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Evaluation of growth rates and establishment patterns of water-elm (Planera aquatica) and baldcypress (Taxodium distichum) in response to hydrologic and climatic conditions at Catahoula Lake, Louisiana

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EVALUATION OF GROWTH RATES AND ESTABLISHMENT PATTERNS OF WATER-ELM (*PLANERA AQUATICA*) AND BALDCYPRESS (*TAXODIUM DISTICHUM*) IN RESPONSE TO HYDROLOGIC AND CLIMATIC CONDITIONS AT CATAHOULA LAKE, LOUISIANA

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ABSTRACT

Hydrologic alterations frequently lead to vegetation changes in floodplain ecosystems. In Louisiana, there has been an expansion of water-elm (*Planera aquatica*) and to a lesser extent baldcypress (*Taxodium distichum*) at Catahoula Lake, a Ramsar Wetland of International Importance. Water-elm and baldcypress both are flood tolerant species; baldcypress growth is known to be influenced by hydrologic conditions more than climate. The expansion of these woody trees has reduced herbaceous vegetation valuable for waterfowl. In this study, I tested two hypotheses that establishment of water-elm trees into the lake increased after the construction of water control structures in the nearby Black River and a diversion canal and water-control structure on the lake in 1971; and that growth rates of water-elm and baldcypress are more correlated with hydrologic regimes than with local climate. Water-elm trees have been found in the lake for at least 140 years, but most (171 of 219) sampled trees were established in the period following the construction of water-control. In addition, 48 of 67 plots consisted of trees established entirely in the post-control period. Hydrologic conditions in the lake changed with the modifications, including reduced variability in June and August lake levels and reduced fall flooding. These changes coincided with apparently increased establishment of water-elm trees during the post-control period. Finally, there are several sources of uncertainty that prevent clear interpretation of the effects of water control on water-elm establishment including prevailing climatic conditions, control measures by Louisiana Department of Wildlife and Fisheries and cattle grazing. My second hypothesis that growth of water-elm and baldcypress would be more correlated with hydrologic regimes than with climate was partially supported. Growth of water-elm was more related to climatic variables than with lake levels, whereas baldcypress radial growth was more correlated with lake levels than with climatic variables. The response of water-

elm radial growth to lake hydrology was limited to a negative relationship with late spring lake levels in the pre-control period; baldcypress had a consistent positive response with lake levels during several seasons in both the pre-and post-control periods.

INTRODUCTION

Timing, depth, duration, and frequency of floods affect tree establishment, growth and species composition in forested wetlands (Hook 1984, Brinson 1990). Flood duration during the growing season, depth of flooding during the dormant season and light availability strongly affect seed germination, seedling establishment, and seedling growth in forested wetlands (Kozlowski 1984, Streng et al. 1989, King and Grant 1996). Flooding during the initial year of seedling establishment can significantly affect the composition of the seedling bank and may strongly influence future overstory composition (Streng et al. 1989, Jones et al. 1994). Streng et al. (1989) found that seedling establishment and survival depend more on flooding than other environmental factors such as light availability and drought. Furthermore, they noted that growing-season flooding during the year of establishment was the most important mortality factor in most light-seeded species. Seedlings produced from heavy-seeded species, such as water oak (*Quercus nigra*), were more tolerant of flooding during their first growing season, presumably due to the larger seed reserve that facilitates resprouting. In both light- and heavy-seeded species, seedling survival increases substantially after the first year in spite of continuous disturbances through flooding and other environmental factors (Streng et al. 1989, Jones et al. 1994).

Flood regime, the timing, depth, duration and frequency of flooding also affects growth of floodplain trees (Brinson 1990). A variety of adaptations to flooding facilitates growth and survival of flood-tolerant tree species (Kozlowski 2002). Growth responses of congeneric tree species can be inconsistent, however, even in similar flood regimes (Mitsch and Ewel 1979, Conner et al. 1981, Stahle et al. 1992). For example, subjecting seasonally flooded bottomland hardwoods to continuous flooding can initially result in either decreased (Mitsch and Ewel 1979, Conner and Brody 1989, Mitsch et al. 1991) or increased growth (Conner and Day 1976, Conner et al. 1981, Keeland and Young 1997). Often tree growth initially increases, and then is followed by a long decline in growth when flooding continues (Stahle et al. 1992, Young et al. 1995). Growth may be increased immediately after floods because of the distribution of supplementary water and a temporary rise in water table post-flooding (Broadfoot and Williston 1973). Flood waters also transport sediments filled with dissolved and undissolved nutrients necessary for tree growth (Mitsch and Rust 1984). Growth is decreased, however, by prolonged flooding during the growing season (Hook 1984, Dickie and Toliver 1990). What defines "prolonged flooding" during the growing season varies among species as well as within a species, based on the age of trees, and/or soil chemical properties (Broadfoot and Williston 1973).

Flooding is not the only controller of tree growth in forested wetlands as climate is also important (Fritts 1976, Stahle et al. 1988, Handerson and Grissino-Mayer 2009). The Palmer Drought Severity Index (PDSI) is a common index of temperature, precipitation and soil moisture (Palmer 1965) that is often used to determine the effects of climate on tree growth. In forested wetland systems, several studies indicate that tree growth responds to PDSI (Stahle et al. 1988, Reams and Vandeusen, 1998, Gee 2012). Stahle et al. (1988) found a positive correlation between baldcypress tree growth and summer PDSI in North Carolina. Similarly, Reams and Vandeusen (1998) found old-growth baldcypress ring widths were best correlated with June PDSI relative to other monthly climatic variables. Gee (2012) found that overcup oak (*Quercus lyrata*) growth was positively related with late non growing season to early growing season PDSI at some sites. At other sites, however, growth response varied from no significant correlation with PDSI to being positively correlated during the late growing season. Bohora (2012) and

Keim and Amos (2012) found that baldcypress tree growth was less correlated to climatic variables compared to water levels in coastal wetland forests of Louisiana.

Because of the close linkages among hydrologic processes and tree establishment and growth, hydrologic alterations, such as dams (Sparks 1995, Poff et al. 1997, Stallins et al. 2010), channelization of streams, and construction of levees and canals (Hupp et al. 2009) have led to changes in many floodplain ecosystems (Bendix and Hupp, 2000). These changes may include decrease in establishment and growth of floodplain trees (Reily and Johnson 1982, Polzin and Rood 2000, Gee 2012), changes in forest community structure and successional processes (Palta et al. 2003), and mortality of overstory trees (Wilder and Roberts, 2004). In addition to these impacts, hydrologic alterations can also lead to changes in the herbaceous community. Weller (1989) observed gradual successional shifts from natural herbaceous plant communities to woody vegetation in a bottomland hardwood forest in east Texas following artificial changes to the flooding regime.

Hydrologic alterations have possibly led to an expansion of woody vegetation into Catahoula Lake, a Ramsar Wetland of International Importance (Emfinger 1991) and the largest freshwater lake in Louisiana (Martin 1986, Lotz 2000). Catahoula Lake lies on the western embankment of the Mississippi River floodplain. Recently, the areal coverage of herbaceous plants has decreased in the lake bed along with a simultaneous increase in woody plants (Bruser 1995). Invasion by woody plants particularly water-elm and to a lesser extent baldcypress (*Taxodium distichum*) in the lake bed has increased at the expense of herbaceous plants, such as chufa (*Cyperus esculentus*), that are valuable for wintering waterfowl. In addition to direct losses of herbaceous communities, productivity of herbaceous plants has been reduced due to reduced light availability resulting from crown closure of the woody vegetation (Bruser 1995).

Water-elm has had a particularly noticeable expansion into the lake bed. Early studies suggested that water-elm was historically present in the lake bed and that its expansion may have begun several decades ago (Brown 1943, Wills 1965). Brown (1943) found a dense population of young water-elm trees and other shrubs throughout the middle elevations of the lake bed between baldcypress trees in the lake's outer, higher elevation boundary and herbaceous vegetation in the center of the lake. Wills (1965) concluded that water-elm was slowly advancing into the Catahoula lakebed, whereas Bruser (1995) noted that water-elm expansion had increased at the time of her study.

The vegetative changes described by Wills (1965) and Bruser (1995) may indeed be related to alterations in the hydrological regime. Willis (2009) noted that major hydrologic changes have occurred in Catahoula Lake due to anthropogenic changes to the Atchafalaya and Mississippi Rivers. The Atchafalaya River had a log raft until 1858 which discouraged water from the Mississippi River entering into the Atchafalaya (Reuss 2004, Willis 2009). The removal of the raft in 1858 increased flow capture from the Mississippi River and resulted in increased downstream flooding and gradual incision of the Atchafalaya River (Willis 2009). Capture of Mississippi River water by the Atchafalaya increased over several decades until it became a threat to capture the majority or the entire flow of the Mississippi River. Thus in 1963, the Old River Structure was built to control the amount of Mississippi River water entering the Atchafalaya River and prevent the complete capture by the Atchafalaya (Willis 2009). Construction of the Old River Structure and gradual incision of the Atchafalaya River brought about a gradual downward shift in the stages of the Black River. The stages of the Black River are important because Catahoula Lake levels are affected by Black River water levels. As a result of the reduced stages, lake levels at Catahoula Lake have decreased substantially (Willis 2009).

In 1971, a diversion canal and water-control structure were built at Catahoula Lake to facilitate attempts to replicate the lake's original natural water regime (Bruser 1995). Bruser (1995) noted that the construction of the diversion canal and water-control structure, however, led to more efficient lake drainage, reduced the length of growing season flooding, and decreased the frequency of fall flooding. Furthermore, Bruser (1995) also found that lake levels were more variable prior to the construction of the diversion canal and water-control structure than after their construction.

Apart from hydrologic alterations, cattle grazing could also have affected woody vegetation establishment and expansion at Catahoula Lake. Free range grazing is believed to have started in the lakebed during the 1700's (Bruser 1995) and certainly occurred several decades prior to its cessation in 2000 (*LSA-R.S. 3:2891*). Cattle grazing could possibly have affected woody establishment as cattle trample and graze the seedlings; it could also have helped in woody expansion as young woody shrubs when browsed by cattle would grow more strongly taking a compact, bushy form (Bruser 1995).

The Louisiana Department of Wildlife and Fisheries (LDWF) became concerned about the expansion of water-elm trees into the lake bed as early as the 1950's. However, fewer measures were implemented to control water-elm during the pre-control period. LDWF increased control measures during the post-control period beginning in the mid-1970's. These measures include mowing as well as cutting and herbiciding water-elm trees. These techniques are costly and of limited success (personal communication with LDWF personnel, Steve Smith). Thus it is hoped that an understanding of species-specific establishment of water-elm trees and growth responses of both water-elm and baldcypress trees to the altered hydrologic regimes at Catahoula

Lake can facilitate the development of more effective and cheaper control measures using managed water levels.

Objectives

The objective of this study was to assess the establishment patterns and growth rates of water-elm trees and growth rates of baldcypress trees at Catahoula Lake.

Specifically, I used water-elm tree ages from the pre- and post-control period to evaluate the age structure of water-elm at Catahoula Lake to provide insights on water-elm establishment in the lakebed. I also used tree rings to evaluate the effects of water levels and climate on water-elm and baldcypress tree growth and to see if their growth responses to hydrology and climate are similar.

Hypotheses

I hypothesized that establishment of water-elm trees into the lake bed increased after the construction of a diversion canal and water-control structure on the lake in 1971. Furthermore, I hypothesized that growth rates of water-elm and baldcypress are more strongly correlated with hydrologic regimes than local climate and that the species have similar patterns of radial growth.

Ecology of Water-elm and Baldcypress Trees

Water-elm is found along riverbanks, in forested wetlands, and in swamps of Gulf and Atlantic Coastal Plains and the Lower Mississippi Alluvial Valley (Rayner 1976, Bruser 1995). It can grow in association with baldcypress in areas with long term flooding and can survive a permanent water depth of up to one meter (Elias 1970). Seedlings of water-elm can shade out the herbaceous species that require sunlight and shallow water (Weller 1989). It is extremely tolerant of flooding (Whitelow and Harris 1979) and water-logging (Theriot 1993).

Water-elm trees growing in flooded, high-light conditions, especially when floodwaters cover part of the crown, produce more seeds (Bruser 1995). Water-elm seeds are produced from fruits that fall from trees one month after their flowering from February to April (Elias 1970, Bruser 1995). Most of the seeds float for up to a few weeks then sink (Rayner 1976). Water-elm seeds remain viable for more than six months in flooded conditions and germinate on the soil surface when floodwaters are removed (Rayner 1976). Water-elm seedlings have the highest chances of mortality from flooding during their first year of life especially in the first few months after their germination, however, the survival rate of seedlings increases substantially in subsequent years (Rayner 1976). Several studies have discussed the characteristic features of water-elm and the physical conditions suitable for its growth (Elias 1970, Rayner 1976); however, I am aware of no studies that have analyzed tree growth and establishment as it relates to hydrologic regimes.

Baldcypress is an important species of deep-water swamps and bottomland hardwood forests of the southern United States in sites with frequent and prolonged flooding (Wharton et al. 1982, Conner 1988). Mature trees can tolerate flood depths of 3m or more (Wilhite and Toliver, 1990). Several studies have analyzed growth responses of baldcypress to changes in natural hydrologic regimes particularly in areas with permanent flooding (Eggler and Moore 1961, Conner and Day 1976, Duever and McCollom 1987, Keeland 1994, Young et al. 1995) but information on the combined effects of climate and reduced variability in flooding patterns on baldcypress tree growth is still needed.

Description of the Study Area

This study was conducted on the 122 km^2 Catahoula Lake. Catahoula Lake is located in LaSalle and Rapides parishes in central Louisiana approximately 32 km northeast of Alexandria at the western boundary of Lower Mississippi River Valley. Catahoula Lake supports large numbers of migratory waterfowl and shorebirds and, as a result, it has been officially declared a Wetland of International Importance by the Ramsar Convention (Emfinger 1991). It is subject to backwater flooding from the Red and Black rivers and head water flooding from the Little River along with adjoining small streams (LDWF 1991). The hydrological regime of this lake is irregular; water levels fluctuate by 7 m annually (Willis 2009) and most of the lake bed is exposed to mud flats during midsummer (Lotz 2000).

In 1971, a diversion canal and a water-control structure were built to facilitate water-level management of the lake (Bruser 1995). Water levels are managed according to an agreement jointly signed by Louisiana Department of Wildlife and Fisheries (LDWF), U.S. Fish and Wildlife Service (FWS) and the U.S. Army Corps of Engineers (USACE) (Woolington and Emfinger 1989, Bruser 1995). The basic goal of water level management is to ensure substantial numbers of waterfowl in the lake during winter for waterfowl conservation and recreational waterfowl hunting (Bruser 1995).

The variance of mean monthly water levels was reduced substantially under artificial conditions after the construction of the diversion canal and the water-control structure (Bruser 1995). Bruser (1995) found reduced variability in mean water levels in August, September and October in the post-control (1974 through 1994) relative to the pre-control (1958 through 1971) period. However, during the post-control period mean variance in water levels was greater in November than during the pre-control period. In all other months there was no significant difference in mean variability of the lake levels during both periods (pre- and post-control) probably because the lake remained flooded during these months in both periods (Bruser 1995). However, when I analyzed the pre-control lake level data from 1950 through 1971 and the post-control lake level data from 1972 through 2009, I found that mean variability of the lake levels pre-control were higher for October and November (Table 1). Post-control lake levels had higher variances for June and August months than pre-control lake levels (Table1). In all other months, no significant difference was found in the mean variability of the lake levels during both periods (Table 1).

Russell (1942) and Brown (1943) termed Catahoula Lake as a rim-swamp lake; valley banks border the lake on the northwest side while natural levees surround it elsewhere. Catahoula Lake historically has been dominated by moist, soil herbaceous plants, particularly chufa (*Cyperus esculentus*), millet (*Echinochloa walteri*), sprangletop (*Leptochloa fusca* ssp. *fascicularis*), and duck potato (*Sagittaria latifolia*) (Wills 1965). Seeds of the herbaceous plants are sources of food for migratory waterfowl during fall and winter (Wills 1972, Hohman et al. 1990, Lotz 2000).

Table 1: Mean and standard errors and variances of monthly lake levels at Catahoula lake with the list of results of two-sample F-test that compared variances of monthly lake levels during the pre-control (1950 -1971; n =21) and post-control (1972 – 2009; n = 38) period.

Months	Mean ± Standard error (m)		Variances (m²)		Two sampled F-test	
	Pre-control	Post-control	Pre-control	Post-control	F-calculated	F-tabulated
January	10.14 ± 3.36	11.12 ± 3.26	11.29	10.63	1.06	2.11
February	11.04 ± 3.68	11.79 ± 2.85	13.54	8.12	1.67	2.11
March	12.19 ± 3.46	12.26 ± 2.89	11.97	8.35	1.43	2.11
April	12.62 ± 3.47	12.39 ± 3.03	12.04	9.18	1.31	2.11
May	12.66 ± 3.90	12.16 ± 3.63	15.21	13.18	1.15	2.11
June	11.19 ± 4.82	11.55 ± 3.30	23.23	10.89	2.13	2.11
July	9.62 ± 3.29	9.63 ± 2.53	10.82	6.40	1.69	2.11
August	8.63 ± 1.33	8.40 ± 0.57	1.77	0.32	5.44	2.11
September	8.35 ± 0.57	8.43 ± 0.83	0.32	0.69	2.12	2.31
October	8.33 ± 0.36	8.55 ± 1.16	0.13	1.35	10.38	2.31
November	8.50 ± 1.01	9.23 ± 2.00	1.02	4.00	3.92	2.31
December	9.34 ± 2.90	10.23 ± 2.66	8.41	7.08	1.19	2.11

*There was no significant difference in variances of monthly lake levels in both periods if F-calculated < F-tabulated (at $\alpha = 0.05$) and significant difference in variances if F-calculated > F-tabulated (at $\alpha = 0.05$).

MATERIALS AND METHODS

Study Sites

I established 7 transect lines scattered across the study area to collect tree cross sections and increment cores (Figure 1). Five of these transects were approximately the same as those of Wills (1965). The remaining two transects had nearly the same location and azimuth as those of Bruser (1995). Transects varied in length and the number of points on a given transect (Table 1). These transects were named by Wills (1965) and Bruser (1995): Mosquito Bend, French Fork, Indian Bayou, Diversion Canal, Willow Springs, Alligator Bayou and Stock Landing. Four transects (Mosquito Bend, Willow Springs, Diversion Canal, and Alligator Bayou) supported trees on the eastern and western end, but mudflats persisted in the lower elevations near the center of the lake and transects. Thus, I divided these 4 transects into two parts designated east and west: Mosquito Bend East and Mosquito Bend West, Willow Springs East and Willow Springs West, Diversion Canal East and Diversion Canal West and Alligator Bayou East and Alligator Bayou West. The remaining 3 transects (French Fork, Indian Bayou and Stock Landing) were sampled only on the eastern end resulting in a total of 11 transects. I moved the initial sampling point forward along the transect line by at least 50 meters if any obstacle such as road, cleared land, etc. was present.

Field Sampling

Sampling points were established at 50 meter intervals along each transect line in the water-elm zones. The water-elm zones are defined as the areas where the number of woody stems of water-elm trees exceeded the number of woody stems of other tree species (Brown 1943). I used the point-quarter sampling method to identify sample trees. At each sampling

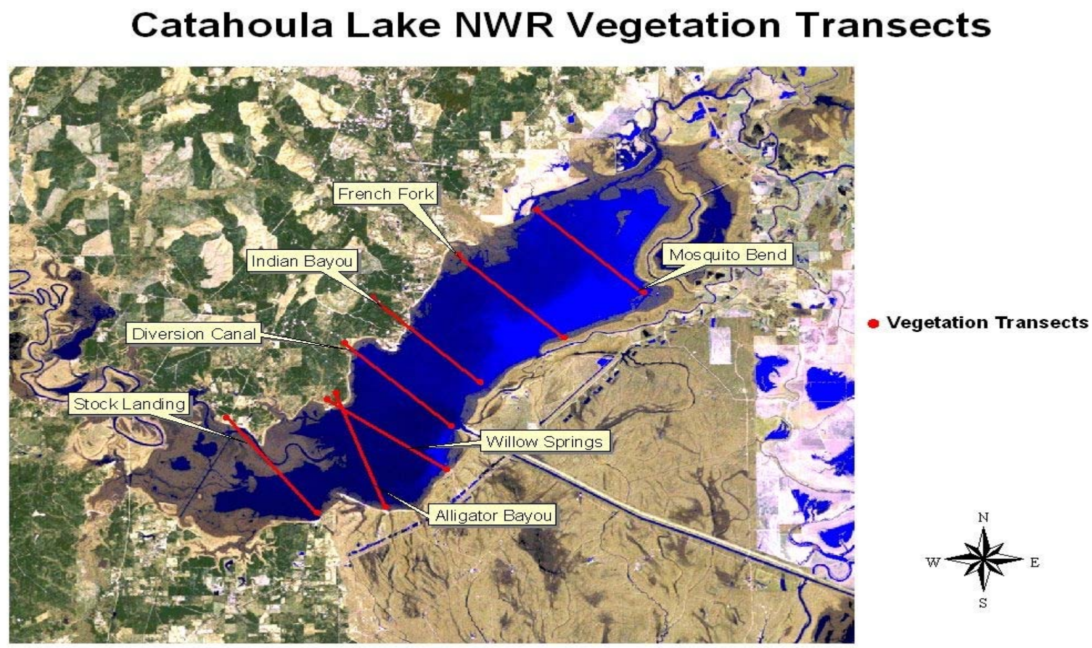

Figure 1: Transect locations at Catahoula Lake, Louisiana.

Table 2: Study sites and sampling transects.

Study Site	Length of transect (meters)	Number of sampling points	Number of samples collected
Mosquito Bend East	550	10	30
French Fork	250	4	10
Indian Bayou	350	5	18
Diversion Canal East	200	3	12
Willow Springs East	400	6	16
Alligator Bayou East	400	7	19
Stock Landing	300	5	15
Mosquito Bend West	600	10	36
Diversion Canal West	250	4	16
Willow Springs West	500	9	33
Alligator Bayou West	250	4	14

point, I defined four quadrants in two perpendicular axes from the point; one axis was along the direction of transect line while another was perpendicular to the transect line. I selected the closest tree in each quadrant ≥ 5 cm diameter-at-breast height (dbh) within 10 m from the origin. If no trees ≥ 5 cm dbh were present within 10 m, a sample was not taken in that quadrant. For each selected tree, I measured the distance from the tree to the plot center. I then collected cross-sections from the largest stem of the tree as close to the base of the tree as possible with a chain saw. For trees > 30 cm dbh, I collected two increment cores per tree by coring the trees at breast height and in opposite directions. Some larger trees were not sampled because it was not possible to collect a suitable core due to twisted stems or they were partially decayed and hollowed. Each sample was labeled with the site, location point, and core or cookie (cross-section) identification number.

Dendrochronological Methods

Standard dendrochronological techniques recommended by Stokes and Smiley (1968) and Phipps (1985) were used to analyze water-elm samples. Cores and cross-sections were transported to the lab and dried at 50ºC for almost one week in a dehydration oven. The dried cores were mounted, and both cores and cross-sections were sanded with progressively finer grits of sandpaper (80-600 grit) until cells were clearly visible under the microscope.

The method of list count described by Fritts (1976) was used to assign years to annual rings. Some cross-sections had a decayed and hollowed pith; in such cross-sections rings were counted only up to their undecayed portion. Final age of these cross-sections was estimated by measuring the length of decay and estimating the number of rings that would have been present in that length according to the number of rings present in the undecayed section. This number was then added to the number of rings already counted. Hollow cross-sections were not subjected to ring measurements and were included only in the analysis of establishment patterns.

Ring widths for all undecayed cross sections were measured and recorded to the 0.01 mm using a Velmex measuring stage (model A60, Bloomfield, New York). In each cross section, ring widths were measured along two axes and then averaged to develop a tree-ring series for each tree. Cross-dating was accomplished graphically using Microsoft Excel 2010. Finally, the program COFECHA was used to verify cross-dating (Holmes 1983, Grissino-Mayer 2001).

Water-elm Chronology Development

After graphical analysis, raw ring widths of water-elm trees were analyzed with COFECHA. Critical level of correlation in COFECHA was retained at 0.328 (Holmes 1983). COFECHA output identified potential problems in each cross-section if the ring widths were flagged for poor correlation (< 0.328) with the master dating series. The cross-sections with potential problems were evaluated, and if necessary, fixed. These cross-sections were reanalyzed in COFECHA; however, cross-sections that could not be fixed were ignored in further analysis. Some cross-sections of older (> 50 years) trees had a poor correlation (> 0.25) with the master dating series but were included in further analysis to lengthen the chronology. Using this procedure COFECHA was rerun several times until acceptable values of series intercorrelation and average mean sensitivity were obtained.

Finally, after verification of cross dating, I used the program ARSTAN to standardize and detrend ring width measurements (Cook and Holmes, 1997). Detrending eliminates endogenous disturbances (such as noise) and maximizes the signal of interest (Cook and Holmes, 1986). I used cubic smoothing spline of 50% frequency response as the detrending method. Final ARSTAN output consisted of four chronologies (i.e., raw, standard, residual and arstan). The raw chronology is mere average of ring width measurements, however, standardization procedures are followed in the Standard, Residual and Arstan chronologies (Speer 2010). Out of these four chronologies, I used the standard and residual chronologies to compare them within a tree species and between two tree species. However, I only used residual chronology for further statistical analysis because; in contrast to standard and arstan chronologies, it had no autocorrelation and represented tree radial growth better than the other three chronologies.

Baldcypress Chronology

Radial growth pattern of baldcypress trees at Catahoula Lake was analyzed using cores collected by Dr. Frank Willis in 2006 from the Bacon Run site (Willis 2009). Dr. Willis had already measured and cross-dated these cores with standard dendrochronological techniques (Stokes and Smiley, 1968, Phipps 1985). For the purpose of this study, a single COFECHA run was enough to support cross-dating efficiency of measured ring widths. After verification of cross-dating, raw ring widths were standardized using program ARSTAN (following the same procedure as in water-elm trees) to develop chronologies for baldcypress. As with water-elm, both residual and standard chronologies were used for comparison within a tree species and between two tree species and the residual chronology was used for further statistical analysis.

Comparison of Water-elm and Baldcypress Chronologies

I compared and contrasted both standard and residual chronologies of water-elm and baldcypress trees at Catahoula Lake to point out similarities and differences in radial growth patterns of two relatively flood tolerant tree species at the same locality experiencing the same hydrologic regimes. In particular, I identified the years in the respective chronologies where low growth in one species contrasted with high growth in the other species and those years where both species responded similarly with noticeably higher or lower growth than other years.

Statistical Methods

Hydrologic Data

To determine the effects of lake levels on tree growth, I used Catahoula Lake level data obtained from Placid Oil Company's gage at French Fork on the east side of Catahoula Lake. The data set extended from 1950 to the start year of the chronology (i.e., 2009).

Exceedance Probability Curves

To analyze if it was possible that flooding had an impact in the first year of establishment of seedlings during the late growing and early non-growing season months (August, September and October), I plotted all of my sample plots on the base map consisting of Catahoula Lake bathymetry given by Michot et al. (2003) using ARCGIS 10 to determine the elevation of sampling plots. Further, I calculated exceedance probability curves for lake levels during August, September, and October for both the pre- and post-control periods

Climate Data

To determine effects of climate on tree growth, I obtained climate data for 1950-2009 from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC) database. For statistical analysis, the climatic variables that I used were monthly mean temperature, monthly precipitation, PDSI and Palmer's Hydrological Index (PHDI). PDSI and PHDI are drought indices used by National Weather Service in order to evaluate wet or dry moisture conditions during the growing season (Stahle et al., 1988). The PDSI is dependent on temperature, precipitation and soil moisture conditions (Palmer 1965); PHDI evaluates long term hydrological impacts (NCDC 2010).

Correlation Analysis

To determine the linear relationship between tree growth and hydrology, correlation between residual chronologies of baldcypress and water-elm and lake levels were calculated (PROC CORR; SAS 9.3).

I also categorized both water-elm and baldcypress chronologies into pre- (1950-1971) and post-control (1972-2009) periods in order to determine if the relationship between hydrology and radial growth of both trees, and the relationship between precipitation and water-elm radial growth changed due to the canal and water-control structure. Finally, correlation values between chronologies and monthly hydrologic variables, water-elm chronology and precipitation for the pre- and post-control periods were calculated separately using Pearson's correlation procedure as mentioned above.

To determine effects of climate on tree growth, I used the same procedures described above to calculate correlation between both trees' chronologies and monthly precipitation, temperature, PDSI and PHDI.

Growing season for trees in southern Louisiana is from March to September of the year of their ring formation (Eggler 1955). However, apart from the possibility of being significantly related to monthly growing season climatic/hydrologic variables for the year of ring formation, tree growth can also be significantly related to variables one year prior to the year of ring formation (Bohora 2012). Therefore, I used monthly climatic/hydrologic variables for 19 months from March of the previous year to September of the year of ring formation. Altogether 95 different variables were used in correlation analyses.

Age Diameter Relationships

Water-elm tree ages were plotted against their corresponding dbh. To determine the linear relationship between establishment dates and dbh of trees, correlation between water-elm tree ages and their dbh were calculated (PROC CORR; SAS 9.3).

Analysis of Water-elm Establishment Patterns

To evaluate stand establishment patterns of water-elm trees during the pre- and post-control period, I first had to distinguish between young trees colonizing new areas and those representing regeneration of previously forested areas to prevent erroneous conclusions about the rate of woody encroachment. Thus, I classified my sampled trees into two age groups; pre-control and post-control period. Similarly, I separated the plots consisting of pre-control trees entirely with plots consisting of post-control trees entirely and plots consisting of both pre- and post-control trees.

Relationship between Tree Age and Distance to the Lake Edge

The analysis of relationship between age of trees and their distance to the lake edge was carried out for transects consisting of both pre- and post-control trees. In each such transect, water-elm tree ages were plotted against the distance of the plots (which consisted of those trees) from the tree line in that transect. The tree line in each transect was the starting point of that transect which was not sampled; sampling points were assigned at 50 m intervals towards the upper bank of the lake up to end of water-elm zones. Since, tree line for each transect was near the center and all sampling points were towards the upper bank of the lake; I hypothesized that the farthest sampling point from the tree line would consist of the oldest tree and there would be decrease in age of trees with decrease in distance of the sampling point from the tree line of the transect.

RESULTS

Description of Sampled Ages

I collected a total of 215 cross-sections and 4 cores (Table 3). Out of the 219 samples, 171 trees were less than or equal to 38 years of age and thus established in the post-control period where as 48 trees established during the pre-control period (Table 3). Five transects supported trees established only in the post-control period: Mosquito Bend East (n=30), Indian Bayou (n=18), Diversion Canal East (n=12), Diversion Canal West (n=16) and Willow Springs West (n=33) (Table 3, Figure 2). The remaining six transects had trees that established during both the pre- and post-control periods: French Fork (n=10), Willow Springs East (n=16), Alligator Bayou East (n=19), Stock Landing (n=15), Mosquito Bend West (n=36) and Alligator Bayou West (n=14) (Table 3, Figure 2). Out of 171 trees established during the post-control period 40 trees were less than or equal to 20 years, 114 trees were between 21-30 years old and 17 trees were between 31-38 years of age (Table 3, Figure 3). Of 45 trees established during the pre-control period, 11 trees were between 39-50 years and 37 trees were greater than 50 years of age. The Mosquito Bend West (n=10), French Fork (n=9), Alligator Bayou West (n=8), and Alligator Bayou East (n=7) transects contained the most trees over 50 years old (Table 3, Figure 3). The four cored trees from the French Fork transect were the oldest in the study, with 3 trees greater than 100 years old and one greater than 90 years old. The oldest tree in this study (131 years) was found on this transect; the youngest tree was 11 years old and was found on the Diversion Canal West transect. Also, the highest number of trees (n=19) were established in the years 1985 and 1987; both of these years were in post-control period (Figure 4). During the pre-control period, the highest number of trees (n=5) were established in the year 1971 (Figure 4).

Table 3: Ages of water-elm as determined from cross-sections and cores (n=4). All four cores were collected on the French Fork transect.

Transect	No. of Samples	No. of samples with age ≤38			No. of samples with age >38		Total ≤38	Total >38
		≤20	21-30	31-38	39-50	>50		
Mosquito Bend East	30	12	18	0	0	0	30	0
French Fork	10*	0	1	0	0	9	1	9
Indian Bayou	18	2	9	7	0	0	18	0
Diversion Canal East	12	1	11	0	0	0	12	0
Willow Springs East	16	2	9	1	4	0	12	4
Alligator Bayou East	19	0	5	5	2	7	10	9
Stock Landing	15	3	5	0	4	3	8	7
Mosquito Bend West	36	5	20	0	1	10	25	11
Diversion Canal West	16	5	9	2	0	0	16	0
Willow Springs West	33	4	27	2	0	0	33	0
Alligator Bayou West	14	6	0	0	0	8	6	8
Total	219	40	114	17	11	37	171	48

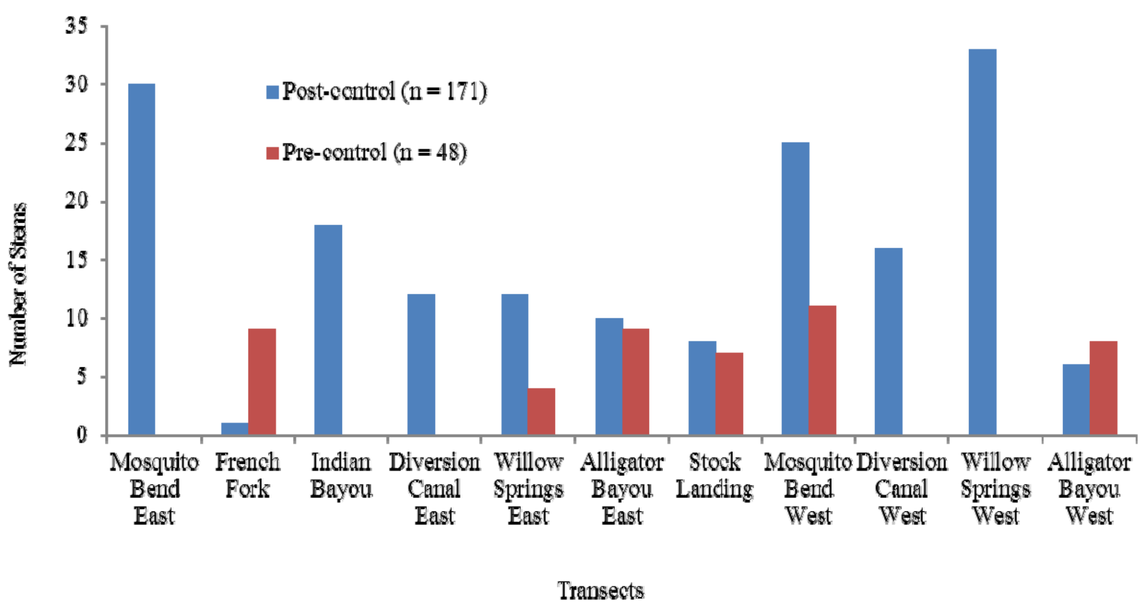

Figure 2: Comparison of the number of sampled trees in each transect established before (pre-control) and after (post-control) the construction of the diversion canal and water-control structure at Catahoula Lake. The diversion canal and water-control structure were constructed in 1971.

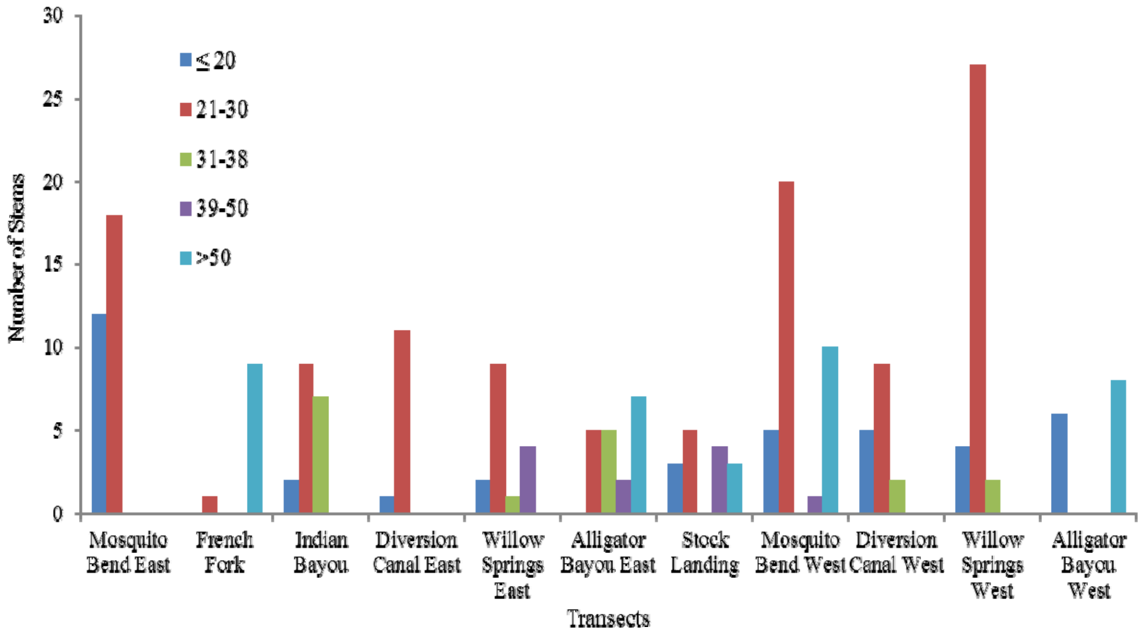

Figure 3: Comparison of the number of sampled trees in each transect at Catahoula Lake in predefined age-classes of 10 years. The first age class was defined as ≤ 20 years because the lowest age recorded was 11 years.

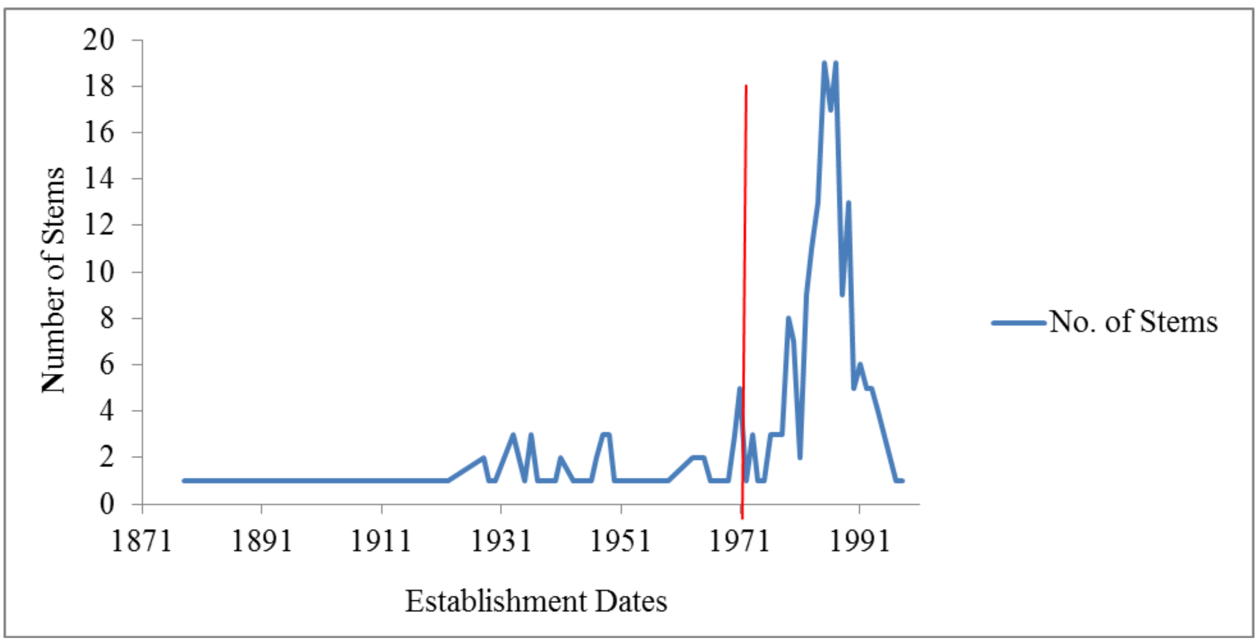

Figure 4: Comparison of number of sampled trees according to their corresponding years of establishment. The red vertical line in 1971 separates trees established during the pre-control period (on its left hand side) with trees established during the post-control period (on its right hand side).

Age of Decayed Cross-Sections

Out of 215 cross-sections, 8 were decayed and hollowed at the pith. A total of 5 decayed cross-sections were collected from Alligator Bayou West and 1 each from Willow Springs East, Stock Landing and French Fork transects (Table 4). The radius of decayed pith was highest in the cross-section GW4D (5.65mm) which belonged to Alligator Bayou West and lowest in GW3B and GW3D (0.7mm) which also belonged to the same transect (Table 4).

Table 4: Logical ring count estimation of cross-sections of water-elm trees with decayed pith.

Name of cross-section	Transect	Number of rings in undecayed portion of cross section	Diameter of decayed portion of pith (mm)	Total Estimated age
WSE1D	Willow Springs East	68	2.15	72
Stock5B	Stock Landing	63	2.55	68
French4A	French Fork	75	1	78
GW3B	Alligator Bayou West	59	0.7	61
GW3C	Alligator Bayou West	54	1.3	60
GW3D	Alligator Bayou West	78	0.7	81
GW4B	Alligator Bayou West	52	3.15	61
GW4D	Alligator Bayou West	70	5.65	87

Water-elm Establishment Pattern at Catahoula Lake

Analysis of individual water-elm trees ages and their distribution according to plots indicated that woody vegetation was established in the lake even before the construction of diversion canal and water-control structure but the number of trees established was greater during the post-control period. French Fork, Alligator Bayou East, Stock Landing, Willow Springs East, Alligator Bayou West and Mosquito Bend West all had plots with trees established during both pre- and post-control periods (Figure 2). On the remaining 5 transects, all sampled trees were established during the post-control period (Figure 2). Of the six transects with mixed ages, 53% of plots (19 out of 36) consisted of both pre-and post-control trees while 48% of plots

(17 out of 36) had post-control trees entirely (Appendix). In all transects, 18% of plots (12 out of 67) consisted entirely of pre-control trees (n=35), 72 % of plots (48 out of 67) had only post-control trees while 10 % of plots (7 out of 67) consisted of both pre-(n=13) and post-(n=11) diversion trees (Appendix).

Age Diameter Relationship

Water-elm tree ages showed a significant positive relationship with their corresponding dbhs ($R = 0.72$ at $\alpha = 0.05$) which indicated that increase in age of a tree was followed by increase in its dbh (Figure 5). Generally, pre-control trees had greater dbh than post-control trees; however, there were some trees which were established during the pre-control period that had a lower dbh than most post-control trees (Figure 5). Also, there were some old trees (≥ 60 years) that had a relatively small dbh (≤ 10 cm) (Figure5). The oldest tree in this study did not have the largest dbh (Figure 5).

Relationship between Tree Age and Distance to the Lake Edge

Analysis of trees ages and distance of their plots from the tree line in transects consisting of both pre- and post-control trees indicated that pre-control trees could either be in the plots near or far from the tree line. Out of 6 transects consisting of both pre- and post-control trees, French Fork supported only one post-control tree found in the plot nearest to the tree line; the pre-control trees in this transect were randomly established over time independent of the distances of their plots from the tree line (Figure 6). Willow Spring East transect demonstrated a curvilinear age-distance relationship, i.e., older pre-control trees were present in the first two plots nearest to the tree line, the next three plots consisted of younger post-control trees while the last plot consisted of 1 pre-control and 2 post-control tress with increased ages (Figure 7). In 3 of 6 transects, Alligator Bayou East, Stock Landing and Alligator Bayou West, tree age increased as the distance of the plots from tree line increased indicating that younger trees were established towards the center and older trees towards the upper bank of the lake in these transects (Figures 8, 9 and 11). However, in the Mosquito Bend transect, the oldest trees occurred in the plots nearest to the tree line and the tree ages decreased pattern with distance of the plots from the tree line (Figure 10).

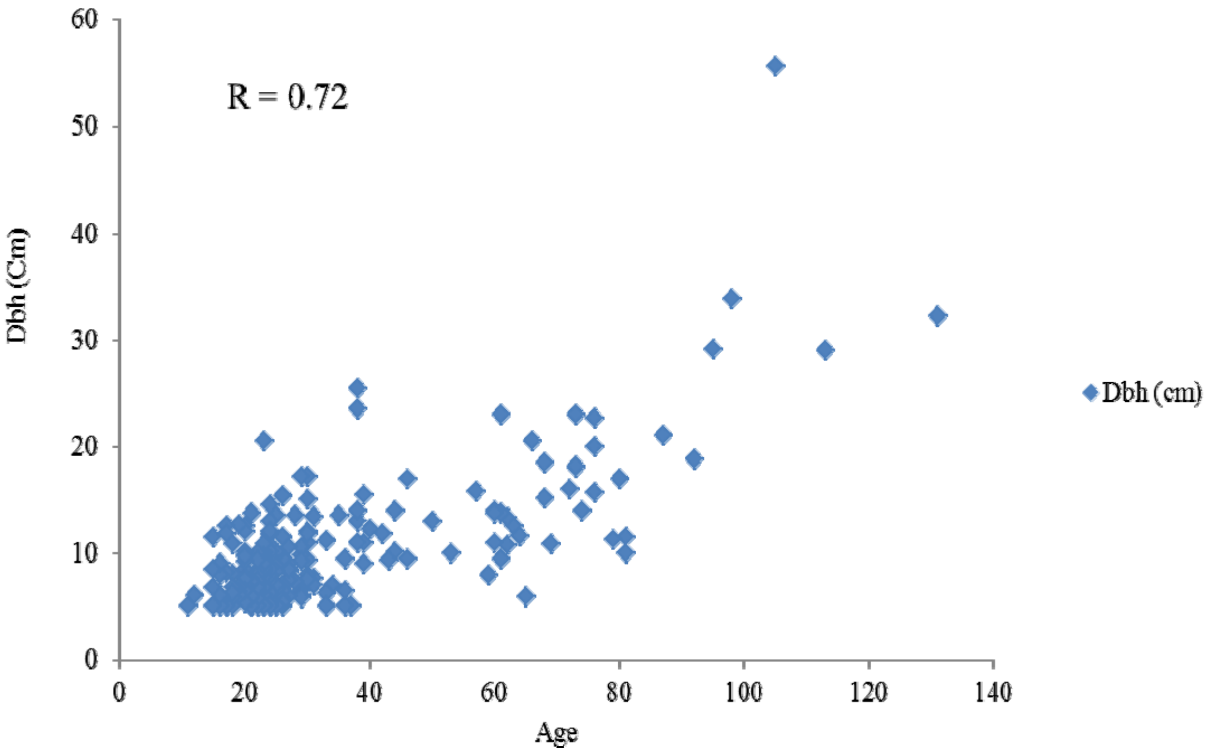

Figure 5: Scatter plot showing the relationship between water-elm tree ages and their corresponding diameter at breast heights (dbhs). "R" represents the correlation coefficient between the two variables (age and dbh) which was found to be statistically significant at $\alpha = 0.05$.

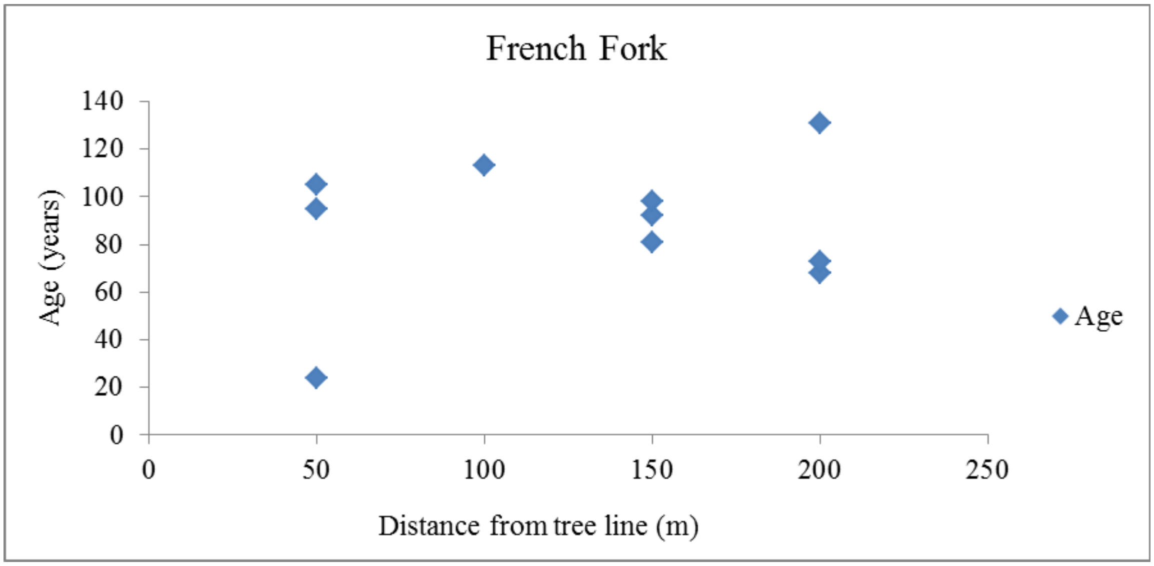

Figure 6: Scatter plot showing the relationship between water-elm tree ages and the distance of the sampling plots including those trees from the tree line in the French Fork transect. The tree line of this transect was near the center of the lake; it ran towards the bank of the lake and finished at the end of the water-elm zone.

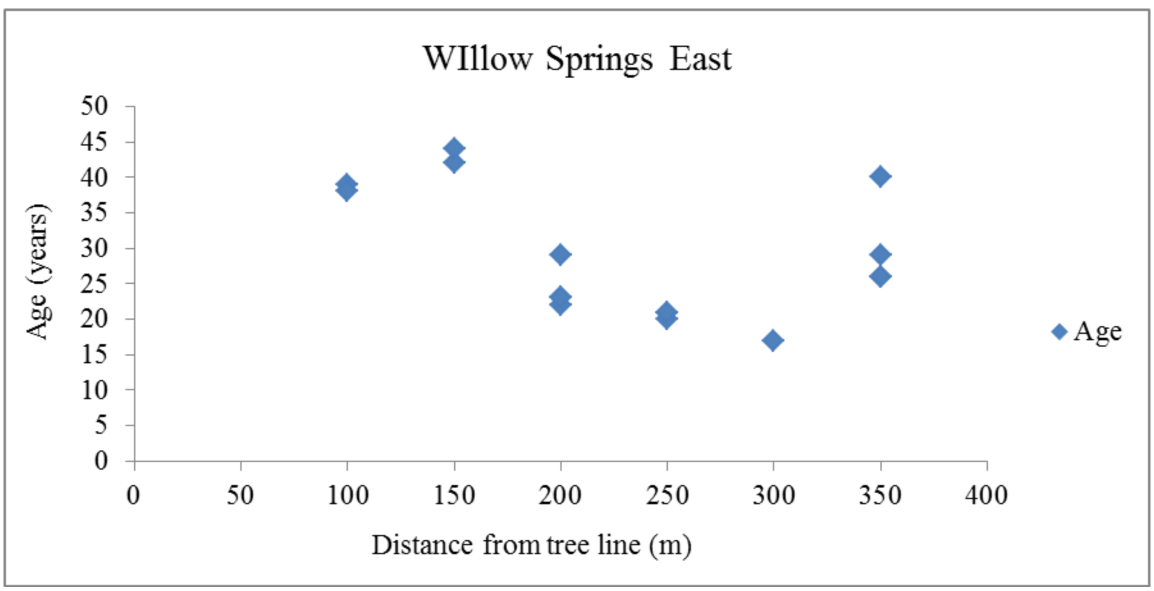

Figure 7: Scatter plot showing the relationship between water-elm tree ages and the distance of the sampling plots including those trees from the tree line in the Willow Springs East transect. The tree line of this transect was near the center of the lake; it ran towards the eastern bank of the lake and finished at the end of the water-elm zone.

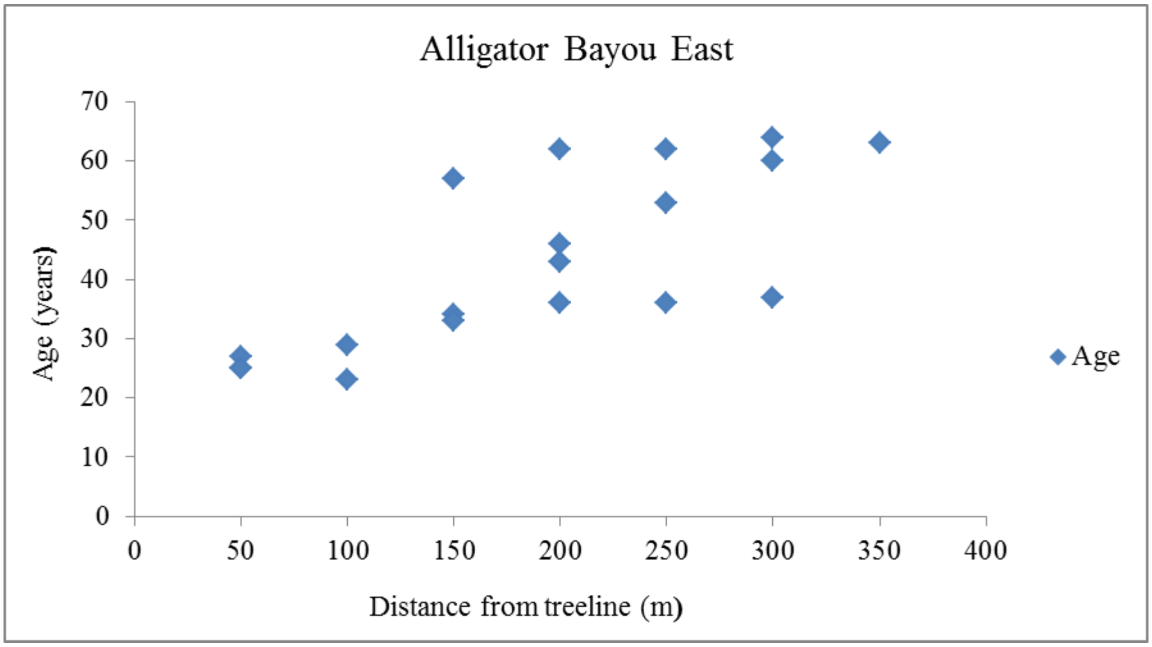

Figure 8: Scatter plot showing the relationship between water-elm tree ages and the distance of the sampling plots including those trees from the tree line in the Alligator Bayou East transect. The tree line of this transect was near the center of the lake; it ran towards the eastern bank of the lake and finished at the end of the water-elm zone.

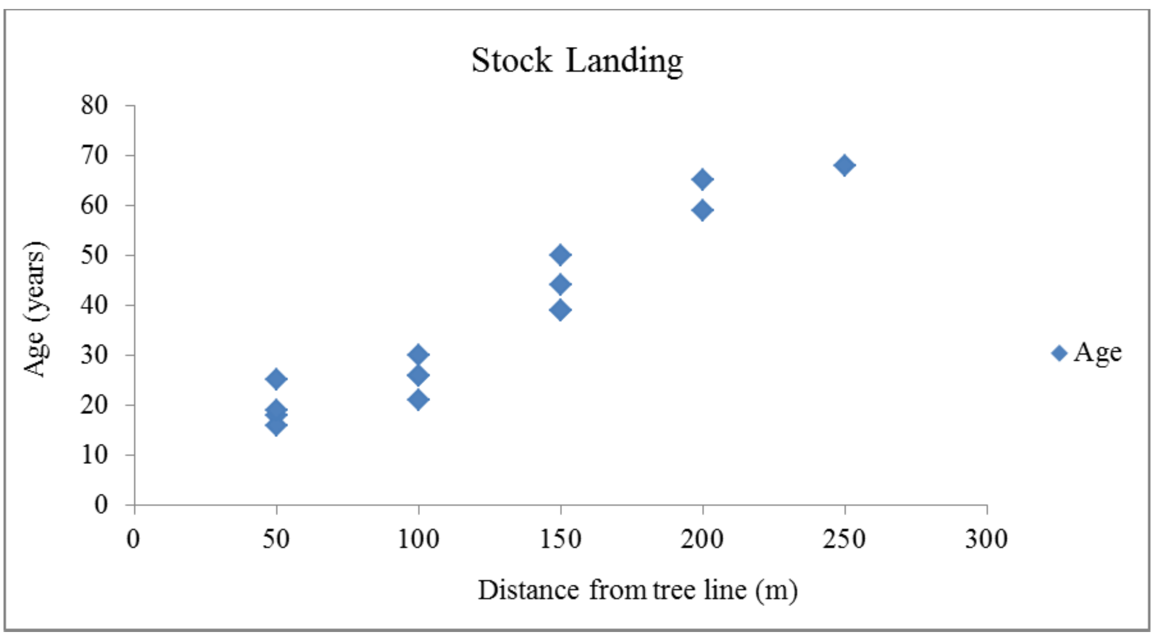

Figure 9: Scatter plot showing the relationship between water-elm tree ages and the distance of the sampling plots including those trees from the tree line in the Stock Landing transect. The tree line of this transect was near the center of the lake; it ran towards the eastern bank of the lake and finished at the end of the water-elm zone.

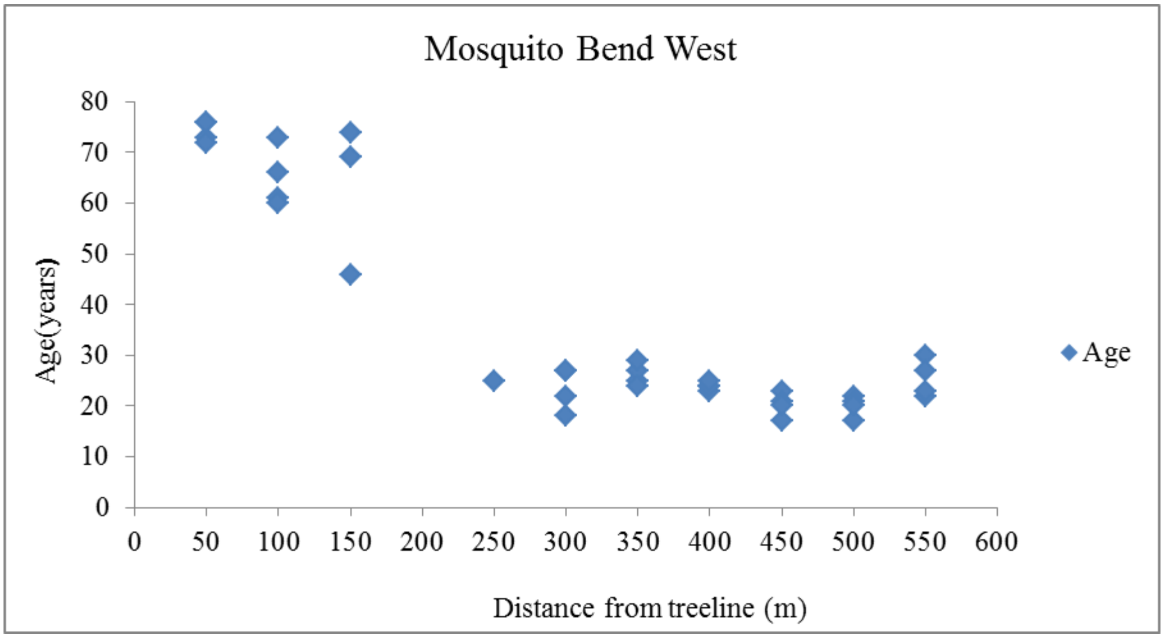

Figure 10: Scatter plot showing the relationship between water-elm tree ages and the distance of the sampling plots including those trees from the tree line in the Mosquito Bend West transect. The tree line of this transect was near the center of the lake; it ran towards the western bank of the lake and finished at the end of the water-elm zone.

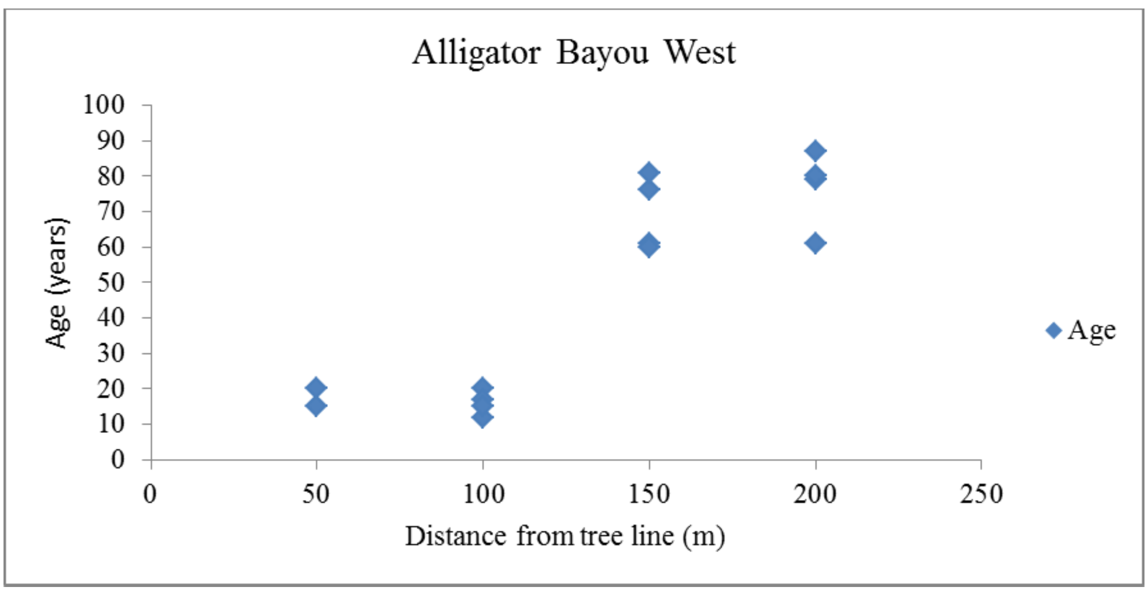

Figure 11: Scatter plot showing the relationship between water-elm tree ages and the distance of the sampling plots including those trees from the tree line in the Alligator Bayou West transect. The tree line of this transect was near the center of the lake; it ran towards the western bank of the lake and finished at the end of the water-elm zone.

Analysis of Exceedance Probability Curves

Analysis of bathymetry data indicated that all but 9 plots were between 9.0 and 10.6 m. The remaining 9 plots were below 9.0 m. The bathymetry data lacked the resolution necessary to determine the exact elevation of the plots. The exceedance probability values for August were numerically lower in the post-control period as compared to the pre-control period for stages from 7.6 to 10.6 m (Figure 12). For all elevations above 9.0 m in August, there was < 10% probability of exceedance during the post-control period, as compared to about a 20% chance during the pre-control period (Figures 12). However, very few differences were detectable for September (Figures 13) and October (Figure 14) for the pre- and post-control periods.

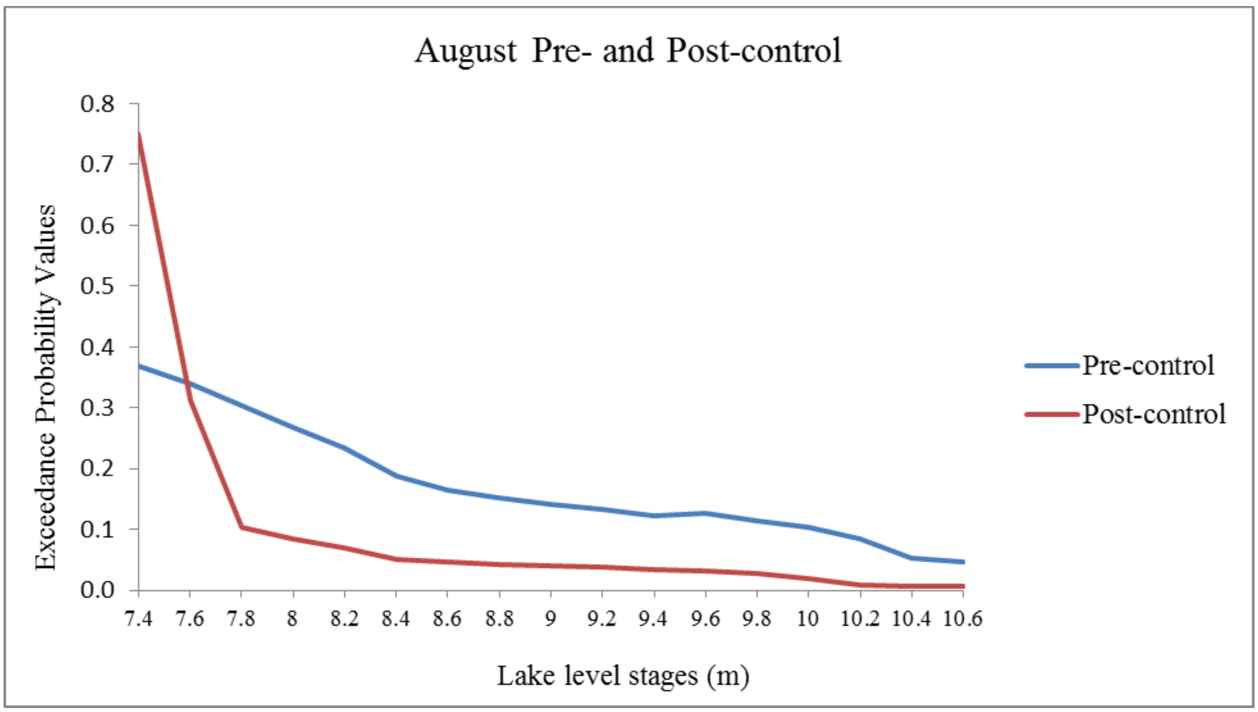

Figure 12: Exceedance probabilities of lake level stages from 7.4 m to 10.6 m at 0.2 m intervals for August during both the pre- and post-control period.

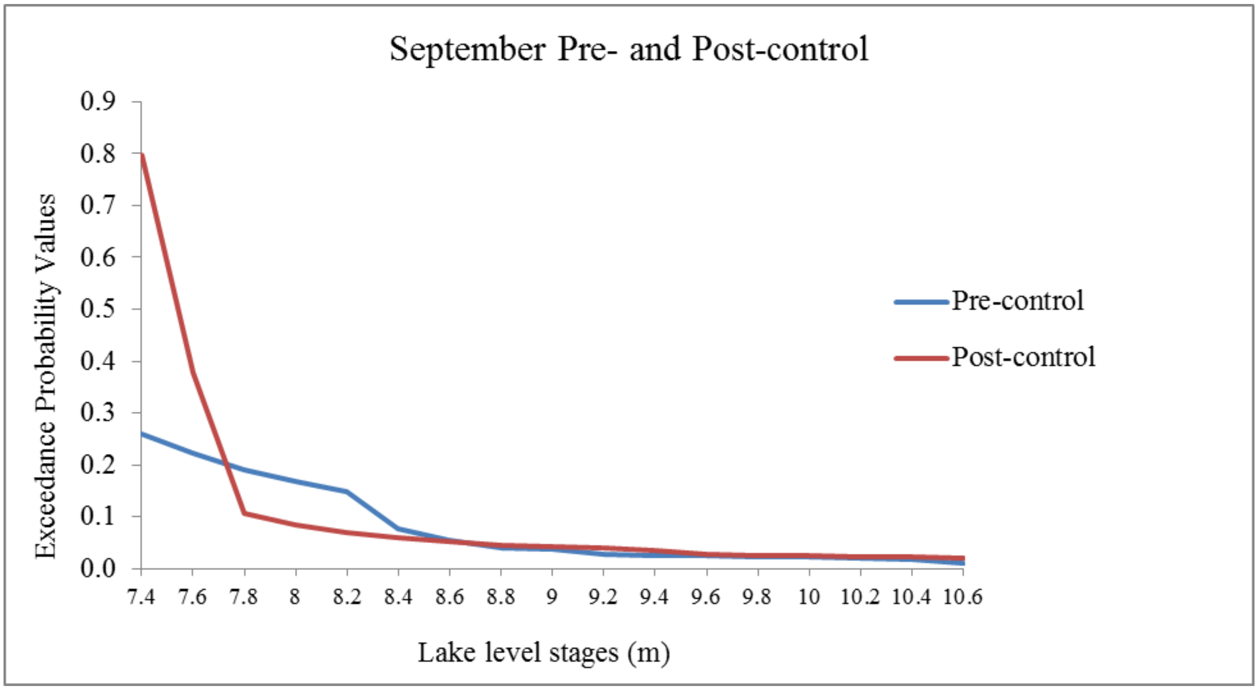

Figure 13: Exceedance probabilities of lake level stages from 7.4 m to 10.6 m at 0.2 m intervals for September during both the pre- and post-control period.

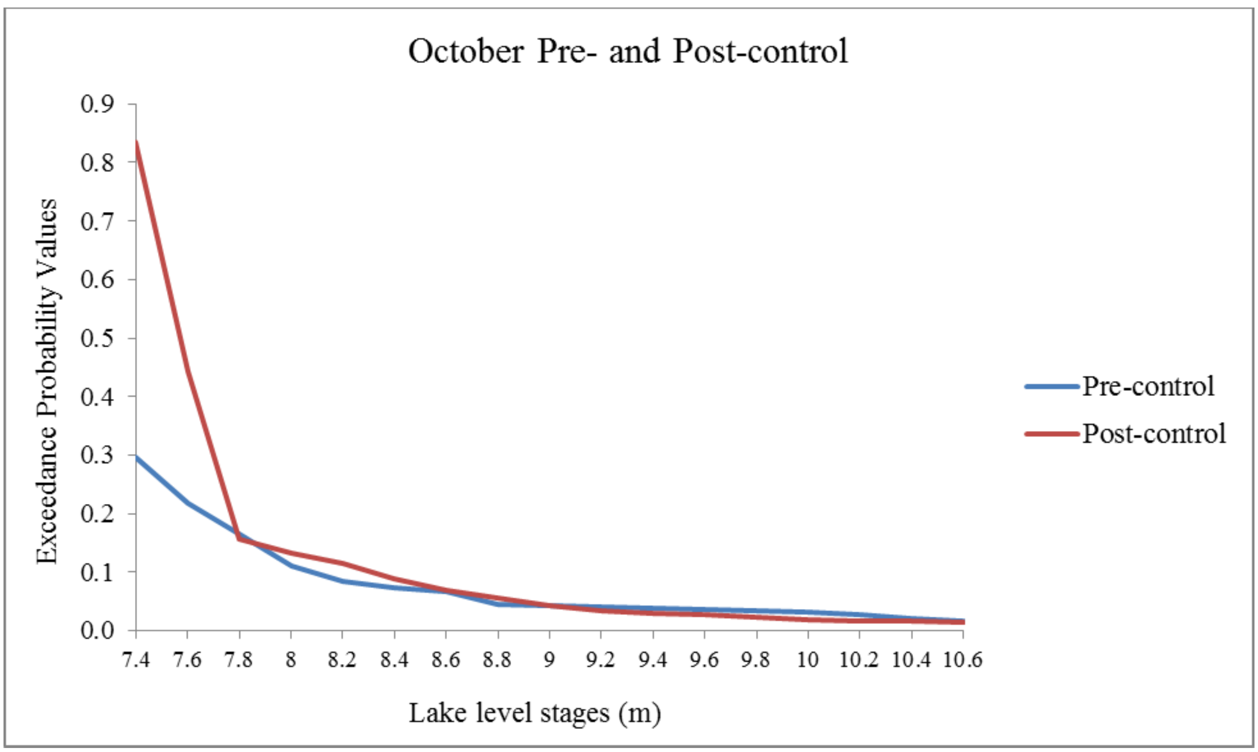

Figure 14: Exceedance probabilities of lake level stages from 7.4 m to 10.6 m at 0.2 m intervals for October during the pre- and post-control period.

Water-elm Chronology

I measured rings from 211 samples which were not decayed and hollowed at the pith, but used only 67 cross-sections in the final chronology due to poor ring structure in most samples. Analyses of COFECHA indicated accurate cross-dating as inter-series correlation (0.439), mean sensitivity (0.359) (Grissino-Mayer 2001) and expressed population signal (0.98 criterion; Wigley et al. 1984) were all adequate. Initially, I used 20-year segments with 5-year lags in COFECHA but this resulted in 163 problem segments. Thus, I changed to a 50-year segment with 25-year lags and reduced the number of problem segments to 10 (Table 5).

The chronologies spanned from 1931 to 2009 (Table 5), however, only 9 trees were established before 1950 and they were dropped from further analysis because a minimum of 10 trees are required to maintain accurate sample depth in a chronology (Speer 2010). Therefore, I truncated my final chronologies to 1950 to 2009 (Figure 15).

Baldcypress Chronology

Final chronologies of baldcypress consisted of 48 trees with rings spanning from 1874 to 2006 (Table 5). However, the chronologies were truncated from 1950 to 2006 in order to match the period of water-elm chronologies (Figure 16). Descriptive statistics of COFECHA analysis indicated adequate values of inter-series correlation (0.638), mean sensitivity (0.586) (Grissino-Mayer 2001), expressed population signal (criterion; Wigley et al. 1984) and low number of potential segment problems (17) in the series (Table 5).

Comparison of Water-elm and Baldcypress Chronologies

The chronologies of water-elm trees indicated highly variable growth among consecutive years and differed from that of baldcypress (Figures 17, 18). Growth of water-elm was highest in 1955, 1960, 1977, 1986 and 2005 but in contrast, baldcypress demonstrated decreased growth in these years (Figures 17, 18). Similarly, 1958, 1993, 1995 and 2004 were years of high growth rates for baldcypress but poor growth for water-elm (Figure 17, 18). Growth patterns in several years, however, were similar between the two species. The years 1951, 1964, 1970, 1972, 1974, 1979, 1981 and 2001 were high growth years for both species whereas 1950, 1952, 1954, 1956, 1959, 1963, 1969, 1971, 1973, 1975, 1980, 2000 and 2006 were poor growth years (Figures 17, 18).

Table 5: Descriptive statistics for final COFECHA analysis of water-elm and baldcypress ring widths using 50-year segments with 25 year lags.

Description of Parameters	Water-elm	Baldcypress
Number of dated series/Sample size	67	48
Master series	1931-2009 (79 years)	1874-2006 (133 years)
Total rings in all series	2149	4706
Total dated rings checked	2146	4696
Series intercorrelation	0.439	0.638
Average mean sensitivity	0.359	0.586
Segments, possible problems	10	17
Mean length of series	32.1 Years	98 years
Expressed Population Signal	98%	98.83%

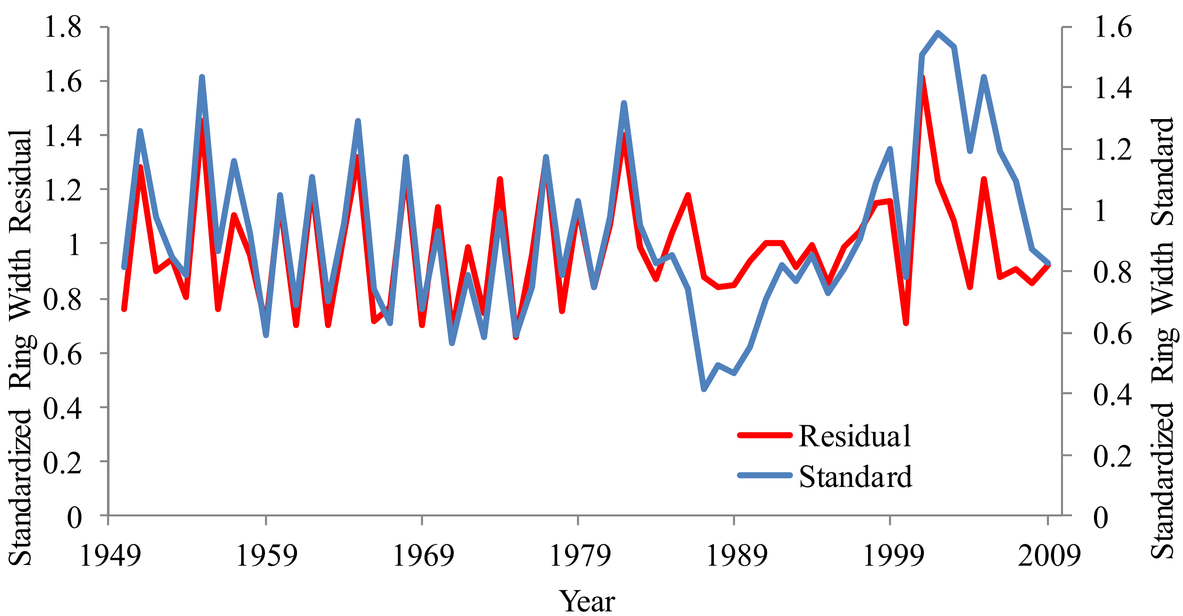

Figure 15: Standard and residual growth chronologies of water-elm (*Planera aquitica*) at Catahoula Lake.

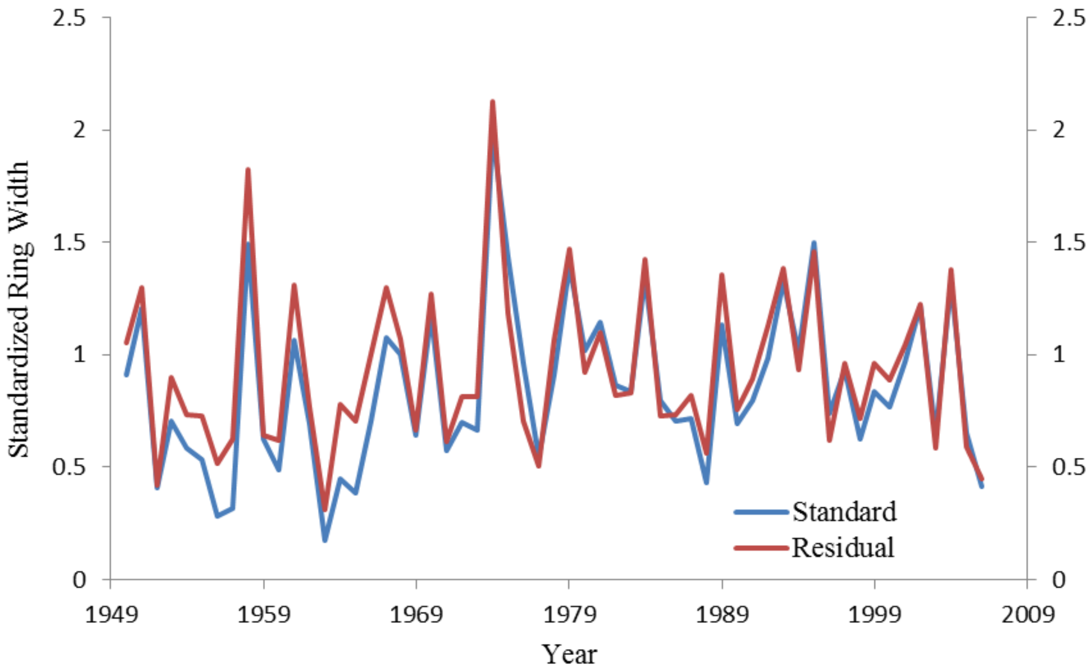

Figure 16: Standard and residual growth chronologies of baldcypress (*Taxodium distichum*) at Catahoula Lake. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

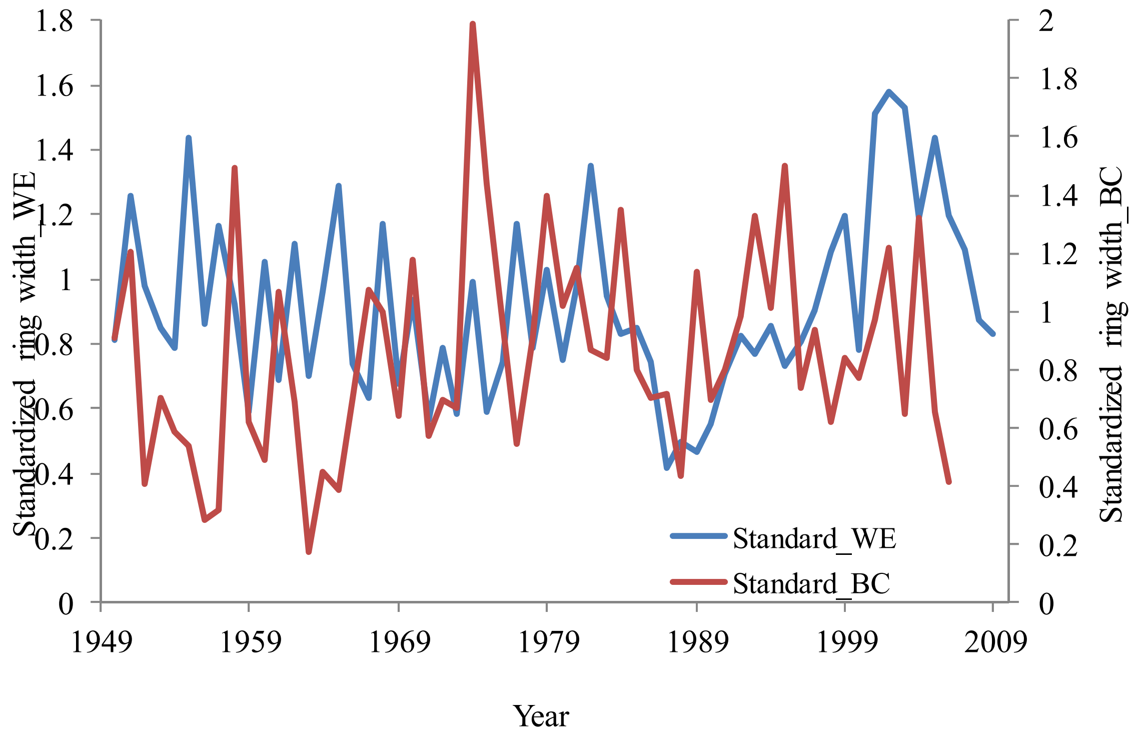

Figure 17: Comparison of standard chronologies of baldcypress and waterelm from Catahoula Lake, Louisiana. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

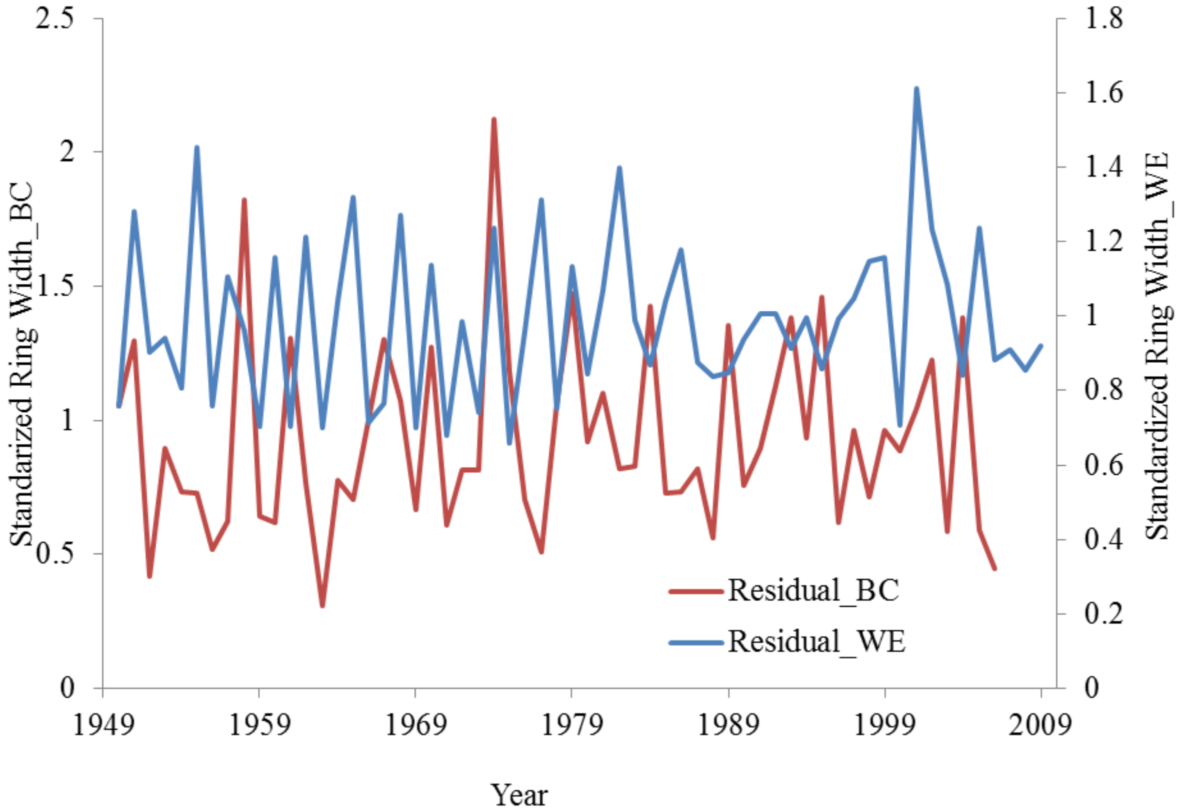

Figure 18: Comparison of residual chronologies of baldcypress and water-elm from Catahoula Lake, Louisiana. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

Growth Responses of Water-elm and Baldcypress to Hydrology and Climate

Water-elm and baldcypress showed different growth responses to lake levels and climate at Catahoula Lake. Baldcypress chronology was significantly positively correlated with late non-growing season (December, January and February) lake levels, late spring to early summer lake levels of current and previous growing seasons (May and June) and late growing season lake levels (August and September) (Figure 19). However, the significant positive correlation of water-elm chronology with monthly lake levels was limited to a couple of months in the late non-growing season (December and January) (Figure 19).

Baldcypress radial growth responded consistently to Catahoula Lake water levels during both the pre- and post-control periods. During either period, the baldcypress chronology was significantly positively correlated with early summer (June) lake levels for the current growing season (Figure 20). During the pre-control period only, the chronology was significantly positively related with late non-growing season (January), late spring and early summer (May and June) and late current growing season (August) lake levels (Figure 20); while during the post-control period only, it had a significant positive relationship with late spring and early summer (May and June) lake levels for the previous growing season and late non-growing season (February), mid-spring (April) and late growing season (September) lake levels (Figure 20). However, water-elm showed slightly different growth responses to Catahoula Lake water levels during pre- and post-control periods. There was no significant positive correlation between the water-elm chronology and monthly lake levels during either period (Figure 21). During the pre-control period, water-elm chronology had a significant negative correlation with late spring (May) lake levels for the current growing season (Figure 21).

Radial growth of both water-elm and baldcypress did not correlate with temperature except one separate month for each tree. Water-elm chronology had a significant positive correlation with mid-spring (April) temperature in the growing season (Figure 22). Baldcypress chronology was correlated negatively with late previous growing season (August) temperature (Figure 22). Water-elm chronology responded positively to mid-spring (April) rainfall during the pre-control period; spring (March, April and May) and late growing season (September) rainfall during the post-control period. However, baldcypress chronology only responded positively to early non-growing season (October) rainfall overall (Figures 23, 24).

Water-elm chronology was significantly positively correlated to several monthly PDSI and PHDI values; spring to early summer (March, April, May and June) and September PDSI and PHDI for current growing season, early spring (March and April) and September PDSI for previous growing season, spring to summer (May, April, May and June) and September PHDI for previous growing season and early non-growing season (October) PHDI (Figures 25, 26). However, baldcypress chronology had low and non-significant values with all the monthly PDSI and PHDI variables at the lake (Figures 25, 26).

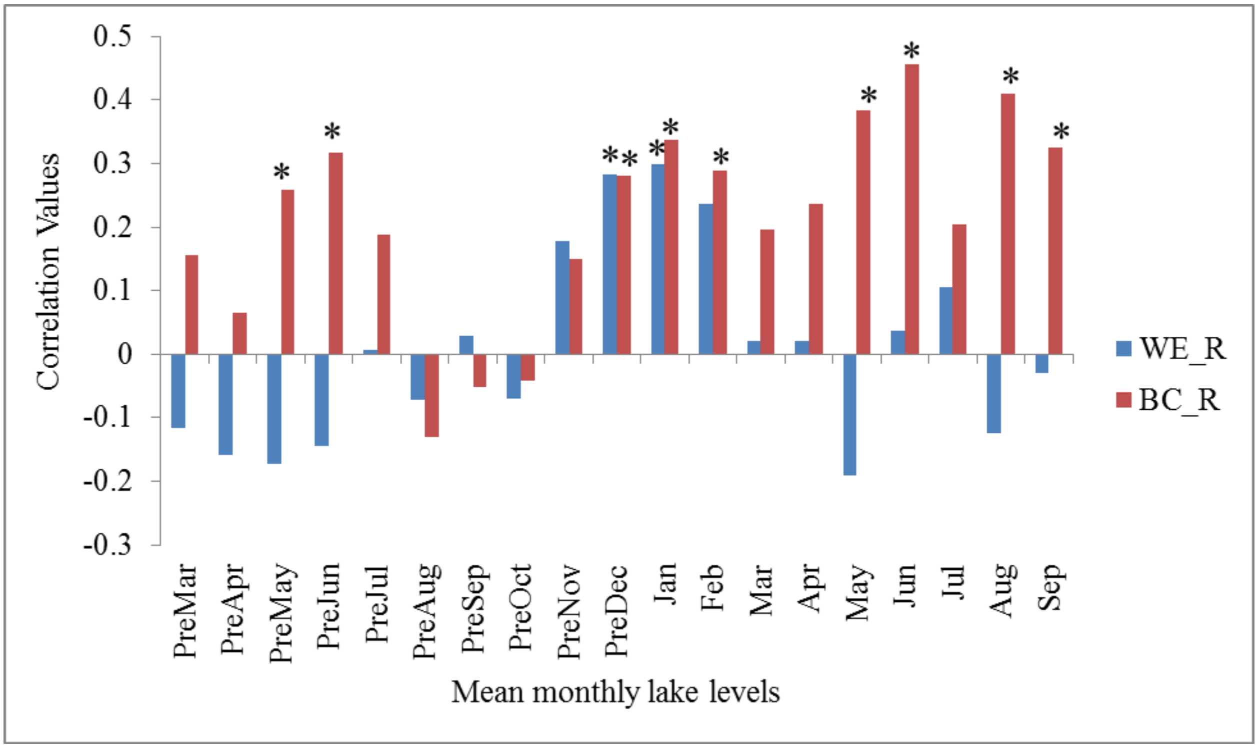

Figure 19: Correlation between radial growth of water-elm and baldcypress trees and mean monthly lake levels at Catahoula Lake. The months with prefix “Pre” added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm, BC = baldcypress, and R = residual chronology. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

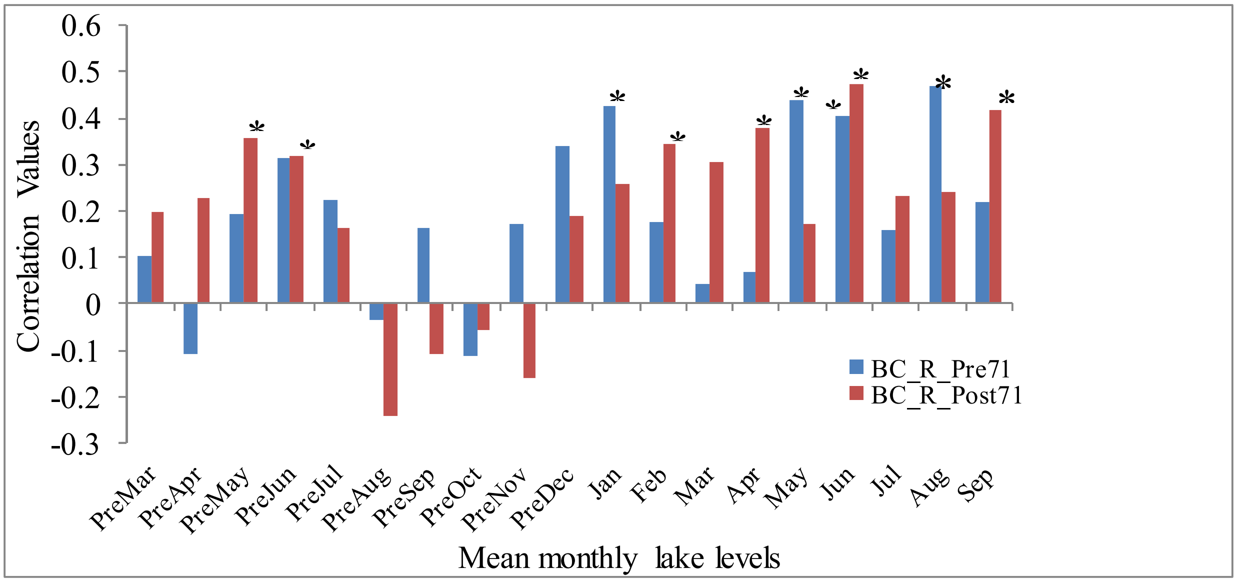

Figure 20: Correlation between radial growth of baldcypress in pre- (n=22) and post-control (n=38) periods and mean monthly lake levels at Catahoula Lake. The months with prefix "Pre" added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. BC = baldcypress and R = residual chronology. Pre71 is the pre-control period and Post71 is the post-control period. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

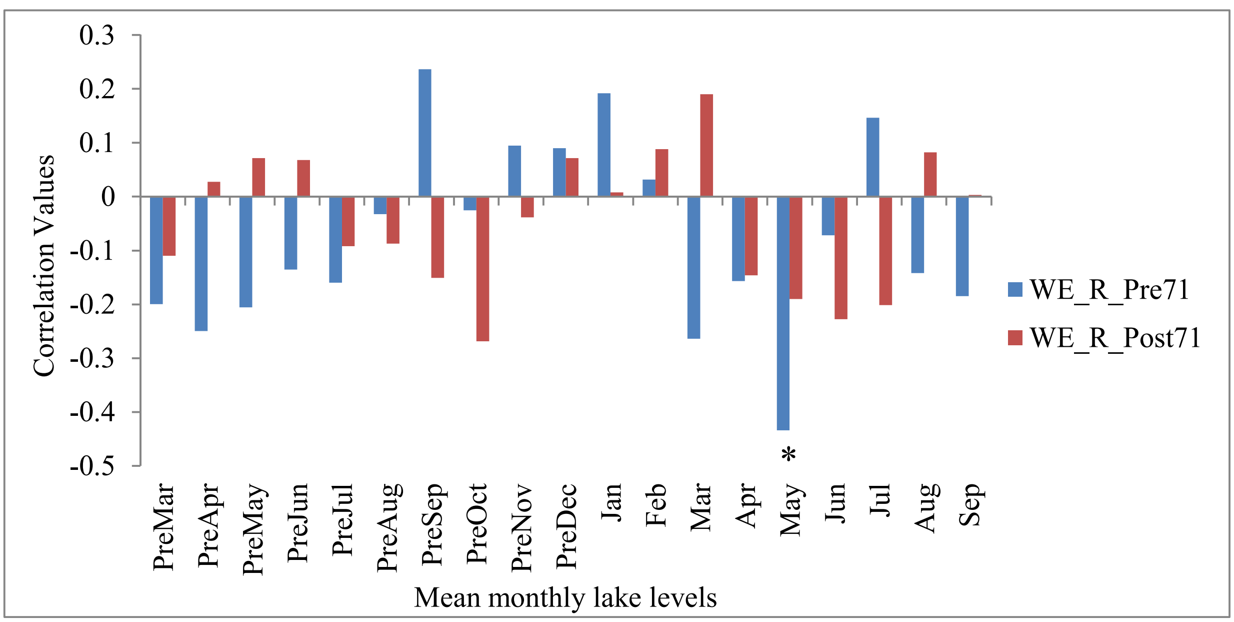

Figure 21: Correlation between radial growth of water-elm in pre- (n=22) and post-control (n=38) periods and mean monthly lake levels at Catahoula Lake. The months with prefix "Pre" added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm and R = residual chronology. Pre71 is pre-control period and Post71 is the post-control period.

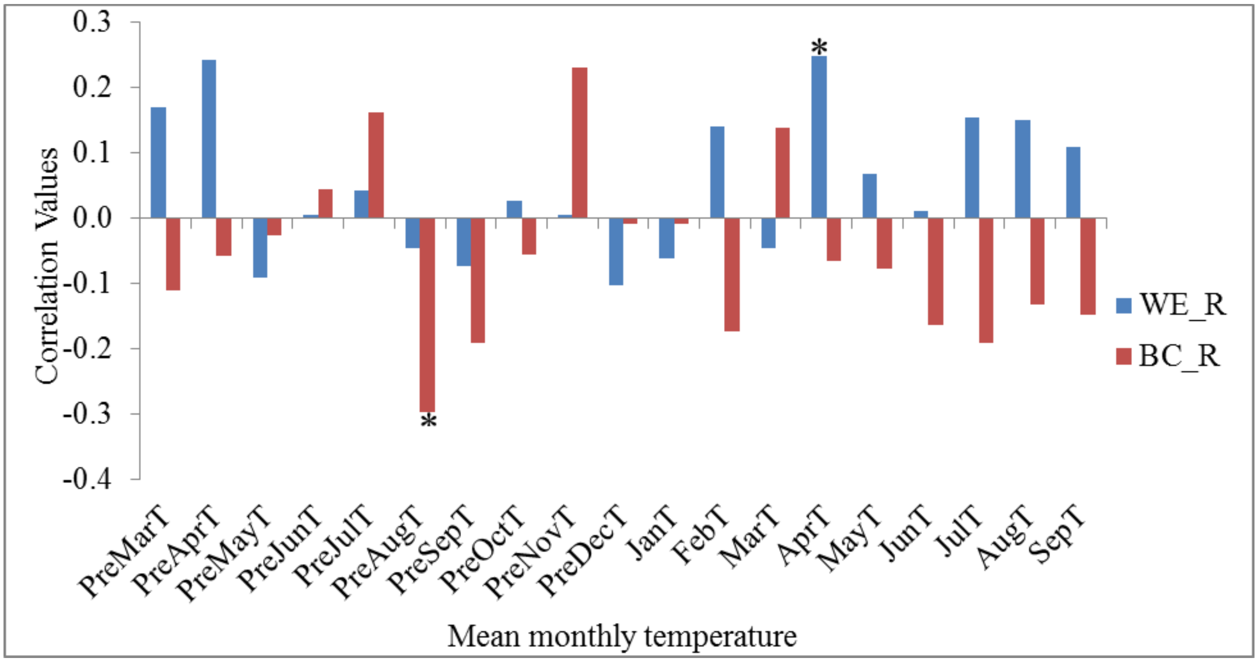

Figure 22: Correlation between radial growth of water-elm and baldcypress trees and mean monthly temperature (T) at Catahoula Lake. The months with prefix "Pre" added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm, BC = baldcypress, and R = residual chronology. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

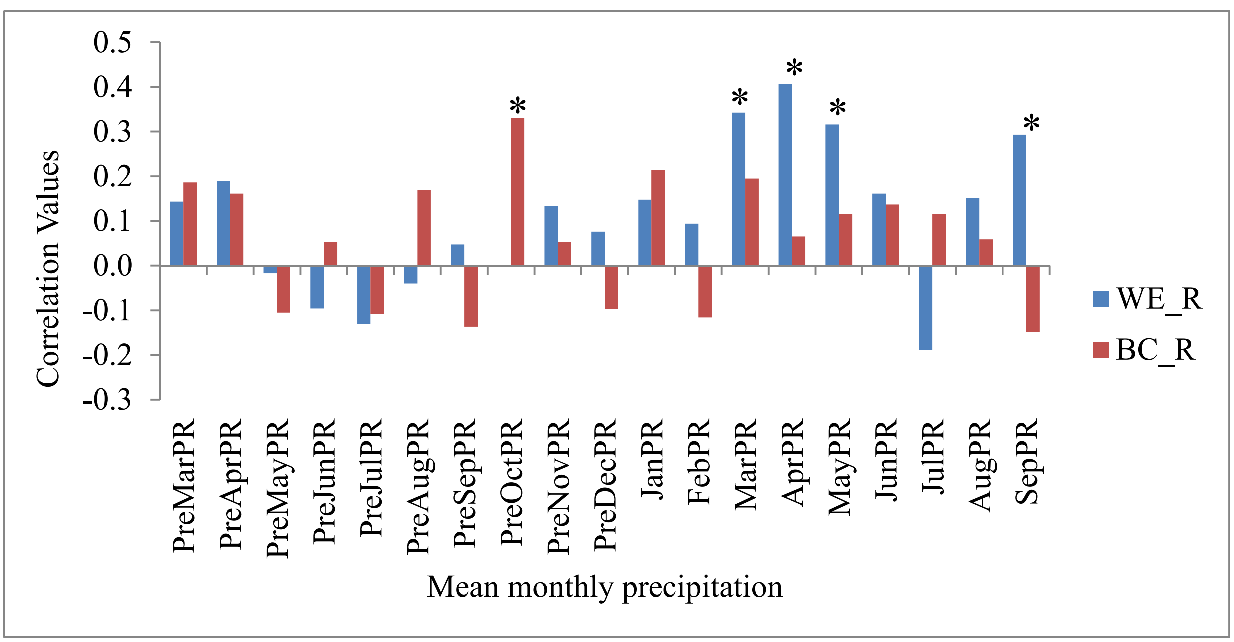

Figure 23: Correlation between radial growth of water-elm and baldcypress trees and mean monthly precipitation (PR) at Catahoula Lake. The months with prefix "Pre" added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm, BC = baldcypress, and R = residual chronology. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

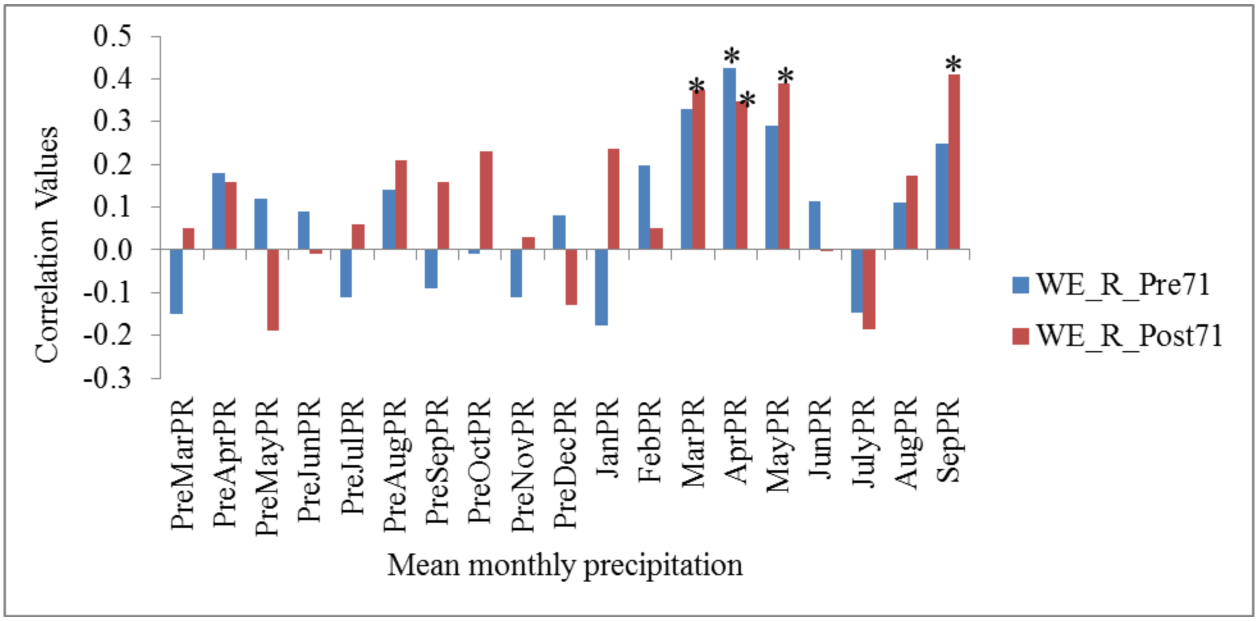

Figure 24: Correlation between radial growth of water-elm in pre- (n=22) and post-control (n=38) periods and mean monthly precipitation (PR) at Catahoula Lake. The months with prefix "Pre" added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm and R = residual chronology. Pre71 is the pre-control period and Post71 is the post-control period.

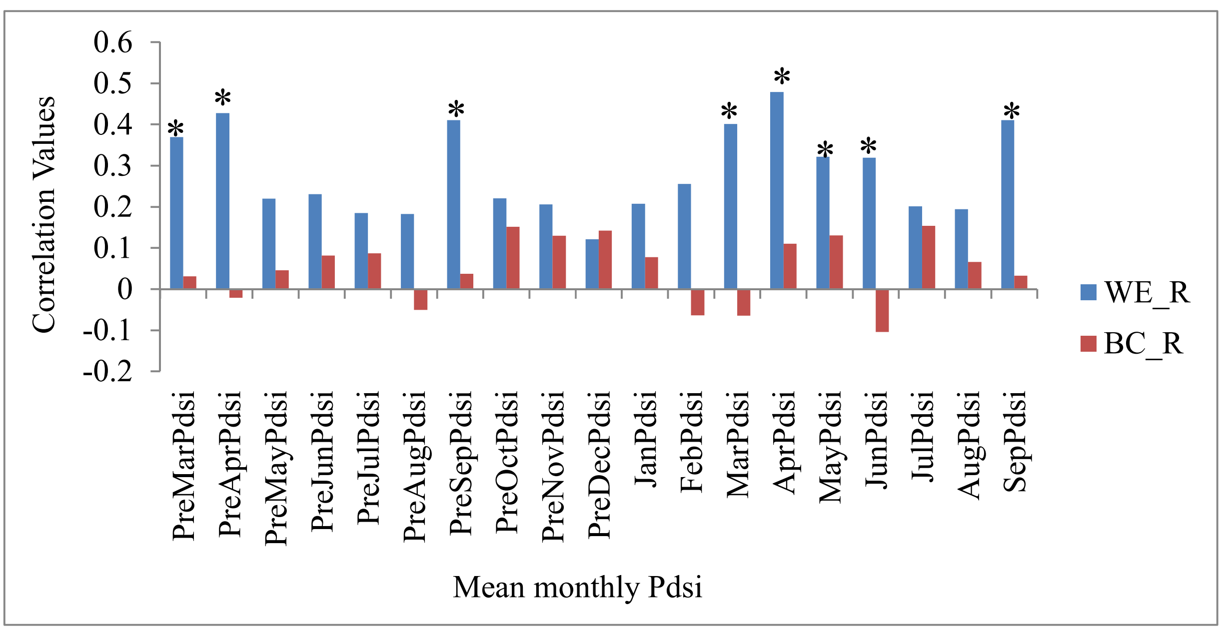

Figure 25: Correlation between radial growth of water-elm and baldcypress trees and mean monthly PSDI at Catahoula Lake. The months with prefix "Pre" added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm, BC = baldcypress, and R = residual chronology. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

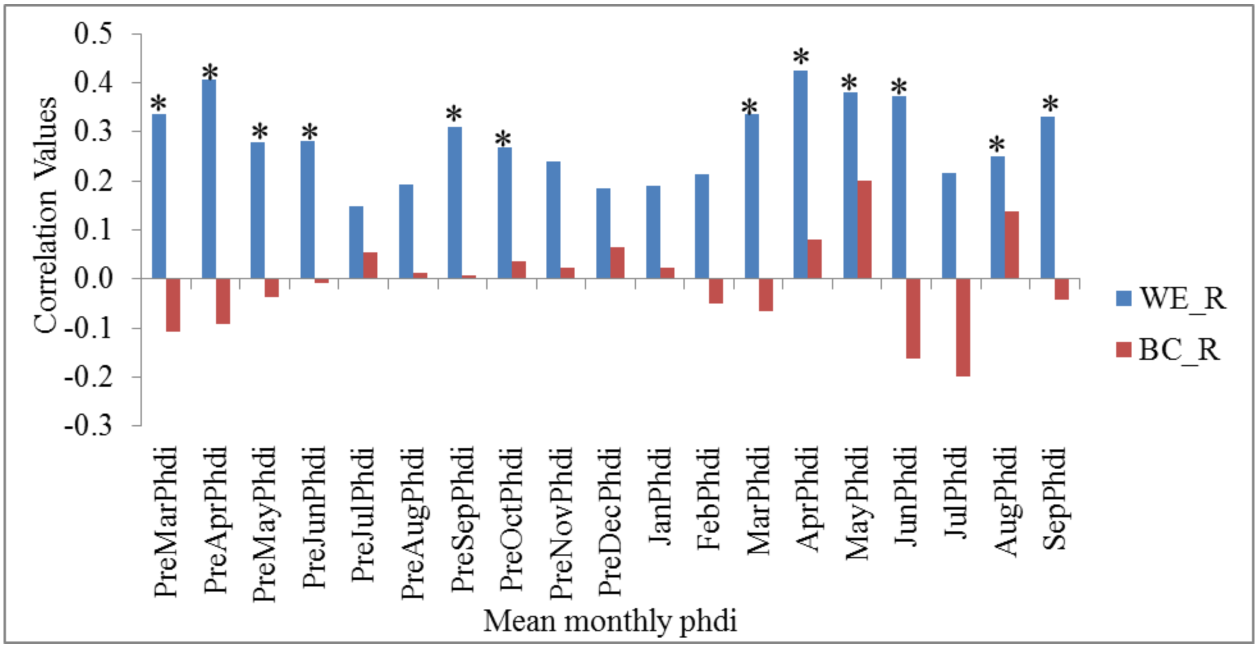

Figure 26: Correlation between radial growth of water-elm and baldcypress trees and mean monthly PHDI at Catahoula Lake. The months with prefix “Pre” added to them are from previous year. Values indicated with asterisks (*) represent statistically significant correlation coefficients at α = 0.05. WE = water-elm, BC = baldcypress, and R = residual chronology. Baldcypress tree cores belonged to Frank Willis (Willis 2009).

DISCUSSION

Establishment of Water-elm Trees in Catahoula Lake

The results of this study indicate that herbaceous plant communities can shift to communities dominated by woody vegetation in a relatively short time period. Specifically, I found that fewer water-elm trees established during the pre-control period (n=48) than during the post diversion period (n=171) at Catahoula Lake. Furthermore, a total of 72% (n=48) of sample plots in this study consisted entirely of post-control trees whereas only 18% (n=12) plots consisted entirely of pre-control trees. My data is consistent with the conclusion of Bruser (1995) that water-elm establishment has increased during the post-control period.

Several factors could be solely or partially responsible for the increased establishment of water-elm trees at Catahoula Lake during the post-control period, none of which receive unequivocal support. Hydrologic alterations during the post-control period such as reduced variability in June and August lake levels, and/or reduced fall flooding are possible explanations. Numerous studies indicate that reduced variability in flooding and reduced peak floods can lead to shifts in wetland plant communities (Weller 1989, Fredrickson and Reid 1990). Toner and Keddy (1997) found that reduced fall flooding can lead to shifts in herbaceous vegetation communities to plant communities dominated by woody vegetation. In fact, the probability of expansion of woody vegetation in wetlands is directly proportional to the length of period between the end of the first growing season flood and the start of the second growing season flood (Toner and Keddy, 1997). Similarly, reduced fall flooding can lead to greater woody seedling survival, particularly of light-seeded species (Streng et al. 1989, Jones et al. 1994). However, the influence of the diversion canal and the water-control structure on hydrologic changes; and specifically on the establishment of water-elm trees could not be directly linked. It is possible that climatic conditions that would have occurred with or without the diversion canal would have resulted in similar hydrologic conditions and establishment patterns. Similarly, water-elm control measures and cattle grazing may also have affected water-elm establishment. LDWF implemented water-elm control measures in both the pre- and post-control period, but the spatial location and type and extent of control measures were inadequately documented to determine their potential impacts on establishment patterns of the trees. Thus, it is possible, although not probable for all plots, that some plots supporting only post-control trees were cleared of trees that established during the pre-control period. Also, cattle were allowed to graze on the lake until 2000. All sampled trees established when grazing was allowed on the lake and trees established during the post-grazing period are not large enough yet to meet the minimum dbh size used in this study.

The analysis of exceedance values of lake levels for August, September and October for both pre- and post-control period did not illustrate any clear linkage between lake levels and water-elm establishment during either of the periods. The exceedance value for August at 9.0 m, the lower end of the elevation class that contained most plots, was slightly higher during the pre-control period (0.18) as compared to the pre-control period (0.05). The low pre-control probability of flooding during August suggests that August flooding was not a major control mechanism for water-elm, at least since 1950. Similarly, for September and October, the exceedance values at 9.0 m were similar and were very low for both the pre- and post-control periods.

Undoubtedly, water-elm establishment into the lake has been influenced by broad-scale hydrologic alterations within the Atchafalaya-Black-Red River watershed that began in the early 1900s (Willis 2009). Lake levels had already started to gradually decrease during the pre-control period due to decreased Black River stages following the Atchafalaya River incision and the construction of the Old River Structure (Willis 2009). The gradual decrease in lake levels may have initiated establishment of water-elm trees into the lake bed during the pre-control period as first described by Wills (1965). The diversion canal and water-control structure may have led to hydrologic conditions that further enhanced woody establishment; however, these changes were likely initiated long before their construction.

The ultimate goal of the diversion canal and water-control structure was to mimic the historical natural water regime of the lake (Bruser 1995) and to minimize consequences of the Black River navigation project on the lake (Willis 2009). However, this lake persisted as a lake dominated by herbaceous vegetation at lower elevations, and presumably within the recently colonized water-elm zone, for at least a few centuries (Tedford 2009). The large number of trees established in the post-control period suggests that the goal of replicating the historical natural water regime has not been achieved, although it is quite possible, if not probable, that without the control structure the impacts of the Black River navigation project would have been even more extreme (Willis 2009). Further analysis of historic hydrologic conditions is needed to determine what hydrologic processes controlled water-elm and facilitated establishment of herbaceous plant communities.

Growth Response of Water-elm and Baldcypress to Hydrology

Although establishment and expansion of water-elm trees at Catahoula Lake were at least partially linked to the prevailing hydrologic conditions pre- and post-control periods, their radial growth generally had a poor relationship with hydrology of the lake. The only linkage between water-elm growth and hydrology was limited to significant positive relationship with lake levels for a couple of non-growing season (December and January) months overall and a significant negative relationship during the pre-control period between growth and late spring lake levels for the current growing season. In contrast, baldcypress radial growth had a significant positive relationship with several mean monthly lake levels for both the current and previous growing seasons overall as well as in both the pre- and post-control periods. Water-elm and baldcypress both are flood tolerant species (Whitelow and Harris 1979, Hook 1984, Wilhite and Toliver 1990), but they responded differently to hydrology even at the same general locality. These results indicate that tree growth responses to hydrologic processes vary even among highly water tolerant species.

Significant negative relationships of water-elm chronology with late spring lake levels during the pre-control period indicate that water-elm radial growth was sensitive to historical lake levels. Spring lake levels had higher variability during the pre-control period than during the post-control period (Table 1) and may have been responsible for the lack of relationships between tree growth and hydrology during the post-control period. Other studies in forested wetlands have also found altered relationships between hydrology and growth following hydrologic changes. Reily and Johnson (1982) found that growth of cottonwood (*Populus deltoides*) along the Missouri River during the pre-dam period was correlated more with high spring stages, while post-dam construction growth was correlated more with precipitation. Gee (2012) found shifts in the relationship between overcup oak (*Quercus lyrata*) growth and river stage due to levee construction along the Mississippi River; growth had significant positive relationship with several mean monthly river stages pre-levee as compared to low and non-significant relationship during the post-levee period.

In contrast to water-elm, positive relationships between baldcypress chronology and several monthly lake levels during both the pre- and post-control periods indicated that baldcypress radial growth was not affected by reduced variability of lake levels during the post-control period. I found significant positive responses of baldcypress chronology with several mean monthly lake levels from the previous and current growing season. Specifically, I found significant positive relationship of baldcypress chronology with late spring and early summer lake levels during both the pre- and post-control periods. Rypel et al. (2009) also found tree radial growth to be positively related with late spring and early summer stages in both regulated and unregulated rives of southeastern U.S. Coastal Plain. Cleaveland (2000) observed a positive relationship between baldcypress chronologies and summer river stage at White River, Arkansas. Smith (2007) suggested that high spring and summer flows on the Appalachicola River could be advantageous to baldcypress growth because the high flows ensured reloading of nutrients on the floodplain and/or decreased the competition with flood intolerant tree species.

It is important to note that the baldcypress tree cores were collected only at the Bacon Run site. Therefore, it is possible that baldcypress trees at other sites on the lake may have different factors affecting growth. In contrast, water-elm cross-sections were collected along multiple transects thus eliminating this type of bias.

Growth Response of Water-elm and Baldcypress to Climate

Water-elm and baldcypress had contrasting growth responses to climate in the lake. Climate was more important for water-elm radial growth but less important for baldcypress radial growth as compared to lake levels. Reams and Van Deusen (1998), Bohora (2012) and Keim and Amos (2012) also concluded that climate was less important than hydrology for baldycpress radial growth in coastal wetland forests of Louisiana. Indeed, strong correlations of climate variables with baldcypress tree rings have not been documented in Louisiana (Keim and Amos 2012). In this study, water-elm radial growth was positively related with several mean monthly climatic variables especially with April temperature, spring precipitation, PDSI and PHDI; however, baldcypress radial growth had low and non-significant correlation values with most climatic variables.

Water-elm chronology was significantly positively related with April temperature of the current growing season. Warm spring temperatures can stimulate tree root systems and ensure rapid tree growth (Babalola et al. 1968, Kozlowski et al. 1991) but water-elm trees remain flooded during April due to spring flooding at Catahoula Lake. Generally, flooding prevents root activity for many species (Coder 1994); however, it is not known how water-elm tree roots interact with flooding; similarly, the phenology of water-elm tree growth needs further study. In this study, baldcypress chronology was only significantly correlated (negatively) with August temperature for the previous growing season. Such negative correlations for baldcypress radial growth were also found by Amos (2006) and Bohora (2012). Both pointed out that due to high summer and early fall temperature there is a reverse effect on production of stored food reserves which might negatively affect tree radial growth in the following year.

Water-elm radial growth was positively related to mid-spring rainfall during both the pre-control period and spring and late growing season (September) rainfall during the post-control period in the lake. Johnson et al. (2002) generalized the concept of a positive relationship between spring precipitation and tree growth by pointing that the years of low spring precipitation result in narrow rings in trees and vice versa. It is unlikely that spring precipitation supports tree growth by increasing soil moisture as soil is moist enough during spring due spring flooding (Keim and Amos 2012) and spring flooding has occurred in Catahoula Lake during both the pre- and post-control periods (LDWF). However, spring rainfall helps in distributing dissolved oxygen in flood waters (Davidson et al. 2006); therefore, it can indirectly benefit tree growth. Furthermore, the significant positive relationship between water-elm chronology and late growing season rainfall during the post-control period suggest that drier fall conditions prevailing during the post-control may have increased the effect of fall rainfall on water-elm radial growth during this period. Fall conditions in the lake post-control have become drier as compared prior to the water-control structure because lake drawdown during late summer and early fall post-control is more rapid and reflooding following drawdown is very rare (Bruser 1995).

In contrast, baldcypress chronology was only significantly positively related to early non-growing season (October) rainfall in this study. In Louisiana, baldcypress has shown variable growth responses to rainfall. Bohora (2012) found negative relationship between October rainfall and baldcypress radial growth. Keim and Amos (2012) did not find a significant relationship between baldcypress growth and October rainfall. They did observe, however, a positive relationship of spring rainfall with radial growth of baldcypress trees, but only when they separated climate from other environmental stresses. The variable responses of baldcypress radial growth with precipitation in this and other studies may be attributed to rainfall variations at different areas and/or to hydrologic conditions prevalent at the sites.

Water-elm chronology was significantly positively related with spring and summer PDSI and PHDI for both current and previous growing seasons; however, none of these variables were significantly correlated with baldcypress chronology. Based on my previous findings that water-elm positively responds to mid-spring (April) temperature and spring precipitation; these findings are sensible as PDSI values are dependent upon temperature, precipitation and soil moisture conditions (Palmer 1965). Similar results were pointed out by Stahle et al. (1988) in southeastern North Carolina and Georgia, and Reams and Van Deusen (1998) in Louisiana;

however, the positive correlation of PDSI in these studies was with baldcypress radial growth (not water-elm) and this positive correlation was limited only with June PDSI.

Probable Reasons for Variable Growth Responses of Water-elm and Baldcypress to Hydrology and Climate

Different radial growth responses of water-elm and baldcypress trees to hydrology and climate at Catahoula Lake may be related to phenological differences in radial growth patterns and root dynamics of both trees. However, studies examining such differences in growth among co-occurring species have been limited especially in southeastern wetland systems. Burke et al. (2003) observed that four oak species in two adjacent wetland habitats had different growth responses to flooding due to variation in the timing of root production in each of the species. They found that spring flooding was detrimental for cherrybark oak (*Quercus pagodaefolia* Raf.) because root growth of this species started early in the growing season; while overcup oak (*Quercus lyrata* Walt.) avoided flooding stress because root growth started later in the growing season and ended sooner than the other three oaks. Haggerty and Mazer (2008) suggested that coexisting species can differ in timing of peak growth, flowering, fruit development and root growth; for example, one individual can have peak growth in spring and least in fall and vice-versa. However, differences in root dynamics and phenology of water-elm and baldcypress are unknown. It is also unknown how these differences can affect their responses to hydrology and climate at the sites they coexist.

CONCLUSIONS

The establishment of water-elm trees into Catahoula Lake has been occurring for many decades; however, it has increased during the post-control period. It is not possible, however, to determine the role of hydrologic alterations resulting from the water-control structure and diversion canal on water-elm establishment. However, it is highly likely that broad-scale hydrologic changes that began in the 1900s initiated vegetation changes in the lake (Willis 2009) and with or without the water-control structure, lake levels would have declined and water-elm would have expanded into the lake.

Water-elm and baldcypress responded differently to prevailing hydrology and climate at Catahoula Lake. Water-elm radial growth had only a significant negative relationship with late spring lake levels in the pre-control period and a significant positive relationship with several mean monthly climatic variables. In contrast, baldcypress radial growth had significant positive relationships with several monthly lake levels overall and in both the pre- and post-control periods. However, most monthly climatic variables were not significantly correlated with baldcypress growth. Hence, water-elm growth was influenced by on a combination of early spring to summer temperature, precipitation and available soil moisture content while contrastingly baldcypress trees depended on lake levels for growth.

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APPENDIX: DETAILED ANALYSIS OF INDIVIDUAL PLOTS AND TREES IN EACH OF THE PLOTS ACCORDING TO THER ESTABLISHMENT IN EITHER THE PRE- OR POST-CONTROL PERIOD.

"Y" represents the presence of trees established in pre-control period in the plot; "N" represents absence of trees established in the pre-control period in the plot. The plots with symbol "Pre" consist entirely of pre-control trees; the plots with symbol "Post" consist entirely of post-control trees while those with symbol "Both" consist of both pre-and post-control trees.

Plot Name	Age > 38 years	Categories according to diversion canal	No. of trees in Pre	No. of trees in Post	No. of (Pre, Post) trees in Both
CanalW_1	N	Post		4	
CanalW_2	N	Post		4	
CanalW_3	N	Post		4	
CanalW_4	N	Post		4	
CanalE_1	N	Post		4	
CanalE_2	N	Post		4	
CanalE_3	N	Post		4	
French_1	Y	Both			2, 1
French_2	Y	Pre	1		
French_3	Y	Pre	3		
French_4	Y	Pre	3		
GatorW_1	N	Post		2	
GatorW_2	N	Post		4	
GatorW_3	Y	Pre	4		
GatorW_4	Y	Pre	4		
GatorE_1	N	Post		3	
GatorE_2	N	Post		2	
GatorE_3	Y	Both			1, 2
GatorE_4	Y	Both			3, 1
GatorE_5	Y	Both			2, 1
GatorE_6	Y	Both			2, 1
GatorE_7	Y	Pre	1		
Indian_1	N	Post		3	
Indian_2	N	Post		4	
Indian_3	N	Post		4	
Indian_4	N	Post		3	
Indian_6	N	Post		4	
MB_W_1	Y	Pre	4		
MB_W_2	Y	Pre	4		

Appendix (continued)

Plot Name	Age > 38 years	Categories according to diversion canal	No. of trees in Pre	No. of trees in Post	No. of (Pre, Post) trees in Both
MBendE_3	N	Post		4	
MBendE_4	N	Post		4	
MBendE_5	N	Post		4	
MBendE_6	N	Post		1	
MBendE_7	N	Post		1	
MBendE_8	N	Post		1	
MBendE_9	N	Post		3	
MBendE_10	N	Post		4	
Stock_1	N	Post		4	
Stock_2	N	Post		4	
Stock_3	Y	Pre	4		
Stock_4	Y	Pre	2		
Stock_5	Y	Pre	1		
WSWest_1	N	Post		4	
WSWest_2	N	Post		4	
WSWest_3	N	Post		4	
WSWest_4	N	Post		1	
WSWest_5	N	Post		4	
WSWest_6	N	Post		4	
WSWest_7	N	Post		4	
WSWest_8	N	Post		4	
WSWest_9	N	Post		4	
WSE_2	N	Both			1,1
WSE_3	Y	Pre	2		
WSE_4	N	Post		4	
WSE_5	N	Post		3	
WSE_6	N	Post		1	
WSE_7	Y	Both			1, 3
Total		Pre = 12	36		
		Post = N = 48		161	
		Both = 7			12, 10

VITA

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