do not drop their leaves until new growth appears in the
spring. *Quercus palustris* is native to eastern North America, and is found from
Connecticut, south to Georgia, and as far west as eastern Kansas. The species is typically
found in poorly drained acidic, clay soils (Grimm 1983).

Acorns of *Q. palustris* are consumed by woodpeckers, *Anas platyrhynchos*
(mallard), *Aix sponsa* (wood duck), *O. virginianus* (white-tailed deer), squirrels, *Meleagris
gallopavo* (wild turkey), *Cyanocitta cristata* (blue jay) and other waterfowl (Burns and

*Quercus phellos* L.

*Quercus phellos* (willow oak) (FACW) is a medium sized tree belonging to the
*Lobatae* section of the *Quercus* family. *Quercus phellos* grows quickly and reaches 20 m
to 30 m in height and 1 m to 1.5 m in trunk diameter. In younger specimens, the bark is
dark gray and smooth, and then becomes even darker, and irregularly fissured, with
increasing age. Leaves are distinctive from other *Quercus* spp., being shaped like *Salix*
leaves. Leaves are green on top and paler and hairy on the bottom ranging from 5 cm to
12 cm in length, and 1 cm to 2.5 cm in width. *Quercus phellos* is native to eastern North
America and ranges from southern New York, south to northern Florida, and west to
eastern Kansas. The species typically grows on floodplains and riparian sites, or other
poorly drained soils that periodically become flooded (Radford et al. 1968, Grimm 1983).
Acorns of *Q. phellos* are eaten by ducks, *Meleagris gallopavo* (wild turkey), *Glaucous Volans* (southern flying squirrel) and other squirrels, *O. virginianus* (white-tailed deer), *Urocyon cinereoargenteus* (gray fox), *Meleagris gallopavo* (wild turkey), *Quiscalus quisca* (common grackle), *Colaptes auratus* (northern flicker), mice (*Peromyscus* spp.), *Cyanocitta cristata* (blue jay), and *Melanerpes erythrocephalus* (red-headed woodpecker) (Van Dersal 1938, Cypert and Webster 1948, Burns and Honkala 1990, Carey 1992, Moore 2002).

These three *Quercus* spp. host a large number of caterpillars, moths, sawflies, acorn weevils, beetles, leafminers, leafrollers, wood borers, gall-wasps, scale insects, aphids, nematodes, midges, sap-suckers, mites, fungi, bacteria and viruses (Johnson and Lyon 1988, Burns and Honkala 1990, Chong et al. 2012).
Structure of Dissertation

In Virginia, many forested headwater wetlands have been destroyed or altered. Restoration of FHW has occurred following the recognition of their importance in the landscape; however, these attempts have not been successful in returning lost ecological structure, functions and services. In particular, successful establishment of trees has proven difficult. There are limited recommendations regarding selection of species and stocktypes with associated economic costs for planting trees in restored FHW. Additionally, there is limited information regarding the biomass accumulation rates of trees planted across hydrologic gradients that has precluded the development of appropriate woody EPSs for CMS. The original research conducted to address these limitations is presented in four chapters followed by a concluding chapter. The overarching goal of this dissertation was to improve the probability of ecologically successful FHW restoration.

CHAPTER 2: EXPERIMENTAL FORESTED WETLAND PLANTED TREE SURVIVAL AND MORPHOLOGY

The objectives of this chapter were to investigate the differences in survival and development of morphological structure (stem diameter, crown diameter, and height) of planted trees over 5 years in response to; 1) species selection, 2) stocktype selection, and 3) soil physical, chemical and hydrologic conditions. The hypotheses of this chapter were; 1) species’ responses (survival and morphology) would vary based on hydrologic treatments, 2) stressful hydrologic treatments would reduce survival and morphological growth, 3) the early successional species would have greater survival and growth than the
late successional (*Quercus* spp.) species, and 4) the larger stocktype (1-gallon container) would have greater survival and growth than the smaller stocktypes (bare root and tubeling).

CHAPTER 3: WOODY BIOMASS DEVELOPMENT OF SEVEN MID-ATLANTIC SPECIES GROWN UNDER THREE HYDROLOGIC CONDITIONS OVER 6 YEARS

The objective of this chapter was to develop biomass estimation models for the seven study species using destructive harvests. In order to reach this objective the following hypotheses were tested; 1) belowground biomass has a non-linear relationship with aboveground woody biomass and 2) total aboveground and belowground biomass has a non-linear relationship with stem cross-sectional diameter at groundline. The resulting biomass estimation model was used to estimate the biomass of all living trees in order to evaluate species and stocktype performance across hydrologic treatments after 6 years.

CHAPTER 4: EFFECT OF HYDROLOGIC CONDITIONS ON ABSOLUTE AND RELATIVE GROWTH RATES OF SEVEN WETLAND TREE SPECIES

The objective of this chapter was to determine the absolute and relative biomass growth rates of the seven study species over six years in response to soil physical, chemical and hydrologic conditions. Absolute and relative growth rates were compared among species and hydrologic treatments, with similar hypotheses to Chapter 2.
CHAPTER 5: DEVELOPING AN ECOLOGICAL PERFORMANCE STANDARD FOR WOODY VEGETATION IN COMPENSATORY MITIGATION WETLANDS OF VIRGINIA

The objective of this chapter was to develop a woody ecological performance standard for use in forested wetland compensatory mitigation site monitoring. In order to address this objective the following hypotheses were tested; 1) morphological measurements are linearly related to each other and 2) existing woody ecological performance standards for Virginia are statistically related to biomass accumulation. Based on the results of testing these hypotheses, an additional ecological performance standard was developed.

CHAPTER 6: ECONOMIC ANALYSIS AND OVERALL CONCLUSIONS

The objective of this chapter was to evaluate the economic cost associated with planting trees in restored forested wetlands and to summarize the results from the individual chapters to draw overarching conclusions.
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CHAPTER 2: EXPERIMENTAL FORESTED WETLAND PLANTED TREE

SURVIVAL AND MORPHOLOGY
Abstract

The destruction or conversion of forested wetland ecosystems has resulted in loss of valuable ecosystem structures, functions and services from the landscape. Assisting the recovery of these degraded ecosystems through restoration practices is often unsuccessful. A major challenge associated with forested wetland restoration has been establishment and growth of trees, driven by a lack of planting recommendations. The purpose of this study was to investigate the differences in survival and development of morphological structure (stem diameter, crown diameter, and height) of planted trees over 5 years in response to: 1) species selection 2) stocktype selection and 3) soil physical, chemical and hydrologic conditions. Seven native wetland trees (*Betula nigra* L., *Liquidambar styraciflua* L., *Platanus occidentalis* L., *Salix nigra* Marshall, *Quercus bicolor* Willd., *Quercus palustris* Münchh., and *Quercus phellos* L.) were planted using three stocktypes (bare roots (BR), tubelings (TB), and 1-gallon containers (GAL)) in a large scale, hydrologically manipulated field experiment. Hydrologic manipulations were applied over three 0.7 ha cells and included: 1) ambient treatment received only precipitation, 2) saturated treatment was saturated within the root-zone (10 cm) for a minimum of 90% of the growing season, 3) flooded treatment was inundated above the root crown for a minimum of 90% of each year and had increased amounts of clay, higher bulk density and decreased nitrogen and phosphorus concentrations compared to the ambient and saturated treatments. Results from the flooded treatment suggest that planting primary successional species (especially *S. nigra*) with larger containerized stocktypes may enhance the return of woody ecosystem structure and ecological functions in stressful environmental conditions of recently restored forested wetlands. In less stressful environmental conditions (ambient and saturated treatment), the bare root stocktype grew similarly to the gallon stocktype, suggesting that the less expensive bare root stocktype could be used successfully. These results apply to a variety of tree planting situations including carbon sequestration projects, wildlife habitat creation and other conservation projects across the landscape.
Introduction

Palustrine forested wetlands, the most abundant wetland type in Virginia, make up a majority of wetland losses in Virginia over the past few decades (Tiner and Finn 1986, USGS 1999, Tiner et al. 2005). These wetlands are valued for the ecological functions and services they provide (Sather and Smith 1984, NRC 1995) including but not limited to, accumulation and retention of sediments (Hupp 1993, Craft and Casey 2000), accumulation, retention and cycling of elements (carbon, nitrogen, phosphorus, etc.) (Craft and Casey 2000, Mitsch et al. 2012, Rheinhardt et al. 2012), maintenance of plant communities (Walbridge 1993, Rheinhardt et al. 2000), provision of animal habitat (Morley 2008), water quality enhancement (Whigham et al. 1988), and surface and subsurface water storage (Brooks et al. 2013). The destruction or conversion of forested wetland ecosystems removes the ecosystem functions and services they provided from the landscape.

Realization of these lost functions and services has led to the restoration of wetlands for a variety of reasons, including but not limited to, compensation for Clean Water Act Section 404 permitted impacts to existing wetlands (wetland compensatory mitigation), state and federal goals (Chesapeake 2000 Agreement), re-establishing bird habitat (Ducks Unlimited) and/or agricultural easements (Agricultural Conservation Easement Program). Regardless of the underlying reason, many attempts at forested wetland restoration have not been ecologically successful (i.e. ecosystem structures, functions and services have not been restored) (Atkinson and Cairns Jr. 2001, Brown and Veneman 2001, Cole et al. 2001, Sudol and Ambrose 2002, Atkinson et al. 2005, Atkinson et al. 2010, Moreno-Mateos et al. 2012, Stefanik and Mitsch 2012). One of the
major challenges associated with forested wetland restoration has been establishment and growth of trees. Numerous studies have found that tree density and tree growth were significantly lower for restored sites as compared to conditions prior to conversion or nearby mature forested wetlands (Brown and Veneman 2001, NRC 2001, Cole and Shafer 2002, Sharitz et al. 2006, Matthews and Endress 2008). This study was designed to assist wetland managers in selecting appropriate species and stocktypes for site conditions in order to increase the probability of successful forested wetland restoration as well as providing insight about the survival and development of planted trees. Successful establishment and growth of trees in restored forested wetlands is important because trees contribute greatly to the ecological structure and multiple ecological functions and services that forested wetland ecosystems provide.

For example, one ecosystem function that trees contribute to is providing and enhancing habitat for plants, animals, fungi, and microbial communities both within the restored wetland and in adjacent and downstream ecosystems. Living and shed bark, wood, roots, flowers, fruits, seeds, leaves and sap are consumed by a number of different organisms, including insects, mammals and birds. Leaf litter and fallen dead wood also provide nutrients for fungus and other microorganisms in the detrital food web. Trees provide shelter from weather and predators in the form of tree cavities, leaf litter and fallen dead wood. Shade provided by trees surrounding streams, estuaries or rivers can reduce air and water temperature, enhancing habitat for aquatic organisms. Trees also provide space for organisms to live, including insects living under and in the bark, birds and mammals building nests in cavities and branches, caterpillars and other insects building nests in the crown, and lichen, moss and fungi living on the bark. Organic matter

Establishing trees in restored wetlands can be achieved through natural colonization or planting seeds or saplings. Saplings are often planted when natural colonization is anticipated to be limited due to insufficient amount of propagules of appropriate species in the existing seed bank or being actively supplied by nearby trees. Additionally, abiotic (hydrology, soil conditions, etc.) and biotic (seed predation, competition, etc.) site conditions can limit natural colonization. If planting is deemed
necessary for restoration, selection of species and stocktype are two critical choices for ensuring survival and subsequent growth following outplanting. These two choices are influenced by the stressful biotic (herbaceous competition, herbivory, deer browsing, pathogens) and abiotic conditions (low soil oxygen concentrations, low organic material, low soil nutrient concentrations, high soil bulk density, and increased rock fragments) typically present in areas undergoing wetland restoration.

Tree species selected for planting should be those that are found naturally in nearby wetland ecosystems that have environmental conditions similar to the anticipated conditions of the restoration site (Nyland 2007). In particular, matching species to restoration site hydrology has been shown to be a key factor for successful establishment of trees in bottomland hardwood forests (Stanturf et al. 2004, McLeod et al. 2006). Following species selection, selection of stocktype (e.g. bare root seedlings of various ages, tubelings or plugs, containerized, balled and burlapped, live stakes, etc.) becomes relevant. These descriptive names can be used to describe the age, size, and production techniques used, which are not uniform throughout the nursery industry. In general bare root seedlings range in age from one to three years old and are typically planted during dormancy without soil surrounding the roots. Tubelings are typically similar in age to bare root seedlings; however, they are planted with tube soil surrounding the roots and are grown in various shaped (square, round) small containers. Seedlings are also grown in larger containers ranging from 1 gallon to >25 gallons. These containerized seedlings are grown to various ages and sizes and are often planted with the soil intact around the root system, which allows for planting later in the season. In general, bare root seedlings are
less expensive and are cheaper to plant, while containerized seedlings are more expensive and require additional labor to plant.

Many studies have investigated how different stocktypes survive and grow following outplanting on upland sites (See Grossnickle and El-Kassaby 2015 for review of >400 containerized and bare-root stocktypes comparison studies). However, few studies have investigated how stocktype selection influences survival and growth in restored forested wetlands (See companion study - Roquemore et al. 2014). Of the studies investigating stocktype selection in relation to wetland restoration the results suggests that the stocktype responses are dependent upon the species used and the environmental conditions. For example, McLeod (2000) found that bare root seedlings had similar survival to more expensive containerized seedlings of *Fraxinus pennsylvanica*, *Nyssa aquatica*, and *Taxodium distichum* when planted in a thermally impacted bottomland hardwood forest. Whereas, a meta-analysis of 122 trials comparing survival between bare-root and containerized stock planted across a variety of upland sites found that containerized stock had greater survival than bare-root stock in 60.7% of the trials (Grossnickle and El-Kassaby 2015). Due to the complexities of the species and stocktypes available and uncertainty regarding the influence of species and stocktype selection on the survival and growth of woody species under various hydrologic conditions, practitioners have encountered difficulties establishing trees in restored forested wetlands that will lead to the desired ecological structures and ecosystem functions and services.

The purpose of this study was to investigate the differences in survival and development of morphological structure (stem diameter, crown diameter, and height) of
planted trees in response to: 1) stocktype selection 2) species selection and 3) soil physical, chemical and hydrologic conditions. Seven native wetland trees common to the mid-Atlantic region of the United States were planted using three stocktypes (bare roots, tubelings, and 1-gallon containers) in a large scale, hydrologically controlled, field experiment.

**Methods**

**Study Site**

The experimental site (hereto referred to as “the site”) was established in New Kent County, Virginia, USA at the Virginia Department of Forestry, New Kent Forestry Center in 2008-2009 (Figure 2-1). The site was located in the Coastal Plain Region of Virginia and the average annual temperature is 15° C and average annual precipitation is 116.2 cm/year (39 year average; WEST POINT 2 NW, Coop ID: 449025). The 1.4-ha experimental site was located 8.8 m above sea level and ~1 km north of the Chickahominy River (latitude 37° 25’ 25.9026” N, longitude -77° 0’ 53.3628” W). The site was located on a terrace adjacent to a mature palustrine forested wetland to the west and north with managed upland fields to the east and south. Soil series (and associated taxonomic class) on the site included Catpoint fine sand (thermic, coated Lamellic Quartzipsamments), State very fine sandy loam (fine-loamy, mixed, semiactive, thermic Typic Hapludults) and Altavista fine sandy loam (fine-loamy, mixed, semiactive, thermic Aquic Hapludults) (USDA NRCS 2015). These soils are classified as somewhat excessively drained, well drained, and moderately well drained respectively. Based on
observations at the site, depth to the natural water table was estimated to be greater than 1 m prior to construction.

The site consisted of three hydrologically distinct cells (ambient (AMB), saturated (SAT) and flooded (FLD)) each 49 m x 95 m in size (Figure 2-1). Each cell was equipped with an on-site irrigation system capable of producing a minimum of 2.54 cm of irrigation per hour. The three cells were hydrologically manipulated such that the ambient treatment received only precipitation, the saturated treatment received irrigation as needed to exhibit saturated soil conditions within the root-zone (upper 10 cm) for a minimum of 90% of the growing season, and the flooded treatment received irrigation as needed to maintain inundations above the root crown for a minimum of 90% of each year. The AMB cell received irrigation when the Palmer Drought Severity Index weekly value was -3 or less indicating a severe drought. Irrigation water was drawn from the non-tidal portion of the Chickahominy River approximately 8 km upriver above Walkers Dam in Walkers, VA. Soils in AMB and SAT treatments were tilled using a finger plow to a depth of 20 cm in February 2009 prior to planting, whereas, the FLD treatment was excavated using a 5-ton backhoe to a depth of 1 m to an existing clay layer.

**Soil Sampling**

Forty four soil samples were collected from each cell (Total=132) in 2013 and analyzed for soil carbon, nitrogen and phosphorus concentrations and soil sand, silt and clay percentages. Samples were evenly spaced within each cell and collected 70 cm diagonally from the tree base. The top 15 cm of soil were collected using a soil probe (tube sampler). Samples were dried in an oven at 60° C until constant mass was obtained.
Bulk density was determined by dividing mass of oven dry soil by volume collected (Brady & Weil 2002). Particle size distribution (sand (>63µm), silt (<63µm-4µm), and clay (<4µm)) was determined by the standard sieve-pipette method (Brady & Weil 2002).

Carbon and nitrogen concentrations from a subsample of homogenized oven dry samples were measured using a PE2400 CHNS/O Elemental Analyzer (Perkin Elmer, Massachusetts, USA). Phosphorus concentrations were measured using a spectrophotometer following a modified ashing and extraction technique (Chambers & Fourqurean 1991). Carbon, nitrogen and phosphorus concentration are presented as percentages of total soil mass.

There were differences in soil physical and chemical characteristics among the cells (Table 2-1). Within each cell there were also differences in the spatial distributions of soil bulk density (Figure 2-2), percentage sand (Figure 2-3), percentage silt (Figure 2-4), percentage clay (Figure 2-5), percentage soil carbon (Figure 2-6), percentage soil nitrogen (Figure 2-7), and percentage phosphorus (Figure 2-8). In general the soil bulk density and percentage clay was higher in the FLD than in the AMB and SAT and the soil elemental concentrations were lower in the FLD than in the AMB and SAT.

**Planting Material**

The seven planted species (and Atlantic and Gulf Coastal Plain wetland indicator statuses (Lichvar et al. 2012; Lichvar 2013)) were *Betula nigra* L. (river birch, FACW), *Liquidambar styraciflua* L. (sweetgum, FAC), *Platanus occidentalis* L. (American sycamore, FACW), *Quercus bicolor* Willd. (swamp white oak, FACW), *Quercus*
palustris Münchh. (pin oak, FACW), *Quercus phellos* L. (willow oak, FACW) and *Salix nigra* Marshall (black willow, OBL).

Three stocktypes of each species were used: bare-root (BR), tubeling (TB), and 1-gallon containers (GAL) (tubelings of *P. occidentalis*, *Q. phellos*, and *S. nigra* had their soil removed by the nursery prior to shipment). Bare root seedlings range in age from one to three years old and were planted during dormancy without soil surrounding the roots. Tubelings are typically similar in age to bare root seedlings; however, they were planted with potting soil surrounding the roots and were grown in small square containers. One gallon containerized seedlings are larger and older than BR and TB and were planted with potting soil intact around the root system. The GAL was most expensive, followed by TB, with BR being the least expensive.

In spring 2009, all combinations of species and stocktypes were planted randomly along rows within each cell. A total of 2,772 trees were planted; ~44 of each species/stocktype combination, for a total of 924 trees per cell. Saplings were arranged in 22 rows per cell (42 saplings per row) that were staggered. Therefore, saplings were spaced 2.29 m from saplings within the row and 2.56 m from saplings in adjacent rows. This led to a density of 1969 stems/ha. In the spring of 2010, a total of 482 additional saplings were planted to ensure adequate survival for biomass sampling, but these were not considered in the present analysis.

Saplings were obtained from four nurseries located in Virginia, North Carolina, New Jersey, and Tennessee. Replacement stock did not necessarily come from the same nursery as the original stock. No fertilizers were applied prior to or following planting. Herbaceous competition was controlled around plantings in AMB and SAT through
bimonthly grass cutting and application of glyphosate at the beginning and middle of the growing season using commercial backpack sprayers.

**Species Grouping**

To facilitate analysis and interpretation of plant material selection, species were assigned to early (primary) or late (secondary) successional categories based on common Mid-Atlantic Coastal Plain regional trends in dominance during stand development as expressed through differences in maturation and growth rates, dispersal mechanisms, and disturbance tolerance. The primary species group (PRI) consisted of four species (*B. nigra*, *L. styraciflua*, *P. occidentalis* and *S. nigra*) that are typically dominant during the early stages of succession, have rapid growth and maturation rates, have wind dispersed seeds and are moderately tolerant of disturbance (Bazzaz 1979). The secondary species group (SEC) consisted of three species (*Q. bicolor*, *Q. palustris*, and *Q. phellos*) typically dominant in the later stages of succession, have slower growth and maturation rates, have large seeds that are dispersed mainly by animals and are generally less tolerant of disturbance. (Guyette et al. 2004).

**Survival and Morphometric Measurements**

Providing habitat for other organisms requires that trees planted in restored wetlands must survive transplanting and grow. Structural measurements of sapling morphology used in this study (crown and stem diameter and height) and survival rates can be used to provide inferences about the amount of habitat provided by individual trees and stands of trees. These measurements are useful since specific amounts of habitat resources provided by trees are difficult to quantify, they are commonly measured in
forest inventories, and they have direct and indirect relationships to the occurrence and abundance of other organisms.

Survival and morphology were measured in mid-April, mid-August, and mid-October for seven years (from April 2009 to October 2015). Individual saplings were considered “live” based on the presence of green leaves or a green layer in the cortex under the bark. We often found it necessary to search for the latter in many saplings that exhibited die-back and re-growth. To check for a live cortex, a small longitudinal incision scratch was made at the highest point on the stem. If brown (i.e. not alive), a second incision was made approximately one half way down the stem. If brown, a final incision was made at the base. If any of the incisions showed a green cortex, the individual sapling was considered alive. Percent survival calculations excluded live trees removed for biomass measurements.

Methods for sampling morphology (stem cross-sectional diameter at groundline, crown diameter (CD), and height of tallest stem (H)) were modified from Bailey et al. (2007). The diameter of stems at ground level was measured using micro-calipers (6-inch stainless steel digital caliper, General, Secaucus, New Jersey) or macro-calipers (127-cm Mantax Precision Blue Calipers, Haglöf, Inc., Långsele Sweden). If root swelling was present (defined as stem diameter > 10% larger than stem above swelling), stem cross-sectional diameter was measured just above the visual top of swelling. For trees with multiple stems originating from below the soil surface, the stem diameter of the five largest stems was measured. A single cross-sectional area at groundline (CSAG) was calculated by summing CSAG for each stem of an individual. In subsequent chapters, this CSAG was then converted to a single stem cross-sectional diameter at groundline.
(referred to as equivalent stem cross-sectional diameter at groundline (ESD). The sum of the area of the measured stems equals an area equivalent to the corresponding diameter of a single stemmed sapling as described in Paul et al. (2013).

Crown diameter was measured in three evenly distributed angles using a meter stick, macro-calipers, 5-m stadia rod, or tape measure. The mean crown diameter was determined by averaging three crown measurements. In subsequent chapters, canopy cover was calculated by converting average crown diameter (cm) to area (cm$^2$).

Total heights were measured with a standard meter stick, 5-m stadia rod, clinometer (PM-5/360 PC, Suunto, Co., Vantaa, Finland), or hypsometer (Vertex III, Haglöf, Inc., Långsele Sweden).

Statistical Analysis

Initial morphological means of stocktypes were compared for each species. Unequal sample size, unequal variance and multiple comparisons were accounted for by modeling variance for each stocktype and using the Games-Howell adjustment (Westfall et al. 2011).

To determine the differences in survival over five years among stocktypes, species, and successional groups, the Cox proportional hazards model was applied to each species or stocktype within each cell (Firth correction and Breslow method for ties). To determine the differences in morphological variables over five years among stocktype, species, and successional groups, repeated measures analysis of variance (rANOVA) was used within each cell (Covariance structure: Autoregressive 1, Estimation method: Residual maximum likelihood). If significant interactions were found for either survival
or morphological variables, a simple effects model was used to determine differences among the stocktypes or successional group for each species within each cell. Least squares post hoc test using a Bonferroni adjustment was used to determine differences among each stocktype. All alpha values were set at 0.05.

Due to the cells unreplicated design the survival and morphology of the 21 unique combinations of species and stocktypes were compared among the cells. Survival was not compared statistically but was compared using only percent survival among species-stocktype combinations. Morphological means after 5 years for each species-stocktype combination were compared across cells. Unequal sample size, unequal variance and multiple comparisons were accounted for by modeling variance for each cell and using the Games-Howell adjustment (Westfall et al. 2011).

Results from each post hoc comparison (stocktype, successional group, cells) for each measured variable (survival, CSAG, H, and CD) were tallied by unique outcome. For example, when comparing the survival among the stocktypes the number of times a particular outcome occurred (BR>GAL, BR=GAL, BR<GAL, TB<GAL, TB=GAL, TB>GAL, BR=TB, or BR<TB) was counted for each cell. The total number of times each outcome occurred across all measured variables was obtained for each cell and in total, to determine which outcome was most common. This analysis also allowed for survival and morphology results to be combined and will be presented as such.
Results

Stocktype Comparison of Initial Morphology

The average initial stem cross-sectional area at groundline (CSAG) for the bare root (BR), gallon (GAL), and tubing (TB) stocktypes across all species was 0.54 cm$^2$ (Standard Deviation (SD = 0.64), 0.56 cm$^2$ (SD = 0.63) and 0.96 cm$^2$ (SD = 0.98) respectively. The average initial height (H) for BR, GAL, and TB across all species was 52.6 cm (SD = 31.0), 70.0 cm (SD = 42.1) and 53.3 cm (SD = 34.0) respectively. The average crown diameter (CD) for BR, GAL, and TB across all species was 8.1 cm (SD = 10.5), 16.2 cm (SD = 17.0) and 8.4 cm (SD = 10.9) respectively. However, there were significant interactions between species and stocktype for each morphological parameter at the time of planting. This suggests that the initial size of the stocktype depended upon the species and vice versa (e.g. GAL stocktype may not be the largest stocktype across all species). As a result of significant interactions, subsequent analysis focused on determining differences among stocktypes for each species separately (Table 2-2).

The GAL CSAG and CD were significantly greater than the BR and TUB stocktypes for all species except *Q. bicolor*. The GAL H was significantly greater than the BR and TUB stocktypes for all species except *L. styraciflua* and *Q. bicolor*. The CSAG and CD were not significantly different between the BR and TB for all species. Initial H was not significantly different between the BR and TB stocktype for all species except *B. nigra*, where the TB was significantly taller than the BR at the time of planting (Table 2-2).
Stocktype Comparison Over 5 Years

There were significant interactions between species and stocktype within the AMB, SAT, and FLD for each parameter (survival, CSAG, H and CD) over the 5 years of monitoring (Figure 2-10). This suggests that within each cell, response of stocktype depended upon species and vice versa (e.g. GAL stocktype may not have greatest survival or H across all species). As a result of significant interactions, subsequent analysis focused on determining differences among stocktype in each cell for each species separately.

Survival

After five years average percent survival across all cells, species and stocktypes was 57%. Average percent survival for BR, GAL, and TB stocktype (across all cells and species) was 48%, 81%, and 43%, respectively. In order to further investigate differences among stocktypes, survival of stocktypes by species were compared within each cell.

In AMB, GAL survival was greater than BR survival for B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, and S. nigra. Similarly, GAL survival was greater than TB survival for B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, and S. nigra. BR survival was greater than TB survival for L. styraciflua, Q. bicolor while Q. palustris had greater survival in BR than TB (Figure 2-11 and Table 2-9). Overall, BR survival was similar to TB for B. nigra and Q. phellos.

In SAT, GAL survival was greater than BR survival for B. nigra, L. styraciflua, P. occidentalis, Q. phellos, and S. nigra and had greater survival than TB for all seven species. BR survival was not different than TB survival for B. nigra, P. occidentalis, Q.
phellos, and S. nigra. However, BR survival was greater than TB survival for L. styraciflua Q. bicolor and Q. palustris (Figure 2-11 and Table 2-9).

In FLD, GAL survival was greater than BR survival for B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, and Q. phellos. GAL survival was greater than TB survival for L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, and Q. phellos. There was no difference in survival between BR and TB for L. styraciflua, P. occidentalis, and Q. palustris. S. nigra had no differences in survival among all stocktypes in FLD (Figure 2-11 and Table 2-9).

Morphology

Stem Cross-sectional Area at Groundline

Average stem cross-sectional area at groundline (CSAG) and standard deviation (SD) for BR, GAL, and TB stocktype (across all cells and species) was 59.6 cm² (n=440, SD=114.6 cm²), 79.8 cm² (n=678, SD=137.4 cm²), and 75.8 cm² (n=346, SD=135.9 cm²), respectively after five years. In order to further investigate differences among stocktypes, CSAG of stocktypes by species were compared within each cell.

In AMB, GAL CSAG was greater than BR CSAG for B. nigra, Q. phellos and S. nigra. There was no difference in CSAG between BR and GAL stocktypes for L. styraciflua, P. occidentalis, Q. bicolor, or Q. palustris. GAL CSAG was greater than TB CSAG for B. nigra, L. styraciflua, Q. bicolor, Q. palustris and Q. phellos. There was no difference in CSAG between TB and BR stocktype for B. nigra, P. occidentalis, Q. palustris, Q. phellos, or S. nigra (Figure 2-12 and Table 2-11).
In SAT, GAL CSAG was greater than BR CSAG for *B. nigra*, *Q. palustris*, and *Q. phellos*. There was no difference in CSAG between BR and GAL stocktypes for *L. styraciflua*, *P. occidentalis*, *Q. bicolor* and *S. nigra*. GAL CSAG was greater than TB CSAG for *B. nigra*, *L. styraciflua*, *Q. bicolor*, *Q. palustris* and *Q. phellos*. There was no difference in CSAG between BR and TB for *B. nigra*, *L. styraciflua*, *P. occidentalis*, *Q. palustris*, *Q. phellos*, and *S. nigra* (Figure 2-12 and Table 2-11).

In FLD, GAL CSAG was greater than BR CSAG for *B. nigra*, *L. styraciflua*, *P. occidentalis*, *Q. palustris*, *Q. phellos*, and *S. nigra*. GAL CSAG was greater than TB CSAG for all seven species. BR CSAG was greater than TB CSAG for *Q. bicolor* only (Figure 2-12 and Table 2-11).

Crown Diameter

BR, GAL, and TB average crown diameter (CD) after five years was 209.3 cm (n=440, SD=158.9 cm), 241.2 cm (n=678, SD=172.6), and 220.2 cm (n=346, SD=189.9 cm) respectively (across all cells and species). In order to further investigate differences among stocktypes, CD of stocktypes by species were compared within each cell.

In AMB, GAL CD was greater than BR CD for *B. nigra*, *Q. palustris*, *Q. phellos*, and *S. nigra*. There was no difference between BR and GAL CD for *L. styraciflua*, *P. occidentalis*, and *Q. bicolor*. GAL CD was greater than TB CD for all seven species except *P. occidentalis* (no difference). BR CD was not different than TB CD for *B. nigra*, *P. occidentalis*, *Q. bicolor*, *Q. phellos* and *S. nigra*. BR CD was greater than TB CD for *L. styraciflua* and *Q. palustris* (Figure 2-13 and Table 2-13).
In SAT GAL CD was greater than BR CD for *B. nigra*, *Q. palustris*, *Q. phellos*, and *S. nigra*. There was no difference between BR and GAL CD for *L. styraciflua*, *P. occidentalis*, and *Q. bicolor*. GAL CD was greater than TB CD for *L. styraciflua*, *Q. bicolor*, *Q. palustris*, *Q. phellos*, and *S. nigra*. There was no difference in CD between TB and GAL stocktype for *B. nigra* and *P. occidentalis*. There was no difference between BR and TB CD for all species except *Q. bicolor* (Figure 2-13 and Table 2-13).

In FLD, GAL CD was greater than BR and TB CD for all seven species. BR CD was greater than TB for all seven species except *Q. bicolor* (Figure 2-13 and Table 2-13).

Height

After five years, average height (H) for BR, GAL, and TB (across all cells and species) was 314.6 cm (n=440, SD=249.1 cm), 345.6 cm (n=678, SD=241.7 cm), and 337.5 cm (n=346, SD=303.0 cm) respectively. In order to further investigate differences among stocktypes, H of stocktypes by species were compared within each cell.

In AMB, GAL H was greater than BR H for *B. nigra*, *Q. palustris*, *Q. phellos*, and *S. nigra*. There was no difference in H between BR and GAL for *L. styraciflua*, *P. occidentalis*, and *Q. bicolor*. GAL H was greater than TB H for *B. nigra*, *L. styraciflua*, *Q. bicolor*, *Q. palustris*, and *Q. phellos*. There was no difference between TB and GAL H for *P. occidentalis* and *S. nigra*. There was no difference in H between BR and TB for *B. nigra*, *P. occidentalis*, *Q. bicolor*, *Q. phellos* and *S. nigra*. BR H was greater than TB H for *L. styraciflua* and *Q. palustris* (Figure 2-14 and Table 2-15).

In SAT, there was no difference in H between BR and GAL for *L. styraciflua*, *P. occidentalis*, *Q. bicolor*, *Q. palustris* and *S. nigra*. GAL H was greater than BR for *B. nigra* and *Q. phellos*. GAL H was greater than TB H for *L. styraciflua*, *Q. bicolor*, *Q. palustris* and *S. nigra*.
palustris, and Q. phellos. There was no difference between TB H and GAL H for B. nigra, P. occidentalis, and S. nigra. There was no difference in H between BR and TB for B. nigra, P. occidentalis, Q. bicolor, Q. phellos and S. nigra. BR H was greater than TB H for L. styraciflua and Q. palustris (Figure 2-14 and Table 2-15).

In FLD, GAL H was greater than BR height for all species except Q. bicolor, for which BR H was greater than GAL height. GAL H was greater than TB H for all species. There was no difference in BR H and TB H for B. nigra, P. occidentalis, Q. phellos, and S. nigra. BR H was greater than TB H for L. styraciflua, Q. bicolor, and Q. palustris (Figure 2-14 and Table 2-15).

Combining survival and morphology

When combining survival and morphological comparisons for each species across all three cells and counting the number of times an outcome occurred, GAL was greater than BR and TB in 67% and 82% of all comparisons respectively and BR was not different than TB in 69% of comparisons (Table 2-6). To further investigate differences among stocktypes, outcomes were counted within each cell.

For all species in AMB, GAL was greater than BR and TB in 61% and 79% of all survival and morphological comparisons respectively and BR was not different than TB in 61% of all comparisons. BR was not different than GAL in 39% of all comparisons and BR was greater than TB in 32% of all comparisons (Table 2-6).

For all species in SAT, GAL was greater than BR in 50% of combined comparisons and was not different than BR in 50% of all comparisons. GAL was greater
than TB in 75% of the comparisons while BR was not different than TB in 75% of all comparisons. BR was greater than TB in 25% of all comparisons (Table 2-6).

For all species in FLD, GAL was greater than BR in 89% of all survival and morphological comparisons and was greater than TB in 93% of all comparisons. BR and TB were not different in 71% of all comparisons (Table 2-6).

Species Group Comparison Over 5 Years

The seven species were divided into two groups (primary and secondary) based on dominance during the traditional forest successional sequence, differences in maturation and growth rates, dispersal mechanisms, and disturbance tolerance in order to facilitate comparisons among species. When analyzing differences in survival, CSAG and H among successional groups and stocktype there were significant interactions between successional group and stocktype within AMB and FLD, SAT and FLD, and FLD respectively. This suggests that the survival, CSAG and H response of stocktype depended upon successional group and vice versa. There was no significant interaction among successional group and stocktype when analyzing differences in CD (Table 2-4). This suggests that CD response was similar among stocktypes for all successional groups and vice versa. As a result of significant interactions, subsequent analysis of each parameter focused on determining differences among successional groups in each cell for each stocktype separately.
Survival

Survival of secondary species (*Quercus* spp.) was greater than survival of primary species when planted as BR in AMB. When planted as GAL or TUB there was no difference between the survival of the primary and secondary successional species (Figure 2-15). In SAT, secondary species (*Quercus* spp.) had greater survival than primary species when planted as BR. When planted as GAL or TUB there were no differences between survival of primary and secondary successional species (Figure 2-15). For all stocktypes primary successional species had greater survival than secondary species in FLD (Figure 2-15).

Morphology

Primary species had greater CSAG and H than secondary species for all stocktypes across all cells (Figure 2-16 and Figure 2-18). Primary species had greater CD than secondary species for all stocktypes in AMB and SAT. In FLD primary species had greater CD than secondary species for GAL and TB stocktype. There was no difference in CD between primary and secondary species for BR (Figure 2-17).

Primary successional species were greater than secondary successional species in 81% of all comparisons when merging survival and morphological comparisons for each stocktype across all three cells (Table 2-7). In order to investigate these results further, survival and morphology comparisons were combined for each cell and differences between stocktype and successional stages were investigated.
**Combining survival and morphology**

In AMB, when combining survival and morphological measurements for each stocktype, primary species were greater than secondary species in 75% of comparisons (Table 2-7). Primary species were greater than secondary species in 75% of combined survival and morphological comparisons in SAT (Table 2-7). In FLD, primary species were greater than secondary species in 92% of all comparisons. There were no differences between primary and secondary species in 8% of comparisons in FLD (Table 2-7).

**Cell Comparison After 5 Years**

Individual species/stocktype combination’s responses after five years were compared among cells in order to make inferences about their responses to environment conditions and to infer about differences among cells. Due to the unreplicated nature of cells, survival was compared using absolute values, while CSAG, H and CD were compared statistically (Table 2-5). The majority of species/stocktype combinations had significantly different responses among the cells, except *Q. palustris* and *Q. phellos* TB and *P. occidentalis* BR (Table 2-5). The results of the individual measurements comparisons are presented below.

**Survival**

BR survival after five years was greater in AMB than SAT for *P. occidentalis*. BR survival in SAT was greater than AMB for *B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos*, and *S. nigra*. All seven species BR survival was greater in AMB
and SAT compared to FLD, except for *S. nigra*. *S. nigra* BR had greater survival in FLD compared to both SAT and AMB (Table 2-10).

GAL survival after five years was greater in AMB than SAT for *B. nigra*, *Q. palustris*, and *S. nigra*. GAL survival in SAT was greater than survival in AMB for *L. styraciflua*, *P. occidentalis*, and *Q. phellos*. While, *Q. bicolor* GAL had no difference in survival between the AMB and SAT. All seven species GAL survival was greater in the AMB and SAT compared to FLD, except for *S. nigra*. *S. nigra* GAL had greater survival in FLD compared to both SAT and AMB (Table 2-10).

TB survival after five years was greater in AMB than SAT for *P. occidentalis* and *S. nigra* while the remaining 5 species TB survival was greater in SAT than AMB. *P. occidentalis*, *Q. bicolor*, *Q. palustris* and *Q. phellos* TB survival in AMB and SAT was greater than FLD. However, *B. nigra*, *L. styraciflua*, and *S. nigra* TB survival in FLD was greater than AMB and SAT (Table 2-10).

*Morphology*

**Stem Cross-sectional Area at Groundline**

The average BR CSAG after five years in AMB, SAT and FLD was 90.7 cm$^2$ (n=182, SD=147.0 cm$^2$), 49.0 cm$^2$ (n=183, SD=89.3 cm$^2$), 10.6 cm$^2$ (n=76, SD=21.3 cm$^2$) respectively. The average GAL CSAG after five years in AMB, SAT and FLD was 126.8 cm$^2$ (n=261, SD=178.2 cm$^2$), 73.3 cm$^2$ (n=268, SD=108.9 cm$^2$), 9.2 cm$^2$ (n=149, SD=12.1 cm$^2$) respectively. Average TB CSAG after five years in AMB, SAT and FLD was 148.5 cm$^2$ (n=111, SD=196.1 cm$^2$), 58.3 cm$^2$ (n=157, SD=84.8 cm$^2$), 7.4 cm$^2$ (n=78,
SD=15.0 cm$^2$) respectively. In order to further investigate differences among cells, CSAG of species within cells were compared for each stocktype.

BR CSAG in AMB was greater than SAT after five years for *L. styraciflua*, *P. occidentalis*, and *Q. palustris*. There was no difference in BR CSAG between AMB and SAT for *B. nigra*, *Q. bicolor*, *Q. phellos*, and *S. nigra*. BR CSAG in AMB was greater FLD for all species except *S. nigra* and BR CSAG in SAT was greater than FLD for all seven species (Table 2-12).

GAL CSAG in AMB was greater than SAT for *B. nigra*, *P. occidentalis*, *Q. bicolor*, and *Q. palustris*. There was no difference between GAL CSAG in AMB and SAT for *L. styraciflua*, *Q. phellos*, and *S. nigra*. All seven species CSAG for GAL was greater in the AMB compared to FLD. GAL CSAG was greater in SAT than FLD for all species except *Q. palustris* (Table 2-12).

TB CSAG after five years was greater in AMB than SAT for *P. occidentalis*, and *Q. bicolor*. There was no difference in TB CSAG between AMB and SAT for *B. nigra*, *L. styraciflua*, *Q. palustris*, *Q. phellos*, and *S. nigra*. TB CSAG was greater in AMB than FLD for *B. nigra*, *L. styraciflua*, *Q. bicolor*, and *S. nigra*. There was no difference in TB CSAG between AMB and FLD for *P. occidentalis* and *Q. palustris*. TB CSAG was greater in SAT than FLD for *B. nigra*, *L. styraciflua*, *Q. bicolor*, and *S. nigra*. There was no difference in TB CSAG between SAT and FLD for *P. occidentalis* and *Q. palustris* after five years (Table 2-12).
Crown diameter

The average BR CD after five years in AMB, SAT and FLD was 277.2 cm (n=182, SD=168.9 cm), 205.5 cm (n=182, SD=131.8 cm), 56.1 cm (n=76, SD=45.0 cm) respectively. Average GAL CD after five years in AMB, SAT and FLD was 326.8 cm (n=261, SD=175.8 cm), 257.9 cm (n=268, SD=136.2 cm), 61.2 cm (n=149, SD=50.7 cm) respectively. Average TB CD after five years in AMB, SAT and FLD was 329.7 cm (n=111, SD=214.1 cm), 228.9 cm (n=157, SD=151.4 cm), 46.7 cm (n=78, SD=42.1 cm) respectively. In order to further investigate differences among cells, CD of species within cells were compared for each stocktype.

BR CD after five years was greater in AMB than SAT for *L. styraciflua*, *P. occidentalis*, *Q. bicolor*, and *Q. palustris*. There was no difference in BR CD between AMB and SAT for *B. nigra*, *Q. phellos* and *S. nigra*. All seven species had greater BR CD in AMB than FLD except *S. nigra* (no difference). All seven species had greater BR CD in SAT than FLD (Table 2-14).

GAL CD was greater in AMB than SAT for *B. nigra*, *P. occidentalis*, *Q. bicolor*, and *Q. palustris*. There was no difference in GAL CD between AMB and SAT for *L. styraciflua*, *Q. phellos*, and *S. nigra*. All seven species GAL CD in AMB and SAT was greater than FLD (Table 2-14).

TB CD was greater in the AMB than SAT for *Q. bicolor*, while the remaining six species had no difference in TB CD between AMB and SAT. TB CD was not different between AMB and FLD for *Q. palustris*, while the remaining six species TB CD was greater in the AMB than FLD. TB CD was greater in SAT than FLD for *B. nigra*, *L.*
*styraciflua, Q. bicolor, and S. nigra*. TB CD was not different between SAT and FLD for *P. occidentalis*, and *Q. palustris* (Table 2-14).

**Height**

The average BR H after five years in AMB, SAT and FLD was 435.7 cm (n=182, SD=278.2 cm), 286.7 cm (n=182, SD=188.8 cm), 91.2 cm (n=76, SD=47.7 cm) respectively. Average GAL H after five years in the AMB, SAT and FLD was 485.8 cm (n=261, SD=251.4 cm), 345.8 cm (n=268, SD=179.4 cm), 99.7 cm (n=149, SD=52.3 cm) respectively. Average TB H after five years in the AMB, SAT and FLD was 545.3 cm (n=111, SD=365.1 cm), 318.1 cm (n=157, SD=210.0 cm), 80.8 cm (n=78, SD=41.3 cm) respectively. In order to further investigate differences among cells, H of species within cells were compared for each stocktype.

BR H after five years was not different between AMB and SAT for *P. occidentalis* and *S. nigra*, while the remaing 5 species BR H was greater in the AMB than SAT. BR H was greater in AMB and SAT than FLD for *B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos*, and *S. nigra* (Table 2-16).

After five years GAL H was greater in AMB than SAT for all species except *L. styraciflua*. GAL H in AMB and SAT were greater than FLD for all 7 species (Table 2-16).

TB H was greater in AMB than SAT for *B. nigra, P. occidentalis, Q. bicolor*, and *S. nigra*. TB H was not different between AMB and SAT for *L. styraciflua, Q. palustris*, and *Q. phellos*. TB H was greater in AMB than FLD for *B. nigra, L. styraciflua*, *P. occidentalis*, *Q. bicolor*, and *S. nigra*. There was no difference in H between AMB and
FLD for *Q. palustris* TB. TB H was greater in SAT than FLD for *B. nigra, L. styrcaciflua, Q. bicolor,* and *S. nigra*. TB H was not different between SAT and FLD for *P. occidentalis* and *Q. palustris* (Table 2-16).

**Combining survival and morphology**

To further analyze the differences among cells, the survival and morphology measurements across all species and stocktypes were combined (Table 2-8). In total, the outcomes of the comparisons of species(stocktype comparisons among cells show that AMB was greater than SAT in 46.4% of comparisons, while there was no difference among AMB and SAT in 36.9% of comparisons and SAT exceeded AMB in 16.7% of comparisons. The SAT exceeded AMB only in percent survival comparisons. When comparing AMB to FLD, AMB was greater than FLD in 85.9% of comparisons and equal to in 7.7%. The SAT exceeded FLD in 84.6% of comparisons and was similar to FLD in 9.0% of comparisons. Based on the responses of the species(stocktype combinations, these results suggest that AMB was more similar to SAT than SAT was similar to FLD, while AMB and FLD are most dissimilar.

**Discussion**

The goal of wetland restoration is to return lost ecological structure and functions to the landscape, including plant, animal, and microbial habitat. Habitat in restored wetlands is obtained primary through the successful establishment of vegetative structure, which provides cover, food and space for a variety of organisms. Numerous studies have found that tree density and tree growth were significantly lower for restored sites as
compared to conditions prior to conversion or nearby mature forested wetlands (Brown and Veneman 2001, NRC 2001, Cole and Shafer 2002, Sharitz et al. 2006, Matthews and Endress 2008). Poor establishment and growth may result from inadequate colonization from surrounding seed sources or low survival of planted woody vegetation (Robb 2002, Morgan and Roberts 2003). Poor survival and growth of planted trees results from unfavorable site conditions (inappropriate hydrology, low organic content, high bulk density, increased rock fragments), competition from non-desired species, improper species or stocktype selection, and/or improper planting techniques (Stolt et al. 2000, Campbell et al. 2002, Bruland and Richardson 2004, Bergshneider 2005, Daniels et al. 2005, Bailey et al. 2007). The effect of stocktype, species and hydrologic and soil conditions on planted tree survival and morphology were the focus of this project.

**Stocktype Comparison of Initial Morphology**

In general the initial morphology of GAL stocktype was greater than the BR and TB stocktypes (except *Q. bicolor*). This suggests that the GAL stocktype with nutrient rich potting soil around the roots may have more initial above and belowground biomass than BR and TB. There were no differences in initial morphology between the BR and TB stocktypes (except H of *B. nigra* TB>BR). The lack of initial morphological differences between the BR and TB suggests that the major difference between these two stocktypes is the presence of potting soil around the roots and possibly other nursery production techniques. However, *P. occidentalis*, *Q. phellos*, and *S. nigra* TB had soil removed by the nursery prior to shipment.
Stocktype Comparison Over 5 Years

In the stressful hydrologic, soil and competitive herbaceous conditions of the flooded cell (FLD), the larger stocktype (GAL) exhibited increased survival, CD (Figure 2-9), and CSAG compared to smaller stocktypes (BR and TB) for most species. The characteristics of GAL (larger initial size, organic rich potting soil surrounding roots) may have increased its ability to overcome transplant shock, competition from herbaceous vegetation and low soil nutrient concentrations in the FLD treatment.

Transplant shock (also called planting check) is a temporary setback in growth that occurs after outplanting, which if severe enough can result in tree mortality (Kozlowski and Davies 1975, Acquaah 2005, Grossnickle 2005, South and Zwolinski 1996). Transplant shock is associated with decreased water absorption as a result of poor root-soil contact, low permeability of suberized roots (older woody roots) and a low amount of roots in relation to shoots (Beineke and Perry 1965, Carlson and Miller 1990, South and Zwolinski 1996, Grossnickle 2005). In order to overcome transplant shock, saplings must absorb enough water to satisfy evapotranspiration and metabolic/physiologic processes. The stressors associated with transplant shock in recently restored wetlands may be greater due to the low oxygen soil conditions present (Kozlowski and Davies 1975).

The larger initial size of GAL suggests that it may have had greater initial aboveground and belowground biomass than the BR and TB stocktypes. Increased belowground biomass has been shown to increase the amount of water absorbed by roots (Carlson 1986) and trees with increased initial aboveground biomass have been shown to overcome herbaceous competition (Grossnickle and El-Kassaby 2015). Additionally, the
gallon stocktype was planted with organic rich potting soil surrounding the root mass, which may have enhanced the probability for survival and overall growth because the roots would have remained in contact with the potting soil and continued to take up water. Furthermore, the potting soil may have provided additional nutrients not available in the surrounding soil. Overall, the initial characteristics of GAL (larger initial size, organic rich potting soil surrounding roots) may be reasons for the greater survival and overall growth than the BR and/or TB stocktypes in FLD.

Previous research has also demonstrated that large containerized woody stock had better survival and/or growth than smaller planting stocks. Burdett et al. (1984) showed that container grown seedlings can have greater root growth during their first growing season after outplanting compared to bare root seedlings. South et al. (2005) also showed that containerized seedlings of Pinus palustris had 20% better survival than bare root seedlings having similar root-collar diameters when outplanted on old-fields and cutover sites. Pinto et al. (2011) found that larger containers of Pinus ponderosa planted at a mesic site had increased total height and basal area. A meta-analysis of 122 trials comparing survival between bare-root and containerized stock planted across a variety of upland sites found that containerized stock had greater survival than bare-root stock in 60.7% of the trials (Grossnickle and El-Kassaby 2015).

In more aerobic soil conditions (AMB and SAT) the GAL stocktype has similar morphology compared to the BR for most species, but was often larger than the TB stocktype (Table 2-6). This suggests that the less expensive BR stocktype may return ecosystem structure and possibly ecosystem habitat functions in a similar manner as a larger stocktype if hydrologic stress and herbaceous vegetation competition is reduced
and there are better soil conditions (low bulk density, high soil nutrient concentrations).
However, the TB stocktype may not be appropriate for planting into restored wetlands
because for many species, the survival was less and the morphology was smaller than the
GAL and BR stocktypes, particularly in FLD (Table 2-6).

Several previous studies have similarly found that bare-root seedlings have
similar survival and growth compared to the more expensive containerized stocktype. A
large scale long term study by McLeod (2000) found that bare root seedlings had similar
survival to more expensive containerized seedlings of *Fraxinus pennsylvanica*, *Nyssa
aquatica*, and *Taxodium distichum* when planted in a thermally impacted bottomland
hardwood forest. Additionally, Denton (1990) investigated the effect of stocktype on the
growth of *T. distichum* in restored forested wetlands in Florida and their results suggest
that in order to obtain 33% canopy closure the initial costs could be reduced by planting
smaller trees (1 gallon container) at ~2500 stems/ha as opposed to planting 7 gallon trees
at ~1000 stems/ha. A large meta-analysis comparing container grown seedlings and bare-
root seedlings found that on a variety of sites with low stress, the two stocktypes had
similar survival rates (Grossnickle and El-Kassaby 2015). While not focusing on
wetlands, these results are similar to the present study.

Recently restored wetlands often have stressful hydrologic conditions (persistent
high water tables) and vegetative competition (Cole and Brooks 2000, Campbell et al.
2002, Bruland and Richardson 2004, DeBerry and Perry 2004). The overall results from
the present study suggest that using a larger stocktype that has increased survival and
grows quickly is returning lost ecological structure and functions more than other smaller
stocktypes when planting in recently restored wetlands. However, less expensive
stocktype could be utilized in less stressful environmental conditions to obtain similar amounts of ecological structure and functioning.

**Species Group Comparison Over 5 Years**

In stressed environmental conditions (FLD) primary successional species (especially *S. nigra*) exhibited greater survival than secondary successional species, while in less stressed conditions (AMB and SAT) the survival of secondary species equaled or exceeded the survival of primary species (Figure 2-15).

Primary successional species have adaptations that allow for establishment following planting in harsh environmental conditions while secondary species may lack these adaptations. The physiological and morphological traits that may enhance establishment of primary successional tree species are high photosynthetic and growth rates, high acclimation potential, fast recovery from resource limitation, fast resource acquisition rates, and high competitive ability in early successional stages (Bazzaz, 1979, Brzeziecki and Kienast, 1994, Huston and Smith 1987).

Simmons et al. (2012) found that the survival, growth and vigor of early successional species were greater than later successional species when planted in different microtopographic treatments (ridges, flats, and mound-and-pool) after 2 years in a riparian forest restoration. They suggested that some early successional species may be more appropriate for restoration if they are adapted to disturbed environmental conditions. Our results confirm that secondary species alone may not be appropriate for returning ecological structure or restoring habitat functions in recently created or restored wetlands because of the harsh environmental conditions often found during this time.
Therefore, we conclude that primary species will more quickly return more tree stem structure and ecological functions than secondary successional species, especially in harsh environmental conditions. For example, *S. nigra*, though short lived, has many adaptations (shallow roots, rapid growth, adventitious rooting etc.) to harsh environmental conditions and appears to be a good species for forested wetland restoration in degraded habitats.

The H, CD and CSAG of primary successional species, regardless of stocktype, were almost always larger than secondary successional species. Primary successional species most often have faster growth rates than secondary species. Farmer (1980) compared first-year growth of six deciduous species grown in nursery conditions and found that early successional species (*Liriodendron tulipifera* and *Prunus serotina*) had higher growth rates, net assimilation rates and higher investment in leaf area than late successional species (*Q. rubra*, *Q. prinus*, *Q. alba*, and *Q. ilicifolia*). Results from Farmer (1980) and the present study suggest that primary successional species are returning ecological structure that provides ecosystem functions (such as habitat) at a faster rate than secondary successional species across a variety of environmental conditions.

**Cell Comparison After 5 Years**

When survival and morphology measurements were combined across all species/stocktype combinations, in general those trees grown in AMB had greater survival and were structurally larger than those in FLD and were greater than or equal in size to those grown in SAT, which generally had greater survival and increased size compared to those grown in FLD. These results suggest that the environmental conditions
in FLD (flooded hydrologic conditions, uncontrolled herbaceous competition, higher clay content, higher bulk density, reduced soil nutrient pools) caused stress to the trees planted there in excess of their physiological tolerances. This also suggests that the initial soil, hydrologic and competitive conditions present during restoration can affect the development of ecological structure and functions provided by trees.

Reduction in tree survival and growth can be attributed to prolonged saturated or flooded soil conditions that remove the plant available oxygen from the soil pore space (Kozlowski and Davies 1975). The reduction in oxygen leads to a lack of aerobic respiration in roots, which decreases the energy available for trees to maintain functions of existing tissues (Hale and Orcutt 1987, Brady and Weil 2002). Many growth chamber, greenhouse, mesocosm and field experiments have investigated the effect of hydrology on a multitude of responses across many species of trees. While species specific responses may vary (e.g. *Taxodium distichum*, mangroves) most species exhibit decreased survival and growth when grown under prolonged inundation. Niswander and Mitch (1995) planted ten tree species (three of which were used in this study, *B. nigra*, *L. styrraciflua*, *Q. palustris*) across a hydrologic gradient in a created wetland. Similar to the results in this study, they found that trees planted in shallow water died or were severely stressed, and that trees planted in the wet meadow portion were able to survive and grow, while trees planted in the upland section were the largest and had the densest foliage. Pennington and Walters (2006) investigated growth and survival four species (two of which were used in this study, *Q. palustris* and *Q. bicolor*) planted in three hydrologic zones (wetland, transition, upland) of created perched wetlands. Again, similar to the present study, trees grown in the transitions zone (high soil water availability with
oxidized root zone) had greater height growth and survival after 5 years than those planted in the wetland zone (reduced oxygen in the root zone). Bailey et al. (2007) investigated the effect of organic matter loading rates and elevation in a created wetland on several vegetation responses, including the growth of planted *B. nigra*. Results suggested that the early growth of planted trees responded to both OM loading rates and hydrology related to elevation. In the lower elevations (higher water table) the tree growth rates were reduced compared to those in the higher elevations, consistent with results of *B. nigra* from the present study. From the present study and previous studies, stressful hydrologic conditions reduce the ecological structure and functions associated with planted trees.

The spatial location of herbaceous vegetation and other trees in relation to planted trees can lead to competition for resources including, light, water, nutrients, CO₂, O₂, and space. Davis et al. (1999) investigated the effect of herbaceous competition along a water-light-nitrogen gradient and found that seedling survival of *Q. macrocarpa* and *Q. ellipsoidalis* was significantly greater when herbaceous vegetation was removed in the wetter shaded plots. These results are consistent with the results from the present study where secondary species had increased survival and growth in SAT where competition was reduced and hydrologic stress was less than FLD. Pinto et al. (2012) investigated the effect of moisture stress caused by vegetative competition on three stocktypes of *P. ponderosa*. The results suggest that small stocktypes had low survival when exposed to low moisture conditions caused by herbaceous competition, while larger stock had somewhat improved survival. They concluded that appropriate moisture is critical for survival and that herbaceous vegetation competes substantially for moisture. A related
finding from the present study was that more species/stocktype combinations had greater survival in SAT than in AMB. This suggests that the hydrologic regime and/or reduction in competition in SAT provided conditions that increased survival, which lead to the restoration of ecological structure and functions.

The soil physical and chemical characteristics of FLD compared to AMB (higher bulk density, higher clay content, lower soil nutrients) are characteristic of restored wetlands in the Mid-Atlantic region (Bishel-Machung et al. 1996, Shaffer and Ernst 1999, Whittecar and Daniels 1999, Stolt et al. 2000, Campbell et al. 2002, Bruland and Richardson 2005, Daniels and Whittecar 2011). Several studies have found that compacted soil reduces the survival and aboveground and belowground growth of planted trees (Alberty et al. 1984, Clevland and Kjelgren 1994, Kozlowski 1999, Siegel-Issem et al. 2005) similar to the results of this study. Clay concentrations influence bulk density and have also been shown to negatively affect planted tree growth. Schaff et al. (2003) found that S. nigra cuttings (posts) planted in fine-grained sediments (higher silt/clay) compared to coarse-grained sediments in a restored streambank had lower biomass accumulation and leaf area. They hypothesized that the fine-grained sediments prevent root elongation and suggested that soil texture be evaluated prior to restoration. Results from the present study similarly show that increased clay concentrations in conjunction with higher bulk density in FLD reduced the survival and growth of all seven species.

Several experiments have shown that decreased abundance of soil nutrients decreases growth of trees. In a greenhouse experiment investigating the effect of flooding and soil nutrients on T. distichum and Nyssa aquatica growth, Effler and Goyer (2006)
found that flooding in combination with low soil nutrients reduced growth, while flooding in combination with fertilization lead to similar growth of trees grown without flooding or fertilization. Day (1987) investigated the effects of flood frequency (no flooding, intermittent flooding and continuous flooding) and nutrient enrichment (no enrichment, nitrogen additions, phosphorus additions and N and P additions) on the biomass production of *Acer rubrum* seedlings within a greenhouse. Continuous flooding reduced biomass production; however, adding nutrients to the continuously flooded trees increased stem and leaf production. Bailey et al. (2007) found that *B. nigra* planted in a created wetland were larger when planted in areas with higher organic amendments that increased the nutrient content of the soil. While the species and treatments may have varied from previous studies, results from the present study similarly show that low soil nutrient concentrations in combination with hydrologic and competitive stress will reduce the survival and size of planted trees. This suggests that in order to ensure the return of ecological structure and functions associated with planted trees in restored forested wetlands, particular attention should be paid to the initial soil physical and chemical characteristics.

**Conclusions**

From this study we conclude that species and stocktypes can be selected to match environmental conditions and to maximize return of ecological structure, functions and services to the landscape. These results can be applied to wetlands undergoing restoration or enhancement that have a range of environmental conditions or to other afforestation or reforestation projects, such as riparian buffers or uplands. Results from this study show
that primary successional species (especially *S. nigra*) planted using larger containerized stock are more appropriate for harsh environmental conditions, such as areas with high water tables, poor soil conditions or heavy herbaceous competition. These areas may correspond to stream banks that experience flooding, post-agricultural wetland restorations or other challenging environments. However, when attempting to restore forested wetland habitat or any other ecosystem the diversity of planted species should be considered.

In areas with less stressful environmental conditions (moderate water table, less compacted and nutrient rich soil conditions and reduced herbaceous competition), primary or secondary species could be expected to have similar survival rates. However, due to the slow growth of secondary species, primary species are preferred for returning their associated ecological structure and functions more quickly. In these less stressful environmental conditions the less expensive bare root stocktype can be expected to develop similar morphological structure as the more expensive gallon stocktype. The tubeling stocktype does not appear to provide added benefit for its intermediate price.

Overall, from comparing differences among cells, the results from this study suggest that initial environmental conditions can have a large influence on survival and growth of planted trees. These results could be used for a variety of tree planting situations besides forested wetland restoration including carbon sequestration projects, wildlife habitat creation and other conservation projects.
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Table 2-1. Description of environmental parameters for the three experimental cells. Numbers represent averages with associated standard deviations. Soil parameters represent 44 samples taken in each cell.

<table>
<thead>
<tr>
<th>Environmental Parameter</th>
<th>Ambient Cell</th>
<th>Saturated Cell</th>
<th>Flooded Cell</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrology</td>
<td>Received only precipitation</td>
<td>Kept saturated for a minimum of 90% of the growing season within the root-zone (10 cm) of the plantings and irrigated as needed</td>
<td>Inundated above the root crown for a minimum of 90% of each year</td>
</tr>
<tr>
<td>Soil Preparation</td>
<td>Disked and Tilled</td>
<td>Disked and Tilled</td>
<td>Excavated to a depth of 1 m to an existing clay layer</td>
</tr>
<tr>
<td>Herbaceous Vegetation Control</td>
<td>Riding Lawnmower, Push mower, weedwacker, Glyphosate application</td>
<td>Riding Lawnmower, Push mower, weedwacker, Glyphosate application</td>
<td>None</td>
</tr>
<tr>
<td>Bulk Density (g/cm³)</td>
<td>1.03 (0.11)</td>
<td>1.1 (0.13)</td>
<td>1.38 (0.14)</td>
</tr>
<tr>
<td>Soil Percentage Sand</td>
<td>85.16 (6.16)</td>
<td>88.35 (4.38)</td>
<td>63.74 (10.05)</td>
</tr>
<tr>
<td>Soil Percentage Silt</td>
<td>10.22 (5.48)</td>
<td>7.57 (3.12)</td>
<td>17.27 (6.44)</td>
</tr>
<tr>
<td>Soil Percentage Clay</td>
<td>4.62 (1.25)</td>
<td>4.08 (1.5)</td>
<td>18.99 (6.64)</td>
</tr>
<tr>
<td>Soil Percentage Carbon</td>
<td>1.47 (0.37)</td>
<td>1.2 (0.4)</td>
<td>0.34 (0.12)</td>
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<tr>
<td>Soil Percentage Nitrogen</td>
<td>0.17 (0.04)</td>
<td>0.15 (0.04)</td>
<td>0.08 (0.03)</td>
</tr>
<tr>
<td>Soil Percentage Phosphorus</td>
<td>0.29 (0.08)</td>
<td>0.26 (0.08)</td>
<td>0.18 (0.04)</td>
</tr>
<tr>
<td>Species</td>
<td>Stocktype</td>
<td>Stem Cross-sectional Area at Groundline (cm²)</td>
<td>Height (cm)</td>
</tr>
<tr>
<td>---------------------</td>
<td>-----------</td>
<td>---------------------------------------------</td>
<td>--------------</td>
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<tr>
<td>Betula nigra</td>
<td>Bare root</td>
<td>0.5 (0.7) b</td>
<td>50.6 (27.2) c</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>1 (1) a</td>
<td>78.8 (48.4) a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>0.6 (0.6) b</td>
<td>61.1 (35.7) b</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>Bare root</td>
<td>0.6 (0.6) b</td>
<td>58.4 (37.8) ab</td>
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<tr>
<td></td>
<td>Gallon</td>
<td>0.8 (0.8) a</td>
<td>62.7 (33.9) a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>0.6 (0.7) b</td>
<td>50.1 (35.8) b</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>Bare root</td>
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<td>48.4 (27) b</td>
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<td>56.4 (29.3) b</td>
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<td>52.2 (30.2) a</td>
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<tr>
<td></td>
<td>Gallon</td>
<td>0.7 (0.6) a</td>
<td>47.3 (28.1) a</td>
</tr>
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<td></td>
<td>Tubeling</td>
<td>0.6 (0.6) a</td>
<td>51.8 (35.9) a</td>
</tr>
<tr>
<td>Quercus palustris</td>
<td>Bare root</td>
<td>0.6 (0.6) b</td>
<td>51.1 (33) b</td>
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<tr>
<td></td>
<td>Gallon</td>
<td>0.8 (0.7) a</td>
<td>66.7 (32.3) a</td>
</tr>
<tr>
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<td>Tubeling</td>
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<td>45 (34.5) b</td>
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<td>Quercus phellos</td>
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<td>55.2 (30.7) b</td>
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<td>Gallon</td>
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<td>73.4 (44.5) a</td>
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<td>Tubeling</td>
<td>0.5 (0.5) b</td>
<td>54 (27.6) b</td>
</tr>
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<td>50.6 (28.8) b</td>
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<td>Gallon</td>
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<td>76.7 (42) a</td>
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<tr>
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<td>Tubeling</td>
<td>0.5 (0.6) b</td>
<td>55.5 (34.7) b</td>
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</tbody>
</table>
Table 2-3. Results of type 3 tests of fixed effects for species and stocktype for each morphological variable over 5 years.

<table>
<thead>
<tr>
<th>Cell</th>
<th>Source of variation</th>
<th>DF</th>
<th>Wald Chi Square</th>
<th>Pr &gt; F</th>
<th>F-value</th>
<th>Pr &gt; F</th>
<th>F-value</th>
<th>Pr &gt; F</th>
<th>F-value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB</td>
<td>Species</td>
<td>6</td>
<td>29.03</td>
<td>0.0014</td>
<td>1.52</td>
<td>&lt;0.001</td>
<td>18.97</td>
<td>&lt;0.001</td>
<td>30.69</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Stocktype</td>
<td>2</td>
<td>21.60</td>
<td>&lt;0.001</td>
<td>33.66</td>
<td>&lt;0.001</td>
<td>22.24</td>
<td>&lt;0.001</td>
<td>20.86</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species x Stocktype</td>
<td>12</td>
<td>57.00</td>
<td>&lt;0.001</td>
<td>8.22</td>
<td>&lt;0.001</td>
<td>4.51</td>
<td>&lt;0.001</td>
<td>6.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SAT</td>
<td>Species</td>
<td>6</td>
<td>18.86</td>
<td>0.0038</td>
<td>13.26</td>
<td>&lt;0.001</td>
<td>22.38</td>
<td>&lt;0.001</td>
<td>27.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Stocktype</td>
<td>2</td>
<td>16.22</td>
<td>&lt;0.001</td>
<td>26.41</td>
<td>&lt;0.001</td>
<td>18.93</td>
<td>&lt;0.001</td>
<td>19.08</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species x Stocktype</td>
<td>12</td>
<td>21.40</td>
<td>0.045</td>
<td>3.67</td>
<td>&lt;0.001</td>
<td>2.42</td>
<td>0.0044</td>
<td>2.10</td>
<td>0.0148</td>
</tr>
<tr>
<td>FLD</td>
<td>Species</td>
<td>6</td>
<td>120.89</td>
<td>0.1036</td>
<td>86.01</td>
<td>&lt;0.001</td>
<td>517.61</td>
<td>&lt;0.001</td>
<td>223.65</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Stocktype</td>
<td>2</td>
<td>4.53</td>
<td>&lt;0.001</td>
<td>79.34</td>
<td>&lt;0.001</td>
<td>87.35</td>
<td>&lt;0.001</td>
<td>71.23</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species x Stocktype</td>
<td>12</td>
<td>44.77</td>
<td>&lt;0.001</td>
<td>3.42</td>
<td>&lt;0.001</td>
<td>21.91</td>
<td>&lt;0.001</td>
<td>6.67</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 2-4. Results of type 3 tests of fixed effects for successional group and species for each morphological variable over 5 years.

<table>
<thead>
<tr>
<th>Cell</th>
<th>Source of variation</th>
<th>Survival DF</th>
<th>Wald Chi Square</th>
<th>Pr &gt; F</th>
<th>Stem Cross-sectional area at Groundline F-value</th>
<th>Pr &gt; F</th>
<th>Height F-value</th>
<th>Pr &gt; F</th>
<th>Canopy Diameter F-value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB</td>
<td>Successional Group</td>
<td>1</td>
<td>0.0987</td>
<td>0.7534</td>
<td>103.16 &lt;0.001</td>
<td>61.31 &lt;0.001</td>
<td>59.06 &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stocktype</td>
<td>2</td>
<td>45.60 &lt;0.001</td>
<td>6.25</td>
<td>0.002</td>
<td>15.67 &lt;0.001</td>
<td>23.83 &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stocktype x Successional Group</td>
<td>2</td>
<td>8.71 0.0128</td>
<td>2.21</td>
<td>0.1104</td>
<td>1.23 0.2929</td>
<td>1.37 0.254</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAT</td>
<td>Successional Group</td>
<td>1</td>
<td>2.027</td>
<td>0.1545</td>
<td>107.53 &lt;0.001</td>
<td>77.63 &lt;0.001</td>
<td>60.14 &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stocktype</td>
<td>2</td>
<td>31.57 &lt;0.001</td>
<td>9.88</td>
<td>&lt;0.001</td>
<td>20.37 &lt;0.001</td>
<td>24.90 &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stocktype x Successional Group</td>
<td>2</td>
<td>3.69 0.158</td>
<td>3.29</td>
<td>0.0379</td>
<td>0.6 0.5513</td>
<td>0.74 0.4758</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FLD</td>
<td>Successional Group</td>
<td>1</td>
<td>86.43 &lt;0.001</td>
<td>102.2</td>
<td>&lt;0.001</td>
<td>179.25 &lt;0.001</td>
<td>39.19 &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stocktype</td>
<td>2</td>
<td>48.48 &lt;0.001</td>
<td>60.93</td>
<td>&lt;0.001</td>
<td>336.23 &lt;0.001</td>
<td>146.19 &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stocktype x Successional Group</td>
<td>2</td>
<td>20.88 &lt;0.001</td>
<td>4.76</td>
<td>0.0088</td>
<td>10.57 &lt;0.001</td>
<td>1.65 0.1923</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2-5. Results of type 3 tests of fixed effects for cell for each morphological variable after 5 years.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stocktype</th>
<th>Source of Variation</th>
<th>Stem Cross-sectional Area at Groundline</th>
<th>Height</th>
<th>Canopy Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>F-value</td>
<td>Pr &gt; F</td>
<td>F-value</td>
</tr>
<tr>
<td>B. nigra</td>
<td>Bare root</td>
<td>Cell</td>
<td>47.83</td>
<td>&lt;0.0001</td>
<td>144.90</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>59.69</td>
<td>&lt;0.0001</td>
<td>276.75</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>53.03</td>
<td>&lt;0.0001</td>
<td>209.13</td>
</tr>
<tr>
<td>L. styraciflua</td>
<td>Bare root</td>
<td>Cell</td>
<td>113.55</td>
<td>&lt;0.0001</td>
<td>319.96</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>135.18</td>
<td>&lt;0.0001</td>
<td>357.83</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>41.74</td>
<td>&lt;0.0001</td>
<td>102.38</td>
</tr>
<tr>
<td>P. occidentalis</td>
<td>Bare root</td>
<td>Cell</td>
<td>16.88</td>
<td>0.0010</td>
<td>24.67</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>33.13</td>
<td>&lt;0.0001</td>
<td>103.85</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>13.25</td>
<td>&lt;0.0001</td>
<td>19.48</td>
</tr>
<tr>
<td>Q. bicolor</td>
<td>Bare root</td>
<td>Cell</td>
<td>15.97</td>
<td>&lt;0.0001</td>
<td>33.89</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>21.95</td>
<td>&lt;0.0001</td>
<td>64.39</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>27.5</td>
<td>&lt;0.0001</td>
<td>64.44</td>
</tr>
<tr>
<td>Q. palustris</td>
<td>Bare root</td>
<td>Cell</td>
<td>31.54</td>
<td>&lt;0.0001</td>
<td>34.96</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>8.06</td>
<td>0.0014</td>
<td>76.54</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>0.26</td>
<td>0.7742</td>
<td>0.29</td>
</tr>
<tr>
<td>Q. phellos</td>
<td>Bare root</td>
<td>Cell</td>
<td>18.9</td>
<td>&lt;0.0001</td>
<td>70.58</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>69.6</td>
<td>&lt;0.0001</td>
<td>119.7</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>0.30</td>
<td>0.5930</td>
<td>0.92</td>
</tr>
<tr>
<td>S. nigra</td>
<td>Bare root</td>
<td>Cell</td>
<td>5.56</td>
<td>0.2872</td>
<td>24.18</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>Cell</td>
<td>29.61</td>
<td>&lt;0.0001</td>
<td>91.29</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>Cell</td>
<td>10.49</td>
<td>0.0005</td>
<td>56.54</td>
</tr>
</tbody>
</table>
Table 2-6. Number of species/measurement combinations that exhibited a particular outcome when comparing stocktypes within each cell. The 28 species/measurement combinations are 7 species paired with each of three morphological measurements (CSAG, H, CD) and survival (e.g. B. nigra H, S. nigra survival, etc.) that were monitored over 5 years. The outcomes (>,<,=) result from post-hoc comparisons of stocktypes (BR vs GAL & TB vs GAL & BR vs TB) for each species/measurement combination. Percent represents percentage of occurrence of each outcome for each group of stocktype post-hoc comparisons (e.g. GAL>BR in 60.7% (17) of the 28 post-hoc BR vs. GAL comparisons in the Ambient cell). Total represents sum of outcomes across all cells and percent occurrence of outcomes for groups of post-hoc comparisons. See following tables representing comparisons of stocktypes for each individual species/measurements combination.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Ambient</th>
<th>Saturated</th>
<th>Flooded</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>BR &lt; GAL</td>
<td>17 (60.7%)</td>
<td>14 (50%)</td>
<td>25 (89.3%)</td>
<td>56 (66.7%)</td>
</tr>
<tr>
<td>BR = GAL</td>
<td>11 (39.3%)</td>
<td>14 (50%)</td>
<td>2 (7.1%)</td>
<td>27 (32.1%)</td>
</tr>
<tr>
<td>BR &gt; GAL</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>1 (3.6%)</td>
<td>1 (1.2%)</td>
</tr>
<tr>
<td>TB &lt; GAL</td>
<td>22 (78.6%)</td>
<td>21 (75%)</td>
<td>26 (92.9%)</td>
<td>69 (82.1%)</td>
</tr>
<tr>
<td>TB = GAL</td>
<td>6 (21.4%)</td>
<td>7 (25%)</td>
<td>2 (7.1%)</td>
<td>15 (17.9%)</td>
</tr>
<tr>
<td>TB &gt; GAL</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td>BR = TB</td>
<td>17 (60.7%)</td>
<td>21 (75%)</td>
<td>20 (71.4%)</td>
<td>58 (69%)</td>
</tr>
<tr>
<td>BR &gt; TB</td>
<td>9 (32.1%)</td>
<td>7 (25%)</td>
<td>7 (25%)</td>
<td>23 (27.4%)</td>
</tr>
<tr>
<td>BR &lt; TB</td>
<td>2 (7.1%)</td>
<td>0 (0%)</td>
<td>1 (3.6%)</td>
<td>3 (3.6%)</td>
</tr>
</tbody>
</table>
Table 2-7. Number of stocktype/measurement combinations that exhibited a particular outcome when comparing successional groups within each cell. The 12 stocktype/measurement combinations are 3 stocktypes paired with each of three morphological measurements (CSAG, H, CD) and survival (e.g. BR H, GAL survival, etc.) that were monitored over 5 years. The outcomes (>,<,=) result from comparison of successional groups (primary vs. secondary) for each stocktype/measurement combination. Percent represents percentage of occurrence of each outcome (e.g. PRI>SEC in 75% (9) of the 12 successional group comparisons in the Ambient cell). Total represents sum of outcomes across all cells and percent occurrence of outcomes for successional group comparisons. See following graphs representing comparisons of successional groups for each individual stocktype/measurement combination.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Ambient</th>
<th>Saturated</th>
<th>Flooded</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pri&gt;Sec</td>
<td>9 (75%)</td>
<td>9 (75%)</td>
<td>11 (91.7%)</td>
<td>29 (80.6%)</td>
</tr>
<tr>
<td>Pri=Sec</td>
<td>2 (16.7%)</td>
<td>2 (16.7%)</td>
<td>1 (8.3%)</td>
<td>5 (13.9%)</td>
</tr>
<tr>
<td>Pri&lt;Sec</td>
<td>1 (8.3%)</td>
<td>1 (8.3%)</td>
<td>0 (0%)</td>
<td>2 (5.6%)</td>
</tr>
</tbody>
</table>
Table 2-8. Number of species/stocktype combinations that exhibited a particular outcome when comparing cells for survival and morphological measurements (CSAG, CD, H) after 5 years. The 21 species/stocktype combinations are 7 species paired with BR, GAL and TB stocktypes (e.g. B. nigra BR, S. nigra TB, etc.). However, due to mortality all 21 combinations are not represented for all comparisons. The outcomes (>,<,=) result from post-hoc comparisons of morphological measurements among cells (AMB vs. SAT, AMB vs. FLD, SAT vs. FLD) for each species/stocktype combinations. Survival was not compared statistically and represents absolute differences. Percent represents percentage of occurrence of each outcome for each group of cell comparisons (e.g. AMB CSAG > SAT CSAG in 42.9% (9) of the 21 post-hoc AMB vs. SAT comparisons). Total represents sum of outcomes across survival and morphological measures and percent occurrence of outcomes for cell groups of post-hoc comparisons. See following tables representing comparisons of cells for each individual species/stocktype combination.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>% Survival</th>
<th>Stem Cross-sectional Area at Groundline</th>
<th>Canopy Diameter</th>
<th>Height</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB&gt;SAT</td>
<td>6 (28.6%)</td>
<td>9 (42.9%)</td>
<td>9 (42.9%)</td>
<td>15 (71.4%)</td>
<td>39 (46.4%)</td>
</tr>
<tr>
<td>AMB=SAT</td>
<td>1 (4.8%)</td>
<td>12 (57.1%)</td>
<td>12 (57.1%)</td>
<td>6 (28.6%)</td>
<td>31 (36.9%)</td>
</tr>
<tr>
<td>AMB&lt;SAT</td>
<td>14 (66.7%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>14 (16.7%)</td>
</tr>
<tr>
<td>AMB&gt;FLD</td>
<td>16 (76.2%)</td>
<td>16 (84.2%)</td>
<td>17 (89.5%)</td>
<td>18 (94.7%)</td>
<td>67 (85.9%)</td>
</tr>
<tr>
<td>AMB=FLD</td>
<td>0 (0%)</td>
<td>3 (15.8%)</td>
<td>2 (10.5%)</td>
<td>1 (5.3%)</td>
<td>6 (7.7%)</td>
</tr>
<tr>
<td>AMB&lt;FLD</td>
<td>5 (23.8%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>5 (6.4%)</td>
</tr>
<tr>
<td>SAT&gt;FLD</td>
<td>16 (76.2%)</td>
<td>16 (84.2%)</td>
<td>17 (89.5%)</td>
<td>17 (89.5%)</td>
<td>66 (84.6%)</td>
</tr>
<tr>
<td>SAT=FLD</td>
<td>0 (0%)</td>
<td>3 (15.8%)</td>
<td>2 (10.5%)</td>
<td>2 (10.5%)</td>
<td>7 (9%)</td>
</tr>
<tr>
<td>SAT&lt;FLD</td>
<td>5 (23.8%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>5 (6.4%)</td>
</tr>
</tbody>
</table>
Table 2-9. Species exhibiting each outcome within each cell. < and > indicate significant difference in percent survival (See Figure 2-11). Total represents a count of how many times each outcome occurred across all cells.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Ambient</th>
<th>Saturated</th>
<th>Flooded</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>BR &lt; GAL</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolour, Q. palustris, Q. phellos</td>
<td>17</td>
</tr>
<tr>
<td>BR = GAL</td>
<td>Q. bicolor</td>
<td>Q. bicolor, Q. palustris</td>
<td>S. nigra</td>
<td>4</td>
</tr>
<tr>
<td>BR &gt; GAL</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>TB &lt; GAL</td>
<td>B. nigra, L. styraciflua, Q. bicolour, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolour, Q. palustris, Q. phellos, S. nigra</td>
<td>L. styraciflua, P. occidentalis, Q. bicolour, Q. palustris, Q. phellos</td>
<td>18</td>
</tr>
<tr>
<td>TB = GAL</td>
<td>P. occidentalis</td>
<td></td>
<td>B. nigra, S. nigra</td>
<td>3</td>
</tr>
<tr>
<td>TB &gt; GAL</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>BR = TB</td>
<td>B. nigra, Q. phellos</td>
<td>B. nigra, P. occidentalis, Q. phellos, S. nigra</td>
<td>L. styraciflua, P. occidentalis, Q. palustris, S. nigra</td>
<td>10</td>
</tr>
<tr>
<td>BR &gt; TB</td>
<td>L. styraciflua, Q. bicolour, Q. palustris</td>
<td>L. styraciflua, Q. bicolour, Q. palustris</td>
<td>Q. bicolour, Q. phellos</td>
<td>8</td>
</tr>
<tr>
<td>BR &lt; TB</td>
<td>P. occidentalis, S. nigra</td>
<td></td>
<td>B. nigra</td>
<td>3</td>
</tr>
</tbody>
</table>
Table 2-10. Species exhibiting each outcome for three stocktypes. < and > indicate significant difference in percent survival (See Figure 2-11). Total represents a count of how many times each outcome occurred across all stocktypes.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Bare root</th>
<th>Gallon</th>
<th>Tubing</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB&gt;SAT</td>
<td>P. occidentalis</td>
<td>B. nigra, Q. palustris, S. nigra</td>
<td>P. occidentalis, S. nigra</td>
<td>6</td>
</tr>
<tr>
<td>AMB=SAT</td>
<td>Q. bicolor</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>AMB&gt;SAT</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>L. styraciflua, P. occidentalis, Q. phellos</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>14</td>
</tr>
<tr>
<td>AMB&gt;FLD</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos</td>
<td>P. occidentalis, Q. bicolor, Q. palustris, Q. phellos</td>
<td>16</td>
</tr>
<tr>
<td>AMB=FLD</td>
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<td></td>
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</tr>
<tr>
<td>AMB&lt;FLD</td>
<td>S. nigra</td>
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<td></td>
<td>5</td>
</tr>
<tr>
<td>SAT&gt;FLD</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos</td>
<td>P. occidentalis, Q. bicolor, Q. palustris, Q. phellos</td>
<td>16</td>
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<tr>
<td>SAT=FLD</td>
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<tr>
<td>SAT&lt;FLD</td>
<td>S. nigra</td>
<td></td>
<td></td>
<td>5</td>
</tr>
</tbody>
</table>
Table 2-11. Number of species exhibiting each outcome within each cell. < and > indicate significant difference in stem cross-sectional area at groundline (CSAG) (See Figure 2-12). Total represents a count of how many times each scenario occurred across all cells.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Ambient</th>
<th>Saturated</th>
<th>Flooded</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>BR &lt; GAL</td>
<td>B. nigra, Q. phellos, S. nigra</td>
<td>B. nigra, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>12</td>
</tr>
<tr>
<td>BR = GAL</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor, S. nigra</td>
<td>Q. bicolor</td>
<td>9</td>
</tr>
<tr>
<td>BR &gt; GAL</td>
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<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>TB &lt; GAL</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>17</td>
</tr>
<tr>
<td>TB = GAL</td>
<td>P. occidentalis, S. nigra</td>
<td>P. occidentalis, S. nigra</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>TB &gt; GAL</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>BR = TB</td>
<td>B. nigra, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>17</td>
</tr>
<tr>
<td>BR &gt; TB</td>
<td>L. styraciflua, Q. bicolor</td>
<td>Q. bicolor</td>
<td>Q. bicolor</td>
<td>4</td>
</tr>
<tr>
<td>BR &lt; TB</td>
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</tr>
</tbody>
</table>
Table 2-12. Number of species exhibiting each outcome for three stocktypes. < and > indicate significant difference in stem cross-sectional area at groundline (CSAG) (See Figure 2-12). Total represents a count of how many times each scenario occurred across all stocktypes.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Bare root</th>
<th>Gallon</th>
<th>Tubeling</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB&gt;SAT</td>
<td>L. styraciflua, P. occidentalis, Q. palustris</td>
<td>B. nigra, P. occidentalis, Q. bicolor, Q. palustris</td>
<td>P. occidentalis, Q. bicolor</td>
<td>9</td>
</tr>
<tr>
<td>AMB&gt;SAT</td>
<td>B. nigra, Q. bicolor, Q. phellos, S. nigra</td>
<td>L. styraciflua, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, Q. palustris, Q. phellos, S. nigra</td>
<td>12</td>
</tr>
<tr>
<td>AMB=SAT</td>
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<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>AMB&gt;FLD</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, Q. bicolor, S. nigra</td>
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<tr>
<td>AMB=FLD</td>
<td>S. nigra</td>
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<td>P. occidentalis, Q. palustris</td>
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<tr>
<td>AMB&lt;FLD</td>
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<tr>
<td>SAT&gt;FLD</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, Q. bicolor, S. nigra</td>
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<tr>
<td>SAT=FLD</td>
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<td>Q. palustris</td>
<td>P. occidentalis, Q. palustris</td>
<td>3</td>
</tr>
<tr>
<td>SAT&lt;FLD</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>
Table 2-13. Number of species exhibiting each outcome within each cell. < and > indicate significant difference in crown diameter (See Figure 2-13). Total represents a count of how many times each outcome occurred across all cells.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Ambient</th>
<th>Saturated</th>
<th>Flooded</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>BR &lt; GAL</td>
<td>B. nigra, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, L. styraciflua, P. occidentalis, Q. bicolor</td>
<td>15</td>
</tr>
<tr>
<td>BR = GAL</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor</td>
<td>6</td>
</tr>
<tr>
<td>BR &gt; GAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TB &lt; GAL</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, L. styraciflua, P. occidentalis, Q. bicolor</td>
<td>18</td>
</tr>
<tr>
<td>TB = GAL</td>
<td>P. occidentalis</td>
<td>B. nigra, P. occidentalis</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>TB &gt; GAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR = TB</td>
<td>B. nigra, P. occidentalis, Q. bicolor, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>17</td>
</tr>
<tr>
<td>BR &gt; TB</td>
<td>L. styraciflua, Q. palustris</td>
<td>Q. bicolor</td>
<td>Q. bicolor</td>
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<tr>
<td>BR &lt; TB</td>
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</tbody>
</table>
Table 2-14. Number of species exhibiting each outcome for three stocktypes. < and > indicate significant difference in crown diameter (See Figure 2-13). Total represents a count of how many times each outcome occurred across all stocktypes.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Bare root</th>
<th>Gallon</th>
<th>Tubeling</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB&gt;SAT</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris</td>
<td>B. nigra, P. occidentalis, Q. bicolor, Q. palustris</td>
<td>Q. bicolor</td>
<td>9</td>
</tr>
<tr>
<td>AMB&gt;SAT</td>
<td>B. nigra, Q. phellos, S. nigra</td>
<td>L. styraciflua, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>12</td>
</tr>
<tr>
<td>AMB&gt;SAT</td>
<td>L. styraciflua, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>AMB=FLD</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, S. nigra</td>
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<tr>
<td>AMB=FLD</td>
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<tr>
<td>AMB=FLD</td>
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<td></td>
<td>0</td>
</tr>
<tr>
<td>SAT&gt;SAT</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, Q. bicolor, S. nigra</td>
<td>17</td>
</tr>
<tr>
<td>SAT&gt;SAT</td>
<td>P. occidentalis, Q. palustris</td>
<td></td>
<td></td>
<td>2</td>
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<tr>
<td>SAT&gt;SAT</td>
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<td>0</td>
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</tbody>
</table>
Table 2-15. Number of species exhibiting each outcome within each cell. < and > indicate significant difference in height (See Figure 2-14). Total represents a count of how many times each outcome occurred across all cells.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Ambient</th>
<th>Saturated</th>
<th>Flooded</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>BR &lt; GAL</td>
<td>B. nigra, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. palustris, Q. phellos, S. nigra</td>
<td>12</td>
</tr>
<tr>
<td>BR = GAL</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, S. nigra</td>
<td>L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, S. nigra</td>
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<tr>
<td>BR &gt; GAL</td>
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<td>Q. bicolor</td>
<td>1</td>
</tr>
<tr>
<td>TB &lt; GAL</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>16</td>
</tr>
<tr>
<td>TB = GAL</td>
<td>P. occidentalis, S. nigra</td>
<td>B. nigra, P. occidentalis, S. nigra</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>TB &gt; GAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR &gt; TB</td>
<td>L. styraciflua, Q. palustris</td>
<td>L. styraciflua, Q. palustris</td>
<td>L. styraciflua, Q. bicolor, Q. palustris</td>
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<tr>
<td>BR &lt; TB</td>
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</table>
Table 2-16. Number of species exhibiting each outcome for three stocktypes. < and > indicate significant difference in height (See Figure 2-14). Total represents a count of how many times each outcome occurred across all stocktypes.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Bare root</th>
<th>Gallon</th>
<th>Tubeling</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMB&gt;SAT</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos</td>
<td>B. nigra, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, P. occidentalis, Q. bicolor, S. nigra</td>
<td>15</td>
</tr>
<tr>
<td>AMB=SAT</td>
<td>P. occidentalis, S. nigra</td>
<td>L. styraciflua</td>
<td>L. styraciflua, Q. palustris, Q. phellos</td>
<td>6</td>
</tr>
<tr>
<td>AMB&lt;SAT</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>AMB&gt;FLD</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, S. nigra</td>
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<td>AMB=FLD</td>
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<td>AMB&lt;FLD</td>
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<tr>
<td>SAT&gt;FLD</td>
<td>B. nigra, L. styraciflua, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, P. occidentalis, Q. bicolor, Q. palustris, Q. phellos, S. nigra</td>
<td>B. nigra, L. styraciflua, Q. bicolor, S. nigra</td>
<td>17</td>
</tr>
<tr>
<td>SAT=FLD</td>
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</tbody>
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Figure 2-1. A) The experimental site is located in the Mid-Atlantic Region of the United States, in the Upper Coastal Plain Province of Virginia. B) The site is on an upland terrace in the Virginia Department of Forestry, New Kent Forestry Center. C) The hydrologically distinct cells (ambient (AMB), saturated (SAT) and flooded (FLD)) are 49 m x 95 m in size.
Figure 2-2. Soil bulk density across experimental site.
Figure 2-3. Percentage sand across experimental site
Figure 2-4. Percentage silt across experimental site.
Figure 2-5. Percentage clay across experimental site
Figure 2-6. Soil percentage carbon across experimental site.
Figure 2-7. Soil percentage nitrogen across experimental site.
Figure 2-8. Soil percentage phosphorus across experimental site.
Figure 2-9. Average crown diameter of stocktypes for three cells. Line represents mean of seven species and ribbons represent 95% confidence interval.
Figure 2-10. Average height of successional groups for all stocktypes across cells. Line represents mean and ribbons represent 95% confidence interval.
Figure 2-11. Simple effects model results for survival of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
Figure 2-12. Simple effects model results for CSAG of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. Ribbons represent 95% confidence interval. Line represents mean. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
Figure 2-13. Simple effects model results for CD of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. Ribbons represent 95% confidence interval. Line represents mean. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
Figure 2-14. Simple effects model results for H of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. Ribbons represent 95% confidence interval. Line represents mean. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates $p$-value $\leq 0.05$, ** indicates $p$-value $\leq 0.01$ and *** indicates $p$-value $\leq 0.001$. 

<table>
<thead>
<tr>
<th>Species</th>
<th>Data Type</th>
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</thead>
<tbody>
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<td>Acer saccharum</td>
<td>Base coat</td>
</tr>
<tr>
<td>Betula nigra</td>
<td>Gallon</td>
</tr>
<tr>
<td>Fraxinus</td>
<td>Sprouting</td>
</tr>
<tr>
<td>Populus</td>
<td>Total</td>
</tr>
</tbody>
</table>

- BR<GL**
- BR=GL*
- BR>GL**
- GL<TB**
- GL=TB
- GL>TB**

Figure 2-14. Simple effects model results for H of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. Ribbons represent 95% confidence interval. Line represents mean. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates $p$-value $\leq 0.05$, ** indicates $p$-value $\leq 0.01$ and *** indicates $p$-value $\leq 0.001$. 

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<tr>
<th>Species</th>
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</thead>
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<tr>
<td>Acer saccharum</td>
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<tr>
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<td>Gallon</td>
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<tr>
<td>Fraxinus</td>
<td>Sprouting</td>
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<tr>
<td>Populus</td>
<td>Total</td>
</tr>
</tbody>
</table>

- BR<GL**
- BR=GL*
- BR>GL**
- GL<TB**
- GL=TB
- GL>TB**

Figure 2-14. Simple effects model results for H of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. Ribbons represent 95% confidence interval. Line represents mean. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates $p$-value $\leq 0.05$, ** indicates $p$-value $\leq 0.01$ and *** indicates $p$-value $\leq 0.001$. 

<table>
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- BR<GL**
- BR=GL*
- BR>GL**
- GL<TB**
- GL=TB
- GL>TB**

Figure 2-14. Simple effects model results for H of stocktypes (lines) among species (columns) and cells (rows). X-axis represents time since planting. Ribbons represent 95% confidence interval. Line represents mean. For stocktype comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates $p$-value $\leq 0.05$, ** indicates $p$-value $\leq 0.01$ and *** indicates $p$-value $\leq 0.001$. 

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- BR<GL**
- BR=GL*
- BR>GL**
- GL<TB**
- GL=TB
- GL>TB**
Figure 2-15. Simple effects model results for survival (time until death) of successional group (lines) among cells (columns) and stocktype (rows). Ribbons represent 95% confidence interval. Line represents mean. For successional group comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
Figure 2-16. Simple effects model results for CSAG of successional group (lines) among cells (columns) and stocktype (rows). Ribbons represent 95% confidence interval. Line represents mean. For successional group comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
Figure 2-17. Simple effects model results for CD of successional group (lines) among cells (columns) and stocktype (rows). Ribbons represent 95% confidence interval. Line represents mean. For successional group comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
Figure 2-18. Simple effects model results for H of successional group (lines) among cells (columns) and stocktype (rows). Ribbons represent 95% confidence interval. Line represents mean. For successional group comparisons, no stars represent no significant difference (p-value > 0.05) while * indicates p-value ≤ 0.05, ** indicates p-value ≤ 0.01 and *** indicates p-value ≤ 0.001.
CHAPTER 3: WOODY BIOMASS DEVELOPMENT OF SEVEN MID-ATLANTIC SPECIES GROWN UNDER THREE HYDROLOGIC CONDITIONS OVER 6 YEARS
Abstract

The primary goal of forested wetland creation and restoration is to replace or return ecosystem structure and functions to the landscape. Production of plant biomass, of which carbon is a large component, is an important ecosystem function that will develop in successfully created and restored forested wetlands. Quantifying accumulation of above and belowground biomass of planted trees is important in understanding this development and may aid in quantification of global chemical cycles. Destructive harvests and tissue elemental analysis of saplings ($n=567$) planted across a hydrologic gradient were used to develop biomass estimation models for seven species common to the Mid-Atlantic region of the United States. The model established that stem cross-sectional diameter at groundline was an adequate predictor of total biomass. The model was then applied to all living trees ($n=1,258$) to evaluate species and stocktype performance over 6 years as well as differences in accumulation across a hydrologic gradient. Early colonizing species accumulated more biomass than late succession species. Larger stocktypes (1-gallon container) accumulated more biomass than smaller stocktypes (bare root and tubeling) in areas with greater hydrologic stress and accumulated biomass decreased with increasing hydrologic stress regardless of stocktype. Aboveground dry woody tissue percentage carbon ranged from 44.2 to 48.5%; however, the proportion of carbon in the woody tissues was not significantly different among the seven species. Biomass in conjunction with elemental concentrations measured in this study can be used to evaluate the development of restored or created forested wetlands and to determine sapling contributions to these global chemical cycles.
**Introduction**

Production and accumulation (storage) of plant biomass, of which carbon is a large component, is an important ecosystem function that develops in successfully created and restored forested wetlands. In early successional created and restored forested wetlands the majority of plant biomass is produced by herbaceous vegetation (Atkinson et al. 2005, DeBerry & Perry 2012). However, as created and restored forested wetlands develop, the production and accumulation of biomass shifts to perennial woody vegetation (woody vines, shrubs, and trees) (Noon 1996, Odland 1997, Battaglia et al. 2002, DeBerry & Perry 2012, Mitsch et al. 2012), where biomass can remain long-term in the boles, stems and roots. Therefore, the intended outcome of the creation or restoration process of forested wetlands is that the majority of biomass/carbon accumulated will be produced by long lived woody species, particularly trees.

If natural colonization by trees is insufficient in a created or restored forested wetland, planting seeds, seedlings and/or saplings of desired woody species becomes necessary (Clewell & Lea 1989, Hudson 2010). The nursery industry uses an assortment of propagation techniques to produce a wide variety of tree seedling and sapling stocktypes (e.g. bare root seedlings of various ages, tubelings or plugs, containerized, balled and burlapped, live stakes, etc.). Very few studies have investigated how species and stocktype selection influences planted tree survival and growth in created/restored forested wetlands (Denton 1990); however, several studies have reported poor survival and growth of planted trees in created/restored wetlands (Morgan & Roberts 2003, Sharitz et al. 2006, Matthews & Endress 2008). Therefore, quantifying standing woody biomass and production of planted trees is important in understanding the development of
ecosystem structure and functions in created and restored forested wetlands. Additionally, accurate quantification of tree biomass, particularly saplings, is an important step in understanding carbon dynamics across a range of forested ecosystems (including wetlands) as saplings play a large, but yet unquantified, role in the global carbon cycle (Temesgen et al. 2015).

Standing biomass of an individual tree is typically estimated by using mathematical relationships between biomass and one or more morphological woody vegetation characteristics, such as stem diameter and/or height (e.g. Jenkins et al. 2003). This method is commonly referred to as dimensional analysis (Whittaker & Woodwell 1968) and relies on consistency in the correlations between the changes in relative dimensions of parts of an organism with changes in overall size, referred to as allometry (Gayon 2000, Stevens 2009). While allometric relationships may be expressed through diverse mathematical formulations (Gould 1966), the mathematical relationships describing the allometry of various characteristics of many organisms (including trees) often conform to power laws (Niklas, 2004, Stevens 2009). Equations that relate biomass and a morphological characteristic were developed and used for this study. These models will be referred to as biomass estimation models (BEM) in this study, but have also been referred to as allometric equations by others (Sileshi 2014).

Development of BEMs for seedlings and saplings is valuable because seedlings and saplings can be a major component of understory (Gemborys 1974) and canopy gaps of mature forests (Ehrenfeld 1980) and can be significant components of the vegetative structure in early successional stages of many ecosystems, including abandoned agricultural fields (Monette and Ware 1983) and recently restored (Hudson 2010) and
created wetlands (DeBerry & Perry 2012). Additionally, BEMs for seedlings and saplings allow more accurate prediction of biomass during tree development, which may allow for improved characterization of factors that affect development.

The purpose of this study was to construct BEMs relating total biomass (leafless woody above and belowground coarse root dry biomass) to sapling stem cross-sectional diameter at groundline for seven native Mid-Atlantic woody wetland species, and to determine how stocktype, soil and hydrologic conditions influenced the amount of biomass accumulated 6 years following planting. We anticipate that the results from this study may enhance the probability of successfully returning ecosystem structure and functions to created and restored forested wetlands through identification of appropriate species and stocktypes for planting and by determining sapling biomass and carbon accumulation across a hydrologic gradient.

**Methods**

Methods used to establish and measure the survival and morphology of saplings planted in the experimental site are the same as Chapter 2.

**Biomass Sampling**

Since the species specific relationships between morphology and biomass change during ontogeny and often in response to environmental conditions, aboveground biomass (AGB) and belowground biomass (BGB) samples were taken in the winter of 2010-2011; AGB was also sampled from additional trees in late winter 2014. The samples included trees from all planting times, cells and stocktypes to incorporate the
maximum variation in morphologies and biomass. A random subsample of saplings \((n=346)\) were removed in the winter of 2010-2011 to measure leafless AGB and coarse root BGB, and a random subsample of trees \((n=221)\) were removed in late winter of 2014 to measure leafless woody AGB. Sample size and average morphology for each species and stocktype are presented in Table 3-1. In order to extract roots from the soil matrix a variety of methods were used based on the size of the tree and planting location. Trees removed from the FLD cell were removed by hand or with trowels and pitchforks. Soil remaining on the roots was washed onsite prior to drying. Small trees \((<0.5 \text{ m tall})\) were removed using similar methods in AMB and SAT. For trees taller than 0.5 m, approximately 0.1 m\(^3\) of soil was excavated around the main stem using a tree spade (Dutchman Model 240o, Ontario, Canada) mounted on a skid steer loader (Bobcat S160, Seoul, South Korea). Following excavation the soil was removed from the roots by hand and with trowels and pitchforks. Any roots that were not excavated using the tree spade were subsequently removed from the soil matrix by hand and with shovels, trowels and pitchforks. All spreading and deep roots were followed to their terminus. Difficult to remove soil around the roots was washed onsite prior to drying. While attempts were made to capture all roots, this method excluded most fine roots smaller than 2 mm diameter.

The complete above and belowground portions of the trees were separated and placed in individual paper bags. Sampling occurred after leaf senescence and leaf biomass was not measured; therefore BGB refers only to coarse roots and AGB refers to stems and branches. All trees were solar dried on-site at approximately 50°C in repurposed greenhouses until constant weight was obtained. The trees were weighed at
the end of the summer in 2011 and 2014 following complete drying. The root-to-shoot ratio (r:s) was calculated for trees harvested in winter 2010-2011 where AGB and BGB was harvested.

Subsamples of trunk and branches AGB (including bark) were collected from trees that were harvested in early spring 2014 (n=103). Each subsample represented a unique stem diameter class determined visually (e.g. If the main trunk was 5 cm diameter, then a subsample was taken from the 4-5 cm diameter stem, 2-3 cm diameter stem, 1 cm diameter and less than 1 cm diameter stem). Subsamples were manually reduced in size using a small sledge hammer and then mechanically ground using a Thomas Wiley Mill Model 4 and Mini-Mill (Thomas Scientific, Swedesboro, NJ). Using a PE2400 CHNS/O Elemental Analyzer (Perkin Elmer, Massachusetts, USA) duplicate dry ground samples were analyzed for percentage carbon and nitrogen elemental concentrations, which were used to determine the carbon to nitrogen ratio (C:N).

**Biomass Estimation Model Development**

The relationship between the above (AGB) and belowground biomass (BGB) was determined for each species from the 2011 samples (AGB and BGB sampled). The 2011 samples were pooled from all three cells due to lack of differences in model coefficients when the AGB to BGB relationship was modeled for each cell separately. The following non-linear equation below was used to determine the relationship between AGB and BGB:

\[ Y = aX^b + \varepsilon \]  

(Equation 1)

\[ Y = \text{BGB (kg)} \]
X = AGB (kg)
a = model estimated intercept
b = model estimated scaling coefficient
ε = residual error term.

Using residual diagnostic plots, a heteroscedastic error structure (variance of BGB increased with greater AGB) was observed. Because of heterogeneous variance, the relationship between AGB and BGB was modeled using a generalized nonlinear least-squares regression (Pinheiro & Bates 2000). The variance structure was modeled using the power of the covariate (Packard 2014, Zuur et al. 2009) since this resulted in homogenization of residuals and lowest Akaike information criterion (AIC) values. Logarithmic transformations were not used because of criticisms associated with these methods and the heterogeneous error structure associated with this dataset (Packard 2014). The resulting model was used to estimate the BGB of the 2014 samples (where only AGB was harvested).

The same non-linear equation was used to determine the relationship between total woody biomass and equivalent stem cross-sectional diameter at groundline (ESD):

\[ Y = aX^b + \varepsilon \]  
*(Equation 2)*

Y = total woody biomass (AGB+BGB)
X = ESD
a = model estimated intercept
b = model estimated scaling coefficient
ε = residual error term.
All samples from 2011 and 2014 \((n=567)\) were used to develop this relationship. Using residual diagnostic plots, a heteroscedastic error structure (variance of biomass increased with greater basal diameter) was observed. As above, generalized nonlinear least-squares regression was used to fit the original untransformed data and the variance structure was modeled using the power of the covariate structure (Packard 2014, Pinheiro & Bates 2000, Zuur et al. 2009). Tree height and crown diameter were not included in the BEM due to multicollinearity among the predictors, despite recent studies that suggest they could be included (Picard et al. 2015).

**Statistical Analysis**

Pairwise t-test were used to compare root-to-shoot \((r:s)\) ratios of trees that were harvested in 2010-2011. Variance was estimated separately for each group, the Welch modification to degrees of freedom was used and Holm’s \(p\)-value adjustment was used to control the family-wise error rate. Percentage carbon \((C)\) and nitrogen \((N)\) and \(C:N\) ratio of AGB subsamples from 2014 harvested trees were compared among species (and species groups) within and across cells using the above methods.

Species specific BEMs were used to determine the biomass of living trees directly following planting and after 6 years. Analysis was limited to trees that were planted in 2009. Using the same methods as above, differences in initial total woody biomass \((BGB+AGB\) directly following outplanting) and woody biomass after 6 years were determined for stocktypes, species and species groups within and across cells. All alpha values were set at 0.05. Data preparation and analysis were completed in R version 3.2.1 (R Core Team 2014).
Results

Root-to-Shoot Ratio

Sampled trees (n=567) ranged in equivalent stem cross-sectional diameter at groundline (ESD) from 0.2 cm to 34.3 cm and heights from 4 cm to 1155 cm. The r:s ratio of all trees harvested in 2010-2011 (aboveground leafless woody biomass and coarse roots harvested) ranged from 0.0068 to 26.7 with an average of 1.82 (Standard error (SE) = 0.117). There were significant differences in r:s among the seven species within each cell (Table 3-2). Life history categories showed that secondary species had greater r:s (mean of 2.26) compared to primary species (1.46) across all cells. When comparing species across cells S. nigra had significantly higher r:s in FLD compared to AMB and SAT and Q. phellos had significantly lower r:s in FLD than in SAT (Table 3-2).

Tissue Elemental Concentrations

There were no differences in percentage C among species within AMB, SAT and FLD cells (Table 3-3). However, when combining all of the species into primary and secondary groups, primary species had significantly greater percentage C than secondary species. Percentage N of species was found to be significantly different within SAT and FLD. Across the cells, only Q. phellos had greater N content in AMB than FLD. These differences in species N content lead to the secondary successional species group having significantly greater N (1.38% SE = 0.023) than primary successional species (1.27% SE = 0.021) (Table 3-3). There were no differences in C:N ratio among species in AMB cell. Across cells only Q. phellos had significantly greater C:N in FLD than AMB (Table 3-3).
Overall, the primary successional species group had significantly greater C:N ratio than the secondary successional species group (Table 3-3).

**Biomass Estimation Model Development**

Using data from the 346 samples collected in 2011, a relationship between AGB and BGB (coarse roots only) for each species was determined using Eq. 1. For each species, samples were pooled across cells because the model estimated coefficients (a and b) were not different when models were developed for each cell.

The resulting model fit the data well for each species based on the standard error of the regression (Table 3-4). Primary species ranged from 0.544 (S. nigra) to 1.334 (L. styraciflua) for the model derived intercept (a) and from 0.7394 (S. nigra) to 0.975 (P. occidentalis) for the model derived exponent. The model derived intercept (a) for secondary species ranged from 0.595 (Q. phellos) to 1.921 (Q. bicolor) and the model derived exponent (b) ranged from 0.732 (Q. phellos) to 0.942 (Q. bicolor). The effect of these ranges for the exponent (b) is evident when comparing the results of primary species (Figure 3-1) and secondary species (Figure 3-2).

Using data from all 567 sampled trees the relationship between ESD and total woody biomass was determined by using Eq. 2 for each species (Table 3-5). BGB of trees harvested in 2014 (AGB only) was estimated using the model. The standard error of the regression suggested that the models described the data well for all species (ranging from 0.522 for P. occidentalis to 1.891 for Q. phellos) (Table 3-5). The model derived intercept (a) ranged from 0.028 (P. occidentalis) to 0.032 (L. styraciflua) for primary species and from 0.047 (Q. palustris) to 0.055 (Q. phellos) for secondary species. The
model derived exponent or scaling coefficient (b) ranged from 2.442 (B. nigra) to 2.788 (P. occidentalis) for primary species and the secondary species range was 2.455 (Q. phellos) to 2.735 (Q. bicolor). The effect of these exponent (b) ranges on the amount of biomass accumulated per centimeter stem diameter is evident when comparing the results among primary species (Figure 3-3) and secondary species (Figure 3-4).

Biomass Estimation Model Implementation

Initial Biomass

Initial total biomass (model derived BGB+AGB directly following outplanting) of all trees ranged from 0.0003 kg to 0.544 kg. Average initial biomass of each species/stocktype combination is presented in Table 3-6. For all species there was no difference in initial biomass between the BR and TB stocktypes. The GAL stocktype had greater initial biomass than TB stocktype for all species except L. styraciflua and Q. bicolor. Additionally, the GAL stocktype had greater initial biomass than BR for all species except Q. bicolor (Table 3-6).

Accumulated Biomass

Stocktype Comparison

In the AMB cell the GAL had significantly greater final biomass than 3 species planted as BR and 1 species planted as TB. Platanus occidentalis was the only species for which both BR and TB final biomass was significantly greater than the GAL final biomass in AMB. For 4 species, there was no difference in final biomass between the BR
and TB stocktypes, while the BR final biomass was significantly greater than TB final biomass for 2 species (Table 3-7).

For 4 species in SAT, there was no difference in final biomass between the GAL and BR and for 2 species there was no difference in final biomass between the GAL and TB. However, the GAL had significantly greater final biomass than 2 species planted as BR and 4 species planted as TB. *Platanus occidentalis* was the only species for which the TB stocktype had significantly greater final biomass than the GAL. For 6 species there was no difference in final biomass between the BR and TB (All BR *P. occidentalis* died or were removed) (Table 3-7).

All species in FLD had no difference in final biomass among stocktypes except *L. styraciflua* for which the GAL had significantly more final biomass than the TB. The lack of statistically significant differences among stocktypes in FLD is a result of poor survival and the stressful environmental conditions (Table 3-7).

Species Comparison

Average final biomass was calculated for each species incorporating all stocktypes in order to make inferences about differences in species and cells, while incorporating the maximum variation for each species (Table 3-8).

In the AMB there was no difference in final biomass among the three *Quercus* species, and they had significantly less final biomass than *P. occidentalis, B. nigra, L. styraciflua,* and *S. nigra* (listed in descending final biomass) (Table 3-8). In SAT, there was no difference in final biomass among *B. nigra, L. styraciflua, P. occidentalis* and *S. nigra,* and all 4 of those species had significantly greater biomass than the *Quercus*
species. Among the *Quercus* species, *Q. phellos* had significantly greater final biomass than *Q. palustris* (Table 3-8). In FLD, only *S. nigra* had significantly greater final biomass than *L. styraciflua, P. occidentalis,* and *Q. bicolor* (Table 3-8).

Species Group Comparison

Species groups (see Methods for description of primary and secondary species groups) were compared within each cell to make broad inferences about the differences between these groups. Primary species had significantly more final biomass than secondary species in each cell (Table 3-9). Additionally, both primary and secondary species groups had significantly more final biomass in AMB than SAT, which had significantly more final biomass than FLD (Table 3-9).

Cell Comparison

The average final biomass for each species (incorporating each stocktype) was compared among the cells in order to make inferences about how the environmental conditions influenced the biomass accumulated for each species (Table 3-8). *B. nigra, P. occidentalis, Q. bicolor, Q. palustris* and *Q. phellos* had significantly greater final biomass in AMB than in SAT. All species had significantly greater biomass in AMB and SAT than FLD.
Discussion

Root-to-Shoot Ratio

The most commonly reported literature value for r:s ratio in forests containing many species, across latitudes, elevation and soil types is approximately 0.2 (Cairns et al. 1997, Mokany et al. 2006, Luo et al. 2012, Hui et al. 2014). The majorities of these ratios were determined for large trees and were measured using partial root samples generalized to forest stands. The r:s ratio in this study averaged 1.8 across all fully harvested individual saplings. Similar investigations focusing on seedlings and saplings suggest that they may have higher r:s ratios than large trees. Day (1987) showed that seedlings of *Acer rubrum* grown in nutrient enrichment experiments have initially high (up to 3.22) r:s ratio. Hui et al. 2014 showed that r:s ratios decrease with increasing diameter at breast height (dbh) and Mokany et al. (2006) showed that stands with lower AGB had greater r:s ratios. Luo et al. (2012) found that stands less than 20 years old had higher r:s ratios than those greater than or equal to 20 years old. The r:s ratio from this study show that saplings as opposed to larger trees, allocate more biomass belowground to coarse roots than aboveground following outplanting. This suggests that belowground biomass is important to consider when evaluating the biomass and carbon accumulation ecosystem functions in restored/created wetlands.

The lower r:s ratio of primary successional species (excluding *P. occidentalis*, see below) compared to secondary successional species suggests that this group of species has the ability to rapidly accumulate belowground biomass and then shift allocation of resources aboveground. These species are appropriate choices for restoration/creation of wetlands for this reason among others.
While not statistically significant, *P. occidentalis* r:s declined from an average of 2.4 in AMB to 0.95 in SAT to 0.88 in FLD. This decline was similar to the decrease in survival *P. occidentalis* exhibited across the cells. This suggests that *P. occidentalis* may not be able to allocate resources effectively belowground under wetter hydrologic conditions and may not be appropriate for planting in restored/created wetlands. The opposite response occurred for *S. nigra*, where the r:s and survival increased moving from AMB to SAT to FLD suggesting that *S. nigra* is able to effectively allocate resources belowground in stressful hydrologic conditions and may be an appropriate choice for planting in restored/created wetlands. The r:s increase of *S. nigra* in FLD is contradictory to the decrease in r:s of *T. distichum* in continuously flooded treatments found by Megonigal and Day (1992), but may be a response to the lower nitrogen concentrations in the FLD. Several studies have found that r:s ratios are higher for a variety of species grown in low nutrient conditions (Dickson and Broyer 1972, Birk and Vitousek 1986, Jerbi et al. 2015).

**Elemental Concentration**

The woody tissue of primary species group had higher C:N (37.3) than secondary species (34.1) mainly because of higher N concentrations in secondary species. Low variation of C and N (and C:N ratios) within and across cells suggests that the species used in this study did not alter the accumulation of these elements in response to the sites hydrologic and soil elemental concentrations. The soil of FLD had lower nitrogen concentrations, resulting from excavation of the topsoil and possibly from increased denitrification from reduced soil oxygen concentrations. Other studies have shown that
soil N concentrations have a positive relationship with tissue N concentrations. Day (1987) found that *Acer rubrum* grown under a variety of hydrologic conditions had greater leaf N concentrations when N was added. The lack of differences in wood C and N concentrations across the site suggest that these species are maintaining the balance among these elements despite soil conditions, possibly through reduction in biomass accumulation.

The wood carbon content from this study (average 46.6% of wood biomass) was consistent with the range of wood carbon content found with temperate/boreal species (43.4-55.6%) (Thomas & Martin 2012). The wood carbon content from this study can be used to determine carbon accumulation of saplings in restored/created wetlands in this region and demonstrates how important saplings are to returning this ecosystem function in these wetlands.

Martin et al. (1998) investigated N content of different woody tissues in 10 Appalachian tree species. All 10 species had very low N concentration in the stem heartwood, sapwood and branches (<4 mg/g) for all species. The low concentrations found in the present study (average 1.3% of wood biomass) suggest that the woody tissue of saplings is a small contributor to removal of N from the environment. However, the long term storage of N in woody tissues is important across longer time scales and as trees accumulate more biomass.

**Biomass Estimation Model Development**

The power-law relationship between BGB and ABG provide a means for non-destructive estimation of coarse root BGB of the seven species used in our study that is
more robust than r:s ratios. This relationship was developed for each species using samples pooled from the three cells, because cell specific model derived coefficients did not differ (confidence intervals overlapped). This may have resulted from the low number of samples taken from each cell but is also evidenced in the lack of species statistical differences in r:s ratios among cells.

Scaling coefficients from this relationship provide insights into how biomass allocation changes as biomass increases. A scaling coefficient of less than 1 (as for most species in this study) suggests that the r:s ratio decreases as saplings accumulate AGB. Departure from an isometric relationship between AGB and BGB have been reported across a range of habitats, species, spatial scales and time scales (Cheng & Niklas 2007, Niklas 2005, Niklas 2004, Enquist & Niklas 2002, Yang & Luo 2011). Hui et al. 2014 showed that as dbh of trees increased, the r:s ratio decreased and the scaling coefficient increased to approximately 1. Results from the current study suggest that inclusion of saplings when determining biomass and carbon accumulation and allocation in restored/created wetlands is important because they may be allocating more resources belowground before shifting allocation of resources aboveground. *L. styraciflua, P. occidentalis* and *Q. bicolor* have scaling coefficients approaching 1 suggesting they are able to quickly allocate resources belowground following outplanting and then shift allocation aboveground. These species may be appropriate for returning these important ecosystem functions to restored/created wetlands.

The BEM developed in this study describing the relationship between stem diameter and total biomass provides a non-destructive estimate of sapling biomass that is useful for determining the development of this ecosystem function in restored/created
wetlands and other forested systems (riparian buffers, uplands, natural forested wetlands etc.). Additionally, it provides an additional way to evaluate planted sapling performance. Current BEMs for the species used in this study (see Jenkins et al. 2003, 2004, Chojnacky et al. 2014) were constructed for large trees (dbh >2.5 cm) and only model AGB. The few studies developing BEMs for saplings focused at the genus taxonomic level for *Salix*, *Betula* and *Quercus* and most only sampled AGB (Tefler 1969, Roussopoulos & Loomis 1979, Smith & Brand 1983, Williams & McClanahem 1984). Comparisons with these studies are further compounded by the methodological differences in stem measurements (several sampled at 15 cm above soil surface) and model fitting (log base 10 transformations of biomass). Despite these differences, the estimated scaling coefficients from this study (Table 3-5) were marginally higher than literature values for these species. The inclusion of BGB in the present study is a potential reason for this but the BEMs developed in this fashion provide a more robust model for estimating total biomass for these species and for evaluating this ecosystem function in restored/created wetlands.

**Accumulated Biomass**

**Stocktype comparison**

In FLD, the choice of stocktype for all species (except *L. styraciflua*) did not affect the biomass accumulated after 6 years. This suggests that larger stocktypes are not able to return this ecosystem function in very stressful environmental conditions; however, it should be noted that the GAL stocktype did have increased survival compared to the BR and TB.
Within SAT, the GAL stocktype had significantly greater biomass after 6 years than the TB for *B. nigra*, *L. styraciflua*, *Q. bicolor*, and *Q. phellos*. This suggests that the larger GAL stocktype may be a better selection than the TB in conditions similar to SAT. In SAT the GAL exceeded the final biomass of BR for only *B. nigra* and *Q. phellos*. This suggests that in these conditions the BR stocktype can accumulate a similar amount of biomass over 6 years as the GAL for most species. In the AMB, there were more differences among the stocktypes than in SAT and FLD. This suggests that when environmental conditions are less stressful, smaller stocktypes are able to accumulate as much or greater biomass than larger stocktypes.

*Species Comparison*

In addition to the stocktype, species selection was shown to influence biomass accumulated after 6 years. Within FLD, *S. nigra* accounted for 55.6% of the total amount of biomass accumulated and is the only species that did not experience substantial mortality. This suggests that in very stressful created and restored wetland conditions *S. nigra* may be a more appropriate choice to replace or return woody biomass to the system. The only other species to have moderate success in FLD was *B. nigra*.

*Species Group Comparison*

In the SAT cell, primary species individually and as a group accumulated more biomass than secondary species. Of the total biomass accumulated, the primary species group accounted for an average of 92.4% and the secondary successional species group accounted for 7.6% across all cells. This suggests that primary successional species as a
group are a better choice when the goal of creation and restoration is to replace lost biomass. However, species and functional diversity of planting material should always be considered.

Cell Comparison

Total biomass accumulated by all living trees after 6 years in AMB, SAT and FLD was 20,077.2 kg, 9035.2 kg, and 195.8 kg respectively. Additionally, primary and secondary species groups both had significantly more biomass in AMB than SAT and FLD and significantly more biomass in SAT than FLD. The reduction in biomass in SAT compared to AMB resulted from the increased hydrologic stress (saturation within the root zone). The substantial reduction in biomass production in FLD resulted from flooding above the root collar, reduced soil nitrogen and phosphorus concentrations, increased clay concentrations, herbaceous competition and poor survival of planted trees.

Reduction in tree survival and biomass accumulation can be attributed to prolonged saturated or flooded soil conditions that remove the plant available oxygen from the soil pore space. The reduction in oxygen leads to a lack of aerobic respiration in roots, which decreases the energy available for trees to maintain functions of existing tissues (Hale & Orcutt 1987, Brady & Weil 2002). Many growth chamber, greenhouse, mesocosm and field experiments have investigated the effect of hydrology on a multitude of responses across many species of trees. While species specific responses may vary (e.g. Taxodium distichum, mangroves) most species exhibit decreased survival and biomass accumulation when grown under prolonged inundation. Niswander & Mitch (1995) planted ten tree species (three of which were used in this study, B. nigra, L.
**Conclusions**

Models relating total biomass and stem cross-sectional diameter at groundline are needed for saplings since most prior models excluded saplings and belowground biomass. Models developed for larger diameter trees underestimate biomass of smaller trees even with inclusion of sapling adjustments (Nelson et al. 2014). Additionally, accurate BEMs are needed to make predictions about carbon storage and exchange in forest ecosystems. The investigation of r:s ratios also provide important information about how saplings transition from allocating biomass belowground to aboveground as they grow.

The results of investigating the biomass accumulated after 6 years for saplings planted under different environmental conditions provides important information for
those attempting creation and restoration of any forested system, particularly for those involving wetland conditions. When planting in stressful hydrologic, soil, and competitive conditions, based on the results from FLD, *S. nigra* appears to be the best choice among these species for returning woody biomass (followed by *B. nigra*). However, it is always important to plant woody species that are found naturally in the type of wetland that is being restored. Meaning, *S. nigra* and *B. nigra* would not be appropriate choices for planting in restored wetlands types in which they do not naturally occur.

In the FLD, the choice of stocktype influenced the survival but did not appear to influence the biomass accumulated after 6 years as all stocktypes were heavily stressed. When planting in less stressful wetland environmental conditions (moderate hydrologic and competitive stress), the primary species used in this study are a better choice to return woody biomass than secondary species. Secondary species (*Quercus* spp.) may be important for additional ecological functions (such as acorn production) but may not be an appropriate planting choice when rapid accumulation of biomass is the goal. The choice of stocktype between GAL and TB appears to be important in areas of moderate environmental stress, where larger stocktypes are a better choice for replacing biomass, even after 6 years. However, in these conditions the BR was able to accumulate similar amounts of biomass as the GAL, suggesting that it may be an acceptable alternative to the larger more expensive stocktype. In areas with low environmental stress, the smaller stocktype are able to equal and exceed the biomass accumulated by the larger stocktype.

In conclusion, the recommended species and stocktypes will help improve the practice of wetland restoration and creation by enhancing the return of lost ecosystem
structure and functions which can be better evaluated using these new sapling biomass estimation models.
Literature Cited


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Dickson, R and Broyer, T (1972) Effects of aeration, water supply, and nitrogen source on growth and development of tupelo gum and bald cypress. Ecology 53:626-634


Roussopoulos PJ, Loomis, RM (1979) Weight and didimension properties of shrubs and small trees of the Great Lakes conifer forest. NC-178 United States Department of Agriculture Forest Service, St Paul, Minnesota


Smith WB, Brand GJ (1983) Allometric biomass equations for 98 species of herbs, shrubs, and small trees. NC-299. United States Department of Agriculture Forest Service, North Central Forest Experiment Station, St Paul, Minnesota


### Tables

Table 3-1. Morphological averages (standard deviation in parentheses) of trees destructively harvested in 2011 and 2014. Species specific and successional group values are averaged across three cells.

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<td>(39.31)</td>
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Species Specific

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<td>(3.56)</td>
<td>82.71</td>
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<td>9.39</td>
<td>(7.06)</td>
<td>92.13</td>
<td>(57.71)</td>
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<td>(0.54)</td>
<td>3.39</td>
<td>(2.18)</td>
<td>43.49</td>
<td>(23.14)</td>
</tr>
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<td>52</td>
<td>1.12</td>
<td>(0.58)</td>
<td>3.09</td>
<td>(1.87)</td>
<td>55.79</td>
<td>(34.89)</td>
</tr>
<tr>
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<td>4.44</td>
<td>(2.42)</td>
<td>74.08</td>
<td>(60.93)</td>
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<td>1.8</td>
<td>(1.1)</td>
<td>7.63</td>
<td>(5.08)</td>
<td>93.44</td>
<td>(38.38)</td>
</tr>
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Successional Groups

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<td>1.94</td>
<td>(1.37)</td>
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<td>(6.8)</td>
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<td>1.16</td>
<td>(0.65)</td>
<td>3.62</td>
<td>(2.21)</td>
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Table 3-2. Average above (AGB) and belowground biomass (BGB), total biomass, and root-to-shoot ratio (R:S) (standard deviation in parentheses) of trees destructively harvested in 2011 and 2014. Species specific and successional group values are averaged across three cells.

<table>
<thead>
<tr>
<th>Cell</th>
<th>Species</th>
<th>BGB (kg) 2011</th>
<th>AGB (kg) 2011</th>
<th>Total Biomass (kg) 2011</th>
<th>R:S Ratio 2011</th>
</tr>
</thead>
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<td>Ambient</td>
<td>Betula nigra</td>
<td>0.52 (0.51)</td>
<td>12.29 (14.44)</td>
<td>0.69 (0.86) 33.14 (46.26)</td>
<td>1.21 (1.34) 45.43 (60.68) 0.97 (0.64)</td>
</tr>
<tr>
<td>Ambient</td>
<td>Liquidambar styraciflua</td>
<td>0.6 (0.77)</td>
<td>8.96 (6.74)</td>
<td>0.62 (0.79) 7.56 (6.02)</td>
<td>1.22 (1.45) 16.53 (12.76) 1.67 (0.93)</td>
</tr>
<tr>
<td>Ambient</td>
<td>Platanus occidentalis</td>
<td>0.29 (0.38)</td>
<td>48.26 (43.36)</td>
<td>0.23 (0.39) 42.08 (38.56)</td>
<td>0.52 (0.75) 90.34 (81.93) 2.4 (2.48) abc; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Quercus bicolor</td>
<td>0.08 (0.12) 2.99 (3.08)</td>
<td>0.04 (0.06) 1.65 (1.78)</td>
<td>0.12 (0.18) 4.64 (4.86)</td>
<td>2.74 (1.39) a; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Quercus palustris</td>
<td>0.09 (0.15) 1.15 (1.61)</td>
<td>0.04 (0.07) 1.36 (2.18)</td>
<td>0.13 (0.22) 2.51 (3.79)</td>
<td>2.24 (0.44) a; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Quercus phellos</td>
<td>0.12 (0.19) 1.53 (1.24)</td>
<td>0.16 (0.3) 4.15 (4.46)</td>
<td>0.28 (0.48) 5.68 (5.7)</td>
<td>2.51 (2.7) abc; yz</td>
</tr>
<tr>
<td>Ambient</td>
<td>Salix nigra</td>
<td>0.08 (0.12) 1.94 (1.99)</td>
<td>0.13 (0.2) 6.74 (9.2)</td>
<td>0.21 (0.32) 8.67 (11.17) 0.76 (0.26) b; z</td>
<td></td>
</tr>
</tbody>
</table>

| Saturated     | Betula nigra        | 0.22 (0.43) 7.01 (6.05) | 0.2 (0.26) 15.81 (16.27) | 0.42 (0.65) 22.82 (22.3) 2.78 (6.89) abc; y |
| Saturated     | Liquidambar styraciflua | 0.08 (0.07) | 5.47 (3.61) | 0.05 (0.05) 4.49 (3.09) | 0.12 (0.11) 9.96 (6.7) | 1.74 (0.63) a; y |
| Saturated     | Platanus occidentalis | 0.05 (0.05) 7.83 (7.4) | 0.08 (0.1) 6.53 (6.28) | 0.13 (0.12) 14.36 (13.69) 0.95 (0.49) bc; y |
| Saturated     | Quercus bicolor     | 0.04 (0.03) 1.63 (2.23) | 0.02 (0.01) 0.88 (1.25) | 0.06 (0.04) 2.51 (3.48) | 2.67 (1.32) a; y |
| Saturated     | Quercus palustris   | 0.06 (0.1) 0.64 (0.7) | 0.05 (0.1) 0.63 (0.81) | 0.11 (0.2) 1.27 (1.5) | 2.35 (1.75) ab; y |
| Saturated     | Quercus phellos     | 0.07 (0.11) 1.21 (1.04) | 0.05 (0.09) 3.05 (3.34) | 0.12 (0.19) 4.26 (4.38) | 2.19 (1.04) a; y |
| Saturated     | Salix nigra         | 0.04 (0.05) 3.22 (3.47) | 0.05 (0.05) 13.58 (18.66) | 0.09 (0.09) 16.89 (22.11) 0.86 (0.44) c; z |

| Flooded       | Betula nigra        | 0.03 (0.04) 0.1 (0.11) | 0.04 (0.06) 0.09 (0.12) | 0.07 (0.1) 0.19 (0.23) | 0.95 (0.48) b; y |
| Flooded       | Liquidambar styraciflua | 0.02 (0.03) | 0.11 (0.15) | 0.02 (0.02) 0.07 (0.1) | 0.04 (0.05) 0.18 (0.25) | 1.42 (0.5) ab; y |
| Flooded       | Platanus occidentalis | 0.01 (0.01) 0.07 (0.08) | 0.02 (0.03) 0.05 (0.06) | 0.03 (0.04) 0.12 (0.15) | 0.88 (0.5) b; y |
| Flooded       | Quercus bicolor     | 0.02 (0.03) 0.23 (0.52) | 0.01 (0.01) 0.12 (0.27) | 0.03 (0.03) 0.35 (0.79) | 2.04 (1.03) a; y |
| Flooded       | Quercus palustris   | 0.02 (0.03) 0.07 (0.07) | 0.02 (0.03) 0.04 (0.05) | 0.04 (0.06) 0.12 (0.13) | 2.62 (1.436) ab; y |
| Flooded       | Quercus phellos     | 0.02 (0.02) 0.08 (0.08) | 0.03 (0.04) 0.07 (0.08) | 0.04 (0.06) 0.15 (0.15) | 1.06 (0.46) ab; z |
| Flooded       | Salix nigra         | 0.11 (0.16) 0.16 (0.13) | 0.13 (0.36) 0.21 (0.23) | 0.24 (0.51) 0.37 (0.35) | 2.29 (2.03) ab; y |

* BGB and total biomass were calculated using the non-linear BGB–AGB relationship developed from the 2011 samples.

a – d letters represent significant differences (p < 0.05) among species within cells
y – z letters represent significant differences (p < 0.05) among cells within species
Table 3-3. Average percentage carbon, nitrogen and C:N ratio of subsamples from trees destructively harvested in 2014. Species specific and successional group values are averaged across three cells. Values in parentheses represent standard deviation.

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<td>5</td>
<td>47.44 (0.82) a; y</td>
<td>1.27 (0.29) a; y</td>
<td>38.69 (7.67) a; y</td>
</tr>
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<td>Ambient</td>
<td>Liquidambar styraciflua</td>
<td>5</td>
<td>46 (0.2) a; y</td>
<td>1.2 (0.1) a; y</td>
<td>38.42 (3.08) a; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Platanus occidentalis</td>
<td>5</td>
<td>46.36 (1.02) a; y</td>
<td>1.13 (0.08) a; y</td>
<td>41.16 (3.51) a; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Quercus bicolor</td>
<td>5</td>
<td>46.42 (0.21) a; y</td>
<td>1.46 (0.22) a; y</td>
<td>32.3 (4.31) a; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Quercus palustris</td>
<td>5</td>
<td>46.3 (0.37) a; y</td>
<td>1.37 (0.11) a; y</td>
<td>34.09 (2.74) a; y</td>
</tr>
<tr>
<td>Ambient</td>
<td>Quercus phellos</td>
<td>5</td>
<td>46.38 (0.36) a; y</td>
<td>1.37 (0.11) a; y</td>
<td>33.97 (2.59) a; z</td>
</tr>
<tr>
<td>Ambient</td>
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<td>5</td>
<td>46.03 (0.58) a; y</td>
<td>1.48 (0.2) a; y</td>
<td>31.48 (4.15) a; y</td>
</tr>
<tr>
<td>Saturated</td>
<td>Betula nigra</td>
<td>5</td>
<td>47.16 (0.48) a; y</td>
<td>1.15 (0.1) cd; y</td>
<td>41.19 (3.11) ab; y</td>
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<tr>
<td>Saturated</td>
<td>Liquidambar styraciflua</td>
<td>5</td>
<td>46.19 (0.67) a; y</td>
<td>1.27 (0.08) abcd; y</td>
<td>36.4 (2.22) abbc; y</td>
</tr>
<tr>
<td>Saturated</td>
<td>Platanus occidentalis</td>
<td>5</td>
<td>46.91 (0.56) a; y</td>
<td>1.17 (0.06) d; y</td>
<td>40.07 (1.92) a; y</td>
</tr>
<tr>
<td>Saturated</td>
<td>Quercus bicolor</td>
<td>5</td>
<td>46.22 (0.36) a; y</td>
<td>1.55 (0.15) ab; y</td>
<td>30.09 (3.03) cd; y</td>
</tr>
<tr>
<td>Saturated</td>
<td>Quercus palustris</td>
<td>5</td>
<td>46.36 (0.78) a; y</td>
<td>1.45 (0.07) ab; y</td>
<td>32.09 (1.43) c; y</td>
</tr>
<tr>
<td>Saturated</td>
<td>Quercus phellos</td>
<td>5</td>
<td>46.13 (0.41) a; y</td>
<td>1.26 (0.02) ad; y</td>
<td>36.74 (0.48) ad; yz</td>
</tr>
<tr>
<td>Saturated</td>
<td>Salix nigra</td>
<td>5</td>
<td>46.34 (0.54) a; y</td>
<td>1.39 (0.04) bc; y</td>
<td>33.38 (0.54) bc; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Betula nigra</td>
<td>5</td>
<td>47.72 (0.53) a; y</td>
<td>1.3 (0.09) ab; y</td>
<td>36.93 (2.62) ab; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Liquidambar styraciflua</td>
<td>5</td>
<td>45.84 (1.05) a; y</td>
<td>1.23 (0.14) ab; y</td>
<td>37.78 (4.19) ab; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Platanus occidentalis</td>
<td>5</td>
<td>47.34 (1.19) a; y</td>
<td>1.22 (0.08) ab; y</td>
<td>38.79 (1.84) a; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Quercus bicolor</td>
<td>5</td>
<td>46.22 (0.76) a; y</td>
<td>1.42 (0.09) a; y</td>
<td>32.57 (2.3) b; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Quercus palustris</td>
<td>4</td>
<td>47.3 (1.0) a; y</td>
<td>1.29 (0.13) ab; y</td>
<td>37.16 (4.6) ab; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Quercus phellos</td>
<td>4</td>
<td>46.16 (1.15) a; y</td>
<td>1.17 (0.05) b; z</td>
<td>39.55 (1.86) a; y</td>
</tr>
<tr>
<td>Flooded</td>
<td>Salix nigra</td>
<td>5</td>
<td>46.98 (1.1) a; y</td>
<td>1.44 (0.1) a; y</td>
<td>32.71 (2.72) ab; y</td>
</tr>
</tbody>
</table>

Species Specific 2014 | 2014 | 2014 | 2014
---|---|---|---
Betula nigra | 15 | 47.44 (0.63) a | 1.24 (0.18) bc | 38.94 (4.98) ab |
Liquidambar styraciflua | 15 | 46.01 (0.69) b | 1.23 (0.11) bc | 37.53 (3.14) ab |
Platanus occidentalis | 15 | 46.87 (0.98) ab | 1.18 (0.08) bc | 40.01 (2.56) a |
Quercus bicolor | 15 | 46.29 (0.47) b | 1.48 (0.16) a | 31.65 (3.28) c |
Quercus palustris | 14 | 46.6 (0.82) ab | 1.37 (0.12) ab | 34.25 (3.5) bc |
Quercus phellos | 14 | 46.23 (0.64) b | 1.27 (0.11) bc | 36.55 (2.88) b |
Salix nigra | 15 | 46.45 (0.83) b | 1.44 (0.13) a | 32.52 (2.79) c |

---|---|---|---
Primary | 60 | 46.69 (0.94) a | 1.27 (0.16) b | 37.25 (4.47) a |
Secondary | 43 | 46.37 (0.66) b | 1.38 (0.15) a | 34.09 (3.75) b |

a – d letters represent significant differences ($p < 0.05$) among species within cells
y – z letters represent significant differences ($p < 0.05$) among cells within species
Table 3-4. Results of fitting Eq. 1 (Y=aX^b + ε) from saplings destructively harvested in 2011. Y=Total dry belowground biomass (kg). X=Total dry aboveground biomass (excluding leaves) (kg).

<table>
<thead>
<tr>
<th>Primary Successional Species</th>
<th>a</th>
<th>a SE</th>
<th>b</th>
<th>b SE</th>
<th>SE of the Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Betula nigra</em></td>
<td>0.787</td>
<td>0.109</td>
<td>0.817</td>
<td>0.091</td>
<td>0.439</td>
</tr>
<tr>
<td><em>Liquidambar styraciflua</em></td>
<td>1.334</td>
<td>0.184</td>
<td>0.948</td>
<td>0.031</td>
<td>0.509</td>
</tr>
<tr>
<td><em>Platanus occidentalis</em></td>
<td>1.272</td>
<td>0.480</td>
<td>0.975</td>
<td>0.092</td>
<td>1.296</td>
</tr>
<tr>
<td><em>Salix nigra</em></td>
<td>0.544</td>
<td>0.162</td>
<td>0.739</td>
<td>0.093</td>
<td>0.578</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Secondary Successional Species</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Quercus bicolor</em></td>
<td>1.921</td>
<td>0.480</td>
<td>0.942</td>
<td>0.059</td>
<td>0.264</td>
</tr>
<tr>
<td><em>Quercus palustris</em></td>
<td>1.019</td>
<td>0.219</td>
<td>0.831</td>
<td>0.064</td>
<td>0.210</td>
</tr>
<tr>
<td><em>Quercus phellos</em></td>
<td>0.595</td>
<td>0.127</td>
<td>0.732</td>
<td>0.055</td>
<td>0.451</td>
</tr>
</tbody>
</table>
Table 3-5. Results of fitting Eq. 1 \((Y = aX^{b} + \varepsilon)\) to saplings destructively harvested in 2011 and 2014. \(Y=\)Total dry biomass (excluding leaves) (kg). \(X=\) Equivalent stem cross-sectional diameter at groundline (ESD) (cm).

<table>
<thead>
<tr>
<th>Primary Successional Species</th>
<th>(a)</th>
<th>(a\ SE)</th>
<th>(b)</th>
<th>(b\ SE)</th>
<th>SE of the Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betula nigra</td>
<td>0.032</td>
<td>0.005</td>
<td>2.442</td>
<td>0.067</td>
<td>0.667</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>0.032</td>
<td>0.010</td>
<td>2.751</td>
<td>0.149</td>
<td>0.908</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>0.028</td>
<td>0.003</td>
<td>2.789</td>
<td>0.049</td>
<td>0.522</td>
</tr>
<tr>
<td>Salix nigra</td>
<td>0.029</td>
<td>0.007</td>
<td>2.519</td>
<td>0.099</td>
<td>0.911</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Secondary Successional Species</th>
<th>(a)</th>
<th>(a\ SE)</th>
<th>(b)</th>
<th>(b\ SE)</th>
<th>SE of the Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus bicolor</td>
<td>0.047</td>
<td>0.007</td>
<td>2.735</td>
<td>0.113</td>
<td>0.571</td>
</tr>
<tr>
<td>Quercus palustris</td>
<td>0.047</td>
<td>0.004</td>
<td>2.502</td>
<td>0.133</td>
<td>1.016</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>0.055</td>
<td>0.007</td>
<td>2.455</td>
<td>0.172</td>
<td>1.891</td>
</tr>
</tbody>
</table>
Table 3-6. Average initial biomass estimates for each species/stocktype combination. Same letters represent no significant difference among stocktype for each species ($p > 0.05$). $n$ represents initial number of trees planted.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stocktype</th>
<th>$n$</th>
<th>Initial Biomass (kg)</th>
<th>Standard Deviation</th>
<th>Within Species Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Betula nigra</strong></td>
<td>Bare root</td>
<td>137</td>
<td>0.021</td>
<td>0.037</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>105</td>
<td>0.046</td>
<td>0.051</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>94</td>
<td>0.025</td>
<td>0.029</td>
<td>b</td>
</tr>
<tr>
<td><strong>Liquidambar styraciflua</strong></td>
<td>Bare root</td>
<td>111</td>
<td>0.024</td>
<td>0.034</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>112</td>
<td>0.040</td>
<td>0.052</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>109</td>
<td>0.029</td>
<td>0.049</td>
<td>ab</td>
</tr>
<tr>
<td><strong>Platanus occidentalis</strong></td>
<td>Bare root</td>
<td>75</td>
<td>0.018</td>
<td>0.034</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>112</td>
<td>0.058</td>
<td>0.075</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>73</td>
<td>0.025</td>
<td>0.034</td>
<td>b</td>
</tr>
<tr>
<td><strong>Quercus bicolor</strong></td>
<td>Bare root</td>
<td>125</td>
<td>0.047</td>
<td>0.061</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>105</td>
<td>0.048</td>
<td>0.056</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>128</td>
<td>0.037</td>
<td>0.057</td>
<td>b</td>
</tr>
<tr>
<td><strong>Quercus palustris</strong></td>
<td>Bare root</td>
<td>127</td>
<td>0.035</td>
<td>0.048</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>116</td>
<td>0.061</td>
<td>0.065</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>96</td>
<td>0.032</td>
<td>0.046</td>
<td>b</td>
</tr>
<tr>
<td><strong>Quercus phellos</strong></td>
<td>Bare root</td>
<td>170</td>
<td>0.039</td>
<td>0.055</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>107</td>
<td>0.083</td>
<td>0.102</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>93</td>
<td>0.035</td>
<td>0.041</td>
<td>b</td>
</tr>
<tr>
<td><strong>Salix nigra</strong></td>
<td>Bare root</td>
<td>112</td>
<td>0.020</td>
<td>0.030</td>
<td>b</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>109</td>
<td>0.055</td>
<td>0.073</td>
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</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>123</td>
<td>0.022</td>
<td>0.028</td>
<td>b</td>
</tr>
<tr>
<td>Species</td>
<td>Stocktype</td>
<td>Final Biomass (kg)</td>
<td>Standard Deviation</td>
<td>Within Species Comparison</td>
<td>Final Biomass (kg)</td>
</tr>
<tr>
<td>--------------------</td>
<td>-----------</td>
<td>--------------------</td>
<td>--------------------</td>
<td>---------------------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>Betula nigra</td>
<td>Bare root</td>
<td>36.88</td>
<td>26.72</td>
<td>b</td>
<td>18.43</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>64.26</td>
<td>41.29</td>
<td>a</td>
<td>40.45</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>8</td>
<td>43.12</td>
<td>ab</td>
<td>27.51</td>
</tr>
<tr>
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<td>Bare root</td>
<td>41.64</td>
<td>23.34</td>
<td>a</td>
<td>31.23</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>36.68</td>
<td>24.01</td>
<td>a</td>
<td>35.76</td>
</tr>
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<td></td>
<td>Tubeling</td>
<td>5</td>
<td>14.40</td>
<td>a</td>
<td>19.77</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>Bare root</td>
<td>151.74</td>
<td>123.38</td>
<td>a</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>71.13</td>
<td>79.44</td>
<td>b</td>
<td>20.12</td>
</tr>
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<td>219.11</td>
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<td>54.77</td>
</tr>
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<td>Bare root</td>
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<td>4.39</td>
<td>a</td>
<td>2.53</td>
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<td>Gallon</td>
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<td>4.74</td>
<td>a</td>
<td>3.72</td>
</tr>
<tr>
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<td>3.18</td>
<td>a</td>
<td>1.45</td>
</tr>
<tr>
<td>Quercus palustris</td>
<td>Bare root</td>
<td>3.17</td>
<td>2.89</td>
<td>a</td>
<td>1.97</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>6.61</td>
<td>8.32</td>
<td>a</td>
<td>3.00</td>
</tr>
<tr>
<td></td>
<td>Tubeling</td>
<td>0.56</td>
<td>0.96</td>
<td>c</td>
<td>1.25</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>Bare root</td>
<td>2.72</td>
<td>3.27</td>
<td>a</td>
<td>2.65</td>
</tr>
<tr>
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<td>Gallon</td>
<td>10.07</td>
<td>8.09</td>
<td>a</td>
<td>6.68</td>
</tr>
<tr>
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<td>Tubeling</td>
<td>2.97</td>
<td>3.78</td>
<td>b</td>
<td>2.99</td>
</tr>
<tr>
<td>Salix nigra</td>
<td>Bare root</td>
<td>NA</td>
<td>NA</td>
<td>a</td>
<td>39.77</td>
</tr>
<tr>
<td></td>
<td>Gallon</td>
<td>18.16</td>
<td>20.57</td>
<td>a</td>
<td>19.34</td>
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<tr>
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<td>Tubeling</td>
<td>28.47</td>
<td>28.69</td>
<td>a</td>
<td>32.87</td>
</tr>
</tbody>
</table>

Table 3-7. Average biomass accumulated 6 years following planted estimated for each stocktype/species combination. Same letter represent no significance difference among stocktype for each species within each cell ($p > 0.05$). $n$ represents count of live trees after 6 years.
Table 3-8. Average biomass accumulated 6 years following planted estimated for each species (incorporating all stocktypes). Average biomass of species is compared within cells and cells are compared for each species. Same letters represent no significant difference ($p<0.05$). $n$ represents count of live trees after 6 years.

<table>
<thead>
<tr>
<th>Ambient</th>
<th>n</th>
<th>Average Total Biomass (kg)</th>
<th>Standard Deviation</th>
<th>Within cell, species comparison</th>
<th>Within species, cell comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Betula nigra</strong></td>
<td>58</td>
<td>54.74</td>
<td>38.53</td>
<td>b</td>
<td>x</td>
</tr>
<tr>
<td><strong>Liquidambar styraciflua</strong></td>
<td>69</td>
<td>37.08</td>
<td>23.79</td>
<td>c</td>
<td>x</td>
</tr>
<tr>
<td><strong>Platanus occidentalis</strong></td>
<td>85</td>
<td>144.38</td>
<td>135.28</td>
<td>a</td>
<td>x</td>
</tr>
<tr>
<td><strong>Quercus bicolor</strong></td>
<td>93</td>
<td>4.41</td>
<td>4.32</td>
<td>e</td>
<td>x</td>
</tr>
<tr>
<td><strong>Quercus palustris</strong></td>
<td>72</td>
<td>4.66</td>
<td>6.40</td>
<td>e</td>
<td>x</td>
</tr>
<tr>
<td><strong>Quercus phellos</strong></td>
<td>60</td>
<td>6.42</td>
<td>7.15</td>
<td>e</td>
<td>x</td>
</tr>
<tr>
<td><strong>Salix nigra</strong></td>
<td>45</td>
<td>20.91</td>
<td>23.13</td>
<td>d</td>
<td>x</td>
</tr>
<tr>
<td><strong>Saturated</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Betula nigra</strong></td>
<td>81</td>
<td>30.41</td>
<td>21.54</td>
<td>a</td>
<td>y</td>
</tr>
<tr>
<td><strong>Liquidambar styraciflua</strong></td>
<td>75</td>
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<td>20.00</td>
<td>a</td>
<td>x</td>
</tr>
<tr>
<td><strong>Platanus occidentalis</strong></td>
<td>55</td>
<td>32.72</td>
<td>47.92</td>
<td>a</td>
<td>y</td>
</tr>
<tr>
<td><strong>Quercus bicolor</strong></td>
<td>96</td>
<td>2.70</td>
<td>3.64</td>
<td>bc</td>
<td>y</td>
</tr>
<tr>
<td><strong>Quercus palustris</strong></td>
<td>80</td>
<td>2.34</td>
<td>2.44</td>
<td>c</td>
<td>y</td>
</tr>
<tr>
<td><strong>Quercus phellos</strong></td>
<td>89</td>
<td>4.19</td>
<td>3.78</td>
<td>b</td>
<td>y</td>
</tr>
<tr>
<td><strong>Salix nigra</strong></td>
<td>60</td>
<td>26.81</td>
<td>35.34</td>
<td>a</td>
<td>x</td>
</tr>
<tr>
<td><strong>Flooded</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Betula nigra</strong></td>
<td>56</td>
<td>0.90</td>
<td>1.83</td>
<td>ab</td>
<td>z</td>
</tr>
<tr>
<td><strong>Liquidambar styraciflua</strong></td>
<td>52</td>
<td>0.37</td>
<td>0.64</td>
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<td>y</td>
</tr>
<tr>
<td><strong>Platanus occidentalis</strong></td>
<td>4</td>
<td>0.31</td>
<td>0.24</td>
<td>b</td>
<td>z</td>
</tr>
<tr>
<td><strong>Quercus bicolor</strong></td>
<td>18</td>
<td>0.41</td>
<td>0.53</td>
<td>b</td>
<td>z</td>
</tr>
<tr>
<td><strong>Quercus palustris</strong></td>
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<td>1.09</td>
<td>ab</td>
<td>z</td>
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<tr>
<td><strong>Quercus phellos</strong></td>
<td>8</td>
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<td>0.75</td>
<td>ab</td>
<td>z</td>
</tr>
<tr>
<td><strong>Salix nigra</strong></td>
<td>98</td>
<td>1.11</td>
<td>1.58</td>
<td>a</td>
<td>y</td>
</tr>
</tbody>
</table>
Table 3-9. Average biomass accumulated 6 years following planted estimated for primary and secondary groups (incorporating all species and stocktypes). Average biomass of species groups are compared within cells and cells are compared for each species group. Same letters represent no significant difference ($p<0.05$). $n$ represents count of live trees after 6 years.

<table>
<thead>
<tr>
<th>Ambient</th>
<th>$n$</th>
<th>Average Total Biomass (kg)</th>
<th>Standard Deviation</th>
<th>Within cell, species group comparison</th>
<th>Within species group, cell comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Primary</strong></td>
<td>257</td>
<td>73.72</td>
<td>95.76</td>
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<tr>
<td>Secondary</td>
<td>225</td>
<td>5.03</td>
<td>5.90</td>
<td>b</td>
<td>x</td>
</tr>
<tr>
<td><strong>Saturated</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primary</td>
<td>271</td>
<td>30.32</td>
<td>31.36</td>
<td>a</td>
<td>y</td>
</tr>
<tr>
<td>Secondary</td>
<td>265</td>
<td>3.09</td>
<td>3.46</td>
<td>b</td>
<td>y</td>
</tr>
<tr>
<td><strong>Flooded</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Primary</td>
<td>210</td>
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<td>1.50</td>
<td>a</td>
<td>z</td>
</tr>
<tr>
<td>Secondary</td>
<td>30</td>
<td>0.53</td>
<td>0.67</td>
<td>b</td>
<td>z</td>
</tr>
</tbody>
</table>

a – b letters represent differences among species within cells
y – z letters represent differences among cells within species
Figures

Figure 3-1. Results of fitting Eq. 1 \(Y=AX^b + \epsilon\) for primary successional species destructively harvested in 2011. \(Y=\)Total dry belowground biomass (coarse roots) (kg) and \(X=\) Total dry aboveground biomass (kg) (excluding leaves) (See Table 3-4 for results of fitting model).
Figure 3-2. Results of fitting Eq. 1 ($Y = aX^b + \epsilon$) for secondary successional species destructively harvested in 2011. $Y =$ Total dry belowground biomass (coarse roots) (kg) and $X =$ Total dry aboveground biomass (excluding leaves) (kg) (See Table 3-4 for results of fitting model).
Figure 3-3. Results of fitting Eq. 1 (\(Y=aX^b + \varepsilon\)) for primary successional species destructively harvested in 2011 and 2014. \(Y=\)Total biomass (kg) and \(X=\)Equivalent stem-cross sectional diameter at groundline (cm) (See Table 3-5 for results of fitting model).
Figure 3-4. Results of fitting Eq. 1 ($Y=aX^b + \epsilon$) for secondary successional species destructively harvested in 2011 and 2014. $Y=$Total biomass (kg) and $X=$Equivalent stem-cross sectional diameter at groundline (cm) (See Table 3-5 for results of fitting model).
CHAPTER 4: EFFECT OF HYDROLOGIC CONDITIONS ON ABSOLUTE AND RELATIVE GROWTH RATES OF SEVEN WETLAND TREE SPECIES
Abstract

Biomass accumulation rates (growth rates) are influenced by many factors and have not been documented for many wetland tree species. Growth rates can be useful in determining the development of created/restored forested wetlands. Successfully restoring these wetlands requires that trees grow and accumulate woody biomass. The purpose of this study was to investigate growth rates of seven Mid-Atlantic wetland tree species (four early successional, three late successional) in response to planting along a controlled hydrologic gradient. Biomass was determined using species specific models and cumulative, absolute (AGR), and relative (RGR) growth rates were determined over 6 years using functional-derived nonlinear models. Growth rates at standardized masses were compared among species and successional groups across the hydrologic gradient. Fast growing early successional species obtained more biomass than late successional species and therefore had increased AGR and RGR rates. At 11 kg, *P. occidentalis* had the greatest AGR (36 g/day) and RGR (3.1 g/g/day) in the least stressful hydrologic treatment. Increased hydrologic stress reduced biomass and biomass accumulation rates; however, moderate hydrologic stress did not reduce AGR or RGR as the selected species are typically found in wetland systems. In the most severe hydrologically stressed conditions, *S. nigra* had the greatest AGR (0.27 g/day) and RGR (2.8 g/g/day) at 0.1 kg standardized biomass. Overall, these results provide needed information about the biomass accumulation rates of planted saplings that are often not accounted for when studying the development of restored forested wetlands.
Introduction

Growth is generally defined as an irreversible change in a measurable quantity (Hunt 1990, Jørgensen et al. 2000). While this definition is simple, a multitude of methods are designed to describe growth. Common measurable quantities can include size, form, or number (Hunt 1982). These measurable quantities can be applied to a vast range of living and non-living systems from individual bacterium to human populations and from crystals all the way to the entire universe. For the purpose of this paper, growth will focus on groups of planted sapling’s increase in total woody biomass.

Many researchers (Blackman 1919, Evans 1972, Causton and Venus 1981, Hunt 1982, Paine et al. 2012 (See Pommerening and Muszta 2016 for review) developed methods to address questions specific to plant growth analysis: through time particular methods have proved more valuable than others and general trends became apparent. Increases in plant mass through time (referred to as cumulative growth) tends to follow the same general sigmoidal pattern that is found elsewhere in nature (Weiner and Thomas 2001, Pommerening and Muszta 2016). Plants start with little to no detectable increases in mass, then mass increases rapidly. As plants reach maturity, the increase in mass slows (reaches an asymptote) and finally ceases (Hunt 1990). This pattern of growth is exhibited by many types of plants; however, the magnitude and symmetry of the curve can change substantially. Further studies have suggested that biomass (or carbon) accumulation of trees may not reach an asymptote (Muller-Landau et al. 2006, Sillett 2010, Stephenson et al. 2014).

From this general sigmoidal pattern, two biomass growth rates can be determined. The first is termed absolute growth rate (AGR) and is defined as the change in mass over
a given time interval (e.g. g/day). Following the above sigmoidal pattern example, AGR will increase rapidly, peak, rapidly decline, and then slowly taper off. AGR yields important information, but presents challenges when comparing growth of individuals of different starting masses (Hunt 1982, Hunt 1990, Rees et al. 2010, Pommerening et al. 2016), which is the focus of this study.

Relative growth rate (RGR) can be used to compare individuals of different sizes when calculated correctly (Rose et al. 2009). Relative growth rate is defined as the increase in mass per unit mass per unit time (e.g. g/g/day) or growth per unit mass. Relative growth rate is referred to as an ‘efficiency index’ because it measures the efficiency of plant material to produce new material (Blackman 1919). It is often compared to the rate of compound interest earned on capital in the financial world (Blackman 1919, Hunt 1990). Relative growth rates of trees decline through time as trees grow larger (ontogenetic drift) and because of self-shading, increased allocation to structural (non-photosynthetic) components, declines in leaf area ratio, and reduced nutrient availability (Evans 1972, Hunt 1982, South 1995, Rees et al. 2010, Paine et al. 2012, Philipson et al. 2012). Therefore, comparisons of RGR among species or experimental treatments must account for differences in mass because high values of RGR can occur when plants are either smaller in size or because they are growing faster (Turnbull et al. 2008, Rees et al. 2010, Turnbull et al. 2012).

Tree growth can be positively or negatively influenced by hydrologic conditions depending on the species and other environmental factors (Kozlowski 1984b). Very few studies, however, measured total biomass (aboveground and belowground) and calculated AGR and RGR for individual seedlings or saplings grown across a hydrologic gradients
Several studies have investigated morphological growth (basal area, stem diameter, tree rings, height, leaf mass, etc.) of trees in different hydrologic regimes and found positive and negative responses (Malecki et al. 1983, Mitsch and Rust 1984, Keeland et al. 1997, Kabrick et al. 2005, Anderson and Mitsch 2008, McCurry et al. 2010, Rodríguez-González et al. 2010, Kabrick et al. 2012, Smith et al. 2013). However, a large proportion of studies fail to account for small trees that have a small stem diameter at breast height (dbh) or are not tall enough to have a dbh at all (Das 2012). In recently restored wetlands and other developing ecosystems, accounting for these trees is important because they are contributing substantially to the overall ecosystem structure and function.

The purpose of this study was to determine biomass growth rates (AGR and RGR) of seven species from the Mid-Atlantic region planted across a hydrologic gradient.

Methods

Methods used to establish and measure the survival and morphology of saplings planted in the experimental site are the same as Chapter 2.

Biomass Estimation Model

Species specific biomass estimation models (BEM) were used to determine biomass of individual saplings for all sample periods over 6 years (See Chapter 3 for BEM development).
Differences in initial and final biomass for each species in each cell were determined using pairwise t-tests. Variance was estimated separately for each group, the Welch modification to degrees of freedom was used and Holm’s p-value adjustment was used to control the family-wise error rate. All alpha values were set at 0.05.

**Growth Rate Calculations**

The methods used to calculate AGR and RGR have been debated extensively (Hunt 1982, Hunt 1990, South 1991, South 1995, Hoffmann and Poorter 2002, Shimojo et al. 2002, MacFarlane and Kobe 2006, Paine et al. 2012, Matsushita et al. 2015, Pommerening and Muszta 2015, 2016). Nonlinear function-derived growth rates presented in Paine et al. (2012) were used to calculate AGR and RGR as a function of mass. These methods of calculating growth rates were used because the repeated biomass estimations made over 6 years allowed for use of these function-derived growth rates that better capture the temporal dynamics of growth than the traditional (classical) growth rate calculations and because of the mathematical support provided for these calculations.

To reduce heterogeneous variance, biomass was transformed using the natural logarithm. The monomolecular function (also known as Mitscherlich function (Zeide 1993)) was fit to the transformed data for each species within each cell using the standard selfStart function, `SSasymp`, in the NLME package (Pinheiro and Bates 2000) in R version 3.2.1 (R Core Team 2015) (Figure 4-2). The following equation was used to model the natural logarithm of biomass:

\[ y_t = K - e^{-rt}(K-M_0) \]  
(Equation 1)

\[ y_t = \text{Natural logarithm of biomass at time } t \]
K = Upper asymptote (model derived)
e = Euler’s number
r = Rate constant (model derived)
t = Time
M₀ = Y intercept (model derived)

This function was selected because the saplings were undergoing rapid increases in biomass and produced lower Akaike information criterion (AIC) values than other functions when modelling the natural logarithm of biomass. The custom function (output.mono.nls) provided by Paine et al. (2012) was used to determine AGR and RGR and associated confidence intervals as a function of biomass. The following equation was used to determine $AGR_m$ (AGR at a specific biomass, variables same as Eq. 1):

$$AGR_m = (re^{rt}(k-M_0))e^{yt} \quad (\text{Equation 2})$$

The following equation was used to determine $RGR_m$ (RGR at a specific biomass, variables same as Eq. 1)

$$RGR_m=r(K-y_t) \quad (\text{Equation 3})$$

Comparing Growth Rates

Several authors suggest comparing species (or treatments) AGR and RGR at particular biomass amounts (Turnbull et al. 2008, Rose et al. 2009, Paul-Victor et al. 2010, Rees et al. 2010, Philipson et al. 2012, Turnbull et al. 2012). This is referred to as size corrected or size standardized growth rates. Most commonly this size standardization is applied to RGR (SRGR); however it can also be applied to AGR (SAGR). This
technique is useful because AGR and RGR trajectories can intersect as experimental units grow larger (Larocque and Marshall 1993, Hautier et al. 2010, Paine et al. 2012).

A standard size was selected at which to compare AGR and RGR for individual species in PRI and SEC groups and differences in rates between AMB and SAT. The size selected represented the maximum biomass obtained by all species in a group from both AMB and SAT. For PRI, 11 kg was selected for comparison and for SEC, 1 kg was selected. Due to the low growth in FLD, the maximum size obtained by all species was 0.1 kg, which was used to compare all species. Importantly, species in these cells obtained these respective biomasses as different times.

Results

Biomass Cumulative Growth

Initial biomass varied among the species (Table 4-1), ranging from 30 g (Standard Deviation (SD) = 42) for B. nigra to 50 g (SD = 72) for Q. phellos. Biomass increased through time for most species in AMB and SAT, while most species exhibited little cumulative growth in FLD (Figure 4-1). As a result, most species had greater biomass after 6 years in AMB than SAT and FLD (Table 3-6 and Figure 4-1). Additionally, there were differences in final biomass among species within each cell (Table 3-6 and Figure 4-1). In the AMB and SAT, PRI species had greater biomass than SEC species. Salix nigra had greater final biomass in FLD than L. styraciflua, P. occidentalis, and Q. bicolor (Table 3-6).
Absolute Growth Rate (AGR)

For most species, AGR increased as sapling size increased (Figure 4-3). For several species, AGR started to reach an asymptote as mass increased; *S. nigra* in FLD reached a peak AGR and then started to decline.

Absolute growth rate differed among PRI and SEC species in AMB. At a standard total biomass of 11 kg, *P. occidentalis* had the greatest AGR (36 g/day), followed by both *B. nigra* (26 g/day) and *L. styraciflua* (23 g/day) (Table 4-2). *Salix nigra* had the lowest AGR at 11 kg (15 g/day) of PRI species in AMB while *Q. phellos* had the greatest AGR at 1 kg total biomass (2.0 g/day) followed by *Q. bicolor* (1.8 g/day) and *Q. palustris* (1.6 g/day) in AMB. The 95% confidence intervals (CI) overlapped for *Q. bicolor* and *Q. palustris*, suggesting that their growth rates may not be significantly different (Table 4-2).

*Liquidambar styraciflua* had the greatest AGR at 11 kg biomass (34 g/day) in SAT. However, CI for *L. styraciflua* overlapped with *S. nigra* (27 g/day) and *B. nigra* (26 g/day). *Platanus occidentalis* had the lowest AGR (22 g/day). *Quercus phellos* had greater AGR at 1 kg (2.0 g/day) than *Q. bicolor* (1.4 g/day) and *Q. palustris* (1.3 g/day). The 95% CI overlapped for *Q. bicolor* and *Q. palustris* (Table 4-2).

*Salix nigra* had the greatest AGR in FLD at 0.1 kg biomass (0.27 g/day). As a result of poor survival and dieback, CI of *L. styraciflua* (0.14 kg/day), *B. nigra* (0.12 g/day) and *P. occidentalis* (0.10 g/day) were overlapping. Similarly, the CI for *Q. phellos* (0.14 g/day), *Q. bicolor* (0.09 g/day) and *Q. palustris* (0.08 g/day) also overlapped at 0.1 kg standard biomass (Table 4-2).

Species AGR were compared between AMB and SAT using 11 kg standardization. Both *L. styraciflua* and *S. nigra* increased AGR in SAT compared to
AMB, while *B. nigra* AGR remained the same (Table 4-2). AGR for *P. occidentalis* declined 38.9% in SAT compared to AMB. Both *Q. bicolor* and *Q. palustris* had decreased AGR in SAT compared to AMB, while *Q. phellos* AGR remained similar. The saplings planted in FLD had lower total biomass after 6 years (Table 3-6) suggesting that their AGR were consistently lower than AMB and SAT.

**Relative Growth Rate (RGR)**

RGR of all species declined rapidly as saplings developed (Figure 4-4). Several species in FLD (*P. occidentalis*, *Q. bicolor*, and *Q. phellos*) exhibited negative RGR due to mortality and die back.

*Platanus occidentalis* had the greatest RGR at 11 kg (3.1 g/g/day) in AMB, followed by *B. nigra* (2.4 g/g/day) and *L. styraciflua* (2.1 g/g/day). The 95% CI overlapped for *B. nigra* and *L. styraciflua* (Table 4-2). *Salix nigra* had the lowest RGR at 11 kg (1.3 g/g/day) of PRI species. *Quercus phellos* had the greatest RGR in AMB at 1 kg total biomass (2.0 g/g/day) followed by *Q. bicolor* (1.8 g/g/day) and *Q. palustris* (1.6 g/g/day). The 95% confidence intervals (CI) overlapped for *Q. phellos* and *Q. bicolor* as well as for *Q. bicolor* and *Q. palustris* suggesting that their growth rates may not be significantly different (Table 4-2).

In SAT, *L. styraciflua* RGR was greatest (3.0 g/g/day) followed by *S. nigra* (2.5 g/g/day) and *B. nigra* (2.3 g/g/day). The CI of *S. nigra* and *B. nigra* overlapped. *Platanus occidentalis* had the lowest RGR (2.0 g/g/day) of PRI species in SAT at 11 kg biomass. *Quercus phellos* had greater RGR at 1 kg (2.0 g/g/day) than *Q. bicolor* (1.4 g/g/day) and
Q. palustris (1.3 g/g/day). There was overlap of CI between the Q. bicolor and Q. palustris (Table 4-2).

When comparing PRI species in FLD, S. nigra had the greatest RGR (2.8 g/g/day). The remaining species, L. styraciflua (1.4 g/g/day), B. nigra (1.2 g/g/day), and P. occidentalis (0.99 g/g/day) had overlapping 95% CI, suggesting that there was no difference in RGR among these species. Similarly, the CI for Q. phellos (1.4 g/g/day), Q. bicolor (0.09 g/g/day) and Q. palustris (0.08 g/g/day) also overlapped at 0.1 kg standard biomass (Table 4-2).

When comparing the RGR of PRI species between AMB and SAT, L. styraciflua and S. nigra exhibited increases in SAT compared to AMB, while B. nigra RGR remained the same and P. occidentalis RGR decreased in SAT (Table 4-2). Quercus bicolor RGR decreased in SAT compared to AMB and Q. palustris and Q. phellos RGR remained similar (Table 4-2).

When observing the entire RGR curves for B. nigra, L. styraciflua, Q. phellos and S. nigra the saplings in SAT had lower initial RGR than AMB. However, at the end of the study, RGR for these species in SAT was greater than AMB (Figure 4-4).

Discussion

Biomass Cumulative Growth

Biomass increased through time for most species in AMB and SAT, but most species planted in FLD had little cumulative growth. As discussed in Chapter 3, this most likely resulted from flooding above the root collar, reduced soil nitrogen and phosphorus concentrations, increased clay concentrations, and herbaceous competition. The reduction
in the amount of biomass accumulated as a result of increased hydrologic stress has been confirmed for *P. occidentalis* (Tang and Kozlowski 1982a), *S. nigra* (Donovan et al. 1988, Pezeshki et al. 1998), *Taxodium distichum* (Mitsch and Ewel 1979), and various flood intolerant species (Kozlowski 1984b). However, *T. distichum* is unique in its adaptations to low oxygen conditions resulting from soil flooding, and other studies have found that the biomass accumulated under stressful hydrologic conditions can be similar to the amount when planted in less stressful hydrologic condition (Megonigal and Day 1992, Dickinson 2007). However, the AGB and BGB allocation patterns of *T. distichum* have been found to shift based on hydrologic conditions (lower BGB production in flooded conditions) (Megonigal and Day 1992). *Salix nigra* has been found to be very tolerant of hydrologic stress (Hook 1984) and Day et al. (2006) showed stem biomass accumulation to be similar in flooded and drained conditions.

Growth rates were compared among species within their respective groups (PRI and SEC) because of the differences in life history strategies between these two groups (Bazzaz 1979). Additionally, the biomass accumulated after 6 years by the SEC species was significantly lower than PRI (Table 3-9). PRI had greater biomass accumulated than SEC in AMB and SAT, while in FLD all species had less biomass accumulated than *S. nigra*.

**Absolute Growth Rate (AGR)**

The increase in AGR as sapling biomass increased is the result of greater ability to capture resources (light, nutrients, water, etc.) with most of the resources being allocated to biomass accumulation as opposed to maintenance and reproduction. Many of
the species had not yet reached a peak in AGR where biomass accumulation is at the maximum rate at the time of sampling. *S. nigra* in FLD appears to have reached a maximum and AGR and started to decline; however, this could be the result of continuing mortality of stems and with additional regrowth this trend could change in the future.

When comparing species AGR at standardized sizes, different species had the greatest AGR in each cell, reflecting their different abilities to tolerate hydrologic stress. *Platanus occidentalis* had the greatest AGR in AMB, *L. styraciflua* had the greatest AGR in SAT, and *S. nigra* had the greatest AGR in FLD. *Quercus phellos* had the greatest AGR in AMB and SAT. Absolute growth rate was not different among SEC species in the FLD. The greater AGR exhibited by *L. styraciflua*, *S. nigra*, and *Q. phellos* suggests that they may be appropriate for planting in restored wetlands or other afforestation/reforestation projects where rapid accumulation of biomass is desired.

Both *L. styraciflua* and *S. nigra* increased AGR in SAT compared to AMB. *Salix nigra* has been shown to be sensitive to dry conditions (McLeod and McPherson 1973, Hook 1984, Schaff et al. 2003), suggesting a reason for the lower AGR in AMB. Although not investigated in this study, the increased size of the trees (particularly *P. occidentalis* and *B. nigra*) in AMB may have caused competition for resources, which may have reduced the AGR of *L. styraciflua* and *S. nigra*. *Platanus occidentalis* AGR declined 38.9% from AMB to SAT suggesting that it has reduced tolerance for hydrologic stress as suggested by Tang and Kozłowski (1982a). In FLD, *P. occidentalis* AGR was the lowest for PRI species, further suggesting that it has a lower tolerance for hydrologic stress than the other species.
AGR of *Q. phellos* was similar in AMB and SAT and was greater than the other SEC species. Both *Q. bicolor* and *Q. palustris* had slightly lower AGR in SAT than AMB. *Quercus phellos* may be more tolerant of hydrologic stress than *Q. bicolor* and *Q. palustris*. All three *Quercus* spp. are considered moderately to somewhat flood tolerant and are typically found on poorly drained soils (Whitlow and Harris 1979, Hook 1984, Burns and Honkala 1990a).

**Relative Growth Rate (RGR)**

Biomass RGR declined rapidly as saplings increased biomass, possibly due to self-shading, increased allocation to structural (non-photosynthetic) components, declines in leaf area ratio, and reduced nutrient availability (Evans 1972, Hunt 1982, South 1995, Rees et al. 2010, Paine et al. 2012, Philipson et al. 2012). Since the species had different initial sizes, several authors suggest comparing species RGR at standardized mass (Turnbull et al. 2008, Rose et al. 2009, Paul-Victor et al. 2010, Rees et al. 2010, Philipson et al. 2012, Turnbull et al. 2012). However, appropriateness of this procedure is still being actively debated (Pommerening and Muszta 2016). Comparison of RGR and AGR for species and cells at standardized masses yielded similar results suggesting that this method may be appropriate and provides additional validation to making planting recommendations based on both measures.

Species that had the greatest biomass RGR were the same species that had the greatest biomass AGR across the cells suggesting that these species also had the greatest growth efficiencies. *Platanus occidentalis* had the greatest RGR in AMB, *L. styraciflua* had the greatest RGR in SAT, and *S. nigra* had the greatest RGR in FLD. *Quercus*
*phellos* had the greatest RGR in AMB and SAT and in FLD there was no difference in RGR among SEC species. These species may be appropriate for planting in restored wetlands or other afforestation/reforestation projects where efficient accumulation of biomass is desired.

Both *L. styraciflua* and *S. nigra* exhibited greater RGR in SAT compared to AMB. This suggests that their growth efficiencies may be reduced in drier conditions. *Platanus occidentalis* RGR was lower in SAT than in AMB, suggesting that growth efficiency is decreased even in moderate hydrologic stress. Consistent with the AGR results, *Q. phellos* RGR was similar in AMB and SAT, while *Q. bicolor* and *Q. palustris* had slightly lower RGR in SAT than AMB. This again suggests that *Q. phellos* may be more tolerant of hydrologic stress than *Q. bicolor* and *Q. palustris*.

*Betula nigra, L. styraciflua, Q. phellos* and *S. nigra* saplings in SAT initially had lower initial RGR than those in the AMB. After 6 years, RGR in SAT was greater than saplings in the AMB for these species. This suggests their growth efficiency was initially higher in AMB and decreased rapidly as biomass increased compared to the saplings grown in SAT (slower decrease in RGR). Similar overlap has been found for grass species grown with and without parasitic plants (Hautier et al. 2010). While not the focus of this study, the rapid decreases in growth efficiency in AMB (dropping below SAT), may suggest that a resource(s) is becoming limited in AMB. This resource limitation may be the result of competition similar to the findings of Larocque and Marshall (1993). Further investigations are needed to elucidate the effect of competition on sapling RGR.
Conclusions

Those species that have greater AGR and RGR under hydrologic stress (*L. styraciflua, S. nigra,* and *Q. phellos*) may be better suited for planting in restored wetlands as they are able to effectively and efficiently accumulate biomass. These species have morphological, physiological, and life history traits (e.g. shallow roots, adventitious roots, hypertrophied lenticels, and seed germination under water) which allow them to grow in soils where oxygen may be limited (Hook 1984).

The novel growth rates presented here can be used to accurately determine woody tissue carbon accumulation rates (from concentrations in Chapter 3). This study illustrates the importance of calculating AGR and RGR across a range of biomass amounts as both of these rates change as saplings grow and suggests that further studies are needed to investigate how resource limitation can influence these rates.
Literature Cited


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Tables

Table 4-1. Initial biomass with standard deviation in parentheses. Same letters represent no significant difference (p<0.05). N represents number of planted saplings.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Initial Biomass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betula nigra</td>
<td>339</td>
<td>30 (42) c</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>332</td>
<td>31 (46) c</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>264</td>
<td>36 (58) abc</td>
</tr>
<tr>
<td>Quercus bicolor</td>
<td>361</td>
<td>43 (58) b</td>
</tr>
<tr>
<td>Quercus palustris</td>
<td>342</td>
<td>43 (55) ab</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>378</td>
<td>50 (72) b</td>
</tr>
<tr>
<td>Salix nigra</td>
<td>351</td>
<td>31 (50) ac</td>
</tr>
</tbody>
</table>
Table 4.2. Species AGR and RGR at standard masses. Values in parentheses represent ±95% confidence intervals.

<table>
<thead>
<tr>
<th>Primary Species</th>
<th>AMB</th>
<th>SAT</th>
<th>FLD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass (kg)</td>
<td>AGR (g/day)</td>
<td>RGR (g/g/day)</td>
<td>AGR (g/day)</td>
</tr>
<tr>
<td>Betula nigra</td>
<td>11</td>
<td>26 (24-29)</td>
<td>2.4 (2.2-2.5)</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>11</td>
<td>23 (21-26)</td>
<td>2.1 (1.9-2.2)</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>11</td>
<td>36 (34-38)</td>
<td>3.1 (3.0-3.2)</td>
</tr>
<tr>
<td>Salix nigra</td>
<td>11</td>
<td>15 (11-18)</td>
<td>1.3 (1.1-1.5)</td>
</tr>
<tr>
<td>Secondary Species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quercus bicolor</td>
<td>1</td>
<td>1.8 (1.6-1.9)</td>
<td>1.8 (1.6-1.9)</td>
</tr>
<tr>
<td>Quercus palustris</td>
<td>1</td>
<td>1.6 (1.3-1.7)</td>
<td>1.6 (1.4-1.7)</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>1</td>
<td>2.0 (1.8-2.2)</td>
<td>2.0 (1.9-2.1)</td>
</tr>
</tbody>
</table>
Figure 4-1. Average predicted biomass of seven species (columns) in each cell (rows). Shading represents 95% confidence intervals around mean.
Figure 4-2. Natural log transformed biomass of seven species (columns) in each cell (rows). Red line represents the results of fitting the monomolecular function.
Figure 4-3. Absolute growth rate (AGR) of seven species (columns) in each cell (rows) as a function of mass. Shading represents 95% confidence intervals around mean.
Figure 4-4. Relative growth rate (RGR) of seven species (columns) in each cell (rows) as a function of mass. Shading represents 95% confidence intervals around mean.
CHAPTER 5: DEVELOPING AN ECOLOGICAL PERFORMANCE STANDARD
FOR WOODY VEGETATION IN COMPENSATORY MITIGATION
WETLANDS OF VIRGINIA
Abstract

Compensatory wetland mitigation sites (CMS) are required to replace ecological structures, functions, and services lost during permitted impacts. Meeting established ecological performance standards (EPS) is the current legislative-mandated method for determining if CMS are meeting this goal. However, existing EPSs often are not adequate measures of ecological functions and services. The purpose of this study was to develop a woody EPS for use in forested CMS in Virginia that is a suitable indicator of woody biomass accumulation, an important ecosystem function. The existing woody EPSs in Virginia (stem density, height growth, canopy cover) were found to be inadequate representations of sapling biomass accumulation. Using data from the previous chapters, a minimum stem cross-sectional area measured at groundline (CSAG) was recommended as an additional EPS. The recommended EPS is that CMS have greater than 5.2 m$^2$/ha CSAG at the end of the 5th year following construction. Sapling CSAG provides a better representation of sapling biomass accumulation than the existing EPSs in Virginia and is more appropriate to determine whether forested CMS are reaching their intended goal of replacing lost ecosystem structure, functions and services.
Introduction

Wetlands are restored for a variety of reasons, including but not limited to: compensation for permitted impacts to existing wetlands (wetland compensatory mitigation); state and federal goals (Chesapeake 2000 Agreement); re-establishing bird habitat (Ducks Unlimited); and agricultural easements (Agricultural Conservation Easement Program). Despite varying motivations for restoration, projects implicitly seek to return lost ecological structures, functions and services to the landscape. Wetlands restored to compensate for permitted impacts often have additional goals they are required to meet as a result of the legal framework they fall within.

Wetland impacts are regulated by the 1972 Federal Water Pollution Control Act, which was amended and renamed the Clean Water Act (CWA) in 1977 (33 U.S.C. 1251 et seq.). Wetland impacts are specifically regulated under Section 404 of the CWA (33 U.S.C 1344) which authorized the United States Army Corps of Engineers (USACE) under the direction of the United States Environmental Protection Agency (USEPA) to issue permits regulating the discharge of dredged or fill material into “waters of the United States”, which include wetlands (40 CFR Part 230.1).

Mitigation was first defined in the 1978 Council on Environmental Quality (CEQ) Regulations for Implementing the Procedural Provisions of the National Environmental Policy Act (NEPA – 42 U.S.C 4321) (40 CFR 1500-1508). In this context, mitigation refers to avoidance, minimization, rectification, reduction over time, or compensation for impacts to any type of environment. The wetland mitigation sequence, in descending order of priority, emphasizes avoidance, minimization and compensation for wetland impacts and was established in the 1990 Memorandum of Agreement between the
Environmental Protection Agency and the Department of the Army. This sequence was devised to allow for permitted wetland impacts while maintaining the physical, biological and chemical integrity of the waters of the United States and remaining in compliance with the CWA. If impacts to existing wetlands are determined unavoidable, four methods of compensation have been deemed acceptable: 1) restoration of converted wetlands, 2) creation of new wetlands, 3) enhancement of existing wetlands, 4) preservation of existing wetlands (listed in descending order of priority (33 CFR PART 332, USACE and USEPA 2008).

Ecological Performance Standards

Wetlands that are created, restored, enhanced, or preserved to offset permitted impacts are often referred to as compensatory mitigation sites (CMS). These CMS are required to replace ecological structures, functions and services lost during permitted impacts (33 CFR PART 332.3). The current legislative-mandated method for determining if a CMS is developing into the desired wetland type and is providing the expected ecological functions is through meeting project specific ecological performance standards (EPS) (aka: success criteria, success standards or release criteria) (33 CFR PART 332.5, USACE and USEPA 2008). Performance standards for all CMS are required to be clear, objective, verifiable, based on the best available science and able to be assessed in a practicable manner (33 CFR PART 332.5, USACE and USEPA 2008).

Ecological performance standards are developed on a project-by-project basis (USACE and USEPA 2008). While EPS vary across USACE districts, the majority are based on soil, vegetation, and hydrologic indicators from the 1987 Federal Delineation

Most EPSs are structural measurements of the vegetative community and/or physical environment (Wilson and Mitsch 1996) and are not direct measurements of wetland functions or services (Mitsch and Wilson 1996, Streever 1999, NRC 2001). Additionally, many EPSs are not adequate indicators of wetland functions or services (Kentula et al. 1992). Cole (2002) suggested that measurement of herbaceous cover (a common EPS) may not serve as an accurate indicator of the replacement of wetland functions. Therefore, meeting site specific EPSs does not guarantee that wetland functions and services are being replaced (the overall goal of compensatory mitigation) (Matthews and Endress 2008).

**Virginia EPS**

In Virginia, the USACE Norfolk District and the Virginia Department of Environmental Quality (VADEQ) (2004) provide recommended hydrologic, soil, and vegetation EPSs for CMS. The VADEQ (2010) also provides a template outlining recommended EPSs specifically for mitigation banks. However, these only serve as guidelines and specific EPSs are developed for each project. These EPSs are designed to ensure that the CMS qualifies as a wetland using the indicators from the 1987 USACE Wetland Delineation Manual (and subsequent supplements) (Environmental Laboratory
To that end, the hydrologic and soil EPS require satisfying their respective criteria in the 1987 USACE Wetland Delineation Manual. Monitoring and compliance reports are required and the current timing in Virginia is to monitor for six years over a 10 year period (typically years 1, 2, 3, 5, 7, and 10) (USACE Norfolk District and VADEQ 2004).

Vegetation EPSs are separated into requirements for herbaceous and woody strata. For both strata, 50% of all the dominant plant species are required to be Facultative (FAC, occurs in wetland and non-wetlands) Facultative Wetland (FACW, usually occurs in wetlands) or Obligate (OBL, almost always occurs in wetlands) (Lichvar 2013). Additionally, areal herbaceous coverage greater than 50% is required in emergent wetland areas after one growing season. Undesirable species (including invasive species and other “weedy” species that may compete with planted saplings) in both strata are required to be quantified and controlled if necessary (USACE Norfolk District and VADEQ 2004).

Specific survival rates of planted herbaceous and woody vegetation may be required in some CMS in Virginia. The particular percentage survival required varies by project; however, planted woody vegetation can be required to exceed 80% survival (Mike Rolband, Personal Communication). In the woody stratum, a stem density of both naturally colonizing and planted trees of 495-990 stems/ha is required until the canopy cover is 30% or greater (USACE Norfolk District and VADEQ 2004). However, in practice most CMS in Virginia are required to have greater than 990 stems/ha (Mike Rolband, Personal Communication).
Possibly because of limited information on growth rates of saplings in created or restored wetlands, few states have established EPSs related to sapling growth in CMS (Denton 1990, Niswander and Mitsch 1995, Streever 1999, Gamble and Mitsch 2006, Pennington and Walters 2006). Virginia is unique in that it has established a height growth EPS for mitigation banks in particular. This EPS states that until the canopy coverage exceeds 30%, average height of all woody stems (including planted and colonizing trees) in each cell, field or block must have an average increase in height of 10% by both the 5th and 10th year following construction. An alternative method for meeting this EPS requires average tree height must be ≥ 1.5 m in the 5th year following construction and 3.0 m in the 10th year following construction (VADEQ 2010). However, few projects have implemented this height-growth EPS (Mike Rolband, personal communication).

In Virginia, the majority of wetland impacts are to non-tidal forested wetlands due to their geographic extent and drier hydrologic conditions (Tiner and Finn 1986, USGS 1999, Tiner et al. 2005, VADEQ 2014). Subsequently forested wetlands have the most compensation area (VADEQ 2014). Therefore, it is important that the woody vegetation EPS in particular be a direct measure of, or proven indicator of, ecological functions that can be compared to those found in natural (reference) systems. They must be quantifiable (in a clear, repeatable, and rapid manner) and ecologically relevant to the region.

The purpose of this study is to determine if the existing woody vegetation EPSs in Virginia are related to woody biomass accumulation (ecological function) and to propose additional woody vegetation EPSs that are representative of this ecological function.
Methods

Methods used to establish and measure the survival and morphology of saplings planted in the experimental site are the same as Chapter 2.

Existing EPS Relationship to Biomass Accumulation

Species specific biomass estimation models (BEM) were used to determine the total biomass of saplings living after 7 years. The BEMs were developed in Chapter 3 and relate ESD to total sapling biomass (aboveground biomass (AGB) and belowground biomass (BGB)). The woody EPSs for Virginia were directly compared to planted sapling biomass accumulation.

Development of Additional Woody EPS

The relationship between ESD and H and ESD and CD for saplings living after 7 years was determined using simple linear regressions. Individual relationships were developed for each species. An additional EPS was developed using stem cross-sectional area at groundline (CSAG).

Results

Sapling Survival EPS (>80% survival) and Stem Density EPS (>990 stems/ha)

After 7 years average percentage survival and stem density in SAT was the highest (66.4% - 1140 stems/ha) followed by AMB (59.0% - 1012 stems/ha) and FLD (27.3% - 449 stems/ha). Greater survival and higher stem density in SAT did not result in biomass greater than AMB (Table 5-1). There was a positive linear relationship between
survival and biomass accumulated after 5 years in the FLD ($r^2 = 0.253$, p-value = 0.02), but not in the AMB ($r^2 = 0.035$, p-value = 0.204) or SAT ($r^2 = 0.003$, p-value = 0.8) (Figure 5-1).

**Height Growth EPSs (>10%/year or > 1.5 m after 5 years)**

After 5 years the average percentage change in average height was greatest in AMB (54.4%), followed by SAT (43.7%) and FLD (8.8%). Similarly, the average height after 5 years was greatest in AMB (4.8 m) followed by SAT (3.2 m) and FLD (0.9 m). FLD was the only cell that did not satisfy both height growth EPSs. Greater percentage change in height and greater average height in AMB did reflect greater biomass than SAT or FLD (Table 5-1). For example the AMB had 54.4% change in height and 38.8 Mg/ha of biomass, while FLD had 8.8% change in height and only 0.55 Mg/ha. There was a positive linear relationship between the 5-year average percentage change in height and biomass accumulated after 5 years in the AMB ($r^2 = 0.376$, p-value = 0.003), but not in the SAT ($r^2 = 0.426$, p-value = 0.396) or FLD ($r^2 = 0.039$, p-value = 0.393) (Figure 5-2).

**Canopy Cover EPS (>30% Canopy Closure)**

If tree canopy cover exceeds 30%, stem density and height growth EPSs are no longer required (USACE Norfolk District 2004, VADEQ 2010). In AMB and SAT cells, 30% canopy closure occurred in years 3 and 4 respectively. After 7 years, AMB had the greatest canopy coverage (165.4%), followed by SAT (120.6%) and FLD (4.9%). Values can exceed 100% due to overlapping canopies. The FLD treatment failed to satisfy the 30% canopy closure EPS. The greater canopy cover in AMB corresponded to greater
biomass than SAT or FLD (Table 5-1). There was a significant positive relationship between percentage canopy cover and average biomass accumulated after 7 years in the AMB ($r^2 = 0.492$, p-value $< 0.001$), SAT ($r^2 = 0.442$, p-value $= 0.001$), and FLD ($r^2 = 0.353$, p-value $= 0.005$) (Figure 5-3).

**Development of Additional Woody EPS**

Equivalent stem cross-sectional diameter at groundline (ESD) was found to have a strong relationship with total AGB and BGB accumulated in individual saplings (Chapter 3). Additionally, there were statistically significant positive relationships (p-value $< 0.001$) between ESD and H for PRI (Figure 5-4) and SEC (Figure 5-5) groups. There were statistically significant positive relationships (p-value $< 0.001$) between ESD and CD for PRI (Figure 5-6) and SEC (Figure 5-7) species groups. *Quercus bicolor* tended to have the lowest coefficient of determination for both relationships which may indicate non-linear relationships in life history strategies and resource allocation patterns.

Stem cross-sectional area at groundline (CSAG) is equivalent to ESD, requires fewer steps to calculate and can be summed across areas (m$^2$/unit area). These characteristics suggest that total CSAG/unit area is a robust and appropriate EPS because it provides a strong indication of an ecological function (biomass accumulation) and can be compared to a natural (reference) wetland.

Total CSAG was greatest in AMB followed by SAT and then FLD at the end of 7 years (Table 5-2). Based on the total CSAG/unit area results from FLD, an appropriate minimum CSAG EPS would be greater than 5.2 m$^2$/ha at the end of the 5th year following construction (Table 5-2). This minimum CSAG EPS corresponds to ~3%
canopy cover and 0.55 Mg/ha total biomass in FLD. Based on the results from SAT, an appropriate maximum CSAG EPS would be 70.1 m$^2$/ha by the 5th year. This corresponds to a stage in site development in which 30% canopy closure occurred and when total biomass reached 14.35 Mg/ha. Additional EPSs could be developed based on CSAG from other points in time during the study.

**Discussion**

The existing EPSs are not strong predictors of sapling biomass accumulation, which is an important ecosystem function necessary for successful forested headwater CMS. These existing EPS may be useful predictors/indicators of other ecosystem functions and sapling characteristics not investigated here. However, the recommended CSAG has the potential to be a more robust EPS for reasons discussed below.

**Sapling Survival and Stem Density EPS**

The relationship between sapling survival (or stem density) and average biomass accumulated was significantly positive in the FLD cell only. However, the percentage of the biomass accumulation variation explained in the FLD by the linear model was low ($r^2=0.253$). The slope of the regression line in the AMB and SAT was not significantly different than zero and the amount of variation explained by the linear model was low in both cells. An example from AMB and SAT can illustrate what this low amount of variation explained represents. Two species/stocktypes combinations had 100% survival in AMB (B. nigra GAL and Q. bicolor GAL) and two combinations had 100% survival in SAT (L. styraciflua GAL and Q. bicolor GAL). The average biomass accumulated by
Q. bicolor in AMB and SAT were 5.25 kg and 5.80 kg respectively; the average biomass accumulated by B. nigra and L. styraciflua was 92.43 kg and 50.58 kg respectively. This large variation in biomass may result from differences in species life history traits among primary and secondary species, as described by Bazzaz (1979), and may also explain why survival was not correlated with biomass accumulation. Additionally, high stem densities with low biomass may result from saplings that grow tall with little accumulation in the main stem or saplings that die back and re-sprout. Several of the individual plantings in this study expressed these growth habits. While survival and stem density are important metrics to track during restoration, the CSAG EPS does take into account these variables and would indicate if survival and stem density were decreasing through time. Overall, survival and stem density are not strongly related to biomass accumulation and may not be appropriate EPSs.

Height Growth EPSs

The significant positive relationship between average percentage change in height and average biomass in AMB and the greater amount of biomass variation explained by the linear model ($r^2=0.376$) suggests that height growth is a more suitable EPS than survival and stem density in less stressful sites with more sapling growth. However, in the SAT and FLD, there was not a significant relationship between height growth and biomass accumulation. This suggests that in sites with moderate or high hydrologic stress where growth is limited, height growth is not a good predictor of biomass accumulation. While, height growth is relatively easy to quantify, the existing calculations hide variation associated with individual growth and have the potential to undervalue larger
trees (with slower height growth) or trees that follow different growth patterns. For example, *S. nigra* tend to be multi-stemmed and expand their crown diameter as opposed to accumulating height. The height growth calculation does not account for this difference in resource allocation and would not provide accurate representations of biomass accumulation for this species. Additionally, measuring heights of individual saplings in CMS is challenging when the saplings are large and the canopies are dense (Mike Rolband, personal communication; and anecdotal evidence from this study).

The positive relationship between ESD and H show there is support for the indirect connection between this EPS and biomass accumulation. However, the more robust relationship between ESD and biomass suggest that using CSAG (equivalent to ESD) would provide a stronger measure of ecosystem function than height.

**Canopy Cover EPS**

Canopy cover can be quantified using a variety of techniques (visual estimation, spherical densiometer, hemispherical photography, remote sensing, etc.). Standardized procedures that can be consistently and efficiently applied are necessary for an appropriate EPS. In this study, canopy cover was quantified by taking three measurements of crown diameter of individual saplings. While time consuming, this allows for a robust and unbiased estimation of canopy cover.

The significant positive relationship between canopy cover and biomass accumulation in all cells and the greater amount of biomass variation explained by the linear model suggest that canopy cover is more appropriate than both height growth and sapling survival. A positive relationship between crown diameter and ESD suggests that
crown diameter has an indirect weak relationship with biomass accumulation. Canopy cover has been used as an indicator of other ecological functions or overall ecosystem development (Rheinhardt et al. 2009). Therefore, of the three existing metrics it has the best support as an appropriate EPS for use in CMS but standardized procedures that are rapid and reproducible are needed.

Development of Additional Woody EPS

The recommended CSAG EPS for headwater wetland CMS in VA is that CSAG should exceed 5.2 m²/ha after 5 years and 6.4 m²/ha after 7 years. By measuring the CSAG earlier than 5 years, it is possible to determine if a CMS is developing toward meeting this EPS and taking corrective actions if it is not.

Stem cross-sectional area at groundline is the most appropriate measure to be used for an EPS for several reasons. The most compelling reason is that ESD (or CSAG) had significant positive relationships explaining a large amount of the variation associated with total biomass accumulation (AGB and BGB) for all species used in this study (Chapter 3).

The relationship between CSAG and biomass is particularly important, because woody biomass (and by extension of the relationship, CSAG) has been shown to be a good indication that other wetland functions and services are occurring. For example, when investigating six wetland functions, Cole (2002) suggested that stem area may be a better predictor of six main wetland ecosystem functions than percent herbaceous vegetation cover.
In addition to the relationship with biomass, ESD (or CSAG) had significant positive relationships with H and CD for all species in this study with high coefficients of determination. Other studies have suggested that measures of stem diameter (diameter at breast height (dbh) in particular) have positive relationship with other morphological measurements (H, trunk taper, volume, stem surface area, leaf surface, etc.) (Whittaker and Woodwell 1968, Niklas 1995). *Quercus bicolor* had the lowest coefficient of determination when relating ESD to H ($r^2 = 0.5563$) and CD ($r^2 = 0.6115$) of all seven species. This suggests that the relationship between these morphologies for *Q. bicolor* may be related in a non-linear fashion. If this is the case it suggests that H and CD increase for *Q. bicolor* was rapid relative to ESD (taller and wider crowns, with smaller stems) initially and as ESD increases the rate of H and CD growth decreases (stems become larger, while H and CD slowly increase). Therefore, *Q. bicolor* may have a different growth strategy (e.g. allocating more resources to height initially and then allocating more resources to the main stem) than the other *Quercus* species used in this study, similar to the results of Guyette et al. (2004).

Sapling GA also has methodological advantages compared to the existing EPSs. Measuring the stem diameter at the groundline allows for the inclusion of saplings that have not yet attained a height of 1.37 (common height for dbh measurements). When trees achieve 1.37 m in height and before they develop a distinct main stem (trunk) it is difficult to determine where to measure dbh, which is not an issue with CSAG. However, using GA precludes the use of traditional comparisons of forests and wetlands that mainly focus on dbh. Measuring dbh on multi-stem saplings presents even more of a problem since energy needed for height growth is usually re-directed to multiple stem
growth. However, measuring groundline diameter is simple for multi-stemmed saplings since each stem that originates belowground is measured individually.

A challenge associated with measuring groundline diameter is root swelling and buttressing. It is recommended that measurements be taken directly above any root swelling or buttressing (defined as stem diameter > 10% larger than stem above swelling), where the stem diameter becomes constant. Irregularly shaped stems should be measured using a dbh tape or by averaging multiple groundline diameter measurements. Measurements should be made in the fall, after the stems have completed the majority of their growth.

The recommended CSAG EPS should be used in conjunction with the existing woody EPS to confirm that this new standard is adequately representing the other EPS. If this CSAG EPS is found to be effective, it has the potential to eliminate some or all of the existing woody EPSs in Virginia. Since this is the first attempt at developing a CSAG EPS, additional measurements in restored/created forested CMS wetlands are needed to confirm that it is set at an appropriate level. Total CSAG can also be compared to natural (reference wetlands); however, most stem area measurements in natural sites are determined at breast height (basal area). Additionally, CSAG (or ESD) can be used to estimate total biomass for comparisons or calculation of carbon accumulation, another important ecosystem function (Chapter 3).

In conclusion, CSAG is easily measured in the field, easily calculated in the office, strongly related to biomass accumulation, related to other morphological measures, comparable to natural reference wetlands and should be considered as an additional EPS in Virginia. Inclusion of this metric will hopefully lead to better
evaluation of new and existing forested headwater CMS and ultimately more successful restorations/creations of this important ecosystem.
Literature Cited


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Virginia Department of Environmental Quality (VADEQ) (2010). *Mitigation Banking Instrument Template*. Template, Virginia Department of Environmental Quality, Richmond, VA.


### Tables

Table 5-1. Total biomass (aboveground and belowground) accumulation (Mg/ha) of all species/stocktype combinations across the 7-year study.

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
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<tr>
<td>Ambient</td>
<td>0.26</td>
<td>1.73</td>
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<td>18.49</td>
<td>38.25</td>
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<td>0.47</td>
<td>2.49</td>
<td>7.52</td>
<td>14.35</td>
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<td>28.81</td>
</tr>
<tr>
<td>Flooded</td>
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<td>0.37</td>
<td>0.19</td>
<td>0.30</td>
<td>0.55</td>
<td>0.42</td>
<td>0.65</td>
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</tbody>
</table>
Table 5-2. Total CSAG (m$^2$/ha) across the 7-year study.

<table>
<thead>
<tr>
<th></th>
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</tr>
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<td>Ambient</td>
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<td>12.0</td>
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<td>70.1</td>
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<tr>
<td>Flooded</td>
<td>1.6</td>
<td>3.7</td>
<td>2.2</td>
<td>3.2</td>
<td>5.2</td>
<td>4.7</td>
<td>6.4</td>
</tr>
</tbody>
</table>
Figure 5-1. Relationship between percentage survival and average biomass accumulated after 7 years for individual species/stocktype combinations. Points represent species/stocktype combinations. Line represents simple linear regression and shading represents 95% confidence interval.
Figure 5-2. Relationship between 5-yr average percentage change in height and average biomass after 5 years. Points represent species/stocktype combinations.
Figure 5-3. Relationship between canopy cover and average biomass after 7 years. Points represent species/stocktype combinations. Line represents linear regression.
Figure 5-4. The relationship between ESD and H after 7 years for primary species. Line represents linear regression.
Figure 5-5. The relationship between ESD (cm) and H (cm) after 7 years for secondary species. Line represents linear regression.
Figure 5-6. The relationship between ESD (cm) and CD (cm) after 7 years for primary species. Line represents linear regression.
Figure 5-7. The relationship between ESD (cm) and CD (cm) after 7 years for secondary. Line represents linear regression.
CHAPTER 6: ECONOMIC ANALYSIS AND OVERALL CONCLUSIONS
Abstract

Ecological restoration is a multibillion dollar industry and research focusing on the economics of restoration is needed to provide better prioritization of finite financial and ecological resources. Maximizing the ecological benefits of forested wetland restoration based on financial investments is necessary because of the costs required in restoring these systems ($98,842/ha to $192,742/ha). The purpose of this study was to investigate the amount of woody biomass of seven Mid-Atlantic wetland tree species (four early successional, three late successional) returned after 5 years based on initial investment. Trees were planted using three stocktypes (bare root, tubeling and 1-gallon container) across a hydrologic gradient to investigate the reduction in planting cost that could be achieved in restoring forested wetlands. The greatest biomass return on initial investment was achieved by *P. occidentalis* tubelings (39.05 kg/$1) in the least hydrologically stressed treatment. In the most stressful conditions (flooding above the root collar with herbaceous competition) *S. nigra* and *B. nigra* had the greatest biomass returns on initial investments (average 0.26 kg/$1 for all 3 stocktypes) and an initial density of 520 stems/ha is recommended for planting of these species. Of the species planted in this study, *S. nigra* and *B. nigra* are the best choices for maximizing biomass accumulation based on initial costs when restoring forested wetlands. In addition to these findings, overall conclusions of this dissertation are provided in this chapter.
Economic Analysis

Economics of restoration is a relatively new area of study that is becoming more widespread (Blignaut et al. 2014). Investigating restoration economics is necessary since restoration has become a multibillion dollar industry (Woodworth 2006). This field broadly encompasses ecosystem valuation, financing restoration, cost-benefit analysis of restoration practices, and economic/socioeconomic effects of restoration. Studying the economics of restoration can lead to better prioritization of finite resources (financial and ecological), which ultimately helps achieve restoration goals.

Since there is finite capital available for each forested wetland restoration project, managers must seek to maximize their ecological returns on their financial investments. However, few studies provided information on the methods that will restore ecosystems at the lowest cost (Robbins and Daniels 2012). Substantial financial investments are required when restoring forested wetlands, that vary substantially based on site specific conditions and goals (King and Bohlen 1994, 1995). Cost estimates are difficult to acquire because restoration work is primary performed by consultants who publish infrequently or view this information as proprietary (Holl and Howarth 2000, Robbins and Daniels 2012). Published total costs to restore 1 ha of freshwater forested wetland range from $98,842/ha to $192,742/ha (King and Bohlen 1994, 1995, Zentner et al. 2003, Daniels et al. 2005). These total costs represent many different aspects of the restoration process, including planning, permitting, materials, construction, maintenance, and monitoring (Zentner et al. 2003). Of this total cost, tree planting can represent a substantial proportion but can be offset by using volunteers to help plant (Zentener et al. 2003).
To recommend cost effective planting material for returning woody biomass to restored forested wetlands, biomass produced per dollar invested (standardized to 1 ha) was determined for the species/stocktype combinations used in this study using the following equation.

\[
\text{Return on investment (kg/$1) = } \frac{\text{total biomass produced after 5 years (kg/ha)}}{\text{initial investment ($/ha)}}
\]

These methods are similar to those applied by Kimball et al. (2015). This robust metric incorporates initial planting costs, survival, and biomass accumulation after 5 years and represents a return (biomass) on the initial investment (planting costs). Initial planting costs included purchase price for the material, installation cost and miscellaneous costs (Table 6-1). It is important to note that greater biomass per dollar does not always represent species/stocktype combinations that have greater biomass production. Greater biomass returns on initial investments with lower overall biomass accumulation can result from species/stocktype combinations that have very low initial planting costs and moderate biomass accumulation.

In AMB, the return on investment ranged from 0 kg/$1 (S. nigra BR had no survivors) to 39.05 kg/$1 (P. occidentalis TB) and the average was 5.51 kg/$1 (Table 6-2). There were many species/stocktypes combinations that would be economically sensible to plant in upland sites that have minimal herbaceous competition (11 combinations had >1 kg/$1). The species/stocktype combination with the greatest return on initial investment was P. occidentalis (TB and BR), followed by L. styraciflua BR and B. nigra (GAL and BR) (Table 6-2). The majority of the Quercus spp. (secondary successional species (SEC)) had lower returns on investment than primary successional species (PRI) because of their slow biomass accumulation rates (Chapter 4). However, Q.
*bicolor* (BR) had greater return on investment than several primary successional species, mainly due to the low initial cost (Table 6-1). The BR and TB stocktypes had greater returns on investment than the GAL for PRI. In comparison, the BR and GAL had greater returns than the TB for SEC (Table 6-2).

In SAT, the return on investment ranged from 0 kg/$1 (*P. occidentalis* BR had no surviving individuals) to 5.66 kg/$1 and the average was 1.67 kg/$1 (Table 6-2). Similar to AMB, there were many species/stocktype combinations that represent good returns on initial investments (10 combinations had >1 kg/$1). The species/stocktype with the greatest return on investment was *S. nigra* BR, followed by *L. styraciflua* (BR), *P. occidentalis* TB and *B. nigra* (BR, GAL, TB). The majority of SEC had lower returns on investment than PRI; however, *Q. bicolor* (BR) had greater return on investment than *L. styraciflua* TB and *S. nigra* GAL, mainly due to the low initial cost (Table 6-1). Similar to AMB, the BR and TB in SAT had greater returns on investment than the GAL for PRI, while the BR and GAL had greater returns than the TB for SEC (Table 6-2).

The average return on investment in FLD (0.08 kg/$1) was lower than AMB (5.51 kg/$1) and SAT (1.67 kg/$1) reflecting the stressful environmental conditions. The return on investment ranged from 0 kg/$1 (7 species/stocktype combinations had 1 or 0 survivors) to 1.08 kg/$1 (Table 6-2). *Salix nigra* BR was the only species/stocktype combination to have >1 kg/$1 return on investment and *S. nigra* TB and GAL were the 2nd and 3rd ranked species/stocktype combinations (Table 6-2). The majority of SEC had very low returns on investment and *Q. bicolor* BR and *Q. palustris* GAL were the only combinations with greater than 0.02 kg/$1. The BR and TB stocktypes had higher returns...
on investment than GAL for PRI, while the GAL had the greater returns than the BR and TB for SEC.

**Initial Planting Density**

The above return on investment metric was based on the initial density used in this study which may not be the density that is appropriate for planting saplings in restored wetlands. To recommend an initial planting density and subsequent planting costs, the stem cross-sectional area at groundline (CSAG) ecological performance standard (EPS) proposed in Chapter 5 (>5.2 m²/ha by year 5) was used as a target.

The initial density required to meet the CSAG EPS was determined for each species/stocktype combination within FLD. This initial density represents planting each combination exclusively and should be adjusted based on the number of species/stocktype combinations used in practice. Additionally, planting a mixture of species is recommended because of the increased ecological benefits associated with greater species diversity in restored wetlands (Allen 1997, Naeem 2006, Aerts and Honnay 2011). Greater biodiversity in a variety of ecosystems has also been shown to provide services that support human well-being (Palumbi et al. 2009). The recommended density was determined using the following equation:

\[
\text{Recommended density (stems/ha)} = \text{initial density (stems/ha)} \times \left( \frac{5.2 \text{ (m²/ha)}}{5\text{th year CSAG (m²/ha)}} \right)
\]

This calculation assumes that the survival and growth trajectories remain the same if planting density was increased.

Based on the results from FLD, the minimum initial densities recommended for *S. nigra* BR, GAL, TB, and *B. nigra* GAL (the top four species/stocktype combinations}
from the economic analysis) was 303, 371, 463, and 519 stems/ha respectively (Table 6-3). These are the initial densities required to meet the recommended CSAG EPS. Based on the average cost of these planting materials, this represents expenditures of approximately $4000/ha for planting and installation of these species/stocktype combinations. Due to slow growth and/or poor survival, minimum initial density recommended increases dramatically beyond the above recommended species/stocktypes. For example, initial density required to meet CSAG EPS for Q. palustris GAL (top recommended Quercus spp.) is 3967 stems/ha (Table 6-3). This increased density leads to a substantial increase in planting costs ($40,000/ha), which is not financially feasible.

**Overall Conclusions**

I provided recommendations in this dissertation regarding selection of species and stocktypes for planting in restored forested wetlands based on survival, morphological development, total biomass accumulated, biomass accumulation rates, and economic costs. Based on all of these factors, I recommend that in restored wetlands (which typically have stressful hydrologic and soil conditions) early successional species (particularly S. nigra and B. nigra) be planted at higher densities (520 stems/ha) than secondary successional species (particularly Q. bicolor and Q. palustris) which should be planted to ensure diverse forest development which mimics natural succession. However, the diversity of species selected for planting should reflect the diversity found in the wetland type that is being restored.

Less expensive stocktypes (BR and TB) should be used for primary species and BR and GAL stocktypes used for secondary species based on their biomass returns on
initial investment. However, larger stocktypes do have greater survival probabilities in stressful conditions and should be considered if funding allows. In afforestation and reforestation projects where hydrologic stress is not a concern, the smaller less expensive stocktypes could be used because they accumulated equivalent biomass for less initial costs than larger stocktypes.

My second recommendation is that the ecological performance standards for forested compensatory wetland mitigation sites in Virginia need to be re-evaluated by the responsible state agencies. I have provided an additional performance standard based on stem cross-sectional area at groundline that requires greater than $5.2 \, \text{m}^2/\text{ha}$ of woody stems be achieved by the 5th year following construction. I have demonstrated that this performance standard can better evaluate the ecological function of woody biomass accumulation in compensatory sites than the existing performance standards and show how this standard could be easily incorporated into the monitoring of these sites.

In conclusion, I hope that this dissertation will contribute to increasing the success of restoring forested headwater wetlands, which are very important to protecting and enhancing the health of our environment, and will contribute to the understanding of how these species respond to environmental stressors.
Literature Cited


Daniels, W. L., Perry, J. E., & Whittecar, R. G. (2005). *Effects of soil amendments and other practices upon the success of the Virginia Department of Transportation’s non-tidal wetland mitigation efforts.* Final Contract Report, Virginia Transportation Research Council, Charlottesville, VA.


Woodworth, P. (2006). What price ecological restoration? In putting a price tag on endangered species and degraded ecosystems, ecologists and economists have

<table>
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<th>Species</th>
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<th>Installation Cost ($/Tree)</th>
<th>Misc. Cost ($/Tree)</th>
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Table 6-1: Source of each species and stocktype and associated costs. Installation and miscellaneous costs were obtained from Wetland Studies and Solutions, Inc. and represent prices in 2012. Material price is based on 2008 purchase price. Miscellaneous costs include mulch, agriform fertilizer, shipping, and terrasorb. No mulch, fertilizer or terrasorb were used in this study, but these products are commonly used in practice.
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Table 6.2. Species/stocktype combinations return on investment ranked within each cell. No surviving individuals. **1 individual surviving.
Table 6-3. Initial densities required to meet 5.2 m²/ha CSAG EPS in FLD. ND represents species/stocktype combinations for which initial density was not determined due to 1 or 0 surviving individuals.

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* No surviving individuals
** 1 individual surviving
VITA

Herman Wesley Hudson III

Wes was born in Richmond, VA on January 26, 1985. After graduating from Varina High School in Henrico, VA in 2003, he went on to earn a B.S. in Biology (concentration in Ornamental Horticulture) from Christopher Newport University in 2008. He completed a M.S. in Environmental Science with Dr. Robert Atkinson at CNU in May 2010 focusing on natural tree colonization into post agricultural restored wetlands in Southeastern Virginia. He entered the Ph.D. program at the Virginia Institute of Marine Science, College of William & Mary under graduate advisor Dr. Jim Perry in the fall of 2010. He was a NSF GK-12 PERFECT Graduate Fellow during 2013-2014 and taught at the Chesapeake Bay Governor School. He will graduate in May 2016 with a Ph.D. in Marine Science.