



Changes in Diameter Growth of *Taxodium distichum* in Response to Flow Alterations in the Savannah River

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Abstract Efforts to maximize or restore ecological function on floodplains impacted by dam construction have increasingly focused on river flow management. Few studies, however, consider floodplain hydrogeomorphic position and annual climatic variation in dam impact assessment. The Savannah River, a large river ecosystem in the Southeastern United States, was impounded in the 1950's. Our study objectives were: (1) Characterize

hydrology in floodplain areas containing *Taxodium distichum*, and determine how it has been affected by dam operations; (2) Identify basal area increment (BAI) response of *Taxodium* to annual flooding and climate (dry, average, wet) conditions; (3) Assess BAI response to dam-induced hydrologic changes. Levee and backswamp sites were significantly drier in the post-dam era, and trees at these sites showed a significant post-dam increase in BAI. Low-elevation river sites did not show significant hydrologic differences between pre- and post-dam eras, but BAI was significantly higher in dry years and significantly less sensitive to hydroperiod in the post-dam era. All trees demonstrated a significant quadratic BAI vs. hydroperiod relationship. This study demonstrates that annual productivity of *Taxodium* trees can be reduced by either drought or flood stress. It also suggests that climate and hydrogeomorphic location mediate dam impacts and productivity-flooding relationships in *Taxodium*.

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Introduction

The dynamic interaction between water and land is the principal process producing, maintaining, and affecting the biota living in river floodplain ecosystems (Bayley 1995). Flood pulses enhance biological productivity and maintain diversity in riverine systems; the principal agents associated with these functions are plants, nutrients, detritus, and sediments (Junk et al. 1989). Human alterations of river hydrology can change the dynamic nature of floodplain ecosystems by prolonging or eliminating inundation of floodplain sites. In addition to reducing or eliminating

inundation in floodplain areas below a dam, impoundments can also increase the duration and depth of inundation at low-lying downstream sites by augmenting low flows. The end result is a floodplain that resembles either a well-drained upland or a poorly-drained deepwater swamp; both are less productive than the former floodplain (Mitsch and Ewel 1979; Conner and Day 1992).

To optimally manage flood dynamics for maximum forest productivity, the relationship between tree populations and flooding gradients must first be determined. The subsidy-stress hypothesis proposed for floodplain forests suggests that the effect of flooding on plant growth can be positive or negative depending on the timing, duration, and hydrologic energy of flood events (Meganigal et al. 1997). Flooding has been defined as a stressor (a) if productivity of a steady-state forest ecosystem decreases following hydrologic alterations that increase flooding (Odum et al. 1979; Meganigal et al. 1997), or (b) if forest productivity is lower on a lowland site than on an upland site (Lugo 1978; Meganigal et al. 1997). In this study, both of these scenarios were examined, by examining growth in populations of *Taxodium distichum* trees (a) before and after the installation of a hydroelectric dam, and (b) in higher and lower elevation areas of the floodplain.

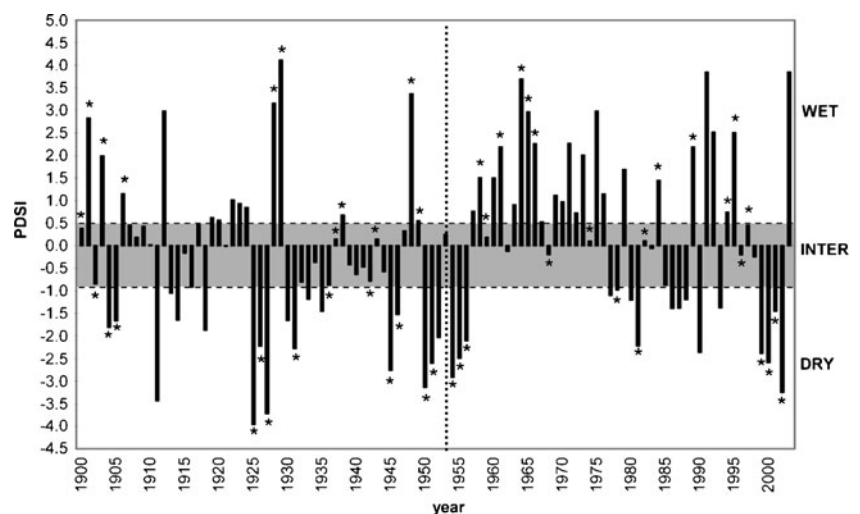
Taxodium is a canopy dominant in the wettest sites of floodplains in the southeastern United States and is highly valued for its role in carbon and nutrient sequestration (e.g., Brantley et al. 2008), its provision of habitat and basal resources (i.e. detritus) in alluvial floodplain ecosystems (e.g., Harrel et al. 1996; McArthur and Moorhead 1996), and its role in the timber industry. Studies of *Taxodium* seedlings and trees have indicated a quadratic relationship between growth variables and flooding: growth is maximal at intermediate levels of flooding (Mitsch and Ewel 1979; Brown 1981; Conner and Day 1992). *Taxodium* is highly drought-sensitive (Elcan and Pezeshki 2002) and is not a

good competitor under dry conditions (Meganigal and Day 1992). Flooding not only increases soil moisture, but can also supply *Taxodium* with nutrient-laden sediments beneficial to growth (Mitsch et al. 1979; Brown 1981; Shanklin and Kozlowski 1985). Oxygen deprivation in the rooting zone under flooded conditions is avoided through several physiological mechanisms, including production of adventitious roots and aerenchyma tissue, or air-filled spaces in the roots. When flood duration is too long or flood depths too great, however, tolerance mechanisms are no longer effective in avoiding root hypoxia, and growth is hindered (Donovan et al. 1989; Effler and Goyer 2006).

The Savannah River was impounded in the 1950's near Augusta, Georgia by Thurmond Dam, a large hydroelectric facility (Fig. 1). Previous studies have suggested adverse effects of longer hydroperiods and large dam releases during the growing season on *Taxodium* regeneration and growth in the Savannah River floodplain (Birch and Cooley 1983; Schneider and Sharitz 1988; Sharitz et al. 1990). Growth and regeneration measurements in these studies were limited, however, to short periods of time in the post-dam era, or to particular hydrogeomorphic areas of the floodplain. Additionally, the relationships between germination, survival, and growth of *Taxodium* and the hydrological conditions of study sites were not directly quantified.

In this study, annual diameter growth of *Taxodium* on the Savannah River floodplain was measured using dendrochronological techniques that allowed for reconstruction of growth patterns over a 103-year period, spanning pre- and post-dam eras. Flooding patterns over this time frame were also reconstructed for the sites at which trees were sampled. The study objectives were twofold: (1) to identify the flooding patterns (depth, duration, and periodicity of floodwaters) of different hydrogeomorphic floodplain areas with *Taxodium*, and determine whether and in which way

Fig. 1 Average PDSI value during the growing season (Apr–Sept) for every year of tree growth record. “Wet” years were defined as having an average growing season value greater than 0.5, and “dry” years were defined as having an average growing season value less than −1.0. “Inter” (intermediate) years were defined as having average growing season values between −1.0 and 0.5. Dashed vertical line separates pre-dam from post-dam era. Asterisks indicate years used in this study



flooding patterns have changed because of dam construction and operation; and (2) to identify responses of *Taxodium* diameter growth to climate and flooding patterns, and to test whether these responses have changed due to alterations in flooding patterns by dam construction and operation.

Study Design and Hypotheses

The geomorphic context of flow alteration is critical in determining ecosystem response to flow alteration, because geomorphic features influence flow and disturbance regime (Poff et al. 2006). Three distinct hydrogeomorphic areas on the Savannah River floodplain supporting populations of *Taxodium* were identified: (1) low-lying areas on the banks of the main channel; (2) higher sites on top of the levee next to the main channel; and (3) low-lying areas behind the levee and away from the main channel, i.e. in the backswamp. These sites are termed river (RI), levee (LE), and backswamp (BS), respectively (Online Resource 1).

Previous work has demonstrated that growth of *Taxodium* trees in the Savannah River basin is positively related to both regional Palmer drought severity index (PDSI, which decreases with increasing severity of drought) (Stahle et al. 1988) and regional precipitation (Stahle and Cleaveland 1992). To isolate the effects of flooding and dam operations on tree growth, we selected years with similar precipitation and PDSI for pre- and post-dam comparisons and for growth contrasts by site. Years in the pre- and post-dam period were assigned to one of three groups (dry, intermediate, or wet) based on the PDSI value that year. Intermediate years were included in analyses in order to identify any potential non-linear trends that might be missed by only analyzing wet and dry years.

At RI sites, we expected that trees were affected little by drought in both the pre- and post-dam era, and that tree roots were saturated throughout the year. We anticipated that considerable surface flooding occurred in both pre- and post-dam eras; however, we expected more continuous surface flooding and fewer dry-down episodes in the post-dam era, particularly during drier years. This expectation was based on studies anecdotally reporting more continuous flooding in lower-lying areas of the Savannah River floodplain (Birch and Cooley 1983; Schneider and Sharitz 1988; Sharitz et al. 1990) and a study documenting higher seven-day low flows and higher baseflow during dry months (August–October) in the Savannah River main channel as a result of dam operations (Hale and Jackson 2003). Given these changes in hydrologic conditions, we hypothesized that RI trees would have higher growth during drier years in the post-dam era (due to reduced drought

stress). During wetter years, we hypothesized that RI trees would not show a change in response to flooding after dam construction, since fairly continuous inundation was expected in both pre- and post-dam eras.

BS sites were expected to experience more continuous periods of inundation and fewer dry-down episodes in the post-dam era than in the pre-dam era. Since the elevations of BS sites are slightly (<1 m) higher than RI sites, however, we anticipated that inundation of BS sites would be slightly more infrequent and of shorter duration than inundation of RI sites. As in RI sites, we hypothesized that the reduction in water level variability at BS sites would result in higher growth during dry years but lower growth during wet years in the post-dam era. Inundation was expected to be of longer duration during the post-dam era at BS sites, resulting in greater levels of stress during wet years in the post-dam period.

At LE sites, which are highest in elevation (~1 m higher than RI or BS sites), we expected less flooding in the post-dam era because of documented changes in hydrologic patterns of the Savannah River as a result of dam operations, i.e. a reduction in the magnitude of peak flows and lower flood recurrence in the main channel (Hale and Jackson 2003). In addition, a preliminary analysis of floodplain inundation using four channel cross-sections downstream of Thurmond Dam indicated that post-dam flows in the main channel have rarely been high enough to overtop the levee (Hale and Jackson 2003). We therefore hypothesized that LE trees would suffer more drought stress during dry years and greater growth during wet years in the post-dam era, since better-drained conditions at LE sites in the post-dam era should translate into less root anoxia during wet years.

Study Site The Savannah River Basin drains an area of 27,575 km² and flows through portions of North Carolina (NC), South Carolina (SC), and Georgia (GA) (USACE 1992). Thurmond Dam is located at river km (RK) 355 (distance from the mouth) on the fall line dividing the Piedmont Province and Coastal Plain (Online Resource 2). Our three study sites were located from 72 (RK 283) to 104 (RK 251) km below the dam (Online Resource 2). This 32-km reach is a low-gradient (mean slope=0.1 m/km), alluvial, meandering river (USACE 1992). Moving downstream, the three sites are: Silver Bluff Plantation at RK 283, Cowden Plantation around RK 270, and the Savannah River Site near Upper Three Runs at RK 251. This stretch was chosen to maximize the signal of hydrologic change in the tree growth record. We avoided areas adjacent to agriculture or areas extensively logged in the last century.

Alterations to the Savannah River Since 1948, the United States Army Corps of Engineers (USACE) has constructed

several impoundments in the Savannah River basin, primarily to reduce flood damage, generate hydropower, and supply water for municipal use (Meyer et al. 2003). Because Thurmond Dam is the oldest and farthest downstream dam, and re-regulates the flows released from all upstream dams, management regimes of the other dams are not directly relevant to flows on the reach of river we studied (Meyer et al. 2003). After dam construction, the USACE further modified the river for navigation below the dam by widening and deepening the channel and by constructing pile dikes and bend cutoffs. Although channel maintenance was discontinued in 1979, these channel modifications changed sediment load, sediment composition, and channel structure (USACE 1992).

Records from two USGS gages on the Savannah River indicate significant alteration in several hydrologic characteristics of flow within the channel following dam construction (Hale and Jackson 2003). Although changes over the last century in the hydrology of the main channel are well documented, little is known about the hydrologic regime of the floodplain. Preliminary analysis using a limited number of floodplain cross-sections suggests that in general, flooding has been greatly reduced on the floodplain (Hale and Jackson 2003). Some studies suggest that the lower-lying sloughs and backswamps adjacent to the channel have experienced greater magnitudes and longer durations of flooding during May and June following dam construction (Schneider and Sharitz 1988; Sharitz et al. 1990; McLeod et al. 2000).

Methods

Tree Sampling To minimize the potentially confounding effects of competition on individual tree growth, only *Taxodium* trees that appeared to be canopy dominants were sampled. To avoid surges in growth caused by release, or sudden availability of light due to death of nearby neighbors, trees located near large and/or obvious stumps were avoided. A total of 34 trees were cored in 2003: 13 RI trees, 10 LE trees, and 13 BS trees. A minimum of two cores were extracted from each tree using an increment borer (Stokes and Smiley 1968) at the same height where tree diameter was measured (above the swollen buttress). Cores were placed in straws, dried at 38°C for 2–3 days, affixed to wooden mounts, and sanded with a sequence of progressively finer-grit sand paper. A third of the trees (8 RI, 3 LE, and 2 BS) exhibited cross-dating problems and were excluded from analysis. Thus 20 of the 34 trees cored were used for statistical analysis: 4 RI, 6 LE, and 10 BS, yielding a total of 2,053 years of growth for potential analysis. We used 990 years of growth for the models described below.

Cross-Dating Trees used for analysis were of comparable age, ranging from 95–104 years old, with the exception of two BS trees (aged 69 and 70). To develop a chronology for RI, LE, and BS tree populations, calendar years were assigned to annual rings by carefully examining cores and noting missing or false rings on each core (Stokes and Smiley 1968). Ring widths were measured to the nearest μm using a Henson stage recorder and optical reader. A few cores had missing rings; those rings identified as missing were assigned a value of 3 μm with the assumption that a small, undetectable amount of growth had occurred in that year, despite the fact that no ring was visible.

Cross-dating for each core was verified using the program COFECHA (Holmes 1983; Grissino-Mayer 1997). If problems in dating (i.e., segments with low correlation to the master chronology) were flagged by COFECHA, increment cores were examined to correct the series if possible. Series that could not be corrected were excluded from growth analyses to ascertain that potential dating errors were not influencing the outcome of the analysis.

Due to the small number of trees in each site type category, analysis was undertaken to identify potential outlier chronologies within each site type. Site type growth averages for each year were recalculated 20 times, excluding one tree each time. The plotted data was then examined to identify any potential outlier trees that may influence subsequent data analysis. No outlier trees were evident upon examining the plotted data; trees within each site type closely conformed to the average growth record for their site type.

Hydrologic Sampling To determine the minimum river discharge required to cause standing surface water (hereafter called “flooding”) in the three types of floodplain sites, water levels were monitored at five points on the levee and two points in the backswamp for 6–9 months (September 2004 to May 2005). Water level data was collected using a Type F Stevens recorder, HOBO temperature loggers, and field observations. When a HOBO logger is submerged with water, the typical daily fluctuations in temperature recorded by the logger are severely dampened. Loggers were secured 15 and 30 cm above ground level (HOBO-15; HOBO-30). Flooding of a site was defined as the period when temperature fluctuations recorded by HOBO-15 were dampened relative to HOBO-30. Flooding at the Stevens recorder was defined as a recorded water level above zero. For RI sites, which were located almost directly on the channel, we used one flood episode to characterize the minimum level of channel water needed to flood RI sites.

Historic mean daily discharge (cfs) values were obtained from USGS gauge 02197000 at RK 302 (Online Resource 2). Precipitation, temperature, and

PDSI data were obtained from the National Oceanic and Atmospheric Administration (NOAA). Total monthly precipitation was obtained from a station in Aiken SC (NOAA Coop ID 380074). When precipitation data were missing from this station's record, data from Augusta GA (NOAA Coop ID 090500), Augusta Bush Field Airport (NOAA Coop ID 090495), and Waynesboro GA (NOAA Coop ID 099194) were used (Online Resource 2). The sites used in this study are located exactly on the border of climate division 5 in SC and 6 in GA. The three weather stations are all in climate division 6 in GA and within a 40 km radius of tree sampling sites. Mean monthly PDSI values were obtained for climate division 6 in GA.

Shallow groundwater depths were monitored every other week using piezometers for 4–9 months (January–September 2004) at four levee and two backswamp points. Both the maximum water level since the last visit and the current water level were recorded.

Growth Calculations Width measurements of rings were used to calculate annual diameter increment ($dinc_t$): $dinc_t = w_{1t} + w_{2t}$, where w_{1t} is the width of the ring assigned to year t on one side of the tree, and w_{2t} is the width of the ring assigned to year t on the other side of the tree. Diameter at core height for each year was then calculated in the following way: $diam_t = diam_i - dinc_t$, where $diam_t$ is the diameter at core height at the beginning of year t , $diam_i$ is the diameter at core height in the year the tree was cored (year i), and $dinc_t$ is the total amount of diameter growth in between years i and t (as determined by summing diameter increments over those years). Basal area increment (BAI) was calculated for each year using: $bai_t = ((diam_{t+1} / 2)^2 * \pi) - ((diam_t / 2)^2 * \pi)$, where bai_t is the BAI of a tree in year t , $diam_{t+1}$ is diameter at core height of the tree in year $t+1$, and $diam_t$ is diameter at core height of the tree in year t .

Selection of Pre- and Post-Dam Years The pre-dam era had, on average, less annual precipitation (data not shown) and lower PDSI values than the post-dam era (Fig. 1). To control for a potential climatic bias toward more flooding in the post-dam era, 48 years were selected (24 pre- and 24 post-dam) that were similar in climatic characteristics for hydrologic and growth analyses. These years were characterized as “dry,” “intermediate,” or “wet” based on PDSI values (Fig. 1).

Average PDSI was determined for the entire year (Jan–Dec), the growing season (GS; Apr–Sept), and the early GS (Apr–Jul). Early GS values were calculated separately for two reasons: (1) most growth of *Taxodium* occurs during the early GS, and growth starts to slow in August (Keeland et al. 1997), and (2) hurricane-induced precipitation is common during the late GS and could drastically alter GS PDSI. Annual, GS, and early GS PDSI were used to assign

years to “dry” (D: $PDSI \leq -1.0$), “intermediate” (I: $-1.0 < PDSI < 0.5$), or “wet” (W: $0.5 \leq PDSI$) categories (Palmer 1965). In six cases (1 D, 1 I, 4 W), categorization based on one of the PDSI measures differed from the others. To ensure a balanced and maximal number of pre- and post-dam years within each category, the average value of annual, GS, and early GS PDSI was used to determine the classification of a given year in these cases. This method appears to have been effective in classifying year type for the following reasons: (1) D, W, and I years had, on average, significantly ($p < 0.05$) different (D < I < W) annual, GS, and early GS PDSI and total precipitation in both pre- and post-dam eras; (2) D, W, and I years did not differ significantly ($p > 0.05$) in annual, GS, or early GS PDSI between pre- and post-dam eras (results not shown).

Surface Water Analyses Discharge at the USGS gage was noted during flooding episodes identified by the HOBO and Stevens recorders to determine the river discharge required to flood LE and BS sites. Because the time lag between increases in discharge at USGS 02197000 and increases in water level at each floodplain site was <24 h, the average of 15-min discharge readings at the gauge was determined for the 24-hr period preceding the time of a flood event at each recorder. The mean river discharge value for all flood events at each recorder was then averaged for all LE and all BS recorders, respectively. This last calculation was used as the minimum discharge at USGS 02197000 required to inundate each site type for the entire period of record (Table 1, 2nd column).

The minimum discharge required to flood RI sites was determined using the average of 15-min discharge measures at USGS 02197000 for a 24-hour period preceding a field observation of 15 cm of surface water at this site. RI sites were inundated with >15 cm of surface water during ~80% of field visits, and were located on the main channel, where there was no lag time between flooding in the main channel and flooding of the tree roots. One observation of the minimum water level required to flood the trees with 15 cm of water was therefore considered sufficient to characterize the hydrologic relationship between RI sites and the main channel.

The number of days annually during which mean daily discharge exceeded the minimum level required to flood each site was determined for each wet, intermediate, and dry year during the pre- and post-dam period. This value, or hydroperiod, was also determined for the growing season (GS) and early GS for LE and BS sites. A t-test assuming unequal variance was used to compare pre- and post-dam hydroperiods during dry, intermediate, and wet years. An ANOVA was used to compare hydroperiod between sites within dry, intermediate, and wet years (SAS Institute 2008).

Table 1 Comparison of hydroperiods among sites in pre- and post-dam eras. Hydroperiod refers to total number of days that a location experienced surface water during the growing season (maximum hydroperiod length=183 days). Discharge refers to the minimum mean daily discharge at USGS 020190000 required to flood a

location. Same letter(s) within a column indicate no significant difference ($p>0.05$) between locations and/or year types as determined by an ANOVA with pairwise Tukey's tests. Same letter(s) within a given row indicate no significant difference between pre- and post-dam means as determined by a t-test assuming unequal variance

Location	Discharge (cfs)	Year Type	Pre-Dam Range	Pre-Dam Mean \pm SE	Post-Dam Range	Post-Dam Mean \pm SE
River	>5,800	Dry	(37–102)	67 \pm 7 ^A	(3–183)	60 \pm 20 ^A
Backswamp	>10,500	Dry	(2–49)	20 \pm 4 ^D	(0–17)	4 \pm 2 ^G
Levee	>15,700	Dry	(0–16)	7 \pm 2 ^D	(0–4)	1 \pm 0.5 ^G
River	>5,800	Intermediate	(86–123)	108 \pm 8 ^B	(112–183)	146 \pm 16 ^B
Backswamp	>10,500	Intermediate	(19–54)	39 \pm 6 ^D	(5–24)	17 \pm 4 ^G
Levee	>15,700	Intermediate	(10–27)	18 \pm 3 ^D	(2–12)	9 \pm 4 ^{GH}
River	>5,800	Wet	(103–183)	152 \pm 9 ^C	(55–183)	146 \pm 13 ^{BC}
Backswamp	>10,500	Wet	(39–108)	75 \pm 8 ^E	(8–97)	43 \pm 8 ^F
Levee	>15,700	Wet	(18–60)	34 \pm 5 ^F	(0–74)	26 \pm 7 ^{FH}

To determine potential changes in the duration of floodwaters between pre- and post-dam periods at a site, the number of floods occurring in each year, GS, and early GS was calculated. A flood was defined as a period of at least 1 day during which mean daily discharge exceeded the minimum level required to inundate a site. The number of pre- and post-dam floods during each year type was compared using a t-test assuming unequal variance.

Analyses of Dam Impact on Growth To study the potential impact of dam construction on diameter growth of *Taxodium*, linear statistical mixed models were fit by SAS (proc MIXED, SAS Institute 2008). To account for year-to-year correlation in growth of a given tree, a repeated measures design was chosen to represent the data, with site type, year type, dam (pre or post), GS hydroperiod, and GS hydroperiod-squared as predictors of BAI. Proc MIXED analysis revealed autocorrelation between years in BAI; an autocorrelated variance structure (ar(1)) was therefore used in all mixed models. Two models were constructed. In the first, fixed effects were site type, year type, and dam; two-

and three-way interaction effects on BAI were also tested. This model was run with all three site types then run again three times for each individual site (Table 2). For the latter three runs, site type and all site type interaction effects were taken out of the model. Contrasts in proc MIXED were used to examine potential differences between site, dam, and year categories.

In the second model, fixed effects were site type, dam, GS hydroperiod, and GS hydroperiod-squared; two- and three-way interaction effects on BAI were also tested. Contrasts in proc MIXED were used to examine potential differences between site and dam categories. To examine more closely the range of hydroperiods under which growth was significantly different between site types and/or significantly different between pre- and post-dam periods, we “reset” the y-axis several times by subtracting the same value from all hydroperiod values used to construct the model. Re-setting was necessary due to the quadratic term in the model: when a quadratic term is included in a proc MIXED model, the linear term in the model represents the linear increase in the outcome variable (BAI) as the predictor variable (hydroperiod) increases with the quadratic term equal

Table 2 Proc MIXED results for the first model with year type (wet, dry, intermediate) and site type (river, levee, backswamp) as predictors; the model has been run separately for each site type to determine specific effects of dam on each site type. The predictand in all models is BAI; each column in the table is a predictor of BAI. P-values ≤ 0.15 are reported below for each variable; p-values above 0.15

are reported in the table as “ns” (not significant). Category contrasts indicate significant ($p \leq 0.05$) differences between BAI at different site types or during different year types for all years (pre- and post-dam). D = dry years, I = intermediate years, and W = wet years. RI = river, LE = levee, BS = backswamp

Site type	site type	year type	dam	year type*dam	Site type*year type	Site type*dam	Category contrasts ($p \leq 0.05$)
All	0.15	<0.0001	0.006	ns	ns	0.02	RI < BS,LE
RI		0.01	ns	ns			D < W
LE		0.0002	ns	ns			D < I < W
BS		<0.0001	0.01	ns			D < I,W

to zero. In our case, this would mean that the linear relationship between hydroperiod and BAI is represented by a straight line that crosses the y axis at $x=0$ days. As hydroperiod increases along the x-axis, linear comparisons between site types or between pre- and post-dam periods become increasingly meaningless, since the hydroperiod vs. BAI relationship is not modified by the curvature introduced by the quadratic term. Subtracting the same value from each hydroperiod value “moves” the y-axis to the right, allowing for growth response comparisons within a higher hydroperiod range. Values used for re-setting the model were chosen by examining regression curves and seeing where inflections in the quadratic curve occurred. Based on observed growth responses (Fig. 3), we re-ran the model with values of 10, 25, 35, 45, 60, and 80 days subtracted from each GS hydroperiod used in the model.

Several precautions were taken in analysis to ensure that the statistical significance of dam effects was not being driven by individual tree records or a difference in tree age between pre- and post-dam eras. To verify that the record from any individual tree was not exerting a disproportionate influence on the statistical significance of a predictor variable or model, both models were re-run 20 times with an individual tree record taken out each time. Since there were no changes in the significance of individual variables or models, we felt confident that no one tree was driving the results obtained. To ensure that pre- and post-dam growth differences were not being driven by a difference in tree age between eras, both models were re-run using the 6 years immediately preceding dam construction (1947–1952) and the 6 years immediately following dam construction (1954–1959); this analysis will subsequently be referred to as the “near-dam analysis.” The 6 year periods had equal proportions of dry, intermediate, and wet years (3 D, 1 I, 2 W), but the range of hydroperiods was narrower than in the analysis including all years, especially for LE sites (LE: 0–44 days, BS: 2–93 days, RI: 32–183 days).

Results

Hydrologic Characteristics of Study Sites Shallow groundwater levels were highly variable at LE sites during the year. BS sites showed a more consistent level of shallow groundwater that was closer to ground surface than LE sites; these sites were also flooded more often than LE sites (data not shown). A higher river discharge was required to inundate LE sites than BS or RI sites, and a higher river discharge was required to inundate BS sites than RI sites (Table 1). Because changes between pre- and post-dam hydrology were nearly identical when examining annual,

GS, and early GS hydrology, only GS data are presented below.

Pre- vs. Post-Dam Hydroperiod During dry years, LE and BS sites showed a highly significant ($p<0.005$) post-dam decrease in hydroperiod (Table 1); post-dam hydroperiod at these sites was ~20% of that seen in the pre-dam era. A decrease in hydroperiod during the post-dam era was also significant in LE and BS during intermediate years; post-dam hydroperiods were 40–60% of pre-dam hydroperiods (Table 1). During wet years, hydroperiods were shorter at BS and LE sites in the post-dam era; the difference was significant for BS sites, and marginally significant ($p=0.07$) for LE sites (Table 1). RI sites did not differ significantly in hydroperiod between pre- and post-dam periods during dry, intermediate, or wet years (Table 1).

RI sites had significantly longer hydroperiods than both LE and BS sites during all year types in both pre- and post-dam eras (Table 1). LE sites had shorter hydroperiods than BS sites, but this difference was usually not significant (Table 1). During wet years in the pre-dam era, all sites differed significantly in hydroperiod, in the order $LE < BS < RI$ (Table 1).

Pre- vs. Post-Dam Floods The number of GS floods was significantly lower post-dam during all year types at LE sites (Fig. 2). At BS sites, the number of floods decreased significantly after dam construction during wet and dry years (Fig. 2). The number of floods at RI sites did not differ significantly between pre- and post-dam periods in any year type (Fig. 2).

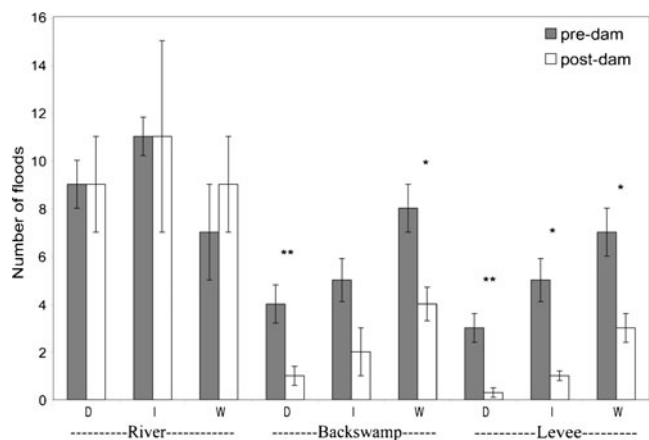


Fig. 2 Number of growing season floods in pre- and post-dam periods. Flood refers to presence of surface water at a site during consecutive days. A flood may, however, last one day (i.e. maximum number of possible floods=183). Significance is based on two-tailed t-tests between pre- and post-dam values for a given year and site type. *=significant ($p<0.05$) difference between pre- and post-dam; **= $p<0.005$. Bars represent standard error of the mean

Growth Responses to Hydrology Basal area increment growth (BAI) of LE and BS trees demonstrated a significant quadratic relationship with GS hydroperiod; growth was highest with intermediate hydroperiods at both sites (Fig. 3). BAI of RI trees also demonstrated a significant quadratic relationship with GS hydroperiod, although the quadratic effect was very small in the post-dam era (Fig. 3).

According to values predicted by the second mixed model, BAI was highest at LE sites at a GS hydroperiod of ~25 days

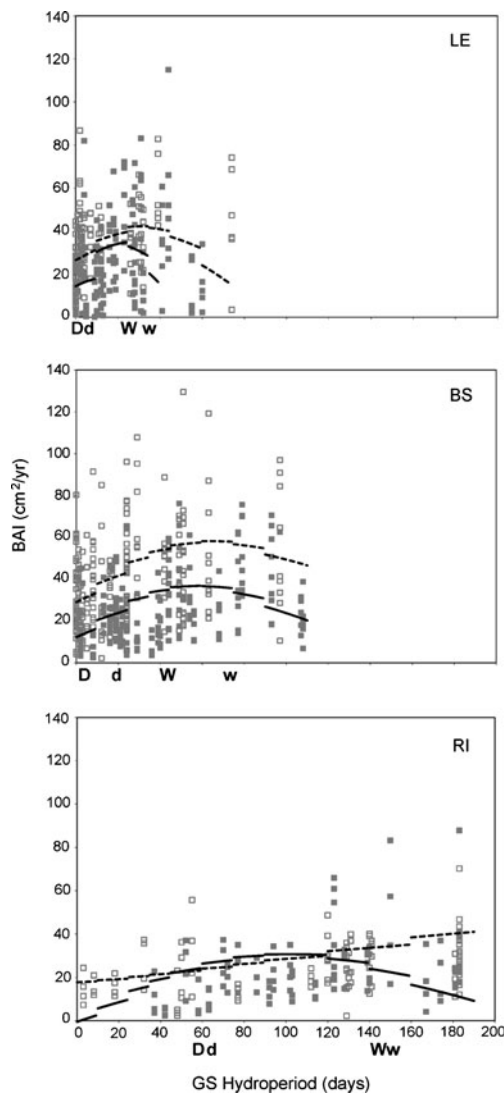


Fig. 3 Relationship between BAI and GS hydroperiod at each site type. Hydroperiod and hydroperiod-squared was a significant ($p < 0.05$) predictor of BAI in all 3 sites. Filled data points & solid lines = pre-dam; unfilled data points & dotted lines = post-dam. Lines are not continuous because the model was re-run for each range of values. Pre- and post-dam lines are significantly different from each other in BS sites; pre- and post-dam lines are significantly different in <10 and >60 day range at LE sites and <60 day range for RI sites. Bold letters below the x axis indicate the mean hydroperiod value for dry (d) and wet (w) years. Lower-case letters indicate the pre-dam era means and capital letters indicate the post-dam era means

in the pre-dam era and at a GS hydroperiod of ~30 days in the post-dam era (Fig. 3). At BS sites, BAI was highest at a GS hydroperiod of ~60 days in pre and post-dam eras (Fig. 3). BAI in RI sites was highest at hydroperiods of 90–120 days pre-dam and >180 days post-dam (Fig. 3). Overall, RI trees had significantly lower BAI than BS and LE trees in all year types (Table 2), significantly lower BAI than BS trees at all comparable GS hydroperiods (Table 3), and significantly lower BAI than LE trees in the 10–80 day GS hydroperiod range (Table 3). BAI was not significantly different between LE and BS trees over the range of hydroperiods and year types observed in this study.

Dam Effects on Growth In the first mixed model, with all site types included, both year type and dam were highly significant ($p \leq 0.001$) predictors of BAI (Table 2). Separate analyses of each site using the same model confirmed that year type was a significant predictor of growth at each site, but differences in growth between year types varied according to site. At RI sites, dry years resulted in significantly less growth than in wet years; at BS and LE sites, dry years resulted in significantly less growth than in intermediate or wet years. Growth during intermediate and wet years was not significantly different except at BS sites. The differences in growth response to year type among sites were not picked up by a significant site type*year type interaction (Table 2).

A site type*dam interaction was a significant predictor of BAI for all sites combined in the first mixed model (Table 2). Separate analyses of each site showed growth was higher in the post-dam era at BS sites, and not significantly different between pre- and post-dam eras at LE and RI sites (Table 2). Dam*year type was not a significant predictor of BAI in the first mixed model. The near-dam analysis using the first mixed model yielded nearly identical p-values to the model using 48 pre- and post-dam years. The one exception was that the dam effect was more significant in the models using only LE ($p = 0.05$) and only BS ($p < 0.0001$) trees, respectively.

The second mixed model indicated significant dam effects on BAI at BS sites due to higher growth at all hydroperiods in the post-dam era (Fig. 3). RI sites exhibited a significant dam effect at hydroperiods <60 days long, and LE sites exhibited a significant dam effect at hydroperiods <10 and ≥ 60 days long due to higher growth in years with these hydroperiods in the post-dam era (Fig. 3, Table 3). A significant site type*dam effect was found for hydroperiods ≥ 60 days (Table 3). This interaction effect indicates that dam construction may have had an influence on whether differences between sites at a given hydroperiod (Table 3, column 2) were significant or not. For example, LE and BS sites did not demonstrate significantly different BAI from one another on average, according to the second

Table 3 Proc MIXED results for the second model; the model has been run multiple times at a new baseline hydroperiod each time to determine the significance of site type, site type*dam, GS hydroperiod, dam and dam*GS hydroperiod effects. Site contrasts indicate significant ($p \leq 0.05$) differences between BAI at two or more site

types for all years (pre- and post-dam). P-values for site*dam and GS hydroperiod*dam effects are also shown (the site associated with the p-value shown is indicated in parentheses; LE sites did not experience hydroperiods >80 days). Ns = not significant

GS hydroperiod value (days)	Site contrasts ($p \leq 0.05$)	Site * dam (for all sites)	GS hydroperiod * dam (for each site)
≥ 0	RI < BS	ns	0.01 (LE), 0.0002 (RI)
≥ 10	RI < BS, LE	0.12	0.02 (LE), 0.001 (RI)
≥ 25	RI < BS, LE	0.09	0.0009 (RI)
≥ 35	RI < BS, LE	0.09	0.07 (LE), 0.0006 (RI)
≥ 45	RI < BS, LE	0.09	0.01 (LE), 0.0005 (RI)
≥ 60	RI < BS, LE	0.02	0.008 (LE), 0.0004 (RI)
≥ 80	RI < BS	0.001	0.0009 (RI)
≥ 120	RI < BS	0.006	

mixed model. But there might have been a significant difference between these two sites at hydroperiods less than 10 days in the post-dam but not the pre-dam era.

BS sites did not exhibit any significant interaction effects on BAI (Table 3). LE and RI sites, on the other hand, demonstrated dam interaction effects with both hydroperiod-squared (over all hydroperiod lengths), and hydroperiod (for all hydroperiods with the exception of the 25–35 day range at LE sites) (Table 3). These interaction effects were due to steeper curvature in the regression line between growth and hydroperiod in the pre-dam period (Fig. 3). In other words, growth at RI and LE sites was less sensitive to changes in hydroperiod in the post-dam era than in the pre-dam era.

The near-dam analysis yielded similar but not identical results to the analysis including all years. Significance of the variables described above was the same, with the exception of the following: (1) the dam effect was significant for LE (in the 10–25 day range) and BS sites (all hydroperiods) only; (2) the site type*dam effect was significant in the 25–60 day range; (3) BS sites exhibited a significant GS hydroperiod*dam effect over the entire range of hydroperiods (due to steeper curvature in the regression line in the post-dam period). These differences in results should be considered within the context of the second model's inclusion of continuous predictor variables (hydroperiod, hydroperiod-squared) rather than solely utilizing categorical predictor variables like the first model, and the smaller ranges of the continuous variables for the near-dam analysis than for the analysis including all years.

Discussion

The hydrology of LE and BS sites has changed significantly since dam construction—these sites have become

drier. The post-dam period has also been characterized by significantly higher annual BAI of *Taxodium* trees growing in several areas of the floodplain: BS trees are experiencing higher growth during all year types (dry, intermediate and wet) and growing season (GS) hydroperiods; LE trees are experiencing higher growth under GS hydroperiods less than 10 days (dry years) and equaling or longer than 60 days (wet years). RI sites, although not significantly drier, have been experiencing slightly shorter GS hydroperiods during wet and dry years; these sites have been experiencing significantly higher post-dam growth at hydroperiods shorter than 60 days (dry years). LE trees and RI trees are also significantly less responsive to increases or decreases in hydroperiod, as evidenced by a significant dam*hydroperiod effect for these sites. That drier conditions decrease flood stress during wet years is not surprising, but given the quadratic relationship found in this study between growth and flooding, drier conditions in the post-dam period during dry years would be expected to increase drought stress, leading to lower growth (Fig. 3). These findings suggest that growth of LE and BS trees may have been inhibited during all year types in the pre-dam period by stress due to root anoxia.

Shallow groundwater dynamics, and the potential development of deeper rooting depths in the post-dam era, may be playing a role in alleviating drought stress and leading to higher post-dam growth at LE and BS sites. Higher low flows in the main channel due to dam operations may be resulting in more available groundwater to tree roots at LE and BS sites during the late GS. The late GS does not typically support high tree growth levels in the Southeast, since it is characterized by high temperatures (and thus high evapotranspiration and drought stress) (Teskey et al. 1987). Certainly the results of stress due to root anoxia were apparent in RI trees, which are located in low-lying, nearly continuously flooded areas of the floodplain and grow in consistently wetter conditions than BS or

LE trees. Low growth of RI trees relative to BS trees over all hydroperiods and LE trees over intermediate hydroperiods suggests that flooding can serve as a stressor in the Savannah River floodplain.

Productivity at Floodplain Sites in Response to Pre- and Post-Dam Inundation Patterns BS sites were expected to be wetter in the post-dam period during wet and dry years, but the opposite was observed. That BS sites are drier in the post-dam era was surprising, given anecdotal observations in earlier studies of deep, continuous flooding in the backswamp attributed to dam operations (Birch and Cooley 1983; Schneider and Sharitz 1988; Sharitz et al. 1990). However, the latter two studies were conducted in backswamp areas more low-lying and more poorly drained than the sites observed in this study. Although hydrology was not explicitly measured in the previous studies, there is a good possibility that the sites were located at elevations intermediate in elevation to BS and RI sites or similar to RI sites. This possibility is supported in part by the observation that RI sites, the lowest-lying sites in this study, had a longer (not significant) GS hydroperiod and a significantly longer annual hydroperiod (data not shown) during intermediate years in the post-dam era.

BS sites were expected to have higher growth during dry years and lower growth during wet years in the post-dam era; this hypothesis was based, however, on the expectation that BS sites would be wetter in the post-dam era. In light of the shorter hydroperiods observed during wet and dry years at BS sites, we would have expected responses at BS sites like those anticipated for LE sites, i.e. lower growth during dry years and higher growth during wet years. Instead, growth of BS trees was significantly higher during all year types and across all hydroperiods in the post-dam era. That shorter hydroperiods and fewer floods at BS sites in the post-dam era would lead to higher growth in wet years is not surprising, since several studies have revealed higher *Taxodium* growth under more periodic vs. more continuous flooding (e.g., Megonigal and Day 1992). During dry years in the post-dam era, however, growth would be expected to be lower, due to higher drought stress (Mitsch and Ewel 1979; Shanklin and Kozlowski 1985; Fig. 3). Higher low flows in the post-dam era due to dam operations (Hale and Jackson 2003) have likely led to higher shallow groundwater levels at floodplain sites, which would reduce water stress during the late GS, leading to more growth during dry years in the post-dam era. As expected, LE sites were drier in the post-dam period during dry years; however, hydroperiod during wet years was not significantly different between pre- and post-dam eras. LE sites did have significantly fewer floods, implying that LE sites are experiencing longer floods during wet years in the post-dam period. The drier conditions during

dry years would be expected to decrease growth in LE trees (Fig. 3). However, LE trees had higher growth during dry years in the post-dam era. Higher growth at LE sites during dry years may, as in the case of BS sites, be due to higher shallow groundwater levels in the post-dam era.

It is possible that floodplain trees in this study developed deeper rooting zones in the post-dam era to better cope with drought stress during dry years. *Taxodium* seedlings and saplings in periodically flooded mesocosms have higher belowground biomass production than in continuously flooded mesocosms, and continuous flooding has been shown to inhibit root elongation in *Taxodium* seedlings (Pezeshki 1991; Megonigal and Day 1992; but see Pezeshki et al. 1999 and Day et al. 2006). There is little evidence of this phenomenon occurring in *Taxodium* past the age of three, however, since root biomass is difficult to assess in adult trees. The fact that the near-dam analysis demonstrated significantly higher average growth in LE and BS trees during all years following dam installation (including dry years) and a significant dam*GS hydroperiod effect in BS, LE, and RI trees also lessens the possibility that root development alone is responsible for higher growth during dry years. The presence of shallow groundwater and high clay content just below the soil surface at BS sites during our monitoring study supports the idea that water may still be available to trees belowground at BS sites. The high clay content of BS surface soils and our anecdotal observations of root content at depth in the field suggest it is unlikely that BS trees developed very deep (>1 m) root systems in the post-dam era. It is possible, however, that a reduction in flooded conditions increased lateral root development (Li et al. 2010), which may be aiding in water uptake during dry years. The LE sites have a clay layer deeper in the profile (1–2 m), with a silty/sandy A horizon; the potential for deeper root development in the post-dam era is therefore higher at LE sites. Since shallow groundwater was monitored at BS and LE sites during an intermediate year (annual PDSI=0.5, GS PDSI=-0.3, early GS PDSI=-0.4), additional monitoring during dry years would be necessary to confirm that groundwater availability is compensating for drought stress in the rooting zone.

A large body of literature supports the idea that long periods of deep, continuous flooding have an adverse effect on *Taxodium* growth (Mitsch and Ewel 1979; Harms et al. 1980; Keeland et al. 1997). Other studies considering the impacts of impoundment on diameter growth and survival of *Taxodium* have primarily looked at populations of trees upstream of impoundments (Harms et al. 1980; Stahle et al. 1992; Young et al. 1995; Keeland and Young 1997). These studies have found conflicting results, in that responses to flood regime change through time and according to pre-conditioning; however, more

continuous, deep flooding does seem to have an adverse effect on diameter growth in *Taxodium*. Our study examined potential differences in growth due to periodic vs. continuous flooding using hydroperiod and number of floods, but did not explicitly consider depth of flooding. A study of backswamp communities dominated by *Taxodium* in Louisiana and South Carolina indicated that depth of flooding may outweigh the importance of periodicity of flooding (Keeland et al. 1997). Trees subjected to shallow flooding, irrespective of whether the flooding was periodic or continuous, demonstrated greater growth and a longer growth phase than trees subjected to deep periodic flooding (Keeland et al. 1997). Flood magnitude in the Savannah River decreased sharply between pre- and post-dam eras (Hale and Jackson 2003), and growth at floodplain sites was often higher in the post-dam era than in the pre-dam era even within the same hydroperiod range. In addition, the growth response curve of RI and LE trees indicated less sensitivity to increases or decreases in hydroperiod length in the post-dam era. These findings support the idea that characteristics of flooding other than hydroperiod length, such as flood magnitude, and morphological reconfigurations of trees in response to flood regime change, such as root biomass allocation, are influencing the growth response of *Taxodium* to inundation at floodplain sites. Nearly continuous flooding at RI sites during wet and intermediate years means that these trees must invest more of their energy into morphological structures that allow the tree to avoid root anoxia. Tree growth at RI sites did exhibit a positive relationship with hydroperiod, but their lower growth in relation to LE and BS trees at comparable hydroperiods again suggests that soil characteristics, shallow groundwater dynamics, or other aspects of flood regime (such as depth) play a role in determining the nature of the relationship between flooding and diameter growth.

Flood Regime and Competition Studies conducted on the Roanoke River, North Carolina, which is similar in size to the Savannah and hydrologically regulated in similar ways, demonstrated that inundation during extremely wet years is the primary determinant of species composition on the floodplain (Townsend 2001). In post-dam wet years on the Roanoke, communities with *Taxodium* as a canopy dominant were flooded 125–275 days annually (Townsend 2001). At annual hydroperiods below 125 days, the relative dominance of *Taxodium* decreased to zero (Townsend 2001). This change in dominance is attributed to reduced seedling recruitment and survival, as well as reduced productivity of mature *Taxodium* relative to other species (Townsend 2001). The average annual hydroperiod at LE sites in our study was well below this range in both pre- and post-dam periods; *Taxodium* was not, however, a very

dominant species at LE sites relative to other species such as sycamore, maple, and elm. In BS sites, on the other hand, annual hydroperiod was within the range of 125–275 days in ~67% of wet years prior to dam construction, and in ~28% of wet years following dam construction.

Recent studies on the Savannah River examining recruitment in bottomland hardwood areas indicate low levels of *Taxodium* germination and recruitment in the post-dam era. A study examining recruitment between 1979 and 1989 in hardwood swamps on the Savannah River Site found that *Taxodium* trees ≥ 4.5 cm dbh showed low or negative net changes in basal area and stem density, and high mortality relative to recruitment (Jones et al. 1994b). In a four-year (1987–1990) study of seedling establishment, basal area of overstory *Taxodium* stems in 1987 was 3.3 m²/ha, but no *Taxodium* seedlings were found that year (Jones et al. 1994a). Further, although mean annual seedfall of *Taxodium* was relatively high throughout the study ($\sim 10^4$ – 10^5 seeds/yr/m² basal area), the mean annual percentage of these seeds germinating was 0% (Jones et al. 1994a). Using the PDSI classification scheme, most of the years of those germination and recruitment studies would be classified as dry, and a few were intermediate or wet. The lack of germination and/or high mortality of seedlings during all year types suggests that recruitment of *Taxodium* in the study examined is likely very low; whether this is due to dam operations is unclear.

Sample Size Sample size was small relative to the total population of *Taxodium* trees growing on the Savannah River floodplain; the trees analyzed may not be representative, therefore, of a larger trend throughout the Savannah River basin. Results were consistent, however, in all sampled trees, even though they were located 10–30 river km apart. Dendrochronological analysis of *Taxodium distichum* populations as small as 16–20 trees have been successfully used to characterize growth response to hydrology and to evaluate changes in growth response due to changes in hydrologic regime at a given site (Stahle et al. 1992; Young et al. 1995). Most RI trees sampled for this study posed crossdating problems and had to be excluded from analysis; more trees, particularly at RI sites, should be sampled in order to verify our results. However, our data provide strong initial evidence that annual productivity of *Taxodium distichum* has changed significantly as a result of construction and operations of Thurmond Dam, at least in areas up to 100 river km downstream of the dam.

Conclusions The hypothesized response of *Taxodium* growth at floodplain sites to hydrologic conditions was based on principles of the subsidy-stress hypothesis (Megonigal et al. 1997), which is the following: the

benefits of water and nutrient subsidies provided by flood waters are negated by physiological stresses imposed by either anaerobic soils (during wet years) or drought (during dry years) (Mitsch and Rust 1984; Magonigal et al. 1997). Findings of this study partly support this expectation: the quadratic relationship between hydroperiod and BAI at floodplain sites confirms findings of other studies suggesting that growth of *Taxodium* is inhibited by stress under conditions that are too wet or too dry (Mitsch and Ewel 1979; Conner and Day 1992). The higher growth patterns relative to RI trees and the positive growth response to dam installation of LE and BS trees, however, suggests that stress due to excessively wet conditions outweighs the stress of dry conditions at these sites. In other words, flood pulses on the Savannah River floodplain prior to dam installation were primarily a stressor, not a subsidy, for *Taxodium* populations on LE and BS sites. Another possibility is that higher low flows in the post-dam era due to dam operations (Hale and Jackson 2003) have also increased shallow groundwater levels, preventing roots from drying out completely during the late growing season, when temperatures and drought stress should typically be highest.

Several groups are in the process of designing and implementing plans to restore and maintain a flow regime on the Savannah River that more closely mimics pre-dam conditions (Richter et al. 2006). Until now, the effects of Thurmond Dam on the hydrologic characteristics of the floodplain have not been known, and the effects of dam operations on forest productivity have not been explicitly studied. Results of this study indicate that hydroperiod is an important determinant of adult tree growth, and that the flooding-growth relationship differs between hydrogeomorphic areas and year types. Hydrogeomorphic location, annual climatic variation, and hydroperiod appear, therefore, highly germane to future research and management designs for forest species on this floodplain and others like it in the Southeastern United States. Productivity studies targeting the relationship between instream flows and floodplain forest canopy dominants are a needed contribution to developing management schemes that optimize ecological integrity of affected river ecosystems such as the Savannah River (Richter et al. 2003).

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References

- Bayley PB (1995) Understanding large river-floodplain ecosystems. *Bioscience* 45:153–159
- Birch JB, Cooley JL (1983) The effect of hydroperiod on floodplain forest production. Technical Completion Report USDI/OWRT, Project No. B-155-GA. Institute of Ecology, University of Georgia, Athens
- Brantley CG, Day JW, Lane RR, Hyfield E, Day JN, Ko JY (2008) Primary production, nutrient dynamics, and accretion of a coastal freshwater forested wetland assimilation system in Louisiana. *Ecological Engineering*. doi:10.1016/j.ecoleng.2008.05.004
- Brown S (1981) A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. *Ecological Monographs* 51:403–427
- Conner WH, Day JW (1992) Diameter growth of *Taxodium distichum* (L.) Rich. and *Nyssa aquatica* L. from 1979–1985 in four Louisiana swamp stands. *American Midland Naturalist* 127:290–299
- Day RH, Doyle TW, Draugelis-Dale RO (2006) Interactive effects of substrate, hydroperiod, and nutrients on seeding growth of *Salix nigra* and *Taxodium distichum*. *Environmental and Experimental Botany*. doi:10.1016/j.envexpbot.2004.10.009
- Donovan LA, Stumpff NJ, McLeod KW (1989) Thermal flooding injury of woody swamp seedlings. *Journal of Thermal Biology*. doi:10.1016/0306-4565(89)90037-5
- Effler RS, Goyer RA (2006) Baldcypress and water tupelo sapling response to multiple stress agents and reforestation implications for Louisiana swamps. *Forest Ecology and Management*. doi:10.1016/j.foreco.2006.02.011
- Elcan JM, Pezeshki SR (2002) Effects of flooding on susceptibility of *Taxodium distichum* L. seedlings to drought. *Photosynthetica*. doi:10.1023/A:1021381204684
- Grissino-Mayer HD (1997) Computer assisted, independent observer verification of tree-ring measurements. *Tree-Ring Bulletin* 54:29–41
- Hale VC, Jackson CR (2003) Hydrologic modifications to the lower Savannah River. In: Hatcher KJ (ed) Proceedings of the 2003 Georgia Water Resources Conference. University of Georgia, Athens
- Harms WR, Schreuder HT, Hook DD, Brown CL, Shropshire FW (1980) The effects of flooding on the swamp forest in Lake Ocklawaha, Florida. *Ecology* 61:1412–1421
- Harrel JB, Allen CM, Hebert SJ (1996) Movements and habitat use of subadult alligator snapping turtles (*Macrocllemys temminckii*) in Louisiana. *American Midland Naturalist* 135:60–67
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bulletin* 43:69–78
- Jones RH, Sharitz RR, Dixon PM, Segal DS, Schneider RL (1994a) Woody plant regeneration in four floodplain forests. *Ecological Monographs* 64:345–367
- Jones RH, Sharitz RR, James SM, Dixon PM (1994b) Tree population dynamics in seven South Carolina mixed-species forests. *Bulletin of the Torrey Botanical Club* 121:360–368
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106:110–127
- Keeland BD, Young PJ (1997) Long-term growth trends of baldcypress (*Taxodium distichum* (L.) Rich.) at Caddo Lake, Texas. *Wetlands*. doi:10.1007/BF03161522
- Keeland BD, Conner WH, Sharitz RR (1997) A comparison of wetland tree growth response to hydrologic regime in Louisiana and South Carolina. *Forest Ecology and Management*. doi:10.1016/S0378-1127(96)03901-1
- Li C, Zhong Z, Geng Y, Schneider R (2010) Comparative studies on physiological and biochemical adaptation of *Taxodium distichum*

- and *Taxodium ascendens* seedlings to different soil water regimes. Plant and Soil. doi:10.1007/s11104-009-0174-z
- Lugo AE (1978) Stress and ecosystems. In: Thorp JH, Gibbons JW (eds) Energy and environmental stress in aquatic systems. US Department of Energy, Washington, D.C., pp 62–101
- McArthur JV, Moorhead KK (1996) Characterization of riparian species and stream detritus using multiple stable isotopes. *Oecologia* 107:232–238
- McLeod KW, Reed MR, Wike LD (2000) Elevation, competition control, and species affect bottomland forest restoration. *Wetlands*. doi:10.1672/0277-5212(2000)020[0162:ECCASA]2.0.CO;2
- Megonigal JP, Day FP (1992) Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. *Ecology* 73:1182–1193
- Megonigal JP, Conner WH, Kroeger S, Sharitz RR (1997) Above-ground production in Southeastern floodplain forests: a test of the subsidy-stress hypothesis. *Ecology* 78:370–384
- Meyer J, Alber M, Duncan W, Freeman M, Hale C, Jackson R, Jennings C, Palta M, Richardson E, Sharitz R, Sheldon J, Weyers R (2003) Summary report supporting the development of ecosystem flow recommendations for the Savannah River below Thurmond Dam. Report to The Nature Conservancy, Savannah
- Mitsch WJ, Ewel KC (1979) Comparative biomass and growth of cypress in Florida wetlands. *American Midland Naturalist* 101:417–426
- Mitsch WJ, Rust WG (1984) Tree growth-responses to flooding in a bottomland forest in northern Illinois. *Forest Science* 30:499–510
- Mitsch WJ, Dorge CL, Wiemhoff JR (1979) Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. *Ecology* 60:1116–1124
- Odum EP, Finn JT, Franz EH (1979) Perturbation theory and the subsidy-stress gradient. *Bioscience* 29:349–352
- Palmer WC (1965) Meteorological drought. Research Paper No. 45, U.S. Department of Commerce Weather Bureau, Washington, D.C.
- Pezeshki SR (1991) Root responses of flood-tolerant and flood-sensitive tree species to soil redox conditions. *Trees-Structure and Function* 5:180–186
- Pezeshki SR, DeLaune RD, Anderson PH (1999) Effect of flooding on elemental uptake and biomass allocation in seedlings of three bottomland tree species. *Journal of Plant Nutrition*. doi:10.1080/01904169909365729
- Poff NL, Bledsoe BP, Cuhaciyan CO (2006) Hydrologic variation with land use across the contiguous United States: Geomorphic and ecological consequences for stream ecosystems. *Geomorphology*. doi:10.1016/j.geomorph.2006.06.032
- Richter BD, Mathews R, Wigington R (2003) Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications* 13:206–224
- Richter BD, Warner AT, Meyer JL, Lutz K (2006) A collaborative and adaptive process for developing environmental flow recommendations. *River Research and Applications*. doi:10.1002/rra.892
- SAS Institute (2008) Version 9.2. SAS Institute, Cary
- Schneider RL, Sharitz RR (1988) Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* 69:1055–1063
- Shanklin J, Kozlowski TT (1985) Effect of flooding of soil on growth and subsequent responses of *Taxodium distichum* seedlings to SO₂. *Environmental Pollution (Series A)* 38:199–212
- Sharitz RR, Schneider RL, Lee LC (1990) Composition and regeneration of a disturbed river floodplain forest in South Carolina. In: Gosselink JG, Lee LC, Muir TA (eds) Ecological processes and cumulative impacts. Lewis Publishers Inc, Chelsea, pp 195–218
- Stahle DW, Cleaveland MK (1992) Reconstruction and analysis of spring rainfall over the Southeast U.S. for the past 1000 years. *Bulletin of the American Meteorological Society*. doi:10.1175/1520-0477(1992)073<1947:RAAOSR>2.0.CO;2
- Stahle DW, Cleaveland MK, Hehr JG (1988) North Carolina climate changes reconstructed from tree rings: A.D. 372 to 1985. *Science*. doi:10.1126/science.240.4858.1517
- Stahle DW, VanArsdale RB, Cleaveland MK (1992) Tectonic signal in baldcypress trees at Reelfoot Lake, Tennessee. *Seismological Research Letters* 63:439–447
- Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. University of Chicago Press, Chicago
- Teskey RO, Bongarten BC, Cregg BM, Dougherty PM, Hennessey TC (1987) Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the characteristics of loblolly pine (*Pinus taeda* L.). *Tree Physiology*. doi:10.1093/treephys/3.1.41
- Townsend PA (2001) Relationships between vegetation patterns and hydroperiod on the Roanoke River Floodplain, NC. *Plant Ecology*. doi:10.1023/A:1011996822576
- US Army Corps of Engineers (1992) Reconnaissance Report: Lower Savannah River Environmental Restoration. Savannah District, South Atlantic Division
- Young PJ, Keeland BD, Sharitz RR (1995) Growth response of baldcypress [*Taxodium distichum* (L.) Rich.] to an altered hydrologic regime. *American Midland Naturalist* 133:206–212