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The effects of hydrologic modifications on floodplain forest tree recruitment and growth in the Mississippi River Alluvial Valley, USA

Hugo Gee
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THE EFFECTS OF HYDROLOGIC MODIFICATIONS ON FLOODPLAIN
FOREST TREE RECRUITMENT AND GROWTH IN THE MISSISSIPPI RIVER
ALLUVIAL VALLEY, USA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University
Agricultural and Mechanical College
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in

The School of Renewable Natural Resources

by
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ABSTRACT

Floodplains forests are productive and diverse ecosystems characterized by frequent riverine flooding. Levees and dams have eliminated or altered riverine flooding which can potentially affect floodplain tree recruitment and growth. Increased light availability from canopy disturbances may increase photosynthesis given sufficient soil moisture, but information on the combined effect of canopy disturbances and hydrologic modifications on tree recruitment and growth is lacking. I used dendrochronological techniques to reconstruct tree recruitment, growth (*Quercus lyrata, Fraxinus pennsylvanica*), and canopy disturbance patterns over a 90-year period at several floodplains in the Mississippi River Alluvial Valley, USA: an unleveed site below dams and two sites within a ring levee. At the site below dams, flood frequency increased in the late non-growing season during the post-dam period, but decreased in the late growing season, although stage may have kept water in the root zone. Mean flood duration of pre-dam and post-dam periods was similar. Interannual variability in flooding may have resulted in recruitment of tree species of varying flood tolerances. Recruitment of shade-tolerant species (*Celtis laevigata, Ulmus americana*) was common during periods of infrequent canopy disturbances, but recruitment and growth of moderately shade-tolerant species such as *F. pennsylvanica* increased following widespread canopy disturbances. Unlike *Q. lyrata, F. pennsylvanica* had positive relationships with river stage during the late growing season in the post-dam period, suggesting riverine influence via groundwater links. At sites within a ring levee, flooding was short duration with longer duration flooding at lower elevations due to ponding of precipitation. Recruitment of flood-intolerant species such as *C. laevigata* expanded after levee construction except at
lower elevations where recruitment of flood-tolerant species such as *Q. lyrata* followed canopy disturbances. In the post-levee period, growth of *Q. lyrata* and *F. pennsylvanica* was closely correlated with surface soil moisture and increased following canopy disturbances. Growth maintained strong relationships with spring stage at low elevations despite the elimination of overbank flooding, suggesting riverine influence via groundwater links. Results of my study indicate that broad-scale hydrologic modifications affected floodplain forest recruitment and growth but local-scale factors such as topography, canopy disturbances, surface soil moisture, and groundwater mediated these effects.
CHAPTER 1: GENERAL INTRODUCTION

1.1 Background

Floodplain forests are among the most productive and diverse ecosystems in the world (Tockner and Stanford 2002). Riverine flooding is essential to the functioning of these ecosystems by transferring water and nutrient-rich sediments between rivers and their floodplain (Pringle 2003). The frequency, timing, depth, and duration of riverine flooding are the primary determinants of tree recruitment (Streng et al. 1989). Changes in flood patterns lead to shifts in tree recruitment and forest stand development (Johnson et al. 2012).

Variation in tree recruitment is constrained by species-specific differences in life-history strategies related to seed production, seed dispersal, seedling emergence, seedling survivorship, and seedling and sapling growth (Streng et al. 1989, Jones et al. 1994, Battaglia et al. 2004, Lin et al. 2004). Few species can tolerate the combined stress of flooding and low light availability, which suggest that species-specific tradeoffs in flood and shade tolerance are important drivers of tree recruitment (Hall and Harcombe 1998, Battaglia and Sharitz 2006). Recruitment also has a stochastic element – for example, the timing of seed arrival and germination in relation to flooding (Streng et al. 1989). Variability in tree recruitment is also related to temporal and spatial effects of a variety of biotic and environmental factors. For instance, seedling survival has been shown to be influenced by competition, disease, herbivory, flooding, and drought (Streng et al. 1989, Jones et al. 1994, Rossell et al. 2005).

Artificial levees, dams, and other flood control activities have eliminated or altered riverine flooding (Wharton et al. 1982). Levees have disconnected floodplains
from riverine flooding with surface flooding now largely dependent on precipitation (Gergel et al. 2002). Dams have altered streamflow patterns and subsequent surface and subsurface water levels on floodplains downstream (Stallins et al. 2010). These flood control activities have altered river stage (Biedenharn and Watson 1997, Jemberie et al. 2008), which may affect the floodplain water table at a variety of spatial and temporal scales (Burt et al. 2002a, Burt et al. 2002b). Altered surface and subsurface water levels in floodplain forests can potentially affect patterns of tree recruitment (Gergel et al. 2002, Lite and Stromberg 2005), growth (Young et al. 1995, Keim and Amos 2012), and stand development (Johnson et al. 2012).

Most studies examining the effects of hydrologic modifications on tree recruitment and growth have focused on a single site and few have examined the effects of long-term hydrologic variability on tree recruitment and growth (Gergel et al. 2002, Stallins et al. 2010, Palta et al. 2011). Increased light availability from canopy disturbances can enhance photosynthesis (Kolb et al. 1990, Hall 1993), but long-term information on the combined effect of canopy disturbances and hydrologic modifications on tree recruitment and growth is uncommon. Long-term studies on tree recruitment and growth following hydrologic modifications at multiple sites can give insights into species-specific responses to flooding and light gradients (Streng et al. 1989).

1.2 Research Objective

My study examines the influence of hydrologic modifications and canopy disturbances on tree recruitment and growth in floodplain forests. To do this, I used dendrochronological techniques to reconstruct recruitment, growth, and canopy
disturbances at several floodplains with relatively few to many hydrologic modifications in the Mississippi River Alluvial Valley (MAV).

1.3 Study Area

The MAV in the USA extends from the confluence of the Ohio and Mississippi rivers at Cairo, Illinois to the Gulf of Mexico Coast of Louisiana, encompassing approximately 10 million ha (Fredrickson 2005). The MAV has been the focus of flood control and channel stabilization efforts since the arrival of early European settlers and is currently under the direction of the US Army Corps of Engineers (Biedenharn and Watson 1997). By the 1900s, a total of 6,880 km of levees had been established in the MAV and virtually all of the 2.8 million ha of remaining floodplain forest has been subjected to some form of hydrologic modification (Interagency Floodplain Management Review Committee 1994).

1.3.1 Study Stands

My study stands are closed canopy forests in Arkansas [Dagmar Wildlife Management Area (WMA; Figure 1A); White River National Wildlife Refuge (NWR; Figure 1B)] and Louisiana [Bayou Cocodrie NWR (Figure 1C); Red River WMA (Figure 1D); Cat Island NWR (Figure 1E)] in the MAV. Dagmar WMA is relatively unaffected by hydrologic modifications, but the study stand does not receive overbank from Cache River. Dam operations on the upper White River watershed have reduced flood duration at White River NWR, but floodplains remain connected to riverine flooding (Bedinger 1971). Channelization of the Mississippi River has decreased annual high stages and
Figure 1: Map of study site locations at (A) Dagmar Wildlife Management Area (WMA), Arkansas (latitude: 34.887401°; longitude: 650597.41°); (B) White River National Wildlife Refuge (NWR), Arkansas (latitude: 34.34288°, longitude: -91.099336°); (C) Bayou Cocodrie National Wildlife Refuge (NWR), Louisiana (latitude: 31.537789°, longitude: -91.61481°); (D) Red River Wildlife Management Area (WMA), Louisiana (Highest elevation – latitude: 31.257855°; longitude: -91.759138°; Mid-elevation – latitude: 31.296633°, longitude: -91.69186°; Lowest elevation – latitude: 31.269699°, longitude: -91.720711°); and (E) Cat Island National Wildlife Refuge (NWR), Louisiana (latitude: 30.774845°, longitude: -91.451582°).
increased annual low stages downstream at Cat Island NWR (Jemberie et al. 2008). Bayou Cocodrie NWR and Red River WMA are disconnected from overbank and backwater flooding of the Mississippi, Red, and Black rivers by a ring levee.

1.4 Dissertation Overview

In chapter 2, I reconstructed tree recruitment and canopy disturbance patterns on three floodplains in the MAV: an unleveed floodplain below a dam (White River NWR) and two floodplains protected by levees (Red River WMA, Bayou Cocodrie NWR). My objectives were (1) to identify differences in surface and subsurface hydrology of various topographic features; and (2) to identify species-specific responses to flooding and canopy disturbances and to determine if recruitment patterns have changed following dam or levee construction. In chapter 3, I reconstructed growth response of overcup oak (Quercus lyrata), a relatively flood-tolerant tree species, to altered flood regimes on floodplains with relatively few to many hydrologic modifications (Dagmar WMA, White River NWR, Cat Island NWR, Red River WMA). My objectives were (1) to identify differences in surface and subsurface hydrology on various geomorphic settings; and (2) to identify responses of overcup oak growth to river stage, climate, soil moisture, and canopy disturbances and to test whether relationships of growth to these variables changed following hydrologic modifications. In chapter 4, I reconstructed growth response of green ash (Fraxinus pennsylvanica), a common floodplain tree species, to hydrologic modifications (White River NWR, Bayou Cocodrie NWR) across floodplain topography. My objectives were (1) to identify differences in surface and subsurface hydrology of various topographic features; and (2) to identify responses of green ash
growth to river stage, climate, soil moisture, and canopy disturbances and I tested whether relationships of growth to these variables changed following dam (White River NWR) or levee construction (Bayou Cocodrie NWR). In chapter 5, I summarized the conclusions of the previous chapters, suggested avenues of future research, and present the management implications of my study.

1.5 Literature Cited


Hall, R.B.W., 1993. Sapling growth and recruitment as affected by flooding and canopy gap formation in a river floodplain forest in southeast Texas. Ph.D Diss., Rice University, Houston, TX.


CHAPTER 2: THE EFFECT OF HYDROLOGIC MODIFICATIONS ON FLOODPLAIN FOREST STAND DEVELOPMENT IN THE MISSISSIPPI RIVER ALLUVIAL VALLEY, USA

2.1 Introduction

Floodplain forest stand development is primarily influenced by changes in flood regime and light availability, which affects tree recruitment (Hall and Harcombe 1998, Battaglia and Sharitz 2006). Hodges (1997) described natural patterns of stand development in the southeastern USA based on changes in rates of deposition and its effect on the elevation of the floodplain. As elevation rises compared to river stage, the floodplain receives less frequent overbank flooding and species of lower flood tolerance become more common in the forest community. Hodges (1997) also described how the frequency, timing, and spatial extent of canopy disturbances can alter a forest’s position along these developmental pathways by changing light availability. Several studies have shown that floodplain forests on the Coastal Plain of the USA tend to be dominated by shade-intolerant species because of frequent large-scale canopy disturbances (Jones et al. 1994, Battaglia et al. 1999). In contrast, small canopy openings limit recruitment of shade-intolerant species on frequently flooded forests further inland in the Mississippi River Alluvial Valley (MAV) of the USA (King and Antrobus 2005, Oliver et al. 2005).

Levees, dams, and other hydrologic modifications have eliminated or altered overbank flooding and subsequent delivery of nutrient-rich sediments (Pringle 2000). The effect of levees and dams on floodplain forest stand development depends on specific changes to the flood regime and the recruitment response of individual species based on flood tolerance (Gergel 2002, Gergel et al. 2002). Several studies have reported increased recruitment of flood-intolerant species after levees or dams eliminated or reduced
overbank flooding (Reily and Johnson 1982, Gergel et al. 2002, Lite and Stromberg 2005). Furthermore, some studies have indicated that the effect of hydrologic modifications on species distributions can vary by topographic feature because differences in elevation, drainage, and soil texture affect the flood regime (Dewine and Cooper 2007, Stallins et al. 2010). These studies highlight the importance of considering broad- and local-scale hydrologic effects on floodplain forest stand development.

Most studies examining stand development on floodplains with altered flood regimes have focused on a single site and few have examined recruitment response over long periods of hydrologic variability (Gergel et al. 2002, Stallins et al. 2010). Increased light availability from canopy disturbances can enhance tree recruitment (Denman and Karnuth 2005, King and Antrobus 2005), but information on the combined effect of canopy disturbances and hydrologic modifications on long-term patterns of recruitment is lacking. Long-term studies on recruitment patterns following hydrologic modifications at multiple sites can give insights into species-specific responses to flooding and light gradients (Streng et al. 1989).

In this study, I used dendrochronological techniques to reconstruct tree recruitment [> 5 cm diameter at breast height (DBH)] and canopy disturbance patterns over a 90-year period at three floodplain forests in the MAV: an unleved floodplain below a dam and two floodplains protected by levees. The study objectives were: (1) to identify differences in surface and subsurface hydrology of various topographic features; and (2) to identify species-specific responses to flooding and canopy disturbances and to determine if recruitment patterns have changed following dam or levee construction.
2.2 Materials and Methods

2.2.1 Study Sites

I reconstructed tree recruitment and canopy disturbance patterns in closed canopy forests in Arkansas (White River National Wildlife Refuge [NWR]) and Louisiana (Bayou Cocodrie National Wildlife Refuge [NWR] and Red River Wildlife Management Area [WMA]), USA (Figure 2). Prior to dam or levee construction, high annual river stages flooded study sites in winter and spring, but river stages were below the elevation of the natural levee during the remainder of the year. Dams completed in 1966 on the upper reaches of the White River have reduced flood duration at White River NWR (hereafter referred to as White River; Figure 2A), but floodplains remain connected to riverine flooding (Bedinger 1971). A ring levee completed from 1940-1955 has disconnected Bayou Cocodrie NWR (hereafter referred to as Bayou Cocodrie; Figure 2B) and Red River WMA (hereafter referred to as Red River; Figure 2C) from overbank and backwater flooding of the Mississippi, Red, and Black rivers.

The geomorphic setting, topography, and soils vary within and among study sites. The geomorphic setting includes Late Wisconsin valley train deposits (White River), meander scroll deposits of an abandoned course of the Mississippi River (Bayou Cocodrie), point bar (Red River – highest elevation stand) and backswamp deposits of the Mississippi River (Red River – mid-elevation stand, lowest elevation stand) (Saucier 1994). The topography at White River and Bayou Cocodrie is characterized by undulating ridges and swales, interspersed with broad flats. The topography at Red River is characterized by broad flats; three stands were selected representing the highest, mid-, and lowest elevation sites. Soils are classified as somewhat poorly drained [White River –
Figure 2. Study sites at (A) White River National Wildlife Refuge (NWR), Arkansas (Latitude: 34.34288, Longitude: -91.099336); (B) Bayou Cocodrie National Wildlife Refuge (NWR), Louisiana (latitude: 31.537789, longitude: -91.61481); and (C) Red River Wildlife Management Area (WMA), Louisiana (Highest elevation – latitude: 31.257855; longitude: -91.759138; Mid-elevation – latitude: 31.296633; longitude: -91.69186; Lowest elevation – latitude: 31.269699, longitude: -91.720711).
Yancopin silty clay loam (Typic Endoaquepts); Bayou Cocodrie – Alligator clays (Chromic dystraquerts) on ridges and swales, and Tensas soils (Chromic Vertic Epiaqualfs) on flats] with the exception of poorly drained soils at Red River [Sharkey clay (thermic Chromic Epiaquerts)] (Martin et al. 1988, NRCS 2008).

2.2.2 Hydrology

To determine hydrologic characteristics at each site, I measured surface and subsurface water levels at monitoring stations with the number of stations varying by topographic feature (ridge, flat, and swale) or stand. I established monitoring stations along transects perpendicular to the river channel crossing each ridge and swale and spread across flats to account for even small differences in elevation. Each station consisted of surface and subsurface water measurements using Odyssey™ capacitance water level probes (accuracy = 0.8-mm; Dataflow Systems PTY Ltd, NZ) that electronically recorded surface and subsurface water levels every 10 minutes for at least one year. I measured surface water levels within a 3.2-cm diameter x 1.5-m length PVC pipe secured to a 5-10 cm diameter tree with rope. I measured subsurface water levels to a depth of 2 m within a 3.2-cm diameter x 3.0-m length PVC pipe casing. I filled the inside of the well bore outside the casing with sand to allow entry of water and filled the top 0.3 m with bentonite clay to prevent infiltration of precipitation. Water entered each pipe through holes measuring 7 mm in diameter at four locations at 10-cm intervals over the length of each pipe and fine solar screen mesh covered holes to prevent sediment from filling the pipe. For monitoring stations, I calculated the number of flood days during the growing season (Arkansas sites – April-September; Louisiana sites – March-
September) and number of days within the root zone during the growing season (approximately 1 m from the forest floor; Phipps 1979).

To determine long-term changes in flood duration at White River, I extrapolated the number of flood days during the growing season (April-September) from river stage data for the highest (44.3 m above msl) and lowest elevation (41.5 m above msl) sampling plots on the floodplain by assuming the difference between stage readings and daily water levels during data collection did not vary (Middleton 2009). I consider this to be a conservatively low estimate of the number of flood days during the growing season because floodwaters may pond in low lying, poorly drained sites. Student’s t-tests were used to compare growing season flood days before (1932-1965) and after (1966-2008) completion of the dams for White River. I did not extrapolate the number of flood days during the growing season for Bayou Cocodrie and Red River because levees have decoupled surface water levels from river stage.

2.2.3 Vegetation Sampling

During summer 2006 to spring 2007, I conducted a forest inventory to determine community composition and structure at each study site. At White River and Bayou Cocodrie, I established a total of 30 sampling plots on each topographic feature (ridge, swale, and flat) as identified using satellite images, topographic maps, and ground truthing. I established plots 50-m apart along ridge crests or at the lowest point of swales, and on a 50-m grid for flats (Figure 3). At Red River, I established a total of 30 sampling plots at each stand on 125-m grids because flats were larger in area than at other sites.
Figure 3: Sampling design stratified by topographic feature (ridge, flat, and swale) on a hypothetical floodplain with meander scroll deposits.

My vegetation sampling plots consisted of two concentric circular plots: a 0.04-ha plot (11.3-m radius) for all live trees ≥ 10 cm DBH and a 0.01-ha plot (5.6-m radius) for trees ≥ 5 cm DBH and < 10 cm DBH. Within sampling plots, I identified all trees to species and classified each tree into four crown classes (dominant, codominant, intermediate, and suppressed) based on the amount and direction of intercepted light (Smith 1986). I measured the heights of 2-3 dominant or codominant trees at each sampling plot using a Haglöf Vertex IV Hyposmeter (height resolution = 0.1 m).

I calculated a modified importance value for each species (Curtis and McIntosh 1951) by crown class at each topographic feature or stand. I calculated the importance value as:

Relative density: stem density of a species ÷ total stem density
Relative dominance: basal area of a species ÷ total basal area
Importance value = Relative density + Relative dominance x 100%  \hspace{1cm} (1)

I used generalized linear models to determine if species importance values at each study site (13 models) could be predicted by sampling plot elevation, topographic feature or stand, and the interaction between elevation and topographic feature or stand (elevation*topographic feature or stand). I used a log link function as the linearizing transformation and normal probability distribution for interpretation of individual models for each species.

To determine sampling plot elevation, I georeferenced (position accuracy 5-8 m) each plot center using the global positioning system (GPS) and referenced coordinates at plot centers with light detection and ranging (LIDAR) data (LSU CADGIS Research Laboratory 2006) with a root mean square error of 9.8-12.5 cm (Watershed Concepts 2006). I calculated elevations at plots centers as the average of the four nearest 5-m x 5-m pixels to compensate for coarse position accuracy of the GPS. LIDAR data was unavailable at White River, so relative elevations at plot centers were based on measured differences in water depth during a flood event in spring 2010 which assuming a level water level was referenced with known elevation points at a benchmark at St. Charles, Arkansas.

2.2.4 Recruitment Patterns

To reconstruct recruitment patterns, I determined the age of 3-5 common species per study site (1,122 trees total) with varying flood and shade tolerances (Table 1). I collected increment cores from at least one tree from each 10-cm diameter class.
Table 1. Flood and shade tolerance ratings of tree species sampled at White River National Wildlife Refuge (1; Arkansas), Bayou Cocodrie National Wildlife Refuge (2; Louisiana), and Red River Wildlife Management Area (3; Louisiana) (Hosner and Boyce 1962, McKnight et al. 1981, Hook 1984, Burns and Honkala 1990).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Symbol</th>
<th>Flood tolerance</th>
<th>Shade tolerance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green ash1,2</td>
<td>FRPE</td>
<td>Moderate to tolerant</td>
<td>Moderate</td>
</tr>
<tr>
<td>Nuttall oak1,2</td>
<td>QUTE</td>
<td>Moderate</td>
<td>Intolerant</td>
</tr>
<tr>
<td>American elm1,2</td>
<td>ULAM</td>
<td>Moderate</td>
<td>Tolerant</td>
</tr>
<tr>
<td>Sugarberry1,2,3</td>
<td>CELA</td>
<td>Intolerant</td>
<td>Very tolerant</td>
</tr>
<tr>
<td>Sweetgum2</td>
<td>LIST</td>
<td>Intolerant to moderate</td>
<td>Intolerant</td>
</tr>
<tr>
<td>Overcup oak1,3</td>
<td>QULY</td>
<td>Tolerant</td>
<td>Moderate</td>
</tr>
<tr>
<td>Honeylocust3</td>
<td>GLTR</td>
<td>Moderate</td>
<td>Intolerant</td>
</tr>
</tbody>
</table>

(minimum 10 cm DBH) to sample the full range of diameters for each species (Appendix A). For each tree, I obtained two cores at 50-cm height when possible to assist in cross-dating. If basal flaring or signs of rot were present, I obtained cores higher on the stem. I returned all tree cores to the laboratory to be oven dried, mounted on core holders, and sanded with increasingly finer grit sandpaper until tree-ring boundaries were visible under a microscope (Stokes and Smiley 1996, Orvis and Grissino-Mayer 2002).

I determined ages of increment cores by tree-ring counts and cross-dated ring widths for each species using narrow signature years (Yamaguchi 1991). To improve the accuracy of tree age determination, I used a pith offset estimation technique that matches the growth pattern from cores where the pith was hit to those where the pith was missed (Villalba and Veblen 1997). Furthermore, I adjusted tree ages of all cores by the mean time to reach the coring height based on a stem analysis conducted at 10-cm increments from the root collar to 1.4 m (Appendix B). For the stem analysis, I randomly collected 3-12 saplings (< 5 cm DBH) of each species from closed canopy forests at Bayou Cocodrie and Red River. Trees could not be aged to the exact year which prevents tying recruitment to particular flood events, so I binned tree ages into 5-year establishment periods (1895-1994) to minimize errors in age determination. I used diameter
distributions and age-diameter models to estimate ages of trees that were not cored. I modeled the age-diameter relationship using third-order polynomial regression models constrained to intercept zero (Condit et al. 1993, Loewenstein et al. 2000).

2.2.5 Canopy Disturbance Patterns

I identified canopy disturbances in increment cores obtained from 357 trees of the main species in the dominant and codominant crown classes from each topographic feature or stand (Appendix C). I obtained two increment cores from each tree at breast height (1.37 m) instead of the standard one core per tree to more accurately identify small-scale canopy disturbances (Copenheaver et al. 2009). After using standard techniques to prepare tree cores (Stokes and Smiley1996), I measured ring widths to the nearest 0.001 mm using a Velmex Unislide positioning stage (Velmex Inc., Bloomfield, NY) and averaged ring widths from the two cores to produce a tree-ring series for each tree. I cross-dated cores to assign exact calendar years to each tree-ring using narrow signature years (Yamaguchi 1991) and I used the software COFECHA to statistically corroborate cross-dating (Holmes 1983).

I used the methods of Black and Abrams (2003) to classify a moderate canopy disturbance event as a ≥ 20% increase in radial growth for at least 10 years, based on a 10 year running mean. This threshold accounts for age, DBH, and crown class and has broad applicability to species of different shade tolerance (Black and Abrams 2004). However, the magnitude of radial growth response to canopy disturbances may be reduced by unfavorable climatic conditions such as drought, or enhanced by favorable climatic events such as an extended growing season (Black and Abrams 2004).
2.3 Results

2.3.1 Hydrology

Hydrographs for monitoring stations at White River indicate that surface and subsurface water levels closely followed stage and precipitation patterns (Figure 4). On September 4, 2008, a heavy precipitation event (12.8 cm) associated with Hurricane Gustav caused a rapid rise in stage on the White River and temporary ponding on all topographic features (Figure 4). Overbank flow from the White River caused temporary flooding on swales in January 2009 and flooded all topographic features from February to June of 2009 (Figure 4). Flood duration during the growing season was longest on swales (95-102 days) compared to ridges (46-92 days) and flats (80-85 days). Subsurface water levels were within the root zone (< 1 m) for > 100 days during the growing season on all topographic features. Growing season flood duration was above average compared to reconstructions from 1932-2008 (Figure 5); hydrographs are representative of wet years.

At White River, water level reconstructions indicate growing season flood duration had high interannual variability (Figure 5). The lowest elevation sampling plot was flooded an average of 72.3 days (SE = 42.3) during the growing season prior to dam construction and a slightly fewer but non-significant (t-test, t-stat = 1.50, P = 0.20) 60.3 days (SE = 39.4) after dam construction. The highest elevation sampling plot was flooded an average of 23.3 days (SE = 28.1) during the growing season prior to dam construction (1932-1965) and a slightly fewer but non-significant (t-test, t-stat = 1.50, P = 0.14) 14.5 days (SE = 20.1) after dam construction (1966-2009). Post-dam flood days were significantly higher by 5.8 days in December (t = 2.29, p = 0.02), but significantly fewer (t = 2.29, p = 0.03) by 3.4 days in July (Figure 6).
Figure 4. Daily surface and subsurface water levels recorded at monitoring stations established along an elevation gradient (identified in m above msl) on ridges, flats, and swales at White River National Wildlife Refuge from August 2008 to July 2009. Precipitation at St. Charles, Arkansas (lowest graph) and stage on the White River at St. Charles, Arkansas (gray line in upper graphs) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
Figure 5. Estimated growing season flood days for the highest elevation (44.3 m above msl) and lowest (41.5 m above msl) sampling plots at White River National Wildlife Refuge, Arkansas. Vertical bars represent cumulative number of flood days.

Figure 6. Estimated days at flood stage (mean and standard error) before (1932-1965) and after (1966-2009) completion of dam construction upstream of White River.
Hydrographs for monitoring stations at Bayou Cocodrie indicate that surface flooding occurred after precipitation events and when subsurface water levels were high in the non-growing season (Figure 7). Surface flooding during the growing season lasted up to four hours following precipitation events on ridges and flats and a maximum of 17 days (0.35 m maximum depth) on swales. Subsurface water levels were deep on ridges and flats and rose for short periods during precipitation events (Figure 7). In contrast, subsurface water levels on swales were in the presumed root zone for 63-71 days during the early growing season. At the end of the year (non-growing season), frequent precipitation events saturated the soil causing subsurface water levels to rise above the forest floor in swales (Figure 7).

Hydrographs for monitoring stations at Red River indicate brief surface flooding after precipitation events and extended flooding occurring when subsurface water levels reached the forest floor (Figure 8). Flood depth was < 0.1 m at each stand and only the low elevation sites at the mid-elevation and lowest elevation stands had more than 30 growing season flood days (Figure 8). The number of growing season flood days had a significant negative relationship ($\beta = -9.9$, $p = 0.05$) with elevation. Subsurface water levels in the root zone (< 1 m) were highly variable (highest elevation stand – 74-80 days; mid-elevation stand – 32-94 days; lowest elevation stand – 70-212 days) during the growing season. Subsurface water levels were within the root zone longer on the lowest elevation sites at each stand. Subsurface water levels declined due to evapotranspiration during the spring at least one month before a similar decline of the Mississippi River stage (Figure 9). The exception was the lowest elevation station at the lowest elevation stand (Figure 9). At the end of the year (non-growing season), longer duration flooding
Figure 7. Daily surface and subsurface water levels recorded at monitoring stations established along an elevation gradient (identified in m above msl) on ridges, flats, and swales at Bayou Cocodrie National Wildlife Refuge in 2009. Precipitation at Natchez, Mississippi (lowest graph) and stage on the Mississippi River at Natchez, Mississippi (gray line in upper graphs) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
Figure 8. Daily surface and subsurface water levels recorded at monitoring stations established along an elevation gradient (identified in m above msl) at the highest elevation, mid-elevation, and lowest elevation stands at Red River Wildlife Management Area in 2009. Precipitation at Marksville, Louisiana (bottom graph) and stage on the Mississippi River at Natchez, Mississippi (gray line in upper graphs) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
Figure 9. Number of flood days recorded during the growing season (March-September 2009) at eleven monitoring stations at the highest elevation, mid-elevation, and lowest elevation stands at Red River Wildlife Management Area, Louisiana.

occurred following frequent precipitation events that caused subsurface water levels to rise above the forest floor at the lower elevation monitoring stations at the mid-elevation and lowest elevation stands (Figure 9). Growing season PDSI at Bayou Cocodrie and Red River in 2009 (-0.2) was similar to the mean for the post-ring levee period (-0.1); hydrographs are representative of normal years in the post-levee period.

2.3.2 Stand Characteristics

There were differences in basal area, stem density, and tree height within and among sites. The highest basal areas were at Bayou Cocodrie and the lowest basal areas
were found at Red River (Table 2). The highest stem densities were at White River while the lowest stem densities were at Bayou Cocodrie (Table 2). The range of stem densities of stands at Red River overlapped with those of Bayou Cocodrie and White River (Table 2). Dominant and codominant trees were tallest on flats and swales at Bayou Cocodrie and shortest at Red River (Table 2).

Table 2. Stand characteristics at White River National Wildlife Refuge (NWR; Arkansas), Bayou Cocodrie National Wildlife Refuge (NWR; Louisiana), and Red River Wildlife Management Area (WMA; Louisiana).

<table>
<thead>
<tr>
<th>Site</th>
<th>Basal area (m²/ha) of stems ≥ 5 cm DBH</th>
<th>Basal area (m²/ha) of stems ≥ 10 cm DBH</th>
<th>Stem density (stems/ha)</th>
<th>Average height (m) of dominant and codominant trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>White River NWR</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ridge</td>
<td>31.0</td>
<td>30.1</td>
<td>475</td>
<td>26.7</td>
</tr>
<tr>
<td>Flat</td>
<td>32.5</td>
<td>32.1</td>
<td>463</td>
<td>27.3</td>
</tr>
<tr>
<td>Swale</td>
<td>31.4</td>
<td>31.3</td>
<td>508</td>
<td>26.7</td>
</tr>
<tr>
<td>Bayou Cocodrie NWR</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ridge</td>
<td>32.1</td>
<td>31.8</td>
<td>353</td>
<td>26.6</td>
</tr>
<tr>
<td>Flat</td>
<td>30.9</td>
<td>30.8</td>
<td>357</td>
<td>29.9</td>
</tr>
<tr>
<td>Swale</td>
<td>34.5</td>
<td>34.4</td>
<td>373</td>
<td>28.6</td>
</tr>
<tr>
<td>Red River WMA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Highest elevation</td>
<td>28.5</td>
<td>28.1</td>
<td>258</td>
<td>24.0</td>
</tr>
<tr>
<td>Mid-elevation</td>
<td>27.1</td>
<td>26.8</td>
<td>446</td>
<td>25.6</td>
</tr>
<tr>
<td>Lowest elevation</td>
<td>29.3</td>
<td>28.8</td>
<td>370</td>
<td>19.3</td>
</tr>
</tbody>
</table>

2.3.3 Canopy Disturbance Patterns

At White River, a series of widespread canopy disturbances occurred from 1895-1934 on every topographic feature (ridges – 5 of 5 plots; swales – 6 of 6 plots; flats – 8 of 8 plots) (Figure 10) although the timing and duration of these disturbance events varied by topographic feature (ridges – 1895-1924; swales – 1925-1934; flats – 1910-1934). Another widespread canopy disturbance event occurred from 1960-1969 in most plots ridges – 13 of 16 plots; swales – 15 of 18 plots; flats – 21 of 21 plots) which overlapped
Figure 10: Percentage of trees of any species indicating a canopy disturbance event by 5-year period at White River National Wildlife Refuge (NWR; Arkansas), Bayou Cocodrie National Wildlife Refuge (NWR; Louisiana), and Red River Wildlife Management Area (WMA; Louisiana). Trees (sample size indicated on top of bars) were collected by topographic feature (R – ridge; S – swales; F – flat) at White River and Bayou Cocodrie NWRs and by stand (highest elevation, mid-elevation, and lowest elevation) at Red River WMA.

with the end of dam construction (Figure 10). This disturbance event occurred slightly earlier on ridges (1955-1969).

At Bayou Cocodrie, a series of widespread canopy disturbances occurred from 1915-1929 in most plots (ridges – 10 of 12 plots; swales – 11 of 12 plots; flats – 16 of 18 plots) (Figure 10). Widespread canopy disturbance events have been absent since 1930 although localized canopy disturbances were recorded (Figure 10).

At Red River, a series of widespread canopy disturbances occurred (highest elevation stand – 7 of 12 plots; mid-elevation stand – 9 of 16 plots; lowest elevation
stand–9 of 12 plots) of varying lengths for each stand (highest elevation stand – 1945-1959; mid-elevation stand – 1935-1964; lowest elevation stand – 1950-1964), however, peak disturbance occurred from 1950-1959. This disturbance event overlapped with completion of the mainline (1940) and ring levees (1955). Prior to this period, canopy disturbances were common during most 5-year periods at the mid-elevation stand (Figure 10). After this period, canopy disturbances were less common at each stand (Figure 10).

2.3.4 Recruitment Patterns

2.3.4.1 White River

Overcup oak occurred on the majority of sampling plots on swales (21 of 30) and flats (19 of 30), but in fewer plots on ridges (9 of 30). Overcup oak had high importance values in the dominant, codominant and intermediate crown classes on swales but only had high importance values in the dominant and codominant crown classes on flats (Figure 11). The generalized linear model identified a significant negative relationship ($\beta = -0.98$, $p = 0.02$) between importance values and elevation indicating that overcup oak was more dominant on lower elevations such as swales. There were small gaps in the overcup oak diameter distributions for each topographic feature; only swales had high stem densities in smaller diameter classes (Figure 12). Tree-ring data indicate that 90% of trees cored on flats germinated before 1915 (27 of 30 trees) and the remaining 10% cored germinated in the 1970s. In contrast, overcup oak germinated during most 5-year periods on swales from 1920-1964 (Figure 13). On swales, a peak in establishment occurred from 1945-1959 (Figure 13); a period estimated to have greater than 60 growing season flood days in almost every year (Figure 5). Smaller-diameter trees (5-10 cm DBH) not cored on
Figure 11: Importance values (%) of species by flood tolerance [most tolerant, highly tolerant, moderately tolerant, and weakly tolerant (Hook 1984)] in 3 crown classes on ridges, flats, and swales at White River National Wildlife Refuge, Arkansas.
Figure 12. Diameter distributions (stems/ha) of green ash, (FRPE), Nuttall oak (QUTE), American elm (ULAM), sugarberry (CELA), and overcup oak (QULY) stems on ridges (R), flats (F), and swales (S) at White River National Wildlife Refuge, Arkansas.
Figure 13. Age distributions of green ash, (FRPE), Nuttall oak (QUTE), American elm (ULAM), sugarberry (CELA), and overcup oak (QULY) trees cored on ridges (R), flats (F), and swales (S) at White River National Wildlife Refuge, Arkansas.
swales were estimated to have germinated during the 1970s to early 1980s (Appendix D) based on significant age-diameter relationships ($r^2 = 0.69, p < 0.0001$; Appendix E). Plot-level comparisons of tree ages with growth patterns indicate that overcup oak germinated only following localized canopy disturbances on swales (9 of 9) and flats (3 of 3).

Nuttall oak was found on about one-third of plots (ridges – 11 of 30; swales – 10 of 30; flats – 12 of 30). Nuttall oak had high importance values in the dominant and codominant crown classes on ridges and flats (Figure 11). The generalized linear model identified no statistically significant relationships ($p > 0.32$) between importance values, elevation, topographic feature, and elevation*topographic feature. Nuttall oak had a bimodal diameter distribution for each topographic feature suggesting a gap in recruitment (Figure 12). Trees germinated primarily before 1910 (ridges – 8 of 14; swales – 6 of 10; flats – 6 of 11) or from 1955-1969 (ridges – 3 of 14; swales – 4 of 10; and flats – 5 of 11) (Figure 13). Smaller diameter trees (5-10 cm DBH) not cored were estimated to have established during the 1970s to early 1990s (Appendix D) based on significant age-diameter relationships ($r^2 = 0.69-0.75$, all $p < 0.0001$; Appendix E). Nuttall oak germinating after 1955 occurred primarily during the recent widespread canopy disturbance (ridges – 5 of 6; swales – 3 of 3; flats – 6 of 6).

Green ash was found on the majority of sampling plots (ridges – 23 of 30; swales – 22 of 30; flats – 23 of 30) on each topographic feature. Green ash had high importance values in the dominant, codominant, and intermediate crown classes on each topographic feature with only swales having high importance values in the suppressed crown class (Figure 11). The generalized linear model identified no significant relationship ($p > 0.47$) between importance values, elevation, topographic feature, and elevation*topographic feature.
feature. Green ash diameter distributions for each topographic feature show trees in every diameter class with high stem densities in smaller diameter classes (Figure 12). Green ash germinated during most 5-year periods on each topographic feature (Figure 14). Based on significant age-diameter relationships ($r^2 = 0.69-0.75$, all $p<0.0001$; Appendix E), smaller diameter trees (5-10 cm DBH) not cored was estimated to have established during a wet period from the 1970s to early 1990s (Appendix D) A high number of trees germinated during two widespread canopy disturbances (ridges – 20 of 30; swales – 15 of 30; flats – 12 of 30). Green ash germinated primarily following widespread and localized canopy disturbances (ridges – 4 of 4; swales – 13 of 13; flats – 11 of 11).

Sugarberry was found on the majority of sampling plots (ridges – 25 of 30; swales – 24 of 30; flats – 28 of 30) on each topographic feature. Sugarberry had high importance values in the intermediate and suppressed crown classes on each topographic feature (Figure 11). In the generalized linear model, topographic feature (ridges, swales), and elevation*topographic feature were statistically significant ($p < 0.01$) predictors of importance value. Importance values were higher on ridges ($\beta = 44.14$), but declined with elevation ($\beta = -1.03$). In contrast, importance values were lower on swales ($\beta = -23.77$), but increased ($\beta = 0.55$) with elevation. Sugarberry diameter distributions for each topographic feature show trees in every diameter class < 50 cm DBH with high stem densities in the smaller diameter classes (Figure 12). The majority of sugarberry cored on each topographic feature germinated (ridges – 28 of 32; swales – 22 of 31; flats – 26 of 32) from 1935-1964 with only swales having trees germinating after this period (Figure 13). Based on significant age-diameter relationships ($p < 0.0001$, $r^2 = 0.57-0.77$; Appendix E), smaller diameter trees (5-10 cm DBH) not cored were estimated to have
established mostly from 1970-1984, with the majority of trees germinating following localized canopy disturbances (ridges – 9 of 9; swales – 11 of 15; flats – 10 of 13). Almost one third of trees cored on each topographic feature (ridges – 11 of 32; swale – 10 of 31; flats – 6 of 32) germinated following a widespread disturbance event in the 1960s.

American elm occurred on the majority of sampling plots (ridges – 23 of 30; swales – 19 of 30; flats – 28 of 30) on each topographic feature. American elm had high importance values in the intermediate (except on swales) and suppressed crown classes on each topographic feature (Figure 11). The generalized linear model identified no significant relationship (\( p > 0.33 \)) between importance values, elevation, topographic feature, and elevation*topographic feature. American elm diameter distributions for each topographic feature show trees in almost every diameter class < 70 cm DBH with low stem densities (Figure 12). Tree-ring data indicate that the American elm cored on each topographic feature (ridges – 29 of 31; swales – 24 of 24; flats – 30 of 31) germinated from 1935-1984 (Figure 13). Smaller-diameter trees (5-10 cm DBH) not cored were estimated to have established during the 1970s to early 1980s (Appendix D) based on significant age-diameter relationships (\( r^2 = 0.65-0.71, \) all \( p < 0.0001 \)). Recruitment was greatest (ridges – 18 of 31; swales – 7 of 24; flats – 13 of 31) following widespread disturbance events in the 1960s (Figure 10). Plot level comparisons of tree ages with growth patterns indicate that American elm was most likely to germinate following localized or widespread canopy disturbances on ridges (11 of 12) and swales (9 of 12). In contrast, a roughly equal proportion of American elm on flats germinated following
localized or widespread canopy disturbances (14 of 25) or in undisturbed areas (11 of 25).

2.3.4.2 Bayou Cocodrie

Sweetgum was found on almost all sampling plots on ridges (28 of 30) and flats (30 of 30), but relatively few plots on swales (9 of 30). Sweetgum had high importance values in all crown classes on ridges and flats (Figure 14). The generalized linear model identified no significant relationship ($p > 0.17$) between importance values, elevation, topographic feature, and elevation*topographic feature. Sweetgum diameter distributions show trees in every diameter class on ridges and flats with high stem densities in smaller diameter classes (Figure 15). The majority of sweetgum cored germinated after the Mississippi River mainline levee on ridges (25 of 27) and flats (23 of 36) (Figure 16). Smaller diameter trees (5-10 cm DBH) not cored were estimated to have germinated during the 1980s to early 1990s (Appendix D) based on significant age-diameter relationships ($r^2 = 0.85-0.87$, all $p < 0.001$; Appendix E). Plot-level comparisons of tree age with growth patterns indicate that sweetgum germinated primarily following localized canopy disturbances (ridges – 13 of 14 trees; flats - 11 of 13 trees).

Nuttall oak was found on the majority of sampling plots on swales (30 of 30) and flats (20 of 30) but was found in fewer plots on ridges (14 of 30). Nuttall oak had high importance values in the dominant and codominant crown classes on each topographic feature but only had high importance values in all crown classes on swales (Figure 14). In the generalized linear model, topographic feature, and elevation*topographic feature were statistically significant ($p < 0.05$) predictors of importance value. Importance values were higher ($\beta = 23.83$) on swales and increased ($\beta = 1.59$) with elevation on this
Figure 14: Importance values (%) of species by flood tolerance [highly tolerant, moderately tolerant, and weakly tolerant (Hook 1984)] on ridges, flats, and swales at Bayou Cocodrie National Wildlife Refuge, Louisiana.
Figure 15. Diameter distributions (stems/ha) of green ash, (FRPE), Nuttall oak (QUTE), American elm (ULAM), sugarberry (CELA), and sweetgum (LIST) stems on ridges (R), flats (F), and swales (S) at Bayou Cocodrie National Wildlife Refuge, Louisiana.
Figure 16. Age distributions of green ash (FRPE), Nuttall oak (QUTE), American elm (ULAM), sugarberry (CELA), and sweetgum (LIST) trees cored on ridges (R), flats (F), and swales (S) at Bayou Cocodrie National Wildlife Refuge, Louisiana.
topographic feature. Nuttall oak diameter distributions show trees in every diameter class with only swales having high stem densities in smaller diameter classes (Figure 15). Almost all Nuttall oak (ridges – 33 of 36; swales – 47 of 47; flats – 34 of 34) germinated before completion of the ring levee (Figure 16). Plot-level comparisons of tree ages with growth patterns indicate that Nuttall oak germinated primarily following localized or widespread canopy disturbances (ridges – 9 of 11 trees; swales – 9 of 9 trees; flats – 10 of 14 trees).

Green ash had high importance values in all crown classes on swales, but only had a high importance value in the dominant and codominant crown classes on flats (Figure 14). In the generalized linear model, topographic feature, and elevation*topographic feature were statistically significant ($p < 0.01$) predictors of importance value. Importance values were higher ($\beta = 10.09$) on swales and increased ($\beta = 10.26$) with elevation on this topographic feature. Green ash diameter distributions show trees in every diameter class (except on ridges) with only swales having high stem densities in smaller diameter classes (Figure 15). Almost all green ash (ridges – 3 of 3; swales – 40 of 41; flats – 21 of 21) germinated before completion of the ring levee (Figure 16). Based on significant age-diameter relationships ($r^2 = 0.53$, all $p < 0.001$; Appendix E), a small number of trees (5-10 cm DBH) not cored on swales were estimated to have germinated following canopy disturbances during the 1970s (Appendix D). Plot-level comparisons of tree ages with growth patterns indicate that the majority of green ash germinated following localized and widespread canopy disturbances (swales – 11 of 14; flats – 11 of 13).
Sugarberry was found on the majority of sampling plots on each topographic feature (ridges – 28 of 30; swales – 22 of 30; flats – 19 of 30). Sugarberry had high importance values in the intermediate and suppressed crown classes on each topographic feature (Figure 14). The generalized linear model identified no significant relationship ($p > 0.23$) between importance values, elevation, topographic feature, and elevation*topographic feature. Sugarberry diameter distributions for each topographic feature show trees in every diameter class < 60 cm DBH with high stem densities in the smaller diameter classes (Figure 15). Smaller diameter trees (5-10 cm DBH) not cored were estimated to have established before the 1970s (Appendix D) based on significant age-diameter relationships ($r^2 = 0.51-0.65$, all $p < 0.01$; Appendix E). The majority of sugarberry trees cored germinated in the 1930s (ridges – 14 of 40; swales – 10 of 39; flats – 15 of 41) or after levee construction (ridges – 14 of 40; swales – 12 of 39; flats – 18 of 41). Plot level comparisons of tree ages with growth patterns indicate that sugarberry trees germinating during these two periods were more likely to germinate in undisturbed areas on ridges (14 of 19) and flats (9 of 15) than on swales (2 of 10).

American elm was found on an intermediate number of sampling plots on each topographic feature (ridges – 17 of 30; swales – 10 of 30; flats – 18 of 30). American elm had its highest importance values in the intermediate crown class on flats (Figure 14). The generalized linear model identified no significant relationship ($p > 0.68$) between importance values, elevation, topographic feature, and elevation*topographic feature. American elm diameter distributions for each topographic feature show trees in almost every diameter class < 70 cm DBH in low densities with the exception of swales (Figure 15). Tree-ring data indicate that almost all American elm cored on each topographic
feature (ridges – 20 of 24; swales – 7 of 8; flats – 30 of 30) germinated before completion of the ring levee (Figure 16). Data were limited for plot level comparisons of tree ages with growth patterns because of insufficient dominant and codominant trees.

2.3.4.3 Red River

Overcup oak was found at all sampling plots at Red River. Overcup oak had high importance values in the dominant and codominant crown classes at all stands, but had relatively low importance values in the suppressed crown class with the exception of the mid-elevation stand (Figure 17). There were overcup oak trees in all diameter classes but only the mid-elevation stand had high stem densities < 30 cm DBH (Figure 18). The majority of overcup oak trees cored at the highest elevation (34 of 44), mid-elevation (28 of 43), and lowest elevation (28 of 39) stands germinated before the Mississippi River mainline levee (Figure 19). All trees cored (17 of 17) that germinated after completion of the ring levee were < 30 cm DBH. The age-diameter relationship for overcup oak was good at all stands ($r^2 = 0.48-0.69$, $p < 0.0001$) indicating that diameter is a useful predictor of tree age (Appendix E). The mid-elevation stand is the only stand with a high density of trees < 30 cm DBH (Figure 18), which suggests that many of these trees germinated after completion of the ring levee. The generalized linear model indicated that importance values of stems > 30 cm DBH (before mainline levee) were higher ($\beta = 11.76$) at the highest elevation stand and decreased ($\beta = 14.18$) with elevation at this stand. In contrast, importance values of stems > 30 cm were lower ($\beta = -14.18$) at the mid-elevation stand and increased ($\beta = 14.18$) with elevation at this stand. In contrast, the generalized linear model indicate that importance values of stems < 30 cm DBH (after mainline levee) were higher at the mid-elevation stand ($\beta = 27.03$, $p = 0.05$), but
Figure 17: Importance values (%) of species by flood tolerance [most tolerant, highly tolerant, moderately tolerant, and weakly tolerant (Hook 1984)] in 3 crown classes at the highest elevation, mid-elevation, and lowest elevation stands at Red River Wildlife Management Area, Louisiana.
Figure 18. Diameter distributions (stems/ha) of overcup oak (QULY), honeylocust (GLTR), and sugarberry (CELA) stems at the highest elevation, mid-elevation, and lowest elevation stands at Red River Wildlife Management Area, Louisiana.

increased at lower elevations ($\beta = -2.47, p = 0.05$) at this stand (11.1-m). Plot level comparisons of tree ages with growth patterns indicate that overcup oak was more likely to germinate following localized or widespread canopy disturbances at all stands (highest elevation stand – 7 of 7; mid-elevation stand – 10 of 12; lowest elevation stand – 6 of 7).

Honeylocust was found at relatively few sampling plots at Red River (highest elevation stand – 6 of 30; mid-elevation stand – 14 of 30) with the exception of the lowest elevation stand (20 of 30). Honeylocust had its highest importance values in all crown classes at the lowest elevation stand (Figure 17), although it was less common than the other species at Red River. The generalized linear model identified no significant
relationship \( (p > 0.13) \) between importance values, elevation, stand, and elevation*stand.

Honeylocust diameter distributions show trees in all diameter classes < 60 cm DBH at the mid-elevation and lowest elevation stands although the highest elevation stand has a bimodal distribution (Figure 18). The majority of honeylocust trees cored at the highest elevation (6 of 6), mid-elevation (26 of 29), and lowest elevation (29 of 32) stands germinated after the Mississippi River mainline levee with most recruitment occurring from 1950-64 (Figure 19). Based on a significant age-diameter relationship for the lowest elevation stand \( (r^2 = 0.79, p < 0.001; \text{Appendix E}) \), a small number of trees (8.5-29.5 cm DBH) not cored were estimated to have germinated after the Mississippi River mainline levee.
levee. Honeylocust was more likely to germinate following localized or widespread canopy disturbances at all stands (highest elevation stand – 6 of 6; mid-elevation stand – 14 of 14; lowest elevation stand – 29 of 30).

Sugarberry was found at the majority of sampling plots at each stand (highest elevation stand – 28 of 30; mid-elevation stand – 17 of 30; lowest elevation stand – 24 of 30). Sugarberry had its highest importance values in the intermediate and suppressed crown classes (Figure 17). In the generalized linear model, stand, elevation, and elevation*stand were statistically significant ($p < 0.001$) predictors of importance value. Overall, importance values increased ($\beta = 2.15$) with elevation. Importance values were higher ($\beta = 27.64$) on the highest elevation stand, but decreased ($\beta = -2.43$) with elevation at this stand. Importance values were lower ($\beta = -21.55$) on the mid-elevation stand, but increased ($\beta = 1.86$) with elevation at this stand. All stands had high stem densities of sugarberry in the smaller diameter classes (Figure 18). All sugarberry trees cored (122 of 122) germinated after the Mississippi River mainline levee (Figure 19) and most stems (highest elevation stand [39 of 42], mid-elevation stand [36 of 40], and lowest elevation stand [39 of 40]) germinated after completion of the ring levee. Reconstructing age distribution of sugarberry using the age-diameter relationship was limited by relatively weak coefficients of determination ($r^2 = 0.25-0.33$) for models (Appendix E). Sugarberry is very shade-tolerant but also responds well to release from suppression (Burns and Honkala 1990), which can result in high variability in the age of similarly sized trees. For instance, one 16.4 cm DBH tree was 29 years old but a similarly sized 15.9 cm DBH tree was 54 years old. Sugarberry was more likely to germinate in undisturbed areas at the RR
stand (13 of 19) and MR stands (17 of 26). At the lowest elevation stand, trees were more likely to germinate in gaps (15 of 26) although these were from relatively few plots (4).

2.4 Discussion

2.4.1 Recruitment Patterns: Unleveed Site Below Dams

Despite alterations to the flood regime following dam construction, floodplain forest recruitment at White River may have been linked to variability in overbank flooding. Similar results have been observed in accompanying studies of radial growth of overcup oak and green ash at White River which was closely associated with overbank flooding despite alterations to the flow regime due to dam operations (see Chapter 3 and 4). Several studies have recorded increased recruitment of less flood tolerant species after dams eliminated overbank flooding (Reily and Johnson 1982, Lite and Stromberg 2005, Dewine and Cooper 2007, Stallins et al. 2010). Unlike these studies, my unlevied site downstream from dams remained connected to riverine flooding and variability in flooding continued to influence recruitment patterns. These findings indicate dams may differ in their effect on the flood regime, which is most important for wetland forest recruitment.

Variability in overbank flooding and the lack of widespread canopy disturbances may have combined to influence recruitment patterns for several decades prior to dam construction at White River. Gaps in recruitment of the shade-intolerant Nuttall oak on all topographic features coincided with an absence in widespread canopy disturbances suggesting that recruitment was limited by light availability. Low light availability prior to dam construction favored recruitment of shade-tolerant to moderately shade-tolerant
species such as green ash, American elm, and sugarberry. Recruitment of moderately flood-tolerant green ash and American elm was common across a wide range of topographic features and flood-intolerant sugarberry tended to be more common on drier sites such as ridges. Flood duration was variable among years and these species would be capable of taking advantage of optimal germination conditions because they produce large seed crops nearly every year (Burns and Honkala 1990, Kennedy 1990).

Variability in overbank flooding and widespread canopy disturbances associated with forest harvest operations may have combined to influence recruitment patterns after dam construction at White River. Recruitment of several moderately flood-tolerant (green ash, American elm) and one flood-intolerant species (sugarberry) expanded following widespread canopy disturbances associated with forest harvest operations. Flood duration was highly variable during this period, but these three species produce large seed crops nearly every year (Burns and Honkala 1990) and would be capable of taking advantage of optimal germination conditions. Greenhouse studies indicate that germination rates of American elm and sugarberry increase in high light conditions as found following forest harvest operations although information on the germination response of green ash to light is lacking (Burns and Honkala 1990, Nijjer et al. 2002). The size of canopy openings and information on which species were removed by this forest harvest operation is unknown (Denman and Karnuth 2005). However, partial harvesting, which leaves a residual overstory, has been found to suppress height growth of red oak species such as Nuttall oak more than it suppresses the height growth of American elm, sugarberry, and green ash (Oliver et al. 2005). Consequently, partial cutting can lead to suppression and eventual mortality of red oak species following canopy closure and favor shade tolerants.
In fact, long-term forest inventories at White River indicate that frequent thinning is required for successful recruitment of shade-intolerant red oak species such as Nuttall oak (Denman and Karnuth 2005).

Differences in flood duration among topographic features and the lack of widespread canopy disturbances may have combined to influence overcup oak recruitment at White River. Phipps (1979) reported that overcup oak dominated sites flooded for 33% of the growing season at White River. In my study, overcup oak dominated on lower elevation sites such as swales where overbank flooding occurred in almost every year. The lowest elevation plots were flooded for 34% of the 210-day growing season in the pre-dam period, but a slightly lower 29% of the growing season in the post-dam period. This slight decrease in flood duration did not limit overcup oak recruitment on swales in the post-dam period. Overcup oak successfully recruited on slightly higher elevation flats in the post-dam period. However, a gap in overcup oak recruitment on flats coincided with the absence of widespread canopy disturbances suggesting that recruitment may have been limited by light availability. Tree-ring counts indicate that overcup oak trees were sexually mature during this period (Burns and Honkala 1990), so seed production was unlikely to have been a limiting factor.

2.4.2 Recruitment Patterns: Leveed Sites

Floodplain forest recruitment shifted from being closely associated with overbank flooding to being closely associated with precipitation following levee construction. A previous study (Reily and Johnson 1982) and my research indicate that radial growth can shift from being closely associated with overbank flooding to surface soil moisture from
precipitation following levee construction. Those studies suggested that trees roots adapted to increased groundwater depth following the elimination of overbank flooding by using surface soil moisture from precipitation. My study is the first that I am aware of to suggest that this shift may occur with tree recruitment after levees eliminated overbank flooding and surface flooding had become precipitation driven.

The shift from overbank flooding to precipitation as a main driver of recruitment is indicated by changes in recruitment after levee construction. At Red River and Bayou Cocodrie, a flood-tolerant (overcup oak) and several moderately flood-tolerant species (green ash, Nuttall oak, American elm) established primarily before completion of the ring levee when overbank and backwater flooding was common, but declined after the ring levee when precipitation was the main source of surface flooding. Changes in recruitment patterns to favor less flood-tolerant species are similar to results in floodplain forests where overbank flooding was eliminated by levees or dams (Reily and Johnson 1982, Gergel et al. 2002, Lite and Stromberg 2005, Dewine and Cooper 2007, Stallins et al. 2010). The lack of recruitment after levee construction suggests that surface flood duration was insufficient to provide a competitive advantage for germination of moderately flood-tolerant to flood-tolerant species in the post-levee period. However, the expansion of moderately flood-tolerant sweetgum within local canopy openings after levee construction indicates that species of the same flood tolerance may have different responses to hydrologic modifications.

Local-scale topography and widespread canopy disturbances mediated the effect of levee construction on recruitment of flood-tolerant species (overcup oak). Before the levee, overcup oak at Red River occurred at all stands across the full elevation range
where this flood-tolerant species was sampled and flood-intolerant sugarberry was absent. After the levee, overcup oak was restricted to canopy openings associated with forest harvest operations (D. Locasio, LDWF, pers. comm.) on lower elevations at the mid-elevation stand and sugarberry began to occupy higher elevations in undisturbed areas. My limited hydrologic data indicates that precipitation driven surface flooding is deeper and longer duration on lower elevations which is similar to previous studies on hydrologically disconnected floodplains (Lewin and Hughes 1980, Gergel. 2002). Furthermore, recruitment patterns are similar to those of Dewine and Cooper (2007) who reported a shift in distribution of a moderately flood-tolerant species to lower elevations after dam operations decreased overbank flooding. Unlike Dewine and Cooper (2007), levees prevent overbank flooding of my sites and surface flooding at lower elevations is limited by the precipitation regime.

At Red River, the decline in recruitment of flood-tolerant species such as overcup oak and water hickory (*Carya aquatica*) and the proliferation of the flood-intolerant sugarberry has been widespread in this forest. The lack of data on species removed during forest harvest operations makes it difficult to determine the relative effect of hydrologic modifications on recruitment patterns. If sugarberry (or flood-intolerant species) were preferentially removed by logging operations at Red River this would indicate that conditions were suitable for germination of sugarberry prior to levee construction. Current species such as overcup oak, water hickory, honeylocust, and sugarberry were likely not logged because they are not preferred species for forest products (Meadows and Stanturf 1997). The location of this site at the confluence of the
Mississippi, Red, and Atchafalaya rivers suggest that it would have received prolonged, deep flooding in most years and would not have been an ideal site for sugarberry.

2.4.3 Tradeoffs Between Flood and Shade Tolerance

My study examined recruitment patterns of common forest species in Southern floodplain forests with varying flood and shade tolerances. Comparisons among species-specific patterns in recruitment, surface flooding, and canopy disturbances indicate that two tradeoffs in flood and shade tolerance were common: 1) species that need flooding and high light availability to be successful (Nuttall oak, green ash, overcup oak) as described by Hall and Harcombe (1998); and 2) species with enhanced recruitment when both flooding and shade are removed (sweetgum, sugarberry) as described by Battaglia and Sharitz (2006).

Recruitment patterns for Nuttall oak, green ash, and overcup oak may represent a flood-shade tolerance tradeoff because these species need both flooding and canopy disturbances to compete with more shade tolerant but less flood tolerant species (Hall and Harcombe 1998). Like Streng et al. (1989), extensive flooding may have favored survival of these relatively late germinating and flood-tolerant species compared to early germinating and flood-intolerant species. Furthermore, Pierce and King (2007) suggested that overcup oak seeds may need immersion in water to activate biochemical processes needed for germination. Like previous studies, my study indicated that canopy disturbances enhanced recruitment of Nuttall oak, green ash, and overcup oak (McCarthy and Evans 2000, King and Antrobus 2005). This flood-shade tolerance tradeoff may have limited the distribution of these species to poorly drained sites within canopy openings in
the post-levee period, whereas the distribution of these species was more widespread prior to levees.

Recruitment of sugarberry and sweetgum was enhanced by release from the joint stresses of flooding and shade (Battaglia and Sharitz 2006). Sugarberry and sweetgum can produce large seed crops nearly every year (Burns and Honkala 1990, Kennedy 1990), which may have contributed to their expansion after levees eliminated overbank flooding. Silviculture studies indicate that sugarberry and sweetgum outgrow shade-intolerant species that were common at Bayou Cocodrie over a broad range of light conditions giving these species a competitive advantage (Oliver et al. 2005). Sugarberry, a very shade-tolerant species, was able to establish without canopy disturbances. However, sugarberry establishment was enhanced by canopy disturbances at lower elevations, which suggests that high light conditions enable this flood-intolerant species to grow fast enough to avoid future floods. Sweetgum, a moderately shade-tolerant species, established during local canopy disturbances after levees eliminated overbank flooding. Battaglia and Sharitz (2006) reported that seedlings and saplings of sugarberry and sweetgum had a higher probability of occurring on sites with a greater depth to the water table and canopy openness than other species sampled in my study. This flood-shade tolerance trade-off may have led to the expansion of these two species after levees eliminated overbank flooding, especially following canopy disturbances.

Results of my study highlight the importance of examining the long-term effects of hydrologic modifications and canopy disturbances on recruitment patterns of common forest species on multiple sites. The lack of common response to hydrologic modifications among species of the same flood tolerance illustrates the importance of
examining the effect of flood and light gradients on multiple species of the same flood
tolerance. Furthermore, species-specific responses to varying flood regimes and canopy
disturbance patterns allows me to group species into categories of flood-shade tolerance
as described by Hall and Harcombe (1998) and Battaglia and Sharitz (2006). These
categories of flood-shade tolerance can give insights into species-specific responses to
hydrologic modifications. For instance, species that respond strongly to release from the
joint stresses of flooding and shade have a competitive advantage on floodplains
disconnected from riverine flooding, especially within small canopy openings.

2.4.4 Stand Development

Hodges (1997) described natural patterns of stand development in floodplain
forests where a forest community progresses towards less flood tolerant species as
elevation rises and the site receives less frequent overbank flooding. Data from my study
indicate that levee construction accelerates this process by eliminating overbank flooding
and favoring less flood tolerant species. Although recruitment responds fairly rapidly to
the elimination of overbank flooding from levee construction, growth of moderately
flood-tolerant to flood-tolerant species may be sustained by precipitation and
groundwater available in the root zone, especially in the presence of canopy disturbances
(see Chapter 3 and 4). In the long-term, precipitation or continued subsurface
connectivity between the river and floodplain water table at leveed stands may keep these
sites wet enough to delay a transition to the end point of succession (oak-hickory)
described by Hodges (1997). For instance, floodplain forest trees may persist for more
than a century after alterations to the flood regime (Howe and Knopf 1991, Trémolières et al. 1998).

Forest communities at each site will continue to be dominated by moderately shade-tolerant (overcup oak, green ash) to shade-intolerant species (sweetgum, Nuttall oak) in the dominant and codominant crown classes in the short-term, but if current successional trajectories continue, these species will be replaced by shade-tolerant species (sugarberry, American elm) in the long-term. In the short-term, moderately shade-tolerant to shade-intolerant species will likely replace themselves in the dominant and codominant crown classes on sites where they have high importance values in the intermediate crown class. The flood regime at the unleveled site favors continued recruitment of species of different flood tolerances while the flood regime at leveed sites favors continued recruitment of flood-intolerant species. However, natural patterns of canopy disturbance in the MAV produce small openings (< 2 ha), which may limit recruitment of shade-intolerant species (King and Antrobus 2005). In the absence of large canopy openings, the most shade-tolerant species (sugarberry, American elm) will eventually replace moderately shade-tolerant (overcup oak, green ash) to shade-intolerant species (sweetgum, Nuttall oak) in the dominant and codominant crown classes. Large canopy openings may enable continued recruitment of moderately shade-tolerant (overcup oak, green ash) to shade-intolerant species (Nuttall oak) to reach the upper crown classes. Stand basal area and stem density fall within the range of other studies (Trémolières et al. 1998, Predick et al. 2009, Lockhart et al. 2010) and indicate that some form of management is necessary to reach desired conditions for a diverse forest community as recommended by the Lower Mississippi Valley Joint Venture Forest
Resource Conservation Working Group (2007). Although stands at Red River and White River can be harvested to produce large canopy openings, this is not possible in the Old Growth Research Natural Area at Bayou Cocodrie where logging is prohibited in order to preserve the forest in a natural state.

2.5 Summary

Broad-scale hydrologic modifications have altered flood regimes in most floodplains throughout the world (Pringle 2000), which may affect forest stand development. My study indicates that the effect of dams on the local flood regime and recruitment patterns may differ among river systems depending on the type of dam and its management (e.g., flood control, navigation, hydroelectric power generation). Forest recruitment remained closely linked to riverine flooding on my floodplain below dams, so a slight reduction in flood duration did not lead to a shift in recruitment patterns. Forest recruitment was disconnected from riverine flooding by a ring levee, which led to expansion of less flood tolerant tree species. Broad-scale hydrologic modifications influenced forest recruitment patterns, but this was mediated by local-scale factors such as canopy disturbances and topography which enhanced recruitment of relatively flood tolerant species on floodplains disconnected from riverine flooding.

2.6 Literature Cited


CHAPTER 3: GROWTH RESPONSE OF OVERCUP OAK TO ALTERED FLOOD REGIMES

3.1 Introduction

Floodplains are productive and diverse ecosystems characterized by frequent riverine flooding and associated delivery of nutrient-rich sediments (Pringle 2003). The flood regime (frequency, timing, depth, and duration of flooding) is the primary driver of tree growth on active floodplains (Brinson 1990). However, levees have disconnected floodplains from riverine flooding with surface flooding now largely dependent on local precipitation (Gergel et al. 2002). Furthermore, dams have altered streamflow patterns and subsequent surface and subsurface water levels on floodplains downstream (Johnson et al. 1976, Stallins et al. 2010). Riverine relationships with floodplain subsurface water levels have received little attention (Burt et al. 2002a, Burt et al. 2002b), but subsurface water levels have been decoupled from river stage on floodplains with hydrologic modifications (Loheide and Booth 2011).

Few studies have examined growth response to long-term (> 30 years) hydrologic and climatic variability on floodplains with altered flood regimes and most have focused on a single species and site (Palta et al. 2011, Keim and Amos 2012). Tree growth on floodplains with reduced overbank flooding has increased reliance on surface soil moisture from precipitation (Reily and Johnson 1982), which may limit tree growth during periods of drought. Furthermore, increased light availability from canopy disturbances can alleviate the effects of excessive or insufficient water by increasing photosynthesis (Kolb et al. 1990, Hall 1993), but information on the interaction between canopy disturbances and hydrologic modifications on tree growth is lacking.
Baldcypress (*Taxodium distichum*), a very flood-tolerant species, has been the focus of most studies on the effect of hydrologic modifications on tree growth in floodplain forests of the southeastern USA. Some studies have reported declines in baldcypress radial growth at seasonally flooded forests following onset of permanent flooding (Conner and Day 1988, Keim and Amos 2012), whereas other studies have reported increases in growth (Conner and Day 1976, Keeland and Young 1997). One study found an initial increase in growth after flooding increased followed by a long-term decline (Young et al. 1995). Species of the same flood tolerance rating can have varying responses to hydrologic modifications (Reily and Johnson 1982, Predick et al. 2009), so information on growth response to altered flood regimes is needed from a wider range of species of similar flood tolerance.

Overcup oak (*Quercus lyrata*) is a flood-tolerant species found on wetter sites such as backswamps and sloughs on floodplains of the Mississippi River Alluvial Valley (MAV) and Coastal Plain regions of the USA (Burns and Honkala 1990). I used dendrochronological techniques to reconstruct annual diameter growth of overcup oak on various geomorphic settings at forest stands in the MAV with relatively few to many hydrologic modifications. The specific objectives of this study were: (1) to identify differences in surface and subsurface hydrology on various geomorphic settings; and (2) to identify responses of overcup oak growth to river stage, climate, soil moisture, and canopy disturbances and to test whether relationships of growth to these variables changed following hydrologic modifications.
3.2 Materials and Methods

3.2.1 Study Sites

I sampled overcup oak from floodplain forests with relatively few to many hydrologic modifications in Arkansas (Dagmar Wildlife Management Area [WMA], White River National Wildlife Refuge [NWR]) and Louisiana (Red River WMA, Cat Island NWR), USA (Figure 20). Dagmar WMA (hereafter referred to as Dagmar; Figure 20A) is relatively unaffected by hydrologic modifications, but beaver dams impound deep sloughs at this site. Dams completed upstream of White River NWR (hereafter referred to as White River; Figure 20B) in 1966 have reduced flood duration at this site, but floodplains remain connected to riverine flooding (Bedinger 1971). Channel cut-offs completed on the Mississippi River in 1933 has led to long-term decrease in high stage and an increase low stage at gauges near Red River WMA (hereafter referred to as Red River; Figure 20C) and Cat Island NWR (hereafter referred to as Cat Island; Figure 20D) (Jemberie et al. 2008). A ring levee completed from 1940-1955 disconnected Red River from overbank and backwater flooding of the Mississippi and Red rivers.

I sampled overcup oak from forest stands on a range of geomorphic settings including backswamp deposits (Red River – mid-elevation stand, lowest elevation stand), point bar deposits of the Mississippi River (Red River – highest elevation stand; Cat Island) or a small stream (Dagmar), and Late Wisconsin valley train deposits (White River) (Saucier 1994). Study stands are topographically flat with the exception of Dagmar where overcup oak was sampled from deep sloughs. Red River is a broad flat, so I selected three stands representing the highest, mid-, and lowest elevation sites. Soils at study stands are classified as poorly drained [Sharkey clay (thermic Chromic
Figure 20. Map of study site locations at (A) Dagmar Wildlife Management Area (WMA), Arkansas (latitude: 34.887401; longitude: 650597.41); (B) White River National Wildlife Refuge (NWR), Arkansas (latitude: 34.34288, longitude: -91.099336); (C) Red River Wildlife Management Area (WMA), Louisiana (Highest elevation – latitude: 31.257855; longitude: -91.759138); Mid-elevation – latitude: 31.296633, longitude: -91.69186; Lowest elevation – latitude: 31.269699, longitude: -91.720711’); and (D) Cat Island National Wildlife Refuge (NWR), Louisiana (latitude: 30.774845; longitude: -91.451582).
Epiaquerts) with the exception of somewhat poorly drained soils at White River [Yancopin silty clay loam (thermic Typic Endoaquepts)] (Martin et al. 1998, NRCS 2008).

At Red River and Cat Island, overcup oak was found in association with water hickory (*Carya aquatica*), baldcypress, and sugarberry (*Celtis laevigata*). Overcup oak was a major component of the dominant and codominant crown classes at Red River (highest elevation stand – 56.0%; mid-elevation stand – 79.2%; lowest elevation stand – 59.2%) and Cat Island (52.0%). At Dagmar, overcup oak was in a mix with Nuttall oak (*Quercus texana*) and water tupelo (*Nyssa aquatica*) and accounted for 16.9% of the basal area in the dominant and codominant crown classes. At White River, overcup oak was in a mix with green ash (*Fraxinus pennsylvanica*) and Nuttall oak and accounted for 25.0% of the basal area in the dominant and codominant crown classes. Stand basal area (Dagmar – 28.3-m²/ha; White River – 32.5-m²/ha; Red River highest elevation stand – 28.2-m²/ha; Red River mid-elevation stand – 28.1-m²/ha; Red River lowest elevation stand – 29.5-m²/ha; Cat Island – 22.7-m²/ha) is typical of southern floodplain forests.

### 3.2.2 Hydrology

To determine hydrologic characteristics at each stand, I measured surface and subsurface water levels at monitoring stations with the number of stations varying among stands. I established monitoring stations across flats or along the deepest point of sloughs to account for even small differences in elevation. Each station consisted of surface and subsurface water measurements using Odyssey™ capacitance water level probes (accuracy = 0.8-mm; Dataflow Systems PTY Ltd, NZ) electronically recorded surface
and subsurface water levels every 10 minutes for at least one year. I measured surface water levels within a 3.2-cm diameter x 1.5-m length PVC pipe secured to a 5-10 cm diameter tree with rope. I measured subsurface water levels to a depth of 2 m within a 3.2-cm diameter x 3.0-m length PVC pipe casing. I filled the inside of the well bore outside the casing with sand to allow entry of water and filled the top 0.3 m with bentonite clay to prevent infiltration of precipitation. Water entered each pipe through holes measuring 7 mm in diameter at four locations at 10-cm intervals over the length of each pipe and fine solar screen mesh covered holes to prevent sediment from filling the pipe. For monitoring stations, I calculated the number of flood days during the growing season (Arkansas sites – April-September; Louisiana sites – March-September) and number of days within the root zone during the growing season (approximately 1 m from the forest floor; Phipps 1979).

To determine long-term changes in flood duration at hydrologically connected sites (Cat Island and White River), I extrapolated the number of flood days during the growing season from river stage data by assuming the difference between stage readings and daily water levels during data collection did not vary (Middleton 2009). I consider this to be a conservatively low estimate of the number of flood days during the growing season because floodwaters may pond in low lying, poorly drained sites. For Cat Island, river stage data is only available after completion of channel cut-offs in 1933 so I used simple linear regression to identify trends in the number of growing season flood days. For White River, I used Student’s t-test to compare extrapolated growing and non-growing season flood days before (1932-1965) and after (1966-2009) completion of the dam.
To determine long-term changes in soil moisture at Red River, I calculated Palmer Drought Severity Index (PDSI – an index of soil moisture and dryness; Palmer 1965) during the growing season (March-September) at Natchez, Mississippi from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC 2011). Student’s t-tests were used to compare growing season PDSI data for periods before (1895-1939) and after completion of the Mississippi River mainline levee (1940-2009).

3.2.3 Tree-ring Chronology Development

For each study stand, I collected increment cores from 21-26 overcup oak trees. Trees were selected in the dominant and codominant crown classes because these trees most accurately reflect growth dynamics of the whole stand instead of being dominated by local competition effects (Fritts 1976). Two increment cores were obtained at breast height (1.37 m) from each tree to assist in cross-dating. Tree cores were oven dried, mounted on core holders, and sanded with increasingly finer grit sandpaper until tree-ring boundaries were visible under a microscope (Stokes and Smiley 1996, Orvis and Grissino-Mayer 2002).

All tree-ring widths were measured to the nearest 0.01-mm using a Velmex Unislide positioning stage (Velmex Inc., Bloomfield, NY) under a dissecting microscope. Ring widths from the two cores were averaged to produce a tree-ring series for each tree. Cores were cross-dated to assign exact calendar years to each tree-ring using narrow signature years (Yamaguchi 1991) and the software COFECHA was used to statistically corroborate cross-dating (Holmes 1983). In COFECHA, only tree-ring series that fell
within a 99% confidence interval of the stand average using Pearson’s correlation (critical correlation of 0.33) were kept for the chronology (Holmes 1983).

Investigating the effect of hydrologic modifications on growth patterns is complicated by multiple factors affecting tree growth. I modeled ring widths based on a modification of Cook (1987) by Amos (2006) as,

\[ R(t) = f(A(t), C(t), H(t), \epsilon(t)), \]

where \( R \) is ring width in year \( t \); \( A \) is the expected age-related variation in ring width; \( C \) is the effect of annual variation in climate; \( H \) is the effect of variations in water level; and \( \epsilon \) is error not accounted for in other terms, including canopy disturbances.

To remove growth trends associated with tree age \( (A) \) while preserving variation that may be related to climate \( (C) \) or hydrology \( (H) \), I created tree-ring chronologies using the Regional Curve Standardization (RCS) method (Briffa et al. 1992, Esper et al. 2003). The RCS method detrends tree-ring series by cambial age as a ratio of observed ring width to the average ring width for a large number of trees from the region. To create the regional curve, all 137 tree-ring series were aligned by cambial age using estimated pith offsets for series where the increment core did not include the pith (Esper et al. 2003). I formed the regional curve by fitting a generalized exponential regression model (Hugershoff curve; Bräker 1981) to the data. To improve the accuracy of tree age determination, I adjusted tree ages by the mean time (5 years) to reach the coring height based on a stem analysis of 8 saplings (< 5 cm DBH) randomly sampled from Red River (Appendix B).

Tree-ring series are autocorrelated because tree rings integrate responses to climatic variation for several years (Fritts 1976). Some of the autocorrelation is due to
canopy disturbances. I used the software ARSTAN (Cook and Holmes 1986) to develop a tree-ring chronology without serial autocorrelation. A residual tree-ring chronology was developed by identifying and detrending significant autocorrelation from each RCS tree-ring series using an autoregressive-moving average (ARMA) model. I compared means from the residual tree-ring chronologies before and after hydrologic modifications using Student’s t-tests. At Red River, these time periods were pre- (1902-1954) and post-ring levee (1955-2006). At White River, these time periods were pre- (1933-1965) and post-dam construction (1966-2006). River stage data was insufficient for similar analyses at Dagmar and Cat Island.

To examine relationships between growth and climate (C), I used Pearson’s correlations between residual tree-ring chronologies and climate over the full-time period with data. Climate variables were examined for correlation with residual tree-ring chronologies, using data obtained at a 4-km resolution using interpolations by (Daly 1994, Daly 1997). Climate data included monthly midpoint temperature and total monthly precipitation.

To examine relationships between tree growth and hydrology (H), I used Pearson’s correlations between residual tree-ring chronologies, water level, and PDSI for periods before and after hydrologic modifications. Water level data were mean monthly river stage data from the nearest US Geological Survey (USGS) or US Army Corps of Engineers (USACE) river gauge with a long history. Monthly PDSI data was from the nearest weather station to each study site using the NOAA National Climatic Data Center (NCDC 2011).
Correlations with climatic and hydrologic variables were obtained from months from the beginning of the previous growing season to the end of the current growing season (Arkansas sites – April-September; Louisiana sites – March-September).

To determine the combined effect of levee construction and drought on tree growth at Red River, I used Student’s t-tests to make comparisons of tree growth before and after levee construction during years with moderate drought (defined as years with PDSI ≤ -2.0) during the growing season (March-September). Red River had at least 6 years with moderate drought before and after levee construction (Figure 21). The Mississippi River gauge at Natchez (Mississippi) reached flood stage in one of the selected years before levee construction. I evaluated all statistical procedures at 0.05-0.10 level of significance using Statistica 6.1 (StatSoft Inc., 2003).

![Figure 21. Mean growing season Palmer Drought Severity Index (PDSI) for Red River from 1895-2006. Asterisks indicate years with moderate drought (PDSI ≤ -2) used for pre- and post-levee comparisons with growth.](image)
To support analyses of the effect of canopy disturbances on growth, I identified canopy disturbances in each tree using the methods of Black and Abrams (2003). Canopy disturbance events were classified as a ≥ 20% percent increase in radial growth for at least 10 years, based on a 10 year running mean. This threshold accounts for age, DBH, and crown class and has broad applicability to varying species and forest types (Black and Abrams 2004). However, the magnitude of radial growth response to canopy disturbances may be reduced by unfavorable climatic conditions such as drought, or enhanced by favorable climatic events such as an extended growing season (Black and Abrams 2004).

3.3 Results

3.3.1 Hydrology

At Red River, hydrographs from monitoring stations indicate that surface flooding occurred after precipitation events and when subsurface water levels were high in the non-growing season (Figure 22). Depth of surface water was < 0.1 m at each monitoring station except for the lowest elevation station at the lowest elevation stand which had > 0.1 m of surface water for short periods (Figure 22). Only the low elevation station at the mid-elevation and lowest elevation stands had more than 30 growing season flood days (Figure 22). Subsurface water levels in the root zone (< 1 m from surface) were highly variable (highest elevation stand – 75-79 days; mid-elevation stand – 31-94 days; lowest elevation stand – 79-214 days) during the growing season. Subsurface water levels generally fell during late spring presumably due to evapotranspiration, with the exception of the lowest elevation site at the lowest elevation stand (Figure 22). At the end of the
Figure 22. Daily surface and subsurface water levels recorded at monitoring stations established along an elevation gradient at the highest elevation, mid-elevation, and lowest elevation stands at Red River in 2009. Precipitation at Marksville, Louisiana (lowest graph) and stage on the Mississippi River at Natchez, Mississippi (thick gray line in upper graphs) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
year (non-growing season), longer duration flooding occurred following frequent precipitation events which caused subsurface water levels at the lowest elevation sites at the mid-elevation and lowest elevation stands to rise above the forest floor (Figure 22).

At Red River, the Mississippi River was at flood stage during the growing season for an average of 99.7 days (SE = 44.1) prior to the Mississippi River mainline levee and a similar \((t = 0.91, p = 0.36)\) 92.0 days (SE = 42.7) after the mainline levee. However, the mainline levee has decoupled surface and subsurface water levels from the Mississippi River, so growing season flood days was not reconstructed based on stage.

At Red River, growing season PDSI was highly variable among years (Figure 21). Mean growing season PDSI was -0.48 (SE = 0.23) prior to the Mississippi River mainline levee (1895-1939) and but a non-significantly different \((t = 1.98, p = 0.18)\) -0.07 (SE = 0.19) after the Mississippi River mainline levee (1940-2009). Growing season PDSI in 2009 (-0.23) was similar to the mean for the post-ring levee period (-0.07); hydrographs are representative of normal years in the post-levee period.

At Cat Island, the hydrograph from the monitoring station indicates that overbank flooding occurred several times during the year (Figure 23). Maximum depth of surface water was 2.9 m with a total of 121 growing season flood days (Figure 23). The subsurface water level was in the root zone for 161 days, but declined in late summer (Figure 23). Growing season flood days was above average (Figure 24); hydrographs are representative of wet years.

At Cat Island, water level reconstructions indicate that there was an average of 80.0 growing season flood days (range = 0-183 days) for 1935-2009 with overbank flooding occurring in 72 of 75 years (Figure 24). Simple linear regression identified no
Figure 23. Daily surface and subsurface water levels measured at Cat Island, White River, and Dagmar in 2009. Precipitation (lower graphs) and stage (thick gray line in upper graphs) from the nearest weather stations and river gauges (Cat Island – Baton Rouge, Louisiana; White River – St. Charles, Arkansas; Dagmar – Brinkley and Brasfield, Arkansas) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
significant trend \((\beta = 0.18, p = 0.41)\) in the number of growing season flood days after channel cut-offs.

At White River, hydrographs from monitoring stations indicate that overbank flooding occurred several times during the year (Figure 23). Maximum depth of surface
water was 1.5 m with a total of 75 growing season flood days (Figure 23). Subsurface water levels were in the root zone for > 131 days during the growing season, but declined in late summer (Figure 23). Growing season flood days was above average compared to reconstructions from 1932-2008 (Figure 24); hydrographs are representative of wet years.

At White River, water level reconstructions indicate there was an average of 55.6 growing season flood days (SE = 38.5) prior to dam construction (1932-1965) and a slightly fewer but non-significant ($t = 1.73, p = 0.09$) 42.3 growing season flood days (SE = 29.4) after dam construction (1966-2009) (Figure 24). Post-dam flood days (over the natural levee) were significantly fewer ($t = 2.29, p = 0.03$) by 3.4 days in July and significantly higher ($t = 2.29, p = 0.02$) by 5.8 days in December (Figure 25).

At Dagmar, hydrographs from monitoring stations indicate that surface flooding in deep sloughs occurred after precipitation events due to ponding or runoff or both (Figure 23). Surface water levels appeared to rise with increased frequency of precipitation events although surface water levels appeared to have a delayed response to an increase in river stage in the early growing season. Flood depth was deepest (1.0 m) at the mid-elevation monitoring station which is between two beaver dams and remained flooded well into the late growing season. Only the lowest elevation monitoring station dried out for a short period during the summer (Figure 23). Water level data are unavailable for a short period during the growing season although subsurface water levels were likely within the root zone for the entire growing season.

At Dagmar, the Cache River reached the elevation of sloughs every year from 1953-2009, but did not reach a stage sufficient for overbank flooding. Growing season
Figure 25. Estimated days at flood stage (mean and standard error) before (1932-1965) and after (1966-2009) completion of dam construction upstream of White River.

PDSI in 2009 (+2.3) was above the long-term mean (-0.3) from 1895-2009; hydrographs are representative of wet years.

3.3.2 Tree-ring Chronologies

Tree-ring chronologies spanned 1754-2006, but were truncated to match the earliest year with river stage data (Table 3). Analyses using COFECHA showed that all tree-ring chronologies were accurately cross-dated and useful for dendroclimatic analyses because of adequate series intercorrelation (> 0.51), mean sensitivity (> 0.29), and expressed population signal (> 0.85 criterion; Wigley et al. 1984), and fewer than 10% problem segments (Grissino-Mayer 2001; Table 3).
Table 3: Descriptive statistics for overcup oak tree-ring chronologies for each study site.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Truncated time period</th>
<th>Series intercorrelation</th>
<th>Mean sensitivity</th>
<th>Expressed population signal</th>
<th>% flags</th>
<th>Sample size</th>
<th>Tree diameter (cm) at breast height (median and range)</th>
<th>Age/year of establishment (median and range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red River (highest elevation)</td>
<td>1902-2006</td>
<td>0.52</td>
<td>0.35</td>
<td>0.87</td>
<td>6</td>
<td>26</td>
<td>46 (24-83)</td>
<td>102 (52-177)/1894 (1829-1954)</td>
</tr>
<tr>
<td>Red River (mid-elevation)</td>
<td>1902-2006</td>
<td>0.51</td>
<td>0.37</td>
<td>0.88</td>
<td>7</td>
<td>21</td>
<td>52 (33-82)</td>
<td>106 (62-317)/1900 (1689-1944)</td>
</tr>
<tr>
<td>Red River (lowest elevation)</td>
<td>1902-2006</td>
<td>0.58</td>
<td>0.37</td>
<td>0.86</td>
<td>5</td>
<td>22</td>
<td>46 (29-87)</td>
<td>94 (57-180)/1912 (1826-1949)</td>
</tr>
<tr>
<td>Cat Island</td>
<td>1936-2006</td>
<td>0.53</td>
<td>0.38</td>
<td>0.95</td>
<td>9</td>
<td>25</td>
<td>48 (32-68)</td>
<td>100 (70-120)/1906 (1886-1936)</td>
</tr>
<tr>
<td>White River</td>
<td>1933-2006</td>
<td>0.62</td>
<td>0.35</td>
<td>0.95</td>
<td>3</td>
<td>22</td>
<td>63 (36-94)</td>
<td>159 (94-253)/1847 (1753-1912)</td>
</tr>
<tr>
<td>Dagmar</td>
<td>1953-2006</td>
<td>0.62</td>
<td>0.29</td>
<td>0.89</td>
<td>0</td>
<td>21</td>
<td>53 (34-81)</td>
<td>96 (45-195)/1910 (1811-1961)</td>
</tr>
</tbody>
</table>
Establishment dates of overcup oak ranged from 1689-1949 at Red River, 1886-1936 at Cat Island, 1753-1912 at White River, and 1811-1961 at Dagmar (Table 3). At Red River, the majority (63 of 69) of trees established before completion of the Mississippi River mainline levee. At Cat Island, almost all (20 of 21) trees established before completion of channel-cutoffs. At White River, all (22 of 22) trees established before completion of dams.

3.3.3 Growth Responses to Climate and Hydrology

Overcup oak growth had similar responses to seasonal patterns in temperature and precipitation at each study site. Most residual chronologies had a significant positive relationship with temperature at the beginning of the growing season (March or April) and a significant negative relationship with temperature during one or several months later in the growing season (Figure 26). Furthermore, most chronologies had a significant positive relationship with precipitation at the beginning of the growing season (March) or later in the growing season (June-September) but occasionally there was a negative relationship with precipitation in late spring (May) (Figure 27).

Overcup oak growth response to river stage and PDSI differed among study sites. Radial growth at Cat Island had a significant positive relationship with stage throughout the growing season (except July) (Figure 28). Growth at Cat Island also had a significant positive relationship with PDSI from late in the non-growing season until the early growing season (January-April) and late in the growing season (September) (Figure 28). Growth at Dagmar had a significant positive relationship with stage from late in the non-growing season until the early growing season (January-April), in the middle (June), and
Figure 26. Correlation between annual radial growth of overcup oak and monthly midpoint temperature (Red River – Natchez, Mississippi; Cat Island – Baton Rouge, Louisiana; White River – St. Charles, Arkansas; Dagmar – Brinkley, Arkansas) for each tree-ring chronology. Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.

end of the growing season (September) (Figure 28). Growth at Dagmar also had a significant positive relationship with PDSI at the beginning (April) and end of the growing season (August-September).
Figure 27. Correlation between annual radial growth of overcup oak and total monthly precipitation (Red River – Natchez, Mississippi; Cat Island – Baton Rouge, Louisiana; White River – St. Charles, Arkansas; Dagmar – Brinkley, Arkansas) for each tree-ring chronology. Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.

At Red River, growth response to river stage and PDSI varied by stand both before and after levee construction. Growth had a significant positive relationship with
stage on one or both rivers (Atchafalaya and Mississippi rivers) during late summer months prior to levee construction (Figure 29-31). After levee construction, growth had a significant positive relationship with stage on the Atchafalaya River in early spring (April) at the mid-elevation and lowest elevation stands (Figure 30-31) and throughout the growing season (April-July, September) at the highest elevation stand (Figure 29). Growth also had a significant positive relationship with PDSI from late in the non-
Figure 29. Correlation between annual radial growth of overcup oak from the highest elevation stand at Red River (Louisiana) with mean monthly stage on the Atchafalaya River (Simmesport, Louisiana), Mississippi River (Natchez, Mississippi) and Palmer Drought Severity Index (PDSI; Natchez, Mississippi) before ($N = 52$) and after the ring levee ($N = 53$). Negative months on x-axis indicate previous year. Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.
Figure 30. Correlation between annual radial growth of overcup oak from the mid-elevation stand at Red River (Louisiana) with mean monthly stage on the Atchafalaya River (Simmesport, Louisiana), Mississippi River (Natchez, Mississippi) and Palmer Drought Severity Index (PDSI; Natchez, Mississippi) before (N = 52) and after the ring levee (N = 53). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at α = 0.05 and plus (+) indicates significant coefficients at α = 0.10.
Figure 31. Correlation between annual radial growth of overcup oak from the lowest elevation stand at Red River (Louisiana) with mean monthly stage on the Atchafalaya River (Simmesport, Louisiana), Mississippi River (Natchez, Mississippi) and Palmer Drought Severity Index (PDSI; Natchez, Mississippi) before ($N = 52$) and after the ring levee ($N = 53$). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$. 

Month
growing season to the end the growing season (January-September) at the highest
elevation stand (Figure 29) and during the early and late growing season (March-April,
July September) at the mid-elevation and lowest elevation stands (Figure 30-31). Growth
in years with moderate drought was not significantly different ($t = 2.16-2.45$, $p = 0.81-
0.88$) between pre- and post-levee periods at all stands.

At White River, growth did not have significant relationships with stage and PDSI
before dam construction (Figure 32). After dam construction, growth had significant
positive relationships with stage from late in the non-growing season to the early growing
season (October-March) and PDSI during the late growing season (July-September)
(Figure 32). Growth in years with moderate drought was not significantly different ($t =
2.05-2.14$, $p = 0.59-0.91$) between pre- and post-dam periods.

3.3.4 Growth Responses to Canopy Disturbances

At Red River, canopy disturbances contributed to above average growth after
levee construction at all stands. A high proportion of trees indicated a canopy disturbance
event (highest elevation – 1945-1959; mid-elevation – 1935-1964; lowest elevation –
1950-1964) prior to a period of above average growth from roughly 1950-1995 (Figure
33).

At White River, canopy disturbances contributed to above average growth before
and after dam construction. A high proportion of trees indicated a canopy disturbance
event (1895-1934, 1960-1969) prior to two periods of above average growth (1928-1940,
1965-2002) (Figure 33).
Figure 32. Correlation between annual radial growth of overcup oak from White River (Arkansas) with mean monthly stage on the White River (St. Charles, Arkansas) and Palmer Drought Severity Index (PDSI; St. Charles, Arkansas) before ($N = 33$) and after the dam construction ($N = 41$). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.

At Cat Island, a high proportion of trees indicated a canopy disturbance event from 1965-1974 prior to a period of above average growth (1972-present) (Figure 33). In contrast, a relatively high proportion of trees indicated a canopy disturbance event (1950-1969) at Dagmar prior to a recent period of above average growth (1964-present), but not prior to an earlier period of above average growth (1915-1946) (Figure 33).
Figure 33. Percentage of overcup oak trees sampled (sample size at base of vertical bars) indicating a disturbance event by 5-year period (left Y-axis) compared to standardized tree-ring index (right Y-axis) at Red River (highest elevation stand, mid-elevation stand, and lowest elevation stand), Cat Island, White River, and Dagmar.
3.4 Discussion

Hydrologic modifications can affect the flood regime, but riverine connectivity during the growing season is important for floodplain tree growth (Stromberg and Patten 1996). Growth-stage relationships remained strong at stands connected to riverine flooding (Cat Island, White River) regardless of alterations to the flow regime. My results support previous studies with very flood-tolerant baldcypress after dam operations reduced overbank flooding along the Savannah River (Palta et al. 2011). Like Palta et al. (2011), these relationships remained strong at my stand downstream of dams at White River despite alterations to the flow regime because the floodplain remained connected to riverine flooding. It is unclear why overcup oak growth at White River did not show significant relationships with stage and PDSI prior to dam construction. The lack of detectable response to stage and PDSI is contrary to previous studies examining overcup oak growth in floodplain forests disconnected from riverine flooding by levees (Bialecki 2009) and with reduced flooding due to dam operations (Smith 2007). The lack of significant relationships between overcup oak, stage, and PDSI at White River prior to dam construction may indicate that hydrology was less important for growth prior to dam construction. However, almost all trees cored established before a canopy disturbance event from 1895-1934 and it is possible that this masked the effects of stage and PDSI on growth in the pre-dam period.

The type of hydrologic modification (e.g., levees, dams) may be unimportant and somewhat unpredictable, but the effect of the modification on local hydrologic processes (e.g., soil moisture in the root zone) is more important for floodplain tree growth (Bassett 1963). At stands behind a ring levee (Red River), overcup oak growth shifted from being
closely correlated with stage and PDSI to being closely correlated with PDSI after levees eliminated overbank flooding. Similar results were found following dam construction by Reily and Johnson (1982). They noted that growth of cottonwood (*Populus deltoides*) along the Missouri River in the Northern Prairie region (USA) changed from being closely correlated with high spring stages before dam construction to being closely correlated with precipitation after dam operations began. Reily and Johnson (1982) suggested that cottonwood roots could no longer access groundwater after dam operations decreased streamflow and shifted to relying on surface soil moisture from precipitation. In contrast, my results at the stand downstream from dams (White River) differed in that growth did not change its main water source because this site remained connected to riverine flooding.

At sites disconnected from riverine flooding by levees, increased reliance of overcup oak growth on surface soil moisture did not decrease growth during periods of drought. My results are unlike Palta et al. (2011), who reported higher growth rates for baldcypress on levees and backswamps during drought years after dams greatly reduced overbank flooding of the Savannah River (Georgia). They postulated that prolonged flooding prior to dam construction had a negative effect on baldcypress growth because of stress from anoxic conditions, which was eliminated after dam operations reduced flood duration. In contrast, my study did not indicate any negative relationships between overcup oak growth and stage prior to levee construction suggesting that flood duration was not long enough to cause stress from anoxic conditions. Growth rates were unchanged after levee construction suggesting that in the absence of overbank flooding, overcup oak trees used other sources of water.
Broad-scale hydrologic modifications may eliminate overbank flooding, but tree growth can be sustained by groundwater in the root zone (Reily and Johnson 1982). At stands disconnected from riverine flooding by a ring levee, overcup oak growth had positive relationships with spring stage on the Atchafalaya River in the post-ring levee period. Growth-stage relationships were strong for more months of the growing season at the highest elevation stand, because relatively coarse-textured point bar deposits beneath this stand have higher subsurface connectivity than relatively fine-textured backswamp deposits beneath other stands at Red River (Cosby et al. 1984). Hydrologic data indicates that the water table was in the root zone primarily during spring at the highest elevation stand. This data was collected during a year with average precipitation so it must be extrapolated beyond this for drought or wet years. Similarly, overcup oak growth had a strong relationship with stage on the Cache River at Dagmar during the winter and spring despite stage not reaching an elevation to cause overbank flooding. Unlike the other hydrologically disconnected site, active beaver impoundments presumably retain precipitation and runoff in sloughs at Dagmar, thus increasing water available for tree growth.

The effect of broad-scale hydrologic modifications on tree growth can be mediated by local canopy disturbances. At stands behind a ring levee, overcup oak growth was expected to decline because of positive relationships between growth and river stage previously reported (Keeland 1994, Cleaveland 2000). However, overcup oak growth increased for at least 40 years at the time of levee construction, presumably because of widespread canopy disturbances. Similar results were observed at another site within the same ring levee where growth of moderately flood-tolerant green ash increased.
presumably because of localized canopy disturbances (See Chapter 4). This supports studies which indicate that increased light availability can alleviate the effects of excessive or insufficient water by increasing photosynthesis (Kolb et al. 1990, Hall 1993). My findings indicate that tree growth can increased on floodplains disconnected from riverine flooding canopy disturbances.

Stand-level differences in species composition may have influenced overcup oak growth rates due to effects on competition. Overcup oak leafs out a month later than most species, giving it a competitive advantage on sites with prolonged flooding into the growing season (Burns and Honkala 1990). Cat Island averaged over 80 growing season flood days, whereas, Red River is located on a low-lying area at the confluence of two rivers and would have had prolonged flooding prior to levee construction when the majority of establishment occurred. As a consequence, overcup oak had the highest basal area in the overstory at these two stands.

Results of my study suggest that broad-scale hydrologic modifications that eliminate overbank flooding can be alleviated by local scale factors such as canopy disturbances, surface soil moisture, groundwater, and competition. However, my study examined growth of a single species and previous studies have documented species of the same flood tolerance rating responding differently to hydrologic variability (Reily and Johnson 1982, Predick et al. 2009). Growth of moderately flood-tolerant green ash was sustained for several decades by canopy disturbances, surface soil moisture, and spring groundwater on depressional swales at another site within the same ring levee (see Chapter 4). Unlike overcup oak, green ash growth on flats at White River was higher after dam operations increased annual low stages. Green ash has a deeper rooting depth
compared to overcup oak (Phipps 1979), which may account for this difference in growth response to groundwater.

3.5 Summary

On floodplains connected to riverine flooding, tree growth is strongly driven by the duration, frequency, depth, and timing of flooding within and among years. Hydrologic modifications to the flood regime, however, do not automatically reduce tree growth of a flood-tolerant species. My study indicates that overcup oak has an increasing dependence on surface soil moisture following levee construction in a humid subtropical region. Increased dependence on surface soil moisture does not necessarily lead to declines in growth during drought years, possibly because riverine influence via groundwater. Information on the relationship between groundwater use and tree growth within and among years requires further investigation. More direct methods (stable isotopes, tree physiology) are needed to determine source water for trees growing on floodplains with altered flood regimes. My results support tree growth studies in floodplain forests of humid continental and semi-arid regions identifying precipitation and groundwater as increasingly important water sources when overbank flooding is removed (Reily and Johnson 1982, Stromberg and Patten 1996). Results of my study indicate that the effects of broad-scale elimination of overbank flooding on growth of flood-tolerant species is complex and can be decreased or amplified by timber harvest, surface soil moisture, groundwater, and other local-scale factors.
3.6 Literature Cited


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CHAPTER 4: INFLUENCE OF HYDROLOGIC MODIFICATIONS ON GREEN ASH GROWTH ACROSS FLOODPLAIN TOPOGRAPHY

4.1 Introduction

Floodplain forests are among the most biologically productive and diverse ecosystems in the world (Tockner and Stanford 2002). Hydrologic connectivity is essential to the functioning of these ecosystems by transferring water, nutrient-rich sediments, and organisms between rivers and their floodplain (Pringle 2003). However, riverine connectivity with floodplains has been altered by levees, dams, and other hydrologic modifications (Pringle 2001). Floodplains behind levees are disconnected from riverine flooding and surface flooding is precipitation-dependent (Gergel et al. 2002). Floodplains downstream of dams experience altered timing, duration, and frequency of flooding (Johnson et al. 1976, Bradley and Smith 1986, Stallins et al. 2010). Detailed understanding of the relationship between river and subsurface water in floodplains is lacking (Burt et al. 2002a, Burt et al. 2002b), but hydrologic modifications often decouple subsurface water levels from river stage (Loheide and Booth 2011).

Hydrologic modifications of surface and subsurface hydrology affect floodplain forest tree growth variously by species (Reily and Johnson 1982, Predick et al. 2009). For example, Reily and Johnson (1982) found that growth of several moderately flood-tolerant species (American elm – *Ulmus americana*; boxelder – *Acer negundo*; and green ash – *Fraxinus pennsylvanica*.) and a flood-intolerant species (burr oak – *Quercus macrocarpa*) declined following completion of Garrison Dam on the Missouri River (North Dakota) because it altered seasonal streamflow, eliminated overbank flooding, and lowered the water table. In contrast, flood-tolerant cottonwood (*Populus deltoides*)
maintained growth by shifting from being primarily influenced by streamflow in the pre-dam period to being influenced by surface soil moisture from precipitation in the post-dam period.

The effect of hydrologic modifications on floodplain tree growth can vary by topographic feature due to differences in elevation, soil texture, drainage, and soil moisture. For example, Predick et al. (2009) reported that the 10-year average growth rate was higher for two moderately flood-tolerant species [green ash and river birch (*Betula nigra*)] on low-lying swales compared to higher ridges and flats after levee construction along the Wisconsin River (Wisconsin).

Most dendrochronological studies in floodplains with altered flood regimes have focused on growth response at a single site and few have examined growth response to long-term (> 30 years) hydrologic and climatic variability (Palta et al. 2011, Keim and Amos 2012). Increased light availability from canopy disturbances can ameliorate the effects of excessive or insufficient water (Kolb et al. 1990, Hall 1993), but it is unknown how canopy disturbances interact with broader scale hydrologic modifications common in floodplain forests.

The objective of my study was to improve the understanding of the influence of hydrologic modifications on green ash growth across floodplain topography. I used dendrochronological techniques to reconstruct annual diameter growth of green ash for at least 30 years before and after major hydrologic modifications at two forest stands in the Mississippi River Alluvial Valley (MAV): an unleveed stand below dams and a stand within a ring levee. The specific objectives of my study were: (1) to identify differences in surface and subsurface hydrology of various topographic features; and (2) to identify
responses of green ash growth to river stage, climate, soil moisture, and canopy disturbances and to test whether relationships of growth to these variables changed following dam or levee construction.

4.2 Methods

4.2.1 Study Sites

I sampled green ash from study sites at White River National Wildlife Refuge (hereafter referred to as White River; Figure 34A), Arkansas and Bayou Cocodrie National Wildlife Refuge (hereafter referred to as Bayou Cocodrie; Figure 34B), Louisiana. Prior to dam and levee construction, high annual river stages flooded study sites in winter and spring, but river stage was below the elevation of the natural levee during the remainder of the year. Dams completed on the upper reaches of the White River watershed from 1944-1966 have reduced flood duration downstream, but floodplains remain connected to riverine flooding (Bedinger 1971). At Bayou Cocodrie, a ring levee completed from 1940-1955 has disconnected the floodplain from overbank flooding of the Mississippi and Black rivers, which was the source of overbank flooding of this site.

I sampled green ash from forest stands across different geomorphic settings and topographic features. The White River stand is on Late Wisconsin valley train deposits and the Bayou Cocodrie stand is on meander scroll deposits of an abandoned course of the Mississippi River (Saucier 1994). Study stands are characterized by ridge and swale topography intermixed with broad flats. Soils on each topographic feature are classified as somewhat poorly drained [White River - Yancopin silty clay loam (Typic
Figure 34. Map of study sites at (A) White River National Wildlife Refuge (NWR), Arkansas (latitude: 34.34288, longitude: -91.09936); (B) Bayou Cocodrie National Wildlife Refuge (NWR), Louisiana (latitude: 31.537789, longitude: -91.61481).
Endoaquepts); Bayou Cocodrie – Alligator clays (Chromic dystraquerts) on ridges and swales, and Tensas soils (Chromic Vertic Epiaqualfs) on flats] (Martin et al. 1988, NRCS 2008).

At White River, the most common overstory species in addition to green ash are sweet pecan (Carya illinoinensis), Nuttall oak (Quercus texana), and overcup oak (Quercus lyrata). At Bayou Cocodrie, green ash is growing in a mix with sweetgum (Liquidambar styraciflua) and oaks (Q. texana, Q. phellos, and Q. nigra). Vegetation sampling of 30 circular sampling plots (0.04 ha) per topographic feature (see Chapter 2) indicate that green ash accounted for greater than 15% of the basal area in the dominant and codominant crown classes at White River (ridges – 18%; flats – 33%; swales – 21%) and greater than 10% of the basal area at Bayou Cocodrie (flats – 10%; swales – 21%).

4.2.2 Hydrology

To determine hydrologic characteristics at each stand, I measured surface and subsurface water levels at monitoring stations established along transects perpendicular to the river channel crossing each ridge and swale and spread across flats to account for even small differences in elevation. Each station consisted of surface and subsurface water measurements using self-logging Odyssey™ capacitance water level probes (accuracy = 0.8-mm; Dataflow Systems PTY Ltd, NZ) that recorded water level every 10 minutes for at least one year. I measured surface water levels within a 3.2-cm diameter x 1.5-m length PVC pipe secured to a 5-10 cm diameter tree with rope. I measured subsurface water levels to a depth of 2 m within a well with a 3.2-cm diameter x 3.0-m length PVC pipe casing. I filled the inside of the well bore outside the casing with sand to
allow entry of water and filled the top 0.3 m with bentonite clay to prevent infiltration of precipitation. Water entered each pipe through holes measuring 7 mm in diameter at four locations at 10-cm intervals over the length of each pipe and fine solar screen mesh covered holes to prevent sediment from filling the pipe. For monitoring stations at each topographic feature, I calculated the number of growing season flood days (range) and the number of days during the growing season that subsurface water levels were in the root zone (approximately 1 m from the forest floor; Phipps 1979).

To determine long-term changes in flood duration at White River, I extrapolated the number of flood days during the growing season (April-September) from river stage for the highest (44.3 m above msl) and lowest elevation (41.5 m above msl) on the floodplain by assuming the difference between gauge readings and daily water levels at monitoring stations did not vary (Middleton 2009). I consider this to be a conservatively low estimate of the number of flood days during the growing season because floodwaters may pond in low lying, poorly drained sites.

To quantify long-term changes in flood frequency at White River, I calculated the percentage of years that stage exceeded several elevations (exceedance probability) for the early growing season (April-June), late growing season (July-September), early non-growing season (October-December), and late non-growing season (January-March) for the periods before (1932-1965) and after (1966-2008) completion of the dams. Student’s t-tests were used to compare monthly flood days and growing season flood days for periods before and after completion of the dams upstream of White River.

To determine long-term changes in soil moisture at Bayou Cocodrie, I calculated Palmer Drought Severity Index (PDSI – an index of soil moisture and dryness; Palmer
1965) during the growing season (March-September) at Natchez, Mississippi from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC 2011). Student’s t-tests were used to compare growing season PDSI data for periods before (1895-1939) and after completion of the Mississippi River mainline levee (1940-2009).

4.2.3 Tree-ring Chronology Development

For each study stand, I collected increment cores from 14-20 green ash trees per topographic feature. Trees were selected in the dominant and codominant crown classes because these trees reflect growth dynamics of the whole stand instead of being dominated by local competition effects (Fritts 1976). Two increment cores were obtained at breast height (137 cm) from each tree to assist in cross-dating. Tree cores were oven dried, mounted on core holders, and sanded with increasingly finer grit sandpaper until tree-ring boundaries were visible under a microscope (Stokes and Smiley 1996, Orvis and Grissino-Mayer 2002).

All tree-ring widths were measured to the nearest 0.01-mm using a Velmex Unislide positioning stage (Velmex Inc., Bloomfield, NY) under a dissecting microscope. Ring widths from the two cores were averaged to produce a tree-ring series for each tree. Cores were cross-dated to assign exact calendar years to each tree-ring using narrow signature years (Yamaguchi 1991) and the software COFECHA was used to statistically corroborate cross-dating (Holmes 1983). In COFECHA, only tree-ring series that fell within a 99% confidence interval of the stand average using Pearson’s correlation (critical correlation of 0.33) were kept for the chronology (Holmes 1983).
Investigating the effect of hydrologic variation on growth patterns is complicated by multiple factors affecting tree growth. I modeled ring widths based on a modification of Cook (1987) by Amos (2006) as,

\[ R(t) = f(A(t), C(t), H(t), \epsilon(t)) \]

where \( R \) is ring width in year \( t \); \( A \) is the expected age-related variation in ring width; \( C \) is the effect of annual variation in climate; \( H \) is the effect of variations in water level; and \( \epsilon \) is error not accounted for in other terms, including canopy disturbances.

To remove growth trends associated with tree age (\( A \)) while preserving variation that may be related to climate (\( C \)) or hydrology (\( H \), I created tree-ring chronologies using the Regional Curve Standardization (RCS) method (Briffa et al. 1992, Esper et al. 2003). The RCS method detrends tree-ring series by cambial age as a ratio of observed ring width to the average ring width for a large number of trees from the region. To create the regional curve, all 87 tree-ring series from the region were aligned by cambial age using estimated pith offsets for series where the increment core did not include the pith (Esper et al. 2003). I formed the regional curve by fitting a generalized exponential regression model (Hugershoff curve; Bräker 1981) to the data. To improve the accuracy of tree age determination, I adjusted trees by the mean time (6 years) to reach the coring height based on a stem analysis of 12 saplings (< 5 cm DBH) randomly sampled from Bayou Cocodrie (Appendix B).

Tree-ring series are autocorrelated because tree rings integrate responses to climatic variation for several years (Fritts 1976). Some of the autocorrelation is due to canopy disturbances. I used the software ARSTAN (Cook and Holmes 1986) to develop a tree-ring chronology without serial autocorrelation. A residual tree-ring chronology was
developed by identifying and detrending significant autocorrelation from each RCS tree-ring series using an autoregressive-moving average (ARMA) model. I compared means from the residual tree-ring chronologies before and after hydrologic modifications using Student’s t-tests. At White River, these time periods were pre- (1933-1965) and post-dam construction (1966-2006). At Bayou Cocodrie, time periods were pre- (1902-1939) and post-levee construction (1940-2006).

To examine relationships between growth and climate (C), I obtained Pearson’s correlations between residual tree-ring chronologies and climate over the full time period with data. Climate variables were examined for correlation with residual tree-ring chronologies, using data obtained at a 4-km resolution using interpolations by Daly (1994, 1997). Climate data included monthly midpoint temperature and total monthly precipitation.

To examine relationships between tree growth and hydrology (H), I used Pearson’s correlations between residual tree-ring chronologies, water level, and PDSI for time periods before and after hydrologic modifications. Water level data were mean monthly river stage data from the nearest US Geological Survey (USGS) or US Army Corps of Engineers (USACE) river gauge with a long history (White River – St. Charles, Arkansas; Bayou Cocodrie – Natchez, Mississippi). Monthly PDSI data was from the nearest weather station to each study site using the NOAA National Climatic Data Center (NCDC 2011).

Correlations with climatic and hydrologic variables were obtained for months from the beginning of the previous growing season to the end of the current growing
season (Arkansas – April-September; Louisiana – March-September). I used Statistica 6.1 (StatSoft Inc., 2003) for all statistical tests ($\alpha = 0.05-0.10$).

To support analyses of the effect of canopy disturbances on growth, I identified canopy disturbances in each tree using the methods of Black and Abrams (2003). Canopy disturbance events were classified as a $\geq 20\%$ percent increase in radial growth for at least 10 years, based on a 10 year running mean. This threshold accounts for age, DBH, and crown class and has broad applicability to varying species and forest types (Black and Abrams 2004). However, the magnitude of radial growth response to canopy disturbances may be reduced by unfavorable climatic conditions such as drought, or enhanced by favorable climatic events such as an extended growing season (Black and Abrams 2004).

4.3 Results

4.3.1 Hydrology

Hydrographs from monitoring stations at White River indicate that surface and subsurface water levels closely followed river stage and precipitation patterns (Figure 35). On September 4, 2008, a heavy precipitation event (12.8 cm) associated with Hurricane Gustav caused a rapid rise in stage on the White River and temporary ponding on all topographic features (Figure 35). Overbank flow caused temporary flooding on swales in January 2009 and flooded all topographic features from February to June of 2009 (Figure 35). Flood duration during the growing season was longest on swales (95-102 days) compared to ridges (46-92 days) and flats (80-85 days). Subsurface water levels were in the root zone ($< 1 \text{ m from surface}$) for $> 100$ days during the growing
Figure 35. Daily surface and subsurface water levels recorded at monitoring stations established along an elevation gradient (identified in m above msl) on ridges, flats, and swales at White River from August 2008 to July 2009. Precipitation at St. Charles, Arkansas (lowest graph) and stage on the White River at St. Charles, Arkansas (gray line in upper graphs) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
season on all topographic features. Growing season flood days was above average compared to reconstructions from 1932-2008 (Figure 36); hydrographs are representative of wet years.

![Graph showing estimated growing season flood days for the highest (44.3 m above msl) and lowest elevation (41.5 m above msl) sampling plots at White River, Arkansas. Vertical bars represent cumulative number of flood days.](image)

Figure 36. Estimated growing season flood days for the highest (44.3 m above msl) and lowest elevation (41.5 m above msl) sampling plots at White River, Arkansas. Vertical bars represent cumulative number of flood days.

At White River, water level reconstructions indicate that growing season flooding occurred during the majority of years on each topographic feature but swales had the longest duration flooding (Figure 36). The lowest elevation sampling plot was flooded an average of 72.3 days (SE = 42.3) during the growing season prior to dam construction and a slightly fewer but non-significant (t-test, t-stat = 1.50, P = 0.20) 60.3 days (SE =
39.4) after dam construction. The highest elevation sampling plot had an average of 23.3 growing season flood days (SE = 28.1) prior to dam construction (1932-1965) and a slightly fewer but non-significant (t-test, t-stat = 1.50, P = 0.14) 14.5 growing season flood days (SE = 20.1) after dam construction (1966-2009).

At White River, overbank flooding was more common during the early non-growing season and low stages increased during the late growing season in the post-dam period (Figure 37). Pre- and post-dam exceedance probabilities were similar on all topographic features during the early growing season, and the effects of the dam were evident mainly in reducing the highest stages above the natural levee (Figure 37A). Although post-dam flood days (over the natural levee) were significantly fewer (t = 2.29, p = 0.03) by 3.4 days in July, exceedance probabilities were higher (more frequent flooding) by 20-21% on topographic features lower than the natural levee during the late growing season (Figure 37B), indicating generally higher annual low stages. Post-dam exceedance probabilities increased by 9-20% on all topographic features during the early non-growing season (Figure 37C) with post-dam flood days being significantly higher (t = 2.29, p = 0.02) by 5.8 days in December.

Hydrographs from monitoring stations at Bayou Cocodrie indicate that surface flooding occurred primarily after precipitation events and also when subsurface water levels were high in the non-growing season (Figure 38). Surface flooding during the growing season lasted up to four hours following precipitation events on ridges and flats and a maximum of 17 days (0.35 m maximum depth) on swales. Subsurface water levels were deep on ridges and flats and rose for short periods during precipitation events (Figure 38). In contrast, subsurface water levels on swales were in the presumed root
Figure 37. Exceedance probabilities at White River near St. Charles, Arkansas for the (A) early growing season (April-June), (B) late growing season (July-September), (C) early non-growing season (October-December), and (D) late non-growing season (January-March) before (1932-1965; \( N = 34 \)) and after (1966-2009; \( N = 44 \)) completion of dam construction.

zone for 63-71 days during the early growing season. At the end of the year (non-growing season), frequent precipitation events saturated the soil causing subsurface water levels to rise above the forest floor in swales (Figure 38).

At Bayou Cocodrie, growing season PDSI was highly variable among years (Figure 39). Mean growing season PDSI was \(-0.48\) (SE = 0.23) prior to the Mississippi River mainline levee (1895-1939) and a non-significantly different \( t = 1.98, p = 0.18 \) - 0.07 (SE = 0.19) after the Mississippi River mainline levee (1940-2009). Growing
Figure 38. Daily surface and subsurface water levels recorded at monitoring stations established along an elevation gradient (identified in m above msl) on ridges, flats, and swales at Bayou Cocodrie in 2009. Precipitation at Natchez, Mississippi (lowest graph) and stage on the Mississippi River at Natchez, Mississippi (gray line in upper graphs) are presented for comparisons. Horizontal dashed lines indicate forest floor at 0 m and horizontal dotted lines indicate maximum rooting depth at -1 m.
season PDSI in 2009 (-0.23) was similar to the mean for the post-ring levee period (-0.07); hydrographs are representative of a normal year.

Figure 39. Mean growing season Palmer Drought Severity Index (PDSI) for Bayou Cocodrie from 1895-2009.

4.3.2 Tree-ring Chronologies

The green ash chronologies spanned 1784-2006, but were truncated to match the period of available river stage data to 1932 for White River and 1902 (Mississippi River) for Bayou Cocodrie (Table 4). Analyses using COFECHA showed that all tree-ring chronologies were accurately cross-dated and useful for dendroclimatic studies because of adequate series intercorrelation (> 0.51), mean sensitivity (> 0.30) (Grissino-Mayer
Table 4. Descriptive statistics for green ash tree-ring chronologies by topographic feature (ridges, swales, and flats) for White River (Arkansas) and Bayou Cocodrie (Louisiana).

<table>
<thead>
<tr>
<th>Study site</th>
<th>Truncated time period</th>
<th>Series intercorrelation</th>
<th>Mean sensitivity</th>
<th>Expressed population signal</th>
<th>Problem segments</th>
<th>Sample size</th>
<th>Tree diameter (cm) at breast height (median and range)</th>
<th>Age/year of establishment (median and range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>White River</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ridges</td>
<td>1933-2006</td>
<td>0.51</td>
<td>0.40</td>
<td>0.91</td>
<td>7</td>
<td>20</td>
<td>49 (18-129)</td>
<td>87 (39-201)/1920 (1806-1968)</td>
</tr>
<tr>
<td>Flats</td>
<td>1933-2006</td>
<td>0.69</td>
<td>0.45</td>
<td>0.94</td>
<td>0</td>
<td>18</td>
<td>63 (28-92)</td>
<td>106 (63-137)/1901 (1870-1944)</td>
</tr>
<tr>
<td>Swales</td>
<td>1933-2009</td>
<td>0.69</td>
<td>0.41</td>
<td>0.90</td>
<td>0</td>
<td>19</td>
<td>52 (25-100)</td>
<td>92 (46-240)/1915 (1767-1964)</td>
</tr>
<tr>
<td>Bayou Cocodrie</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Flats</td>
<td>1902-2006</td>
<td>0.56</td>
<td>0.35</td>
<td>0.90</td>
<td>0</td>
<td>14</td>
<td>53 (33-80)</td>
<td>114 (69-149)/1893 (1858-1938)</td>
</tr>
<tr>
<td>Swales</td>
<td>1902-2006</td>
<td>0.62</td>
<td>0.37</td>
<td>0.94</td>
<td>2</td>
<td>16</td>
<td>57 (24-72)</td>
<td>89 (55-195)/1918 (1812-1952)</td>
</tr>
</tbody>
</table>
2001), and expressed population signal (> 0.85 criterion; Wigley et al. 1984), and fewer than 10% of all series having problem segments (Grissino-Mayer 2001; Table 4).

Establishment dates of green ash trees ranged from 1767-1968 at White River and 1812-1952 at Bayou Cocodrie (Table 4). At White River, the majority (46 of 57) of trees established before dam construction and the remainder established within 3 years after dams were completed. At Bayou Cocodrie, the majority (26 of 30) of trees established before completion of the Mississippi River mainline levee in 1940 and all trees established before completion of the ring levee in 1955.

4.3.3 Growth Responses to Climate and Hydrology

At Bayou Cocodrie, radial growth of green ash had a negative relationship with temperature during several months in the late growing season (flats – July-August; swales – June-August) (Figure 40) and a significant positive relationship with precipitation for most of the early growing season (February-June) (Figure 41). At White River, radial growth of green ash had significant positive relationships with temperature on flats only during a few months in the non-growing season (January, March) and a negative relationship with temperature on swales during the summer (July) (Figure 40). Furthermore, radial growth of green ash had a significant positive relationship with precipitation for individual months during the non-growing and growing season on flats (December, May) and swales (January, May) (Figure 41). Radial growth of green ash responded to temperature and precipitation during more months of the year at Bayou Cocodrie compared to White River.
Figure 40. Correlation between annual radial growth of green ash and monthly midpoint temperature at White River (ridges, flats, swales) and Bayou Cocodrie (flats, swales). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.

Radial growth of green ash had varying responses to river stage and PDSI within sites by topographic feature and between sites. At White River, radial growth of green ash had a significant positive relationship with early growing season stage (swales –
Figure 41. Correlation between monthly precipitation and annual radial growth of green ash at White River (ridges, flats, swales) and Bayou Cocodrie (flats, swales). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.

March-June; ridges and flats – April-June) and a negative relationship with late growing season stage (ridges – July; flats – July-September; swales – July-August) before dam construction (Figure 42). Furthermore, radial growth of green ash had a significant negative relationship with late growing season PDSI (ridges – July- September; flats – May-September; swales – June-September) before dam construction (Figure 43). After
Figure 42. Correlation between mean monthly stage on the White River (St. Charles, Arkansas) and annual radial growth of green ash from White River (ridges, flats, swales) before \((N = 33)\) and after dam construction \((N = 51)\). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at \(\alpha = 0.05\) and plus (+) indicates significant coefficients at \(\alpha = 0.10\).

dam construction, radial growth of green ash had a significant positive relationship with stage from late in the non-growing season to the end of the growing season (ridges – January-September; flats – February-September; swales – previous December-
Figure 43. Correlation between monthly Palmer Drought Severity Index (PDSI) and annual radial growth of green ash from White River (ridges, flats, swales) before ($N = 33$) and after dam construction ($N = 51$). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at $\alpha = 0.05$ and plus (+) indicates significant coefficients at $\alpha = 0.10$.

September) (Figure 42) and with PDSI from early in the non-growing season until the end of the growing season (ridges – previous September-current September; flats – previous December-September; swales – previous October-September) (Figure 43). At
Bayou Cocodrie, radial growth of green ash had a significant positive relationship with Mississippi River stage (flats – April-July; swales – April-August) and PDSI (flats – March-July; swales – March-August) during most of the growing season prior to levee construction (Figure 44). After levee construction, radial growth of green ash had a significant positive relationship with stage during a few months in the early growing season on swales (April-May) (Figure 44) and with PDSI during most of the growing season (May-August) on both topographic features (Figure 45).

![Correlation charts for flats and swales before and after levee construction]

Figure 44. Correlation between mean monthly stage on the Mississippi River (Natchez, Mississippi) and annual radial growth of green ash from Bayou Cocodrie (flats, swales) before \((N = 38)\) and after levee construction \((N = 67)\). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at \(\alpha = 0.05\) and plus (+) indicates significant coefficients at \(\alpha = 0.10\).
Figure 45. Correlation between monthly Palmer Drought Severity Index (PDSI) and annual radial growth of green ash from Bayou Cocodrie (flats, swales) before \( N = 38 \) and after levee construction \( N = 67 \). Negative months on x-axis indicate previous year. Asterisks (*) indicates significant coefficients at \( \alpha = 0.05 \) and plus (+) indicates significant coefficients at \( \alpha = 0.10 \).

4.3.4 Growth Responses to Canopy Disturbances

The number and frequency of canopy disturbances varied between sites and within sites by topographic feature. At White River, a relatively high percentage of trees indicated canopy disturbances on ridges and flats prior to growth rising above average starting in the 1960s (Figure 46). At Bayou Cocodrie, a relatively high percentage of trees indicated canopy disturbances prior to growth rising above average around 1920 on flats and swales (Figure 46). Growth fell below average on flats (1947) in the post-levee
Figure 46. Percentage of green ash trees sampled (sample size at base of vertical bars) indicating a disturbance event by 5-year period (left Y-axis) compared to RCS tree-ring index (right Y-axis) for White River (ridges, flats, and swales) and Bayou Cocodrie (flats and swales). Horizontal dotted line indicates mean growth.

... period, but a relatively high percentage of trees indicated canopy disturbances on swales around 1950 and growth remained above average until 1963 (Figure 46).
4.4 Discussion

Broad-scale hydrologic modifications may have varying effects on local-scale hydrologic processes (e.g., soil moisture within the rooting zone) which is most important for floodplain forest tree growth (Bassett 1963). At the hydrologically disconnected site (Bayou Cocodrie), green ash growth shifted from being closely correlated with high stages and surface soil moisture (PDSI) to being closely correlated with surface soil moisture following completion of the ring levee. A similar shift in the main factors affecting tree growth was observed with flood-tolerant overcup oak within the same ring levee (see Chapter 3) and in another study with moderately flood-tolerant cottonwood following dam construction on the Missouri River in North Dakota (Reily and Johnson 1982). Reily and Johnson (1982) suggested that cottonwood roots adapted to a decrease in groundwater levels after dam construction by depending on surface soil moisture from precipitation. Unlike Reily and Johnson (1982), my stand downstream from dams (White River) did not have a shift in the main factors affecting growth suggesting that green ash roots continue to access water available in the root zone at this hydrologically connected site.

Hydrologic modifications can affect local surface and subsurface water levels, but water availability in the root zone is most important for floodplain tree growth (Palta et al. 2011). At the hydrologically connected site (White River), green ash growth maintained a strong relationship with river stage despite alterations in the flow regime. Before dam construction, growth relationships with stage indicate that high stages in the early growing season enhanced growth on all topographic features, but high stages in the late growing season decreased growth. Prolonged flooding in the late growing season as
indicated by Palta et al. (2011) led to decreased growth and may be a response to anoxic conditions decreasing production of photosynthates (Gravatt and Kirby 1998). After dam construction, growth on all topographic features was positively affected by stage from the late non-growing season until the end of the growing season. High stages leading to overbank flooding during the late non-growing season was more likely to occur in the post-dam period, which can enhance growth by increasing soil moisture and nutrient availability during the growing season (Broadfoot and Williston 1973, Mitsch et al. 1979). Furthermore, high stages leading to prolonged flooding into the late growing season was less likely to occur and stage was more likely to be at the elevation of all topographic features during the late growing season. Like other studies which show close relationships between stage and water table (Cabezas et al. 2011), my study suggests that stage kept the water table in the root zone on all topographic features during the late growing season when temperature and drought stress is highest. However, hydrologic data is based on a single year so this does not preclude relationships between stage and water table from differing in the past or in the future.

The effect of broad-scale hydrologic modifications on tree growth can be mediated by local canopy disturbances. At the hydrologically disconnected site, I expected green ash growth to decline based on previous long-term studies where overbank flooding was eliminated (Johnson et al. 1976, Reily and Johnson 1982). However, growth increased on swales for at least 20 years following completion of the mainline levee (1940) presumably because of local canopy disturbances. This supports studies which report that increased light availability can alleviate the effects of excessive or insufficient water by increasing photosynthesis in seedlings and saplings (Kolb et al.
My findings suggest that canopy disturbances can enhance tree growth despite the elimination of overbank flooding.

Local topography can mediate the effects of broad-scale hydrologic modifications on tree growth. At the hydrologically disconnected site, growth on both flats and swales continued to maintain a strong relationship with surface soil moisture (PDSI) from the late spring until the end of the growing season, but only growth on swales maintained a strong relationship with stage on the Mississippi River during the early spring. My findings suggest that trees growing on swales within the ring levee have a strong river influence via groundwater links. Lin et al. (2006) reported higher soil moisture and subsurface water levels on swales. In contrast, green ash growth at the hydrologically connected site maintained a strong relationship with stage on all topographic features, but growth on flats had higher growth rates. Flats had a different species mix than ridges and flats, which may have resulted in higher green growth rates.

My results highlight the importance of long-term studies (> 30 years) on tree growth response to climatic and hydrologic variation that considers floodplain topography. For instance, Predick et al. (2009) recorded higher green ash growth on lower topographic features for 10 years following levee construction on the Wisconsin River. Unlike Predick et al. (2009), my long-term study captured the effect of canopy disturbances and between 40 and 70 years of hydrologic and climatic variation on tree growth following hydrologic modifications. Results of my study suggest that canopy disturbances can enhance green ash growth despite the elimination of overbank flooding. Furthermore, long-term green ash growth can be sustained for several decades following
hydrologic modifications by surface soil moisture and/or groundwater, both of which vary by topographic feature.

My study focused on growth of a single species and previous studies have reported species of the same flood tolerance rating having different responses to hydrologic variability (Reily and Johnson 1982, Galuszka and Kolb 2002, Predick et al. 2009). Within the same ring levee, growth of flood-tolerant overcup oak in lower elevation stands increased for several decades presumably because of canopy disturbances before declining following a recent drought (see Chapter 3). Unlike green ash, overcup oak growth on flats at White River did not respond to the higher summer low stages after dam construction (see Chapter 3). Overcup oak has a shallower root depth compared to green ash (Phipps 1979), which may account for this difference in growth response. Higher summer low stages from dam operations are common in the United States (Graf 2006) so interspecific differences in tree growth response to these hydrologic modifications require further investigation. Furthermore, tree physiology and stable isotope studies are needed to make direct links between tree water use and growth at hydrologically altered floodplains on short and long time scales (Smith et al. 1991, Ehleringer and Dawson 1992).

4.5 Summary

The flood regime is the main determinant of tree growth patterns in floodplain forests connected to riverine flooding. Hydrologic modifications that increase flooding during the late non-growing season and decrease flooding during the late growing season may maintain the water table in the root zone which can enhance growth of moderately-
flood tolerant species such as green ash. Hydrologic modifications that eliminate overbank flooding cause green ash to become increasingly correlated with local climate (temperature, precipitation, soil moisture), while growth on lower topographic features can maintain a strong relationship with high spring stages. My study indicates that the effects of broad-scale hydrologic modifications differ in their effects on the flood regime (timing, duration) and that the effect of these modifications on tree growth can be mediated by local-scale factors such as canopy disturbances and topography.

4.6 Literature Cited


Hall, R.B.W., 1993. Sapling growth and recruitment as affected by flooding and canopy gap formation in a river floodplain forest in southeast Texas. Ph.D Diss., Rice University, Houston, TX.


CHAPTER 5: CONCLUSIONS

Broad-scale hydrologic modifications have altered flood regimes in most floodplains throughout the world which may affect tree recruitment and growth. My study indicates that the effect of dams on the local flood regime and recruitment patterns may differ among river systems depending on the type of dam and its management (e.g., flood control, navigation, hydroelectric power generation). My site below dams remained connected to riverine flooding, so recruitment and growth patterns continued to be driven by variability in overbank flooding. Dam operations actually enhanced green ash growth by increasing flooding during the late non-growing season and decreasing flooding during the late growing season, while maintaining the water table in the root zone. In contrast, tree recruitment and growth shifted from being driven by overbank flooding and precipitation to being driven only by precipitation at forest stands disconnected from riverine flooding by levees. The precipitation driven flood regime favored recruitment of less flood tolerant species. However, growth did not immediately decline for green ash on lower topographic features (swales) and for overcup oak at all stands because trees were able to obtain sufficient water from surface soil moisture and groundwater. Tree physiology and stable isotope studies can improve our understanding of short- and long-term tree water use on floodplains with hydrologic modifications. The finding that canopy disturbances mediated the effects of levees by enhancing recruitment and growth of relatively flood tolerant species on poorly drained sites may have important management implications. It suggests that management practices can be implemented to create canopy openings and soil moisture conditions to enhance recruitment and growth of relatively flood tolerant species on floodplains disconnected from riverine flooding.
**APPENDIX A: DESCRIPTIVE STATISTICS OF TREES CORED**

Sample size, age, and diameter at breast height (DBH) (median and range) of tree species cored at White River National Wildlife Refuge (NWR; Arkansas), Bayou Cocodrie National Wildlife Refuge (NWR; Louisiana), and Red River Wildlife Management Area (WMA; Louisiana).

<table>
<thead>
<tr>
<th>Species</th>
<th>White River NWR</th>
<th>Bayou Cocodrie NWR</th>
<th>Red River WMA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sample size</td>
<td>Age (years)</td>
<td>DBH (cm)</td>
</tr>
<tr>
<td>Green ash</td>
<td>112</td>
<td>57</td>
<td>28.9</td>
</tr>
<tr>
<td></td>
<td>(30-240)</td>
<td>(7.1-129.2)</td>
<td></td>
</tr>
<tr>
<td>Nuttall oak</td>
<td>35</td>
<td>101</td>
<td>45.3</td>
</tr>
<tr>
<td></td>
<td>(40-262)</td>
<td>(10.1-109.7)</td>
<td></td>
</tr>
<tr>
<td>American elm</td>
<td>87</td>
<td>42</td>
<td>17.1</td>
</tr>
<tr>
<td></td>
<td>(24-171)</td>
<td>(9.7-70.3)</td>
<td></td>
</tr>
<tr>
<td>Sugarberry</td>
<td>96</td>
<td>55</td>
<td>14.7</td>
</tr>
<tr>
<td></td>
<td>(32-197)</td>
<td>(9.5-69.5)</td>
<td></td>
</tr>
<tr>
<td>Sweetgum</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overcup oak</td>
<td>52</td>
<td>129</td>
<td>52.0</td>
</tr>
<tr>
<td></td>
<td>(32-254)</td>
<td>(5.7-93.6)</td>
<td></td>
</tr>
<tr>
<td>Honeylocust</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Age (mean and range) of green ash (FRPE; $N = 12$), Nuttall oak (QUTE; $N = 12$), American elm (ULAM; $N = 12$), and sugarberry (CELA; $N = 10$), sweetgum (LIST; $N = 9$), overcup oak (QULY; $N = 8$), and honeylocust (GLTR; $N = 3$) stems at 10 cm height increments (0-140 cm height) from stem analysis.
APPENDIX C: SAMPLE SIZE OF DOMINANT AND CODOMINANT TREES CORED

Sample size of dominant and codominant trees cored of each species to identify canopy disturbance events at White River National Wildlife Refuge (NWR; Arkansas), Bayou Cocodrie National Wildlife Refuge (NWR; Louisiana), and Red River Wildlife Management Area (WMA; Louisiana).

<table>
<thead>
<tr>
<th>Species</th>
<th>White River NWR</th>
<th>Bayou Cocodrie NWR</th>
<th>Red River WMA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ridge</td>
<td>Flat</td>
<td>Swale</td>
</tr>
<tr>
<td>Green ash</td>
<td>20</td>
<td>18</td>
<td>19</td>
</tr>
<tr>
<td>Nuttall oak</td>
<td>9</td>
<td>4</td>
<td>-</td>
</tr>
<tr>
<td>American elm</td>
<td>4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sugarberry</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Sweetgum</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Overcup oak</td>
<td>-</td>
<td>25</td>
<td>7</td>
</tr>
<tr>
<td>Sweet pecan</td>
<td>-</td>
<td>-</td>
<td>19</td>
</tr>
<tr>
<td>Willow oak</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>50</td>
<td>47</td>
</tr>
</tbody>
</table>
### APPENDIX D: ESTIMATED TIME OF ESTABLISHMENT

Estimated time of establishment of 5-10 cm DBH trees not cored using age-diameter models by topographic feature [ridges (R), flats (F), and swales (S)] at White River National Wildlife Refuge (NWR; Arkansas) and Bayou Cocodrie National Wildlife Refuge (NWR; Louisiana).

<table>
<thead>
<tr>
<th>Species</th>
<th>Study site</th>
<th>Number of stems</th>
<th>Size range (cm DBH)</th>
<th>Years of establishment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sweetgum</td>
<td>Bayou Cocodrie NWR (R)</td>
<td>3</td>
<td>5.7-6.7</td>
<td>1989-1991</td>
</tr>
<tr>
<td></td>
<td>Bayou Cocodrie NWR (F)</td>
<td>7</td>
<td>5.3-9.8</td>
<td>1981-1992</td>
</tr>
<tr>
<td>Green ash</td>
<td>White River NWR (R)</td>
<td>16</td>
<td>5.4-8.3</td>
<td>1981-1991</td>
</tr>
<tr>
<td></td>
<td>White River NWR (F)</td>
<td>7</td>
<td>6.2-9.4</td>
<td>1973-1983</td>
</tr>
<tr>
<td></td>
<td>White River NWR (S)</td>
<td>8</td>
<td>5.1-9.2</td>
<td>1982-1992</td>
</tr>
<tr>
<td></td>
<td>Bayou Cocodrie NWR (S)</td>
<td>3</td>
<td>5.5-7.8</td>
<td>1973-1982</td>
</tr>
<tr>
<td>Sugarberry</td>
<td>White River NWR (R)</td>
<td>23</td>
<td>5.1-9.3</td>
<td>1964-1984</td>
</tr>
<tr>
<td></td>
<td>White River NWR (F)</td>
<td>22</td>
<td>5.6-9.8</td>
<td>1969-1985</td>
</tr>
<tr>
<td></td>
<td>White River NWR (S)</td>
<td>22</td>
<td>5.2-9.7</td>
<td>1969-1984</td>
</tr>
<tr>
<td></td>
<td>Bayou Cocodrie NWR (R)</td>
<td>12</td>
<td>7.1-9.8</td>
<td>1956-1966</td>
</tr>
<tr>
<td></td>
<td>Bayou Cocodrie NWR (F)</td>
<td>14</td>
<td>5.6-9.8</td>
<td>1948-1964</td>
</tr>
<tr>
<td></td>
<td>Bayou Cocodrie NWR (S)</td>
<td>3</td>
<td>9.0-9.5</td>
<td>1960-1962</td>
</tr>
<tr>
<td>American elm</td>
<td>White River NWR (R)</td>
<td>14</td>
<td>5.7-9.3</td>
<td>1974-1983</td>
</tr>
<tr>
<td></td>
<td>White River NWR (F)</td>
<td>32</td>
<td>5.0-9.9</td>
<td>1971-1981</td>
</tr>
<tr>
<td></td>
<td>White River NWR (S)</td>
<td>6</td>
<td>5.0-9.7</td>
<td>1975-1983</td>
</tr>
<tr>
<td>Overcup oak</td>
<td>White River NWR (S)</td>
<td>9</td>
<td>5.5-8.9</td>
<td>1974-1986</td>
</tr>
</tbody>
</table>
APPENDIX E: AGE-DIAMETER MODELS

Descriptive statistics for age-diameter models of green ash, Nuttall oak, American elm, sugarberry, sweetgum, overcup oak, and honeylocust. Age diameter models are for ridges (R), swales (S), and flats (F) at White River National Wildlife Refuge (WRNWR) (Arkansas) and Bayou Cocodrie National Wildlife Refuge (BCNWR) (Louisiana), and on the highest elevation, mid-elevation, and lowest elevation stands at Red River Wildlife Management Area (RRWMA) (Louisiana).

<table>
<thead>
<tr>
<th>Green ash</th>
<th>Age-diameter model (A-D)</th>
<th>Coefficient of determination ($r^2$)</th>
<th>Sample size</th>
<th>Population size</th>
</tr>
</thead>
<tbody>
<tr>
<td>WRNWR (F)</td>
<td>$A = 0.0003D^3 - 0.05D^2 + 4.1D$</td>
<td>0.75</td>
<td>37</td>
<td>45</td>
</tr>
<tr>
<td>WRNWR (S)</td>
<td>$A = 0.0003D^3 - 0.04D^2 + 3.1D$</td>
<td>0.73</td>
<td>35</td>
<td>81</td>
</tr>
<tr>
<td>BCNWR (R)</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>BCNWR (F)</td>
<td>$A = 0.0006D^3 - 0.03D^2 + 3.9D$</td>
<td>0.30</td>
<td>21</td>
<td>37</td>
</tr>
<tr>
<td>BCNWR (S)</td>
<td>$A = 0.0004D^3 - 0.07D^2 + 4.9D$</td>
<td>0.53</td>
<td>39</td>
<td>65</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nuttall oak</th>
<th>Age-diameter model (A-D)</th>
<th>Coefficient of determination ($r^2$)</th>
<th>Sample size</th>
<th>Population size</th>
</tr>
</thead>
<tbody>
<tr>
<td>WRNWR (R)</td>
<td>$A = -0.0007D^3 - 0.07D^2 + 3.91D$</td>
<td>0.81</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>WRNWR (F)</td>
<td>$A = -0.00009D^3 - 0.008D^2 + 2.2D$</td>
<td>0.85</td>
<td>11</td>
<td>12</td>
</tr>
<tr>
<td>WRNWR (S)</td>
<td>$A = 0.0003D^3 - 0.06D^2 + 4.3D$</td>
<td>0.96</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>BCNWR (R)</td>
<td>$A = -0.00005D^3 - 0.01D^2 + 3.1D$</td>
<td>0.65</td>
<td>36</td>
<td>38</td>
</tr>
<tr>
<td>BCNWR (F)</td>
<td>$A = -0.009D^3 - 1.7D^2 + 39.8D$</td>
<td>0.26</td>
<td>34</td>
<td>41</td>
</tr>
<tr>
<td>BCNWR (S)</td>
<td>$A = 0.0007D^3 - 0.1D^2 + 5.0D$</td>
<td>0.23</td>
<td>47</td>
<td>124</td>
</tr>
<tr>
<td>Tree Type</td>
<td>Form</td>
<td>Equation Description</td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>-------------------</td>
<td>----------</td>
<td>------------------------------------------</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td><strong>American elm</strong></td>
<td>WRNWR (R)</td>
<td>(A = 0.003D^3 - 0.2D^2 + 5.2D)</td>
<td>0.64</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>WRNWR (F)</td>
<td>(A = -0.0002D^3 - 0.05D^2 + 3.8D)</td>
<td>0.65</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>WRNWR (S)</td>
<td>(A = 0.001D^3 - 0.5D^2 + 6.7D)</td>
<td>0.71</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>BCNWR (R)</td>
<td>(A = -0.00004D^3 - 0.03D^2 + 4.3D)</td>
<td>0.63</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>BCNWR (F)</td>
<td>(A = 0.0003D^3 - 0.07D^2 + 4.9D)</td>
<td>0.42</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>BCNWR (S)</td>
<td>(A = -0.000006D^3 - 0.02D^2 + 3.3D)</td>
<td>0.87</td>
<td>8</td>
</tr>
<tr>
<td><strong>Sugarberry</strong></td>
<td>WRNWR (R)</td>
<td>(A = 0.0004D^3 - 0.007D^2 + 4.6D)</td>
<td>0.57</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>WRNWR (F)</td>
<td>(A = 0.0003D^3 - 0.5D^2 + 4.1D)</td>
<td>0.75</td>
<td>37</td>
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<tr>
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<td>WRNWR (S)</td>
<td>(A = 0.002D^3 - 0.2D^2 + 5.2D)</td>
<td>0.77</td>
<td>30</td>
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<td>BCNWR (R)</td>
<td>(A = 0.003D^4 - 0.3D^2 + 7.4D)</td>
<td>0.26</td>
<td>40</td>
</tr>
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<td>BCNWR (F)</td>
<td>(A = 0.01D^3 - 0.5D^2 + 10.2D)</td>
<td>0.65</td>
<td>41</td>
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<td>BCNWR (S)</td>
<td>(A = 0.001D^3 - 0.1D^2 + 6.1D)</td>
<td>0.51</td>
<td>39</td>
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<tr>
<td><strong>RRWMA</strong></td>
<td>(RR)</td>
<td>(A = 0.002D^3 - 0.2D^2 + 4.3D)</td>
<td>0.24</td>
<td>42</td>
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<td></td>
<td>(MR)</td>
<td>(A = 0.002D^3 - 0.2D^2 + 4.7D)</td>
<td>0.32</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>(INT)</td>
<td>(A = 0.001D^3 - 0.1D^2 + 4.1D)</td>
<td>0.33</td>
<td>42</td>
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</tbody>
</table>
### APPENDIX E CONTINUED

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Equation</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
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<tbody>
<tr>
<td>Sweetgum</td>
<td>BCNWR (R)</td>
<td>$A = 0.0004D^3 - 0.06D^2 + 3.1D$</td>
<td>0.87</td>
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<td>118</td>
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<td>BCNWR (F)</td>
<td>$A = 0.0002D^3 - 0.03D^2 + 2.9D$</td>
<td>0.85</td>
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<td>Overcup oak</td>
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<td>$A = 0.002D^3 - 0.06D^2 + 6.1D$</td>
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<tr>
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<td>WRNWR (S)</td>
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<td>RRWMA (RR)</td>
<td>$A = 0.0003D^3 - 0.05D^2 + 3.9D$</td>
<td>0.69</td>
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<td>$A = 0.0007D^3 - 0.1D^2 + 5.0D$</td>
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<td>135</td>
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<tr>
<td>Honeylocust</td>
<td>RRWMA (MR)</td>
<td>$A = 0.0004D^3 - 0.3D^2 + 6.7D$</td>
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<td>29</td>
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<tr>
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<td>RRWMA (INT)</td>
<td>$A = 0.004D^3 - 0.3D^2 + 5.9D$</td>
<td>0.79</td>
<td>32</td>
<td>53</td>
<td></td>
</tr>
</tbody>
</table>
VITA

Hugo Gee was born in Montreal, Quebec (Canada,) in 1973. He graduated from Concordia University (Montreal, Quebec), in 1995 with a Baccalaureate in Commerce degree in marketing. Hugo worked as a project coordinator in the printing and publishing industry for the next 3 years before returning to school to follow his passion for conservation. He received a Bachelor of Science degree in wildlife biology from McGill University (Montreal, Quebec,) in 2002. Hugo caught the wetland bug and studied “Habitat characteristics of taro lo’i and managed wetlands used by endangered Hawaiian waterbirds at Hanalei National Wildlife Refuge, Hawaii”, for his graduate studies. He received his Master of Science in fisheries and wildlife sciences from South Dakota State University (Brookings, South Dakota), in 2007. In May of 2012, he will receive a Doctor of Philosophy in wildlife and fisheries sciences from the School of Renewable Natural Resources at Louisiana State University.