12-2006

Flood Tolerance of Hardwood Bottomland Oak Seedlings

Jonathan Ray McCurry

Recommended Citation

McCurry, Jonathan Ray, "Flood Tolerance of Hardwood Bottomland Oak Seedlings. " Master's Thesis, University of Tennessee, 2006.
https://trace.tennessee.edu/utk_gradthes/9363

To the Graduate Council:

I am submitting herewith a thesis written by Jonathan Ray McCurry entitled "Flood Tolerance of Hardwood Bottomland Oak Seedlings." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Matthew J. Gray, Major Professor

We have read this thesis and recommend its acceptance:

Jennifer A. Franklin, Ray C. Albright

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a thesis written by Jonathan Ray McCurry entitled "Flood Tolerance of Hardwood Bottomland Oak Seedlings." I have examined the final paper copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Matthew J. Gray, Major Professor

We have read this thesis
and recommend it acceptance:

J. Franklin

Jennifer A. Franklin

Ray C. Albright

Ray C. Albright

Accepted for the Council:

Linda R. Painter

Interim Dean of Graduate Studies

Flood Tolerance of Hardwood Bottomland Oak Seedlings

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Jonathan Ray McCurry
December 2006

DEDICATION

To my parents for all of the wonderful opportunities they have given me in life. They have always been there for me and supported me no matter what path I chose. Thank you mom and dad, I love you.

ACKNOWLEDGMENTS

This study was funded by the Department of Forestry, Wildlife and Fisheries and the West Tennessee Research and Education Center (WTREC) of the University of Tennessee   Funds for seedlings were provided by the Natural Resources Conservation Service through a Conservation Reserve Program agreement with WTREC under the Forested Riparian Buffer Practice. I especially thank Dr Bob Hayes, Gordon Percell, and Ronnie Staggs at WTREC for study assistance and guidance. I also would like to thank Dr. David Mercker for conceiving the sampling design and playing an integral role in implementing my study. Gates for the water control structures were provided by the Tennessee Wildlife and Resources Agency, and special thanks to Ed Harsson for orchestrating acquisition. Thank you to Robert Wheat and John Taylor of U.S. Fish and Wildlife Service at Tennessee National Wildlife Refuge for loaning me one of their gator pumps each spring to flood my impoundments

I would also like to thank my committee members, Drs. Ray Albright and Jennifer Franklin for their guidance in forest hydrology and seedling physiology, respectively. Also, I especially would like to thank Dr. Franklin for letting me use her tree physiology lab, where I spent many hours processing samples

Special thanks to Dr. Matthew Gray for his guidance as my major professor. His input and drive were paramount in the completion of my thesis. I am honored to have had the opportunity to work under him for the past 2 ½ years, and it has been an exciting and memorable learning experience   Thanks again, Matt.

Special thanks to Zach Steele, Drew Hardin, Liz Burton, and John Rizza for spending many hours in the field with me measuring seedlings. I would also like to thank

the students in the Department of Forestry, Wildlife and Fisheries, and other volunteers and technicians that helped me collect data. Lastly, I would like to thank Ashley Speck, John Mulhouse and John Laux for providing initial editorial comments on my thesis.

ABSTRACT

The afforestation of hardwood bottomlands is an expanding conservation practice in the southeastern United States. Understanding relative flood tolerance of hardwood bottomland seedlings is fundamental to ensuring restoration success. Thus, I examined the combined effects of 3 early growing-season flood duration treatments (0, 15, and 30 days) and the natural flood regime on willow (*Quercus phellos*, WIO), Nuttall (*Q nuttallii*, NTO) and overcup (*Q lyrata*, OCO) oak seedlings in a 6-ha replanted west Tennessee bottomland. Seedlings (*n* = 5,003) were planted from January–March 2004 in a randomized design. All seedlings were uniquely tagged, survival assessed, and height and diameter measured for each individual in fall 2004 for pre-treatment baseline data. In 2005 and 2006, I applied flood treatments after seedling bud break initiated, which was mid-April each year. Survival was measured in July and fall 2005 and July 2006 Overall survival was 96%, 89%, and 84% for OCO, NTO, and WIO, respectively. Survival of NTO and WIO was greatest in control impoundments that did not experience prescribed early growing-season flooding. I measured height and diameter in fall 2004 and 2005, and calculated second growing-season growth as the difference between 2004 and 2005 measurements. All species exhibited the least growth when subjected to the 30-day treatment. Interestingly, growth of NTO and WIO were greater in the 15-day treatment than in the control treatment, which suggests a possible benefit of short duration early growing-season flooding. Seedlings of each species were collected in May 2005 and 2006 (*n* = 36/species/year), and shoot and root biomass, root length, and root sugar and starch concentrations measured. Seedling transpiration was measured for 36 seedlings/species in July 2005 and 72 seedlings/species in July 2006; soil respiration was measured for the same seedlings in July 2005. In general, all physiological variables decreased as flood duration increased. My results suggest that early growing-season flooding may negatively impact survival, growth and physiology of bottomland oak seedlings. Furthermore, I ranked relative flood tolerance given the magnitude of seedling response variables, and suggest that flood tolerance decreases from OCO to NTO to WIO. Managers should consider planting seedlings in a candidate bottomland based on species-specific flood tolerances. Inasmuch as elevation and flooding depth and duration are correlated, I recommend that natural resource practitioners manage low elevations in bottomlands that flood frequently as moist-soil wetlands, plant NTO at medium elevations, plant WIO with NTO at medium-high elevations, and plant WIO exclusively at higher elevations that flood infrequently to increase the likelihood of restoration success. Although OCO seedlings are very flood tolerant and likely could withstand frequent and deep flooding, I do not recommend planting OCO at lower bottomland elevations, because their acorns are not preferred by waterfowl and the value of OCO timber is low.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Hardwood bottomland ecosystems are forested wetlands adjacent to riverine systems (Mitsch and Gosselink 2000). These wetlands are important for timber production and provide habitat for various fish and wildlife species (Langdon et al. 1981, Wharton et al. 1981). Forested wetlands are critical areas for floodwater storage, nutrient cycling, and they improve water quality by naturally filtering sediments and contaminants from runoff. Hardwood bottomland forests also help stabilize river channels and stream banks and reduce erosion (Gosselink and Lee 1989) Annual profits from timber in hardwood bottomlands in the United States are $3–8 billion (Gosselink and Lee 1989).

Approximately 30% of the hardwood bottomlands in the conterminous United States have been drained or deforested (Turner et al. 1981) Within the lower Mississippi Alluvial Valley (LMAV), only 25% of the original hardwood bottomland acreage remains (Turner et al. 1981). Tennessee has lost almost 60% of its wetlands, most of which were hardwood bottomlands (Turner et al. 1981) Drainage of forested and other wetlands was encouraged (via the Swamp Lands Acts) from the late 1800s through the 1970s for agriculture and other human land-use developments (MacDonald et al. 1979).

The Clean Water Act of 1975 authorized protection of hardwood bottomlands and other wetlands. In addition, the Swampbuster Provision of the 1985 Food Security Act disqualified farmers from receiving federal subsidies if wetland areas were cultivated (Gosselink and Lee 1989). This legislation, along with the creation of federal conservation programs (e g., Conservation Reserve Program, CRP; Wetland Reserve Program, WRP), has decreased the rate of wetland loss and increased interest in hardwood bottomland restoration (Stanturf et al. 2001). These programs pay landowners to restore erodible lands and wetlands to native vegetation

In Tennessee, most wetland restoration efforts have focused on forested wetlands. For example, 89 8% (3,605 ha) of wetlands restored by the National Resources Conservation Service (NRCS) in Tennessee are forested. Similarly, Tennessee Wildlife Resource Agency (TWRA) has acquired almost 21,022 ha of wetlands via the Tennessee Wetland Acquisition Act, most of which are hardwood bottomlands (J Hopper, TWRA, *unpublished data*). Often these areas are replanted with oak seedlings (e.g., around 70% of NRCS easements) in an attempt to restore native vegetation and animal communities. Interestingly though, very little information exists on the ideal oak species to plant given the current hydrology of a candidate restoration site. Some species may be more flood tolerant, thus ideal if flooding during the growing season is extended due to river channelization, sedimentation, or lock and dam structures (King et al. 1998).

Flooding occurs naturally in hardwood bottomlands during winter and for short durations in spring (Mitsch and Gosselink 2000) However, human modifications of landscapes (e.g., river channelization, agricultural fields, and urbanization) can increase sheet flow runoff, soil erosion, and sediment deposition in bottomlands, and correspondingly alter hydrology. Changes in flooding duration and depth may induce stress on plants in bottomlands (Cairns et al. 1981) Inasmuch as most river systems in the southeastern United States have been altered, it is important to understand the relative flood tolerance of bottomland hardwood species. Seedlings are the natural regeneration unit in a forest, and they are commonly planted in forest wetland restoration projects (Schoenholtz et al. 2001). Hence, a basic understanding of the influences of flooding on seedling physiology, growth and survival is paramount to restoration success (Kozlowski 2002).

Flooding stresses plants by reducing oxygen in the soil. When soils are flooded, oxygen is quickly used by plant roots and microorganisms, eventually resulting in an anoxic state (Kozlowski 1984). Flooding also increases soil temperature and pH, decreases redox potential and electrical conductance, and causes chemical transformations that can result in the accumulation of phytotoxic chemicals (Ponnamperuma 1984). Together these variables can inhibit metabolic processes and cause necrosis, ultimately reducing seedling growth and survival (Kozlwoski 1984, 2002).

Woody plants that are stressed from flooding may exhibit reduced shoot and root growth, leaf chlorosis, defoliation, reduced leaf size and growth, reduced mycorrhizae, epicormic sprouting, and crown dieback in trees (Kozlowski 1984). Flooding causes stomata to close thus reduces transpiration, which triggers a series of metabolic steps that can decrease growth and survival (Kozlowski and Pallardy 1984) Reductions in photosynthesis, carbohydrate synthesis and translocation, and ion absorption also occur following flooding, and can further negatively influence plants that are not adapted to cope with decreases in oxygen (Kozlowski and Pallardy 1984).

An array of morphological and physiological adaptations allow bottomland plants to survive periodic flooding including formation of hypertrophied lenticels, development of aerenchyma tissues, root regeneration, redirection of protein synthesis, changes in utilization of minerals, alterations in amounts and balances of growth hormones, and metabolic adaptations (e.g., stimulation of glycolysis, production of ethanol, and synthesis of adenosine triphosphate (Kozlowski 2002). These changes in morphology facilitate oxygen uptake, oxygen diffusion, toxic compound release, and glucose maintenance, which increase plant survival during soil inundation (Kozlowski and Pallardy 1984 and Kozlowski 2002).

Oaks commonly occur in bottomlands, and many can withstand periodic flooding (Whitlow and Harris 1979). In general, they also have a high timber value and produce mast for wildlife, which makes them particularly attractive candidates for bottomland restoration projects (Langdon et al 1981, Hook 1984, Young et al. 1995). Three oak species that are found in Southeast bottomlands and used in restoration are: willow (*Quercus phellos*, WIO), Nuttall (*Q nuttallii*, NTO) and overcup (*Q lyrata*, OCO).

Overcup oak occurs in bottomlands extending from Delaware and Maryland south to Georgia and west to eastern Texas (Solomon 1990). Overcup oak is common in the Mississippi Alluvial Valley (MAV), and is predominately found on alluvial floodplains with poorly drained clay soils (Solomon 1990). It generally grows in warm climates that receive 1140 to 1520 mm of precipitation per year and have annual temperatures ranging from 7 to 28 C. Overcup oak is considered a very flood-tolerant species (Hook 1984). As a mature tree, it can survive deep flooding for >1 year (Whitlow and Harris 1979). Overcup oak is most commonly associated with willow oak, Nuttall oak, water hickory (*Carya aquatica*), American elm (*Ulmus americana*), cedar elm (*Ulmus crassifolia*), green ash (*Fraxinus pennsylvanica*), common persimmon (*Diospyros virginiana*), and red maple (*Acer rubrum*) (Solomon 1990). Despite its flood tolerance, OCO often is considered undesirable in bottomlands by natural resource managers, because its timber is relatively low value and it has large acorns, which are not preferred by waterfowl (Young et al. 1995, Barras et al. 1996).

Nuttall oaks have a smaller native range than OCO, constricted primarily to the MAV and the Gulf Coastal Plain (Filer 1990). It grows best in alluvial bottomlands of the Mississippi River and its primary tributaries (Filer 1990). Nuttall oak is found in areas with an average annual precipitation between 1270 – 1650 mm and annual temperatures ranging from 10 to 27 C (Filer 1990) Nuttall oak is often associated with sweetgum (*Liquidambar styraciflua*), willow (*Salix* spp.), laurel and bur oak (*Quercus laurifolia* and *macrocarpa*), red and silver maple (*Acer rubrum* and *saccharinum*), black willow (*Salix nigra*), cedar elm (*Ulmus crassifolia*), and persimmon (*Diospyros virginiana*) (Filer 1990). Nuttall oak is considered a moderate to very flood-tolerant species (Hook 1984), and studies have shown that mature NTO can tolerate 2 years of flooding (Broadfoot and Williston 1973). Whitlow and Harris (1979) showed that Nuttall oak seedlings could survive 2 months of flooding. Nuttall oak timber also is valuable and mature trees produce moderately-sized acorns each year, making this species a good candidate for bottomland restoration (Filer 1990).

The range of WIO extends from New Jersey and Pennsylvania south along coastal plain and through most of the Southeast (Schlaegel 1990). The climate where it is found can be characterized with an average annual precipitation ranging from 1020 to 1520 mm and annual temperatures ranging from 10 to 27 C (Schlaegel 1990) Willow oak is most commonly found on higher elevations within a bottomland on alluvial soils, and generally does not occur in the upland. It grows best in loamy or silt soils without clay pans (Schlaegel 1990) Willow oak is commonly associated with water oak (*Quercus* *nigra*), red maple (*Acer rubrum*), cedar elm (*Ulmus crassifolia*), eastern cottonwood (*Populus deltoides*), honeylocust (*Gleditsia triacanthos*), and persimmon (*Diospyros virginiana*) (Schlaegel 1990). Willow oak generally is considered a moderately flood-tolerant species (Hook 1984). As a mature tree, it is able to survive flooding or saturated soils for 30 consecutive days during the growing season (Broadfoot and Williston 1973). Similar to NTO, WIO is a commercially important timber species and is important to wildlife due to its large mast production and small acorns, which are easily ingested (Schlaegel 1990, Barras et al. 1996).

Greenhouse and uncontrolled field studies in forested wetlands have provided evidence that flood tolerance may differ among bottomland oak seedlings, and increase in the order of WIO to NTO to OCO (Broadfoot and Williston 1973, Hook 1984, Gray and Kaminski 2005, McCurry et al. 2006) However, no controlled studies have been conducted examining seedlings for these species under different growing-season flood regimes for an actual bottomland restoration endeavor. Approximately 24 ha of a previously farmed hardwood bottomland at the West Tennessee Research and Education Center (WTREC; Jackson, TN, USA) have been replanted in seedlings as part of a restoration effort associated with the Forested Riparian Buffer Practice of CRP. About ¼ of this acreage is planted exclusively in oak seedlings of these 3 species and enclosed by levees with water control structures forming 6 impoundments. Water in each impoundment can be independently manipulated, thus creating a unique opportunity to experimentally examine WIO, NTO, and OCO seedling responses under different prescribed early growing-season flood treatments. Bottomland elevation also differs among these impoundments (McCurry et al. 2006), allowing the influences of natural flooding and elevation on seedling responses to be explored. Based on previous research, seedling response variables that can be influenced by flooding include survival, growth, height, diameter, shoot and root biomass, root length, non-structural carbohydrates, leaf transpiration, and soil respiration. Furthermore, the state of bud activity can influence the ability of a seedling to endure stress associated with flooding. It is believed that dormant seedlings are less affected by flooding than seedlings which have experienced bud break (Hall and Smith 1955). Given the aforementioned, I performed the following study.

CHAPTER II

RESEARCH DIRECTION

Goal

My goal was to determine effects of early growing-season flooding on seedlings of 3 oak species commonly used in hardwood bottomland restoration.

Objectives

1. Quantify and compare seedling survival and growth among 3 early growing-season flood treatments for each species,
2. Quantify and compare soil respiration and seedling leaf transpiration during summer among flood treatments for each species;
3. Quantify and compare root carbohydrates, root and shoot biomass, and root length among flood treatments for each species; and,
4. Based on seedling responses in 1–3, make decisions on relative flood tolerance of these 3 oak species, and provide planting recommendations for candidate bottomland restoration sites.

Hypotheses

Based on research performed in greenhouses, which suggests extended flooding during the growing season influences physiology of most bottomland oak seedlings,

H_1: I hypothesized that survival and growth will differ among flood duration treatments, and differences in these responses will exist among species and be related to their flood tolerance

H_2: I hypothesized that soil respiration and leaf transpiration will differ among flood duration treatments, and differences in these responses will exist among species.

H_3: I hypothesized that carbohydrate resources, shoot and root biomass, and root length will differ among flood duration treatments and differences in these responses will exist among species and be related to their flood tolerance.

H_4: I hypothesized that flood tolerance will decrease in the order of overcup oak, Nuttall oak, and willow oak.

H_0: The above trends did not exist.

Nuisance Variables

McCurry et al. (2006) documented that elevation was an important predictor of first-year growth of oak seedlings in this bottomland. Given that elevation differed among impoundments, I considered bottomland elevation a nuisance variable of treatment effects in my study. The state of bud break also can influence growth, thus I also considered it a nuisance variable of treatment effects in my study.

CHAPTER III

STUDY AREA

I conducted my study in a 6-ha bottomland at the University of Tennessee West Tennessee Research and Education Center (WTREC) located in Jackson, Tennessee (35° 37′ 37″ N, 88° 51′ 36″ W, 120 m mean elevation). The WTREC bottomland contained six 1-ha impoundments (numbered 2–7) with 1-m high levees that contained drop-board water control structures at their lower end and connected to a drainage channel (Figures 1–2). The impoundments differed predictably in elevation, with the gradient sloping upward from 2 to 7 and northeast to southwest. Existing surface and groundwater hydrology was a consequence of localized rainfall, runoff, and water levels in the channelized South Fork of the Forked Deer River. At high water levels, the river can back into the drainage canal that extends into the bottomland, and flow through the water control structures into the impoundments. Water flow into the bottomland from the river can be stopped (except for groundwater) by placing gates in the water control structures or by closing screw gates in the canal. When these gates are closed, hydrology in the bottomland is predominately a result of surface runoff from the upland, rainfall and groundwater flow. A permanent pump also exists in the canal and can be used to drain the bottomland if necessary (Figures 1–2). The predominant soil type is an uneroded to slightly eroded Waverly silt loam with a level slope (0–2%). A small finger of Lalaya loamy sand, overwashed phase, with identical slope and erosion characteristics extended into the highest elevations of impoundments 4 and 5 (Sease and Springer 1957).

Impoundments can flood during natural rain events or by pumping water from the canal using a towable PTO-driven pump (e.g., Gator® pump). Water can be retained in

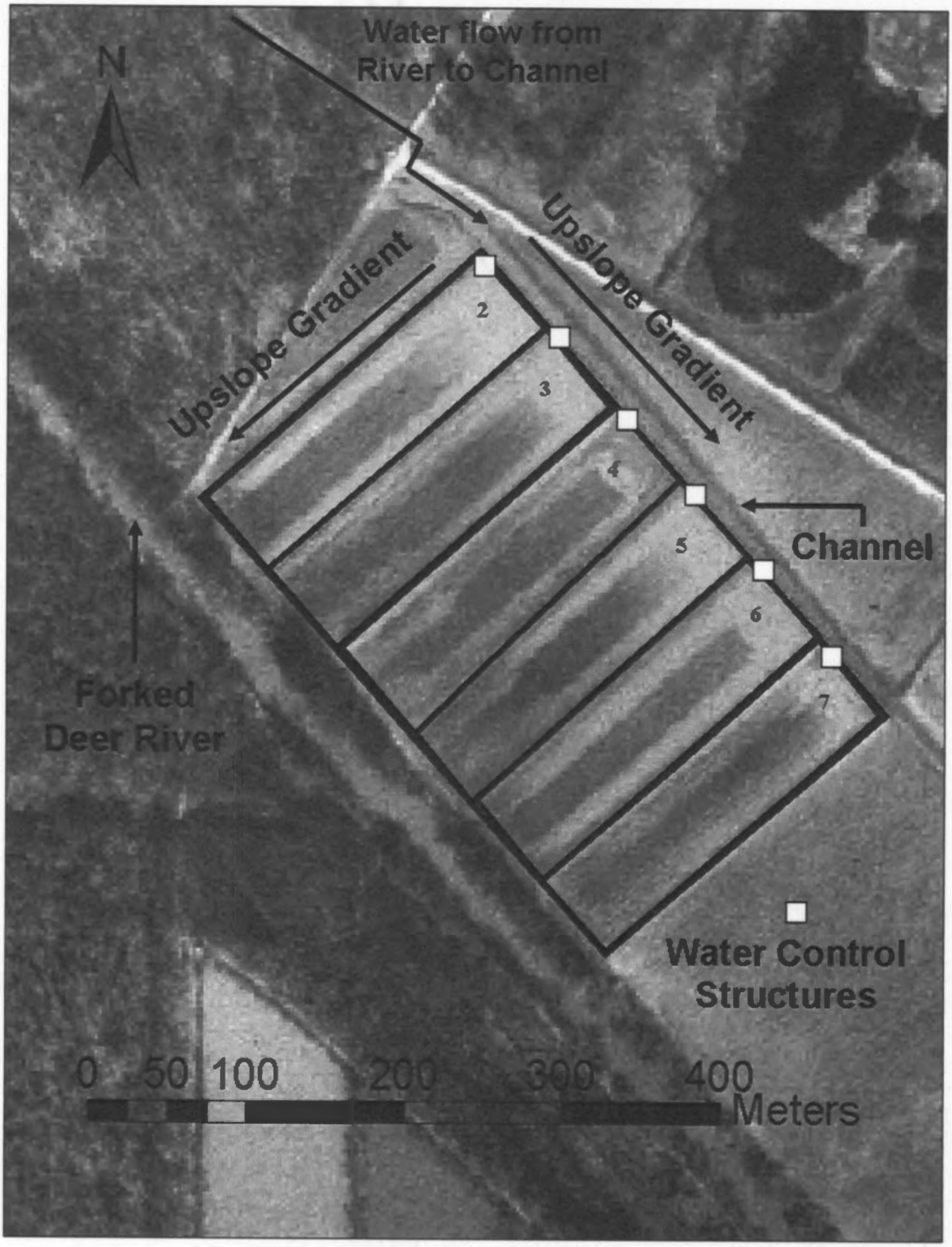


Figure 1. Impoundments 2–7 at the West Tennessee Research and Education Center, Jackson, Tennessee, USA.

Figure 2. Impoundments, water control structures, canal, and permanent pump at the West Tennessee Research and Education Center, Jackson, Tennessee, USA.

impoundments by placing gates in the water control structures. Natural flooding of the bottomland occurs on average 10 times per year, but usually ≤ 2 times per year during the growing season (McCurry et al. 2006). Flooding depth can occasionally be substantial (e g., 2 m) and overtop impoundment levees. Water typically drains quickly from the bottomland after flood events. Surface water is present rarely >10 days continuously during the growing season (McCurry et al. 2006)

CHAPTER IV

METHODS

Seedlings

Seedlings of Nuttall oak (*Quercus nuttallii* Palmer, NTO), overcup oak (*Q. lyrata* Walt., OCO), and willow oak (*Q. phellos* L , WIO) seedlings were planted in monospecific plots with 3 × 3 m spacing in six 36 × 36 m elevation blocks per impoundment (Figure 3). Impoundments were experimentally divided into low and high ends to randomly assign species to elevation blocks. Within each impoundment and end, seedling species were randomly assigned without replacement to each elevation block, thereby ensuring that a species was not clustered at low or high elevations. Approximately 144 seedlings per elevation block were planted, although portions of some blocks in impoundments 5, 6, and 7 could not be planted because of a gas line. Also, water oak (*Q nigra*) was planted instead of overcup oak in impoundments 6 and 7, but was not included in the analyses, because it had replication in only one treatment (Figure 3).

All seedlings (1–0 stock) were acquired from the Tennessee Division of Forestry State Nursery, and maintained at 4 C in a walk-in cooler at WTREC until planted. Nuttall oak and WIO seedlings were grown at the state nursery in Pinson, TN, and OCO was grown at the state nursery in Dellanow, TN. Overcup and WIO acorns were purchased from Mid-South Forest Seed located in Searcy, AR, and NTO acorns were purchased from Forest Seed Products located in Bells, TN.

To standardize planting conditions, 1-m width rows were sub-soiled at 36 cm depth along planting locations. Seedlings were planted during January – March 2004

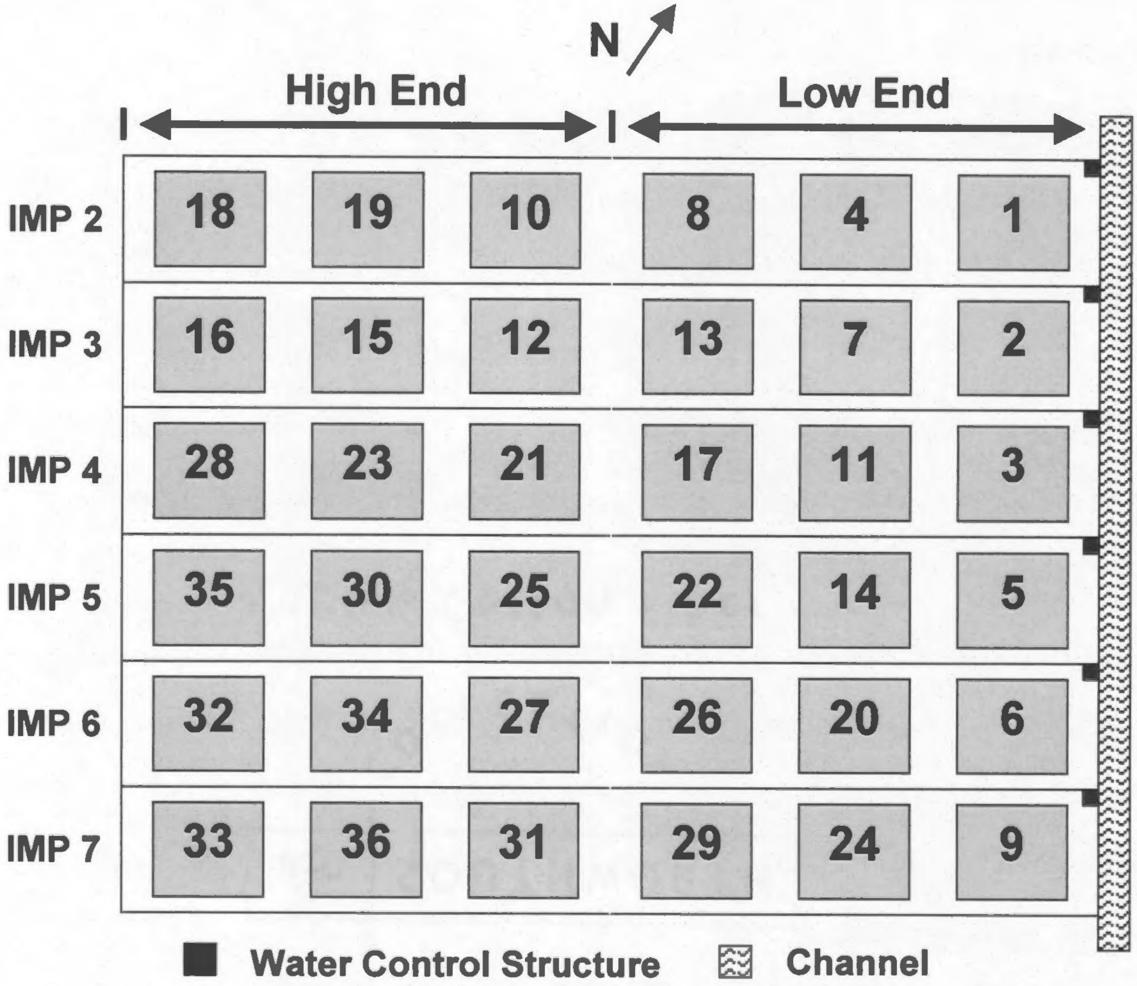


Figure 3. Planting and elevation schematic of hardwood bottomland seedlings in 6 impoundments (IMP 2–7) in a west Tennessee bottomland. Species were randomly assigned to numbered elevation blocks within impoundments and ends. Elevation increased with ordinal ranking of blocks. Willow oak (*Quercus phellos*) were planted in blocks 2, 6, 8, 9, 12, 14, 17, 18, 23, 25, 34, and 36. Nuttall oak (*Q. nuttallii*) were planted in blocks 1, 3, 7, 15, 19, 20, 21, 22, 29, 31, 32, and 35. Overcup oak (*Q. lyrata*) were planted in blocks 4, 5, 10, 11, 13, 16, 28, and 30.

using a Whitfield® Tree Planter (R. A. Whitfield Manufacturing, Mableton, Georgia), which is designed specifically for planting hardwood seedlings. At the time of planting, all seedlings within species appeared in similar physical condition, and individuals of each species were planted randomly within elevation blocks. Due to this designed randomization, I assumed that all seedling response variables (discussed on pages 22-31) were not correlated with elevation and no differences existed in these variables among impoundments (i.e., treatments) at the time of planting. To limit potential effects of herbaceous vegetation on seedling responses, herbicide was applied twice per year uniformly around seedlings during my study Oust® XP (sulfometuron methyl, DuPont, Wilmington, Delaware) was sprayed at a concentration of 91.4 ml per 112.2 L of water per ha prior to bud break in March 2004, 2005 and 2006. Roundup® (glyphosate, Monsanto, St. Louis, Missouri) also was applied in June 2004.

Flood Treatments and Procedures

Pairs of impoundments were assigned the following early growing-season flood treatments: control (0 days), 15-day, and 30-day. These treatments corresponded to flood duration in controlled greenhouse experiments (e.g., Hosner and Boyce 1962). Impoundments 2 and 3 = 30 days, 4 and 5 = 15 days, and 6 and 7 = 0 days (Figure 1). Flooding constituted surface water presence not inundated seedlings.

Impoundments were flooded starting 18 April 2005 and 17 April 2006, after seedlings initiated bud break. Bud break was monitored by Gordon Percell, David Mercker, and me. Prior to flooding, relative bud activity (dormant=0, bud swell=1, bud break=2, and leafed out=3) were recorded for every seedling. The intention was to begin flooding after >75% of seedlings initiated bud break; however, the 2005 survey indicated that 17% had bud activity (i.e., activity > 1). In 2006, 70% of seedlings had bud activity Immediately following completion of the bud survey, flooding was initiated. Water was pumped using a Gator® pump from the canal into impoundments 2–5 Water depth was maintained by placing gates in the water control structures for the treatment duration. Gates were not placed in the water control structures for impoundments 6 and 7, because they served as experimental controls. After 15 and 30 days of flooding (04 and 20 May 2005 and 03 and 19 May 2006), gates were removed from impoundments 4–5 and 2–3, respectively. As the gates were removed, water was pumped from the canal using the permanent pump to facilitate draining and prevent water from backing into other impoundments. After impoundments were drained, boards were not replaced and screw gates in the canal remained open to allow all impoundments to experience unrestricted hydrology.

Hydrology

To measure surface and groundwater hydrology in impoundments during natural and prescribed flooding, I installed water-level recorders (Infinities USA, Inc) and PVC wells in the center of 12 elevation blocks, and programmed them to measure water depths twice daily (Figure 4). Six wells were installed fall 2004 and 6 additional wells were installed spring 2005, for a total of 2 wells per impoundment, with 4 wells per treatment. Flooding frequency, depth and duration were calculated by averaging readings from the 4 wells in each treatment.

Flooding in the 30-day treatment impoundments occurred 12 75 times from 17 April 2005 – 9 July 2006 for 103.3 days with a mean depth of 28.21 cm (Table 1, Figure 5). In the 15-day impoundments, flooding occurred 12.5 times during the same time

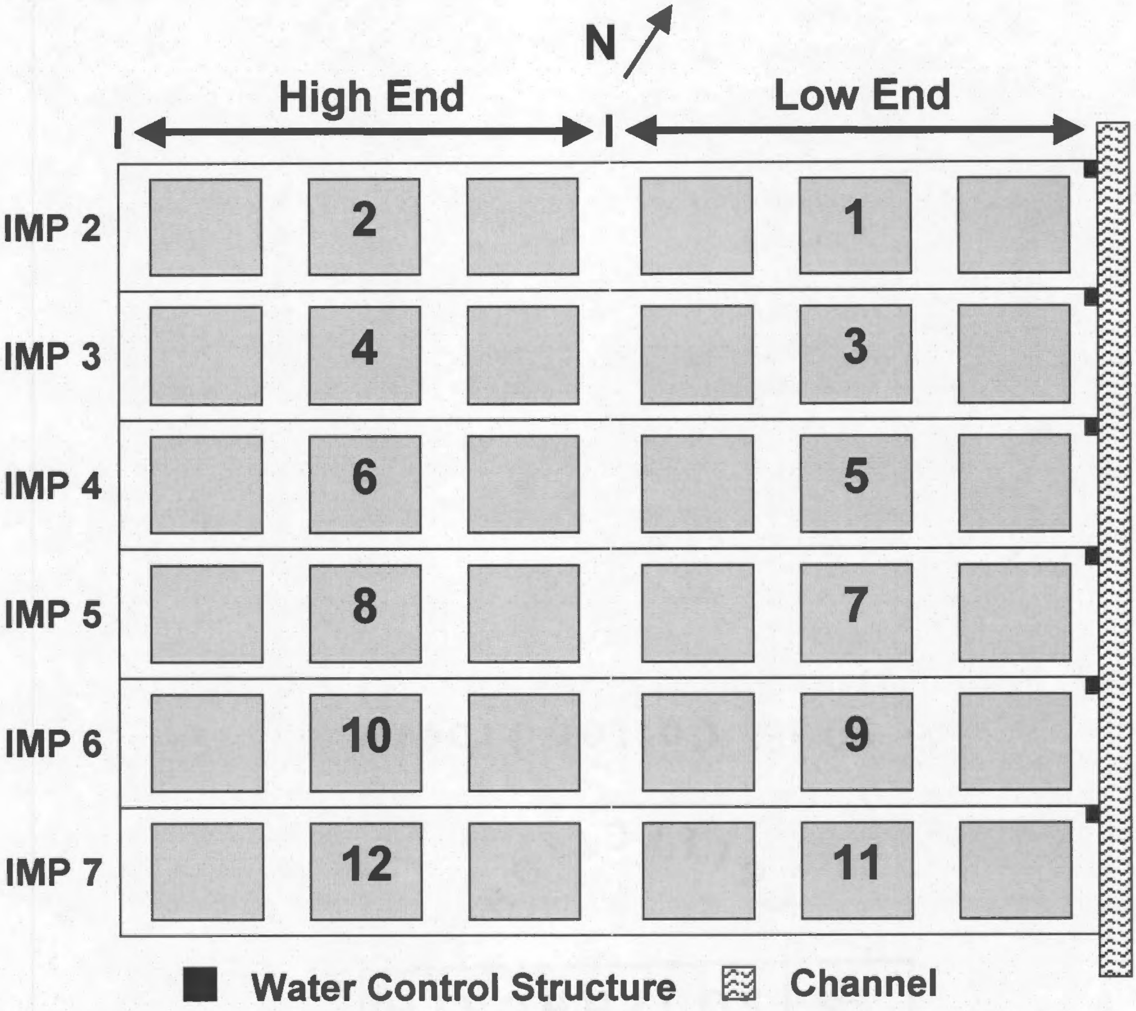


Figure 4. Locations of water-level meters and PVC wells in 6 impoundments (IMP 2–7) in a replanted west Tennessee, USA, bottomland.

Table 1. Flooding duration, frequency, and depth in a replanted west Tennessee, USA, bottomland, 2005 and 2006.

Treatment[1]	Flooding Period[2]	Duration (d)		Frequency		Depth (cm)	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Control	Treatment 2005	0	0	0	0	0	0
	Treatment 2006	0	0	0	0	0	0
	Non-treatment	22.63	1.71	6.00	0.71	23.58	1.07
	Total	23.50	1.74	6.50	0.65	23.05	1.05
15-day	Treatment 2005	14.9	0.13	1.00	0.00	21.74	0.59
	Treatment 2006	15.0	0.35	1.00	0.00	21.62	0.79
	Non-treatment	47.63	3.21	10.50	0.50	36.84	1.28
	Total	77.38	3.49	12.50	0.50	31.04	0.86
30-day	Treatment 2005	26.3	2.37	1.00	0.00	22.09	0.79
	Treatment 2006	23.13	4.51	1.00	0.00	20.13	0.77
	Non-treatment	54.0	9.35	10.75	0.63	34.60	1.22
	Total	103.3	14.56	12.75	0.63	28.21	0.73

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Flooding periods when treatments were applied were 18 April – 20 May 2005 (Treatment 2005) and 17 April – 19 May 2006 (Treatment 2006), when treatments were not applied were 21 May 2005 – 18 April 2006 and 20 May – 09 July 2006 (Non-treatment), and for the entire study period was 17 April 2005 – 09 July 2006 (Total).

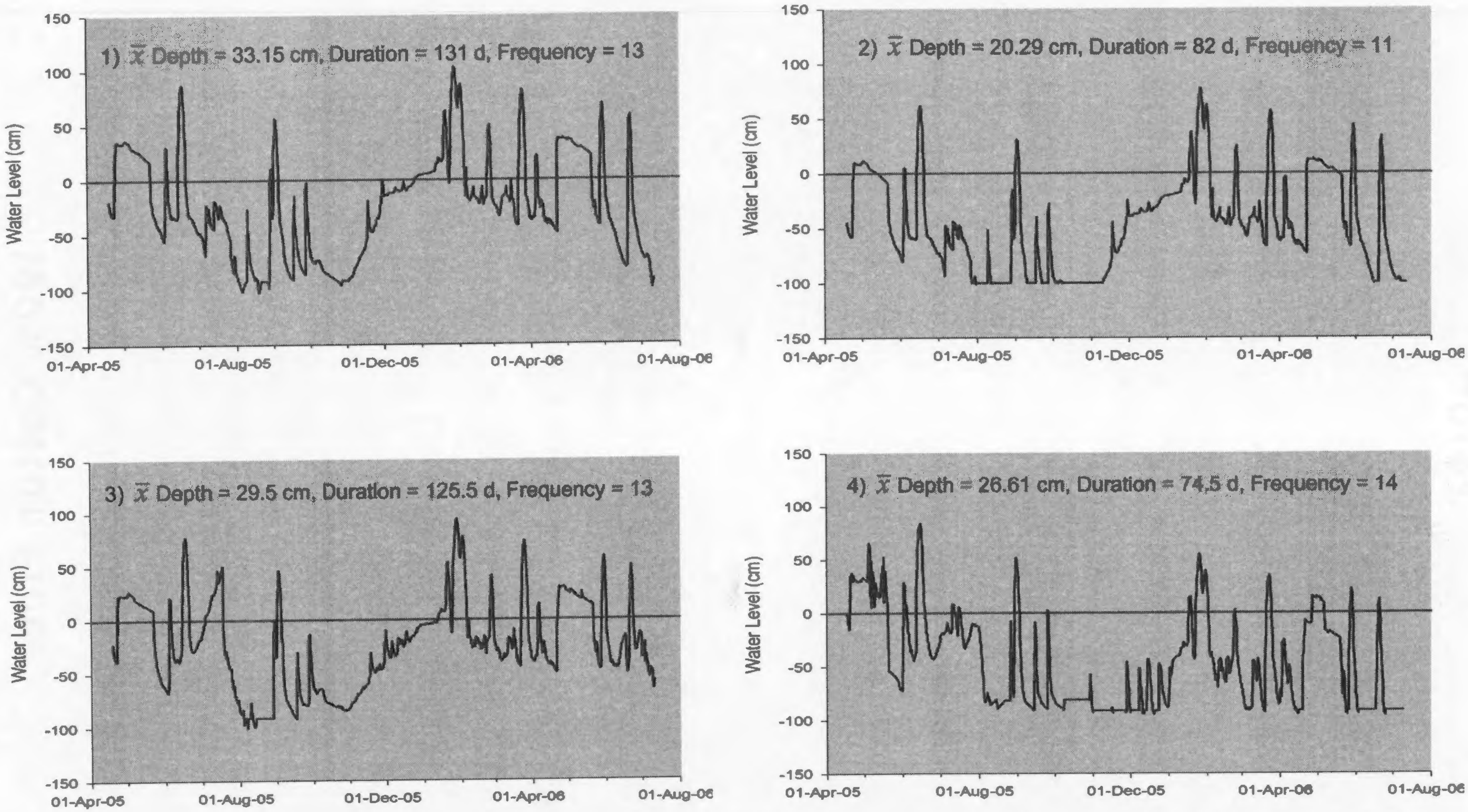


Figure 5. Hydrographs from water meters (1–4) in the 30-day treatment impoundments 2 (meters 1–2) and 3 (meters 3–4) in a replanted west Tennessee, USA, bottomland, 17 April 2005 – 9 July 2006.

period for 77.4 days with mean depth of 31.04 cm (Figure 6, Table 1). In the control impoundments, flooding occurred 6.5 times for 23.5 days with a mean depth of 23 05 cm (Figure 7, Table 1). Natural flooding of impoundments occurred 6–11 times during the non-treatment period with durations ranging from 1–20 days (Figure 8).

Seedling Sampling

Collection of pre-treatment seedling data began on 13 October 2004 after the first growing season. All seedlings were marked individually with numbered metal tags (*n* = 5,003, Figure 9). Survival, height and root-collar diameter also were measured for each seedling Survival was assessed in October 2004 and 2005, and July 2005 and 2006. A seedling was considered dead if leaves were not present and its cambium was not green (determined by scraping a small section of the bark). Seedling height and diameter was measured in October 2004 and 2005. Seedling height was measured to the nearest 0.5 cm from the ground to the terminal bud using a meter stick Root-collar diameter was measured to the nearest 0 5 mm at ground level using calipers.

Seedling transpiration was measured from 6–10 July 2005 and 2006 Soil respiration was measured at the same time except only during July 2005, because no significant trends were detected in 2005, and I wanted to increase the sample size for seedling transpiration in 2006. I measured seedling transpiration for and soil respiration associated with 96 randomly selected seedlings (*n* = 3 individuals per species per elevation block) in 2005. During 2006, I measured transpiration for 192 randomly selected seedlings (*n* = 6 individuals per species per elevation block). Transpiration rates were measured in mornings (before 1000 hrs) using a steady state porometer (LI-1600, Licor Inc , Lincoln, NE) Soil respiration was measured between 1000 – 1400 hrs *in situ*

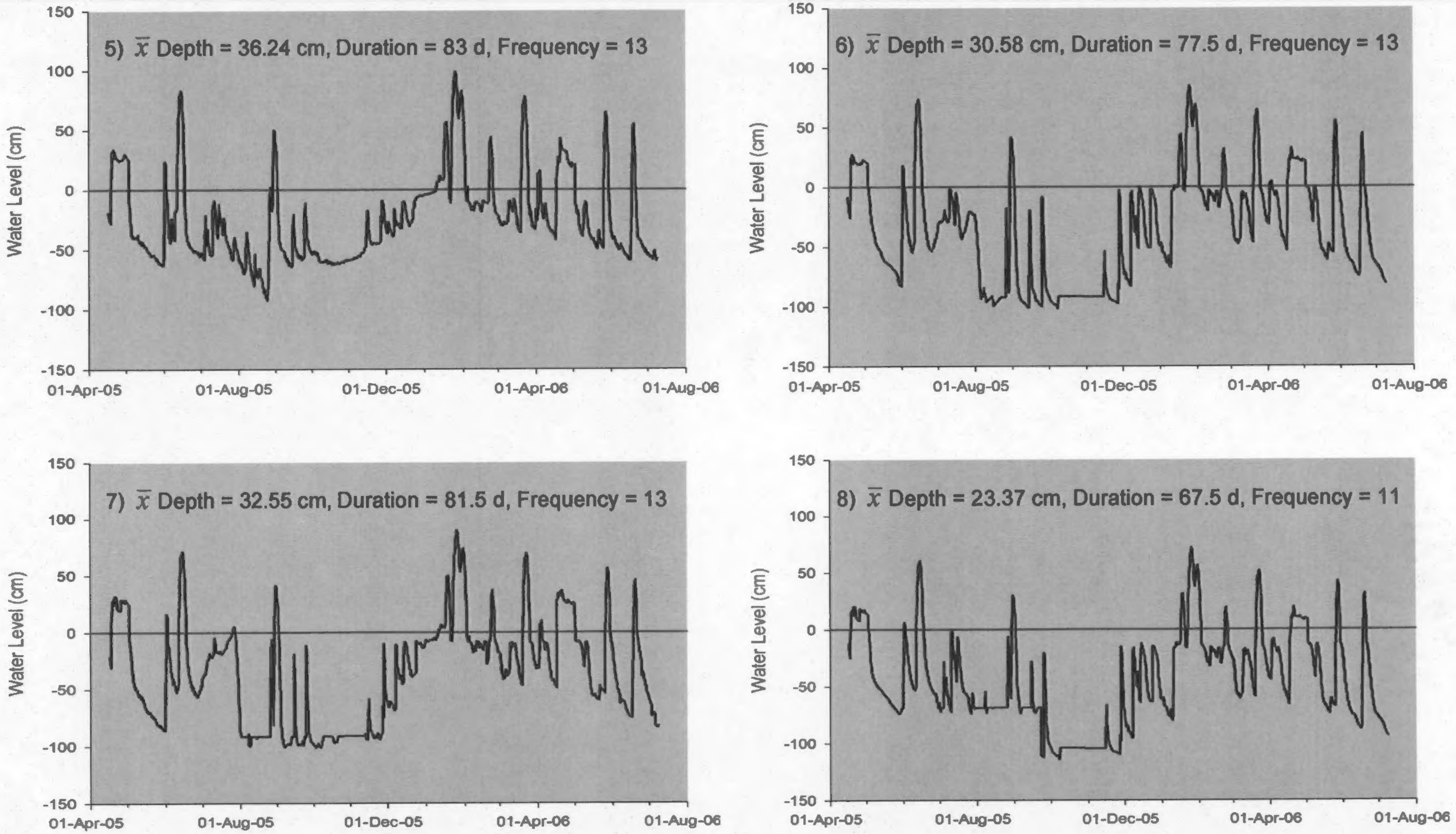


Figure 6. Hydrographs from water meters (5–8) in the 15-day treatment impoundments 4 (meters 5–6) and 5 (meters 7–8) in a replanted west Tennessee, USA, bottomland, 17 April 2005 – 9 July 2006.

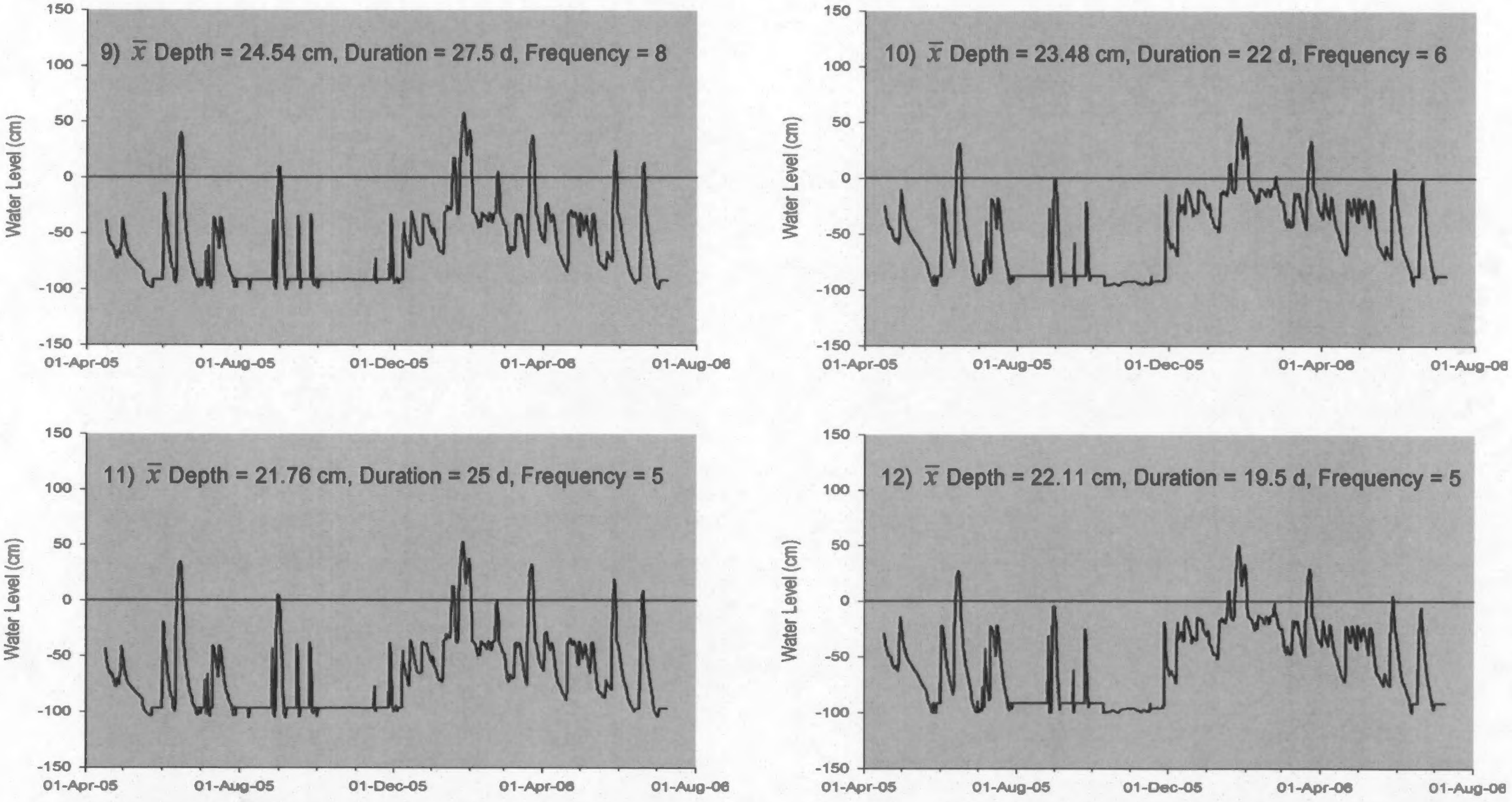


Figure 7. Hydrographs from water meters (9–12) in the control impoundments 6 (meters 9–10) and 7 (meters 11–12) in a replanted west Tennessee, USA, bottomland, 17 April 2005 – 9 July 2006.

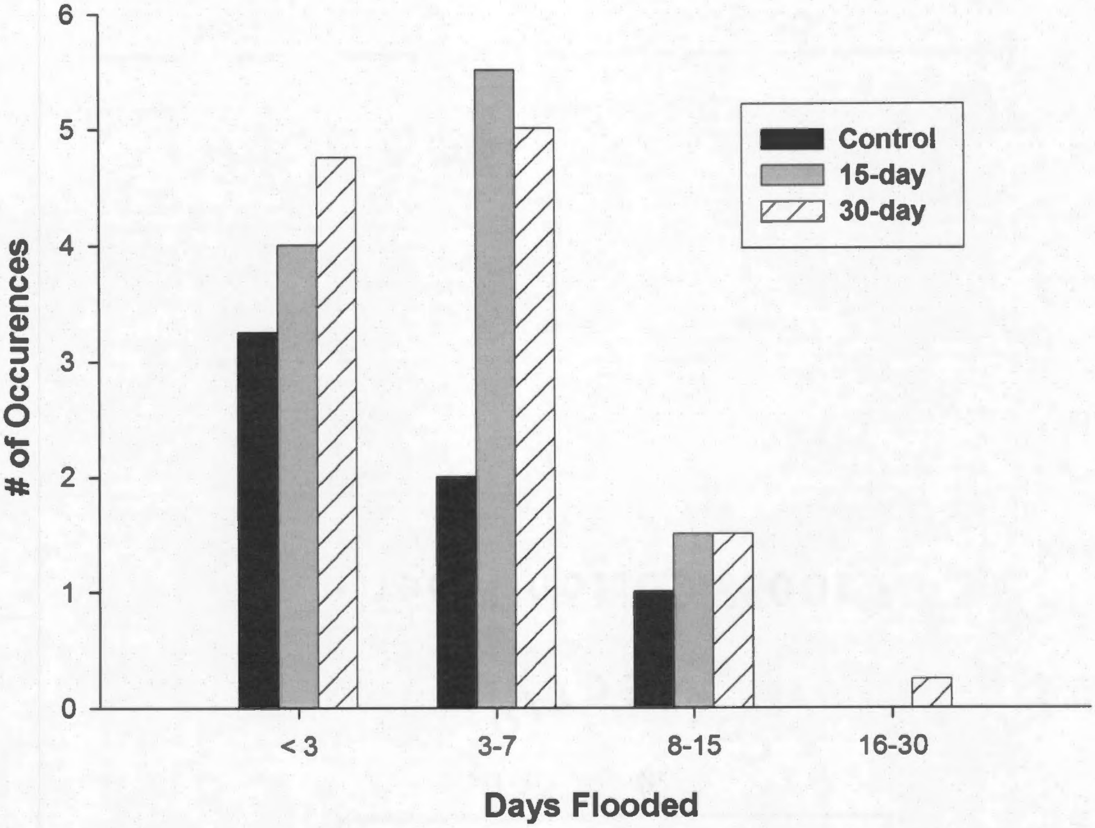
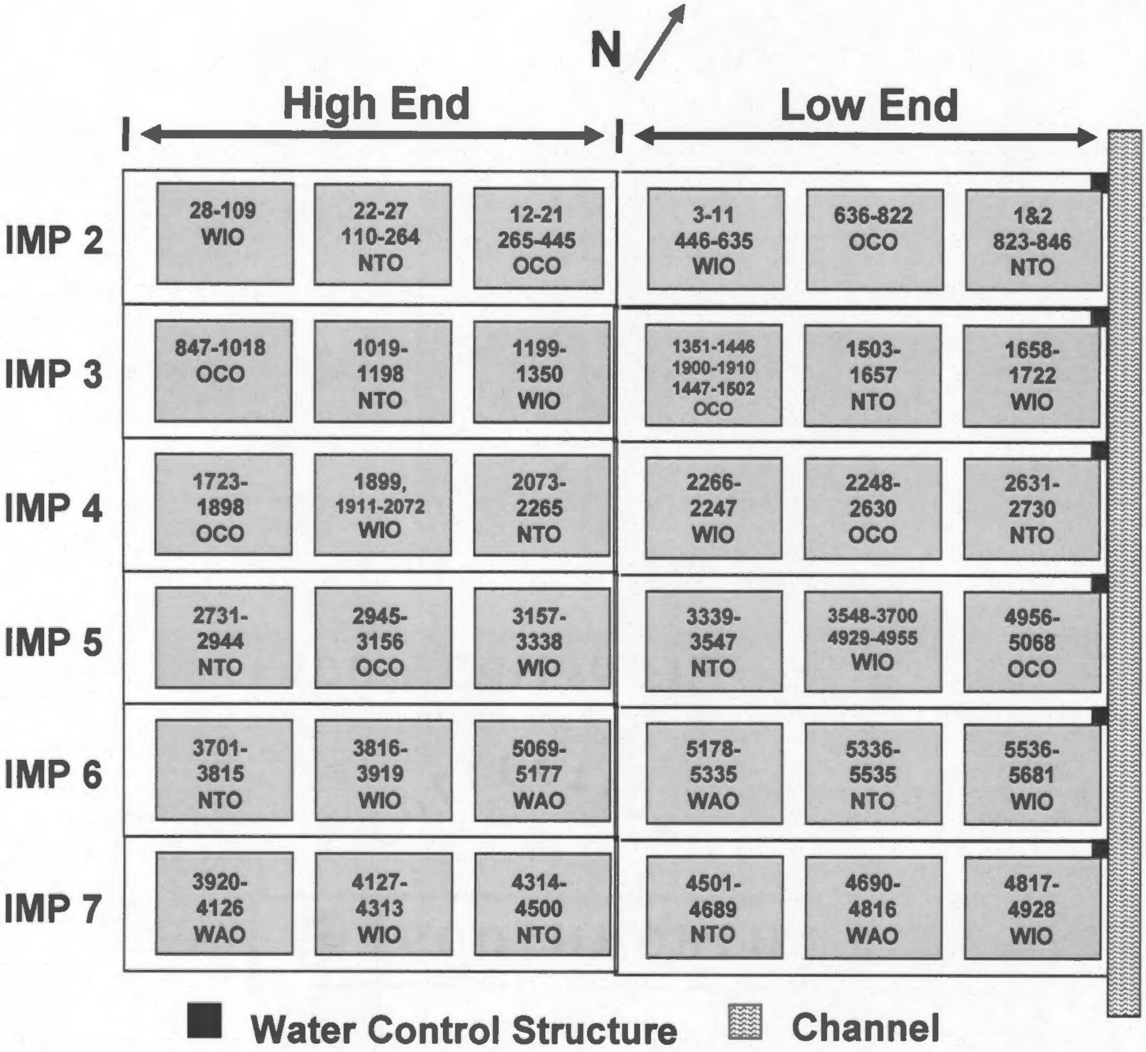


Figure 8. Number of occurrences and duration of natural flood events during the non-treatment period (21 May 2005 – 18 April 2006 and 20 May – 09 July 2006) in control, 15-day, and 30-day impoundments, West Tennessee Research and Education Center, USA.



	High End			Low End		
IMP 2	28-109 WIO	22-27 110-264 NTO	12-21 265-445 OCO	3-11 446-635 WIO	636-822 OCO	1&2 823-846 NTO
IMP 3	847-1018 OCO	1019- 1198 NTO	1199- 1350 WIO	1351-1446 1900-1910 1447-1502 OCO	1503- 1657 NTO	1658- 1722 WIO
IMP 4	1723- 1898 OCO	1899, 1911-2072 WIO	2073- 2265 NTO	2266- 2247 WIO	2248- 2630 OCO	2631- 2730 NTO
IMP 5	2731- 2944 NTO	2945- 3156 OCO	3157- 3338 WIO	3339- 3547 NTO	3548-3700 4929-4955 WIO	4956- 5068 OCO
IMP 6	3701- 3815 NTO	3816- 3919 WIO	5069- 5177 WAO	5178- 5335 WAO	5336- 5535 NTO	5536- 5681 WIO
IMP 7	3920- 4126 WAO	4127- 4313 WIO	4314- 4500 NTO	4501- 4689 NTO	4690- 4816 WAO	4817- 4928 WIO

Figure 9. Seedling numbers and species (overcup oak, OCO, Nuttall oak, NTO, willow oak, WIO, and water oak, WAO) in 6 impoundments (IMP 2–7) in a replanted west Tennessee, USA, bottomland.

using a soil respiration chamber attached to an infrared gas analyzer (LI-6400, Licor Inc., Lincoln, NE) Soil respiration was measured at the midpoint distance between the randomly selected individual and the neighboring seedling directly north of it.

Soil moisture was measured in July 2005 and 2006, and used as a covariate in respiration and transpiration analyses. In July 2005, I collected soil cores (n = 96) at a depth of 16 cm. Soil cores were weighed (wet) to the nearest 0.01g, dried for 48 hours at 50 C, and then weighed again (dry). Soil moisture was calculated as: (wet soil weight – oven dry weight) / oven dry weight. In July 2006, I measured soil moisture (n = 96) using a Trace Time Domain Reflectometry (TDR) probe (Soilmoisture Corp Santa Barbara, CA). Readings were taken in percent volumetric soil moisture at 15 cm depth Thirty-six individuals per species (3 seedlings per elevation block) were collected in November 2004, May 2005 and May 2006 for carbohydrate analyses. Root length and root and shoot biomass also were measured for these seedlings. These seedlings were transported to the University of Tennessee on ice and refrigerated at 4 C if processing occurred in <1 week. If processing started >1 week following collection, seedlings were frozen at -20 C Seedlings were washed, leaves stripped, and roots cut from stems in the lab. Root length was measured to the nearest 1 mm from the root collar to the end of the root. I did not decide to measure root length until 2005, so it was not measured in November 2004. Roots and shoots were dried for 48 hours at 50 C, and mass measured to the nearest 0 01 g (Figure 10)

Non-structural Carbohydrates

Roots were ground using a Willey Mill (Figure 11), and stored non-structural carbohydrates measured. Carbohydrate analyses protocol followed Ashwell (1957) and

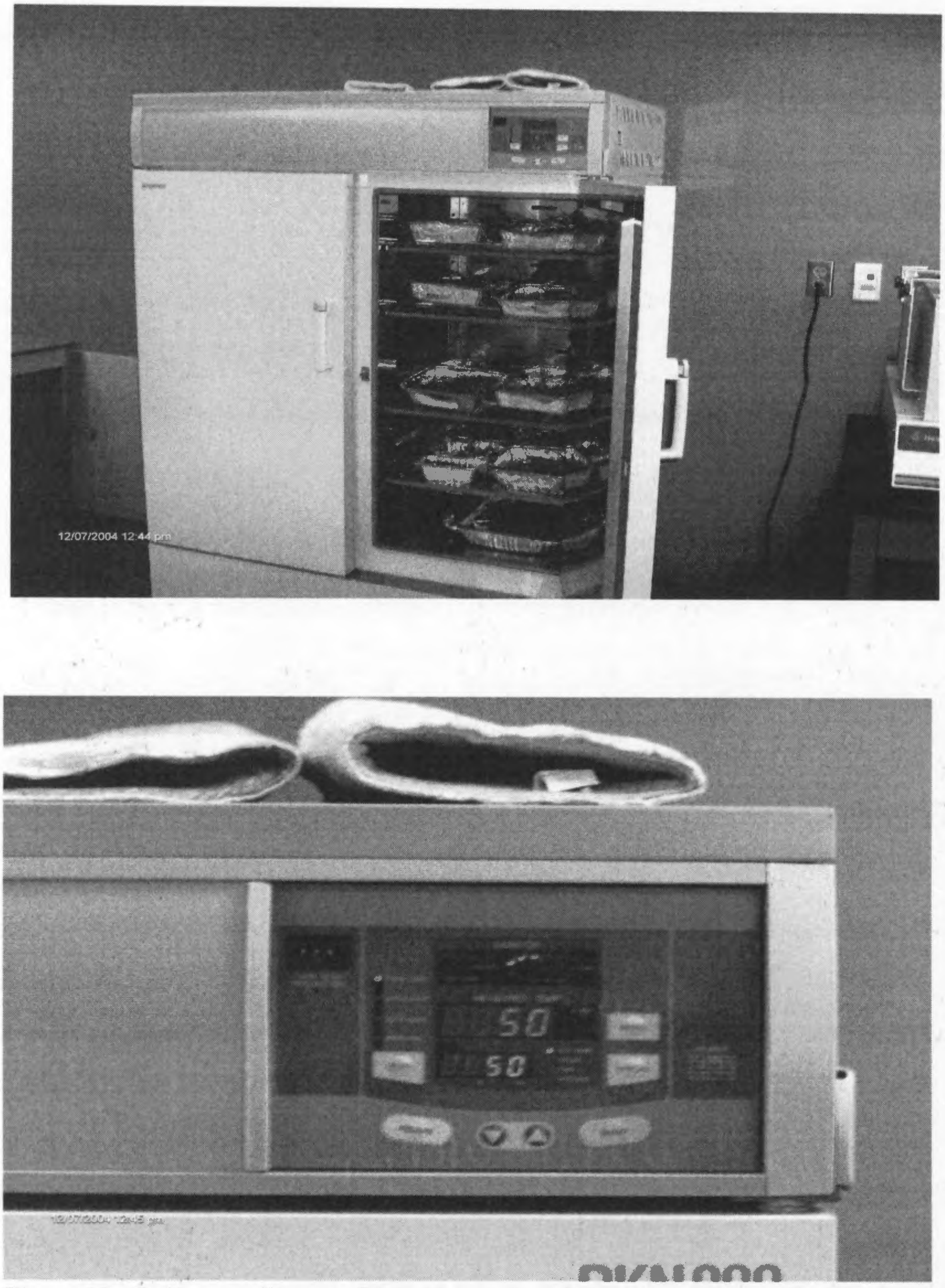


Figure 10. Drying seedlings at 50 C, University of Tennessee, Knoxville, Tennessee, USA.

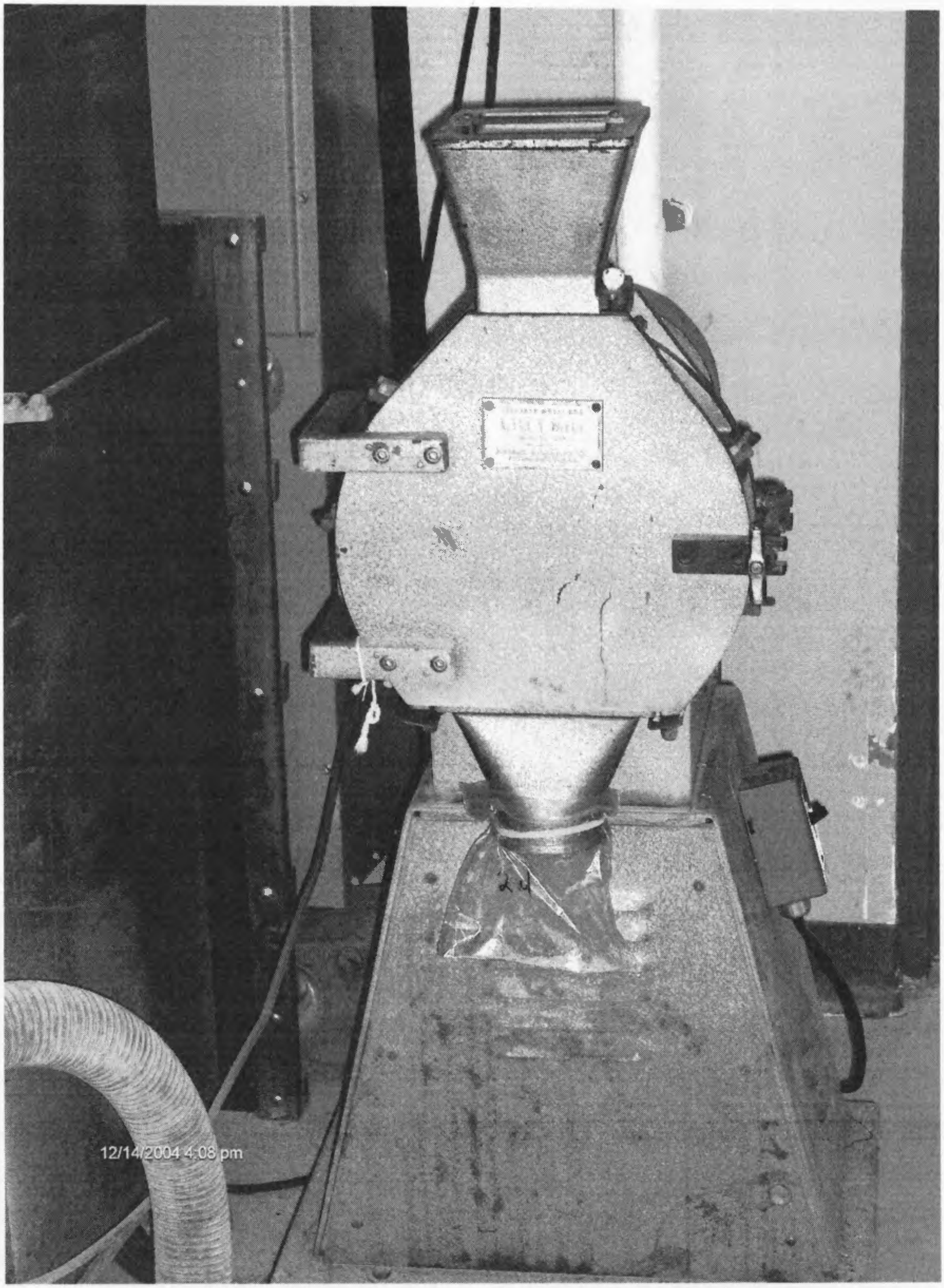


Figure 11. Willey Mill used for grinding seedling roots, Forest Products Center, University of Tennessee, Knoxville, Tennessee, USA.

Hendrix (1993) To calculate sugar concentrations, 0.15–0.20 g of root tissue for each seedling was heated to 90 C in 85% ethanol. Ethanol was pipetted into a 15-ml plastic test tube leaving the starch residue, put into a speed-vac until ≤ 2 ml of solution remained, and then topped off with deionized water to 10 ml. The starch residue was dried at 50 C and frozen at -30 C for later analysis (discussed below). Next, I added 10 ml of a 2 g/L anthrone reagent to a 50-ml test tube. Approximately 0.2 ml of each sugar sample and 4.8 ml of distilled water were added slowly to the anthrone reagent. I vortexed these samples and placed them in an ice bath for 10 minutes. Samples were removed from the ice bath, allowed to warm to room temperature, and placed into a 90 C bath for 15 minutes. Then, I measured sugar concentration of each sample using a spectrophotometer.

To convert starches to sugars, I prepared an amyloglucosidase solution in a dialysis tube and mixed 0.8 ml of the solution with 39 2 ml of 0.5 M sodium acetate buffer (pH = 4 5). I weighed 0.0025 g, 0.005 g, 0.01 g, 0.025 g, and 0.05 g of starch standard into test tubes Next, I added 1 ml of 0 1 M KOH to the standards and the remaining starch residue from the sugar analysis, and boiled it for 1 hour. Samples were allowed to cool, water added until total volume was 2 ml, then 20 µl of 1 M acetic acid was added. I added 0.2 ml of amylase solution to the samples and standards, vortexed them, pipetted off the liquid and placed them into an 85 C bath for 30 minutes, shaking intermittently The samples were cooled to room temperature, and acetic acid was added until pH was < 5. I added 1 ml of amyloglucosidase solution to the samples and heated in a bath to 55 C for 40 min, then boiled for 4 minutes to stop enzyme reaction. Distilled water was added to samples and standards until total volume was 5 ml. Then, I followed sugar extraction methods beginning at the anthrone reagent step to calculate sugar concentrations from the converted starch.

Statistical Analysis

McCurry et al (2006) reported that elevation influenced first-year growth of oak seedlings in the WTREC bottomland. Thus, I used elevation block as a covariate in all statistical analyses I used logistic regression to test for differences ($\alpha = 0.05$) in survival among flood treatments and species (Stokes et al. 2000). When the main-effect chi-square tests associated with logistic regressions were significant, I used large-sample *Z*-tests for 2 proportions that were Bonferroni corrected ($\alpha = 0.017$) for pairwise comparison of percent survival between treatments (Milton and Arnold 1995). I used an analysis-of-variance (ANOVA) to test for differences ($\alpha = 0.05$) in all remaining response variables among treatments and species. In all cases, species and treatment effects interacted, thus analyses were performed by species In addition to elevation, I also included state of bud activity as a blocking variable in the ANOVA models for seedling height, diameter and growth (Milton and Arnold 1995), because I hypothesized the state of bud break during flooding would influence growth. I did not include bud break as a blocking variable for other response variables, because there was insufficient replication per bud break category. Ryan's-Q multiple comparison test was used for pairwise treatment comparisons when the overall ANOVA was significant (Westfall et al. 1999). This test maintains experimentwise error rate at $\alpha \leq 0.05$ given all post-hoc comparisons made. I used the SAS® system v.9.1 and Minitab® v.14 for all analyses.

CHAPTER V

RESULTS

Survival

Across all flood treatments and sample periods, survival was 96%, 89%, and 84% for OCO, NTO, and WIO, respectively. Survival of WIO was different among treatments in July 2005 ($\chi^2_{(2)} = 21.2$, $P < 0.001$, Table 2); survival was greater in the control than in the 15-day and 30-day treatments ($Z > 4.33$, $P < 0.001$). No differences were detected among treatments for WIO during other sample periods ($\chi^2_{(2)} = 1.8$, $P > 0.40$). Survival of NTO was different among treatments in July 2005 ($\chi^2_{(2)} = 6.3$, $P = 0.04$); survival was greater in the control than in the 15-day treatment ($Z = 2.41$, $P = 0.016$). No differences among treatments were detected for NTO during other sample periods ($\chi^2_{(2)} < 0.6$, $P > 0.19$). No differences in survival were detected for OCO among treatments during all sample periods ($\chi^2_{(1)} < 1.4$, $P > 0.24$, Table 2). Bottomland elevation explained significant variation in percent survival of NTO and WIO in fall 2005 and OCO and NTO in July 2005 ($\chi^2_{(1)} > 4.1$, $P < 0.04$).

Survival was different among species in the 15-day and 30-day treatments in July 2005 ($\chi^2_{(2)} > 42.4$, $P < 0.001$, Table 2); OCO survival was greater than NTO and WIO ($Z > 5.3$, $P < 0.001$). Survival was different among species in the 30-day treatment in fall 2005 ($\chi^2_{(2)} = 13.8$, $P = 0.001$); OCO survival was greater than NTO and WIO ($Z > 3.49$, $P < 0.04$). Survival was different among species in the 15-day and control treatments in July 2006 ($\chi^2_{(2)} > 4.5$, $P < 0.03$) Survival of OCO and NTO was greater than WIO in the 15-day treatment ($Z > 3.1$, $P < 0.002$), and NTO was greater than WIO in the control ($\chi^2_{(1)} = 4.5$, $P = 0.03$, Table 2). Bottomland elevation explained significant variation in

Table 2. Survival of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallu*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, 2005 and 2006.

Date[2]	Species	Treatments[1]					
		Control[3]		15-day		30-day	
		n	$\hat{S}$[4]	n	$\hat{S}$	n	$\hat{S}$
July 2005	OCO		NA	661	0.969 Aa	677	0.972 Aa
	NTO	671	0.929 Aa	688	0.891 Bb	492	0.898 ABb
	WIO	507	0.941 Aa	663	0.854 Bb	448	0.857 Bb
Fall 2005	OCO		NA	646	0.991 Aa	659	0.988 Aa
	NTO	628	0 986 Aa	626	0.991 Aa	444	0.962 Ab
	WIO	481	0 975 Aa	566	0.990 Aa	382	0.953 Ab
July 2006	OCO		NA	640	0.997 Aa	651	0.997 Aa
	NTO	618	0.998 Aa	609	0.997 Aa	427	0 998 Aa
	WIO	469	0.985 Ab	545	0.976 Ab	365	0.984 Aa

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days

[2] Month that survival was assessed, fall 2005 assessment occurred from 28 October – 05 November.

[3] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[4] Survival estimates in rows followed by unlike uppercase letters are different ($P \leq 0.04$); estimates for species within columns and dates followed by unlike lowercase letters are different ($P \leq 0.03$) by pairwise Bonferroni-corrected chi-square tests.

percent survival in the 15-day treatment during all sample periods and in the 30-day treatment fall and July 2005 ($\chi^2_{(1)} > 6.2$, $P < 0.01$).

Aboveground Seedling Responses

Differences in mean height growth during the second growing season existed among treatments for all species in fall 2005 ($F_{2,1215} > 39.4$, $P < 0.001$, Table 3). Height growth was the lowest for all species in the 30-day treatment and greatest in the control for WIO. Differences also existed in mean diameter growth among treatments for all species ($F_{1,1259} > 125\ 1$, $P < 0.001$, Table 3). Diameter growth was the lowest in the 30-day treatment for all species; no other differences among treatments were detected. Bottomland elevation and state of bud break explained significant variation in height growth for NTO and WIO and diameter growth for all species ($F_{1,1259} > 3.2$, $P < 0.02$).

Mean height of NTO was greater in the control than in the 15-day and 30-day treatments in fall 2004 ($F_{2,1911} = 13.1$, $P < 0.001$, Table 4). No differences existed for OCO and WIO among treatments in fall 2004 ($F_{1,1378} < 2\ 1$, $P > 0.15$). Differences in height of OCO and WIO existed among all treatments in fall 2005 ($F_{2,1361} > 36.5$, $P < 0.001$); mean height was the lowest in the 30-day treatment for both species (Table 4). Mean height of NTO was greater in the control and 15-day treatments than in the 30-day treatment ($F_{2,1636} = 45.5$, $P < 0.001$, Table 4). Bottomland elevation explained significant variation in mean height for all species ($F_{11,1676} > 10.0$, $P < 0.001$). State of bud break also explained significant variation in mean height of NTO and WIO ($F_{3,1361} > 19.1$, $P < 0.001$).

Table 3. Growth of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, 2005.

Variable	Species	Treatments[1]								
		Control[2]			15-day			30-day		
		n	$\bar{x}$[3]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Height	OCO		NA		580	34.05 A	0.78	583	23.52 B	0.68
(cm/yr)	NTO	579	42.65 A	0.90	580	46.88 B	1.05	393	31.40 C	1.01
	WIO	446	30.27 A	1.00	482	26.50 B	0.79	304	18.94 C	0.99
Diameter	OCO		NA		635	10.65 A	0.19	635	8.14 B	0.18
(mm/yr)	NTO	614	12.80 A	0.24	600	12.94 A	0.25	413	7.78 B	0.24
	WIO	467	8.79 A	0.19	537	9.16 A	0.23	346	4.70 B	0.16

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days

[2] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[3] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

Table 4. Height (cm) of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, fall 2004 and 2005.

		Treatments[1]								
Year	Species	Control[2]			15-day			30-day		
		n	$\bar{x}$[3]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2004	OCO		NA		685	50.37 A	0.66	701	51.61 A	0.63
	NTO	695	48.66 A	0.52	712	45.63 B	0.53	519	45.07 B	0.63
	WIO	530	41.85 A	0.56	688	41.80 A	0.52	472	41.37 A	0.62
2005	OCO		NA		640	80.48 A	1.09	652	72.00 B	1.05
	NTO	618	88.30 A	1.21	609	90.98 A	1.36	427	74.93 B	1.45
	WIO	469	70.05 A	1.18	545	63.90 B	1.01	364	57.18 C	1.25

[1] Flooding treatments were applied 18 April – 20 May 2005, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[3] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

Similar to height, mean diameter of NTO was greater in the control than in the 15-day and 30-day treatments in fall 2004 ($F_{2,1911} = 14.3$, $P < 0.001$, Table 5). No differences existed for OCO and WIO among treatments in fall 2004 ($F_{1,1378} < 1.10$, $P > 0.30$). Diameter was the lowest in the 30-day treatment for all species in fall 2005 ($F_{1,1280} > 80.3$, $P < 0\ 001$); no other differences existed among treatments (Table 5). Bottomland elevation and state of bud break explained significant variation in mean diameter for all species ($F_{12,1911} > 7\ 1$, $P < 0.001$).

Shoot biomass for NTO in the control and 15-day treatments was greater than in the 30-day treatment in May 2006 ($F_{2,24} = 5.5$, $P = 0.01$, Table 6). No other differences were detected among treatments ($F_{2,22} < 2.9$, $P > 0.07$, Table 6). Bottomland elevation explained significant variation in mean shoot biomass for OCO in fall 2004 ($F_{6,16} = 3.2$, $P = 0.03$).

Belowground Seedling Responses

Root length was significantly greater in the control than in the 30-day and 15-day treatments for NTO in May 2005 ($F_{2,23} = 5.96$, $P = 0\ 008$, Table 7). No other differences in root length existed among treatments ($F_{2,24} < 1.80$, $P > 0.19$), although in general, mean root length was the shortest for all species in the 30-day treatment (Table 7). Bottomland elevation explained significant variation in mean root length for OCO in May 2005 ($F_{6,18} = 3.1$, $P = 0.03$).

Root biomass for NTO and WIO in the control and 15-day treatments was greater than in the 30-day treatment in May 2006 ($F_{2,24} > 6.5$, $P < 0.006$, Table 8). No other significant differences in root biomass were detected among treatments ($F_{2,22} < 2.3$, $P > 0.13$, Table 8). Bottomland elevation explained significant variation in mean root

Table 5. Diameter (mm) of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, fall 2004 and 2005.

		Treatments[1]								
Year	Species	Control[2]			15-day			30-day		
		n	$\bar{x}$[3]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2004	OCO		NA		685	9.83 A	0.14	701	9.65 A	0.12
	NTO	695	10.35 A	0.13	712	9.68 B	0.14	519	9.34 B	0.13
	WIO	530	7.04 A	0.11	688	6.96 A	0.10	472	7.16 A	0.11
2005	OCO		NA		640	20.44 A	0.25	651	17.65 B	0.26
	NTO	618	23.27 A	0.30	609	22.66 A	0.32	427	17.10 B	0.34
	WIO	468	15.90 A	0.22	545	16.04 A	0.27	364	11.70 B	0.22

[1] Flooding treatments were applied 18 April – 20 May 2005, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days

[2] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[3] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

Table 6. Shoot biomass (g) of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, 2004 – 2006.

Year[2]	Species	Treatments[1]								
		Control[3]			15-day			30-day		
		n	$\bar{x}$[4]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2004	OCO		NA		12	15.77 A	3.57	12	11.56 A	1.84
	NTO	12	16.11 A	3.39	12	11.78 A	1.59	13	10.54 A	1.43
	WIO	12	9.20 A	1.22	12	8.96 A	2.55	11	6.76 A	0.98
2005	OCO		NA		12	18.80 A	4.27	14	18.16 A	3.29
	NTO	12	24.11 A	5.65	12	19.14 A	5.52	11	12.26 A	2.55
	WIO	11	15.40 A	5.30	12	6.36 A	1.49	11	5.78 A	1.05
2006	OCO		NA		12	60.08 A	12.14	11	44.72 A	14.48
	NTO	12	184.98 A	25.60	12	175.51 A	51.27	12	44.50 B	18.05
	WIO	12	86.80 A	20.96	12	76.34 A	36.73	13	21.52 A	5.39

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Samples were collected in November 2004 and May 2005 and 2006.

[3] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[4] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

Table 7. Root length (cm) of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, May 2005 and 2006.

Year	Species	Treatments[1]								
		Control[2]			15-day			30-day		
		n	$\bar{x}$[3]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2005	OCO		NA		12	21.01 A	1.53	14	22.49 A	1.51
	NTO	12	28.64 A	2.01	12	20.35 B	2.15	11	20.89 B	1.87
	WIO	11	22.24 A	1.32	12	21.40 A	1.90	11	18.20 A	1.36
2006	OCO		NA		12	38.25 A	3.03	11	36.55 A	2.64
	NTO	12	42.59 A	2.40	12	44.74 A	3.71	12	37.63 A	4.15
	WIO	12	34.72 A	2.50	12	38.67 A	2.30	13	31.85 A	2.21

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[3] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

Table 8. Root biomass (g) of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, 2004–2006.

Year[2]	Species	Treatments[1]								
		Control[3]			15-day			30-day		
		n	$\bar{x}$[4]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2004	OCO		NA		12	21.24 A	3.58	12	17.65 A	2.80
	NTO	12	25.90 A	4.55	12	23.45 A	2.36	13	21.13 A	4.04
	WIO	12	12.52 A	1.89	12	15.41 A	3.40	11	10.86 A	1.16
2005	OCO		NA		12	23 66 A	4.45	14	21.35 A	3.72
	NTO	12	30.47 A	6.76	12	20.61 A	4.70	11	18.14 A	2.86
	WIO	11	13.76 A	3.66	12	8.19 A	1.38	11	7.56 A	1.22
2006	OCO		NA		12	54.65 A	10.46	11	63 33A	17.12
	NTO	12	175.80 A	27.87	12	175.62 A	36.08	12	52.35 B	18.13
	WIO	12	85.22 A	18 67	12	64.99 A	19.97	13	24.18 B	5.15

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Samples were collected in November 2004 and May 2005 and 2006.

[3] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[4] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

biomass for OCO in fall 2004 ($F_{6,16} = 3.2$, $P = 0.03$) and for WIO in May 2006 ($F_{10,24} = 3.1$, $P = 0.01$).

Seedling Physiology

Willow oak sugar concentration in the roots was different among treatments in May 2005 ($F_{2,22}$ = 14 9, $P < 0.001$), concentrations were lowest in the 30-day treatment and greatest in the 15-day treatment (Table 9). No differences in sugar concentration were detected among treatments for WIO during other sample periods ($F_{2,23} < 1.7$, $P >$ 0.21) Sugar concentration was greater in the 15-day treatment than in the 30-day treatment for OCO and NTO in May 2005 ($F_{2,23} > 6.2$, $P < 0.007$). In May 2006, sugar concentrations were greater in the 30-day than in the 15-day treatment for NTO ($F_{2,24} = 6.0$, $P = 0.008$). No other differences in sugar concentrations were detected among treatments for OCO and NTO ($F_{1,15} < 1.8$, $P > 0.20$, Table 9). Bottomland elevation explained significant variation in mean sugar concentrations for NTO in May 2006, and WIO in May 2005 and 2006 ($F_{9,24}$ > 2 8, $P < 0.02$).

Starch concentration in the control and 30-day treatments was greater than in the 15-day treatment for NTO in fall 2004 ($F_{2,24} = 4.4$, $P = 0.02$, Table 10). Similarly, starch concentration in WIO was greater in the 30-day treatment than in the 15-day treatment in fall 2004 ($F_{2,23} = 3.6$, $P = 0.04$). In May 2005, WIO starch concentration was greater in the 30-day treatment than in the 15-day and control treatments ($F_{2,22} = 5.4$, $P = 0.01$). However, WIO starch concentration was the lowest in the 30-day treatment compared to 15-day and control treatments in May 2006 ($F_{2,24} = 7.4$, $P = 0.003$). Starch concentration was greatest in the control for NTO in May 2006 ($F_{2,24} = 11.6$, $P = 0.003$, Table 10). No other differences were detected among treatments ($F_{2,23} < 2.8$, $P >$ 0 08). Bottomland

Table 9. Sugar concentration (mg g^{-1} dw) in the roots of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, 2004–2006

Year[2]	Species	Treatments[1]								
		Control[3]			15-day			30-day		
		n	$\bar{x}$[4]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2004	OCO		NA		12	64.67 A	7.26	11	78.39 A	8.02
	NTO	12	58.01 A	7.33	12	54.90 A	7.16	13	46.07 A	4.52
	WIO	12	60.63 A	3.94	12	52.99 A	3.40	11	61.92 A	4.93
2005	OCO		NA		12	75.66 A	10.09	14	37.06 B	3.41
	NTO	12	43.92 AB	3.46	12	53.42 A	6.77	11	31.83 B	1.64
	WIO	11	49.22 A	2.72	12	60.33 B	5.88	11	36.13 C	2.20
2006	OCO		NA		12	39.17 A	2.67	10	33.98 A	4.03
	NTO	12	43.59 AB	3.35	12	32.26 B	3.97	12	51.42 A	6.49
	WIO	12	43.90 A	3.29	12	41.13 A	3.39	13	42.20 A	4.20

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Samples were collected in November 2004 and May 2005 and 2006.

[3] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[4] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

Table 10. Starch concentration (mg g^{-1} dw) in the roots of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, 2004–2006.

		Treatments[1]								
Year[2]	Species	Control[3]			15-day			30-day		
		n	$\bar{x}$[4]	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
2004	OCO		NA		12	0.6174 A	0.121	11	0.8571 A	0.184
	NTO	12	0.9886 A	0.116	11	0.4830 B	0.115	13	0.9507 A	0.175
	WIO	12	0.7088 AB	0.092	12	0.5979 B	0.103	11	1.0642 A	0.194
2005	OCO		NA		12	0.0213 A	0.004	14	0.0273 A	0.004
	NTO	12	0.0188 A	0.003	12	0.0127 A	0.003	11	0.0230 A	0.003
	WIO	11	0.0147 A	0.001	12	0.0117 A	0.002	11	0.0311 B	0.006
2006	OCO		NA		12	0.5605 A	0.065	11	0.7419 A	0.121
	NTO	12	0.8191 A	0.097	12	0.4103 B	0.074	12	0.3981 B	0.070
	WIO	12	0.7259 A	0.080	12	0.6180 A	0.095	13	0.3588 B	0.045

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Samples were collected in November 2004 and May 2005 and 2006.

[3] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[4] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test

elevation explained significant variation in mean starch concentration for NTO during the fall 2004 and May 2005 sampling periods ($F_{6,18} > 3.0$, $P < 0.03$).

Transpiration rate of NTO was greater in the control than in the 30-day treatment in July 2005 ($F_{2,23} = 4.4$, $P = 0.02$, Table 11) However, in July 2006, the transpiration rate of NTO was greater in the 30-day treatment than in the control ($F_{2,60} = 3.2$, $P = 0.05$). No differences were detected among treatments for OCO or WIO either year ($F_{2,60} < 2.4$, $P > 0.10$). No differences in soil respiration rates were detected among treatments for any species in July 2005 ($F_{2,23} < 1.7$, $P > 0.20$, Table 11), although in general, the lowest soil respiration rates occurred in the 15-day treatment. Soil respiration was not measured in July 2006 Bottomland elevation explained significant variation in mean transpiration rate for OCO during both sampling periods ($F_{6,40} > 2.6$, $P < 0.03$), and it explained significant variation in mean respiration rate of NTO in July 2005 ($F_{10,23} = 2.3$, $P = 0.05$).

Table 11. Leaf transpiration rate (mmol H_2O $m^{-2}s^{-1}$) and soil respiration rate (mmol CO_2 $m^{-2}s^{-1}$) of overcup (*Quercus lyrata*, OCO), Nuttall (*Q. nuttallii*, NTO), and willow (*Q. phellos*, WIO) oak seedlings exposed to 3 early growing-season flood treatments in a replanted west Tennessee, USA, bottomland, July 2005 and 2006.

Variable	Year	Species	Treatments[1]								
			Control[2]			15-day			30-day		
			n	$\bar{x}$[3]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Transpiration	2005	OCO		NA		12	36.12 A	2.44	12	37.47 A	2.93
		NTO	12	43.51 A	2.43	13	39.64 AB	2.52	11	34.39 B	2.39
		WIO	11	39.58 A	3.16	12	37 57 A	2.78	13	38.64 A	2.40
	2006	OCO		NA		24	33.49 A	2.68	24	34.32 A	2.55
		NTO	24	29.66 A	1.39	24	35.25 AB	2.93	24	36 82 B	1 99
		WIO	24	32.27 A	1.62	24	38.94 A	3.18	24	37.47 A	1.89
Respiration	2005	OCO		NA		12	3.08 A	0.42	12	3.61 A	0.60
		NTO	12	5.54 A	1.31	13	3.51 A	0.56	11	4.61 A	0.81
		WIO	11	3.39 A	0.58	12	2 94 A	0.24	13	3.47 A	0.55

[1] Flooding treatments were applied 18 April – 20 May 2005 and 17 April – 19 May 2006, and constituted soil inundation for 0 (control), 15 (15-day), and 30 (30-day) days.

[2] Overcup oak seedlings were not available (NA) for sampling in the control treatment.

[3] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple comparison test.

CHAPTER VI

DISCUSSION

Survival

Overall survival was 96%, 89%, and 84% for OCO, NTO, and WIO, respectively. Extended early growing-season flooding negatively affected the survival of NTO in 2005 and WIO both years. Overcup oak survival was not influenced by flooding treatments. Also, NTO and OCO survival generally was greater than WIO for all treatments. My survival results seem to support findings from other field studies. Gray and Kaminski (2005) found that OCO seedlings had 10% greater survival than WIO seedlings in a Mississippi hardwood bottomland that was continuously flooded during winter. Day et al (1998) reported that spring flooding significantly decreased the survival of NTO and WIO seedlings in the Mississippi Delta, and NTO survival was greater than WIO. Further, McLeod et al. (2000) found that OCO seedlings had greater survival than NTO and WIO over a 3-year period in South Carolina bottomlands that periodically flooded ($\bar{x} = 5$ times/year) during the growing season and winter

Extended early growing-season flooding probably negatively influenced survival of NTO and WIO, because of negative impacts on seedling physiology associated with anoxic conditions in the soil. When soils are flooded, available oxygen in the soil is quickly used by respiring roots and microorganisms (Kozlowski 1984) Reduction of oxygen in the soil decreases aerobic metabolism, ultimately decreasing photosynthetic rates, carbohydrate synthesis and ion absorption, which can negatively affect survival of seedlings (Kozlowski and Pallardy 1984) Anaerobic respiration is not as efficient as aerobic respiration at metabolizing energy necessary for survival and growth (Kozlowski

2002). Flooding also reduces aerobic mycorrhizae, which play a key role in uptake of essential macronutrients from the soil (Filer 1975). Rates of photosynthesis are reduced during flooding because stomata close, which decreases CO_2 absorption, ultimately lowering ATP production (Kozlowski 1997). Extended flooding also can reduce leaf chlorophyll a and b, and contribute to lower photosynthetic rates (Anella and Whitlow 2000, Franklin et al. 2005).

Another possibility is that flooding may have negatively influenced seedling survival through accumulation of toxic chemicals. Flooding causes transformation of chemicals in the soil from an oxidized to a reduced state (Kozlowski 1997). For example, nitrogen, manganese, iron, and sulfur are quickly reduced (<2 weeks) in flooded soils (Mitsch and Gosselink 2000). When these chemicals accumulate (e.g., $Fe^{2+} > 750$ μM), they are toxic to seedlings (Jackson and Drew 1984, Laan 1991) Extended flooding also can produce hydrocarbons, alcohols, phenolic acids, and volatile sulfur in the soil, which can inhibit seedling physiological processes (Kozlowski 2002).

My results further suggest that short duration flooding during the second growing season may positively influence survival of NTO and WIO seedlings. Although significant differences were not detected, NTO and WIO survival was greatest in the 15-day treatment in fall 2005. Chamberlain and Leopold (2005) suggested that short duration periodic flooding may increase 30-day-term survival of bottomland oak seedlings. Burkett et al (2005) reported that natural flooding in a reforested wetland in Mississippi increased survival of NTO seedlings. I hypothesize that the mechanism driving this response is related to an ideal range of soil moisture for these species I measured soil moisture in July 2005 and 2006, and it was greater in the 15-day treatment

($\bar{x}$ = 20.5%, S = 0.52) than in the control ($\bar{x}$ = 18.2%, S = 0.43). Increased soil moisture can positively influence survival of bottomland oak species by reducing rodent herbivory, vegetation competition and drought stress (Burkett et al. 2005, Chamberlain and Leopold 2005). However, given that survival generally was lower in the 30-day treatment than in the 15-day and control treatments for NTO and WIO, there must be a threshold for these species, where duration of flooding and increased soil moisture negatively affects seedlings. My results suggest that this threshold is between 15 and 30 days of 100% soil moisture during the first month of the growing season. Soil moisture in July was on average 23% (S = 1.00) in the 30-day treatment.

Aboveground Seedling Responses

Extended early growing-season flooding appeared to negatively impact second-year growth, height and diameter for all species Also, NTO and WIO generally experienced the greatest growth in the 15-day treatment, again suggesting a possible benefit of short duration (≤ 15 days) early growing-season flooding. Similar results have been found in other bottomland studies. Conner et al. (1998) reported that 17 weeks of growing-season flooding in a greenhouse significantly reduced first-year height and diameter growth of NTO and OCO seedlings. McCasland et al. (1998) found that first-year height and diameter of NTO seedlings exposed to 1 month of continuous and intermittent flooding in a greenhouse were significantly lower than seedlings not flooded. Day et al (1998) reported that flooding negatively influenced height growth of NTO seedlings in the Mississippi Delta. Several other studies also have documented reduced growth of *Nyssa aquatica, Nyssa sylvatica, Acer rubrum* and *Taxodium distichum* in response to growing-season flooding in bottomlands (Donovan et al. 1988, Keeland et al. 1997).

Flooding generally reduced the amount of aboveground shoot biomass for all species. Pezeshki et al. (1999) found that flooding reduced shoot biomass of NTO seedlings that were flooded for 70 days in a greenhouse. Pezeshki et al. (1996) reported that shoot biomass of OCO seedlings was reduced when flooded for 22 days during the growing season. Conner et al. (1998) also found that shoot biomass of NTO seedlings was negatively affected if flooded for 17 weeks during the growing season. Reduction in shoot biomass in response to flooding has been documented for other bottomland species as well (e.g., *Nyssa aquatica, Sapium sebiferum, and Fraxinus pennsylcanica*; Conner et al 1997), although to my knowledge, this is the first documentation of reduced shoot biomass for WIO exposed to growing-season flooding.

Reduced growth of seedlings is a typical response to flooding, because anaerobic conditions in the soil thwart energy storage and metabolism (Kozlowski 1984). Flooding also induces stomatal closure in various woody plants, which can reduce photosynthetic activity thus growth potential (Kozlowski and Pallardy 2002). Flooding can negatively affect active transport of essential nutrients into the roots due to the anoxic state, which can reduce growth (McKevlin et al 1998, Kozlowski 2002). In addition, flooding can reduce growth by affecting the quantity and ratio of growth hormones in the plant (Kozlowski 2002).

Similar to survival, apparently short-duration flooding during the growing season may be beneficial to bottomland seedlings. In general, the largest seedlings and greatest growth occurred in the 15-day treatment. I hypothesize that short-duration flooding during the first month of the growing season provides optimal soil moisture later in the growing season for these seedling species, possibly enhancing growth. Further, as suggested previously, moderate flooding may reduce girdling by rodents and vegetation competition, thus facilitate increased growth (Burkett et al. 2005, Chamberlain and Leopold 2005).

It should be noted that pre-treatment mean height and diameter of NTO were greater in the control than in the 15-day and 30-day treatments. In 2005, however, NTO overcame the pre-treatment difference in the 15-day treatment, because mean height and diameter were greater in the control and 15-day treatments than in the 30-day treatment. Nonetheless, I suggest NTO growth results be interpreted cautiously, given differences existed among treatments prior to application. This likely occurred because elevation was positively correlated with first-year seedling growth (McCurry et al. 2006), and 30-day treatment impoundments were at lower elevations in the bottomland (Figure 1).

Belowground Seedling Responses

Root length generally was shortest for all species in the 30-day treatment, suggesting that extended early growing-season flooding reduced root elongation Pezeshki et al (1996) found that OCO root elongation was reduced by 78% when seedlings were flooded for 22 days, providing evidence that anoxic conditions may hinder root growth. To my knowledge, my study was the first to document reduced WIO and NTO root length associated with growing-season flooding. Similar to previous response variables, some flooding during the growing season may be beneficial to seedlings given that root lengths were generally longest in the 15-day treatment for all species

Root biomass was lowest in seedlings exposed to the 30-day flood duration treatment. Pezeshki et al. (1996, 1999) reported that root biomass of NTO and OCO seedlings was significantly reduced when flooded for 22 and 70 days, respectively. Conner et al (1998) found that flooding NTO and OCO seedlings for 17 weeks during the growing season in a greenhouse significantly reduced root biomass. Other studies have shown that flooding causes a decrease in root biomass when seedlings are flooded, except for a few extremely flood-tolerant species (e.g., *Taxodium distichum, Nyssa aquatica*; Donovan et al 1988, Megonigal and Day 1992, Pezeshki and DeLaune 1998, Burke and Chambers 2003, and Kercher and Zedler 2004)

I hypothesize that reduced root length and biomass in the 30-day treatment was due to dieback and metabolism of root carbohydrates. Root dieback in response to flooding has been reported for various species, including bottomland oaks (Hook and Brown 1973, McKevlin et al. 1998), presumably because most of the oxygen in flooded soils occurs in the upper horizon (Burke and Chambers 2003) Carbohydrate stores in the roots also were likely utilized to compensate for ATP reduction associated with decreases in photosynthesis (Kozlowski and Pallardy 1984).

Seedling Physiology

In general, sugar concentrations decreased in all species as flood duration increased. To my knowledge, this study is the first to examine the influences of flooding on sugar concentrations in roots for OCO, NTO, and WIO. It has been reported that sugar concentrations in roots of other seedling species decrease when flooded (Angelov et al. 1996, Islam and Macdonald 2004). For example, sugar concentrations in black spruce (*Licea mariana*) and tamarack (*Larix laricina*) seedlings decreased after flooding for 34 days during the growing season (Islam and Macdonald 2004).

In May 2006, however, sugar concentrations in NTO roots were greatest in the 30-day treatment, which is contradictory to the above hypothesis that flooding negatively affects sugar concentrations. It has been suggested that some flood-tolerant species may alter their biochemical processes to maintain sugar reserves when soils conditions are anoxic (Kozlowski and Pallardy 2002). Albrecht and Biemelt (1998) found that there was a larger accumulation of carbohydrates in roots of known wetland plants compared to non-wetland plants when flooded. Further, it has been suggested that flood tolerance may be related to the ability of a plant to maintain carbohydrate reserves in its roots when they are flooded (Crawford and Braendle 1996, Kreuwieser et al. 2004). Perhaps, NTO seedlings in my study underwent an adaptation (or acclimation) to flooding, such that by the second growing season, NTO seedlings maintained sugars more efficiently than the other species. Indeed, future research is needed to test this hypothesis Similar to previously discussed response variables, some flooding during the growing season may be beneficial to seedlings given that in May 2005 the largest concentrations of sugars were in the 15-day treatment for all species.

Starch concentrations in NTO and WIO were greatest in the control and 30-day treatments in fall 2004 prior to treatment application, thus the following discussion of results must be interpreted cautiously. As a general trend, starch concentrations in all species were greatest in the 30-day treatment in May 2005 However, in May 2006, starch concentrations of NTO and WIO were lowest in the 30-day treatment, and OCO levels appeared unaffected. To my knowledge, this study is the first to examine the influences of flooding on starch concentrations in roots of OCO, NTO, and WIO seedlings Previous studies have reported trends similar to my results in May 2006. Gravatt and Kirby (1998) found a significant decrease in root starch concentrations in *Q alba* and *Q nigra* seedlings exposed to 32 days of flooding in a greenhouse. Castonguay et al. (1993) demonstrated that flooding caused root starch concentrations to decrease in alfalfa (*Medicago sativa*). Su et al. (1998) also found similar results when they exposed luffa (*Luffa aegyptiaca*) and bitter melon (*Momordica balsamina*) to flooding A possible explanation for the trend observed in May 2005 is related to bud activity. In 2005, there was only 17% bud activity, thus it is possible that seedlings had not used substantial starch stores prior to flooding and had greater quantities after flooding. Differences may have existed between 15- and 30-day treatments in 2005, because seedlings in the 15-day treatment were not collected until after the 30-day treatment, allowing seedlings in the 15-day to resume growth and utilize starches prior to collection.

Carbohydrates produced by photosynthesis have multiple fates including oxidation for respiration, growth, storage for reserves, production of defense chemicals, and loss to root grafts and parasites (Kozlowski 1992). Soil flooding decreases the rate of photosynthesis, which in turn reduces the rate of carbohydrate production and translocation (Kozlowski and Pallardy 1984). In anoxic conditions, seedlings rely on carbohydrate reserves to maintain respiration and growth (Gravatt and Kirby 1998). Due to the increased demand for carbohydrates by flood-stressed roots, there is a decrease in availability of translocated carbohydrates for other physiological processes throughout the plant (Kroen et al 1991). The exact mechanism by which flooding blocks translocation of carbohydrates is not well understood. One possibility is that flooding inhibits phloem transport (Kozlowski and Pallardy 1984, Gravatt and Kirby 1998). Furthermore, flooding effects on starch and sugar concentrations appear to be tied closely with species-specific flood tolerance (Angelov et al. 1996). For example, Angelov et al. (1996) found that starch concentrations of sweetgum and swamp tupelo seedlings roots where higher than cherrybark oak seedlings when subjected to 2 years of continuous flooding In fact, in this study, starch concentrations increased in swamp tupelo when flooded, which is a highly flood-tolerant species (Angelov et al. 1996). Furthermore, Albrecht and Biemelt (1998) found that there was a larger accumulation of carbohydrates in roots exposed to flood stress in wetland species compared to non-wetland species.

Leaf transpiration rates of NTO seedlings were negatively affected by flooding in July 2005. Conversely, leaf transpiration rates of NTO seedlings were positively affected by flooding in July 2006. Transpiration rates for WIO and OCO appeared to be unaffected by flooding treatments. Thus, I am assuming differences in other response variables were not associated with transpiration. To my knowledge, this study is the first to examine the influences of flooding on leaf transpiration rates for WIO and NTO. It is hypothesized that transpiration rates decrease in response to flooding, because flooding decreases oxygen and nutrient uptake by the roots, which in turn reduces transpiration (Parker 1950, Kozlowski and Pallardy 1984). Several bottomland species, including overcup oak (Parker 1950), showed declines in transpiration rates when flooded (Nash and Graves 1993, Kreuzwieser et al. 2004). Furthermore, flooding decreased transpiration rates in *Q. robur* saplings and 2-year-old *Fagus sylvatica* and *Prunus armeniaca* seedlings (Kreuzwieser et al. 2002, Nicolas et al 2005). Anderson and Pezeshki (1999) found that NTO seedlings subjected to intermittent flooding (5 days flooded and 5 days drained for 3 cycles) had reduced stomatal conductance. Stomatal conductance rates are comparable to transpiration rates, because both measurements are taken in mmol H_2O $m^{-2}s^{-1}$ and positively correlated.

Elevation and Bud Break

My results suggest that elevation and bud break are important mechanisms influencing seedling physiology and growth The parameter estimates for elevation in all ANOVA models were positive for all response variables, indicating that as elevation increased, the value of the response variables increased also. Elevation may influence seedlings through its correlation with hydrology (i.e., lower elevations are flooded more frequently and for longer duration) McCurry et al (2006) reported that bottomland elevation explained significant variation in first-year height and diameter of NTO and WIO seedlings. In general, height and diameter of seedlings were greater at higher elevations than at lower elevations in the bottomland. Furthermore, McLeod et al. (2000) found that elevation was positively correlated with WIO survival and growth. Presumably, seedlings at lower elevations are exposed to hydrologic stress more often, owing to their reduced rate of growth.

Bud break also was positively correlated with seedling growth, indicating that seedlings that had experienced bud activity when flooding occurred were less affected. Growth, height and diameter were lowest for individuals that were still dormant at the time of flood treatment application. Flooding decreases energy stores, thus I hypothesize that dormant seedlings depleted their energy stores in an effort to maintain respiration and survive anoxic conditions. Therefore, dormant seedlings may not have had as much energy for subsequent growth. This emphasizes the importance of flood timing on growth of bottomland seedlings (King 1994), and suggests that flooding during the first month of the growing season prior to bud break negatively affects seedlings. Gray and Kaminski (2005) found that continuous winter flooding decreased the survival of OCO and WIO Contrary to my findings, Hall and Smith (1955) concluded that growing season flooding was more stressful than dormant season flooding. However, flooding can negatively affect seedlings during the dormant season as depth increases (Fredrickson and Batema 1993). Overall, it appears that seedling survival and growth can be affected by both growing- and dormant-season flooding. To my knowledge, there have been no studies directly comparing the effects of dormant- and growing-season flooding on growth and survival of bottomland seedlings

Flood Tolerance

A basic understanding of species-specific flood tolerance is fundamental to restoration success (Kozlowski 2002). Hook (1984) classified flood tolerance of OCO, NTO and WIO as very flood tolerant, moderate to very flood tolerant, and moderately flood tolerant, respectively. McKnight et al. (1981) ranked flood tolerance of OCO and NTO as moderately flood tolerant and WIO as weakly to moderately flood tolerant. McCurry et al. (2006) ranked flood tolerance, decreasing from OCO to NTO to WIO. Based on my results, I propose the ranking of flood tolerance for these species follows previous research in the order of OCO, NTO and WIO being least flood tolerant. I am ranking OCO as the most flood-tolerant species, because of its high survival and general lack of differences between treatments for all response variables. I suggest that NTO is the next most flood tolerant, because for most response variables, the magnitude was less for NTO than OCO. Note that some of the growth variables were greater for NTO than

OCO, however, I attribute this to the typical slow growth rate of OCO (Morris 1965). Lastly, I conclude that WIO is the least flood tolerant among these 3 species, because in general, response variables were lowest for it.

The differences in flood tolerance I observed suggest differences in species-specific physiological responses to flooding. I observed several trends where the largest magnitude, of a particular variable, was in the 15-day treatment. This suggests that the short-duration early growing-season flooding was beneficial to seedling growth and survival as others have suggested (Chamberlain and Leopold 2005, Burkett et al 2005).

CHAPTER VII

MANAGEMENT IMPLICATIONS

Flood duration, depth and timing are primary mechanisms that regulate plant survival, growth and composition in hardwood bottomland ecosystems (Hosner and Boyce 1962, Whitlow and Harris 1979, McKnight et al. 1981, Streng et al. 1989, Mitsch and Gosselink 2000, Burke et al. 2003). These allogenic factors influence plant function and composition based on species-specific tolerance to anoxic conditions and other chemical transformations in the soil during flooding (Kozlowski and Pallardy 1984, Hodges 1997) My results suggest that wildlife managers and foresters should not replant hardwood bottomlands in a random species arrangement. Seedlings of bottomland species differ in flood tolerance, and flood frequency and depth are typically correlated with elevation (McCurry et al. 2006).

Overcup oak seedlings appeared to be the most flood tolerant among my species. Thus, managers should consider planting OCO at sites with longer and more frequent flooding, and at lower elevations Unfortunately, OCO is an oak species that is generally considered poor by wildlife managers, because it has low timber value and its acorns are large hence not preferred by waterfowl (Young et al. 1995, Barras et al. 1996). Thus, this species may not be ideal for bottomland restoration in the Southeast. Alternatively, wildlife biologists and foresters may consider managing low elevations that flood frequently in candidate bottomlands as moist-soil wetlands. Moist-soil wetlands are highly productive (Gray et al 1999), and important natural habitats for various species, including waterfowl and amphibians (Baldassarre and Bolen 1994, Gray and Smith 2005).

I ranked NTO as moderately flood tolerant, thus I recommend planting NTO in bottomlands that receive short (≤ 30 days) periodic flooding during the growing season. In fact, it appears that some flooding (e.g., 15 days) in the growing season benefits NTO survival and growth. Because flood duration is usually correlated with elevation (McCurry et al. 2006), I recommend planting NTO seedlings at medium elevations. In the WTREC bottomland, medium elevations were 0.5 – 0.75 m above the incipient point of overbank flow. Given that NTO has a high timber value and its acorns are generally smaller than OCO (Young et al. 1995, Barras et al. 1996), I suggest NTO is a better species for bottomland restoration than OCO. Willow oak was the least flood tolerant among species given its low survival rate and lower magnitude in response variables in the 30-day flood treatment. Thus, I recommend planting WIO at higher elevations (e g., >0.75 m above the incipient point of overbank flow). Despite its lower flood tolerance, WIO is a good species to plant for bottomland restoration, because it has a high timber value and its acorns are small and preferred over most other oak species by waterfowl (Young et al. 1995, Barras et al. 1996). Based on my results, I recommend the following planting design in a bottomland. manage low elevations that flood frequently as herbaceous moist-soil wetlands, plant NTO at medium elevations, plant WIO with NTO at higher medium elevations, and continue planting WIO at higher elevations that flood infrequently. Based on my hydrographs, I would classify annual flood frequency at low, medium, and high elevation as >12, 8–12, and <8 times per year, respectively. Implementing this planting design, which is based on species-specific flood tolerance and flooding depth, duration, and timing in a bottomland, should increase the likelihood of restoration success.

LITERATURE CITED

Albrecht, G., and S. Biemelt. 1998. A comparative study on carbohydrate reserves and ethanolic fermentation in the roots of two wetland and non-wetland species after commencement of hypoxia. Physiologia Plantarum 104:81–86.

Anderson, P. H., and S R. Pezeshki. 1999. The effects of intermittent flooding on seedlings of three forest species Photosynthetica 37:543–552.

Anella, L. B., and T. H. Whitlow 2000. Photosynthetic response of flooding of acer rubrum seedlings from wet and dry sites. American Midland Naturalist 143:330–341.

Angelov, M N., S. J. S Sung, R. L. Doong, W R. Harms, P. P Kormanik, and C. C. Black Jr. 1996. Long- and short-term flooding effects on survival and sink-source relationships of swamp-adapted tree species. Tree Physiology 16:477–484.

Ashwell, G 1957. Colorimetric analysis of sugars. Methods in Enzymology 3:73–105.

Baldassarre, G A. and E. G. Bolen. 1994. Waterfowl ecology and management, Wiley, New York, New York, USA.

Barras, S. C., R. M. Kaminski, and L. A. Brennan. 1996. Acorn selection by female wood ducks Journal of Wildlife Management 60:592–602

Broadfoot, W. M., and H. L. Williston. 1973. Flooding effects on southern forests. Journal of Forestry 71 584–587.

Burke, M K , and J. Chambers. 2003. Root dynamics in bottomland hardwood forests of the Southeastern United States Coastal Plain. Plant and Soil 250:141–153.

______, S. L. King, D. Gartner, and M. H. Eisenbies. 2003. Vegetation, soil, and flooding relationships in a blackwater floodplain forest. Wetlands 23:988-1002.

Burkett, V. R., R. O. Draugelis-Dale, H. M. Williams, and S. H. Schoenholtz. 2005. Effects of flooding regime and seedling treatment on early survival and growth of Nuttall oak. Restoration Ecology 13:471–479.

Cairns, J. Jr., M. M. Brinson, R L. Robert, W. B. Parker, R. E. Turner, and P. V. Winger. 1981. Impacts associated with southeastern bottomland hardwood forest ecosystems. Pages 303-332 *in* J. R. Clark, and J Benforado editors. Wetlands of bottomland hardwood forests. Elsevier Scientific, Amsterdam, the Netherlands.

Castonguay, Y., P. Nadeau, and R. Simard. 1993 Effects of flooding on carbohydrate and ABA levels in roots and shoots of alfalfa. Plant Cell Environment 16:695–702

Chamberlain, M. J. and B. D. Leopold. 2005. Survival and cause-specific mortality of hardwood seedlings in the Mississippi Alluvial Valley. Pages 137–141 *in* L H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri, Gaylord Memorial Laboratory Special Publication Number 10, Puxico, Missouri, USA.

Conner W. H., K. W McLeod, and J. K McCarron. 1998. Survival and growth of seedlings of four bottomland oak species in response to increases in flooding and salinity. Forest Science 44:618–624

______, ______, and ______. 1997. Flooding and salinity effects on growth and survival of four common forested wetland species. Wetlands Ecology and Management 5·99–109.

Crawford, R. M. M., and R. Braendle. 1996. Oxygen deprivation stress in a changing environment. Journal of Experimental Botany 47:145–159.

Day, C. P. III., J. D. Hodges, S. H. Schoenholtz, and K. L. Belli. 1998. Influence of hydrology on artificial regeneration of oaks in the Mississippi Delta. Pages 295–299 *in* T. A. Waldrop, editor. Proceedings of the 9th Biennial Southern Silvicultural Research Conference, General Technical Report SRS-20, United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina USA.

Donovan, L. A., K. W. McLeod, K. C. Sherrod, and N. J. Stumpf. 1988. Response of woody swamp seedlings to flooding and increased water temperatures I: Growth, biomass, and survivorship. American Journal of Botany 75:1181–1190.

Filer, T. H. 1975. Mycorrhizae and soil microflora in a green tree reservoir. Forest Science 24:36–39.

Filer, T. H. Jr. 1990. Quercus nuttallii Palmer Nuttall Oak. *in* R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. United States Department of Agriculture, Forest Service, Washington, DC. http://www.na.fs.fed.us/Spfo/pubs/silvics_manual/table_of_contents.htm

Franklin, J. A , N N. V. Kav, W. Yajima, and D. M. Reid. 2005. Root temperature and aeration effects on the protein profile of canola leaves. Crop Science 45:1379–1386

Fredrickson, L. H., and D. L. Batema. 1993. Green-tree reservoir management handbook. Gaylord Memorial Laboratory Wetland Management Series. No. 1. Univ. of Missouri, School of Natural Resources, Gaylord Memorial Laboratory, Puxico, MO.

Gosselink, J. G., and L. C. Lee. 1989. Cumulative impact assessment in bottomland hardwood forests. Wetlands 9·89–174.

Gravatt, D. A., and J. C. Kirby. 1998. Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. Tree Physiology 18:411–417.

Gray, M. J. and R. M. Kaminski. 2005. Effect of continuous versus periodic winter flooding on survival of oak seedlings in Mississippi greentree reservoirs. Pages 487–493 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri, Gaylord Memorial Laboratory Special Publication Number 10, Puxico, Missouri, USA.

______, ______, G. Weerakkody, B D. Leopold, and K C. Jensen. 1999. Aquatic invertebrate and plant responses following mechanical manipulations of moist-soil habitat. Wildlife Society Bulletin 27.770–779

______, and L. M. Smith. 2005. Influence of land use on postmetamorphic body size of playa lake amphibians. Journal of Wildlife Management 69:515–524.

Hall, T F., and G. E. Smith. 1955. Effects of flooding on woody plants, West Sandy dewatering project, Kentucky Reservoir. Journal of Forestry 53:281–285.

Hendrix, D. L. 1993. Rapid extraction and analysis of nonstructural carbohydrates in plant tissues. Crop Science 33:1306–1311.

Hodges, J. D. 1997. Development and ecology of bottomland hardwood sites. Forest Ecology and Management 90:117–125.

Hook, D. D 1984. Waterlogging tolerance of lowland tree species of the south. Southern Journal of Applied Forestry 8:136–148.

_______, and C. L. Brown. 1973. Root adaptations and relative flood tolerance of five hardwood species. Forest Science 19:225–229.

Hosner, J. F , and S. G. Boyce. 1962. Tolerance to water saturated soil of various bottomland hardwoods. Forest Science 8.180–186.

Islam, M. A., and S. E. MacDonald. 2004. Ecophysiological adaptations of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) seedlings to flooding. Trees 18.35–42.

Jackson, M. B., and M. C. Drew. 1984. Effects of flooding on growth and metabolism of herbaceous plants. Pages 47–128 *in* T. T. Kozlowski, editor. Flooding and plant growth. Academic, Orlando, Florida USA.

Keeland, B. D., W. H. Conner, and R. R. Sharitz. 1997. A comparison of wetland tree growth response to hydrologic regime in Louisiana and South Carolina. Forest Ecology and Management 90:237-250.

Kercher, S. M., and J. B. Zedler. 2004 Flood tolerance of wetland angiosperms: a comparison of invasive and noninvasive species. Aquatic Botany 80:89–102.

King, S L. 1994. Effects of water regimes and green-tree reservoir management on succession of bottomland hardwoods. Ph.D Dissertation, Texas A&M University, College Station, Texas.

King, S L., J. A. Allen., and J. W McCoy. 1998 Long-term effects of a lock and dam and greentree reservoir management on a bottomland hardwood forest. Forest Ecology and Management 112:213–226.

Kozlowski T. T., and S. G. Pallardy. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Botanical Review 68.270–334.

______, and ______ 1984. Effects of flooding on water, carbohydrates, and mineral relations. Pages 165–194 *in* T. T. Kozlowski, editor. Flooding and plant growth Academic, Orlando, Florida, USA.

_______ 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands 22:550–561.

______. 1997. Responses of woody plants to flooding and salinity. Tree Physiology Monograph No. 1. http://www.heronpublishing.com/tp/monograph/kozlowski.pdf.

______. 1992. Carbohydrate source and sinks in woody plants Botanical Review 58.107–222

______. 1984. Response of woody plants to flooding. Pages 129–164 *in* T T. Kozlowski, editor. Flooding and plant growth. Academic, Orlando, Florida USA.

Kroen, W K., D. M. Pharr, and S C. Huber. 1991. Root flooding of muskmelon *(cucumis-melo*L) affects fruit sugar concentration but not leaf carbon exchange-rate. Plant and Cell Physiology 32.467–473.

Kreuzwieser, J., E. Papadopoulou, and H. Rennenberg. 2004. Interaction of flooding with carbon metabolism of forest tress Plant Biology 6:299–306.

______, S. Fürniss, and H. Rennenberg. 2002. Impact of waterlogging on the N-metabolism of flood tolerant and non-tolerant tree species. Plant, Cell and Environment 25:1039–1049.

Laan, P , A. Smolders, and C. W. P. H. Blom. 1991. The relative importance of anaerobiosis and high iron levels in the flood tolerance of *Rumex* species. Plant and Soil 136·153-161

Langdon, O. G., J. P. McClure, D. D Hook, J. M. Crockett, and R. Hunt. 1981 Extent, condition, management, and research needs of bottomland hardwood-cypress forests in the southeastern United States. Pages 71-86 *in* J. R. Clark and J Benforado, editors. Wetlands of bottomland hardwood forests. Elsevier Scientific, Amsterdam, Netherlands.

MacDonald, P. O., W. E. Frayer, and J. K. Clauser. 1979. Documentation, chronology, and future projections of bottomland hardwood habitat losses in the Lower Mississippi Alluvial Plain U.S. Department of the Interior, Fish and Wildlife Service, Washington, D. C. Vols. 1 and 2.

McCasland, C. S., S. R. Pezeshki, and R. J. Cooper. 1998. Relationship between flooding regime and increased herbivory of Nuttall oak. Pages 304–308 *in* T. A. Waldrop, editor Proceedings of the 9th Biennial Southern Silvicultural Research Conference, General Technical Report SRS-20, United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA.

McCurry, J. R., M. J. Gray, J. A. Franklin, and D. C. Mercker 2006. Relationship of oak seedling height and diameter with bottomland elevation. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 59.

McKevlin, M. R., D. D. Hook, and A. A. Rozelle 1998. Adaptations of plants and soil waterlogging. Pages 173–203 *in* M. G. Messina and W. H. Conner editors. Southern Forested Wetlands. Ecology and Management. CRC Press, Boca Raton, Florida, USA.

McKnight, J S., D. D. Hook, O G. Langdon, and R. L. Johnson. 1981. Flood Tolerance and related characteristics of tress of bottomland forests of the southern United States Pages 26–69 *in* J. R. Clark and J. Benforado, editors. Wetlands of bottomland hardwood forests. Elsevier Scientific, Amsterdam, Netherlands.

Mcleod, K. W., M. R. Reed, and L. D. Wike. 2000. Elevation, competition control, and species affect bottomland forest restoration. Wetlands 20· 162–168.

Megonigal, J. P., and F. P. Day. 1992 Effects of flooding on root and shoot production of bald cypress in large experimental closures. Ecology 73: 1182–1193.

Milton, J. S , and J. C. Arnold. 1995 Introduction to probability and statistics, Third edition. McGraw-Hill, New York, USA.

Mitsch, W. J. and J. G Gosselink. 2000. Wetlands, Third edition. John Wiley, New York, New York, USA.

Morris, R C 1965. Overcup oak (*Quercus lyrata* Walt.). Pages 600–602 *in* H. A. Fowells, editor. Silvics of forest trees of the United States, United States Department of Agriculture, Agriculture Handbook 271. Washington D.C.

Nash, L. J., and W. R. Graves. 1993. Drought and flood stress effects on plant development and leaf water relations of 5 taxa of trees native to bottomland habitats. Journal of the American Society for Horticultural Science 118:845–850.

Nicolas, E , A. Torrecillas, J. Dell'Amico, and J. Alarcon 2005. The effect of short term flooding o the sap flow, gas exchange and hydraulic conductivity of young apricot trees. Trees-Structure and Function 19:51–57.

Parker, J 1950. The effects of flooding on the transpiration and survival of some southeastern forest tree species. Plant Physiology 25:453–460.

Pezeshki, S. R., R. D. DeLaune, and P. H. Anderson. 1999. Effect of flooding on elemental uptake and biomass allocation in seedlings of three bottomland tree species. Journal of Plant Nutrition 22·1481–1494.

_______, and _______ 1998. Responses of seedlings of selected woody species to soil oxidation-reduction conditions Environmental and Experimental Botany 40:123-133.

_______, J. H Pardue, R D. Delaune, and E. D. Moser. 1996. Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. Tree Physiology 16:453–458.

Ponnamperuma, F. N. 1984 Effects of flooding on soils. Pages 10-47 T. T. Kozlowski, editor. Flooding and plant growth. Academic, Orlando, Florida, USA.

Schoenholtz, S. H., J. P. James, R. M. Kaminski, B D. Leopold, and A. W. Ezell. 2001. Afforestation of bottomland hardwoods in the lower Mississippi Alluvial Valley: Status and Trends. Wetlands 21:602–613.

Schlaegel, B.E. 1990. *Quercus phellos* L. willow oak. Pages 715-720. *in* R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. United States Department of Agriculture, Forest Service, Washington, DC.

Sease, C. S., and M E Springer. 1957. Soil Map of the West Tennessee Experiment Station, Jackson, Tennessee. United States Department of Agriculture, Soil Conservation Service, Washington, D.C

Solomon, J D. 1990. *Quercus lyrata* Walt. Overcup oak. *in* R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. United States Department of Agriculture, Forest Service, Washington, DC. http://www.na.fs fed.us/Spfo/pubs/silvics_manual/table_of_contents.htm

Stanturf, J A., S. H. Schoenholtz, C. J Schweitzer, and J. P Shepard. 2001. Achieving restoration success: myths in bottomland hardwood forests. Restoration Ecology 9:189–200.

Stokes, M. E., C. S. Davis, and G. G Koch. 2000 Categorical data analysis using the SAS® system. SAS Institute, Cary, North Carolina, USA

Streng, D. R., J. S. Glitzenstein, and P. A Harcombe. 1989. Woody seedling dynamics in an east Texas floodplain forest. Ecological Monographs 59: 177–204.

Su, P. H., T. H. Wu, and C. H. Lin. 1998. Root sugar level in luffa and bitter melon is not referential to their flooding tolerance. Botanical Bulletin of Academica Sinicia 39: 175–179.

Turner, R. E , S. W. Forsythe, and N. J. Craig. 1981 Bottomland hardwood forests of the southeastern United States. Pages 13-28 *in* J. R. Clark, and J. Benforado editors. Wetlands of bottomland hardwood forests. Elsevier Scientific, Amsterdam, Netherlands.

Westfall, P. H., R. D. Tobias, D. Rom, R. D. Wolfinger, and Y. Hochberg 1999. Multiple comparisons and multiple test using the SAS® system. SAS Institute Inc., Cary, North Carolina, USA

Wharton, C. H., V. W. Lambou, J Newson, P V. Winger, L. L. Gaddy, and R. Mancke. 1981 The fauna of bottomland hardwoods in southeastern United States. Pages 87–160 *in* J R. Clark and J Benforado, editors. Wetlands of bottomland hardwood forests: proceedings of a workshop on bottomland hardwood forest wetlands of the southeastern United States. Elsevier, New York, New York, USA.

Whitlow, T. H., and R. W. Harris. 1979. Flood tolerance in plants: a state-of-the-art review. U.S. Army Corps of Engineers, Waterways Experiment Station, Environmental Laboratory, Vicksburg, Mississippi, USA. Technical Report E-79-2.

Young, G. L., B. L. Karr, B. D. Leopold, and J. D. Hodges. 1995. Effect of greentree reservoir management on Mississippi bottomland hardwoods. Wildlife Society Bulletin 23:525–531.

VITA

Jonathan R. McCurry was born in Knoxville, Tennessee on September 02, 1981 to J. Dennis and Linda O. McCurry. He was raised on Fort Loudoun Lake in Louisville, TN, where under the wing of his father he learned to appreciate the outdoors and enjoy many of the activities it has to offer. At an early age, and continuing to the present, he accompanied his father on hunting and fishing trips throughout the Southeast. Jonathan took this love and appreciation for the outdoors to the mountains of Colorado in the fall of 1999, where he attended Western State College of Colorado in Gunnison and graduated with a Bachelor of Arts in Biology with an environmental biology and ecology emphasis in spring of 2003 After graduation, Jonathan took a year off to rehabilitate an injured knee and to enjoy life prior to beginning his Master of Science degree at the University of Tennessee in the fall of 2004. Working under the direction of Dr. Matthew J. Gray, Jonathan earned a M.S. in Wildlife and Fisheries Science in December 2006