Estuaries and Coasts
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Periodicity in Stem Growth and Litterfall in Tidal Freshwater Forested Wetlands: Influence of Salinity and Drought on Nitrogen Recycling

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Abstract Many tidally influenced freshwater forested wetlands (tidal swamps) along the south Atlantic coast of the USA are currently undergoing dieback and decline. Salinity often drives conversion of tidal swamps to marsh, especially under conditions of regional drought. During this change, alterations in nitrogen (N) uptake from dominant vegetation or timing of N recycling from the canopy during annual litter senescence may help to facilitate marsh encroachment by providing for greater bioavailable N with small increases in salinity. To monitor these changes along with shifts in stand productivity, we established sites along two tidal swamp landscape transects on the lower reaches of the Waccamaw River (South Carolina) and Savannah River (Georgia) representing freshwater ($\leq$0.1 psu), low oligohaline (1.1–1.6 psu), and high oligohaline (2.6–4.1 psu) stands; the latter stands have active marsh encroachment. Aboveground tree productivity was monitored on all sites through monthly litterfall collection and dendrometer band measurements from 2005 to 2009. Litterfall samples were pooled by season and analyzed for total N and carbon (C). On average between the two rivers, freshwater, low oligohaline, and high oligohaline tidal swamps returned 8,126, 3,831, and 1,471 mg $\mathrm{N\,m^{-2}\,year^{-1}}$, respectively, to the forest floor through litterfall, with differences related to total litterfall volume rather than foliar N concentrations. High oligohaline sites were most inconsistent in patterns of foliar N concentrations and N loading from the canopy. Leaf N content generally decreased and foliar C/N generally increased with salinization (excepting one site), with all sites being fairly inefficient in resorbing N from leaves prior to senescence. Stands with higher salinity also had greater flood frequency and duration, lower basal area increments, lower tree densities, higher numbers of dead or dying trees, and much reduced leaf litter fall (103 vs. 624 $\mathrm{g\,m^{-2}\,year^{-1}}$) over the five study years. Our data suggest that alternative processes, such as the rate of decomposition and potential for N mineralization, on tidal swamp sites undergoing salinity-induced state change may be more important for controlling N biogeochemical cycling in soils than differences among sites in N loading via litterfall.

Keywords Sea-level rise · Tidal swamps · Forested wetlands · Leaf litterfall · Diameter increment · Carbon · Nitrogen · Resorption · Salinity

Introduction

Tidal freshwater forested wetlands (or tidal swamps) generally exist as a consequence of river flow and tidal reach. Tidal swamps normally occupy the upper intertidal zone between upland nontidal swamp or hardwood forests and tidal marsh. Regions with large tidal range (2–3 m), such as the Atlantic coast of the USA from north Florida to southern North Carolina, have the largest percentage of tidal swamps, ranging to over 60 % of the Nation's inventory (Field et al. 1991). Of an estimated 6.4 million ha of freshwater and saltwater wetlands within watersheds of the Atlantic coast, freshwater forested wetlands occupy 3.5 million ha compared to 0.7 million ha of freshwater marsh (Stedman and

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Dahl 2008). Where freshwater tides influence coastal wetlands, swamp vegetation generally performs quite well; collectively, freshwater tidal wetlands are recognized for plant species diversity and high rates of productivity (Neubauer et al. 2000; Mitsch et al. 2009; Whigham 2009). While management of species diversity and productivity within tidal swamps may be related strongly to hydrology (cf., Rheinhardt and Hershner 1992), state change from tidal swamp to marsh is often mediated by two primary natural drivers: small, permanent changes in hydrology (Rheinhardt 1992) and salinity (Brinson et al. 1985; Hackney et al. 2007).

Altered hydrology, drought, coastal land development, agriculture, accelerated sea-level rise, and persistent river dredging to support navigation have reduced the distribution of tidal swamps in the Southeast (Brinson et al. 1995; Doyle et al. 2007). Indeed, a number of research studies have documented sea-level rise and salinity-induced change among upper intertidal forested watersheds in Louisiana (Salinas et al. 1986; Pezeshki et al. 1987), Mississippi (Keeland and McCoy 2007), Florida (Williams et al. 1999, 2003; DeSantis et al. 2007; Light et al. 2007), North Carolina (Brinson et al. 1985; Hackney and Yelverton 1990), and Maryland/Delaware (Rheinhardt 1992; Baldwin 2007). While these studies have described the role of certain environmental variables responsible for altering productivity and community composition on a holistic spatial scale, identifying inter-annual patterns in productivity and nutrient recycling will provide insight into the edaphic and biogeochemical processes driving change.

In one of the first comprehensive studies on tidal swamps, Brinson et al. (1985) described premature litterfall on salt-impacted, streamside swamps in North Carolina, and hypothesized that premature leaf fall potentially leads to a build-up of nitrogen (N) in the litter deposited on the soil surface. Higher soil N at moderate salinity levels (1.2–2.1 psu) was found in tidal swamps in Louisiana, South Carolina, and Georgia, leading Krauss et al. (2009) to suggest that, in addition to the aforementioned hypothesis, perhaps moderate salinity (1.2–2.0 psu) could result in increased N retention in soils receiving greater N concentrations in leaf litter or, at even higher salinities (>2.1 psu), drive greater N mineralization rates, increasing N loss from the soil and contributing directly to marsh encroachment. Some biogeochemical studies do support this latter possibility (e.g., Weston et al. 2006), but no comprehensive assessment of growth periodicity and nutrient composition has been reported from additional tidal swamps in order to verify the role of litterfall in influencing N budgets.

The primary goal of this study is to determine the effect that increased salinity during drought has on primary productivity and N cycling in tidal swamps. In doing so, we replicate components of the research of Brinson et al. (1985) by selecting sites farther south, and include replicate rivers along with multiple wet and dry years. We focus on salinity gradients occurring along the Waccamaw River (South Carolina) and Savannah River (Georgia), and test whether location along a river transition from intact freshwater tidal swamp to degraded swamp with marsh invasion of the understory gives rise to distinctive patterns of stem growth and litterfall periodicity, as well as facilitates different patterns of N recycling. Our data span a half-decadal period of low rainfall for the Southeast. While the tide may buffer swamps from drought effects (cf., Reich and Borchert 1984; Young et al. 1993; Day et al. 2007), drought alone can concentrate salinity in some tidal swamps and have strong influences on growth patterns in current and future years (Hinckley et al. 1979; Schöngart et al. 2002; Davidson et al. 2006).

Materials and Methods

Site Characteristics

Studies were conducted along coastal reaches of the Waccamaw River near Georgetown, South Carolina and the Savannah River near Port Wentworth, Georgia (Fig. 1). Three sites (upper, middle, lower) were established along each river, and located on the floodplain within 100 m of river's edge. Both rivers maintain large areas of healthy tidal swamps beginning upstream from approximately river-km 30. The Waccamaw River is a predominantly "black water" river that receives drainage from 11 watersheds encompassing an area of nearly 253,000 ha, with approximately 20 % categorized as forested (SCDHEC 2000). "Black water" rivers are typically acidic and transparent, but are dark stained by the high amount of tannins in the river. The Pee Dee (a "red water" river) and Black Rivers flow into the Waccamaw River, which join Sampit River discharge in Winyah Bay. The Waccamaw Lower site was actually located along the Sampit River, but close to where the Waccamaw and Sampit Rivers converge into the bay. The Waccamaw River doubles as the Atlantic Intracoastal Waterway and therefore has much recreational and industrial boat traffic. The Pee Dee River is regulated by a series of impoundments upstream of its convergence with the Waccamaw River and Winyah Bay. The Savannah River, which is a "red water" river that drains an area of approximately 2.7 million ha (Bristol et al. 2005), is heavily used for shipping and is undergoing persistent dredging just seaward of established sites. "Red water" rivers typically carry red, eroded soils of the Piedmont and generally have higher silt and clay loads than "black water" rivers. Hydrology of the Savannah River has been altered further by damming upstream and through the operation of a decommissioned, one-

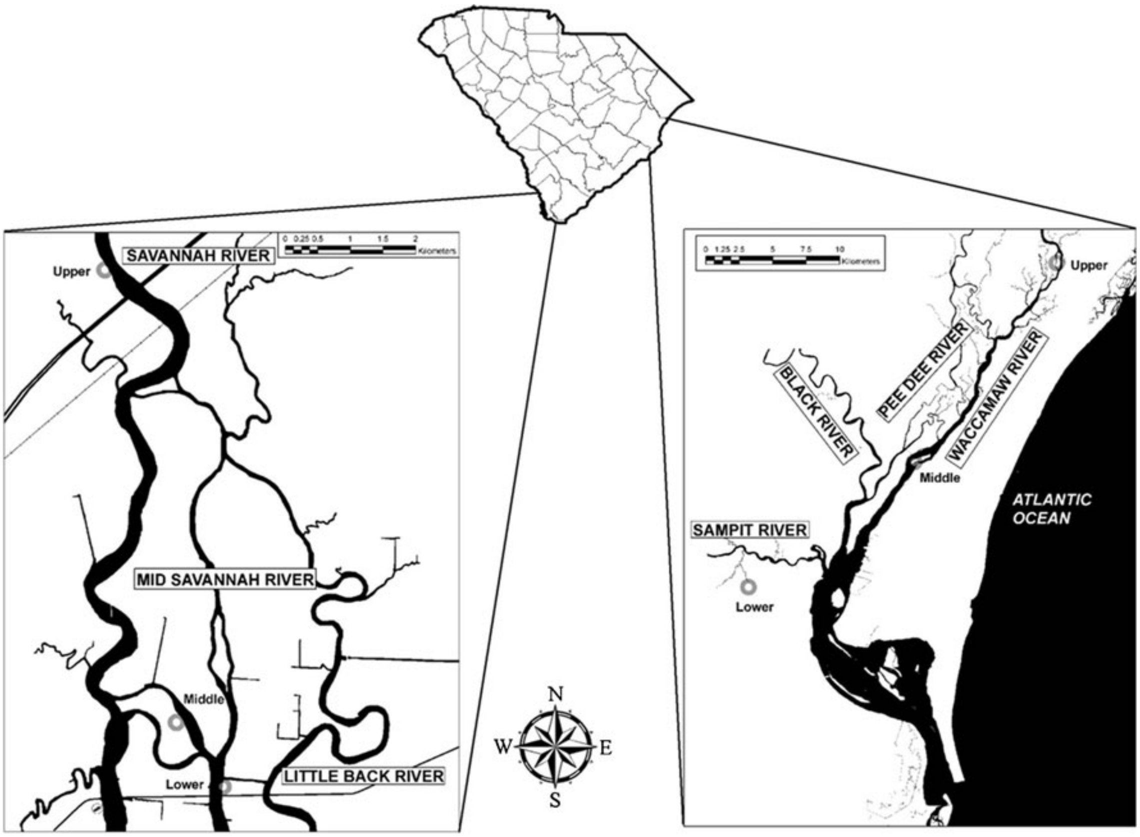

Fig. 1 Location of the Waccamaw River in South Carolina and Savannah River in Georgia, USA. The mouths of these rivers are approximately 200 km apart, and both discharge into bays feeding into the Atlantic Ocean

way tidal flap gate downstream, which forced vegetation shifts as salinities increased over 14 years of operation (Pearlstein et al. 1993).

Each site consisted of paired, 20×25-m plots encompassing an area of 1,000 m^2 (0.1 ha). Study sites differed in overstory species composition, standing basal area, mean canopy height, individual tree diameter, flood duration, and soil porewater salinity from upstream to downstream positions in the estuary (Table 1; Krauss et al. 2009). Waccamaw and Savannah Upper sites were established as true tidal freshwater swamps, in areas having no salt water incursion. Overstory species included *Taxodium distichum* [L.] L.C. Rich., *Nyssa aquatica* L., *Nyssa biflora* Walt., *Fraxinus* spp., and/or *Acer rubrum* (L.). *Alnus serrulata* (Aiton) Willd. was present as a shrub on both sites. The herbaceous community was composed mostly of *Polygonum hydropiperoides* Michx., *Polygonum arifolium* L., *Thelypteris* sp., *Carex* spp., *Commelina diffusa* Burm. f., *Toxicodendron radicans* (L.) Kuntze, and *Iris* sp. Waccamaw and Savannah Middle sites (low oligohaline) were established at the seaward limit of tidal forest, and represented sites undergoing early stages of stress, including some epicormic branching, fewer overstory species, and presence of oligohaline marsh species. Overstory species were restricted to *T. distichum*, with a sparse mid-story of *N. biflora*, and the herbaceous communities were composed of *Peltandra virginica* (L.) Schott, *Sagittaria lancifolia* L., *Lilaeopsis chinensis* (L.) Kuntze, and some *Schoenoplectus robustus* (Pursh) M.T. Strong. Finally, Waccamaw and Savannah Lower sites (high oligohaline) were composed of a salt-stressed monoculture of *T. distichum* in the overstory, including several dead stems, with an understory of oligohaline marsh plants, including *Zizaniopsis miliacea* (Michx.) Döll & Asch., *Spartina cynosuroides* L., *Schoenoplectus robustus*, and *Sagittaria lancifolia*.

Hydrology

Tides along both river systems are semi-diurnal. The mean tidal range is 1.1 and 2.3 m for the Waccamaw and Savannah Rivers, respectively. Flooding depth and duration varies according to local conditions, so we measured water levels of each site between the paired plots. PVC wells (7.6 cm diameter) were inserted to approximately 1 m into the soil, and pressure sounds (model #138, Infinities USA, Port Orange, Florida, USA) recorded water levels at hourly intervals from 2005 to 2009. Salinity was measured from the four extreme corners of each site with permanently emplaced, 3.8-cm-diameter PVC wells inserted to

Table 1 Summary of forest structure and soil physico-chemical properties (mean ± SE) on tidal swamp sites along the Waccamaw River (South Carolina) and Savannah River (Georgia)

	Forest structure				Soil physico-chemical properties		
	Mean forest height (m)	Mean dbh (cm)	Mean basal area (m^2 ha^{-1})	Tree density (ind ha^{-1})	TN (%)	TC (%)	Atomic C:N
Waccamaw River							
Upper	25.3±0.31	23.0±0.96	59.46	1,190	1.26±0.09	19.5±1.64	15.5
Middle	18.4±0.38	31.9±1.34	44.29	510	1.09±0.05	18.6±1.06	17.1
Lower	15.9±0.44	20.2±1.12	25.38	660	1.29±0.15	22.9±2.67	17.8
Savannah River							
Upper	25.6±0.48	23.5±1.04	65.19	1,220	0.63±0.10	10.1±1.50	16.1
Middle	23.4±0.34	29.5±1.33	59.97	760	1.17±0.08	22.0±1.36	18.8
Lower	13.5±0.50	20.7±0.63	23.06	650	0.58±0.08	10.9±1.61	18.8

The forest structure and TN data were originally reported in Krauss et al. (2009)

approximately 60 cm into the soil. Wells were capped and residual water was removed prior to monthly salinity readings. Salinity was measured with a portable conductivity meter (YSI Model 30, Yellow Springs, Ohio, USA), tested periodically against standards. Thirty-year annual rainfall averages for the study area ranges from 117.9 to 130.8 cm. Normal monthly precipitation is lowest in the months of April, May, October, November, and December; normal monthly precipitation typically peaks in July and August (http://www.ncdc.noaa.gov/oa/climate/online/ccd/nrmlprcp.html). Rainfall amount can be highly variable, especially along the coast, and droughts often have pervasive effects regionally. Therefore, the balance among wet and dry years here was described as meteorological drought severity using the Palmer Drought Severity Index (PDSI: Palmer 1965). The PDSI measures the duration and intensity of long-term drought based upon regional moisture balance in a given month (Guttman 1998). Data were obtained from the National (U.S.) Climate Data Center (http://www7.ncdc.noaa.gov/CDO/), as “South Carolina Northeast Division” for Waccamaw River sites and “Georgia Southeast Division” for Savannah River sites.

Stem Growth Increment

Stem growth was measured monthly from January 2005 to December 2009 on 10 co-dominant *T. distichum* trees associated with each plot, for a total of 20 trees from each site. *T. distichum* was the only tree species occurring on all sites. We used stainless steel dendrometer bands affixed at stem heights ranging from 1.3 to 2.0 m above ground in order to account for several trees with high basal swelling. Trees were scraped to ensure a tight fit and fastened to the tree with springs. Dendrometer bands measure fractions of millimeters in individual tree circumference increment (Hall 1944; Cattelino et al. 1986), and are very precise (Keeland and Sharitz 1993). First, circumference changes were converted to monthly diameter increment adjusted by individual tree size, providing for some standardization among trees of different initial sizes. Next, individual tree basal area was determined for each measurement. Finally, the initial basal area of each tree was subtracted from its new monthly basal area measurement to obtain a basal area increment for all trees studied. Stem growth is reported in units of individual tree basal area increment (square centimeter per month). This metric is different than stand basal area, typically reported as square meter per hectare, and represents only the growth associated with select individual trees.

Litterfall

Ten, 0.5×0.5-m, wooden litter baskets with fiberglass screening were elevated to 1 m above ground on each site, and positioned to collect leaves, twigs, fruits, and flowers falling from the canopy. Five baskets were placed systematically and evenly on each of the two plots per site. Litter was collected monthly from January 2006 to December 2009, dried in an oven for at least 48 h at 60°C, then sorted into two categories: (1) foliage and reproductive material (including caterpillar frass), and (2) woody structures (including bark, lichens, Spanish moss). Sorted litter from each trap was then weighed to the nearest 0.01 g.

Foliage made up the largest percentage of litterfall, and was analyzed further for tissue N and carbon (C) content. Foliage from each trap was separated from caterpillar frass and pulverized, then pooled and homogenized for each site in 3-month groups (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec) by year for samples collected in 2004, 2005, and 2006. Total N and total C of the leaf litter were measured with a CN elemental analyzer (Flash EA 1112, ThermoFinnigan, Wigan, UK). Foliar concentrations of N and C (percent) were multiplied by monthly litterfall biomass (grams) to attain rates of N and C loading from the canopy to the forest floor.

Soil Nutrients

Soil samples to a depth of 30 cm were collected from three of the four corners of each plot, for a total of six soil samples per site. These soils were collected at the time of plot installation in 2005; some of the soils data and the complete sample methods were originally reported in Krauss et al. (2009). Total N and total C were also determined using a CN elemental analyzer (Flash EA 1112, ThermoFinnigan, Wigan, UK) on dried and pulverized samples. TN and TP data are reported here as percent concentrations.

Statistical Analyses

Replicate litterfall traps in each site ($n=10$) were averaged for each month from January 2005 to December

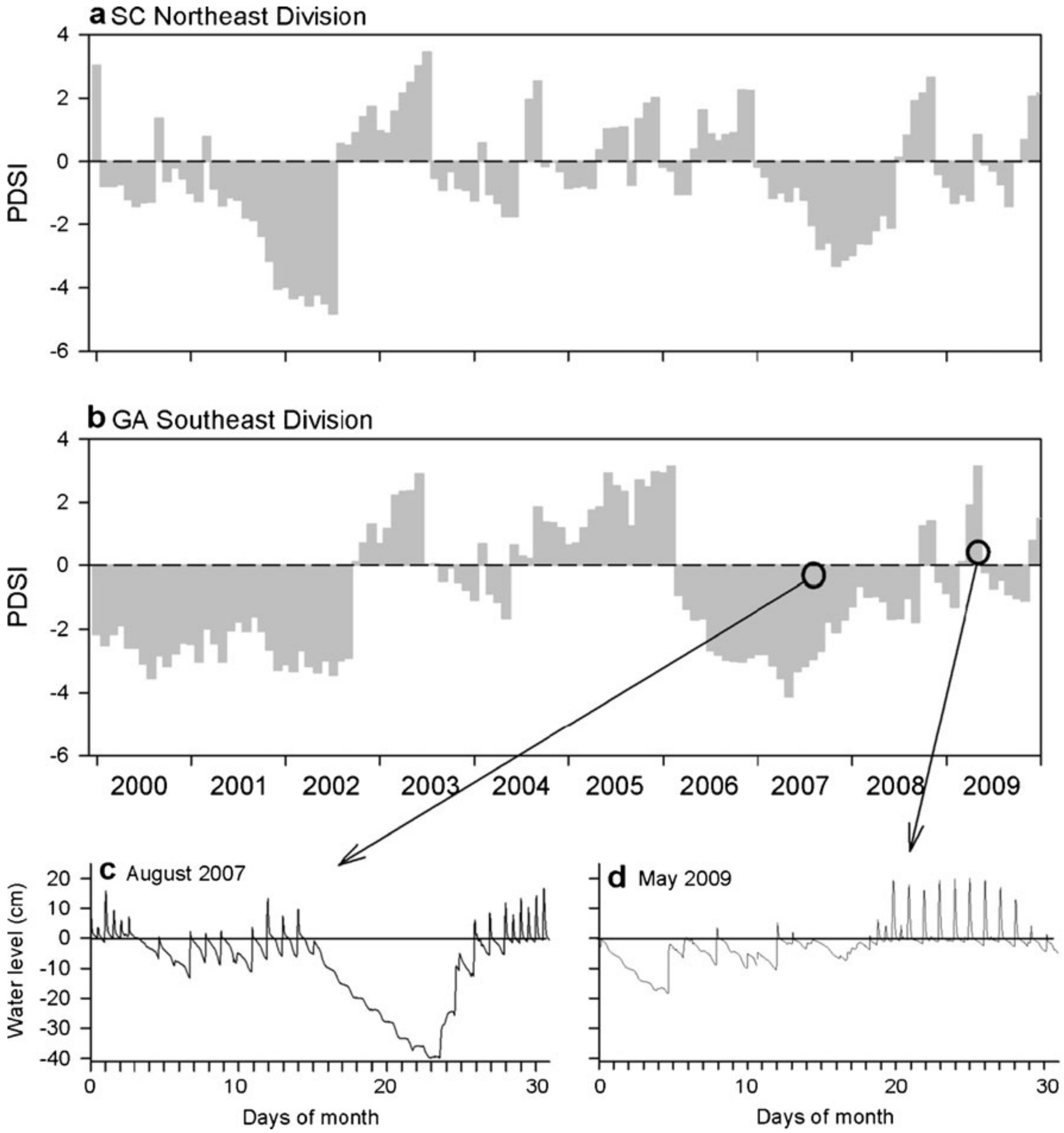

Fig. 2 Calculated values for the Palmer Drought Severity Index (PDSI) for regions of South Carolina and Georgia that encompass the **a** Waccamaw River and **b** Savannah River, respectively, and examples of Savannah River hydrographs from **c** August 2007 (severe drought) and **d** May 2009 (very moist). Data from National (U.S.) Climate Data Center, referenced in text. *Key:* Extreme drought, <−4; severe drought, −3 to −3.99; moderate drought, −2 to −2.99; middle range (normal), −1.99 to 1.99; moderately moist, 2 to 2.99; very moist, 3 to 3.99; extremely moist, >4

2009; monthly data from each site were combined to obtain annual estimates of leaf litterfall. Raw treeband data from up to 20 trees per site were used to calculate diameter increments and individual tree basal area increment at each site per month from January 2006 to December 2009. Significant mortality has occurred since the onset of the experiment at the lower sites on both rivers. As a result, dead trees were eliminated from further analysis; only 13 trees on Waccamaw Lower and 8 trees on Savannah Lower remain for analysis. Different time intervals were selected for analyses (i.e., month versus year). In order to account for some missing months and to tease out whether seasonal differences in litterfall productivity or growth increment existed among the six sites, months were combined in sets of two. For the remainder of the manuscript, "month" represents 2-month averages (n=6 per year) for all litterfall and treeband data.

All data were analyzed using a cubic spline interpolation to account for missing data, which were rare since data were pooled by 2-month averages. We used a general linear model (Proc GLM, SAS Institute, 2007) to compare river, site, and time. Because there were many more time points from which data were collected, but only six sites, standard repeated measures could not be used. We tested for homogeneity of residual variances for each response variable model and determined that log transformation was most appropriate for both datasets. We then ran least squared means comparisons for site by year and site by two-month averages, adjusting for the study-wise alpha level (0.05/180 comparisons= 0.000278). All statistical analyses were performed using SAS, Version 9.2 (Statistical Analysis Software, 2009).

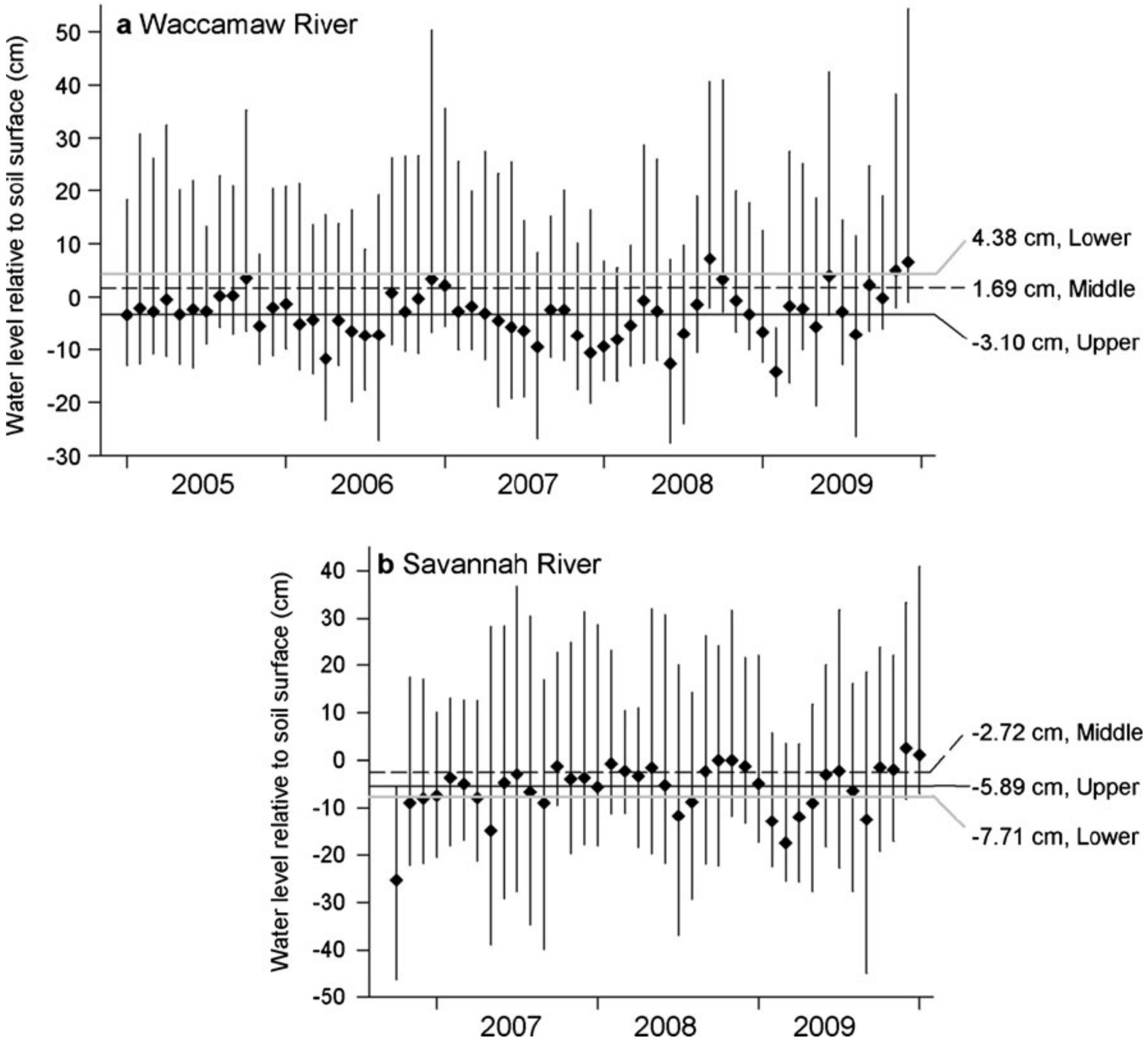

Fig. 3 Summary of monthly hydrological conditions on the **a** Waccamaw River and **b** Savannah River, including mean (*diamond symbol*), maximum, and minimum water levels (format after Brinson et al. 1985). Hydrological time series are from Upper sites, and are arranged relative to ground level (y=0) of Upper sites as a base. Because all sites were strongly tidal, hydrology among sites differed most in terms of flood depths, and not frequency. *Horizontal reference lines and values* represent 5-year mean annual water table depths for upper, middle, and lower sites

Results

Drought Indices, Water Level Variability, and Soil Salinity

Drought conditions along the South Carolina and Georgia coasts in 2006 and 2007 were prevalent, but followed a 2-year period of moderate moisture in both regions (Fig. 2a, b). The earlier part of the decade was also characterized by drought (2000–2002; Fig. 2a, b). While many tidal wetlands may be buffered somewhat from drought effects by having reliable delivery of tidal flood waters, fluctuations in many parts of the estuary are dependent upon river stage. This becomes evident when hydrographs from similar locations are compared in wet and dry years. The month of August 2007 (Fig. 2c), which experienced a moderate to severe drought (PDSI=−2.95), and the month of May 2009 (Fig. 2d), which was very moist (PDSI=3.14), had similar projected tidal ranges (2.96–2.98 m) along the Savannah River; however, the hydrograph during the drought (Fig. 2c) indicated greater dewatering between spring tidal events than during wetter periods (Fig. 2d). It should be noted that the number of surface floods between wet and dry periods do not necessarily differ at all locations. Similar patterns were repeated along the Waccamaw River.

Contrasts among sites become more evident when mean, maximum, and minimum water levels are reported relative to ground level on all Waccamaw River and Savannah River study sites over a 60- and 40-month period, respectively (Fig. 3a, b). Low mean water table depths in 2006 and 2007 tend to linger into 2008 until a short wet period beginning in September. As expected with a transition seaward, water table depths were 4.8 and 7.5 cm higher on Waccamaw Middle and Lower, respectively, than on Waccamaw Upper as mean site elevations relative to sea level decrease. Mean water table depths span 5 cm for Savannah River sites (Fig. 3). However, while Savannah Middle maintained a 3.2-cm-greater water-table depth than Savannah Upper, Savannah Lower broke this pattern by maintaining the lowest water table depth among all sites along both rivers (–7.7 cm); Savannah Lower was established on a slightly elevated area.

Coupled to low atmospheric moisture availability and a corresponding six-month decrease in mean water table depths on all sites after a persistent 2006–2007 drought (Fig. 3a, b), soil porewater salinity increased in middle and lower sites along both rivers (Fig. 4a, b). Upper sites remained fresh throughout the study (≤0.1 psu), while salinity of middle sites averaged 1.1 to 1.6 psu and lower sites averaged 2.6 to 4.1 psu. Salinity was lower in the wetter year of 2005 but began to increase as PDSI index values decreased into 2006. Site salinities increased consistently toward the latter months of each year, and decreased into winter months. This was most evident in 2007 along the Waccamaw River, when salinity for middle and lower sites increased by nearly 5 psu from October to December 2007, followed by a decrease in salinity to approximately 2 psu by April 2008 (Fig. 4a). Summer increases in salinity were not as evident along the Savannah River until 2008, but even there, major salinity pulses were restricted to Savannah Lower (Fig. 4b).

Stem Growth Increment

Seasonal patterns of basal area increment were fairly consistent for upper and middle sites from both rivers; peaks occurred in late spring and summer (May–August), with relatively little basal area increment in fall and winter months (Fig. 5a, b). Seasonal patterns were much less distinctive on lower sites (Fig. 5c). While the magnitude of individual tree basal area increment differs between Savannah Upper and Middle sites at salinities below 2 psu (Table 3), growing season length is affected above 2 psu along both rivers, and is tempered by seasonal variation in salinity. For example, the greatest monthly growth rate of 2.1 $\text{cm}^2\ \text{month}^{-1}$ on Waccamaw Lower (Fig. 5c) corresponded to salinities below 2 psu in 2007, just prior to a large increase in salinity in subsequent months with drought (Fig. 4a).

Hence, for all years and months, mean patterns among sites are always the same; decreasing individual tree basal area increment from fresher to more saline environments (Fig. 6). Tree diameter growth even among surviving trees

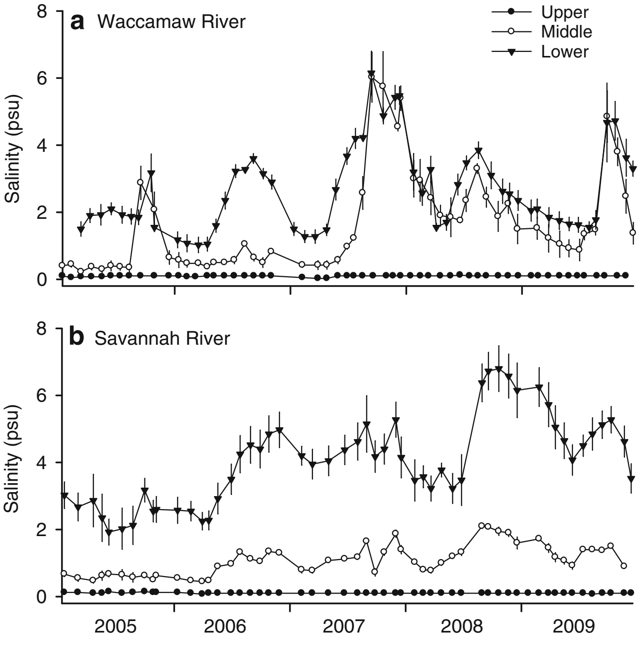

Fig. 4 Mean monthly soil salinity (psu ± SE) for upper, middle, and lower study sites along the **a** Waccamaw River and **b** Savannah River from 2005 to 2009

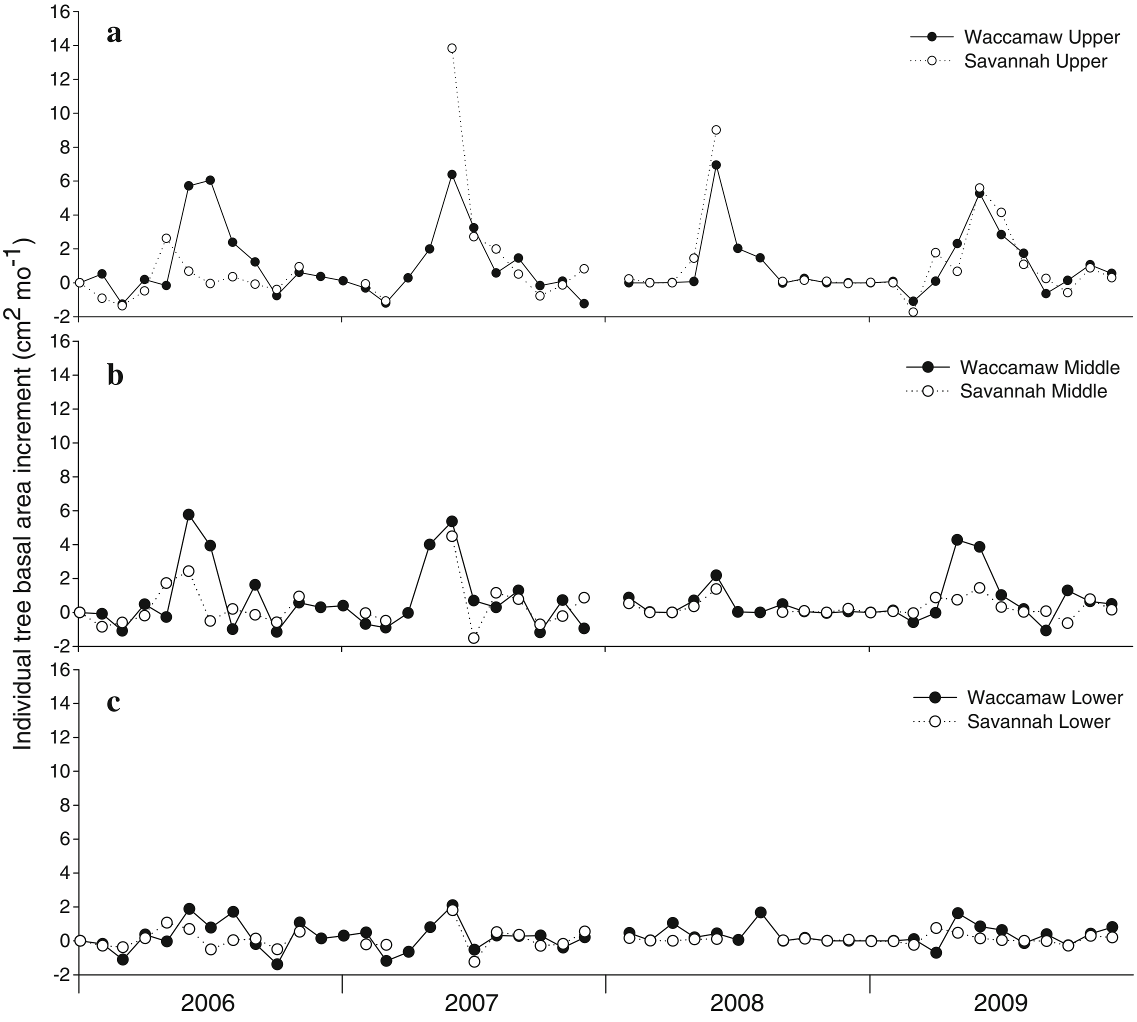

Fig. 5 Mean individual tree basal area increment by month for the **a** upper, **b** middle, and **c** lower study sites along the Waccamaw and Savannah Rivers from 2006 to 2009

is suppressed at the lower sites (more saline sites) for both watersheds beyond what would be considered sustainable; lower sites are rapidly converting to marsh. Statistically, monthly individual tree basal area increments are highly variable because of complete growth cessation in deciduous trees during winter months, making site by month interactions more important than site by year interactions (Table 3).

Litterfall

Mean forest canopy leaf litterfall differed significantly among sites (Table 3) ranging from as high as 732 g m^{-2} year^{-1} on an upper, freshwater site, to as low as 64 gm^{-2} year^{-1} on a lower, saline site (Table 2). Maximum monthly rates of leaf litterfall occurred in the fall (October to December) at all sites with a second smaller peak in the spring (April and May) at the upstream sites (Fig. 7). Fall peaks represent senesced leaves from late spring and summer foliar growth; the much smaller peaks in the spring on upper and middle sites correspond to annual defoliation from caterpillars. Significant differences were evident among sites, years, and months (Table 3). On average, annual litterfall was 233 and 527 % higher on middle and upper sites, respectively, than lower sites on the same river; however, the differential was much more distinct along the Waccamaw River (Table 2; Fig. 7). Furthermore, there were no clear differences among sites in terms of onset or duration of litterfall on a temporal resolution of months; physical leaf fall from canopies is driven by similar weather events on all sites (e.g., wind from cold fronts). Litter dropped from the canopy quicker at lower sites than upper and middle sites in early fall (Fig. 7). When sites had increased salinity due to drought conditions, like those present in 2007 and 2008 (Figs. 2 and 4), the overall capacity for leaf litterfall was suppressed (Fig. 7), providing less C and nutrient return to the forest floor.

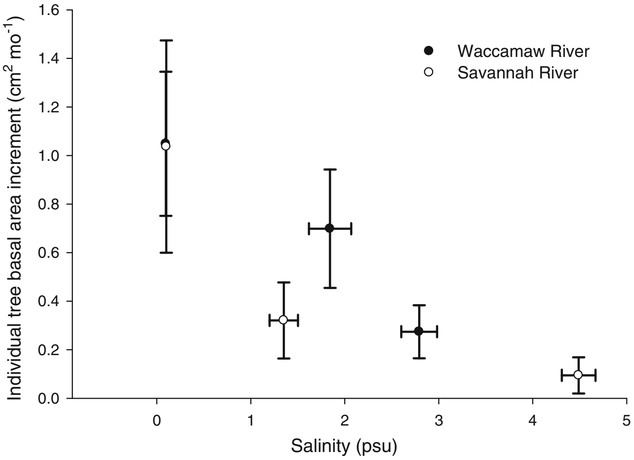

Fig. 6 Individual tree basal area increments for the six sites versus salinity (±1 SE). The data represent the averages of individual tree basal area increments for monthly measurements of 20 trees at each site from January 2006 to December 2009. Salinities are site averages of monthly samples of four wells per site from January 2006 to December 2009. Regression analysis yielded an r^2 of 0.843 for a quadratic fit with variation associated with means for y ($y=1.05-0.3936x+0.0409x^2$)

N and C Loading to the Forest Floor

The two watersheds did not differ significantly in the amount of C ($F=2.23$, $P=0.0963$) or N ($F=1.56$, $P=0.2208$) returned to the forest floor annually by way of leaf litterfall (Table 4). The concentration of C in senesced leaves was uniform among sites, ranging narrowly from 0.50 to 0.52 g g^{-1}. The concentration of N in senesced leaves was high at Savannah Lower (14.2 mg g^{-1}), 38 % greater than at Waccamaw Lower (10.3 mg g^{-1}). However, concentrations of N in senesced leaves at the Savannah Lower site was similar to the Waccamaw Upper and Savannah Upper sites (Table 4) despite much lower total litterfall at the lower sites (Fig. 7). When concentrations of N in senesced leaves were multiplied by total annual leaf litterfall, litterfall N fluxes at the Waccamaw Lower and Savannah Lower sites were only about 11 and 27 %, respectively, of those at the upper freshwater sites along the same rivers (Table 4). Differences in litterfall N fluxes are partly influenced by concentrations of N in the litter, but are primarily driven by differences in total mass of litterfall among our study sites.

Generally, N concentrations in senesced leaves decreased with increasing salinity, while leaf C/N ratios increased. Savannah Lower was the exception, with proportionally more N in senesced leaves. Total N in underlying soils was also reduced in both Savannah Lower and Savannah Upper locations (Table 1).

Discussion

Past investigations have documented the vegetation transition of tidal swamps to marsh at rather low salinity concentrations around 2 psu (Hackney et al. 2007; Krauss et al. 2009). While hydrology certainly mediates transitions to some degree, state change appears to be driven strongly by salinity, with examples of similar change along rivers and watersheds with vastly different hydrologies (Day et al. 2007).

Rates of Litterfall

Leaf litterfall rates from our tidal swamps were comparable to other reports. In another location along the Waccamaw River, the rate of leaf litterfall was 564–667 gm^{-2} year^{-1} (Ratard 2003), and a study from the Donnelley Wildlife Management area farther south along the South Carolina coast documented rates ranging from 355 to 655 g m^{-2} year^{-1} (Burke et al. 1999). Along the Savannah River, Megonigal et al. (1997) and Muzika et al. (1987) documented leaf litterfall rates of 644–972 and 337–544 g m^{-2} year^{-1}, respectively. Other studies in forested wetlands along the east coast reported a variety of leaf litterfall rates: Ogeechee River, Georgia (627–902 gm^{-2} year^{-1}; Cuffney 1988), Ichauway Ecological Reserve, Georgia (243–582 g m^{-2} year^{-1}; Watt and Golladay 1999), Great Dismal Swamp, Virginia (455–536 gm^{-2} year^{-1}; Gomez and Day 1982), and

Table 2 Annual leaf litterfall for 5 years at tidal swamp sites along the Waccamaw and Savannah Rivers

Year	Annual leaf litterfall (g m^{-2})					
	Waccamaw River			Savannah River		
	Upper	Middle	Lower	Upper	Middle	Lower
2005	645.87	337.21	97.73	618.44	337.70	165.31
2006	732.18	402.53	114.19	504.01	320.00	130.76
2007	645.36	358.45	82.99	613.43	340.73	147.58
2008	719.54	345.88	64.38	551.47	280.26	74.49
2009	688.64	324.36	82.01	527.10	298.00	72.96
X (S.E.)	686.32 (18.06)^{a}	353.69 (13.42)^{c}	88.26 (8.36)^{d}	562.89 (22.93)^{b}	315.34 (11.61)^{c}	118.22 (18.97)^{d}

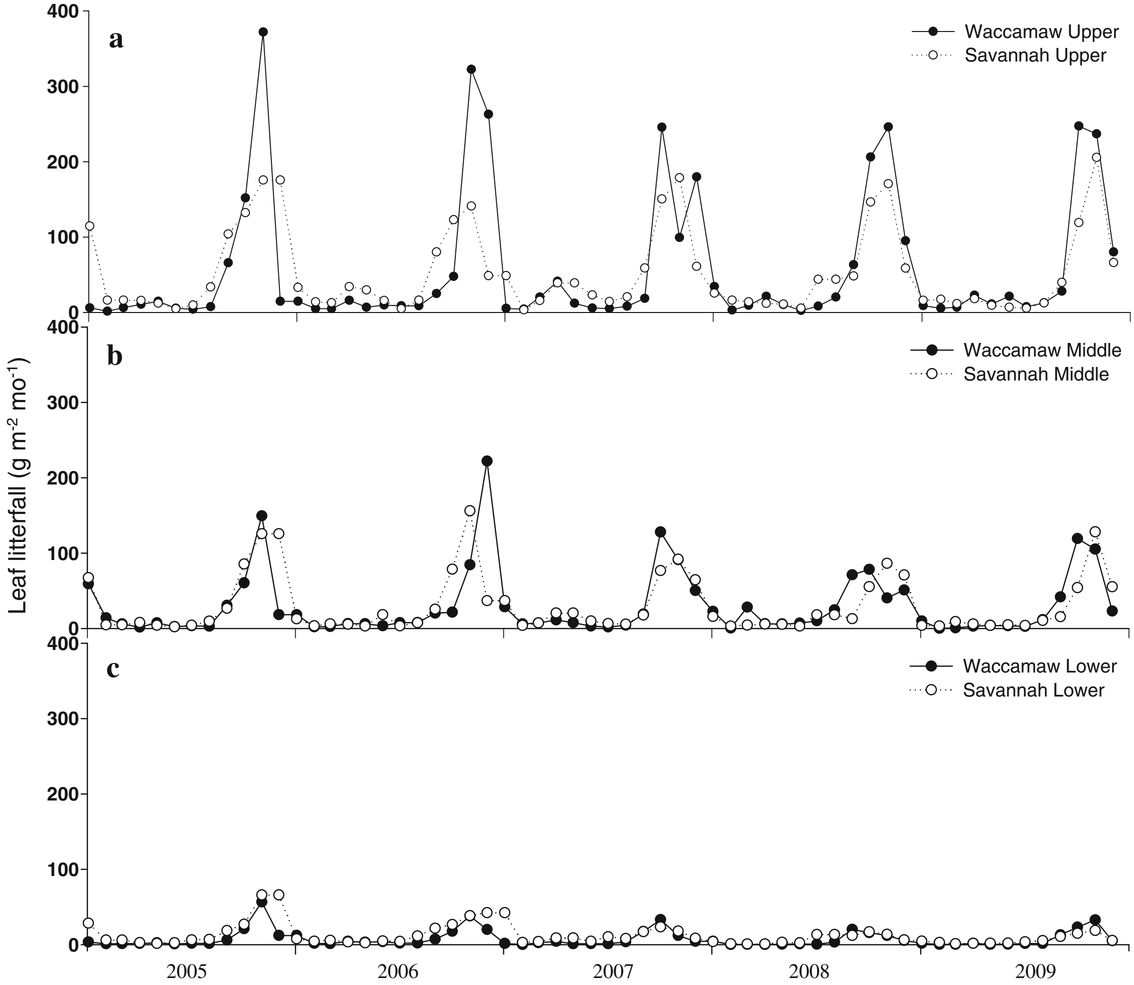

Fig. 7 Leaf litterfall by month for the **a** upper, **b** middle, and **c** lower study sites along the Waccamaw and Savannah Rivers from 2005 to 2009

Okefenokee Swamp, Georgia (231–595 gm^{-2} year^{-1}; Schlesinger 1978). Rates as low as 252 gm^{-2} year^{-1} were also reported in a tidal bottomland hardwood forest in Virginia (Fowler and Hershner 1989). Lower leaf litterfall rates reported by the literature mimic what we found on Waccamaw and Savannah Upper and Middle sites, but rates from the literature were greater than the litterfall rates at our higher salinity lower sites (Table 2). Brinson et al. (1985) also found lower leaf litterfall rates in downstream, more frequently flooded sites (290 and 381 gm^{-2} year^{-1}) than in upstream, less frequently flooded sites (600 and 731 gm^{-2} year^{-1}), suggesting similarly to our study that salinity can reverse the positive, nutrient-mediated relationship between litterfall and flood duration commonly documented from forested wetlands in the southeastern USA (Conner et al. 1981; Gomez and Day 1982; Megonigal et al. 1997).

Influence of Salinity on Litterfall, Growth, and N Recycling

Salinity tended to affect the mass of litter but neither the timing of leaf litter fall nor the concentration of foliar N consistently over five study years. Brinson et al. (1985) found that peaks in tidal swamp litterfall occurred slightly later on freshwater sites than on salt-impacted sites along tidal creeks in the Pamlico Sound, North Carolina. A 1-week shift in timing of litterfall in Brinson's study equated to 60–73 % of total litterfall dropping in October instead of November for more saline, downstream sites versus 38–55 % for upstream sites. While these differences in timing may seem small, foliar concentrations of N were higher in salinity stressed stands, potentially forcing greater amounts of N to surface litter during this early leaf abscission (Brinson et al. 1985). Leaves developing under true tidal freshwater conditions are expected to return many of the N-based compounds (including nucleosides and amino acids) to branches through phloem transport just prior to leaf abscission at the end of each year (Pennell and Lamb 1997), thus conserving N within deciduous stems. We did find that concentrations of foliar N were considerably higher for litter falling from April to September versus October to December (Table 4), such that premature leaf fall could add proportionally more N to the soil per leaf.

Table 3 Significance values for main effects and interactions of ANOVA comparisons for individual tree basal area increment and litterfall for tidal swamps along the Waccamaw and Savannah Rivers

Source of variation	DF_{num}, DF_{den}	MSE	*F* value	Pr>*F*
Individual tree basal area increment				
River	1, 144	0.04181	0.39	0.5330
Site	2, 144	0.78138	7.30	0.0010
River × site	2, 144	0.06294	0.59	0.5568
Month	5, 144	2.86676	26.78	<0.0001
River × month	5, 144	0.10616	0.99	0.4251
Site × month	10, 144	0.47000	4.39	<0.0001
River × site × month	10, 144	0.04588	0.43	0.9307
Year	3, 144	0.13606	1.27	0.2867
River × year	3, 144	0.25716	2.40	0.0701
Site × year	6, 144	0.03895	0.36	0.9007
Litterfall				
River	1, 180	11.02988	27.22	<0.0001
Site	2, 180	62.69820	154.72	<0.0001
River × site	2, 180	1.63124	4.03	0.0195
Month	5, 180	62.56346	154.39	<0.0001
River × month	5, 180	1.43288	3.54	0.0045
Site × month	10, 180	1.06959	2.64	0.0050
River × site × month	10, 180	0.47829	1.18	0.3068
Year	4, 180	1.90459	4.70	0.0012
River × year	4, 180	0.66640	1.64	0.1650
Site × year	8, 180	0.64720	1.60	0.1284

Month refers to bimonthly or 2-month averages (*1*: Jan/Feb, *2*: Mar/Apr, *3*: May/Jun, *4*: Jul/Aug, *5*: Sept/Oct, *6*: Nov/Dec)

However, we found no indication that leaves were shed out of phase, earlier or otherwise, among our study sites at monthly resolutions (Fig. 7). Perhaps more frequent collections would have revealed smaller-scale differences in litterfall timing among sites, but the differences in litterfall volume among sites were so great (Table 4) that within-month shifts in timing would be masked. Monthly variation in stem growth increment was consistent among our study sites despite increasingly saline conditions (Fig. 5), indicating an inherent, in lieu of relative, timing for growth patterns. Furthermore, as lower sites became progressively saltier in late 2007 through 2009, litterfall volume was reduced, but timing remained unchanged. Instead, it appeared that at the scale of an individual river, wind associated with frontal passages standardized pulses of litter to the forest floor. Litter did tend to fall over shorter time periods on more saline sites, especially after 2007 (Fig. 7), perhaps reflecting less canopy structure with reduced overstory species diversity. Peaks in litterfall were also linked more directly to high precipitation and wind events for a *Pterocarpus* forest in Puerto Rico undergoing transition to mangrove with salinity increases (Eusse and Aide 1999).

Resorption proficiency of N from leaves prior to senescence can be determined when compared with values from the literature (Killingbeck 1996); resorption is highly proficient when foliar N values in senesced leaf material are below 0.7 %. However, N made up 1.03–1.42 % of senesced leaf biomass from our tidal swamp sites, with one lower and one upper site tying for most inefficient (Table 4). Compared with many deciduous species surveyed (median=0.87 % foliar N; Killingbeck 1996), resorption proficiency from litter in our tidal swamps was not strong regardless of salinity. Furthermore, during periods of maximum leaf fall in October through December, the highest concentration of foliar N (12.8 mg g^{-1}) was found on Savannah Lower, yet this same site registered among the lowest concentration of soil total N (Table 1). Otherwise, reductions in litter N concentrations appeared linear from freshwater sites to saline sites along both rivers. It is possible that soil total N concentrations may be related to site-level differences in the refractory nature of litter N balanced against supply of N from flood waters (sensu Noe and Hupp 2007). Foliar C content, which ranged narrowly from 0.50 to 0.52 g g^{-1}, offered little insight per se.

Hydrological Variation among Study Sites

The effect that increased salinity has on primary productivity at these sites may be confounded by the influence of the frequency and duration each site is flooded. Both Waccamaw and Savannah Lower sites were flooded between 591 and 633 h year^{-1} over the first several years of study, while flood duration for upper and middle sites ranged from 256 to 390 h year^{-1} over that same interval (Krauss et al. 2009). However, in terms of flood frequency, middle and lower sites were more similar, receiving between 137 and 169 floods per year. Waccamaw and Savannah Upper sites were flooded between 48 and 97 times per year. Hence, litterfall was greatest on sites that had among the lowest flood durations along with the lowest flood frequencies (Fig. 7). Stem growth patterns were variable by river in patterning between middle and either upper or lower sites (Fig. 5). This indicates that relative flood frequency may be as important as duration for maintaining forest productivity during drought.

A few studies have indicated that wetland trees experience less seasonal variation in growth because of a more reliable supply of soil water (Reich and Borchert 1984; Young et al. 1993), which may be extrapolated to wet versus dry years (but see Davidson et al. 2006). More importantly, flood frequency is also a primary driver for soil N dynamics in floodplain forests (Conner et al. 1981; Gomez and Day 1982; Noe and Hupp 2007). Mean N concentrations in the peak leaf litterfall of *T. distichum* and *N. aquatica* species were higher in more frequently flooded *T. distichum* stands than in either cedar or mixed hardwood forests (Gomez and Day 1982). Variation in when water is delivered via surface

Table 4 Annual contributions of litterfall carbon and nitrogen to the forest floor, and carbon and nitrogen concentrations in senesced leaf litter in all six sites from 2004 to 2006 along the Waccamaw and Savannah Rivers

	Waccamaw River			Savannah River		
	Upper	Middle	Lower	Upper	Middle	Lower
Annual leaf litterfall						
Carbon (g m^{-2})	370.93	195.89	50.12	322.69	194.34	74.81
Nitrogen (mg m^{-2})	8,893	3,961	955	7,359	3,701	1,987
Concentration in senesced leaves						
Carbon (g g^{-1})						
January–March	0.52	0.53	0.51	0.50	0.52	0.52
April–June	0.51	0.52	0.53	0.50	0.52	0.51
July–September	0.49	0.50	0.50	0.50	0.50	0.50
October–December	0.50	0.52	0.52	0.50	0.51	0.51
Average (S.E.)	0.51 (0.004)	0.52 (0.006)	0.51 (0.006)	0.50 (0.002)	0.51 (0.004)	0.51 (0.004)
Nitrogen (mg g^{-1})						
January–March	13.4	9.0	8.4	11.5	10.0	12.9
April–June	17.4	15.0	12.0	18.9	13.9	16.5
July–September	14.8	12.6	11.5	11.1	12.3	14.6
October–December	11.4	10.1	9.4	10.5	9.1	12.8
Average (S.E.)	14.2 (1.25)	11.7 (1.32)	10.3 (0.87)	13.0 (1.98)	11.3 (1.09)	14.2 (0.86)
Atomic ratio of leaves						
C/N						
Average (S.E.)	36 (3.2)	46 (5.4)	51 (4.3)	41 (4.9)	47 (4.6)	36 (2.2)

flooding should influence productivity interactively with soil nutrient status.

Relative to our hypothesis, greater flood frequencies would tend to flush surface litter from sites more efficiently, perhaps forcing a greater role for litter dynamics to influence N biogeochemistry on upstream sites with less frequent flooding, especially during drought. Furthermore, with such a large discrepancy in the volume of litter N falling in the two less frequently flooded, upstream freshwater sites (8,126 mg N m^{-2} $year^{-1}$) versus the four downstream sites (2,651 mg N m^{-2} $year^{-1}$: Table 4), any increase in soil total N stores with higher salinity would have to be related to differential flushing, decomposition, and/or mineralization in lieu of litter N loading alone. Accordingly, flushing of litter from our sites is expected to be higher on seaward sites flooded more frequently, while litter decomposition may be faster on freshwater sites because of generally lower C:N concentrations in leaf litter (Table 4; Taylor et al. 1989). Regardless, the six sites we selected indicated enough variation in soil total N, foliar N concentrations, and litter C/N ratios to cloud clear patterns; hydrological control over biogeochemical cycling provides a likely explanation for variable patterns (Clawson et al. 2001).

Conclusions

Forest stands with higher salinity had greater flood frequency and duration, lower basal area increments, lower tree densities, higher numbers of dead or dying trees, and reduced leaf litter fall. We also tested the hypothesis that higher soil total N concentrations at moderate salinities may be explained by greater amounts of N loading to the soil from litterfall on salt-impacted sites. Overall, our data did not indicate that litterfall N is a likely source for the increased soil total N on our study sites at moderate salinities. However, this conclusion may be masked by the lack of data from litterfall and N content of plants less than 1 m (the height of our litter traps). These results are based on litter N inputs from the dominant vegetation in the overstory and do not reflect the inputs from understory herbaceous vegetation. Alternatively, the rate of decomposition and potential for N mineralization on our study sites undergoing salinity-induced state change may be more important for controlling N biogeochemical cycling in soils than N loading via litterfall. Further study of organic matter mineralization rates is needed as well as a comprehensive study of nitrogen fluxes from soil respiration and dissolution of N gas in the porewater and surface water to determine the influence of these proposed processes on N cycling in these tidal forest systems.

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References

Baldwin, A.H. 2007. Vegetation and seed bank studies of salt-pulsed swamps of the Nanticoke River, Chesapeake Bay. In *Ecology of tidal freshwater forested wetlands of the Southeastern United States*, ed. W.H. Conner, T.W. Doyle, and K.W. Krauss, 139–160. The Netherlands: Springer.

Brinson, M.M., H.D. Bradshaw, and M.N. Jones. 1985. Transitions in forested wetlands along gradients of salinity and hydroperiod. *Journal of the Elisha Mitchell Scientific Society* 101: 76–94.

Brinson, M.M., R.R. Christian, and L.K. Blum. 1995. Multiple states in the sea-level induced transition from terrestrial forest to estuary. *Estuaries* 18: 648–659.

Bristol, P.L., R.J. Devlin, D.G. Baize, and A.C. Boozer. 2005. South Carolina—Savannah River basin facilities water use report 2004. Technical Report No. 010-05, South Carolina Department of Health and Environmental Control, Bureau of Water, Columbia, SC, USA.

Burke, M.K., B.G. Lockaby, and W.H. Conner. 1999. Aboveground production and nutrient circulation along a flooding gradient in a South Carolina Coastal Plain forest. *Canadian Journal of Forest Research* 29: 1402–1418.

Cattelino, P.J., C.A. Becker, and L.G. Fuller. 1986. Construction and installation of homemade dendrometer bands. *Northern Journal of Applied Forestry* 3: 73–75.

Clawson, R.G., B.G. Lockaby, and B. Rummer. 2001. Changes in production and nutrient cycling across a wetness gradient within a floodplain forest. *Ecosystems* 4: 126–138.

Conner, W.H., J.G. Gosselink, and R.T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. *American Journal of Botany* 68: 320–331.

Cuffney, T.F. 1988. Input, movement and exchange of organic matter within a subtropical coastal blackwater river-floodplain system. *Freshwater Biology* 19: 305–320.

Davidson, G.R., B.C. Laine, S.J. Galicki, and S.T. Threlkeld. 2006. Root-zone hydrology: Why bald cypress in flooded wetlands grow more when it rains. *Tree-Ring Research* 62: 3–12.

Day, R.H., T.M. Williams, and C.M. Swarzenski. 2007. Hydrology of tidal freshwater forested wetlands of the Southeastern United States. In *Ecology of tidal freshwater forested wetlands of the Southeastern United States*, ed. W.H. Conner, T.W. Doyle, and K.W. Krauss, 29–63. The Netherlands: Springer.

DeSantis, L.R.G., S. Bhotika, K. Williams, and F.E. Putz. 2007. Sea-level rise and drought interactions accelerate forest decline on the Gulf Coast of Florida, USA. *Global Change Biology* 13: 2349–2360.

Doyle, T.W., C.P. O’Neil, M.P.V. Melder, A.S. From, and M.M. Palta. 2007. Tidal freshwater swamps of the Southeastern United States: Effects of land use, hurricanes, sea-level rise, and climate change. In *Ecology of tidal freshwater forested wetlands of the Southeastern United States*, ed. W.H. Conner, T.W. Doyle, and K.W. Krauss, 1–28. The Netherlands: Springer.

Eusse, A.M., and T.M. Aide. 1999. Patterns of litter production across a salinity gradient in a *Pterocarpus officinalis* tropical wetland. *Plant Ecology* 145: 307–315.

Field, D.W., A. Reyer, P. Genovese, and B. Shearer. 1991. Coastal wetlands of the United States: An accounting of a valuable national resource. Office of Oceanography and Marine Assessment, National Ocean Service, National Oceanic and Atmospheric Administration, Rockville, MD, USA.

Fowler, B.K., and C. Hershner. 1989. Primary production in Cohoke Swamp, a tidal freshwater wetland in Virginia. In *Freshwater wetlands and wildlife symposium: Perspectives on natural, managed and degraded ecosystems*, eds. R.R. Sharitz and J.W. Gibbons, 365–374. U.S. Department of Energy, Office of Scientific and Technical Information, CONF-8603101, DOE Symposium Series No. 61, Oakridge, TN, USA.

Gomez, M.M., and F.P. Day Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. *American Journal of Botany* 69: 1314–1321.

Guttman, N.B. 1998. Comparing the Palmer Drought Index and the Standardized Precipitation Index. *Journal of the American Water Resources Association* 34: 113–121.

Hackney, C.T., and G.F. Yelverton. 1990. Effects of human activities and sea level rise on wetland ecosystems in the Cape Fear River Estuary, North Carolina, USA. In *Wetland ecology and management*, ed. D.F. Whigham, R.F. Good, and Y. Kvet, 55–61. Dordrecht: Kluwer Academic Publishers.

Hackney, C.T., G.B. Avery, L.A. Leonard, M. Posey, and T. Alphin. 2007. Biological, chemical, and physical characteristics of tidal freshwater swamp forests of the Lower Cape Fear River/Estuary, North Carolina. In *Ecology of tidal freshwater forested wetlands of the Southeastern United States*, ed. W.H. Conner, T.W. Doyle, and K.W. Krauss, 183–221. The Netherlands: Springer.

Hall, R.C. 1944. A vernier tree-growth band. *Journal of Forestry* 42: 742–743.

Hinckley, T.M., P.M. Dougherty, J.P. Lassoie, J.E. Roberts, and R.O. Teskey. 1979. A severe drought: Impact on tree growth, phenology, net photosynthetic rate and water relations. *The American Midland Naturalist* 102: 307–316.

Keeland, B.D., and J.W. McCoy. 2007. Plant community composition of a tidally influenced, remnant Atlantic white cedar stand in Mississippi. In *Ecology of tidal freshwater forested wetlands of the Southeastern United States*, ed. W.H. Conner, T.W. Doyle, and K.W. Krauss, 89–111. The Netherlands: Springer.

Keeland, B.D., and R.R. Sharitz. 1993. Accuracy of tree growth measurements using dendrometer bands. *Canadian Journal of Forest Research* 23: 2454–2457.

Killingbeck, K.T. 1996. Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology* 77: 1716–1727.

Krauss, K.W., J.A. Duberstein, T.W. Doyle, W.H. Conner, R.H. Day, L.W. Inabinette, and J.L. Whitbeck. 2009. Site condition, structure, and growth of baldcypress along tidal/non-tidal salinity gradients. *Wetlands* 29: 505–519.

Light, H.M., M.R. Darst, and R.A. Mattson. 2007. Ecological characteristics of tidal freshwater forests along the Lower Suwannee River, Florida. In *Ecology of tidal freshwater forested wetlands of the Southeastern United States*, ed. W.H. Conner, T.W. Doyle, and K.W. Krauss, 291–320. The Netherlands: Springer.

Megonigal, J.P., W.H. Conner, S. Kroeger, and R.R. Sharitz. 1997. Aboveground production in southeastern floodplain forests: A test of the subsidy-stress hypothesis. *Ecology* 78: 370–384.

Mitsch, W.J., J.G. Gosselink, C.J. Anderson, and L. Zhang. 2009. *Wetland ecosystems*. New Jersey: Wiley.

Muzika, R.M., J.B. Gladden, and J.D. Haddock. 1987. Structural and functional aspects of succession in southeastern floodplain forests following a major disturbance. *American Midland Naturalist* 117: 1–9.

Neubauer, S.C., W.D. Miller, and I.C. Anderson. 2000. Carbon cycling in a tidal freshwater marsh ecosystem: A carbon gas flux study. *Marine Ecology Progress Series* 199: 13–30.

Noe, G.B., and C.R. Hupp. 2007. Seasonal variation in nutrient retention during inundation of a short-hydroperiod floodplain. *River Research and Applications* 23: 1088–1101.

Palmer, W.C. 1965. *Meteorological drought*. Research paper no. 45, U.S. Weather Bureau, Washington, DC. 58 pp.

Pearlstein, L.G., W.M. Kitchens, P.J. Latham, and R.D. Bartleson. 1993. Tide gate influences on a tidal salt marsh. *Water Resources Bulletin* 29: 1009–1019.

Pennell, R.I., and C. Lamb. 1997. Programmed cell death in plants. *The Plant Cell* 9: 1157–1168.

Pezeshki, S.R., R.D. DeLaune, and W.H. Patrick Jr. 1987. Response of baldcypress (*Taxodium distichum* L. var. *distichum*) to increases in flooding salinity in Louisiana's Mississippi River Deltaic Plain. *Wetlands* 7: 1–10.

Ratard, M.A. 2003. *Factors affecting growth and regeneration of baldcypress in a South Carolina tidal freshwater swamp*. PhD thesis, Clemson University, Clemson, South Carolina.

Reich, P.B., and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* 72: 61–74.

Rheinhardt, R. 1992. A multivariate analysis of vegetation patterns in tidal freshwater swamps of lower Chesapeake Bay, USA. *Bulletin of the Torrey Botanical Club* 119: 192–207.

Rheinhardt, R., and C. Hershner. 1992. The relationship of belowground hydrology to canopy composition in five tidal freshwater swamps. *Wetlands* 12: 208–216.

Salinas, L.M., R.D. DeLaune, and W.H. Patrick Jr. 1986. Changes occurring along a rapidly subsiding coastal area: Louisiana, USA. *Journal of Coastal Research* 2: 269–284.

SCDHEC. 2000. Watershed water quality management strategy: Pee Dee Basin. Technical Report No. 015-00. South Carolina Department of Health and Environmental Control, Bureau of Water, Columbia, SC, USA.

Schlesinger, W.H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee cypress swamp-forest. *Ecological Monographs* 48: 43–65.

Schöngart, J., M.T.F. Piedade, S. Ludwigshausen, V. Horna, and M. Worbes. 2002. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology* 18: 581–597.

Stedman, S., and T.E. Dahl. 2008 Status and trends of wetlands in the coastal watersheds of the Eastern United States 1998 to 2004. National Oceanic and Atmospheric Administration, National Marine Fisheries Service and U.S. Department of the Interior, Fish and Wildlife Service. 32 pp.

Taylor, B.R., D. Parkinson, and W.F.J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology* 70: 97–104.

Watt, K.M., and S.W. Golladay. 1999. Organic matter dynamics in seasonally inundated, forested wetlands of the Gulf Coastal Plain. *Wetlands* 19: 139–148.

Weston, N.B., R.E. Dixon, and S.B. Joye. 2006. Ramifications of increased salinity in tidal freshwater sediments: Geochemistry and microbial pathways of organic matter mineralization. *Journal of Geophysical Research* 111: G01009.

Whigham, D.F. 2009. Primary production in tidal freshwater wetlands. In *Tidal freshwater wetlands*, ed. A. Barendregt, D.F. Whigham, and A.H. Baldwin, 115–122. Weikersheim: Margraf Publishers.

Williams, K., K.C. Ewel, R.P. Stumpf, F.E. Putz, and T.W. Workman. 1999. Sea-level rise and coastal forest retreat on the west coast of Florida, USA. *Ecology* 80: 2045–2063.

Williams, K., M. MacDonald, and L.D.S.L. Sternberg. 2003. Interactions of storm, drought, and sea-level rise on coastal forest: A case study. *Journal of Coastal Research* 19: 1116–1121.

Young, P.J., J.P. Megonigal, R.R. Sharitz, and F.P. Day. 1993. False ring formation in baldcypress (*Taxodium distichum*) saplings under two flooding regimes. *Wetlands* 13: 293–298.