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Baldcypress and Black Willow Growth Response to Contrasting Flood Regimes, Climate, and Competition, in the Atchafalaya Basin, Louisiana

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REGIMES, CLIMATE, AND COMPETITION, IN THE ATCHAFALAYA RIVER BASIN,
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ABSTRACT

Wetlands are dynamic ecosystems distinguished by their dependence on fluctuations of hydrologic influence. Although it is generally accepted that that flooding is a strong influence on growth, and that effects vary depending on whether water is stagnant or flowing, several aspects of flood characteristics and several tree species remain poorly investigated. One source of variability that has not been investigated is how flooding, climate, and competition among trees interact to control growth of individual trees. The objective of this study was therefore to 1) investigate effects of temporally varying hydrology and climate on growth of baldcypress and black willow trees and to 2) compare the effects of competition and hydrology on growth of baldcypress and black willow trees. Both objectives were addressed using tree ring measurements on three sites of varying flood connectivity to a side channel in the Atchafalaya River Basin, Louisiana. Consistent with previous studies of baldcypress, water depth was the most important variable for growth when compared with climate variables; black willow showed similar relationships. Among climatic variables, temperature had the greatest effects on growth for both species, but particularly for black willow. Higher temperature increased growth between fall- previous to the year of ring formation and spring of the year of ring formation, but decreased growth during late spring and summer of the year of ring formation. In contrast, precipitation and Palmer's Drought Severity Index were poorly related to growth of both species, particularly for black willow. Competition for growing space, analyzed through linear mixed modeling in combination with hydrologic, climatic, and site variables, had significant influence on growth of baldcypress trees and was best described by local stand density index measured by a 20 basal area factor prism. Although effects of site (hydrologic connectivity) on tree growth were not statistically significant because of high among-tree variability, differences in mean tree growth rates by site varied by about 20%.

CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

Wetlands are dynamic ecosystems distinguished by their dependence on fluctuations of hydrologic influence (Hammer and Bastian, 1989). This influence is imparted by the hydrologic regime, which encompasses factors such as timing, duration, depth, seasonality, and frequency of surface flooding and soil saturation (Bunn et al., 1997). Variations in hydrologic influence have created numerous wetland types such as coastal and freshwater marshes, bays, depression swamps, and forested floodplains (Brinson, 1993). Although having different properties and characteristics, wetlands in general are considered among the most diverse and important ecosystems worldwide due to the ecosystem services they provide (Costanza et al. 1997; Clarkson et al., 2013). Examples of ecosystem services are biogeochemical processes affecting nutrient conversion and retention and structural and compositional attributes providing diverse habitat and flood control (Allen, 2016). Numerous studies have been conducted to understand changes in ecosystem processes in response to ecological stimuli, however, ecosystem processes are affected by multiple complex effects.

Vegetation is a key component of wetlands that is influenced by variations in hydrology and climate that vary both spatially and temporally (Rodriguez-Iturbe et al., 1999). Although wetland plants are adapted to flooding, both positive and negative growth responses of wetland vegetation to flooding have been observed (Anderson and Mitsch, 2008). Many studies have concluded that seasonal flooding results in higher growth than does permanent flooding (Conner and Day, 1976; Mitsch and Ewel 1979, Brinson et al., 1981, Heiler et al. 1995), but other studies have found the opposite (Brown and Peterson, 1983; Burke et al., 1999). This contradiction highlights the importance of further study on the impact of hydrology on wetland functions. As natural and manmade changes continue, knowing how they will affect vegetation is pertinent (Kroes and Kraemer, 2014).

Growth response to climate conditions is relevant for wetland plants as well. Much wetland research has been done on coastal wetlands that are vulnerable to impacts from sea level rise, which will alter the hydrologic regime and erosion (Day et al., 2008). Effects of climate change on wetlands will not only be from sea level rise in coastal areas, but also from decreased temperature (as a result of increased cloudiness) and increased precipitation patterns that are projected to affect vegetative growth in Southeastern freshwater wetlands; (Molholland et al., 1997; Burkett and Kusler, 2000). Although studies have evaluated the effects of climate influence on vegetative growth in freshwater wetlands (Dudek et al, 1998; Dang and Lieffers, 1989), few have been done involving the comparison of climate effects on growth based on differences in freshwater hydrologic influence.

Competition is an important control on local stand structure, composition, and growth (Rodriguez-Iturbe et al., 1999). Many studies have evaluated the effects of competition (on the bases of growing space) on growth, but often in terms of stand level productivity. In wetlands affected by multiple disturbances, stand level productivity may not be a suitable measurement to evaluate site conditions and resources for tree growth. Allen (2016) suggested, based on evidence from Keeland and Young (1997), that in wetlands, particularly for baldcypress, lower stand productivity may occur from effects of flood disturbance (such as lack of regeneration potential and mortality of less tolerant species) by reducing growing stems, but this does not indicate lower growth of individual baldcypress trees. With this consideration, evaluation of growth response to the combined hydrologic and competitive environment should be done on an individual tree basis to understand hydrologic influence free of complication by variation in competition.

Although numerous studies have evaluated hydrologic, climate, and competitive effects on vegetative growth, a multidisciplinary approach observing the combined environmental influences should be used to provide a more comprehensive understanding of effects and growth response feedbacks. With this consideration, the specific objectives of this thesis are
- to investigate inter-annual effects of hydrology and climate on flood tolerant tree growth and
- to determine the effect of local competition versus hydrology on flood tolerant tree growth.

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CHAPTER 2: BALDCYPRESS AND BLACK WILLOW GROWTH RESPONSE TO HYDROLOGIC CONNECTIVITY AND CLIMATE

2.1 INTRODUCTION

Floodplains are among the most dynamic and diverse systems globally, providing substantial ecosystem services (Tockner and Stanford, 2002) such as flood abatement, nutrient conversion and storage, and biodiversity. Anthropogenic effects coupled with changes in climatic influence have the potential to alter and reduce the ecosystem services such as water quality, flood control, and carbon storage (Zedler and Kercher, 2005; Palmer et al., 2008). Increased awareness of the importance of ecosystem services provided by wetlands, particularly floodplains, has prompted numerous studies aimed at improving understanding of the influences on floodplain functionality (Junk, 1997).

Surface water connectivity between rivers and floodplains is an important determinant of natural processes in floodplains (Junk et al., 1989; Thomaz et. al., 2007). Connectivity influences the nature and effects of flooding because the exchange of water modifies the characteristics of floodwaters. The topography (bank elevations and channel depths) and hydraulic gradient influence the degree of connectivity of surface water flow between river and floodplain and throughout the floodplain (Trigg et al., 2013). Generally, as floodwaters rise, connectivity increases; therefore, floodplains that experience water exchange at from lower levels of flooding, are considered to have higher connectivity (Ward and Stanford, 1995). Floodplains with greater hydrologic connectivity often have greater habitat heterogeneity, biodiversity, and productivity (Ward and Stanford, 1995).

In the southeastern United States, the flood-tolerant tree species baldcypress (*Taxodium distichum* (L). Rich.) and black willow (*Salix nigra (*Marsh.)) are common on wet sites in floodplains. Life histories of baldcypress and black willow are distinctly different. Baldcypress is a slow-growing, long-lived species that often succeeds black willow stands (Kozlowski, 2002), whereas black willow is a pioneer, short lived species (Hodges, 1997). Because of the variability of flood disturbance within the floodplain, both species can be found growing amongst each other in some stands. In those cases, there is an opportunity to better understand flood effects on species with varying growth patterns.

Odum et al. (1979) hypothesized that flooding could be a net subsidy or stressor of growth. Many studies have been conducted to evaluate the effects of flooding on growth of baldcypress and black willow, but contrasting conclusions in regards to growth response to differences in flooding duration (Anderson and Mitsch, 2008) and soil moisture (Pezeshki et al., 2007) —both of which are driven by hydrologic connectivity—have been reported. Comparing among wetland ecosystems, many studies on mature baldcypress have concluded that there is faster forest or tree growth in wetlands that experience a seasonal flood pulse than wetlands that experience continual flooding (Conner and Day, 1976; Mitsch and Ewel 1979; Brinson et al., 1981; Heiler et al., 1995). Other studies, however, have found that trees in continually flooded wetlands grow slower than those with seasonal flooding (Brown and Peterson, 1983; Burke et al., 1999; and Anderson and Mitsch, 2008). Similarly, the majority of black willow studies on young trees have found that prolonged flooding or drought reduces growth (Li et al., 2004; Li et al., 2005), but there are variations in growth sensitivity to these influences (Hosner, 1958, 1960). Additionally, studies on flooding effects on black willow have focused on cuttings or saplings, but there may be differences in growth patterns between young and mature trees (Bond, 2000; Day et al, 2001) and there has been very little investigation of the growth of mature black willow.

Although flooding is often a dominant environmental factor influencing growth in floodplains, climatic variables such as temperature, precipitation, and drought, also affect tree growth in wetlands (Dudek et al., 1998). There are interactive effects of temperature and precipitation on growth response during the growing season for baldcypress (Stahle et al., 1985; Keim and Amos, 2012) potentially in response to secondary effects on dissolved oxygen, and water vapor deficit (Stahle and Cleaveland, 1992; Allen, 2016). Although some floodplains experience seasonal flooding, droughts occur. Palmer's Drought Severity Index (PDSI), which can be used as an indicator of soil wetness and drought, based on precipitation and temperature, has been used in assessing growth response (Conner et al., 2014). Positive relationships of growth with PDSI for baldcypress has been reported, particularly for values measured during the spring and summer (Day et al., 2012; Stahle et al.. 1988; Stahle and Cleaveland, 1992; Keim and Amos, 2012).

Tree rings record long-term information on environmental influences and have been used in numerous studies to evaluate the effects and predict future influences of flooding and climate on tree growth (Mitsch and Ewel, 1979; Young et al., 1995; Keim and Amos, 2012). Several studies using tree ring analysis to evaluate growth response to both flood and climate have been done on baldcypress but none have been done on black willow. With growth pattern variability and knowledge gaps, it is important for additional research to be conducted before predicting future growth patterns to environmental variables which in turn could affect ecosystem services. Therefore, the goal of this study was to improve understanding of baldcypress and black willow growth response to flood and climate. Specifically, the objectives of this study were (1) to compare growth response of baldcypress and black willow to flood and climate influences among sites of different flood connectivity and (2) to compare differences of growth response patterns between baldcypress and black willow.

2.2 STUDY SITE

Located in south-central Louisiana, the Atchafalaya River (ARB) is the largest distributary of the Mississippi River Basin. In response to expectations that the Mississippi River would eventually diverge into the ARB, threatening the economy of New Orleans (Ford and Nyman, 2011), the U.S. Army Corps of Engineers constructed levee systems and the Old River Control Structure, in 1963, to divert 30% of the combined flows of the Mississippi and Red rivers into the Atchafalaya River. The ARB is thus a modified wetland with high rates of sediment accretion within the floodplain, especially at the study sites (Hupp et al., 2008).

In the Atchafalaya River Basin, the sites for this project were on the Atchafalaya Basin Preserve (ABP) managed by The Nature Conservancy as part of an initiative to restore floodplain ecosystem services that may have become reduced in response to high sediment accretion rates, thus causing reduction in hydrologic connectivity. To understand differences in ecosystem services based on hydrologic connectivity, three sites were selected for this study: seasonally flooded, bottomland hardwood backswamps that receive brownwater (sediment-rich water) through overbank or channelized flooding, or blackwater (sediment-poor water) from backwater flooding (Figure 2.2). Specifically, the ABP property is adjacent to Bayou Sorrel, which receives direct water flow from the Atchafalaya River. Water levels in the Atchafalaya River are highly variable, resulting in high annual water level variability in Bayou Sorrel. A flood pulse occurs annually, often with highest flows generally in April (Rutherford et al., 2011). On the southern side of Bayou Sorrel, field experience shows the connected and partially connected sites receive overbank flooding beginning at 4.57 and 5.48 meter river stages recorded at the Bayou Sorrel Lock water gauge (USACE water gauge #49630). The disconnected site, on the north side of Bayou Sorrel, receives overbank flooding at 5.48 meters, however, at overbanking stage, river water does not flow readily into the site due to the natural southerly water flow toward the Gulf of Mexico. Although all three sites shared similar soil types (Fausse/Dowling), defined by fine clay accumulation from riverine influence that characteristically causes ponding of water in backswamp areas (NRCS, 2018), differences in drainage paths resulted in greater ponding and slower drainage in the disconnected site.

In this study, 37 dominant baldcypress (*Taxodium distichum*) and 39 black willow (*Salix nigra*) trees were sampled. Although both are found within the backswamp of floodplains in Louisiana, they have different life histories and physical characteristics that increase functional diversity and response within the wetlands. Black willow is a pioneer species that becomes established in newly deposited sediments, grows quickly, and is shade intolerant. Once reaching maturity, black willow can remain a dominant competitor for approximately 20 years before senescence begins (Krinard, 1985). In contrast, baldcypress is a slow-growing, moderately shade-tolerant, long-lived species that is commonly found on floodplains (Hodges 1997).

For the purpose of this study, sample trees were chosen to be in dominant or codominant canopy positions, with minimum visible signs of damage, and far enough away from other sampled trees such that they shared no common competing trees according to the measures used. All sampling plots were located within the interior floodplain forests determined by the change (decrease) in elevation from the natural levee to the interior floodplain forests and change in species composition. Bottomland hardwood species baldcypress (*Taxodium distichum*), black willow (*Salix nigra*), green ash (*Fraxinus pennsylvania*), water tupelo (*Nyssa aquatica*), planertree (*Planerea aquatica*) and swamp-privet (*Forestiera aquatica*) were common among all sites.
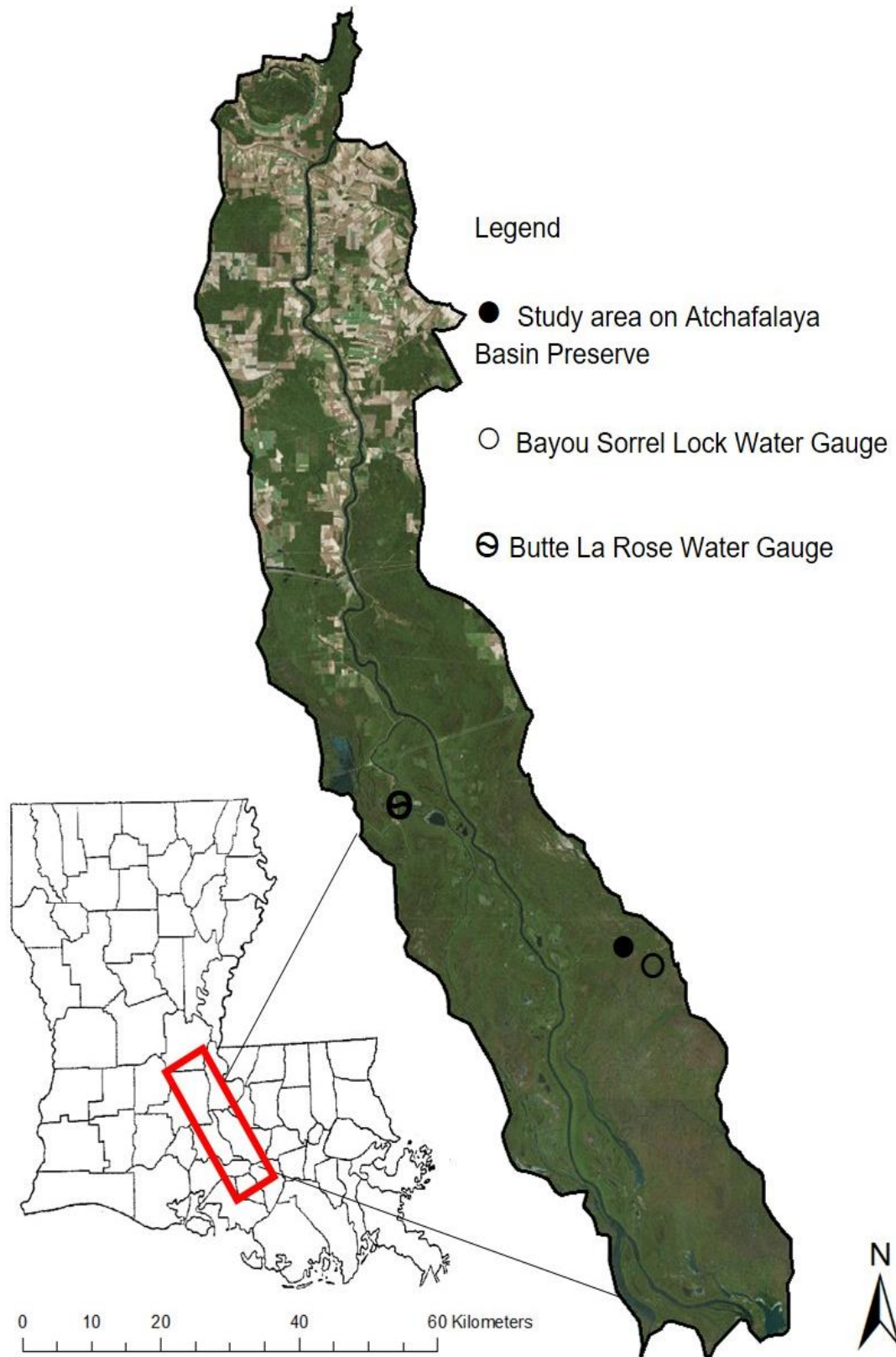
Figure 2.1 Location of study area in the Atchafalaya Basin in south-central Louisiana
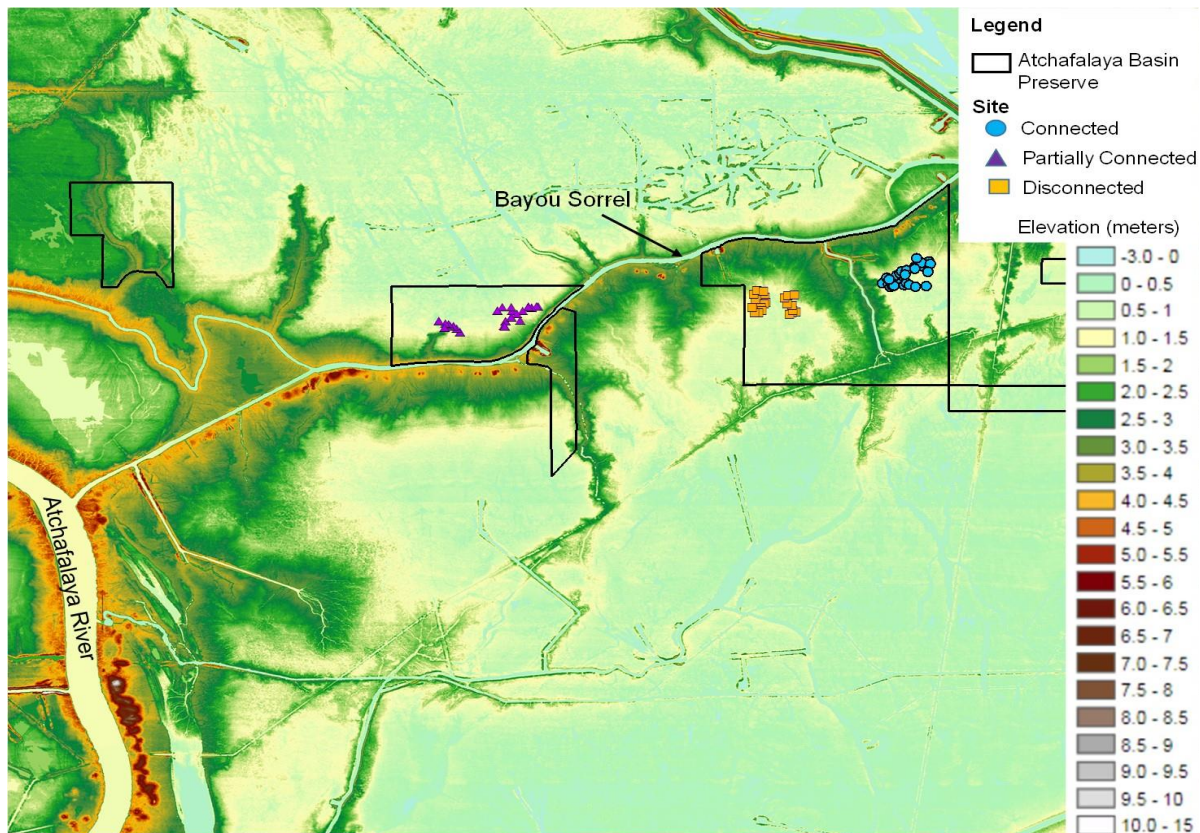
Figure 2.2. 2012 Lidar digital elevation map of the sample trees located on the Atchafalaya Basin Preserve (atlas.lsu.edu). Sites identified as hydrologically connected (blue circles), partially connected (orange squares) and disconnected (purple triangles).

2.3 METHODS

2.3.1 Dendrochronological measures

In each site, a minimum of 10 dominant or codominant baldcypress and black willow trees were sampled. Dominant trees with minimum visible signs of crown damage, split stem, or disease were selected because their growth response to environmental conditions, such as climate and hydrology, is less complicated by individual variability (Fritts 1976). Trees were cored using a 5.15 mm increment borer. Two cores were collected from each tree at 90 degrees to account for ring-width variance and missing or false rings. Cores were taken at breast height (1.3 meters) for black willow, and above buttressed trunks for baldcypress at normal diameter, defined as the stem diameter approximately equivalent to diameter at breast height (Parresol and Hotvedt, 1990).

In the lab, cores were dehydrated, mounted, and sanded in preparation for crossdating and measurement following the methods of Stokes and Smiley (1968), Estes (1970), and Fritts (1976), Yamaguichi (1990). Ring boundaries were identified under visible light for both species and black willow cores required fluorescent light and wetting of the wood to identify ring boundaries, particularly in the sapwood, because rings are diffuse to semi-diffuse porous (Krinard, 1985). Specifically, diffuse to semi-diffuse porous rings show pore size variation between earlywood and latewood growth in some rings, while no variation is evident in others (uniform pore sizes throughout ring) (Thomas, 2000). Annual rings were measured with 0.001 mm precision, from bark to pith for each core, using a Velmex measuring stage. Using real-time plots of ring widths for visual representation of growth patterns and marker years (years of significantly good or poor growth), individual tree cores were manually crossdated by tree, then collectively by site. To assess accuracy of the cross-dating, the time sequences of rings in individually dated series were statistically analyzed using the software COFECHA to ensure accurate date assignment of each ring (Holmes, 1983; Grissino-Mayer, 2001).

Radial increment is influenced by a wide variety of factors. Tree-ring analysis attempts to separate inherent patterns, due to age and internal factors, from the external factors that correlate with ring width. The external factors that are correlated with ring width are considered the desired signal that is filtered from the internal factors, considered noise, through modeling (Cook, 1990). One such internal factor is the biological age of a tree which has a strong influence on growth (Cook, 1985). Because radial increment from the biological age of a tree can interfere with signal to flooding or climate, its effect on growth must be accounted for when creating chronologies. To create chronologies for evaluation, the ARSTAN program (Cook and Holmes (1986) was used. Many detrending methods can be used in ARSTAN to remove age and endogenous stand disturbance effects on growth (Cook and Holmes, 1986). The age-related trend in tree rings is often modeled using a negative exponential curve applying the knowledge that tree ring widths decrease with age. However, age growth behavior in closed canopy forests deviates from the negative exponential curve as a result of competition and disturbance influences (Cook, 1987). In uneven-aged forests, the cubic smoothing spline method is a better method of standardization because it does not assume a pattern of growth across the life of the tree, but instead is fitted to the natural growth pattern (Cook and Peters, 1981), therefore better retaining desirable high frequency growth responses to environmental conditions (Holmes, 1983). To model these effects, a 20-year cubic smoothing spline retaining 50 percent variance was fitted to each individual tree ring series. In addition to age-related effects, growth is autocorrelated between years, meaning growth of a previous year has statistical correlation to subsequent years (Fritts, 1976; Speer, 2010). To increase the desired signal of high frequency growth response to environmental influences, effects of autocorrelation were filtered through autoregressive moving average modeling (Cook, 1985). In the program ARSTAN, chronologies created with pooled autoregressive modeling were chosen for evaluation because common growth to environmental signal response among all tree cores are retained within the chronologies (Cook, 1985). The resulting chronologies, useable for analysis, have no biological age effects, no autocorrelation effects, and are indexed growth around the mean 1 (Fritts, 1976; Cook and Peters, 1981; Speer, 2010).

2.3.2 Hydrological data

Mean monthly water level data from 1955-2016 were recorded at the nearby Bayou Sorrel Lock (U.S. Army Corps of Engineers water gauge #49630) approximately 5 km downstream from study sites (Figure 2.1).Although records of water levels have been recorded since 1955, geomorphology and flow patterns of channels in the Atchafalaya River Basin have changed naturally (through increased flows; Mossa, 2013) or through manmade impacts (dredging, soil banks, pipeline river crossings, flood control structures) over time (Mossa, 2016). These changes may have modified the relationship between the gauge and local water levels in the study area over time. The correlation between the Bayou Sorrel Lock gauge and the Butte La Rose gauge, located above the confluence of the Atchafalaya River and Bayou Sorrel, was nearly perfect (r=.97), despite the decline in the mean daily gauge height of Butte La Rose (and likewise Bayou Sorrel Lock) from 1959-2009 (Alford and Walker, 2011). Therefore, over time some discrepancy between water level and water influence to sites may have occurred, such as higher water levels now may be required for water flow through the floodplain sites than in previous decades, but there is no evidence that the meaning of gauge data has shifted differently by study site.

2.3.3 Climatic data

Aside from surface water flow, three climatic variables that are known to affect ring width were used to assess influence on growth: temperature, precipitation, and Palmer's Drought Severity Index (Stahle et al., 1985; Stahle et al., 1988; Orwig and Abrams, 1997). The data for the climatic variables were obtained from the National Oceanic Atmospheric Administration (NOAA) from the National Climatic Data Center (NCDC) database (https://www.ncdc.noaa.gov/cag/divisional/time-series/). Monthly data were used from years 1900 to 2016 from the south-central, region 8, divisional area of Louisiana where the sites are located.

2.3.4 Statistical analysis

Correlations between ARSTAN chronologies and mean monthly water depth and mean monthly temperature, precipitation, and Palmer's Drought Severity Index were evaluated using SAS (Statistical

Analytical System 9.4) program. A lag effect of environmental influence on radial increment is known to sometimes occur; therefore, analyses included months in the year prior to ring formation (Janurary1- to December1- and months in the year of ring formation until completion of the ring (January to October).

2.4 RESULTS

Tree establishment dates varied by approximately 190 years for baldcypress at all sites. The connected site had the oldest tree establishment date in 1692, the partially connected site having the most recent date (1871) for the oldest tree establishment. Of the 37 trees sampled, 13 were established prior to 1900. Establishment dates of the oldest black willows of all sites were from 1954 to 1958, with the connected site having the oldest tree establishment date, and the disconnected site having the youngest tree establishment date.

Prior to 1900 coherence in growth patterns among the cores was low, resulting from missing or false rings, to the point where crossdating techniques became ineffective. Therefore, baldcypress chronologies were truncated to begin in 1900. In contrast, black willow establishment dates were between late 1950s and early 1960s and the chronologies did not require truncation (Table 2.1; Figure 2.4).

For both species, series intercorrelation (>0.471), expressed population signal (>0.91), and mean sensitivity (>0.444) provided evidence that all chronologies were accurately cross-dated and sufficient for dendroclimatic analyses (Grissino-Mayer, 2001). There was higher interseries correlation for baldcypress chronologies than for black willow chronologies at all sites (Table 2.1). Series inter-correlations at 0.50 or greater, are desirable for tree ring crossdating, as it indicates tree ring sensitivity to environmental effects and crossdating accuracy (Grissino-Mayer, 2001). However, black willow in connected and partially connected sites resulted in series intercorrelation slightly less than 0.50.

Table 2.1 Summary statistics from the study sites.

Site[a]	No. of Trees	Mean Diameter (cm)	Mean Height (m)	Tree Initiation Range (yr)[b]	Trees >250 yrs old	Chronology (yrs)	Series inter-Correlation	EPS[c]	Mean sensitivity
Baldcypress									
C	14	51.4	23.8	1692-	2	1900-2016	.572	.95	.497
P	13	47.6	24.3	1890-	0	1900-2016	.665	.96	.512
D	10	48.9	22.4	1871-	0	1900-2016	.715	.96	.524
Black willow									
C	15	70.5	23.4	1954-	0	1958-2016	.471	.93	.451
P	10	48.8	23.9	1955-	0	1960-2016	.499	.91	.465
D	13	55.5	24.1	1958-	0	1963-2016	.536	.94	.444

[a]C, connected; P, partially connected; D, disconnected
[b]Assumes 10 years for trees to grow to height of coring for baldcypress and 3 years for black willow.
[c]EPS, expressed population signal (Wigley et al. 1984),

2.4.1 Raw Ring Widths

Ring widths of baldcypress, with the exception of 3 trees, were small between 1900 and 1926 (Figure 2.4). In 1927, an event resulting in greater radial increment for all individual, and from 1927 to 2016 there was greater growth and variability in growth than prior to 1927. Years of particularly good growth included 1927, 1945, 1957, 1975, 1979, 1995, and 2008 (Figure 2.7). Years of poor growth included 1934, 1946, 1958-1960, 1971, 1978, 1980, 2000, and 2005 (Figure 2.7).

Trees in the connected site had the highest variability in growth. Greatest variability occurred between the years of 1927 through 2005. After the poor growth year of 2005 all trees grew with relatively low variability through 2016. There was low growth variation at the partially connected site until some apparent stand disturbance occurred in 1980. From 1980 until 2016, high variability among individual cores was still evident. Overall the lowest variability among all sites occurred for the disconnected site. Among all sites, between the years 1936 and 1944, extremely high growth variability occurred (Figure 2.3 & 2.4). High variability among individual trees became evident again between 1962 and 1970, for only the connected and disconnected sites.

Black willow growth was less ordered than it was for baldcypress (Figure 2.5 & 2.6). The highest variability in radial increment was between 1957 and 1967. For individual tree growth patterns, the connected and partially connected site qualitatively had the overall highest and lowest interstand variability, respectively. Some notable years of good growth were 1967, 1974, 1979, 1982, 1989, 2001, and 2013 (Figure 2.7). Some notable years of poor growth were 1972, 1978, 1980, and 2000, 2012, and 2015 (Figure 2.7). During years of generally better growth, higher variability in growth occurred than for poor years in which all trees resulted in similar behavior.

2.4.2 Chronologies

Temporal variation of indexed tree growth, averaged by sites, was similar (Figures 2.7, 2.8) for baldcypress and black willow. In 1900, 14 baldcypress had been established in total for all 3 sites. Establishment continued until 1963. In contrast, at year 1960, 4 black willow trees were established and establishment continued until 1985.
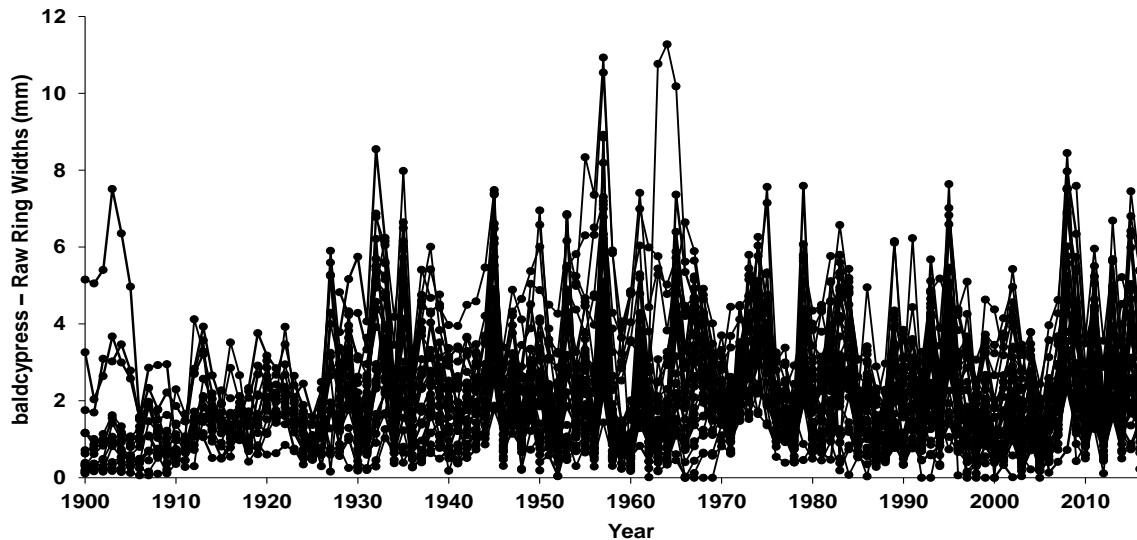
Figure 2.3. Individual raw ring widths of all sampled baldcypress for years 1900-2016.
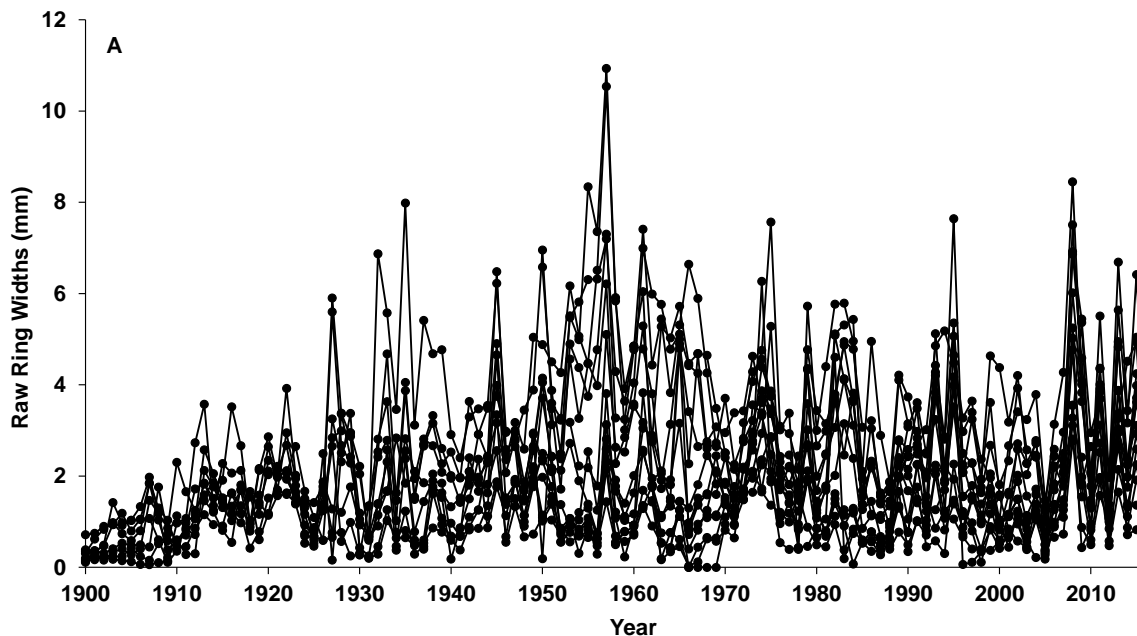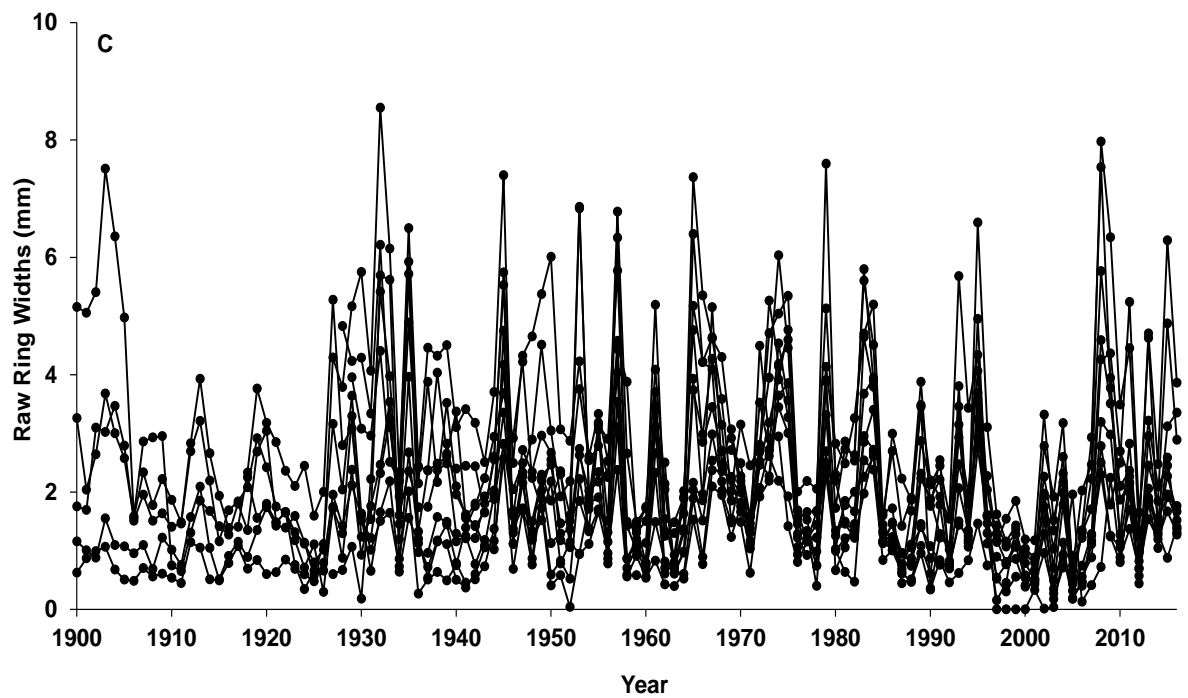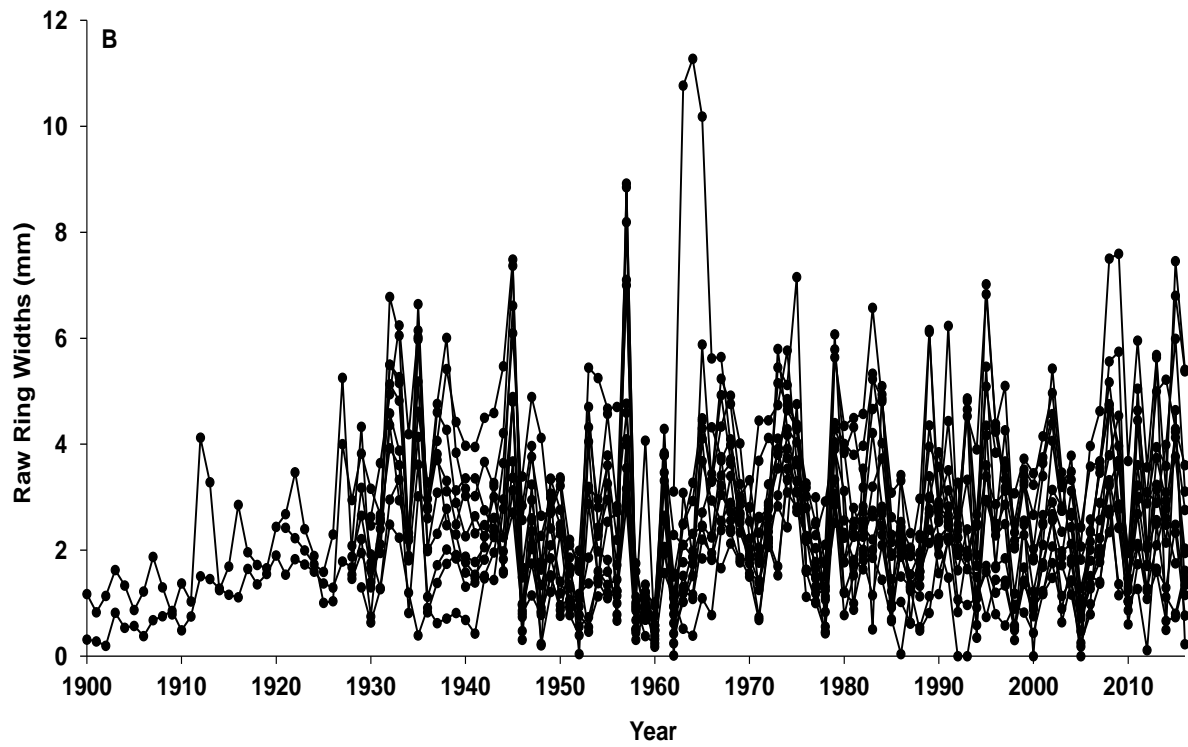
Figure 2.4. Individual raw ring widths for baldcypress in the flood connected (A), partially connected (B) and disconnected (C) sites for years 1900-2016
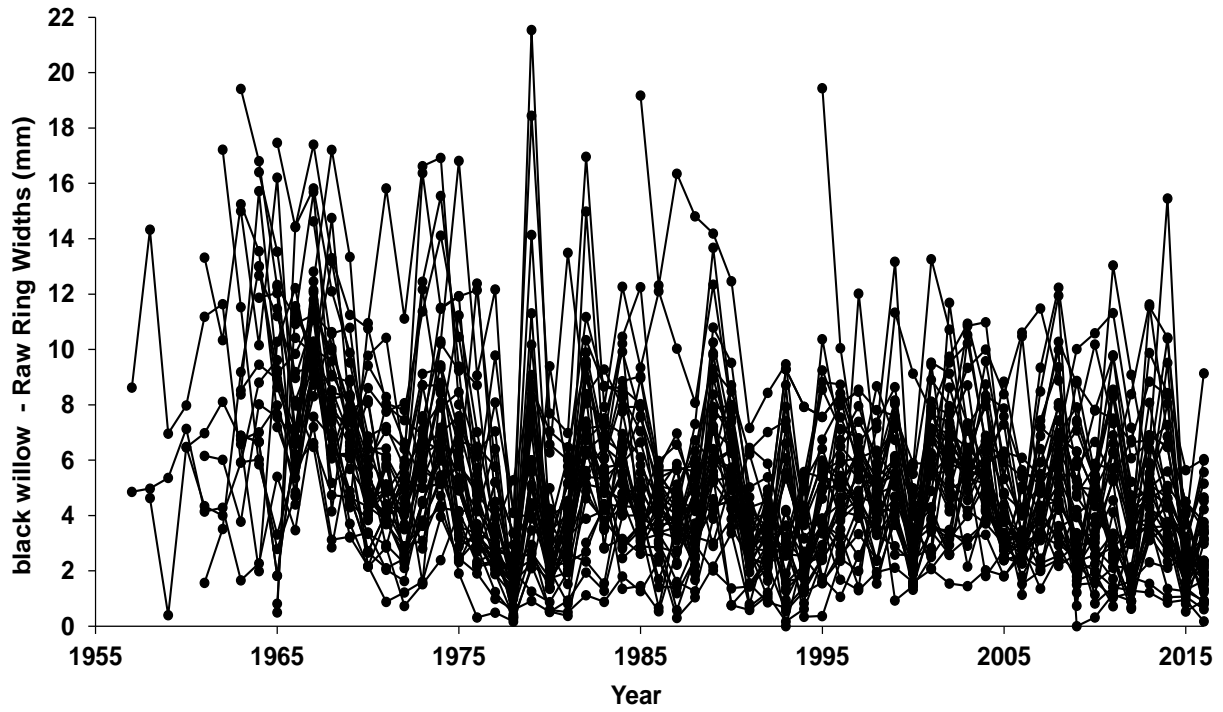
Figure 2.5. Individual raw ring widths of all sampled black willow for years 1957-2016
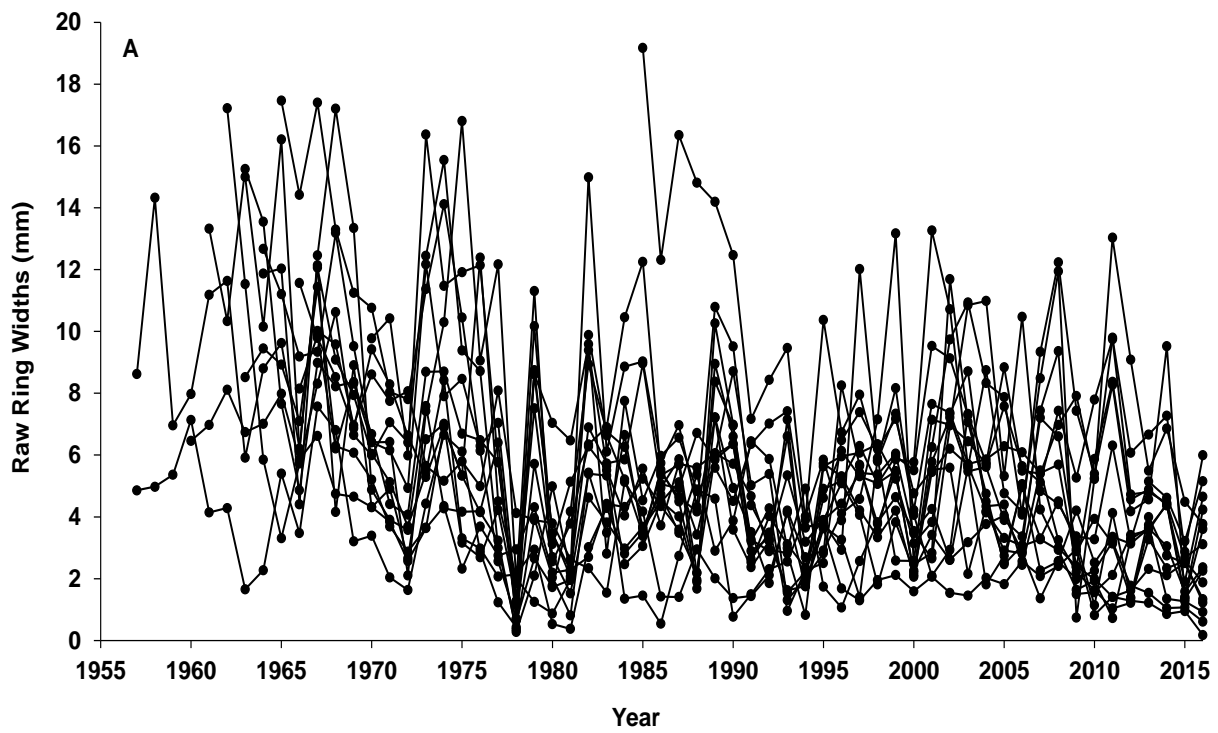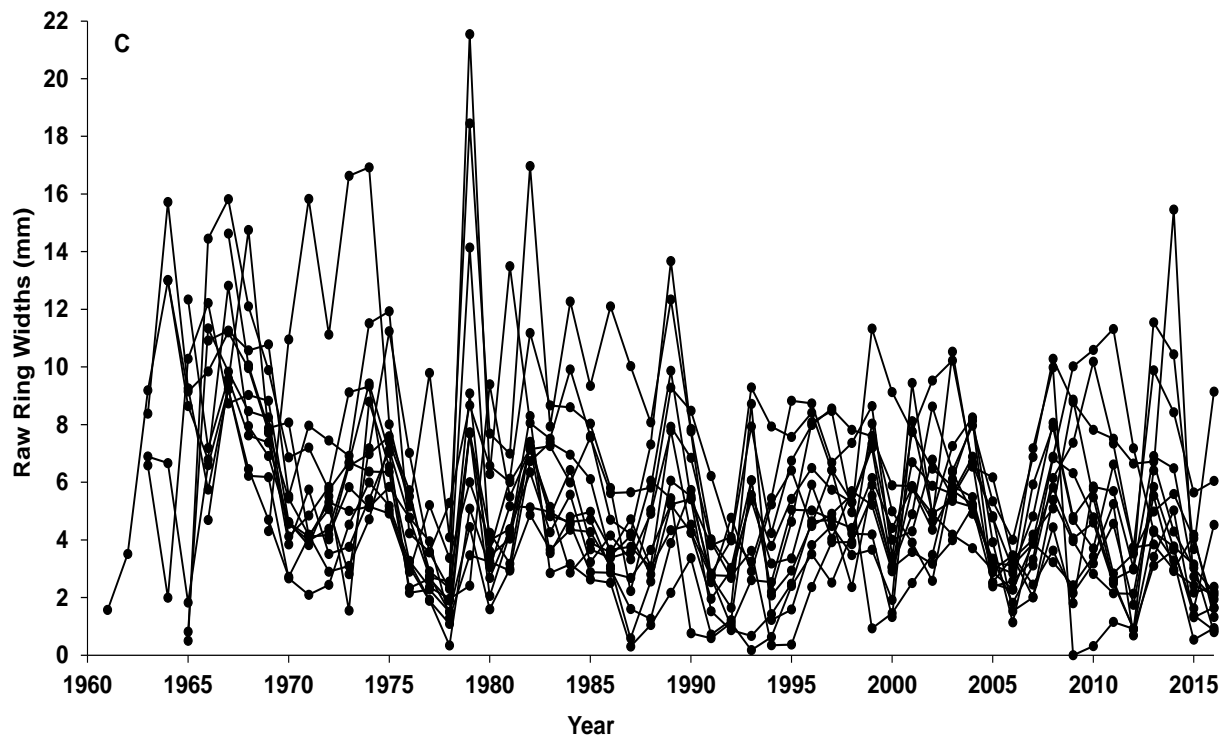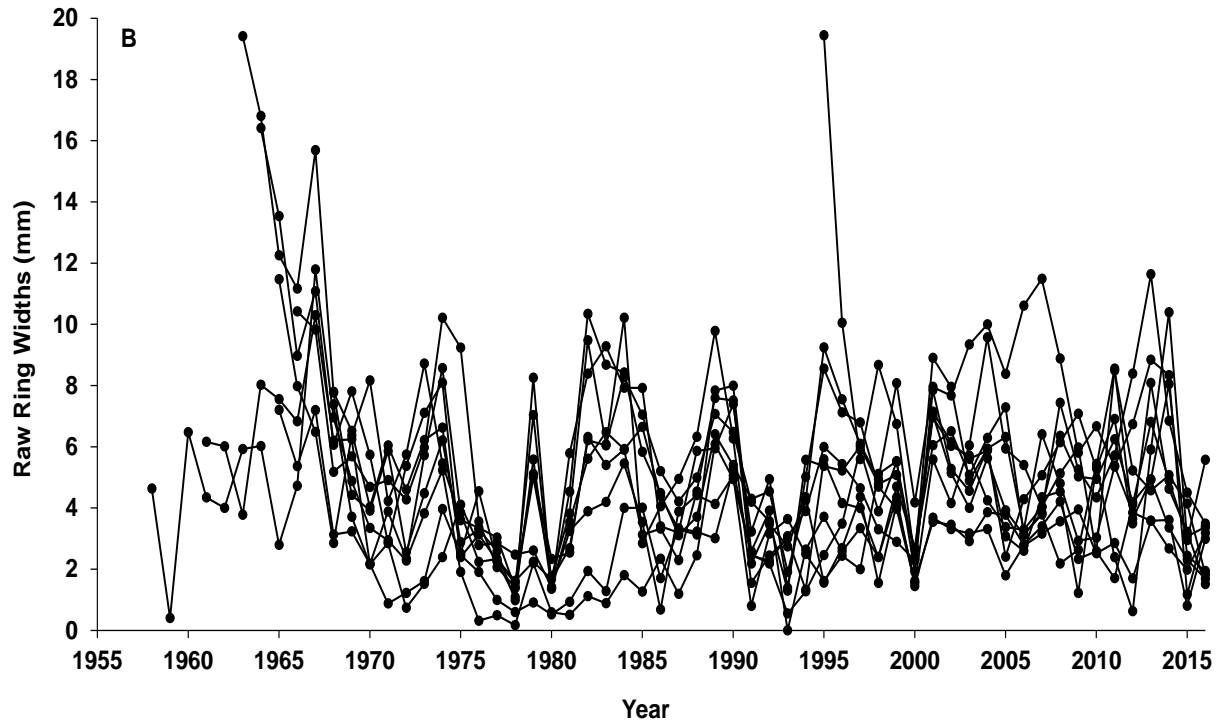
Figure 2.6. Individual raw ring widths for black willow in the flood connected (A), partially connected (B) and disconnected (C) sites.
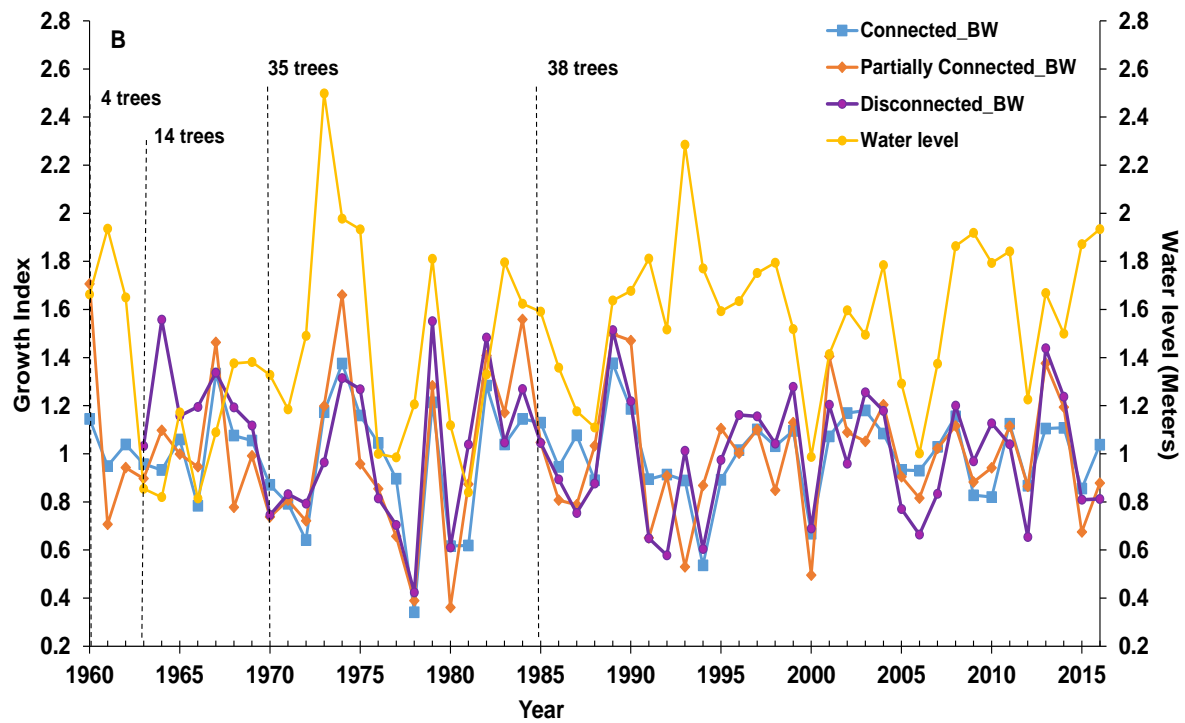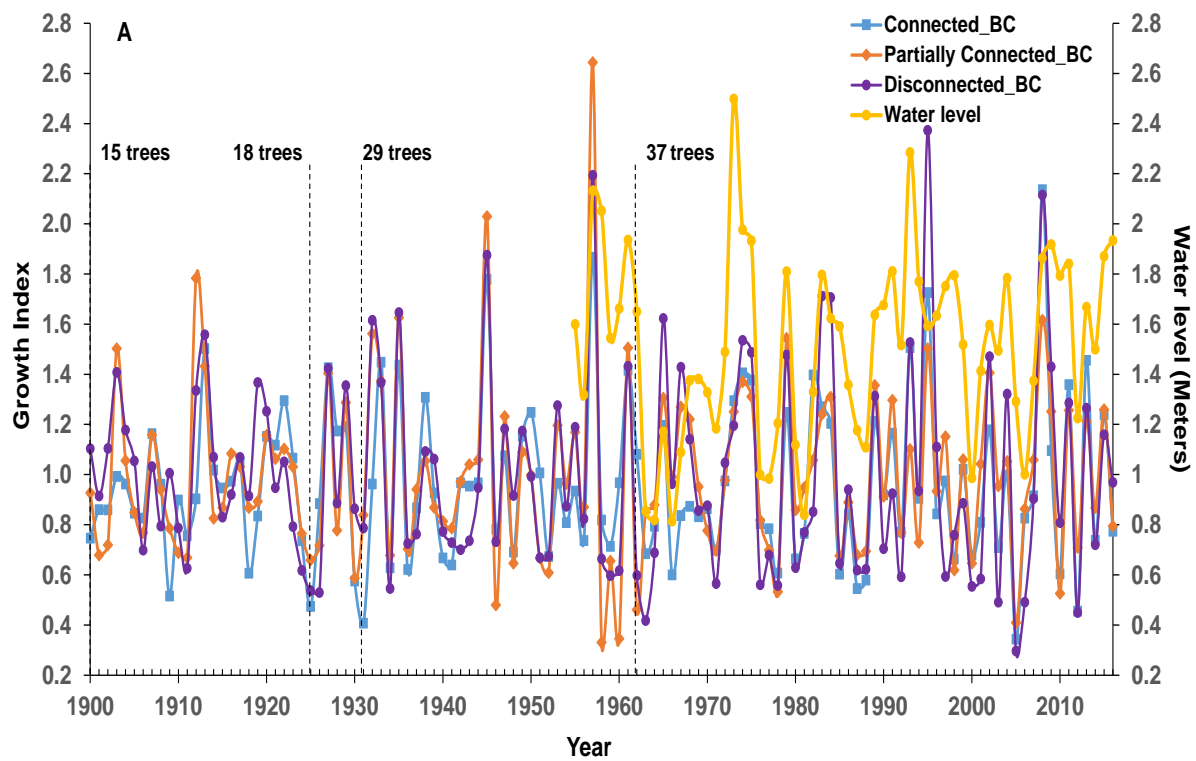
Figure 2.7. Age-normalized, cubic-spline-standardized ARSTAN chronologies for baldcypress (A) and black willow (B) in the flood connected, partially connected, and disconnected sites. Tree numbers along dotted lines represent total sample number in the chronologies.
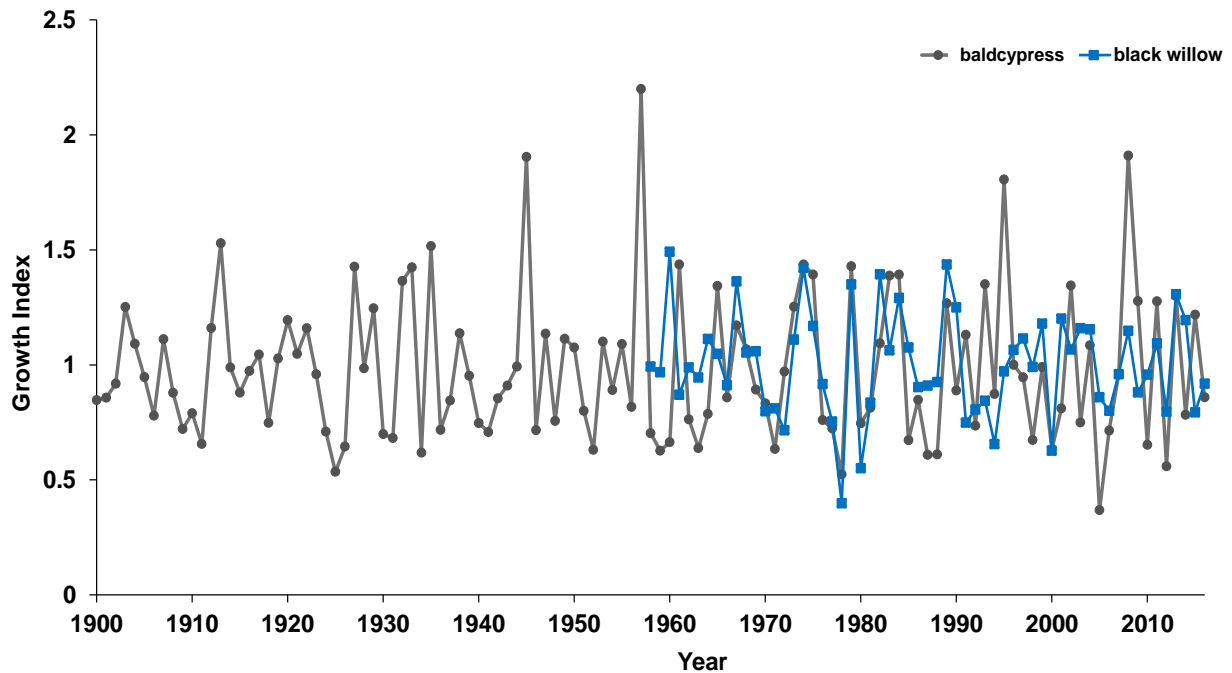
Figure 2.8. Comparison of age-normalized, cubic-spline-standardized ARSTAN chronologies averaged of all sampled baldcypress and black willow.

2.4.3 Simple climate correlations with chronologies

There were several significant correlations between age-normalized, standardized chronologies (index growth) and monthly water depth for both species (Table 2.2). All significant correlations of radial increment with water depth in months of the year prior to ring formation (lag year) (Jan1- through Dec1-) were negative, but all significant correlations between incremental growth and water depth in months of the year of formation (Jan-Oct) were positive. Most significant correlations involving conditions in the year prior to ring formation were between September and December, but most relationships across sites and species were not statistically significant.

There were significant correlations between radial increment of baldcypress and water depth in March through October, and the strongest correlations were for the months of June and July (Table 2.2). For black willow, there were significant correlations between incremental growth and water depth in February through July, and correlations were stronger in the connected site than other sites. The strengths of correlations between chronologies and water depth were generally weaker for black willow than for baldcypress.

Table 2.2. Simple correlation coefficients, r, between mean monthly water depth and age-normalized, standardized growth indices, for baldcypress and black willow on connected, partially connected, and disconnected sites

Water depth	baldcypress			black willow		
	C[1]	P[2]	D[3]	C[1]	P[2]	D[3]
Jan1-	0.08	-0.06	0.03	0.07	0.00	-0.06
Feb1-	0.21	0.08	0.08	0.12	0.04	-0.09
Mar1-	0.07	-0.03	0.03	-0.10	-0.11	**-0.32 c**
Apr1-	-0.05	-0.07	-0.05	-0.10	-0.09	-0.10
(table cont'd)						

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	baldcypress			black willow		
Water depth	C[1]	P[2]	D[3]	C[1]	P[2]	D[3]
May1-	-0.08	-0.10	-0.03	0.00	0.03	-0.14
Jun1-	-0.11	-0.15	-0.10	0.16	0.11	-0.04
Jul1-	0.04	-0.17	-0.09	0.08	-0.02	-0.12
Aug1-	0.03	-0.19	-0.05	-0.12	-0.1	-0.19
Sep1-	0.09	-0.09	0.06	**-0.24 d**	-0.14	-0.17
Oct1-	-0.15	**-0.35 b**	-0.19	**-0.23 d**	-0.13	**-0.27 c**
Nov1-	-0.18	**-0.37 b**	-0.21	-0.01	0.00	-0.16
Dec1-	-0.03	-0.20	0.02	-0.04	-0.03	**-0.25 d**
Jan	0.08	-0.06	0.09	0.16	0.06	-0.14
Feb	0.17	0.01	0.11	**0.26 c**	**0.26 c**	0.06
Mar	**0.28 c**	0.10	0.11	**0.39 b**	**0.29 c**	0.20
Apr	**0.44 a**	**0.25 d**	**0.27 c**	**0.30 c**	0.10	0.17
May	**0.59 a**	**0.40 b**	**0.52 a**	**0.23 d**	0.16	0.15
Jun	**0.63 a**	**0.53 a**	**0.60 a**	**0.32 c**	**0.31 c**	**0.28 c**
Jul	**0.64 a**	**0.47 a**	**0.55 a**	**0.37 b**	**0.36 b**	**0.34 c**
Aug	**0.39 b**	0.18	**0.34 b**	0.05	-0.02	0.07
Sep	**0.48 a**	**0.23 d**	**0.38 b**	0.19	0.05	0.13
Oct	**0.35 b**	0.21	**0.35 b**	0.10	-0.02	0.10

[1] C, Connected
[2] P, Partially Connected
[3] D, Disconnected
Note: letters represent p-value significance; a, < 0.0001; b, < 0.001; c, < 0.05; d, < 0.10

There were several significant relationships between chronologies and temperature, in both the positive and negative directions (Table 2.3). There were positive correlations for both species for temperature November1-, and for December1- to March for baldcypress (Table 2.3). Relationships were generally consistent among sites. There were negative correlations between chronologies and temperature in the late spring and summer, especially for June (baldcypress), and late summer (both species, but stronger for black willow).

Table 2.3. Simple correlation coefficients, r, between temperature and age-normalized, standardized growth indices for baldcypress and black willow on connected, partially connected, and disconnected sites

	baldcypress			black willow		
Temperature	C[1]	P[2]	D[3]	C	P	D
Jan1-	0.04	-0.03	-0.08	0.02	0.04	0.02
Feb1-	0.07	0.02	-0.02	-0.11	-0.13	-0.29
Mar1-	-0.10	-0.13	-0.04	0.03	-0.03	-0.02
Apr1-	-0.15	-0.05	-0.12	-0.01	-0.18	-0.01
May1-	-0.05	-0.03	-0.09	0.15	**0.23 d**	0.16
Jun1-	-0.03	0.00	-0.05	-0.17	-0.10	-0.16
Jul1-	-0.02	-0.01	-0.05	-0.07	0.00	-0.03
Aug1-	-0.07	-0.07	-0.12	-0.12	0.02	-0.13
Sep 1-	0.00	-0.03	-0.13	-0.12	-0.03	-0.04
Oct1-	0.04	0.01	-0.02	0.12	0.11	0.05
Nov1-	0.08	0.12	**0.16 d**	**0.27 c**	**0.23 d**	**0.23 d**
Dec1-	**0.19 c**	**0.21 c**	**0.20 c**	-0.07	-0.18	-0.20
Jan	**0.25 b**	**0.2 c**	**0.16 d**	0.19	0.12	0.06
Feb	**0.19 c**	**0.18 d**	0.09	0.12	0.04	-0.08
Mar	**0.16 d**	**0.19 c**	0.12	0.14	0.00	-0.16
(Table cont'd)						

Temperature	baldcypress			black willow		
	C[1]	P[2]	D[3]	C	P	D
Apr	-0.03	0.13	0.01	-0.03	0.05	0.02
May	0.03	0.02	0.03	-0.07	-0.17	-0.04
Jun	-0.12	**-0.26 b**	**-0.22 c**	-0.17	-0.13	-0.11
Jul	-0.06	-0.11	-0.05	-0.20	-0.20	**-0.25 d**
Aug	-0.03	-0.15	-0.13	-0.13	-0.20	-0.09
Sep	**-0.19 c**	**-0.22 c**	**-0.19 c**	**-0.38 b**	**-0.38 b**	**-0.40 b**
Oct	-0.05	-0.09	0.01	0.04	0.09	0.01

[1] C, Connected
[2] P, Partially Connected
[3] D, Disconnected
Note: letters represent p-value significance; a, < 0.0001; b, < 0.001; c, < 0.05; d, < 0.10

There were several significant relationships between radial increment and precipitation for both species, but generally correlations were weak (Table 2.4). The only significant negative relationship for black willow was with May1- temperature on the disconnected site. For baldcypress, there were positive relationships between chronologies and precipitation during August1- and between March and May.

Table 2.4. Simple correlation coefficients, r, between precipitation and age-normalized, standardized growth indices, for baldcypress and black willow on connected, partially connected, and disconnected sites

Precipitation	baldcypress			black willow		
	C[1]	P[2]	D[3]	C	P	D
Jan1-	0.10	0.09	0.13	0.03	0.00	0.06
Feb1-	0.01	-0.01	0.06	0.18	0.13	0.07
Mar1-	0.14	0.04	0.09	0.04	0.07	0.07
Apr1-	-0.01	-0.07	0.06	-0.17	-0.09	-0.17
May1-	-0.02	-0.06	-0.08	-0.12	-0.10	**-0.23 d**
Jun1-	0.06	-0.05	-0.06	0.21	0.19	0.09
Jul1-	0.00	-0.03	0.01	0.04	0.04	-0.04
Aug1-	**0.16 d**	**0.23 c**	**0.23 c**	0.13	0.07	0.22
Sep1-	0.00	-0.01	-0.02	0.01	0.16	0.11
Oct1-	-0.08	-0.14	-0.11	-0.03	-0.06	-0.15
Nov1-	-0.02	-0.02	0.00	-0.05	0.00	0.00
Dec1-	0.09	0.07	0.11	-0.04	-0.06	0.01
Jan	0.02	0.00	0.04	-0.08	-0.10	-0.08
Feb	-0.12	0.00	-0.01	0.05	0.16	0.20
Mar	**0.16 d**	0.15	0.13	-0.06	-0.05	-0.14
Apr	**0.20 c**	**0.16 d**	**0.16 d**	-0.03	-0.11	-0.05
May	0.13	**0.17 d**	**0.16 d**	-0.06	-0.08	-0.01
Jun	0.00	0.07	-0.07	0.12	0.11	0.12
Jul	-0.09	-0.08	-0.08	0.00	-0.06	0.19
Aug	-0.09	-0.08	0.00	0.08	0.07	-0.13
Sep	0.07	0.03	0.00	0.06	-0.05	-0.09
Oct	0.01	0.08	0.11	0.05	0.07	0.08

[1] C, Connected
[2] P, Partially Connected
[3] D, Disconnected
Note: letters represent p-value significance; a, < 0.0001; b, < 0.001; c, < 0.05; d, < 0.10

There were several positive significant relationships between chronologies and Palmer's Drought Severity Index for baldcypress but none for black willow (Table 2.5). The time periods of positive

relationships were summer months of the year prior to ring formation, and spring months of the year of ring formation.

Table 2.5. Simple correlation coefficients, r, between Palmer's Drought Severity Index and age-normalized, standardized growth indices, for baldcypress and black willow on connected, partially connected, and disconnected sites

	baldcypress			black willow		
PDSI	C[1]	P[2]	D[3]	C	P	D
Jan1-	0.11	0.12	**0.16 d**	-0.04	-0.12	-0.09
Feb1-	0.09	0.08	0.14	0.06	0.00	-0.06
Mar1-	0.14	0.09	0.15	0.06	0.01	-0.01
Apr1-	0.09	0.02	0.13	-0.05	-0.03	-0.07
May1-	0.08	0.00	0.09	-0.09	-0.08	-0.15
Jun1-	0.15	0.03	0.11	0.11	0.09	-0.04
Jul1-	**0.17 d**	0.07	0.14	0.16	0.11	0.01
Aug1-	**0.20 c**	0.13	**0.19 c**	0.17	0.11	0.07
Sep1-	**0.17 d**	0.10	**0.17 d**	0.18	0.19	0.14
Oct1-	0.10	0.01	0.10	0.18	0.12	0.01
Nov1-	0.05	-0.02	0.03	0.09	0.12	0.07
Dec1-	0.05	0.00	0.06	0.04	0.09	0.09
Jan	0.07	0.03	0.08	-0.03	-0.04	-0.03
Feb	-0.01	0.00	0.05	-0.05	0.00	0.05
Mar	0.10	0.10	0.13	-0.09	-0.04	0.00
Apr	**0.18 d**	**0.15 d**	**0.19 c**	-0.10	-0.10	-0.04
May	**0.19 c**	**0.20 c**	**0.23 c**	-0.04	-0.05	0.03
Jun	0.12	**0.15 d**	0.13	0.02	0.00	-0.01
Jul	0.03	0.07	0.05	0.02	0.06	0.03
Aug	0.03	0.03	0.07	0.10	0.10	0.03
Sep	0.05	0.06	0.06	0.10	0.11	0.01
Oct	0.03	0.11	0.10	0.09	0.11	0.00

[1] C, Connected
[2] P, Partially Connected
[3] D, Disconnected
Note: letters represent p-value significance; a, < 0.0001; b, < 0.001; c, < 0.05; d, < 0.10

2.5 DISCUSSION

2.5.1 Hydrologic Influence

Consistent with previous studies of baldcypress, water depth had the greatest influence on radial increment compared to climatic drivers, and the relationship was similar for black willow. Highest growth for baldcypress has been previously shown to be associated with water levels, commonly linked with flood events (Conner and Day, 1976; Mitsch and Ewel 1979). Various studies in riverine-floodplain systems have found that spring and summer water levels often have highest influence on growth. Another example is the findings of Rypel et al. (2009), who found the strongest relationship between baldcypress radial increment and high spring water flow in a seasonally flooded floodplain. Bohora (2012) also found highest growth correlations for baldcypress with water level in the late spring and early summer in the Atchafalaya Basin.

This study also found that black willow growth was positively and significantly correlated with flooding depth, in contrast to previous findings from laboratory studies of young trees (Pezeshki et al., 1998; Li. et al., 2005). It is unclear whether these relationship differences to water levels may be attributed to differences in maturity, but there are physiological differences in morphology (i.e. water roots

and knees) by trees age, that can mediate effects of flooding. Similar differences between behavior of seedlings and mature trees have been observed previously (Allen and Keim 2017).

2.5.2 Air Temperature

Tree radial increment in southern Louisiana floodplains has been found to have lower correlations to climate variables as a result of greater influence by flood (Reams and van Deusen, 1998; Keim and Amos, 2012). Where and when flooding is less important, however, radial increment may become more dependent on climatic conditions that affect soil moisture and thus radial increment growth (Boggess, 1956; Fritts, 1956; Phipps and Gilbert, 1961; Robertson, 1992). Depending on season, there were both positive and negative growth responses to higher temperature, mainly for baldcypress, which may be related to root and stem processes. Soil temperature may improve root growth during late fall through early spring of baldcypress, because it is an important influence to root growth in many species (Teskey and Hinckley 1981). Additionally, higher temperatures may stimulate earlier bud release and growth (Arora et al. 2003): cambial activity, which creates incremental growth, is stimulated by hormones from developing buds, and that growth can begin before full development of leaves (Meyer and Anderson, 1952; Eggler, 1955).

In contrast to baldcypress there was little relationship between temperature and growth between fall1- and spring for black willow. The differences between baldcypress and black willow responses to temperature could be linked to their differing phenological processes involving mechanisms that regulate bud release. Caffara and Donnelly (2011) observed growth response of two long-lived, late-successional species and two short-lived, pioneer species (one of which was a willow, (*Salix x smithiana*)). Their study found that the short-lived, pioneer species (particularly willow) were less affected by high temperatures and were often stimulated to begin growing earlier in the growing season, in contrast to the long-lived European beech (*Fagus sylvatica)* and littleleaf lindon (*Tilia cordata)* which are more temperature regulated. These conclusions may be applicable in explaining the growth responses of the long-lived species (baldcypress) and short-lived species (black willow) in this study.

For both species, there were negative correlations between radial increment and temperature between June and September, potentially in response to vapor pressure deficits. In the Atchafalaya Basin at the study sites, peak flooding generally occurs in April (though with great interannual variability), followed by an overall decline to lowest water levels in September. The most significant negative correlation between radial increment and temperature was for September, which is consistent with a period of more sensitivity to the dry conditions. Both species depend on high water tables, accessed by shallow root systems to avoid anaerobic soils, so the combination of surface water recession and higher temperatures may have a larger effect on floodplain species than upland species (Mahoney and Rood, 1998; Pezeshki, 2001; Allen et al., 2016).

2.5.3 Precipitation

Radial increment response to precipitation for baldcypress and black willow, similar to other studies (Bohora, 2012; Keim and Amos, 2012), was not a strong determinant of growth in the Atchafalaya Basin. Although not there were no strong correlations, there were some weakly positive relationships between baldcypress radial increment and precipitation that are consistent with the relationships to temperature in the late summer: rainy conditions subsidize soil moisture and also reduce evapotranspiration (which results from a combination of solar radiation, air temperature, and vapor pressure deficit; Abtew, 1996). Radial increment of baldcypress was positively correlated with precipitation during the spring, March through May, even though the peak flood pulse during this time means that water availability is high. Increased precipitation during these months may stimulate radial growth by reducing water vapor deficit or oxygenating flood waters. There was little relationship between radial increment and precipitation for black willow.

2.5.4 Palmer's Drought Severity Index

Palmer's Drought Severity Index (PDSI) was weakly related to baldcypress and black willow chronologies, although there were some significant relationships for baldcypress. All relationships were positive (wetter correlate with higher growth), which is consistent with the results of the relationships with

precipitation and temperature. Day et al. (2012) found that spring drought, specifically during the month of May had negative effects on baldcypress growth, and Bohora (2012) and Keim and Amos (2012) also found a significant positive relationship between radial increment response and PDSI for the spring of the year of ring formation. One reason for apparently weaker relationships between growth and PDSI for this study and others may originate in the fact that PDSI is not strictly applicable in floodplains it is a model of upland soil moisture but floodplains are dominated by riverine water and groundwater (Reams and Van Deusen, 1998; Sims et al., 2002). Conner et al. (2014) suggested that PDSI was also not a good measure in floodplains, particularly in Louisiana, because of frequent hurricane disturbances and flood disturbance that could alter growth conditions not accounted for by PDSI.

2.5.5 Stand history

Overall, growth patterns among trees and stands varied through time and among trees in response to timber harvesting, flooding, and drought. Growth suppression of baldcypress from 1900-1926 was released by a timber harvest in 1927 (pers. comm. from Joseph Baustian) and trees from all sites showed a growth release. There were no other comparable periods of suppression, although growth rates were low at all stands during droughts of the late 1930s, 1978, 1980, 1987-1988, and 2000 (NOAA, 2017; NASA 2017). In contrast, radial increment strongly increased during flood events in 1927, 1945, 1957, 1979, and 2011 (Zaninetti et al., 2012; Roberts et al., 1980, Khan et al., 2013). This stand history is consistent with correlations between environmental factors and chronologies.

A concentrated period of establishment of black willow in the 1950s-1960s coincides with dates of the onset of rapid geomorphic change in the Atchafalaya Basin, and with the dates of channel manipulations in Bayou Sorrel that were the most likely apparent cause of disturbance at the study sites. The open stand conditions may persist both because of flooding that inhibits regeneration, but also rapid sediment deposition on these sites (Hupp et al., 2008).

Species comparison

In general, baldcypress chronologies were more correlated to environmental drivers than were black willow chronologies. The advanced age of the willow, combined with frequent wind disturbance in the area (Doyle et al. 1995) meant that crowns were irregular and all sampled trees showed signs of disturbance. In contrast, none of the baldcypress trees were close to senescence, and crowns were generally intact, vigorous, and undamaged. Thus, correlations of ring growth in black willow to environmental conditions was likely degraded by other, stronger, non-environmental drivers of inter-tree variability in growth rates. In only one case—temperature—were black willow chronologies more correlated with an environmental variable than were baldcypress chronologies, which suggests temperature dependence is distinctly greater in black willow. The weaker relationships to other variables may simply indicate poor correlation because of tree condition rather than indicating ecophysiological differences between species.

2.6 CONCLUSIONS

Both baldcypress and black willow showed similar radial increment responses to environmental conditions, although correlations were stronger overall for baldcypress. Of all flooding and climate variables, flooding depth had the strongest, and positive, effect on radial increment of both species across all sites. Widest rings occurred correlation with high pulses in the late spring and early summer. Of the climatic variables, temperature had the strongest effect on both species. Precipitation and PDSI were both weak predictors of growth.

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CHAPTER 3: USING GROWTH EFFICIENCY MODIFIED BY INDIVIDUAL TREE COMPETITION MEASURES TO ASSESS SITE QUALITY IN DISTURBED, BROWNWATER AND BLACK WATER FORESTED WETLANDS

3.1 INTRODUCTION

Forest growth depends on the combined, complex ecological influences of a site; commonly referred to as the site quality. The flood regime is widely considered to be a strong determinant of site quality in wetlands (Junk et al., 1989), but many details as to why it is a strong determinant of site quality remains poorly understood. Flood influence in wetlands is variable and can be affected by the variability in hydrological connectivity between flowing waters and the floodplain. Connectivity, defined as the transfer of energy, materials, and organisms between areas by water (Pringle, 2001), is often categorized into two general groups: surface and subsurface connectivity. In riverine wetland systems, hydrologic connectivity is often defined as the potential of surface water flow to occur between a river and the floodplain (Mitsch et. al., 1991; Keeland et al., 1997; Trigg et. al, 2013), although subsurface connectivity can also be important for water and solute exchange (Newman and Keim 2013).

Site quality is used to quantify potential productivity (Carmean, 1975). In even-aged forests, particularly plantations, site quality is commonly quantified as site index, which is easily measured using tree height and age (Chapman 1921; McLeod and Running, 1987), because uniform structure of the forest minimizes tree-specific factors such as disturbance or competition. However, in uneven-aged forests, heterogeneity results in competition influence throughout the lifespan of individual trees; this lack of a free-to-grow environment creates variations in the relationship between height and age.

An alternative to measure site quality in uneven-aged forests is to estimate growth efficiency. Growth efficiency is defined as the amount of stemwood volume produced per unit of crown leaf area (Waring 1981; Waring, 1983). Greater growth efficiency occurs with higher site quality as a response to better and more available environmental resources (Binkley et al., 2004). As an example, a general characteristic that influences site quality is the soil characteristics such as texture, which affects nutrient and soil moisture availability for plant uptake and growth (Diebold, 1935; Burger and Kelting, 1999). In wetlands, the nutrient and water dependency of plants is often sustained through inputs from flooding events (Venterink et al., 2003).

Although wetland species such as baldcypress (*Taxodium distichum*) and black willow (*Salix nigra*) have morphological and physiological adaptations to flooding, no common responses to the effects of flooding on tree growth have been determined (Anderson and Mitsch, 2008). Conner and Day (1976) and Mitsch et al. (1991) found that growth (biomass productivity) in Louisiana bottomland hardwood wetlands characterized by seasonally flooded, flowing water was greater than in permanently flooded wetlands. In contrast, in wetlands in Illinois, Brown and Peterson (1983) found tree growth was greater in a wetland with stagnant water and longer duration flooding. Although both sites had comparable nutrient availability, the depth of floodwaters in the seasonally flooded wetland was deeper, potentially affecting dissolved oxygen. In South Carolina, Burke et al. (1999) observed lower growth in seasonally flooded wetlands but attributed this to varying flood effects on soil chemistry and ultimately nutrient availability. Although there have been contradictory results of wetland flood influence on growth, different results may have been due to differences in the site qualities created by flooding.

Growth efficiency however, is not only dependent on site quality (influenced by flooding) but also competition. Competition is often considered the most important in terms of growth (Waring, 1987; Dobbertin, 2005) and is often measured through its negative effect on tree crown leaf area. Therefore, by measuring competition effects on growth, and having measures of growth efficiency, measures of site quality than then be obtained.

Numerous measures have been used to quantify effects of competition on growth. A group of competition measures known as distance-dependent measures is commonly used to assess the competitive effect of local neighbors on trees (Tome and Burkhart, 1989). Examples of distance-dependent measures, including local basal area, trees per hectare, and stand density index, have been used as simple linear indices or as the basis for modified indices to predict growth (Daniels et al., 1986). Previous work to compare competition indices (Curtis 1970; Johnson 1973; Lorimer 1983; Holmes and Reed 1991) has found variability in their performance (Daniels et al., 1976) as predictability of competitive

effect on individual tree growth and stand productivity (Daniels et al., 1986), therefore, it is still unclear which local distance-dependent measure best represents influence on growth.

Another common group of competition measures used to infer local stand competition is based on competitive effects on crown dimensions of subject trees. Crown shape and size are influenced by the interaction of local competition and light resource availability (Zimmerman and Brown; 1971), so tree height, crown length, and live-crown ratio are often used to evaluate competition results and, inversely, the dominance of a tree. Previous studies have found increased competition, regardless of dominance class (e.g., dominant, codominant), results in reduction of these crown dimensions, so they can provide insight to competitive effects (Holdaway, 1986). An example of one measure is the number of neighboring trees that influence crown of subject trees through shading. The effects of neighboring trees is dependent on distance (crowding) and shade influence (Canham et al., 2004). Another example of such a tool was created by Meadows et al. (2001) for bottomland hardwoods in the southern US, which has proven to be a useful measure of the results of competitive effects on tree growth (Dimov et al., 2008). The Meadows method was specifically created for uneven-aged stands, and uses measures of (1) direct sunlight from above, (2) direct sunlight from sides, (3) crown balance, and (4) crown size to quantify crown dimensions and infer tree dominance. By understanding competition influence on crown leaf area and growth, the specific effect of site quality on growth can then be separately evaluated.

Although many studies have evaluated competition measures and growth efficiency (Waring, 1983; O'Hara et. al., 1999; Ryan, 1986), none have done so with relation to site quality, particularly by using the combined measures to definitively predict site quality in seasonally flooded, wetland systems, dominated by uneven-aged floodplain forests. Therefore, the overall goal is to develop tools to evaluate site quality in an environment that is highly disturbed by flooding and competition, where site quality is difficult to measure. To achieve this goal, the specific objectives for this study are (1) to determine which measures are good predictors of growth efficiency, 2) to determine whether various measures give similar assessments of competition faced by individual trees, and (3) determine whether variation in competition or site quality in three contrasting hydrologic regimes is a larger effect on tree growth in two important floodplain species, baldcypress and black willow.

3.2 STUDY SITE

The study sites were located in the Atchafalaya Basin in south-central Louisiana, the largest distributary of the Mississippi River. In response to damage from historically high flood events in the late 1800s and early 1900s, and fear that the Mississippi River would eventually diverge into the ARB, threatening the economy of New Orleans (Ford and Nyman, 2011), the U.S. Army Corps of Engineers constructed levee systems and the Old River Control Structure, in 1963, to divert 30% of the Mississippi and Red river flow into the Atchafalaya. The ARB is thus a modified wetland that is experiencing high rates of sediment accretion within the floodplains (Hupp et al., 2008).

In the Atchafalaya River Basin, the sites for this project were on the Atchafalaya Basin Preserve (ABP) managed by The Nature Conservancy as part of an initiative to restore floodplain ecosystem services that may have become reduced in response to high sediment accretion rates, thus causing reduction in hydrologic connectivity. To understand differences in ecosystem services based on hydrologic connectivity, three sites were selected for this study: seasonally flooded, bottomland hardwood backswamps that receive brownwater (sediment-rich water) through overbank or channelized flooding, or blackwater (sediment poor water) from backwater flooding (Figure 2.2). Specifically, the ABP property is located adjacent to Bayou Sorrel which receives direct water flow from the Atchafalaya River. Water levels in the Atchafalaya River are highly variable resulting in high annual water level variability in Bayou Sorrel. A flood pulse occurs annually, often with highest flows in April (Rutherford et al., 2011). On the southern side of Bayou Sorrel, the connected and partially connected sites receive overbank flooding beginning at 4.57 and 5.48 meter river stages, recorded at the Bayou Sorrel Lock water gauge (USACE water gauge #49630). The disconnected site, on the north side of Bayou Sorrel, receives overbank flooding at 5.48 meters, however, at overbanking stage, the water does not flow readily into the site due to the natural southerly water flow toward the Gulf of Mexico. Although all three sites shared similar soil types (Fausse/Dowling), defined by fine clay accumulation from riverine influence that characteristically causes ponding of water in backswamp areas (NRCS, 2018), differences in drainage paths resulted in greater ponding and slower drainage in the disconnected site.

In this study, 37 dominant baldcypress (*Taxodium distichum*) and 39 black willow (*Salix nigra*) trees were sampled. Although both occur within the backswamp of floodplains of Louisiana, they have different life histories and physical characteristics that increase functional diversity and response within the wetlands. Black willow is a pioneer species that becomes established in newly deposited sediments, often along river banks. Black willow grows quickly and is shade intolerant. Once reaching maturity, black willow can remain a dominant competitor for approximately 20 years before senescence in growth occurs (Krinard, 1985). On the contrary, baldcypress is a slow growing, moderately shade tolerant, long lived species, that is commonly found on floodplains (Hodges 1997).

For the purpose of this study, subject trees were chosen to be in dominant or codominant canopy positions, with minimum visible signs of damage, and far enough away from other sampled trees such that they shared no common competing trees according to the measures used. All sampling plots were located within the interior floodplain forests determined by the change (decrease) in elevation from the natural levee to the interior floodplain forests and chance in species composition. Bottomland hardwood species baldcypress (*Taxodium distichum*), black willow (*Salix nigra*), green ash (*Fraxinus pennsylvania*), water tupelo (*Nyssa aquatica*), planertree (*Planerea aquatica*) and swamp-privet (*Forestiera aquatica*) were common among all sites.

3.3 METHODS

3.3.1 Competition Measures

Multiple measurements were made of each sample tree. Diameter at breast height (black willow) and above buttressing (baldcypress) was measured using a Wheeler pentaprism to the nearest 1 cm. Total height and height to crown base were measured using a TruPulse 200x laser rangefinder to the nearest 1 m. Crown length and live crown ratio (LCR) were calculated from these measurements. A numerical rating system for crown classification developed by Meadows et al. (2001) was used to quantify the crown of each sample tree, using visual estimates of (1) on a scale 1-10, amount of sunlight the crown received from above (MTop), (2) on a scale of 1-10, the amount of sunlight the crown received from the sides, (MSide) (3) on a scale of 1-4, overall crown balance, (MBal) and (4) on a scale of 1-4, crown size (MSize).

To assess crown competition, we also evaluated a new metric: the number of trees occupying an inverted cone defined from the crown base of the sample tree. The number of trees with crowns occupying a 30, 35, 40, 45-degree angle (from vertical) from the base of the crown of each sample trees, were measured (to the nearest meter) for total height and distance from sample tree using the TruPulse 200x rangefinder. These competitive trees are hereafter referred to as cone trees.

To measure local stand density based on tree size and spatial distribution, two variable radius point samplings were done using 10 and 20 basal area factor (BAF; $ft^2/ac^{-1}/tree^{-1}$) angle prisms centered on sample trees. Both prisms were used because each differently measures local competition. Diameters were measured for all trees in the variable-radius plots, which enabled measurements of local basal area (local BA 20 and 10), trees per hectare (local TPH 20 and 10), and Reineke's (1933) stand density index (local SDI 20 and 10).

3.3.2 Growth Efficiency

Growth efficiency (GE) is defined as defined as the amount of stemwood volume produced per unit of crown leaf area (Waring 1981; Waring, 1983). An alternative, but related, measure to growth efficiency is annual growth increment (BAI) per sapwood basal area (SBA) (O'Hara, 1988; Dean et al., 1988; Allen, 2016). To estimate GE, two tree cores per tree were taken using a 5.15 mm increment borer at breast height for black willow or above buttressing for baldcypress. All rings in all cores were measured and cross-dated using techniques described in chapter 2. To calculate BAI, total basal area was first calculated using the summation of tree ring widths (mm) per tree, estimating in cases where the core did not intersect the pith by assuming circular growth dimensions. Basal area was calculated per year and the differences of basal areas between years was annual BAI.

For each core extracted, sapwood width was identified in the field by observing differential light transmission (Vertessy et al, 1995), and measured using calipers to the nearest 1 mm. Sapwood basal area was calculated by the subtraction of heartwood area from total basal area of each core, then

averaged per tree. Growth efficiency over periods of 3, 5, and 7 years was calculated as the ratio of periodic BAI (3, 5, and 7 years) to SBA. Assuming no change in SBA, these time intervals were arbitrarily chosen, and the most relevant basis was inferred to be the time interval at which the most frequent correlations with competition measures were observed subsequently. Longer time intervals were not used to avoid possible effects of hurricanes prior to 2010: Hurricane Gustav caused crown damage in the Atchafalaya Basin in 2008 (Conner et al. 2014).

The relationships between competition measures and growth efficiency were evaluated using linear regression analysis. For analysis, competition and growth variables were grouped into three categories of influence: (1) measures of local stand density, (2) measures of crown characteristics, and (3) measures of growth. Specifically, local stand density measures were BA/ha (20 and 10), TPH (20 and 10), SDI (20 and 10), and cone tree competition (number of trees within inverted 30, 35, 40, 45 40 degree angles of sample tree cone). Measures of crown characteristics included Meadows scores (from Meadows et al., 2001), crown length, and live-crown ratio. Measures of radial increment growth included SBA, BAI, and GE. Significant bivariate correlations between competition measures and GE were selected as candidate members for a generalized, mixed-linear model of tree growth. Multiple mixed-linear models with selected competition measures and sites, were fit to the data, (using the SAS 9.4 statistical program), and models with the lowest Akaike Information Criterion (AIC) values were considered the best given these data.

3.4 RESULTS

3.4.1 Tree dimensions vs growth relationships

There were positive but weak relationships between Meadows crown scores and individual tree growth measures for both species (Table 3.1). The strongest relationship (r=0.3162) was between crown balance (MBal) and sapwood basal area (SBA) for baldcypress. In contrast, the relationship between crown size (MSize) and sapwood basal area was the strongest for black willow. Relationships between Meadows crown scores and basal area increments (BAI) were positive for both species, although there were more significant relationships for black willow. Specifically, for black willow, there were significant relationships between all Meadows crown scores and individual tree growth measures, with the exception of crown side measure (MSide). In contrast, for baldcypress, the only significant relationships were between Meadows crown scores and basal area increment averaged 5 years (BAI5) and basal area increment averaged 7 years (BAI7), and those relationships were weaker than all relationships for black willow.

Table 3.1. The coefficient of correlation (r) from ordinary least square regressions between crown dimension measures (Meadows crown score) and individual growth measures for baldcypress and black willow.

Size and Growth Measure	Crown Dimension Measure				
	MTop[a]	MSide	MBal	MSize	MTotal
Baldcypress					
DBH[b]	-0.0151	0.0239	-0.0278	0.0413	0.0239
SBA[c]	0.0320	-0.0003	0.3162*	-0.0011	-0.0255
BAI3[d]	-0.0252	-0.0269	0.0790	0.0321	0.0070
BAI5[d]	-0.0161	-0.0270	0.0822*	0.0411	-0.0149
BAI7[d]	-0.0175	-0.0270	0.0840*	0.0389	-0.0146
GE3[e]	-0.0191	0.0001	-0.0251	-0.0016	0.0006
GE5[e]	-0.0204	-0.0147	-0.0127	-0.0022	-0.0180
GE7[e]	-0.0180	-0.0108	-0.0043	-0.0027	-0.0170
Black willow					
DBH	-0.0270	0.0242	-0.0216	-0.0241	-0.0171
SBA	0.0388	-0.0278	0.0451	0.1694*	0.0840{*}
BAI3	0.1664{*}	-0.0193	0.1013*	0.0951*	0.0885*
BAI5	0.0954*	-0.0222	0.1417*	0.1258*	0.1087*
(Table cont'd)					

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Size and Growth	Crown Dimension Measure				
Measure	MTop[a]	MSide	MBal	MSize	MTotal
BAI7	0.0975*	-0.0130	0.0918*	0.1308*	0.1150*
GE3	0.0382	-0.0096	0.0080	-0.0277	0.0068
GE5	0.0973{*}	-0.0169	0.0408	-0.0266	0.0094
GE7	0.1231*	0.0232	0.0186	-0.0273	0.0515

[a] MTop, Meadows top score; MSide, Meadows side score; MBal, Meadows balance score, MSize, Meadows size score; MTotal, Meadows total score
[b] DBH, Diameter at breast height
[c] SBA, Sapwood basal area
[d] BAI3-7, Basal area increment averaged 3-7 years
[e] GE3-7, Growth efficiency averaged 3-7years
* $p < 0.05$
{*} $P < 0.05$ after log transformation

There were positive correlations between crown dimensions and tree growth measures for both species (Table 3.2). Height was related to diameter at breast height (DBH) for both species as expected. Between crown dimension measures and other individual tree measures, crown length and SBA were weakly positively correlated to both species, with the stronger relationship resulting for black willow. Additionally, through log transformations, height and basal area over 5 and 7 years were related to height for black willow, with BAI7 resulting in the stronger relationship. No crown dimension measures were significant predictors of growth efficiency.

Table 3.2. The coefficient of correlation (r) values of relationships between crown dimension measures and size and growth measures for baldcypress and black willow.

Size and Growth	Crown Dimension Measure		
Measure	Ht[a]	CLth[b]	LCR[c]
Baldcypress			
DBH[d]	0.1454*	-0.0064	-0.0275
SBA[e]	0.0180	0.0803*	0.0600
BAI3[f]	0.0359	0.0404	0.0077
BAI5[f]	0.0203	0.0610	0.0309
BAI7[f]	0.0261	0.6050	0.0295
GE3[g]	-0.0103	-0.0063	-0.0177
GE5[g]	-0.0244	-0.0072	-0.0127
GE7[g]	-0.0233	-0.0115	-0.0169
Black willow			
DBH	0.1549*	0.00278	-0.0232
SBA	0.1468	0.0978*	-0.0240
BAI3	0.0150	0.0581	0.0035
BAI5	0.0999{*}	0.0583	-0.0091
BAI7	0.1443{*}	0.0484	-0.0229
GE3	-0.0251	-0.0260	-0.0145
GE5	-0.0243	-0.0276	-0.0200
GE7	-0.0266	-0.0273	-0.0272

[a] Ht, Height
[b] CLth, Crown length
[c] LCR, Live crown ratio
[d] DBH, Diamter at breast height
[e] SBA, Sapwood basal area
[f] BAI3-7, Basal area increment averaged 3-7 years
[g] GE3-7, Growth efficiency averaged 3-7 years
* $p < 0.05$

3.4.2 Competition measures vs tree dimensions

There were significant, negative correlations between distance-dependent measures (local basal area, trees per hectare, and stand density index) and crown dimension measures (crown length, live crown ratio, tree height), although they varied by species (Table 3.3). A strong relationship existed between SDI10 for both crown length and live crown ratio measures, whereas there were no significant relationships with the SDI20 measure. Additionally, although not strong correlations, there were negative relationships between logBA20 and logTPH20 to LCR. In contrast to baldcypress, there was one weak positive relationship between BA10 and height for black willow.

Table 3.3. The coefficient of correlation (r) values of relationships between local distance dependent measures and crown dimension measures for both baldcypress and black willow.

Crown Dimension Measure	Competition Measure					
	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]	SDI10[f]
Baldcypress						
Ht[g]	0.0190	0.0190	-0.0277	-0.0262	-0.0285	-0.0209
CLth[h]	0.1035*	-0.0031	0.0038	0.0709	0.1110*	0.1951*
LCR[i]	0.0875{*}	0.0877{*}	0.0043	0.1135*	0.1267*	0.2046
Black willow						
Ht	0.0000	0.0000	0.0094	0.0865*	-0.0247	0.0226
CLth	-0.0281	-0.0185	-0.0261	-0.0177	-0.0283	-0.0281
LCR	-0.0192	-0.0020	0.0210	-0.0215	-0.0283	-0.0147

[a] BA20, Basal area using Basal area factor (BAF) prism 20
[b] TPH20, Trees per hectare BAF 20
[c] SDI20, Stand density index BAF 20
[d] BA10, Basal area BAF 10
[e] TPH10, Trees per hectare BAF 10
[f] SDI10, Stand density index BAF 10
[g] Ht, Height
[h] CLth, Crown length
[i] LCR, Live crown ratio
* p < 0.05
{*} P< 0.05 after log transformation

There were negative relationships between distance-dependent measures and Meadows crown scores only for black willow (Table 3.4). Of four significant relationships, only the correlation between Meadows crown balance (MBal) and trees per hectare of 10 BAF prism (TPH10) was naturally linear, and the other relationships resulted from log transformations. The strongest relationship (r = 0.1491) resulted between meadows top score (MTop) and logBA10 and the weakest relationship (r = 0.1281) was observed between MTotal and logBA10. Because of high variance and low range of data for Meadows scores (all codominant and dominant trees), these relationships are not particularly meaningful.

Table 3.4. The coefficient of correlation (r) values of relationships between local distance dependent measures and crown dimension measures (Meadows crown score) for baldcypress and black willow

Crown Dimension Measure	Competition Measure					
	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]	SDI10[f]
Baldcypress						
MTop[g]	-0.0182	-0.0299	-0.0234	-0.0250	-0.0202	-0.0080
MSide	-0.0248	-0.0059	0.0154	-0.0236	-0.0131	-0.0312
MBal	-0.0218	-0.0285	0.0718	-0.0298	-0.0299	-0.0308
MSize	-0.0258	-0.0286	-0.0038	0.0288	-0.0248	-0.0198

(Table cont'd)

Crown Dimension	Competition Measure					
Measure	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]	SDI10[f]
MTotal	-0.0271	-0.0101	-0.0298	-0.0174	-0.0273	-0.0283
Black willow						
MTop	-0.0235	-0.0159	-0.0246	0.1491{*}	-0.0054	0.0314
MSide	0.0215	-0.0181	0.0414	0.0307	-0.0167	-0.0006
MBal	0.1355{*}	-0.0159	-0.0285	-0.0077	0.1217*	0.0669
MSize	0.0185	-0.0181	-0.0226	-0.0276	-0.0275	-0.0285
MTotal	0.1281{*}	-0.0285	0.0048	-0.0044	-0.0246	0.0058

[a] BA20, Basal area using Basal area factor (BAF) prism 20
[b] TPH20, Trees per hectare BAF 20
[c] SDI20, Stand density index BAF 20
[d] BA10, Basal area BAF 10
[e] TPH10, Trees per hectare BAF 10
[f] SDI10, Stand density index BAF 10
[g] Mtop, Meadows top score; MSide, Meadows side score; MBal, Meadows balance score, MSize, Meadows size score; MTotal, Meadows total score
* $p < 0.05$
{*} $P < 0.05$ after log transformation

There was one negative significant relationship between Meadows side measure (MSide) and number of cone trees in 30-degree angle of sample tree (CT30), for black willow (Table 3.5). Although predictively negative, there were no significant relationships for sample trees that had less than 4 cone trees.

Table 3.5. The coefficient of correlation (r) values of relationships between local distance dependent competition (number of cone trees) and crown dimension measures (Meadows crown scores) for baldcypress and black willow

Crown Dimension	Competition Measure			
Measure	CT30[a]	CT35	CT40	CT45
Baldcypress				
MTop[b]	-0.0286	-0.0286	-0.0285	-0.0283
MSide	-0.0121	-0.0283	-0.0162	0.0565
MBal	-0.0249	0.0050	0.0274	0.0166
MSize	-0.0177	-0.0289	-0.0237	-0.0268
MTotal	-0.0173	-0.0224	-0.0286	-0.0042
Black willow				
MTop	0.0228	-0.0207	-0.0269	-0.0238
MSide	0.0830*	0.0403	-0.0051	0.0042
MBal	-0.0266	-0.0247	-0.0269	-0.0258
MSize	0.0026	0.0108	-0.0153	-0.0267
MTotal	0.0106	-0.0179	-0.0231	-0.0145

[a] CT30-45, Cone trees within 30-45 degree angle of base of subject tree crown
[b] MTop, Meadows top score; MSide, Meadows side score; MBal, Meadows balance score, MSize, Meadows size score; MTotal, Meadows total score.
* $p < 0.05$

No significant relationships between crown dimensions (height, crown length, live crown ratio) and cone tree measures were evident (Table 3.6).

Table 3.6. The coefficient of correlation (r) values of relationships between local distance dependent competition (number of cone trees) and crown dimensions for baldcypress and black willow

Crown Dimension	Competition Measure			
Measure	CT30[a]	CT35	CT40	CT45
Baldcypress				
Ht[b]	-0.0275	-0.0275	-0.0263	-0.0137
CLth[c]	0.0129	-0.0271	0.0027	0.0852
LCR[d]	0.0220	-0.0285	-0.0078	0.0586
Black willow				
Ht	-0.0212	-0.0266	-0.0269	-0.0265
CLth	0.0167	0.0200	0.0141	-0.0055
LCR	-0.0052	0.0144	0.0163	-0.0017

[a] CT, Cone trees within 30-45 degree angle of base of sample tree crown
[b] Ht, Height
[c] CLth, Crown length
[d] LCR, Live crown ratio
* $p < 0.05$

3.4.3 Relationships among comparable variables

There were many significant relationships between similar measures; such relationships among similar measures verified the reliability and accuracy of using the variables to measure relationships to growth.

There was only one positive relationship between Meadows crown scores (MTop) and tree dimensions (height) (Table 3.7), but the data range for MTop was mostly between 9 or 10, with only 3 trees having MTop score of 9; therefore the relationship is not particularly meaningful.

Table 3.7. The coefficient of correlation (r) values between relationships of crown dimension measures (Meadows crown score) and other crown dimensions for baldcypress and black willow

Crown Dimension	Crown Dimension Measure				
Measure	MTop[a]	MSide	MBal	MSize	MTotal
Baldcypress					
Ht[b]	-0.0246	-0.0250	-0.0007	-0.0143	-0.0079
CLth[c]	0.0255	-0.0136	-0.0274	-0.0072	-0.0283
LCR[d]	0.0430	-0.0152	-0.0165	0.0136	-0.0275
Black willow					
Ht	0.0994*	-0.0183	0.0534	0.0604	0.0088
CLth	0.0318	-0.0178	0.0828	-0.0174	-0.0109
LCR	-0.0270	-0.0215	-0.0099	-0.0127	-0.0257

[a] MTop, Meadows top score; MSide, Meadows side score; MBal, Meadows balance score, MSize, Meadows size score; MTotal, Meadows total score
[b] Ht, Height
[c] CLth, Crown length
[d] LCR, Live crown ratio
* $p < 0.05$

There were positive correlations between cone tree and local distance-dependent measures only for black willow (Table 3.8). There were significant relationships between basal area (20) and all cone tree measures (CT), the strongest relationship with CT45. Relationship significance resulted from sample

points that had greater than 6 trees (for CT30 and CT35) or greater than 10 trees (for CT40 and CT45). Significant correlations also resulted for stand density index (20) and basal area (10) with CT45.

Table 3.8. The coefficient of correlation (r) values of relationships between local distance-dependent measures and number of cone trees for baldcypress and black willow

Competition Measure	Competition Measure					
	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]	SDI10[f]
Baldcypress						
CT30[g]	-0.0310	-0.0227	-0.0312	-0.0273	-0.0230	-0.0244
CT35	-0.0293	-0.0301	-0.0198	-0.0277	-0.0309	-0.0307
CT40	-0.0297	-0.0303	-0.0218	-0.0291	-0.0252	-0.0304
CT45	-0.0260	-0.0177	-0.0177	-0.0227	-0.0134	-0.0258
Black willow						
CT30	0.1382*	-0.0216	0.0584	0.0460	-0.0286	0.0440
CT35	0.0810*	-0.0285	0.0498	0.0395	-0.0253	0.0172
CT40	0.1206*	-0.0264	0.0692	0.0542	-0.0285	0.0384
CT45	0.1971*	-0.0220	0.1200*	0.1123*	-0.0276	0.0787

[a] BA20, Basal area using Basal area factor (BAF) prism 20
[b] TPH20, Trees per hectare BAF 20
[c] SDI20, Stand density index BAF 20
[d] BA10, Basal area BAF 10
[e] TPH10, Trees per hectare BAF 10
[f] SDI10, Stand density index BAF 10
[g] CT, Cone trees within 30-45 degree angle of base of sample tree crown
* $p < 0.05$

There were positive correlations between sapwood basal area (SBA) and all basal area increments (BAI) for both species, but there were no significant correlations between SBA and GE measures (Table 3.9). The correlations between SBA and BAI measures were greater for black willow than for baldcypress, with an increasing level of significance for baldcypress with increasing length of BAI interval. As expected, correlations among all BAI measures were significant to GEs for both species with baldcypress attaining the highest correlations ($p<.0001$). The correlations for black willow, although significance for logGE3 and GE5 to BAI7, were weak (r =.0950 and .0984 respectively).

There were also positive relationships between diameter at breast height (DBH) and internal growth measures, specifically SBA for both species, and GE3 and GE5 for black willow. The strongest relationship with DBH was for SBA of black willow (r=0.2713), but the relationship was much weaker for baldcypress (r=0.1095). There were weak relationships between DBH and growth efficiency measures for black willow. Additionally, there were positive relationships among all individual tree growth measures to all basal area increment measures, with strongest relationships all for baldcypress.

Table 3.9. The coefficient of correlation (r) values of relationships between size and growth measures vs size and growth measures for baldcypress and black willow.

Size and Growth Measure	Size and Growth Measure				
	DBH[a]	SBA[b]	BAI3[c]	BAI5[c]	BAI7[c]
Baldcypress					
SBA	0.1095*				
BAI3	-0.0229	0.1921*			
BAI5	-0.0166	0.2627*	0.9274*		
BAI7	-0.0191	0.3105*	0.8883*	0.9730*	
GE3[d]	-0.0193	-0.0111	0.6112*	0.4907*	0.4112*
GE5[d]	-0.0197	0.0037	0.4963*	0.4855*	0.4072*
GE7[d]	-0.0110	0.0052	0.4753*	0.4682*	0.4299*
(Table cont'd)					

Size and Growth	Size and Growth Measure				
Measure	DBH[a]	SBA[b]	BAI3[c]	BAI5[c]	BAI7[c]
Black willow					
SBA	0.2713*				
BAI3	0.0145	0.4645*			
BAI5	0.0192	0.5736*	0.9088*		
BAI7	0.0744	0.0725*	0.7146*	0.8929*	
GE3	0.0877{*}	-0.0146	0.3373*	0.2128*	0.0950{*}
GE5	0.1545*	0.0064	0.1952*	0.1791*	0.0984{*}
GE7	0.0777	-0.0267	0.2117*	0.2526*	0.2207*

[a] DBH, Diameter at breast height
[b] SBA, Sapwood basal area
[c] BAI3-7, Basal area increment averaged 3-7 years
[d] GE3-7, Growth efficiency averaged 3-7 years
* $p < 0.05$
{*} $p < 0.05$ after log transformation

There were strong correlations between crown dimensions and crown dimension measures live crown ratio (LCR) and crown length (CLth) for both species, but no significant correlations with height (Table 3.10).

Table 3.10. The coefficient of correlation (r) values of relationships between crown dimensions and crown dimensions for baldcypress and black willow.

Crown Dimension	Crown Dimension Measure	
Measure	Ht[a]	CLth[b]
Baldcypress		
CLth	0.1609	
LCR[c]	-0.0214	0.8662*
Black willow		
CLth	0.2126	
LCR	0.0100	0.5667*

[a] Ht, Height
[b] CLth, Crown length
[c] LCR, Live crown ratio
* $p < 0.05$

As expected for both species, there were strong relationships between local basal area (BA), trees per hectare (TPH), and Reineke's stand density index (SDI), for both BAF prism points (BAF 10 and 20); however, there were some differences by species (Table 3.11). When evaluated as singular measures, not separated by species, all comparative relationships of local distance-dependent measures were significant.

Table 3.11. The coefficient of correlation (r) values of relationships between local distance-dependent measures and local distance-dependent measures for baldcypress and black willow.

Competition	Competition Measure				
Measure	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]
Baldcypress					
TPH20	0.5657*				
SDI20	0.2731*	0.1104*			
BA10	0.3968*	-0.0229	0.5579*		
(Table cont'd)					

Competition	Competition Measure				
Measure	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]
TPH10	0.1355*	0.3467*	0.0368	0.1202{*}	
SDI10[f]	0.6196*	0.3600*	0.2039*	0.3630*	0.6769*
Black willow					
TPH20	0.2255*				
SDI20	0.5076*	0.1752*			
BA10	0.5031*	0.1404*	0.5675*		
TPH10	0.0575	0.3012*	0.0901*	0.2422*	
SDI20	0.5427*	0.2679*	0.4266*	0.8444*	0.4844*

[a] BA20, Basal area using Basal area factor (BAF) prism 20
[b] TPH20, Trees per hectare BAF 20
[c] SDI20, Stand density index BAF 20
[d] BA10, Basal area BAF 10
[e] TPH10, Trees per hectare BAF 10
[f] SDI10, Stand density index BAF 10
* $p < 0.05$
{*} $p < 0.05$ after log transformation

3.4.4 Competition measures vs. growth measures

Competition influence on stem growth was most correlated with stand density index calculated from trees included in BAF20 prism points (SDI20) (Table 3.12). For only baldcypress, SDI20 was significantly negatively correlated with all stem growth measures. The strongest correlation was between SDI20 and growth efficiency averaged over 7 years (GE7). Significance of relationships increased with increasing length of time over which GE was based (i.e., correlations with GE7 were generally highest). Likewise, there was similar increase in relationship strength for basal area increments as average increased from 3 to 7 years. For black willow, there were no statistically significant relationships between local stand density and individual tree growth measures, although the insignificant relationships were negative as for baldcypress.

Table 3.12. The coefficient of correlation (r) values between local density-dependent measures and individual size and growth measures of baldcypress and black willow.

Size and Growth	Competition Measure					
Measure	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]	SDI10[f]
Baldcypress						
DBH[g]	-0.0253	-0.0312	0.0215	0.0141	-0.0165	-0.0181
SBA[h]	-0.0295	-0.0188	-0.0288	-0.0022	-0.0169	-0.0077
BAI3[i]	0.0150	-0.0141	0.1105*	0.0078	-0.0084	-0.0114
BAI5[i]	0.0111	-0.0051	0.1306*	0.0341	0.0109	0.0045
BAI7[i]	0.0244	0.0053	0.1519*	0.0318	0.0194	0.0059
GE3[j]	-0.0001	-0.0310	0.1419*	-0.0119	-0.0279	-0.0294
GE5[j]	-0.0121	-0.0312	0.1629*	0.0011	-0.0254	-0.0283
GE7[j]	0.0050	-0.0294	0.2208*	0.0038	-0.0212	-0.0270
Black willow						
DBH	-0.0112	-0.0222	-0.0176	0.0012	-0.0286	-0.0197
SBA	-0.0272	-0.0188	-0.0250	0.0369	-0.0245	0.0151
BAI3	0.0186	-0.0050	0.0292	-0.0292	-0.0230	-0.0231
BAI5	0.0058	-0.0138	0.0034	-0.0212	-0.0294	-0.0289
BAI7	-0.0182	-0.0282	-0.0125	-0.0009	-0.0194	-0.0116

(Table cont'd)

Size and Growth	Competition Measure					
Measure	BA20[a]	TPH20[b]	SDI20[c]	BA10[d]	TPH10[e]	SDI10[f]
GE3	-0.0186	-0.0258	0.0083	0.0016	-0.0052	0.0146
GE5	-0.0233	-0.0294	-0.0202	-0.0216	-0.0257	-0.0152
GE7	-0.0294	-0.0120	-0.0222	-0.0293	-0.0242	-0.0294

[a] BA20, Basal area using basal area factor prism (BAF) 20;
[b] TPH20, Trees per hectare BAF 20;
[c] SDI20, Stand density index BAF 20
[d] BA10, Basal area BAF 10
[e] TPH10, Trees per hectare BAF 10
[f] SDI10, Stand density index BAF 10
[g] DBH, Diameter at breast height
[h] SBA, Sapwood basal area
[i] BAI3-7, Basal area increment averaged 3-7 years
[j] GE3-7, Growth efficiency averaged 3-7 years
* $p < 0.05$

There were significant positive relationships between the number of trees in the 40 and 45 degree cones and BAI for baldcypress (Table 3.13). Relationship strength increased from BAI3 to BAI7 for both cone tree competition measures, with CT45 having the strongest relationship for all cone shapes. Similarly, SBA, the relationship between CT45 and SBA was the strongest of all cone shapes. Although there was no significant relationships for black willow, the slopes of the insignificant relationships were also negative.

There were positive relationships between both CT40 and CT45 and GE3 for black willow (Table 3.13). These relationships were unexpected, because growth efficiency generally decreases with increased crown competition. These relationships apparently resulted from a single outlier. Most trees had fewer than 10 competing cone trees, so that there was a limited range of competition represented in the samples.

Table 3.13. The coefficient of correlation (r) values of relationships between local density dependent measures (number of cone trees) and size and growth measures for baldcypress and black willow.

Size and Growth	Competition Measure			
Measure	CT30[a]	CT35	CT40	CT45
Baldcypress				
DBH[b]	0.0529	0.0610	0.0271	-0.0120
SBA[c]	-0.0271	0.0175	0.1140*	0.1730*
BAI3[d]	0.0014	0.0408	0.1020*	0.1264*
BAI5[d]	-0.0088	0.0342	0.1280*	0.1674*
BAI7[d]	-0.0152	0.0327	0.1330*	0.1690*
GE3[e]	0.0170	-0.0119	-0.0146	-0.0153
GE5[e]	0.0055	-0.0197	-0.0127	-0.0124
GE7[e]	0.0007	-0.0200	-0.0133	-0.0158
Black willow				
DBH	0.0140	0.0149	0.0458	0.0391
SBA	-0.0005	0.0030	0.0178	0.3064
BAI3	-0.0217	-0.0262	-0.0278	-0.0278
BAI5	-0.0171	-0.0226	-0.0242	-0.0275
BAI7	0.0019	-0.0053	-0.0104	-0.0221
GE3	-0.0098	0.0233	0.0813*	0.0837*
GE5	-0.0185	0.0089	0.0479	0.0753
GE7	-0.0267	-0.0244	-0.0002	0.0281

[a] CT30-35, Cone trees within 30-45 degree angle of base of subject tree crown
[b] DBH, Diameter at breast height

3.4.5 Modeling Site and Competition Effects on Growth

There were significant negative correlations between competition measures SDI20, cone tree angles 40 and 45, and growth efficiency (Table 3.12 & 3.13); however, cone tree measurements were excluded from the regression models as the strong correlations was determined to have resulted from outliers. Similarly, there were isolated significant relationships between Meadows crown score, logDBH, and DBH, and growth efficiency, but both Meadows and logDBH measurements were omitted because of inconsistent or illogical correlations. Therefore, only SDI20 and DBH variables were included in mixed models of GE.

Linear mixed modeling and Akaike Information Criterion (AICc) values indicated growth efficiency was most significantly ($p<0.0023$) influenced by stand density index 20 (SDI20) for baldcypress (Table 3.14). In contrast, the competition influence was not as strong on growth efficiency for black willow. Instead, the best model for black willow included SDI20 and the covariate DBH, although neither variable was statistically significant individually. Although there were no significant relationships between GE7 for DBH variable of black willow, DBH in the model GE7=SDI20 + DBH had the lowest p (.0709) and AIC. To evaluate influence of site (based on flood influence), site, competition, and covariate variables were modeled in combination; however, there was weak effect ($p> 0.05$) of site on growth for both species (Table 3.14) indicating again that SDI20 alone was the best predictor of growth efficiency among baldcypress with these analyses.

Table 3.14. Model fits, including Akaike Information Criterion for small samples (AICc) and p-values for linear mixed models using combination of competition, covariate, and site variables.

Model	AICc	p-value X_1	p-value X_2	p-value X_3
Baldcypress GE7				
=SDI20	276.9**	0.0023*	-------	-------
=SDI20 + DBH	279.2	0.0039*	0.5840	-------
=Site	309.1	0.1471	-------	-------
=Site + SDI20	279.6	0.2685	0.0016*	-------
=Site + DBH	310.5	0.1081	0.2645	-------
=Site SDI20 + DBH	281.9	0.2188	0.0122*	0.5541
Black willow GE7				
=SDI20	331.8	0.6180	-------	-------
=SDI20 + DBH	331.0**	0.7239	0.0709	-------
=Site	347.0	0.1665		
=Site + SDI20	333.6	0.1872	0.6351	-------
=Site + DBH	348.5	0.4941	0.2886	-------
=Site + SDI20 + DBH[1]	335.5	0.5850	0.6611	0.0614

[1]Site, combined effect of connected, partially connected, and disconnected sites; SDI20, stand density index BAF 20; DBH, diameter at breast height
** Strongest model for each species
* , $p < 0.05$

With regards to competition effect on growth, there was a negative relationship between SDI20 and GE7 for only baldcypress, (Figure 1). Measurements of SDI20 for baldcypress ranged between 57 and 983 (SI units), over which range growth efficiency decreased by almost half (47%) (Figure 1). There was no significant relationship between SDI20 and GE7 for black willow.

The variable Site did not attain statistical significance in the linear mixed model, and p = 0.17 and 0.15 for bivariate models of GE with site as the sole predictor for baldcypress and black willow, respectively. Hence, the null hypothesis of no site effect cannot be rejected at p=0.05 for this dataset.

Nevertheless, the magnitude of variation in mean growth responses of baldcypress and black willow by site is useful for comparison to other sources of variation (Figure 2). The non-significant differences in mean growth efficiency across sites in this study were a range of about 22% (baldcypress) and 18% (black willow) of the overall mean. Thus, despite much among-tree variation, the best estimate of the effect of hydrologic connectivity variations represented in this study is a difference of about 20% in site quality.
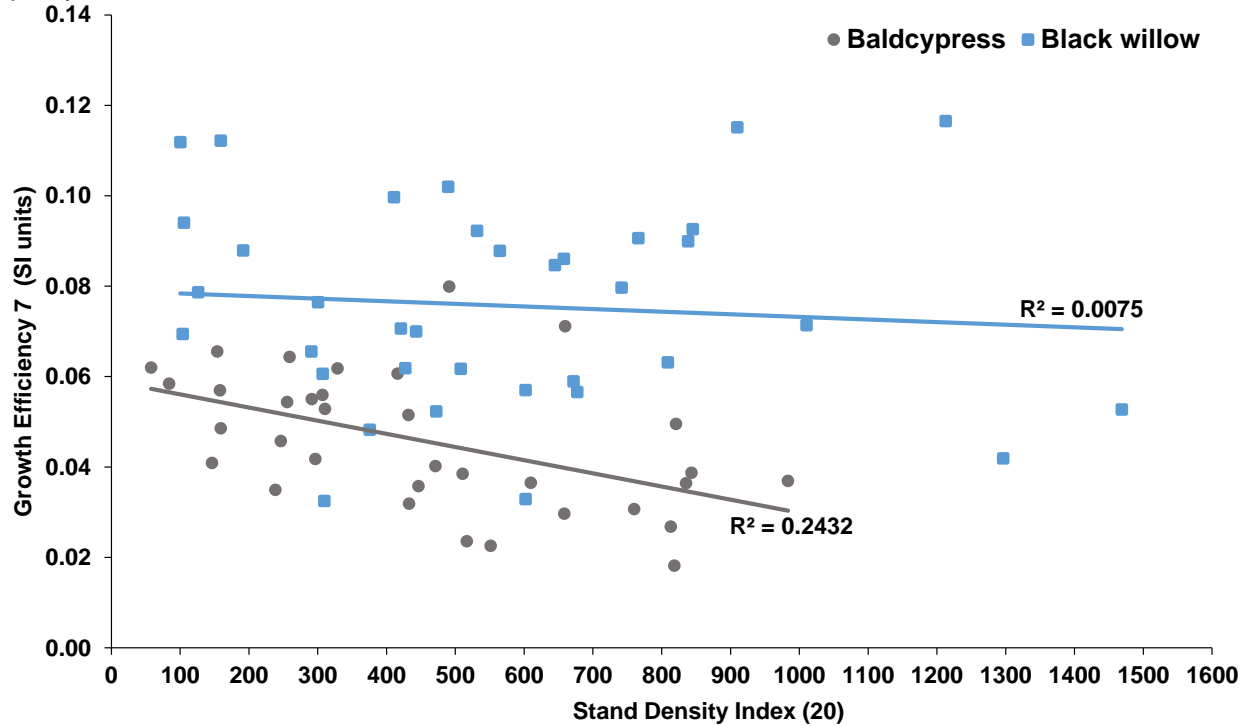

Figure 3.1. Stand density index (20) competition influence on growth efficiency of baldcypress and black willow
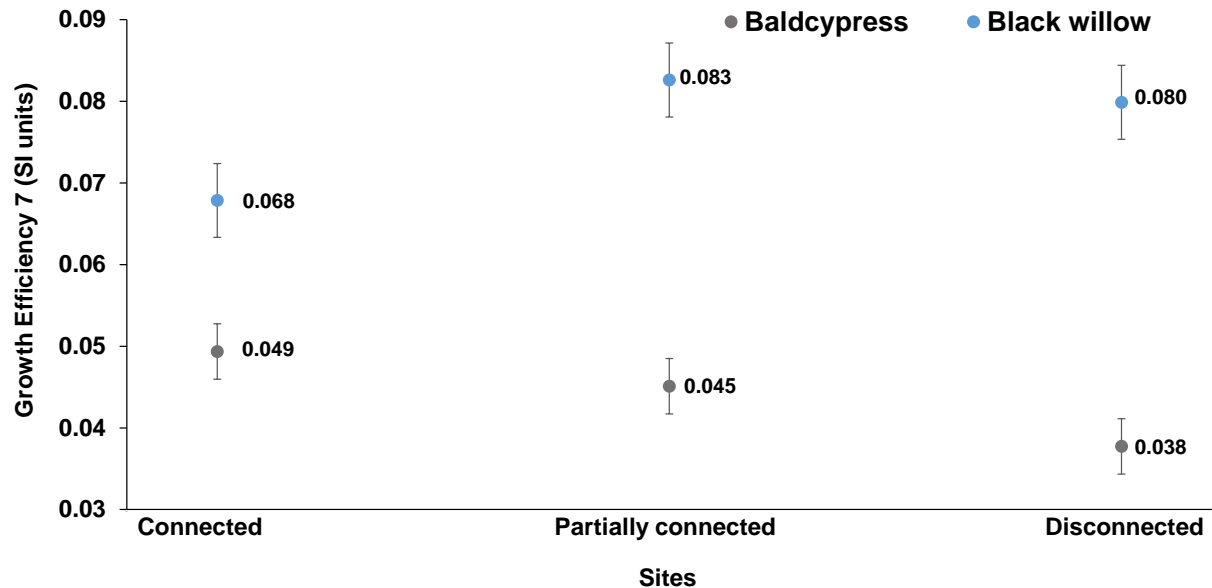

Figure 3.2. Mean growth efficiencies averaged across 7 years for baldcypress and black willow by site (connected, partially connected, disconnected) with bars of standard error.

3.5 DISCUSSION

3.5.1 Site vs Competition Effects

Site quality and competition both have the potential to affect growth of individual trees. Generally, an increase in site quality results in accelerated development of competition (Forrester et al., 2013) due to resource availability. In wetlands, however, flooding, considered the crucial determinant of growth (Anderson and Mitsch, 2008) and can cause conflicting relationships between site quality and competition; an example of such is that flooding can reduce regeneration (Kroschel et al., 2016) and therefore competition.

The conclusion of this study is that that competition has the strongest effect on growth, and there is some indication that connectivity does affect growth to a lesser degree. Among all competition variables, SDI20 was the best descriptor, across the range of observed density, of growth efficiency for baldcypress. Although growth efficiency decreased by almost 50 percent across this range, the sampled trees were not in stands of maximum density, which occurs around 1200 SDI (Keim et al. 2010); therefore, there is potential for competition to have an even greater effect on growth at higher densities.

The lack of a statistical relationship between SDI20 and growth efficiency for black willow was probably due to variability in crown structure and growth that was not a direct consequence of local competition. Additionally, recent hurricane damage to stands within the area may have caused greater damage to black willow than to baldcypress crowns. Doyle et al. (1995) found that baldcypress are resilient to hurricane effects, while black willow is brittle and subject to frequent crown damage.

Although disturbance, including storms, flooding, and sedimentation, may have affected stand and tree structure and hence growth, a likely cause of differences in the relationship between competition and growth between the two species is differences in their lifespans and general life history. Whereas baldcypress is a long-lived species reaching several hundred years of age, black willow has a maximum life span of 55-60 years growth (Krinard, 1985; Yin, 1998). The black willow in this study were approximately 55-60 years of age and were reaching senescence; therefore, the change in growth pattern as a result of age and general vigor were probably responsible for some of the low correlations between competition and growth.

Despite the lack of statistical significance for site effect on growth efficiency, the means of growth efficiency were interpretably different among all sites, providing some indication that hydrologic connectivity may influence growth but is not the major determinant of growth for the range of connectivity examined here. Wetlands with greater variability in connectivity or other hydrologic factors may affect growth more. For example, Allen (2016) reported growth efficiencies of baldcypress varying by much more than observed here.

To fully understand site quality in terms of connectivity, tree adaptations and morphologic plasticity must be better understood. For example, trees exposed to flooding have physiological characteristics such as water roots and epicormic branching that may have mediated flood effects on growth (Megonigal and Day, 1992; Meadows, 1995). Within this study, only trees of dominant or codominant crown classifications were sampled for analyses. The small data range may have excluded potential growth responses to site quality which may have been observed in less dominant, younger trees of the same species. Studying the growth of species to the site quality between seedling to mature stage may increase the understanding of the effect of hydrologic connectivity, as flood tolerances differs by age, and species (Parker, 1950; Gill, 1970).

3.5.2 Variability among relationships

Many variable relationships occurred between the competition indices and growth measures in this study; specifically, among relationships between similar measures and growth. Variation in relationships may result from stand heterogeneity, species light tolerance, canopy structure, and growth patterns.

Because the sites are in wetlands with frequent disturbance, the forest is typified by gaps and uneven-aged structure, creating complexity of influences on growth of individual trees, specifically, the spatial heterogeneity of tree location and size influences competition among trees (Curtis, 1970; Suzuki et al., 2013). Light interception and use efficiency vary according to canopy structure and shade tolerance.

Differences between baldcypress and black willow likely influence their response to competition; for example, baldcypress have pyramidal crowns in contrast to the spreading, irregular crowns of black willow. From open-grown to closed-canopy conditions, crown size decreases as a result of light competition (Farrar, 1961; Larson, 1963; Sprinz and Burkhart, 1987). Terborgh (1992) discussed light availability for understory and midstory competition; he suggested areas with complex canopy gaps (as in uneven aged stands of high heterogeneity) receive greater light and that such gaps are influenced by crown shapes, (i.e., pyramidal crowns inhibit transmission of most sunlight to the forest floor). Therefore, for this study, the pyramidal shape of baldcypress may have blocked more direct light to the ground than did black willow, inhibiting competition more than the black willow crowns, having irregular shape (Li et al., 1995). Although having differences in crown specifics, baldcypress had less growth efficiency with increased competition than black willow, even under similar competition influence. The differences in growth efficiency possibly can be attributed to the fact that sapwood basal area is only a proxy for crown leaf area and crown leaf area to growth relations are species specific due to species morphological differences (conifer vs broadleaf), as such differences have previously been found between similar conifer species (Waring, 1983).

3.6 CONCLUSIONS

In this study, competition for growing space had a larger effect on growth efficiency than did hydrologic connectivity. Local stand density index for BAF 20 prism points (SDI20) was the best measure of competition for baldcypress, but there were no strong relationships between competition indices and growth for black willow. Although statistical significance among most competition measures for both species were weak, trends between the competition indices and growth indicated that as competition increased, growth efficiency, measured at the cross section of the stem, decreased.

Although it was a marginally statistically significant predictor of tree growth, site quality appears to have varied by about 20% across the range of hydrologically connectivity examined in this study. The effect of site on growth efficiency of individual trees was lower than was the effect of competition for baldcypress: trees in the densest parts of the stand grew with only ~1/3 the efficiency.

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CHAPTER 4: CONCLUSIONS

Both baldcypress and black willow showed similar radial increment responses to environmental conditions, although correlations were stronger overall for baldcypress. Of all flooding and climate variables, flooding depth had the strongest, and positive, effect on radial increment of both species across all sites. Widest rings occurred correlation with high pulses in the late spring and early summer. Of the climatic variables, temperature had the strongest effect on both species. Precipitation and PDSI were both weak predictors of growth.

Wetlands again are defined by the influence of flooding to sites and vegetation. However tree growth is not only influenced by flooding but also by competition. In this study, competition for growing space had a larger effect on growth efficiency than did hydrologic connectivity. Local stand density index for BAF 20 prism points (SDI20) was the best measure of competition for baldcypress, but there were no strong relationships between competition indices and growth for black willow. Although statistical significance among most competition measures for both species were weak, trends between the competition indices and growth indicated that as competition increased, growth efficiency, measured at the cross section of the stem, decreased.

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VITA

Alicia Louise McAlhaney is a native to Varnville, South Carolina. Alicia attended Clemson University in South Carolina from 2012-2016, receiving her Bachelor of Science degree in Forest Resource Management. During her time at Clemson University, Alicia participated in a variety of research opportunities such as invasive species management, water quality, and stream and wetland restoration. Through her experiences, Alicia realized a passion for research and wetland functions, particularly tree growth response; therefore, she decided to continue her education.

In June 2016, Alicia began a graduate assistantship with Dr. Richard Keim in the Forest and Wetland Ecohydrology Lab at Louisiana State University to complete a Master's of Science degree in Renewable Natural Resources, with a focus in wetland science. Her research, funded by The Nature Conservancy, focused on floodplain tree growth to hydrologic, climatic, and competitive influence, using dendrochronological – tree ring- analyses. Upon competition of her Masters of Science degree, Alicia plans to begin her career as a research associate at LSU, applying her knowledge of dendrochronological methods for other students' research needs.