SITE CONDITION, STRUCTURE, AND GROWTH OF BALDCYPRESS ALONG TIDAL/NON-TIDAL SALINITY GRADIENTS

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Abstract: This report documents changes in forest structure and growth potential of dominant trees in salt-impacted tidal and non-tidal baldcypress wetlands of the southeastern United States. We inventoried basal area and tree height, and monitored incremental growth (in basal area) of codominant baldcypress (*Taxodium distichum*) trees monthly, for over four years, to examine the inter-relationships among growth, site fertility, and soil physico-chemical characteristics. We found that salinity, soil total nitrogen (TN), flood duration, and flood frequency affected forest structure and growth the greatest. While mean annual site salinity ranged from 0.1 to 3.4 ppt, sites with salinity concentrations of 1.3 ppt or greater supported a basal area of less than 40 m^2/ha. Where salinity was < 0.7 ppt, basal area was as high as 87 m^2/ha. Stand height was also negatively affected by higher salinity. However, salinity related only to soil TN concentrations or to the relative balance between soil TN and total phosphorus (TP), which reached a maximum concentration between 1.2 and 2.0 ppt salinity. As estuarine influence shifts inland with sea-level rise, forest growth may become more strongly linked to salinity, not only due to salt effects but also as a consequence of site nitrogen imbalance.

Key Words: climate change, fertility, flooding, hydroperiod, nitrogen, phosphorus, tidal swamp

INTRODUCTION

Tidal freshwater forested wetlands (or tidal swamps) comprise at least 200,000 ha in the southeastern United States. The greatest concentration of these wetlands occurs along the Atlantic Coast of Georgia, South Carolina, and Virginia where tidal range is relatively broad (Field et al. 1991, Doyle et al. 2007b). Tidal swamps normally occupy the upper intertidal zone between uplands and marsh, and thus have the capacity to influence water quality both downstream and upstream with tidal ebbs and flows. Yet, they are very responsive to subtle changes in climatic extremes (e.g., drought, storm surge, chronic salinization) that may influence site condition. This has historically led to the inland migration of tidal swamps under rising sea levels (Wanless 1989, Brinson et al. 1995, Williams et al. 1999). In addition, a number of historically tidal swamps have been isolated from tidal influence by human alteration of the landscape (Conner et al.

1981, Gresham and Hook 1982). Changes in forest growth potential that occur as habitats shift between non-tidal and tidal states, or in mean salinity concentrations, are not well understood.

Many coastally restricted wetlands are at least periodically influenced by salinity. Tidal freshwater wetlands in general are defined as occurring at salinities below 0.5 ppt (Odum et al. 1984, see also Simpson et al. 1983), but during periods of drought, storm surge, or even strong tides, they must periodically cope with salinity pulses (Baldwin 2007, Doyle et al. 2007a). An important transition occurs as mean salinity levels creep to 2 ppt, at which point many freshwater swamp forests are at advanced stages of conversion to oligohaline or brackish marsh (Hackney et al. 2007). During these transitory stages, salt tolerance of both woody and herbaceous plants may replace flood tolerance in controlling plant community composition, growth, and productivity. Salt tolerance studies have been conducted on a
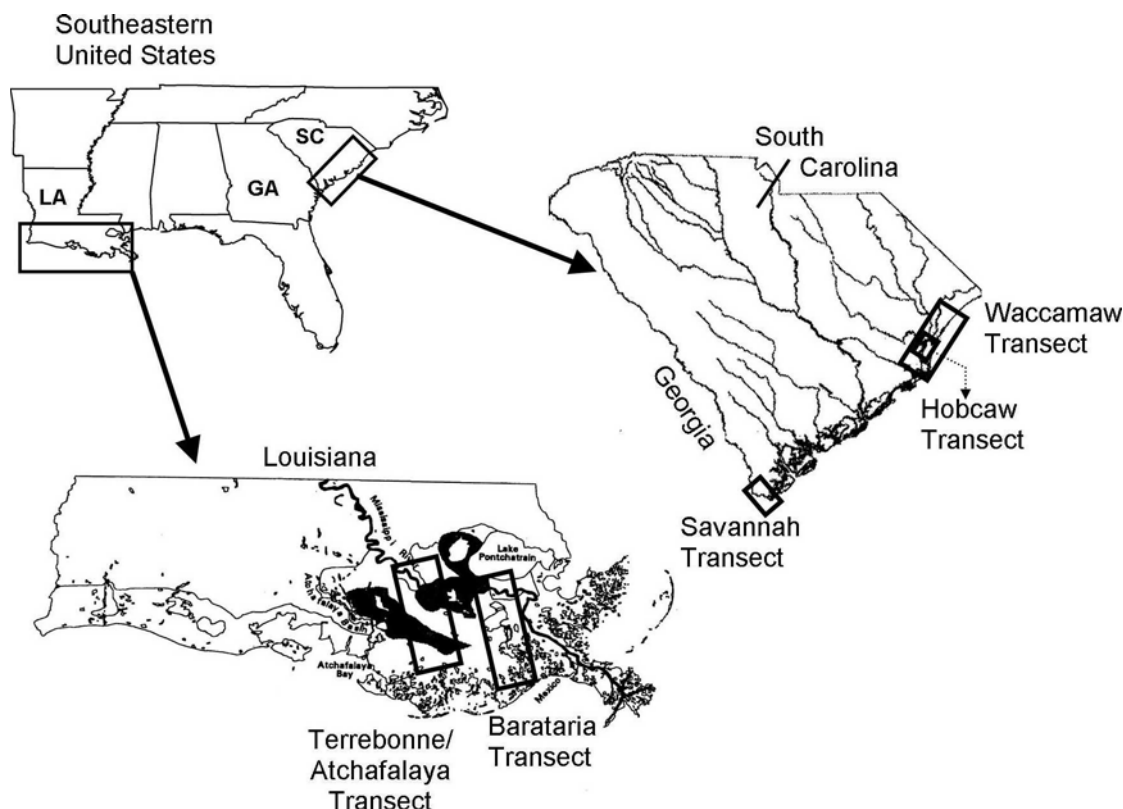
Figure 1. General location of landscape transects in South Carolina (SC), Georgia (GA), and Louisiana (LA). Three or four tidal/non-tidal baldcypress swamp sites were located along each transect, representing a range of site conditions indicative of degradation along respective coastlines.

range of tidal swamp species, from flood sensitive oaks (*Quercus* spp.) to hardwoods and baldcypress (*Taxodium distichum* (L.) L.C. Rich.) (see review by Krauss et al. 2007). Among all native tree species examined, baldcypress exhibits the greatest degree of salt tolerance both as seedlings (Pezeshki 1990, Conner and Askew 1992, McLeod et al. 1996) and as mature canopy trees (Conner et al. 2007). Hence, along with flood regime, climate change-induced salinization has the effect of driving tidal and non-tidal swamp stands to a baldcypress monoculture as a stage of degradation.

In this study, we report on several years of field measurement from coastal baldcypress-dominated tidal and non-tidal swamp sites established along landscape transects in Louisiana, South Carolina, and Georgia. Each landscape transect includes at least three sites established under salinity gradients ranging from fresh to oligohaline, under hydrological gradients ranging from non-tidal to strongly tidal, and under a range of relative fertilities. Our specific interest lies in determining how standing forest structure of tidal and non-tidal baldcypress swamps is affected by reductions in individual tree growth rates along various salinity and hydrologic gradients.

METHODS

Study Sites

Sites were selected along five landscape transects in coastal Louisiana, South Carolina, or Georgia (Figure 1). Each landscape transect had one degraded site established alongside marsh, with the other two sites located progressively upstream to represent moderately degraded and healthy stands. For South Carolina and Georgia, transects were associated with rivers and tidal creeks, while in Louisiana, transects were associated with more complex systems of interconnected bayous and open water bodies. Degree of degradation was determined by apparent tree stress and understory invasion by marsh species into stands (especially *Sagittaria lancifolia* L., *Typha* sp., *Spartina cynosuroides* (L.) Roth). Hence, we hypothesized in advance that these sites were being degraded by proximity to the estuary and that salinity was our principal driver of environmental degradation.

Sites in South Carolina and Georgia were selected along the Waccamaw and Savannah Rivers (Figure 1). The Waccamaw River, which doubles as the Atlantic Intracoastal Waterway, includes 11 water-

sheds and encompasses an area of approximately 253,000 ha, slightly over 20% of which is forested wetland (SCDHEC 2000). The Waccamaw River flows across the South Carolina and North Carolina state line to join the Sampit and Pee Dee Rivers in Winyah Bay. Two transects were located within the drainage basin of the lower Waccamaw River. The first transect, referred to as the "Waccamaw Transect", includes a freshwater site on Richmond Island (Waccamaw Upper, approximately river-km 50), a moderately degraded site on Butler Island (Waccamaw Middle, approximately river-km 31), and a degraded site along the lower Sampit River (Waccamaw Lower, approximately river-km 17). The second transect, referred to as the "Hobcaw Transect," is composed of four sites, including two freshwater sites within Hobcaw Barony in George-town, South Carolina. Hobcaw Barony connects with Winyah Bay via a tidal distributary within the Waccamaw River's drainage basin; tidal influences to the sites are delayed by the presence of a causeway with small culverts. Hobcaw Transect length is shorter relative to all other transects, with hydrologically perched (Crabhaul Swamp) and hydrologically connected (Reserve Upper) freshwa-ter sites between 3 km and 0.25 km from the marsh edge, respectively. Moderately (Reserve Middle) and highly (Reserve Lower) degraded sites were located approximately 150 m and 0 m from the edge of the marsh, respectively, and are connected by surface and groundwater flow to a nearby marsh, and to Reserve Upper.

The "Savannah Transect" was established along the lower Savannah River on the South Carolina and Georgia border. Savannah River discharges are affected by three dams upstream, constant dredging of the river, and historically by a one-way tidal flap gate installed along one of three channel braids to the Savannah River at river km-23 just upstream of the City of Savannah (Duberstein and Kitchens 2007). As tides flowed upstream, a salt water wedge was pushed farther up the Savannah River and, along with greater flow areas as a consequence of dredging, influenced wetlands via salinization (Pearlstein et al. 1993). The cumulative impacts of a tide gate that was commissioned in 1977 and removed in 1991 led to dramatic shifts in marsh salinity and vegetative community structure (La-tham 1990, Georgia Ports Authority 1998), and minor shifts in tidal swamp salinity (< 1 ppt) with the possibility of residual growth impacts to the tidal forests in Savannah National Wildlife Refuge (Duberstein and Kitchens 2007). Sites along the Savannah Transect were established at approxi-mately river-km 39 (Upper, fresh water), river-km 28

(Middle, moderately degraded), and river-km 26 (lower, highly degraded).

Sites in Louisiana were associated with either the Terrebonne/Atchafalaya Basin or the Barataria Basin (Figure 1). The three sites on the "Terre-bonne/Atchafalaya Transect" ranged from perma-nently to periodically flooded. Historically, large areas of this basin were tidal, but intense land manipulation within the Louisiana coastal zone has confined much tidal swamp area to remnant tidal positions within levees. None of the three sites along this transect are actively tidal. Highly degraded (Mandalay), moderately degraded (Bayou Teche), and freshwater sites (Bayou Chevreuil) were located near Houma, Franklin, and Thibodaux, Louisiana, respectively. The "Barataria Transect" was estab-lished in the Barataria Basin of Louisiana, and includes a strongly degraded, seasonal microtidal site (Fleming) near the Town of Lafitte. This transect also includes a moderately degraded micro-tidal site (Treasure Island) and impounded freshwa-ter site (Jean Lafitte) in Jean Lafitte National Historical Park and Preserve.

Conditions found in tidal and non-tidal baldcy-press swamps reported here span a range of site histories, diversity of flood frequencies and dura-tions, and salinity. Hydrographic detail further demonstrates the variation in tidal signature, flood frequency, and flood duration between coasts and along specific transects (Figure 2).

Plot Establishment and Forest Measurements

Peak years of rice agriculture (circa. 1670–1860) and logging (circa. 1880–1920) began the conversion of nearly all coastal swamps from old-growth to either regenerating forests, or where regeneration could not occur, marsh. Climatic conditions of the 1920's and 1930's were favorable for regeneration of baldcypress, which require water drawdown for germination (Mattoon 1915, Demaree 1932). Thus, all of the tidal/non-tidal baldcypress swamps reported here are second-growth forests with different site histories, are greater than 75 years of age based on ring counts (T.W. Doyle, unpubl.), and have closed canopies or deteriorating canopies that were once closed.

Sites were established using paired, rectangular 20 $\times$ 25-m plots encompassing a combined area of 1000 m^2 (0.1 ha). Freshwater stands were always continuous with multiple ha of swamp forest, while highly degraded stands were almost always small and often just large enough to establish a 0.1 ha sampling design. All plots were established with a buffer at least as wide as the dominant tree height from open areas, levees, and water bodies. Plots
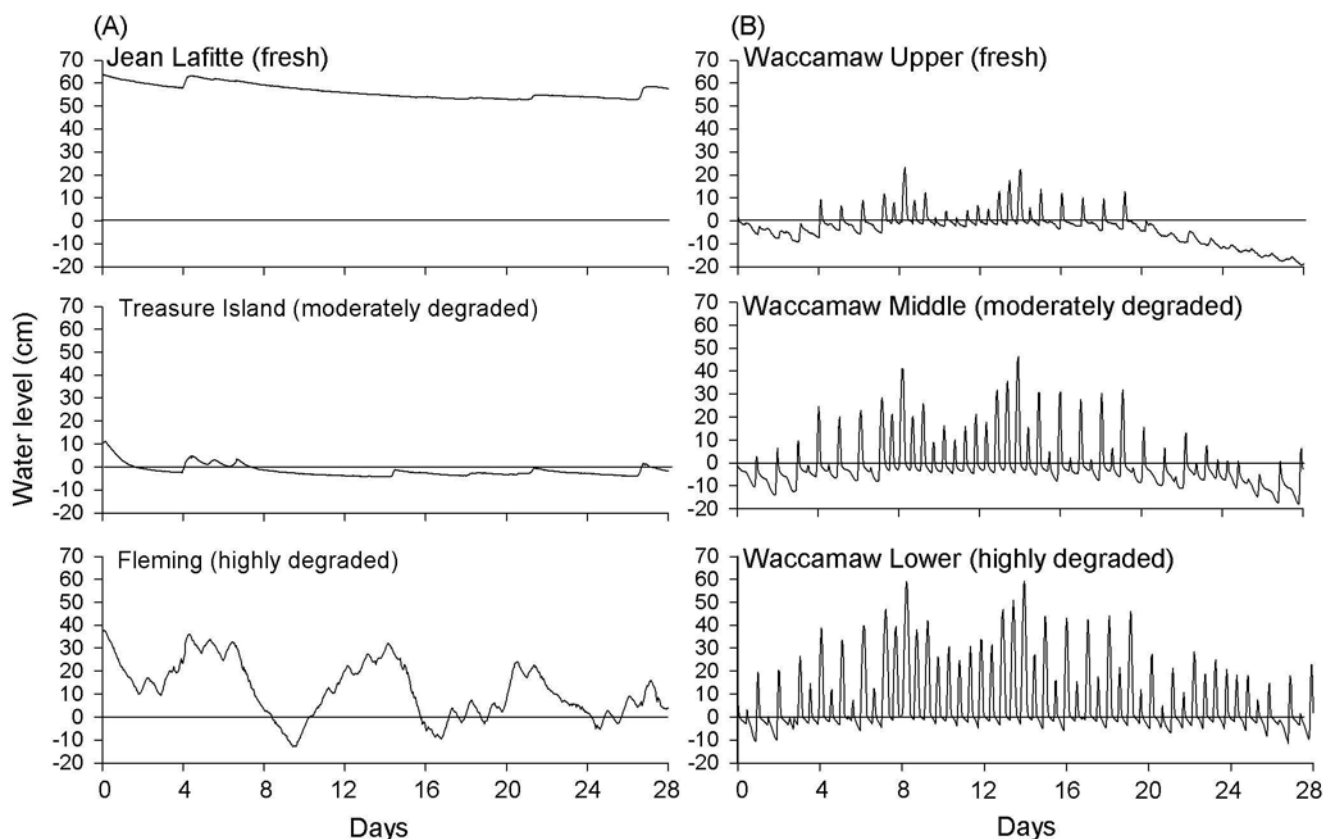
Figure 2. Representative hydrographs from sites along the A) Barataria Transect and B) Waccamaw Transect. A zero reading on the y-axis depicts the soil surface of topographic lows (hollows).

along the Waccamaw, Savannah, Terrebonne/Atchafalaya, and Barataria Transects were established within 100 m of a major river or canal corridor; "backswamp" locations were not sampled (*sensu* Duberstein and Kitchens 2007). Sites along the Hobcaw Transect were established along a small drainage at the landward edge of a tidal marsh.

Basal area (i.e., cumulative diameter of standing trees at a height of 1.3 m: DBH), stand density, and species composition of all trees greater than 10-cm DBH were assessed within each plot on every site using standard diameter tapes. Height measurements were taken on at least 20 representative codominant baldcypress trees on each site using a laser height device (Impulse 200, Laser Technology, Inc., Englewood, Colorado, USA).

We installed dendrometer bands on 20 codominant baldcypress trees on each site and re-measured bands monthly from August 2004 (for many plots) through July 2007. Dendrometer bands are designed to attach firmly around the entire circumference of a tree at standard DBH (i.e., avoiding fluted portions of stem), and to measure fine-scale circumference shrink and swell (Hall 1944, Cattelino et al. 1986). Small changes in circumference increment are converted to individual tree basal area increment (BAI), which provides a relative growth rate that better accounts for differences in initial tree size (Allen et al. 2005). Stainless steel dendrometers were installed and tightened with stainless steel springs after first scraping spongy bark off of each tree with a rasp to ensure a tight fit. Dendrometers are precise in measurement (Keeland and Sharitz 1993) and have a decadal life-span.

Physico-chemical Characterization

A water level recorder was placed between plots on each site to record hydrologic character on an hourly basis. Wells were dug within interior swamp locations. Each 7.6-cm-diameter PVC pipe was inserted at topographic low positions (within hollows) to a depth of approximately 1 m, and backfilled with gravel. Vented pressure transducers were placed at the bottom of each well and connected to a data logger sealed with a plastic cap (Infinities USA, Port Orange, FL, USA). Data were downloaded every five months from August 2004 to July 2007, and were used to calculate flood duration, flood frequency, and water table depth.

Four salinity wells were inserted on each site and were positioned to represent the four extreme corners of the two-plot layout. Screened, 3.2-cm PVC wells were slotted and inserted to a 0.6-m depth and capped. Salinity and temperature were measured monthly with a portable meter (Model 30, YSI Inc., Yellow Springs, OH, USA) after wells were first pumped of residual water and allowed to backfill with fresh pore water.

In June 2005, soil samples were collected from three of the four corners of each plot, for a total of six soil samples per site. Samples were taken at depths of 0–15 cm and 15–30 cm using a longitudinally sectioned, 10-cm-diameter PVC extractor. Since results varied little by depth, depths were pooled. Soil bulk density (BD), total nitrogen (TN), and total phosphorus (TP) were determined for each sample. Soil BD was calculated as a simple function of dry weight and sample volume assuming minimal compaction. Where surface compaction did occur (on two sites), we used density data from the 15–30 cm horizon only, where compaction was minimal. TN concentrations were determined with a CN elemental analyzer (Flash EA 1112, ThermoFinnigan, Wigan, UK) on dried and pulverized samples. Total phosphorus concentrations (TP) were determined by a contract laboratory (Louisiana State University, Wetland Biogeochemical Analytical Services, Baton Rouge, Louisiana, USA) by ashing samples at 550°C and extracting TP with 1 N hydrochloric acid. TP was measured through spectroscopy after an acid-fluoride extraction (Aspila et al. 1976). Soil TN and TP data were reported as bulk-density-adjusted concentrations to account for a broad range of bulk density values among sites (0.125–0.544 g/cm^3: Table 1).

Statistical Analyses

Sample units for individual parameters varied. For stand basal area, the sample unit was the individual site. The sample unit for tree height and mean BAI was the individual tree, which was replicated consistently among plots within site. The sample unit for soil data was the individual location within each site. All data were analyzed for among-site differences with an analysis of variance (ANOVA) after a square-root transformation (Proc Mixed, SAS Institute 2007). Plots were nested within site in a split-plot analysis framework. All data were normal with homoscedastic variance after transformation. Hence, this first analysis was used to determine whether differences existed for all parameters among sites ($\alpha = 0.05$).

We then used non-metric multidimensional scaling (PC-ORD, Version 5.1, McCune and Mefford 2006) to ordinate basal area, tree height, and BAI variables by plot. Non-metric multidimensional scaling ordinations (NMS) used a Sorensen distance measure, a random starting configuration, and 250 runs of both real and randomized data to determine the optimal dimensionality (number of axes). After evaluating the reduction in stress obtained by inclusion of each axis (see Results), a two-dimensional solution (final stress of 3.41) was chosen and 100 runs with real data were used in the final ordination. Vector overlays of all site edaphic factors measured were used as a guide for hypothesis generation and subsequent confirmatory analyses (i.e., multiple regression, quantile regression, and univariate analyses as described below). Those variables with correlations greater than $r^2 = 0.24$ to either axis were included in further analyses.

Second, we analyzed tree height and mean BAI with a step-wise, multiple regression procedure (Proc GLMSelect: SAS Institute 2007). Individual salinity, hydrology, and soil parameters were swapped in and out and tested against height and BAI of codominant baldcypress trees for best fit. The step-wise procedure used a Schwarz Bayesian Information Criterion (SBC) that ranks variables most likely to fit data and most useful for modeling relationships (Burnham and Anderson 2002). We then used quantile regression to explore some of the stronger relationships suggested by multivariate techniques. Standard regression techniques explore relationships associated with a mean response (50th quantile), yet if the combination of factors associated with individual sites are expected to limit growth (BAI), the capacity for swamps to respond incidentally to salinity, flood duration, and flood frequency might best be described using upper quantiles (see Cade et al. 1999, Cade and Guo 2000). These analyses were conducted using Proc Quantreg (SAS Institute 2007).

Finally, univariate relationships of significant general trends were presented, and the potential for autocorrelation among physico-chemical parameters was tested through correlation analyses, replicated by plot within site.

RESULTS

Site Characteristics

Overstory species composition among sites shifted dramatically along salinity gradients, coincident also with changes in flood frequency (Table 1). Freshwater sites were composed of baldcypress, water tupelo (*Nyssa aquatica* L.), swamp tupelo (*Nyssa*

Table 1. Summary of site history, forest structure, hydroperiod (3-year record), and physico-chemical properties ± 1 SE) for tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. For water table depth, negative values represent an average hourly belowground water table.

| Site | History | | | | Forest Structure | | | | Hydroperiod | | | | Physico-chemical Properties | |
	Degradation State	Tidally Influenced Currently?	Historically Tidal?	Number of Overstory Species	Mean Forest Height (m)	Mean dbh (cm)	Mean Basal Area (m²/ha)	Tree Density (ind/ha)	Flood Duration (h/year)	Flood Frequency (floods/year)	Water Table Depth (cm)		Salinity (ppt)	Soil Bulk Density (g/cm³)
South Carolina														
Hobcaw Transect														
Crabhaul	Freshwater	N	N	3	30±0.92	39.8 ± 2.27	87.12	590	6626	1.5	35.6		0.28±0.02	0.231 ± 0.057
Reserve Upper	Freshwater	N	N	7	35±0.54	41.4 ± 2.61	86.05	530	2173	11.1	−3.9		0.61 ± 0.16	0.544 ± 0.060
Reserve Middle	Moderately	N	Y	6	30±0.47	28.4 ± 1.72	71.95	870	4844	11.0	5.3		0.37±0.17	0.227 ± 0.051
Reserve Lower	Highly	Y	Y	4	22±1.00	32.8 ± 1.80	39.86	420	333	40.9	−4.6		1.29 ± 0.19	0.140 ± 0.003
Waccamaw Transect														
Waccamaw Upper	Freshwater	Y	Y	4	25±0.31	23.0 ± 0.96	59.46	1190	256	96.9	−2.8		0.09 ± 0.00	0.198 ± 0.009
Waccamaw Middle	Moderately	Y	Y	3	18±0.38	31.9 ± 1.34	44.29	510	279	167.3	−3.4		0.66 ± 0.11	0.260 ± 0.005
Waccamaw Lower	Highly	Y	Y	2	15±0.44	20.2 ± 1.12	25.38	660	591	169.3	−0.4		2.08 ± 0.17	0.219 ± 0.026
Georgia														
Savannah Transect														
Savannah Upper	Freshwater	Y	Y	6	25±0.48	23.5 ± 1.04	65.19	1220	303	48.0	−9.0		0.11 ± 0.01	0.387 ± 0.032
Savannah Middle	Moderately	Y	Y	2	23±0.34	29.5 ± 1.33	59.97	760	390	136.9	−2.0		0.83 ± 0.05	0.242 ± 0.011
Savannah Lower	Highly	Y	Y	1	13±0.50	20.7 ± 0.63	23.06	650	633	155.5	−1.9		3.36 ± 0.17	0.368 ± 0.036
Louisiana														
Terrebonne/Atchafalaya Transect														
Bayou Chevreuil	Freshwater	N	N	4	23±0.3	26.3 ± 1.1	56.19	890	6565	3.4	4.6		0.57±0.05	0.141 ± 0.007
Bayou Teche	Moderately	N	Y	3	17±1.3	30.9 ± 2.5	53.35	600	8760	0.5	32.6		0.42±0.02	0.352 ± 0.045
Mandalay	Highly	N	Y	2	19±0.8	34.5 ± 4.2	26.85	220	7610	3.8	11.5		1.62±0.15	0.380 ± 0.049
Barataria Transect														
Jean Lafitte	Freshwater	N	N	2	24±0.6	29.9 ± 1.3	70.61	860	8760	0.4	44.6		0.42±0.04	0.216 ± 0.025
Treasure Island	Moderately	Y (seasonally)	Y	2	16.9±0.6	23.3 ± 1.1	36.89	750	1523	18.9	−2.1		2.01 ± 0.06	0.125 ± 0.005
Fleming	Highly	Y (seasonally)	Y	1	18±0.6	27.9 ± 1.4	36.06	520	3066	29.3	15.2		2.13±0.16	0.227 ± 0.030
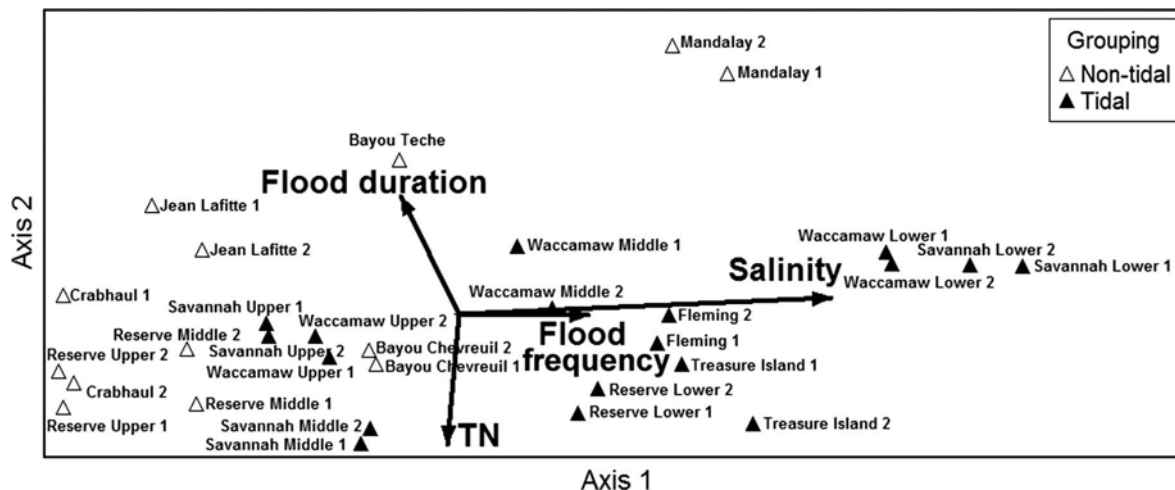
Figure 3.   Non-metric multidimensional scaling (NMS) ordination graph resulting from the plot × variable data matrix. Response variables include basal area, tree height, and basal area increment (BAI). The proportion of variance explained, based on the r^2 between distance in the ordination space and distance in the original space, is 0.935 and 0.056 for Axis 1 and 2, respectively. Edaphic factors were overlaid as vectors (solid lines with arrows), and used to infer their relative importance in each plot. Longer lines indicate stronger relationships. TN = soil total nitrogen.

biflora Walt.), ash (*Fraxinus* spp.), red maple (*Acer rubrum* L.), and/or oak (*Quercus* spp.). At higher salinity (and flood frequency), species progressively fell out of this assemblage leaving only baldcypress and a scattering of swamp tupelo and red maple on stump sprouts at the very highest salinity (Table 1). Wax myrtle (*Morella cerifera* (L.) Small) and, in some cases, Chinese tallow (*Triadica sebiferum* (L.) Small) invaded the understory of Louisiana swamps at all salinities, especially on microtopographic highs (hummocks). In South Carolina and Georgia, wax myrtle invaded the understory notably on only two sites, Reserve Lower and Reserve Middle, where salinity was moderate (0.8 to 1.3 ppt); Chinese tallow was not prevalent on South Carolina or Georgia sites.

Hydrological characteristics ranged widely among study sites. Annual flood frequency varied from 0.4 to 169 floods/yr, and annual flood duration varied from 256 to 8760 h/yr (Table 1). Sites in South Carolina and Georgia were more tidal in nature than those in Louisiana (Figure 2), which tended to exhibit the classic characteristics of southern deepwater swamps: long flood durations, high water table depths, low flood frequency, and lower soil bulk density. Two sites in Louisiana (i.e., Fleming, Treasure Island) registered higher water levels when winds were from the south for extended periods of time and lower water levels when winds were from the north. Many sites in Louisiana were near small levees, but they maintained estuarine connectivity either directly or during storm surges that provided an occasional source of salinity (Conner et al. 2007: 243).

Differences were detected among sites for every dependent and independent variable ($p < 0.05$). Therefore, all data were considered in the NMS analysis. While salinity and flood frequency were important correlates with response along Axis 1, TN and flood duration were important correlates with response along Axis 2 (Figure 3). Groupings of tidal versus non-tidal sites were fairly distinct, separating largely on the basis of salinity and flood frequency (Axis 1): saline sites tended to be more consistently tidal (greater flood frequency). However, some tidal plots (Savannah Middle, Savannah Upper, Waccamaw Upper) were confounded with freshwater sites due to the low salinities and flood frequencies that result from either placement at an extreme of the tidal reach (Waccamaw Upper) or the presence of a natural berm (Savannah Middle and Upper). Non-tidal sites separate along both Axes 1 and 2, indicating that variables associated with Axis 2 (flood duration and TN) are relatively more important in non-tidal sites. In order to decipher important trends associated with basal area, stand height, and BAI of codominant baldcypress, our subsequent analyses focused on relationships with salinity, flood duration, flood frequency, and TN as suggested by the NMS (Figure 3).

Basal Area and Stand Height

Mean annual site salinity ranged from 0.1 to 3.4 ppt across all sites and affected forest structural attributes non-linearly (Figure 4). Sites with salinity concentrations of 1.3 ppt or greater supported a basal area of less than 40 m^2/ha. Stand height
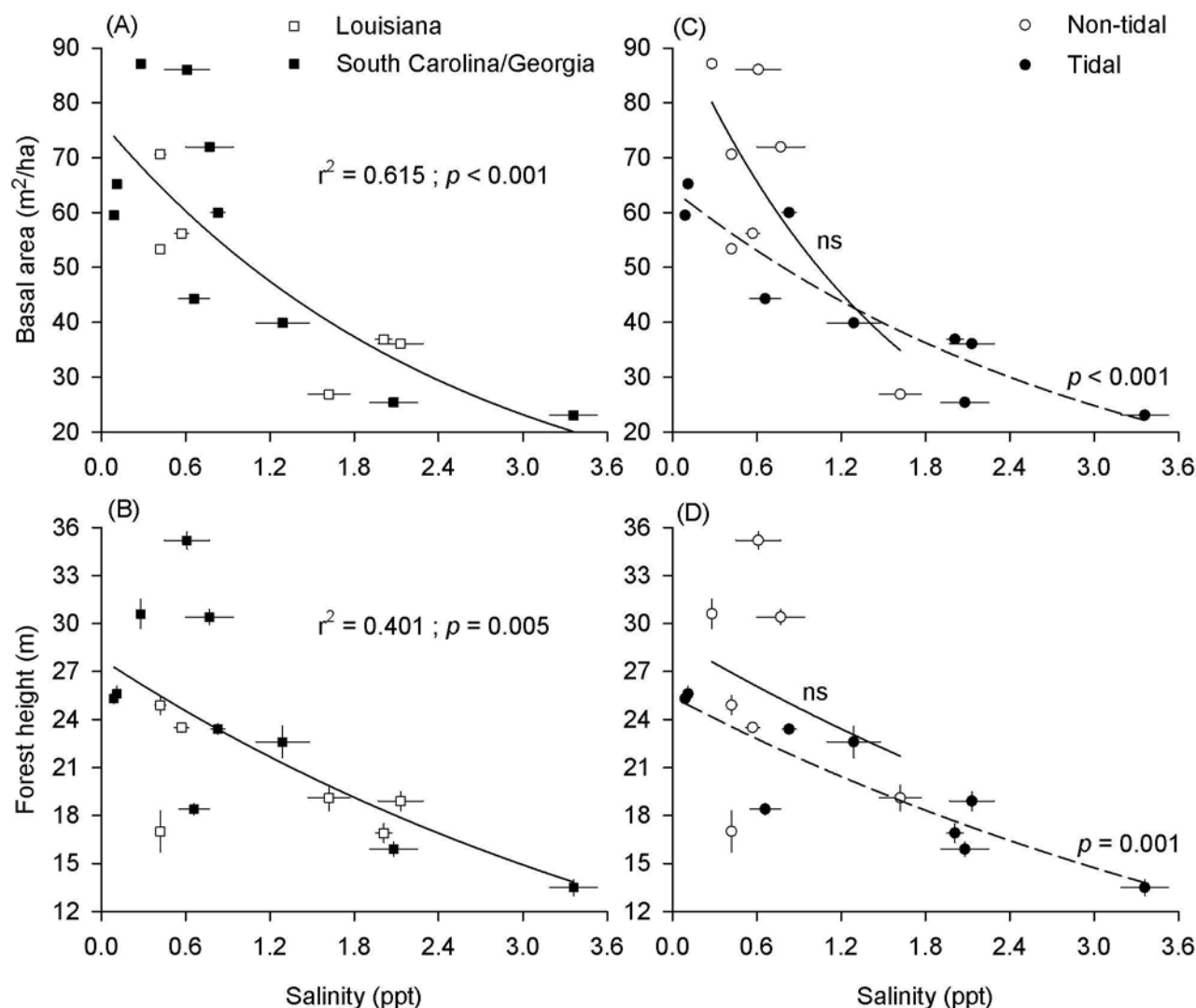
Figure 4. A) Basal area (m^2/ha) of trees $\geq$ 10 cm DBH and B) height (m, $\pm$ 1 SE) of codominant baldcypress trees relative to mean annual salinity concentrations (ppt, $\pm$ 1 SE) in tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. Graphs C) and D) present the same data, but are segregated based upon whether the site is tidal (dashed regression) or non-tidal (solid regression). Data are graphed by site.

differed among sites ($F_{15,257}$ = 78.9; p < 0.001), and regression analyses indicated that stand height and basal area were logistically related to salinity (Figure 4A,B). Where salinity was < 0.7 ppt, basal area was as high as 87 m^2/ha (Table 1). When analyzed separately, non-tidal sites did not approximate this logistic fit (Figure 4C,D). The greatest basal areas and tallest forest stands were present in South Carolina in locations with no tidal activity: Reserve Upper, Reserve Middle, and Crabhaul.

Baldcypress Tree Growth in Relation to Salinity, Soil Fertility, and Hydrology

BAI of individual codominant baldcypress ranged from 2–22 cm^2/yr and differed among sites ($F_{15,275}$

= 22.6; p < 0.001). BAI generally decreased along transects as sites transgressed from fresh to saline in South Carolina and Georgia (Figure 5). All sites with BAI > 8 cm^2/yr (n = 10) had salinities of 1.62 ppt or less and all but one had salinities of 0.77 ppt or less. Multivariate model selection procedures were consistent in identifying salinity and flood duration as the primary drivers for mean BAI (Table 2). For example, BAI of codominant trees on the highly degraded Savannah Lower site (3.36 ppt salinity) was only 17% of BAI for baldcypress trees on the fresh Savannah Upper site (0.11 ppt salinity). Such growth reduction with salinity was not the case for the Terrebonne/ Atchafalaya Transect, where baldcypress trees at Bayou Chevreuil (freshwater) had a lower BAI
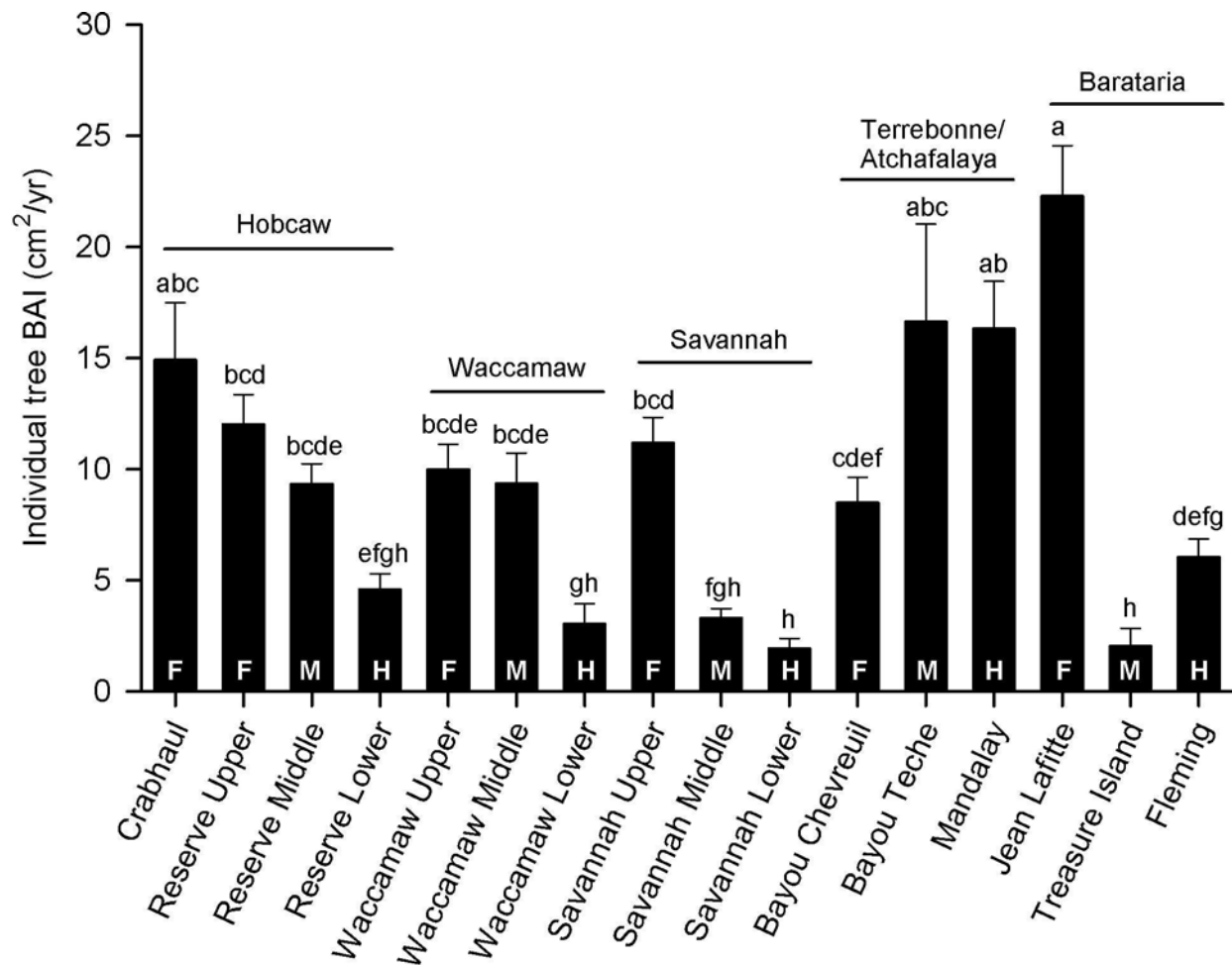
Figure 5. Mean basal area increment (BAI) of codominant baldcypress trees by site (± 1 SE), with landscape transects and relative degree of site degradation noted for tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. BAI for sites sharing a letter do not differ significantly at $\alpha = 0.05$. F = freshwater site; M = moderately degraded; H = highly degraded.

relative to the highly degraded Mandalay site (1.6 ppt salinity). However, the four sites with the greatest BAI (Mandalay, Bayou Teche, Crabhaul, Jean Lafitte) also had the longest flood durations (6626–8760 h/yr); five of eight sites with flood durations less than 2000 h/yr had BAI less than 4.5 cm^2/yr.

Overall, BAI of codominant baldcypress decreased with salinity (Figure 6A), increased with flood duration (Figure 6B), and decreased slightly relative to increasing flood frequency (Figure 6C). All relationships involving hydrological measurements were accentuated at higher regression quantiles (Table 3), and indicated better growth potential

Table 2. Stepwise selection summary for determining the influence of site physico-chemical factors on codominant baldcypress tree height and basal area increment (BAI) on tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. SBC = Schwarz Bayesian Information Criterion.

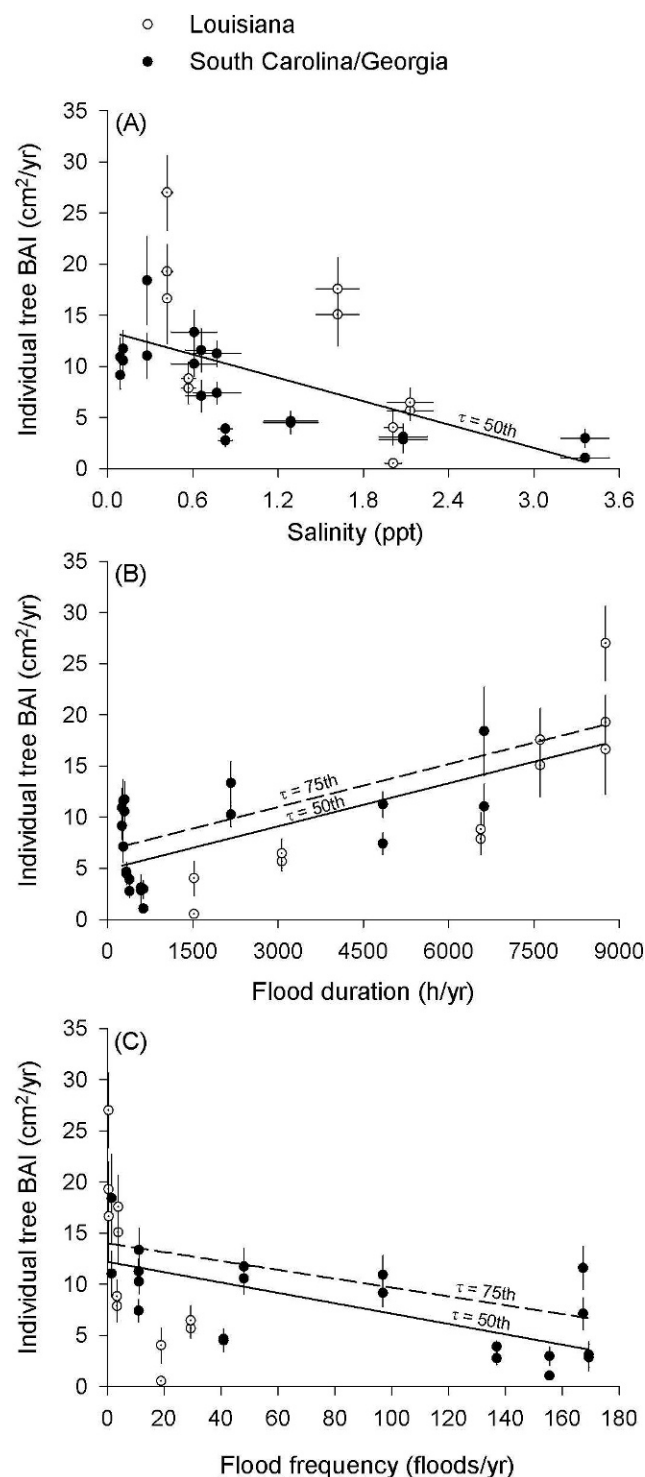|	Tree Height (m)		Mean BAI (cm^2/yr)	
Step	Effect Entered	SBC	Effect Entered	SBC
0	Intercept	115.365	Intercept	114.926
1	Salinity	99.529	Flood duration	95.366
2	TN	93.779	Salinity	86.074
3	TN:TP ratio	85.909	Bulk density	80.658
4	Flood frequency	85.414	–	–

Figure 6. Observed relationships for site salinity (ppt, ± 1 SE), flood duration (h/yr), and flood frequency (floods/yr) with mean BAI (cm²/yr, ± 1 SE) of codominant baldcypress trees on tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. The strongest fit for all relationships was through linear regression, although slight BAI enhancements at 0.4 ppt are noteworthy. Regressions of 75th quantiles (τ) are shown for flood duration and flood frequency; the 50th quantile was the largest significant quantile for salinity (Table 3). Data are graphed by plot within site.

at greater flood durations and flood frequencies than standard regression analyses might otherwise suggest. Predictability beyond a 50% quantile for salinity, or 75% quantile for flood duration and frequency, was not strong (at $\alpha = 0.05$). Slopes of estimates are also important to consider (Table 3). Change in growth per additional hour of annual flooding ($b_1 = 0.0001$ to 0.0003) or per flood event ($b_1 = -0.003$ to -0.008) was far less from among all quantiles than for the addition of an increment in salinity ($b_1 = -0.194$ to -0.983).

Interactions among Dependent and Independent Variables

Soil TN was more strongly correlated to mean forest height (Figure 7A) than was TP or TN:TP ratios. However, soil TN concentrations were not correlated with BAI of codominant baldcypress (Figure 7B). Using step-wise regression, soil TN ranked second only to salinity as an influence on forest height, followed by TN:TP ratio and flood frequency (Table 2). SBC values indicated that TN had a much stronger influence on tree height than on mean BAI (Table 2).

When influences of salinity, hydroperiod, and soil nutrient concentrations were analyzed relative to forest structure and growth in tidal and non-tidal baldcypress swamps, it was important to understand how these groups of variables might interact. Of all the combinations tested, salinity related only to TN concentrations (Figure 8A) and TN:TP ratios (Figure 8C). Data fit a bell-shaped curve, with TN:TP ratios reaching a peak between 1.2 and 2.0 ppt salinity. No such peak was evident for TP (Figure 8B). There was also no apparent relationship between hydrological metrics (flood frequency and duration) and soil concentrations of either TN or TP.

DISCUSSION

Importance of Flood Duration and Flood Frequency

Tidal swamps along Atlantic coastal rivers persist because they maintain a connection between seasonal river floods and more frequent tidal activity. Connected floodplain ecosystems of this type receive mineral nutrients from riverine flood pulses (Tockner et al. 2000) and tidal subsidies (Odum and Fanning 1973, Odum et al. 1979), while contributing in critical ways to decomposition and export of organic matter to support metabolism in nearby ecosystems (Brinson et al. 1981, Meyer et al. 1997, but see Noe and Hupp 2007). BAI of codominant

baldcypress tended to be lower on all sites at higher flood frequencies in our study (Figure 6C). Therefore, much of the productivity in South Carolina and Georgia swamps may be restricted to sites less frequently flooded by tides (i.e., even if flooding occurs for longer durations). More frequent flooding along strongly tidal rivers tended to decrease growth (e.g., Savannah and Waccamaw Rivers), while increased flood durations associated with longer-term ponding of non-tidal sites tended to increase growth (e.g., Crabhaul Swamp). Accordingly, enhanced growth and greater flood duration related strongly at all but one Louisiana site (Bayou Chevreuil).

Tides can influence not only the physical environment of coastal wetlands, but also can supply nutrients and oxygen to soils while flushing them of phytotoxic respiratory byproducts (Odum et al. 1983). A general theory suggests that a trade-off exists between an energy subsidy with low to moderate levels of tidal flushing and an energy drain, or stress, with greater flood influence (Subsidy-Stress Hypothesis; Odum et al. 1979). For our sites, it makes sense that short-duration tidal floods might deliver nutrients in the form of soluble reactive phosphorus, dissolved oxygen, and organic and inorganic forms of nitrogen, while permanent flooding would produce anaerobic soils and increase respiratory demands on individual trees, thus reducing BAI. While increasing flood durations on our sites were related to greater BAI in baldcypress, there were no inflections, or stress responses, along a nearly complete flood duration range of 256 to 8760 hours flooded per year (Figure 6). The only imposed stress for baldcypress was related to increased flood frequency. Baldcypress is an extremely flood tolerant species (Hook 1984), and on our sites, potential growth detriments provided by continuous flooding may have been countered by the overwhelming influence of salinity in what should be a functionally freshwater ecosystem.

Importance of Salinity

Salinity poses a major barrier to coastal swamp persistence (Pezeshki et al. 1987, Allen et al. 1996, Krauss et al. 2000). Growth of baldcypress in our study was reduced considerably in tidal and non-tidal swamps at mean annual salinity concentrations above 2 ppt. Working on the Lower Cape Fear River, North Carolina, USA, Hackney et al. (2007) suggested that 2 ppt is an important threshold for conversion from swamp to oligohaline or brackish marsh. Our Waccamaw Lower (2.1 ppt salinity) and Savannah Lower (3.4 ppt salinity) sites are both

Table 3. Estimates of β_0 and β_1, 95% confidence interval for β_1, and p for determining whether β_0 differs from 0 for regression quantiles (τ) associating salinity, flood duration, and flood frequency with mean individual tree basal area increment (BAI) for codominant baldcypress trees on tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. Significant relationships (α = 0.05) are denoted in bold font.

| τ	Salinity (ppt)				Flood Duration (h/yr)				Flood Frequency (floods/yr)			
	β_0	β_1	95% CI for β_1	$p > t$	β_0	β_1	95% CI for β_1	$p > t$	β_0	β_1	95% CI for β_1	$p > t$
5th	2.41	−0.9826	−2.09–(0.12)	0.080	0.57	0.0002	−0.0002–0.0007	0.254	1.74	−0.0065	−0.0638–0.0508	0.818
10th	2.41	−0.9825	−1.91–(−0.06)	**0.038**	0.56	0.0003	−0.0001–0.0006	0.120	2.06	−0.0085	−0.0377–0.0206	0.553
25th	2.50	−0.5531	−1.03–(−0.08)	**0.024**	1.26	0.0002	0.0001–0.0003	**0.001**	2.20	−0.0064	−0.0150–0.0023	0.143
50th	2.60	−0.4893	−0.72–(−0.26)	**0.001**	1.66	0.0001	0.0001–0.0002	**0.001**	2.50	−0.0066	−0.0112–(−0.0021)	**0.006**
75th	2.95	−0.4673	−1.00–(0.07)	0.083	2.30	0.0001	0.0000–0.0002	**0.036**	2.87	−0.0057	−0.0113–(−0.0001)	**0.045**
90th	3.09	−0.1942	−1.09–0.70	0.659	2.51	0.0001	−0.0000–0.0002	0.165	3.01	−0.0055	−0.0127–0.0018	0.133
95th	3.48	−0.3420	−1.38–0.70	0.505	2.51	0.0001	−0.0000–0.0002	0.111	3.01	−0.0029	−0.0156–0.0098	0.649
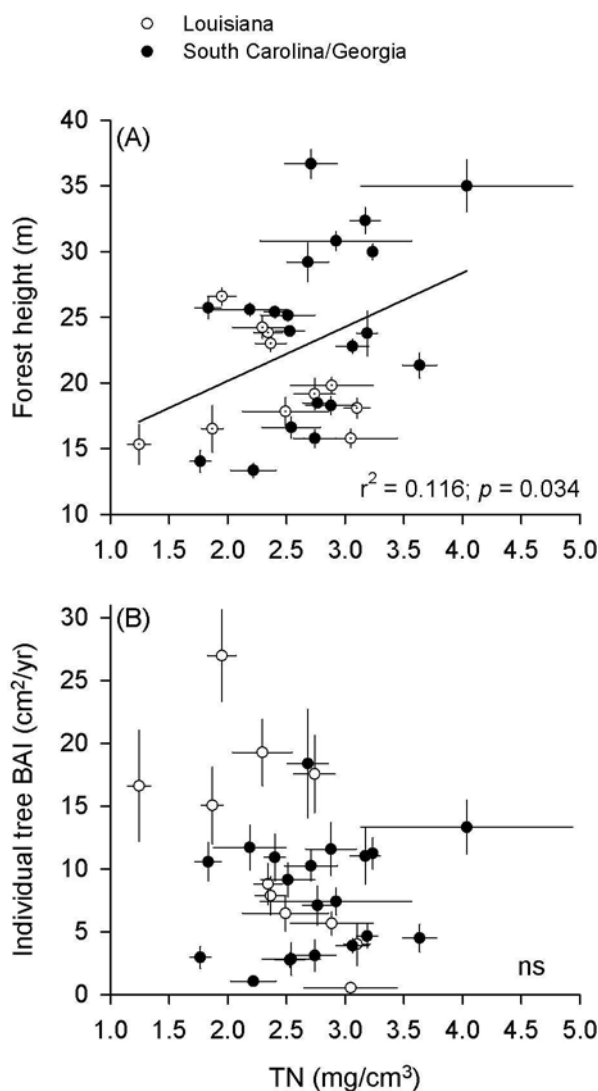
Figure 7. Observed relationships between A) height (m, ± 1 SE) of codominant baldcypress and TN (± 1 SE) and between B) BAI (cm²/yr, ± 1 SE) of codominant baldcypress and TN (± 1 SE) for tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. When significant, the strongest fit for all relationships was through linear regression. Data are graphed by plot within site.

actively converting to marsh; some trees that were monitored died, while the understory marsh environment was becoming dominant. For the Treasure Island (2.0 ppt) and Fleming (2.1 ppt) sites in Louisiana that are at or above the 2 ppt salinity threshold, conversion appears to be occurring more slowly. However, encroachment of *Sagittaria lancifolia* in the understory, degradation of soils to unconsolidated slurries with little root sustenance, and the unstable condition of surrounding tidal swamps suggest that these sites were also deteriorating.
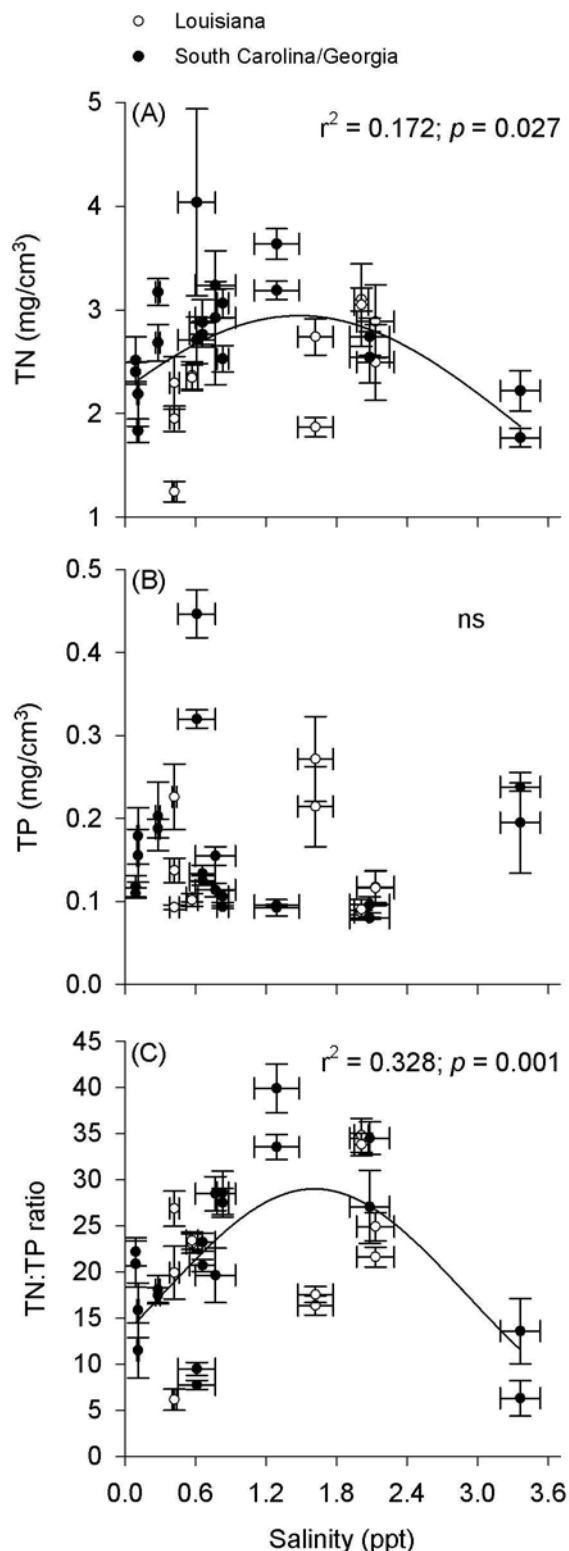
Figure 8. Relationships between porewater salinity (ppt, ± 1 SE), and A) soil TN, B) soil TP, and C) soil TN:TP ratio (± 1 SE) for tidal/non-tidal baldcypress swamps in South Carolina, Georgia, and Louisiana. Gaussian peaks provided the strongest fit for data associated with (A) and (C), while there were no significant correlations for (B). Data are graphed by plot within site.

While the distribution of water tupelo (*N. aquatica*) in the overstory of tidal and non-tidal swamps was limited to salinities < 1 ppt, swamp tupelo (*N. biflora*) occurred at salinities as high as 2.1 ppt (Waccamaw Lower). This contradicts results for swamp tupelo from greenhouse studies where cessation of physiological activity and complete mortality of swamp tupelo seedlings occurred at 2 ppt salinity after only 70 d of exposure (McCarron et al. 1998). Swamp tupelo seedlings might be less tolerant to salinity than mature trees, which would indicate that salinity conditions during regeneration may have been lower on some sites than it is now. However, larger trees may also be able to escape salt stress by accessing fresher water through deeper roots. This has been demonstrated in cabbage palm (*Sabal palmetto* (Walt.) Lodd. Ex J.A. & J.H. Schultes) and southern redcedar (*Juniperus virginiana* var. *silicicola* (Small) J. Silba) communities that are actively transitioning to salt marsh along the northern Gulf Coast of Florida, USA (Williams et al. 1999). Because mature southern redcedar uses less fresh groundwater as stands decline, southern redcedar stands closer to the ocean are more susceptible to salinization resulting from drought or storm surge because of their greater dependence on estuarine waters within the rhizosphere (Williams et al. 2003). Large-statured baldcypress trees, and perhaps even some swamp tupelo and red maple, on our most salt stressed sites may benefit from a similar strategy of water use.

Flooding, Salinity, and Nutrients: Interactive Effects with Climate Change

On our sites, soil TN was positively correlated with standing forest height, and greatest soil TN coincided with moderate porewater salinities. This suggests that less nitrogen is available to coastal baldcypress-dominated stands at both low and high porewater salinities. The relative balance between soil TN and TP may be critical (as indicated by stepwise regression analysis, Table 2), as prominent nitrogen sources (upland flow) give way to phosphorus sources from seawater (see also Chen and Twilley 1999). Phosphorus mineralization, for example, is likely to be more important on non-tidal sites; persistent flooding affects biological mineralization and supply of phosphorus in floodplain forests (Wright et al. 2001).

Although the relative balance of salinity might trump many ecological processes in coastal baldcypress swamps as sea-level rises or riverine flows decrease, retention of important mediating nutrients will also be important to consider along tidal

reaches (Verhoeven et al. 2001). Our detection of peak soil TN and TN:TP ratios at moderate salinities could be influenced by shifts in vegetation uptake among different tree species across the salinity gradient as well as by hydrological inputs of these nutrients. Along a tidal swamp to marsh continuum, dead or dying trees eventually give way to broken marsh where more nitrogen is likely to be retained by the soils during annual cycles of marsh growth and senescence. Eventually, marsh grasses may become vigorous enough to assume the prominent role in nitrogen cycling, and they may benefit from an increase in soil TN at moderate salinities.

This scenario was evident on our moderately degraded Waccamaw River and Savannah River sites where soil TN averaged 2.8 mg/cm^3 compared to either the upstream freshwater sites (mean = 2.2 mg/cm^3 TN) or the highly degraded downstream sites (mean = 2.3 mg/cm^3 TN). Brinson et al. (1985) suggested that higher nitrogen concentration in leaf fall of salinity-stressed trees reflects premature dropping of leaves and might affect nutrient reabsorption mechanisms. Processes associated with organic matter mineralization may also promote greater site fertility with salinity intrusion (at least to 9.9 ppt, Weston et al. 2006).

We suggest that a threshold may exist whereby salt stressed trees lose their capacity for nutrient retention or reabsorption in tidal and non-tidal baldcypress swamps. Salinities approaching 2.0 ppt coincide with concentrations required to induce leaf-level ion ratio imbalances for baldcypress and promote leaf photosynthetic dysfunction (Allen et al. 1997, Krauss et al. 2000). Changes in alternating periods of wetting and drying might also affect tidal swamp soils, forest productivity, and tidal swamp persistence. Reduced capacity for nutrient conservation, especially of nitrogen, might be one way in which tidal and non-tidal baldcypress trees respond to sea-level rise and salinization. Strong links among increasing salinity, diminished growth, and increased mortality of tidal swamp trees are likely to overwhelm the more subtle processes inherent to nutrient conservation.

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