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Hydrological shifts and tree growth responses to river modification along the Apalachicola River, Florida

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Shifts in the hydrologic regime of Florida's Apalachicola River have been attributed to anthropogenic changes throughout its watershed, including local dam construction. To assess impacts of those shifts on floodplain forests, we reconstructed tree growth using dendrochronology and compared these trends with hydrological and climatic variables. Comparisons of stream-gage data before and after dam construction on the Apalachicola River revealed statistically significant mean declines in annual average stage. Mean minimum annual stages, rise rates, and fall rates also decreased, while hydrograph reversals increased. Growth in four tree species correlated strongly with site-specific inundation parameters. A wetter climate in the two decades following dam construction and fine-scale fluctuation of the hydrograph may have set the stage for positive growth releases. Logging and hurricane wind throw events may have also contributed. However, drier conditions in the last two decades are now exacerbated by stage-discharge declines that had been masked previously. Tree growth rates and recruitment have decreased and, in the absence of a major disturbance, the forest canopy is composed of an older cohort of individuals. Our findings highlight how hydrograph variability, climate change, and vegetation disturbance are all relevant for gaging and anticipating the range of impacts of river modification on floodplain forests.

Keywords: dams; riparian; forest; disturbance; Apalachicola River

Introduction

Direct and indirect anthropogenic impacts on riparian ecosystems constitute one of the most dramatic environmental changes of the past century (Graf, 1999, 2001). The most visible of these impacts has been the construction of dams. The observed downstream impacts of dams include changes in flood regime, shifts in the patterns of sediment erosion and deposition, fragmentation of floodplain habitat, and a restructuring of the geomorphic complexity (Brandt, 2000; Dynesius & Nilsson, 1994; Graf, 2006; Petts & Gurnell, 2005; Williams & Wolman, 1984). These changes also have the potential to influence floodplain forest composition, structure, and dynamics (Bendix & Hupp, 2000; Corenblit, Steiger, Gurnell, & Naiman, 2009; Osterkamp & Hupp, 2010).

Dammed rivers typically undergo reductions in peak discharge. Morphological changes, such as channel bed degradation or channel width modification may also alter flood regime (Magilligan & Nislow, 2005). However, the actual downstream effects of

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dams are context-dependent. Williams and Wolman (1984) found that changes in annual peak discharge, rate of initial downcutting, and adjustments in channel width varied significantly among alluvial channel rivers. For some rivers, a generalized trend of channel incision downstream of dams is valid. Yet examination of the changes at smaller spatial extents (i.e., individual cross sections) can reveal considerable variability in morphological response (Phillips, Slattery, & Musselman, 2005). Rates of adjustment to dam construction can also exhibit different tempos, some proceeding relatively rapidly, others extending over longer time scales (Wellmeyer, Slattery, & Phillips, 2005). Fluvial landscapes are best characterized as circumstantial, contingent outcomes of deterministic laws operating in specific environmental and historical contexts (Phillips, 2007).

This context dependency underscores the need to conduct site-specific investigations of the changes that occur in floodplain forests after dam construction. If hydrologic, climatic, and geomorphic variables interact idiosyncratically as a function of geography, then one could also expect that changes in floodplain forests may likewise have more diverse responses. The effects of the alteration of river flow may not necessarily propagate through a biogeomorphic landscape in the same manner from one location to another (e.g., Phillips, 2010). Local forest patch dynamics may also shape the response of riparian forests to river regulation.

This paper characterizes biogeomorphic changes in floodplain forest associated with dam construction along northwest Florida's Apalachicola River. First, we describe the changes in hydrological conditions coincident with dam construction in the late 1950s. We then quantify the association of these changes with annual growth signals in the tree rings of four floodplain tree species distributed across a long-term monitoring site. Earlier studies have documented stage declines and channel incision following dam construction on the Apalachicola (Light, Darst, & Grubbs, 1998; Light, Vincent, Darst, & Price, 2006). Coincident with these changes has been a general drying of the floodplain forest and a paucity of recruitment in former canopy dominants (Darst & Light, 2008; Gibson, Meyer, Poff, Hay, & Georgakakos, 2005; Stallins, Nesius, Smith, & Watson, 2010). However, these studies are based on forest inventories conducted after the dam was constructed. They characterize vegetation change based only on two points in time. Dendrochronology allows us to characterize floodplain tree growth in the decades before dam construction and at an annual resolution commensurate with historical river gaging data.

A small number of dendrochronological studies have assessed the impact of dams on forested floodplains along alluvial rivers in humid climates. Tree rings from north Florida have been shown to be sensitive to stream flow (Crockett, Martin, Grissino-Mayer, Larson, & Mirti, 2010). However, the relationship between river flows and tree growth has not been consistent from study to study, even when detailed streamflow and elevation data were available. For a baldcypress-dominated lake in east Texas, Keeland and Young (1997) found no strong growth declines in response to hydrologic alteration, but new recruitment had ceased. For a dam-modified river in southwest Florida undergoing increased flow due to agricultural irrigation, Ford and Brooks (2002) found counterintuitive results. Annual growth in slash pine had a positive correlation with streamflow despite higher water levels and observed plant stress. They postulated that increased streamflow may have had indirect, deleterious impacts on slash pine (possibly by increasing competition) that counteracted its direct positive effect. Cleveland (2000) documented a strong positive correlation between baldcypress growth and streamflow, while Stahle, Van Arsdale, and Cleveland (1992), and Young, Keeland,

and Sharitz (1995) found a temporary surge in baldcypress growth, followed by a period of depressed growth, after onset of increased inundation. Amos (2006) also observed differences in the responses of baldcypress to riverine (positive) versus stagnant (negative) flooding. These studies suggest that binary (wetter vs. drier) classifications of dam impacts on riparian habitats, although potentially valid at some time and space scales, may miss critical details about forest responses.

Study area

The Apalachicola River (Figure 1) is a major alluvial river on the coastal plain of northwest Florida. Flowing for 170 km before emptying into the Apalachicola Bay, the river has a mean annual discharge of 630 m³/s (Light et al., 1998). The Apalachicola shows considerable seasonal variation in flow (~280–2800 m³/s), with a major flood pulse regularly occurring in late winter or early spring (January–April), and a period of low flow typically occurring in fall (September–November; Elder, Flagg, & Mattraw, 1988). Streamflow is the principal component of the river's water budget. Precipitation, groundwater discharge, and other inputs contribute little to the magnitude or variability of flow (Mattraw, & Elder, 1984). Flooding along the river is important as it supports the largest forested floodplain in Florida, at 450 km² (Leitman, Sohm, & Franklin, 1983).

However, a different situation exists in the basins of the Apalachicola's main tributaries, the Chattahoochee and Flint Rivers, from which it derives approximately 80% of its water (Florida Natural Areas Inventory, 2005; Pederson et al., 2012). The Chattahoochee and Flint flow through areas of Georgia and Alabama that have undergone extensive development for urbanization and agriculture. The city of Atlanta, near the headwaters of the Chattahoochee, has grown over the past half century from a population of 500,000 to over 4 million. Because groundwater is largely inaccessible, Atlanta draws heavily on water from the Chattahoochee, the smallest river to support a major American city. Downstream, increasing demand from the agricultural sector has placed further strain on these water resources. The consumptive withdrawals that now occur in the Apalachicola-Chattahoochee-Flint basin during the summer (agricultural, industrial, and municipal withdrawals combined) are over half the river's minimum discharge levels for those months (Leitman, 2005).

Several anthropogenic factors have influenced the Apalachicola directly. One is the Jim Woodruff Dam, on which construction began in 1950 at the confluence of the Chattahoochee and Flint Rivers, where the Apalachicola begins. The dam itself functions primarily for hydroelectricity and navigation, while its associated reservoir, Lake Seminole (filled from 1954 to 1957), is primarily recreational. In addition to this, the main channel of the Apalachicola has been periodically dredged to facilitate barge traffic. Dredging began intermittently in the nineteenth century, and in 1956, concurrent with the construction of the dam, the US Army Corps of Engineers began maintaining a channel 30 m wide and 3 m deep. Dredged material, on the order of 800,000 m³/yr, was initially placed on the floodplain, leading to localized tree mortality (Leitman et al., 1983). In response to a steadily dwindling volume of barge traffic and to growing complaints about harmful effects of dredging and disposal, the Corps halted this practice in April 2005. Other anthropogenic changes to the river made for the benefit of transportation have included the implementation of navigation windows, the timed storage and release of water by the Jim Woodruff Dam during periods of low flow (Light et al., 1998).

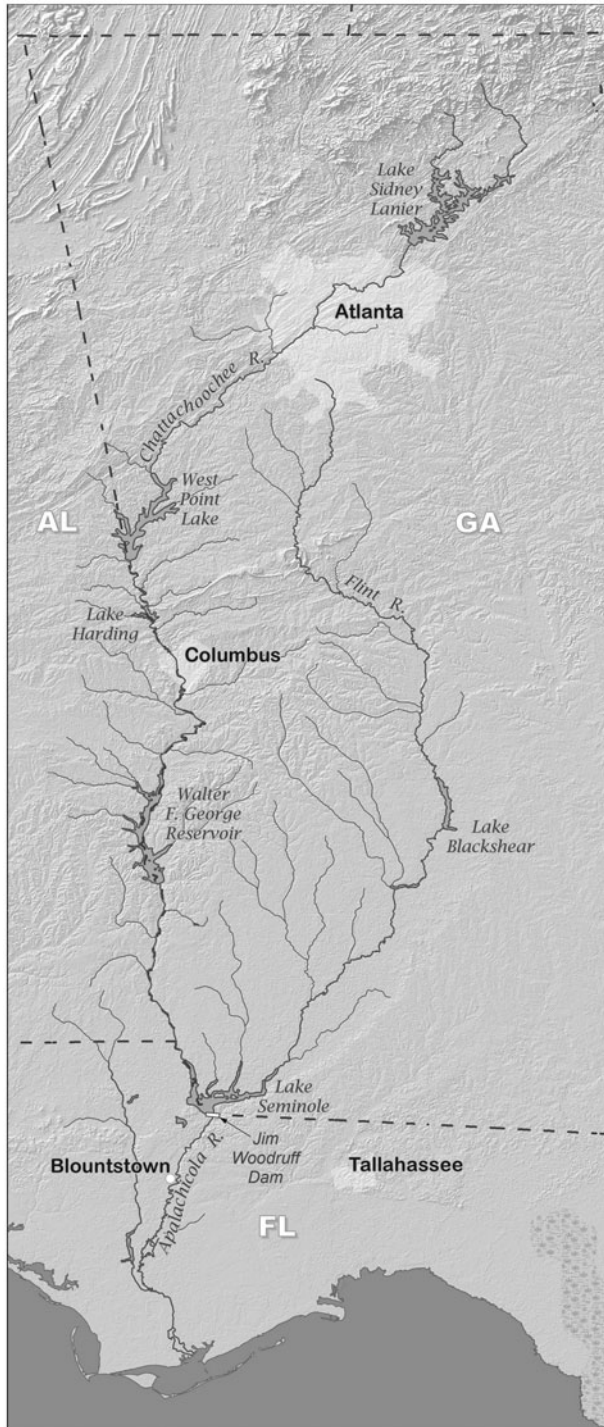


Figure 1. Study region.

The cumulative effects of these alterations on the hydrology of the river were first investigated in the 1980s as part of the US Geological Survey's Apalachicola River Quality Assessment (Elder et al., 1988). Leitman et al. (1983) noted a decline in the stage-duration curve, which represents the percentage of time that a given river stage is equaled or exceeded. Shortly thereafter, a Corps of Engineers study (Simons, Li, and Associates, 1985) took a closer look at the response of Apalachicola channel morphology to anthropogenic impacts. The authors concluded that entrenchment of the bed had occurred over the two decades following dam closure (Simons, Li, and Associates, 1985). A US Geological Survey study (Light et al., 1998) quantified the areas of aquatic habitat that were hydrologically connected to the main channel during various flow levels. They observed that many of these connections at low flows had been effectively severed by falling river stages. In another USGS report, Light et al. (2006) found that decreases in river stage driven by entrenchment have been pronounced at low flows. At a flow of 280 m³/s, stage at the Chattahoochee gage (directly below the dam) is now nearly 1.5 m lower than at the corresponding flow during the pre-dam period. The effects of bed degradation extend approximately 100 km downstream of the dam, while the magnitude of the stage decrease tapers as downstream distance increases. However, in terms of ecological consequences, this downstream attenuation may be partially offset by the progressively flatter floodplain topography. At the Blountstown gage, ~2 km downstream of the plot used for the present study, the decrease in stage at low flows has been greater than 0.75 m. In addition to degradation of the channel bed, the channel has widened locally, likely contributing in certain places to the observed stage decrease (Light et al., 2006).

On the Apalachicola River floodplain, the flooding regime of the river exerts an overarching influence on the establishment, growth, and reproduction of plant species. Each species has a distinct envelope of tolerance to inundation and saturation (Kozłowski, 2002; Messina & Conner, 1998; Mitsch & Gosselink, 2000). As a result of these individual tolerance curves, distinct zonation of plant communities typically develops along alluvial rivers, which track changes in topography and flooding regime. Anthropogenic modification of flooding regimes alters the conditions within these communities, causing changes in growth and potentially redirecting recruitment and succession.

The tree species referenced in this study were distributed across a 350 m by 30 m plot aligned perpendicular to the west bank of the Apalachicola River, 127 km upstream from its mouth and 44 km downstream from the Jim Woodruff Dam (30.44° N, 85.01° W). The site consisted of bottomland hardwood forest owned by the Neal Land and Timber Company, which purchased the forest in the early 1920s. The plot was originally established in 1977, and was selected because of its proximity to the Blountstown gaging station (Leitman, 1978). Four generalized forest types occur along the plot: upland forest on the levees, low and high bottomland forest, and backswamps.

Methods

We used Indicators of Hydrologic Alteration (IHA) to detect temporal shifts and trends in the hydrologic regime of the Apalachicola River. This method quantifies the impact of dam and reservoir construction on the hydrologic characteristics of rivers (Richter, Baumgartner, Powell, & Braun, 1996). IHA uses daily stage or discharge measurements as input, and allows for the specification of an "impact date" (dam construction in this case), which divides output into two periods for comparison. The output is

Table 1. IHA Variables for hydrologic and climatic parameters. All variables are for Blountstown, Florida, for the water year of October through September.

Variable	Description
PAnn	Annual cumulative precipitation
POct-PSep	Cumulative monthly precipitation
TAnn	Annual mean temperature
TOct-TSep	Mean monthly temperature
PDSIAnn	Annual average Palmer Drought Severity Index
PDSIOct-PDSISep	Monthly Palmer Drought Severity Index
SAnn	Annual mean stage
SOct-SSep	Monthly mean stage
S1dMin-S90dMin	Min annual daily stage averaged over 1, 3, 7, 30, 90 days
S1dMax-S90dMax	Max annual daily stage averaged over 1, 3, 7, 30, 90 days
SBase	Annual base stage
SMinTime, SMaxTime	Julian date of each annual 1-day minimum/maximum stage
SRise, SFall	Rise and fall rates
SRev	Number hydrologic reversals per year
SEventFreq*	Frequency of inundation
SEventDur*	Duration of inundation
SEventTime*	Mean Julian date of all inundation events during a year
SEventPeak*	Mean of all peak stages during inundation events
SEventRise*, SEventFall*	Mean rise rate and fall rate during inundation events

*These variables were calculated separately for each of five different stage thresholds: the average basal elevation of each of the four species for which chronologies were developed, and the average basal elevation of all trees used in the overall chronology.

32 hydrologic parameters that measure inter-annual statistical variations in hydrologic regimes (Table 1). IHA analyzes were performed on stage and discharge data to isolate the effects of a declining stage-discharge relation. We obtained daily mean discharge measurements from a USGS gage at Chattahoochee, Florida. Daily mean stage measurements were acquired from a gage operated by the US Army Corps of Engineers at Blountstown, Florida, approximately 2 km downstream from the Blountstown plot. The period of record used in this study extends from 1 October 1928 to 30 September 2004, corresponding to the period of overlap between available stage and discharge measurements.

Annual base stage was calculated as the annual minimum 7-day-averaged stage divided by annual mean stage. Rise rate and fall rate are the means of all positive differences and means of all negative differences, respectively, between consecutive daily stages. The number of hydrologic reversals is a count of the shifts from rising stages to falling stages, or vice versa, over consecutive days per year. The frequency of inundation is the number of events per year during which stages climbed above the average basal elevation of all trees on the plot. Duration of inundation was tabulated as the average length of an inundation event, in number of consecutive days.

An important feature of the IHA model is the ability to customize the stage or discharge threshold used for classifying high pulse events. From the perspective of a floodplain tree, the important stage threshold will correspond to an elevation at or near the base of the tree. Therefore, to obtain the most relevant IHA results for the Blountstown plot, separate analyzes were conducted with the average basal elevation of each species, in turn, set as the high pulse threshold. A final analysis was conducted using the average basal elevation of all trees on the plot. Basal elevations were obtained from Leitman (1978); selected remeasurements demonstrated that changes in

elevation have been negligible on the whole since then. Each of these analyzes yields the approximate frequency, average duration, and average timing of events linked to the inundation of the corresponding group of trees.

Statistical comparisons of pre- and post-dam periods were carried out for a number of the IHA parameters. The pre-dam period, from 1929 to 1956, encompassed the beginning of the stage and discharge record to the year before completion of Lake Seminole. A period of equivalent length, from 1977 to the end of 2004, was chosen to represent post-dam conditions. These two 28-year periods bracketed the transitional interval during which the majority of channel degradation occurred following dam construction. To identify significant shifts in mean and variance of the IHA parameters, the Student's t-test and Fisher's F-test were used, respectively. Climatic variables were obtained from the National Climatic Data Center for the Blountstown, Florida weather station.

The process of selecting individual trees for coring began with the elimination of species unsuited for dendrochronological study. Core samples were taken from at least one individual of every tree species present on the plot (24 species total out of 544 stems greater than 7.5 cm DBH). Following examination of the wood characteristics of each, 20 of these species were eliminated from consideration. Reasons for elimination included an insufficient number of individuals for chronology-building (e.g., *Ulmus alata*), the difficulty of identifying annual rings in diffuse-porous wood (e.g., *Acer rubrum* and *Liquidambar styraciflua*), and the complications introduced by unusual growth characteristics (e.g., *Nyssa ogeche*, which commonly occurs as multiple stems around a hollow center). Four final species were chosen for tree-ring analysis: baldcypress, overcup oak (*Quercus lyrata*), laurel oak (*Quercus laurifolia*), and sugarberry (*Celtis laevigata*). On the Blountstown plot, only seven viable bald cypress individuals were identified. To obtain a sufficient sample, additional tree cores were taken from a stand <1 km from the main plot. These four species cover a wide ecological spectrum, and were representative of each of the forest types found in the floodplain.

Baldcypress is classified as an obligate wetland species. It is an exceptionally long-lived and commercially important tree with growth rings amenable to cross dating. It has received by far the most intensive dendrochronological study of wetland trees in the Eastern USA (Cleaveland, 2000; Stahle et al., 1992; Young et al., 1995). Laurel and overcup oak are both classified as facultative wetland species, although overcup oak is typically associated with somewhat moister conditions (Burns & Honkala, 1990). Sugarberry is classified as a facultative upland species. In comparison to baldcypress, tree-ring analysis of floodplain hardwood species has generally yielded more ambiguous results (Copenheaver, Yancey, Pantaleoni, & Emrick, 2007; Dudek, McClenahan, & Mitsch, 1998; Mitsch & Rust, 1984).

Duplicate tree-ring samples were extracted at breast height from each of these four tree species. Annual growth increments for each core were measured using a Velmex measuring stage with a precision of 0.001 mm. Measurements were tabulated and dated automatically using Measure J2X (VoorTech Consulting, Holderness, NH). The program COFECHA (Grissino-Mayer, 2001; Holmes, 1983) was subsequently used for validation of cross dating. ARSTAN (Cook, 1985) was used to generate standard and residual chronologies. Because significant autocorrelation was found in all raw series used in this study, residual chronologies were selected for analysis (Fritts, 1976; Cook & Kairiukstis, 1990). Examination of the raw series revealed that the only species with an obvious age-related growth component was sugarberry. Most individual trees of this species displayed a clear negative exponential trend that required detrending in ARSTAN.

Pearson's product-moment correlation coefficient (r) was calculated between each chronology and each environmental parameter for the period of record (1929–2004). A stepwise multiple regression was then performed for each selected chronology using only those parameters demonstrating significant correlations with that chronology. Parameters were progressively eliminated until all remaining coefficients were significant ($p < 0.05$). The resulting model was interpreted as providing the best available explanation of variance in tree growth. All correlation and regression analyses were performed in the statistical package R (R Development Core Team, 2006).

Intervention detection analysis was used to characterize changes in tree growth. This technique was originally developed for generic time-series data by Box and Jenkins (1970) and Box and Tiao (1975), and has been more recently applied to tree ring series (Downing & McLaughlin, 1990; Druckenbrod, 2005) in an attempt to reconstruct forest disturbance history. The series for each individual tree was input into the time-series analysis program AutoBox (Automatic Forecasting Systems, 2004), which first generates an autoregressive integrated moving-average (ARIMA) model for each series. An ARIMA model uses a combination of autoregressive, differencing, and moving-average operators to characterize the general behavior of a time-series. Following ARIMA modeling, an intervention detection analysis was performed on the resulting series to identify growth features of three types: pulses (transient "shocks" of unusually high or low values), steps (significant increases or decreases in the series mean), and trends (periods of relatively consistent increases or decreases). A minimum of five consecutive years is required to classify a given event as a step or trend intervention (Druckenbrod, 2005). To summarize the output of this process, the number of interventions detected in a given year was summed over all series, separating the three intervention types from each other as well as positive interventions from negative. This generated graphs highlighting patterns of disturbance that may not have been evident in the original chronologies.

Results

Hydrologic analyzes

Decline in average stages for the Apalachicola was evident although obscured to some extent by the large year-to-year variability. There was a gradual divergence in stage and discharge during the 1960s and 1970s from its tighter pre-dam relationship (Figure 2(a)). Mean decline in stage for eight of the 12 months of the water year were significantly different between the two 28-year periods (pre-dam and recent; Table 2). These declines have been greatest in the spring and summer. Minimum annual stages, rise rates, and fall rates have decreased significantly, while the number of hydrograph reversals has seen a significant increase. Only four parameters demonstrated significantly different increases in variance following dam construction. However these parameters are important controls of tree physiology: rise and fall rates, frequency of inundation of the plot, and average duration of a plot inundation event. The average date of minimum flow moved up almost a month from 10 October to 17 September, while the average date of maximum flow moved up by approximately the same interval, from 1 May to 9 April. The average date of all plot inundation events moved up by a full month and a half, from 10 June to 26 April.

There were abrupt changes in rise rate, fall rate and the number of reversals coincident with the completion of Lake Seminole in 1957. Reversals in that year exceeded any previous year, while in 1958 they reached a level 50% higher than the

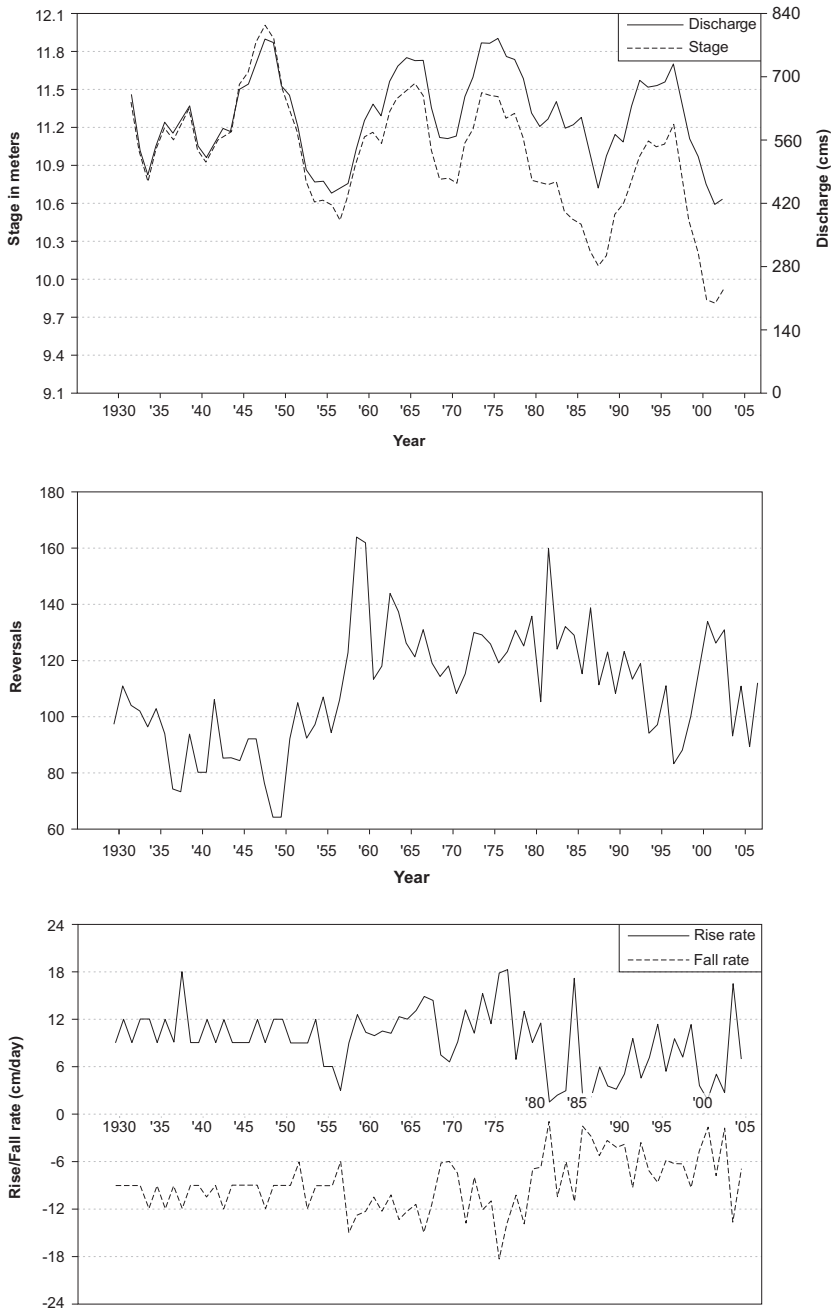


Figure 2. (a) 5-year running averages of mean annual stage, in meters, and discharge, in cubic meters per second (cms), for the Apalachicola River at the Chattahoochee gage; (b) number of reversals per year between daily average stage values; (c) annual average rate of rise and fall of stages at the Blountstown gage, in cm per day.

highest pre-dam number (Figure 2(b)). Meanwhile, rise rate and fall rate, which had been locked into a remarkably steady regime during the pre-dam period, suddenly

Table 2. Mean and standard deviation for hydrologic and climatic variables with statistically significant changes ($p < 0.05$) for pre-dam and recent periods.

Variable	Pre-dam (1929–1956)	Recent (1977–2004)
SAnn	36.8 ± 2.5	34.8 ± 2.6
SOct	33.3 ± 3.1	31.5 ± 2.7
SJan	39.1 ± 4.4	36.6 ± 4.7
SApr	41.1 ± 3.7	37.9 ± 4.1
SMay	37.9 ± 3.4	35.0 ± 4.0
SJun	35.3 ± 2.8	32.9 ± 2.9
SJul	35.6 ± 3.0	33.0 ± 4.2
SAug	35.3 ± 2.8	32.5 ± 3.3
SSep	33.6 ± 2.3	31.8 ± 2.6
S1dMin	31.1 ± 1.4	28.9 ± 1.4
S90dMin	33.3 ± 2.3	31.0 ± 2.0
SRev	85.0 ± 10.3	97.7 ± 14.0
SRise ^a	0.33 ± 0.1	0.2 ± 0.2
SFall ^a	-0.3 ± 0.1	-0.2 ± 0.1
SEventFreq ^b	6.2 ± 2.6	6.1 ± 4.3
SEventDur ^b	11.7 ± 8.7	12.1 ± 16.0

^aMean and variance are significantly different

^bOnly the variance is significantly different

entered a period of much greater year-to-year variability (Figure 2(c)). These changes indicate a systematic alteration of the fine-scale structure of the hydrograph, a phenomenon of a different nature than changes in its average lows and highs. This suggestion is borne out by examination of hydrographs for individual years directly preceding and following completion of the reservoir (Figure 3(a) and (b)). The comparatively abrupt day-to-day changes occurring in 1958 give its hydrograph a spiky, erratic quality not found in hydrographs from any previous year.

Tree growth chronologies

Of the four species identified as useful for developing chronologies, we cored all individuals of suitable size and condition (Table 3). All chronologies except laurel oak spanned the entire period of hydrologic record. Although many cores contained a longer growth record (up to ~300 yr for some cypress samples), only the time period of correspondence to the hydrological data was used. The common interval shared by the 12 laurel oaks sampled extended back to 1957. Sensitivity values of all four chronologies were above 0.3 and would thus be considered high (Grissino-Mayer, 2001; Speer, 2010); baldcypress was remarkably sensitive, with an exceptionally high value of 0.54. Intercorrelation values ranged from the marginally adequate (baldcypress and sugarberry) to the more securely adequate (laurel and overcup oaks). In general, values above 0.4 are recommended for trustworthy chronologies (Grissino-Mayer, 2001; Speer, 2010).

Residual chronologies for baldcypress, overcup oak, laurel oak, sugarberry, and for all four species (Figures 4 and 5) suggested how canopy dynamics exert an influence on riparian forest growth. The overcup oak series, for instance, is dominated by what appear to be two major disturbance events, in the early 1960s and late 1980s. A similar growth signal is present in the sugarberry chronology. The composite chronology for all four species also conveyed these growth increases. In the baldcypress series, a

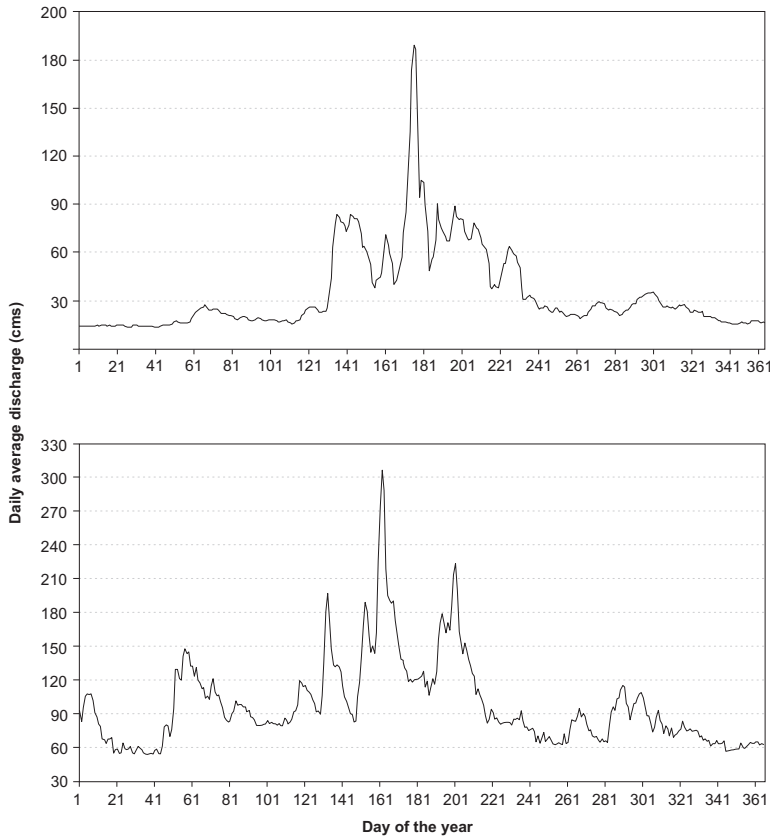


Figure 3. (a) Apalachicola River hydrograph for the water year of 1956, the year prior to completion of Lake Seminole, using daily average discharges at the Chattahoochee gage; (b) Apalachicola River hydrograph for the water year of 1958, the year following completion of Lake Seminole, illustrating the increased short-term fluctuations typically observed in hydrographs after this date.

Table 3. Descriptive statistics for each of the five tree growth chronologies.

	Overall	<i>T. distichum</i>	<i>Q. lyrata</i>	<i>Q. laurifolia</i>	<i>C. laevigata</i>
No. cores/trees	124/62	34/17	30/15	24/12	36/18
Common interval	1929–2006	1929–2006	1929–2006	1957–2006	1929–2006
Intercorrelation	0.39	0.46	0.53	0.52	0.49
Mean sensitivity	0.39	0.54	0.35	0.33	0.35
1st-order autocorrelation	0.59	0.42	0.71	0.62	0.61

gradual increase in growth can be observed prior to the mid-1970s, at which point annual increments began to conspicuously decline. There has been an increasing trend in the overall growth rates of laurel oak, yet these rates have declined during the 2001–2006 period. Over the past 78 yr, the four years of lowest overall tree growth were 2002, 2003, 2004, and 2006; and eight of the 14 lowest-growth years have occurred since 1999. These same years of decline were also noted by Maxwell and Knapp (2012) in their dendrochronology of *Nyssa ogeche* (white tupelo) along the Apalachicola River.

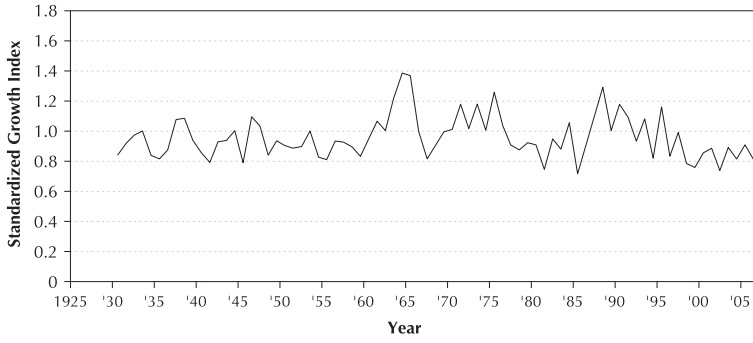


Figure 4. Residual growth chronologies for all four species combined.

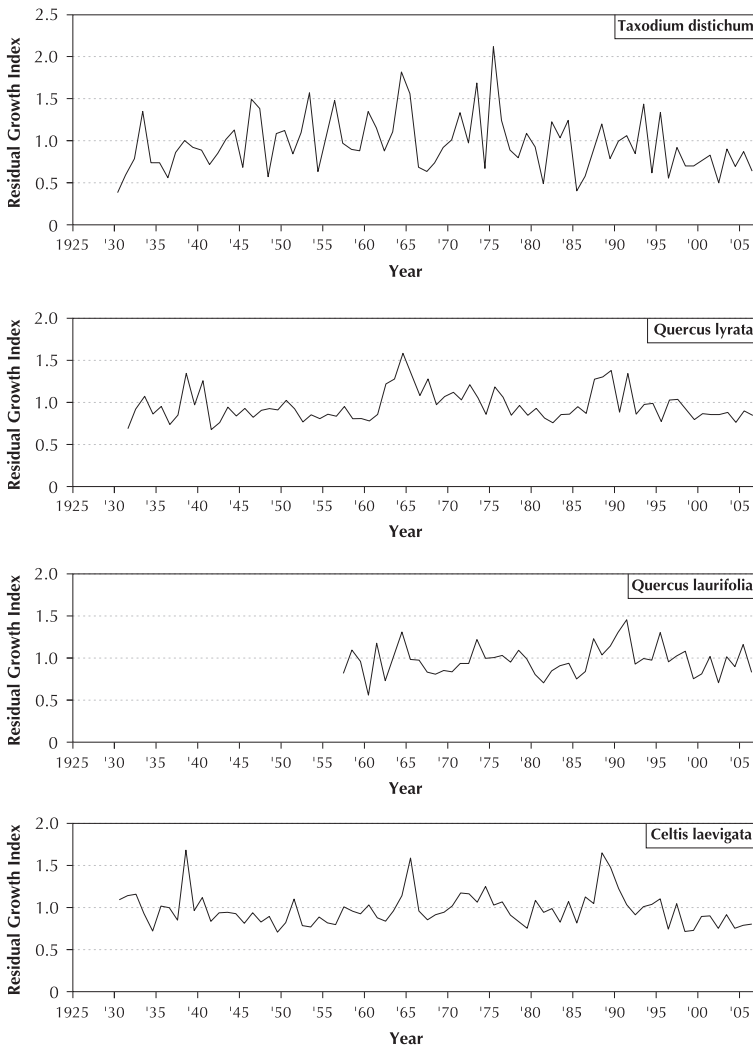


Figure 5. Residual growth chronologies for individual species.

Table 4. Significant ($p < 0.05$) Pearson's correlation coefficients for relationships between residual growthchronologies and hydrologic or climatic parameters.

Overall Variable	<i>T. distichum</i>		<i>Q. lyrata</i>		<i>Q. laurifolia</i>		<i>C. laevigata</i>	
	<i>r</i>	Variable	<i>r</i>	Variable	<i>r</i>	Variable	<i>r</i>	Variable
SEventFreq	0.45	SEventFreq	0.49	SEventFreq	0.45	SEventTime	0.59	SEventPeak
SBase	-0.42	SFall	-0.48	SEventTime	0.35	SBase	-0.57	SMinTime
S90dMax	0.41	S90dMax	0.47	TJul	-0.34	PDSIMar	0.48	SEventTime
SAnn	0.38	SAnn	0.47	SEventDur	-0.31	PDSIMay	0.46	TJun
SEventTime	0.36	SMay	0.47	SEventPeak	-0.31	PDSIJan	0.45	TMay
SMay	0.35	PApr	0.47	PJan	0.28	SEventFreq	0.40	
SJan	0.34	SApr	0.46	TJun	-0.26	SAnn	0.40	
PDSIMar	0.34	SEventTime	0.41	SJul	0.26	PDSIApr	0.40	
PDSIApr	0.33	SBase	-0.40	PDSIJul	0.23	S90dMax	0.40	
SApr	0.32	SMar	0.39	SRev	0.23	PDSIFeb	0.39	

Correlation and regression analyzes

Correlations indicated that the hydrologic parameters strongly outperformed the climatic parameters with respect to predicting tree growth (Table 4). There were some exceptions. Local spring drought severity (PSDI values) was a significant predictor of laurel oak growth. High summer temperatures had the ability to inhibit the growth of overcup oak and sugarberry.

Frequency of inundation was the strongest hydrologic predictor of growth in baldcypress ($r = 0.49$) and overcup oak ($r = 0.45$), as well as in all four species combined ($r = 0.45$). It was also significantly correlated with laurel oak growth, although the correlation was slightly weaker ($r = 0.40$). Average timing of inundation events was the only parameter that was significant for all species, ranging from $r = 0.27$ in sugarberry to $r = 0.59$ in laurel oak. Growth in all species was positively correlated with this parameter, signifying increased growth when inundation events fell later, on average, in the calendar year. Bald cypress and laurel oak growth were negatively correlated with base flow ($r = -0.40$ and $r = -0.57$, respectively), signifying more growth during years in which minimum flow constituted a greater proportion of average flow. Among the four species, sugarberry stands out due to the lack of strong correlations. As this is a species usually found in somewhat higher elevations and drier conditions than the other species considered here, it is understandable that its growth remains more independent of river hydrology.

Model fit was generally significant but not strong, explaining a quarter to half of the variance in growth (Tables 5 and 6). Examination of observed and model-predicted

Table 5. Statistically significant ($p < 0.05$) multiple regression models for each growth chronology.

Chronology	Variable	Direction of relationship	Adjusted r^2
Overall	S90dMax	+	0.29
	SEventDur	-	
<i>T. distichum</i>	SEventFreq	+	0.28
	SApr	+	
<i>Q. lyrata</i>	SEventFreq	+	0.28
	SEventDur	-	
	SEventTime	+	
<i>Q. laurifolia</i>	SEventTime	+	0.45
	SBase	-	
<i>C. laevigata</i>	SEventPeak	-	0.26
	SEventTime	+	
	TJun	-	

Table 6. Variance explained and associated probabilities for the regression models in Table 5, with data for the designated outlier years excluded. All models are significant at $p < 0.001$.

Chronology	Years removed	Adjusted r^2
Overall	1948, 1988, 1998	0.44
<i>T. distichum</i>	1930, 1936, 1948	0.41
<i>Quercus lyrata</i>	1960, 1962, 1976	0.36
<i>Quercus laurifolia</i>	1960, 1965, 1991	0.52
<i>Celtis laevigata</i>	1931, 1955, 1976	0.36

growth increments revealed the presence of outlier years that were poorly predicted by the model for each of the five chronologies. Removal of up to three of the largest outliers and redevelopment of the regression substantially improved each model, particularly in the case of baldcypress (from $r^2 = 0.28$ to 0.41) and the overall chronology (from $r^2 = 0.29$ to 0.44). Eight of the 15 outlier years detected fell within disturbance peaks, in the early 1960s and late 1980s, respectively. During these periods, disturbance effects likely overwhelmed the year-to-year influence of river hydrology and climate. After removing outlier years, regression models based on hydrologic

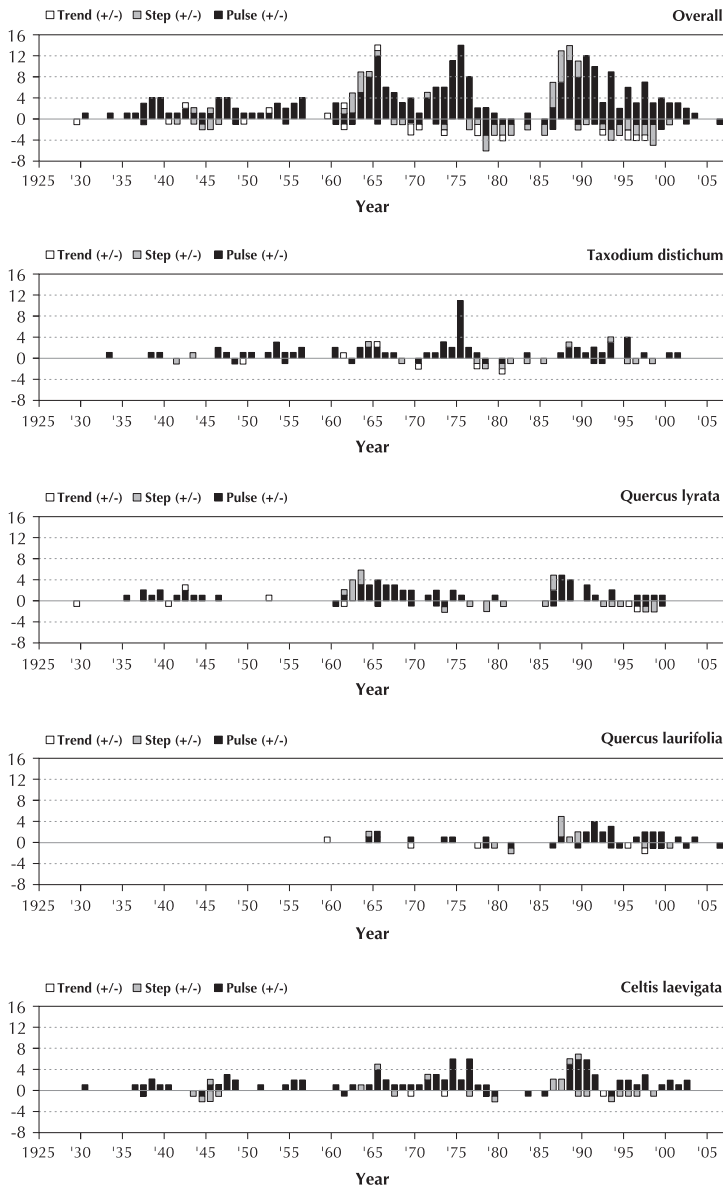


Figure 6. Sum of intervention features detected per year, by type and sign, in the individual tree growth records for the following species.

parameters explained between 36 and 52% of the variance in growth in the four tree species examined.

Annual trends, steps, and pulse interventions were detected in each of the five growth chronologies (Figure 6). Pulses were not common until the years coinciding with dam construction. Two major disturbance peaks appear on the composite graph, centered on the mid 1960s and mid 1980s. The majority of the interventions detected in these years, and in most other years, are positive pulse interventions, signifying transient shocks to the system rather than prolonged shifts in average growth or direction of growth rate. Positive pulse interventions are characteristic of isolated suppression-release events (Downing & McLaughlin, 1990) initiated by canopy opening.

Discussion

Significant relationships between tree growth and inundation-event parameters were evident. Hydrological variables may be more important than climate in relation to the growth signal expressed in the tree rings of the tree species in this study, a finding similar to that of Keim and Amos (2012). Growth in all four species studied here was positively correlated with timing of inundation, implying that inundation events later in the calendar year, on average, are more auspicious for tree growth. Maxwell and Knapp (2012) also observed recent shifts in *Nyssa ogeche* radial growth responses to November and July flows that could reflect the temporal shift in inundation we detected.

While the overall shape of the Apalachicola River's annual hydrograph has remained largely intact, the more specific characteristics of the hydrograph revealed a fundamental alteration of its fine-scale structure developing simultaneously with completion of Lake Seminole in 1957. For the two decades following this event, rise and fall rates in the hydrograph, as well as the number of hydrologic reversals, were exceptionally high in comparison with pre-reservoir levels. In addition, the two decades (1958–1979) following dam construction had higher average annual flows than the equivalent period (1929–1957) preceding it (Leitman et al., 1983; Elder et al., 1988). These higher annual average flows following dam construction and corresponding with a more variable hydrograph increased the frequency of inundation events on the Blountstown plot. This phenomenon may have been beneficial to growth in baldcypress, overcup oak, and sugarberry directly, or indirectly through the suppressed establishment of less flood-tolerant competitors via repeated, inhibitory flooding events. Although trees may have benefited from longer and more frequent flooding, wet conditions can also become stressful if too frequent or persistent. The negative correlation found between the duration of inundation and laurel oak growth confirms that this higher bottomland species has a much lower threshold of tolerance to inundation events.

The abrupt nature of the changes in the hydrograph and its exact coincidence with the completion of the reservoir make climatic explanations implausible. One possible factor is the operation of dams for hydropower generation, a process that has been implicated in similar hydrologic shifts in the nearby Tombigbee-Alabama system (Mobile Register, 2007). Some hydropower dams store water so as to concentrate power generation during times of peak demand, a process known as hydropeaking. However, this is not the case for the Jim Woodruff Dam, a run-of-the-river dam with limited control over storage and outflow. Although hydropeaking does occur at several dams upstream, notably at the Walter F. George Lock and Dam (~160 km upstream), its effects would attenuate over the intervening distance. While a precise explanation for the initiation of noisiness in the hydrograph is lacking, intervention detection

analysis confirmed that the tree ring growth signal also changed markedly immediately after dam construction. Positive growth pulses and steps increased, suggesting that fine-scale changes in the hydrograph could have fostered changes in flood regime that benefitted tree growth.

Although the relationship between Apalachicola River hydrology and floodplain tree growth has been convincingly demonstrated, over half of the variance in growth remains unaccounted for. Local disturbance events are potential explanatory factors, particularly for the two major growth peaks in the mid-1960s and mid-1980s that far exceed average year-to-year variability in growth. Much of the floodplain forest along the Apalachicola has a history of historic and recent logging. Logging of cypress, tupelo, and hardwoods could account for the growth release signal seen in the tree ring record around these dates. The positive pulse interventions detected by the IDA software are characteristic of isolated suppression-release events, such as those caused by logging or storms (Downing & McLaughlin, 1990). According to a spokesman for a local timber company, the Blountstown plot had last been selectively logged in the early 1960s and was scheduled for more logging in the late 1980s (Leitman, 1978). Although this later episode has not been confirmed, and no evidence of logging is presently apparent on the site, this would be the most parsimonious explanation for the disturbance signal observed in these tree rings. The trees exhibiting the largest growth response were those in the small-to-medium size range, which likely occupied the subcanopy layer at the time of logging (Darst & Light, 2008). Tropical cyclones also have the capacity to cause widespread growth release signals through extensive windthrow. Hurricane Kate passed almost directly over the Blountstown plot in November 1985. It is notable that the disturbance peaks identified in the mid-1960s and the mid-1980s are somewhat diffuse, rather than abruptly concentrated within one year. This could signify a delayed and/or differential recovery of growth from a strong but isolated event, or a prolonged disturbance event.

Overall growth in the four species studied has declined more since 2000 than at any other time during the period of record. This has been an exceptionally dry period, with lower flows exacerbated by the decline in the stage-discharge relation. Accordingly, inundation of the plot has become infrequent. Even in the flood years of 2003 and 2005, growth was far below average. Although these trees experienced initial transient benefits during the 1960s and 1970s from shifts in hydrograph structure and a wetter climate, those have now been overridden by a combination of factors, including long-term climatic trends culminating in record drought, and channel degradation resulting in lower river stages. On top of these phenomena, the trees have been forced to contend with streamflow that exhibited greater variability and less predictability under regulated conditions, which may pose severe challenges to species that are finely adapted to natural flooding regimes for reproduction. Stands of baldcypress and tupelo today are generally older and are not regenerating (Stallins et al., 2010). Another factor contributing to this recent decline in growth and recruitment may be the significant shifts in seasonality of flooding documented in this study. Without late season inundation events, the advancement of the average date of inundation events by a month and a half may be stressful for all four tree species.

Conclusions

Our results confirm that hydrological, climatic, and land-use contexts must be accounted for in attempts to discern the impacts of river regulation on riparian forests

(DeWeese, Grissino-Mayer, & Lam, 2007; Gibson et al., 2005; Konrad, 1998). Rather than examine riparian forest response to dams through a singular causal framework, the more salient question is how different drivers of change overlap in time and space, and the extent to which their effects propagate, amplify, or attenuate. For the Apalachicola River, the years immediately after dam construction coincided with a shift to wetter climate conditions, which may have attenuated any effects of channel entrenchment and stage declines. Drier conditions in the last two decades have magnified the influence of the geomorphic modifications that unfolded following river regulation. Superimposed upon these climatic and hydrological influences are the effects of land-use history and natural disturbances like tropical storms. Fine-scale local variability in flood regime may also be important. As observed in this study, daily fluctuation in the water levels detected in the hydrograph after dam construction could play a strong role in plant growth and regeneration dynamics, even though most studies of dam impacts concentrate on the larger macro-scale flood regime.

There are also other complexities to consider. Moisture availability in the water-retaining backswamps can vary considerably due to local factors. With stage decline, connectivity of the floodplain with the adjacent river channel determines inundation. As side channels become cut off from the main channel, the backswamps can be deprived of river water. Local site precipitation and the contingencies of microtopography may then increase in importance where these elevational relationships arise. Consequently, strong pulses of growth in riparian trees may be more local in character and less associated with flood regime and climate derived from the larger geographic setting (Franklin et al., 2001; Stallins et al., 2010). One would also need to consider the physiological attributes of different species in relation to these local controls on moisture. Cypress is more responsive to the hydrological inputs in the current growing season, while other bottomland trees, like *Nyssa ogeche*, may be responsive to hydrological inputs from the previous year (Keim & Amos, 2012; Maxwell & Knapp, 2012; Palta, Doyle, Jackson, Meyer, & Sharitz, 2012; Stahle, Cook, & White, 1985).

There is considerable controversy over the availability and intended uses of water in the Apalachicola-Flint-Chattahoochee river system. The findings from this study suggest that the simplistic narratives about ecological change that dominate in this water “war” are unlikely to correspond to how they actually play out. Contingencies in vegetation dynamics, land use, climate variability, and local controls of moisture availability may diversify the range of possible forest floodplain responses to hydrological alteration. For large alluvial rivers in humid subtropical climates, the outcomes of river modification may be difficult to generalize without considerable loss of resolution of the critical biological, hydrological, and ecological details. Consequently, a wider range of compositional and structural changes in the floodplain forests of the Apalachicola River are possible, and the manner in which they might emerge is perhaps more non-linear and capable of surprise than is presently recognized.

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