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Forest composition and growth in a freshwater forested wetland community across a salinity gradient in South Carolina, USA

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A B S T R A C T

Tidal freshwater forested wetlands (TFFW) of the southeastern United States are experiencing increased saltwater intrusion mainly due to sea-level rise. Inter-annual and intra-annual variability in forest productivity along a salinity gradient was studied on established sites. Aboveground net primary productivity (ANPP) of trees was monitored from 2013 to 2015 on three sites within a baldcypress (*Taxodium distichum*) swamp forest ecosystem in Strawberry Swamp on Hobcaw Barony, Georgetown County, South Carolina. Paired plots (20×25-m) were established along a water salinity gradient (0.8, 2.6, 4.6 PSU). Salinity was continuously monitored, litterfall was measured monthly, and growth of overstory trees $\geqslant 10$ cm diameter at breast height (DBH) was monitored on an annual basis. Annual litterfall and stem wood growth were summed to estimate ANPP. The DBH of live and dead individuals of understory shrubs were measured to calculate density, basal area (BA), and important values (IV). Freshwater forest communities clearly differed in composition, structure, tree size, BA, and productivity across the salinity gradient. The higher salinity plots had decreased numbers of tree species, density, and BA. Higher salinity reduced average ANPP. The dominant tree species and their relative densities did not change along the salinity gradient, but the dominance of the primary tree species differed with increasing salinity. Baldcypress was the predominant tree species with highest density, DBH, BA, IV, and contribution to total ANPP on all sites. Mean growth rate of baldcypress trees decreased with increasing salinity, but exhibited the greatest growth among all tree species. While the overall number of shrub species decreased with increasing salinity, wax myrtle (*Morella cerifera*) density, DBH, BA, and IV increased with salinity. With rising sea level and increasing salinity levels, low regeneration of baldcypress, and the invasion of wax myrtle, typical successional patterns in TFFW and forest health are likely to change in the future.

1. Introduction

Tidal freshwater forested wetlands (TFFW) ecosystems provide an opportunity for understanding the unique structuring of freshwater forests along hydroperiod, salinity, and microtopographical gradients (Williams et al., 1999; Morris et al., 2002; Craft et al., 2009; Anderson et al., 2013). TFFW with seasonal hydrology are generally more productive than their stagnant or drained counterparts (Conner and Day, 1976, 1992). Likewise, rapid hydrological pulsing of tidal systems can likely be a factor in the relatively high primary productivity found in TFFW (Ratard, 2004; Duberstein and Kitchens, 2007). This productivity makes them an important component in global carbon sequestration, thus the importance of understanding processes in these wetlands. However, tidal fluctuations, local precipitation, and freshwater inputs drive most variations in salinity and inundation (Ungar, 1991; Schile et al., 2011). Therefore, TFFW are likely the most sensitive ecosystems to the very trend that carbon sequestration efforts hope to ameliorate: global climate change (Doyle et al., 2007). The effects of increased salinity have been documented in greenhouse gas and streamside forest studies (e.g., DeLaune and Lindau, 1987; Conner and Brody, 1989; Pezeshki et al., 1990), and include decreased productivity, death of trees, and transformation to alternate stable states (Pezeshki et al., 1987; Hackney et al., 2007; Krauss et al., 2009, 2012). Furthermore, both salinity and inundation regimes within tidal wetlands are likely to be affected by future climate change through increased rates of sea level rise and changes in local precipitation and watershed runoff (Hopkinson et al., 2008; Nicholls

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and Cazenave, 2010). Sea level rise poses potentially greater threats to backswamp areas due to decreased flushing once salt intrudes.

TFFW and other types of coastal swamp forests of the southeastern U.S. are degrading in many oligohaline (low salinity) locations (Conner et al., 2007). This degradation is related both to natural climate change factors and anthropogenic influences, with sea level rise and saltwater intrusion being dominant factors (Williams et al., 1999, 2007). Our working hypothesis is that ecosystem productivity will vary in predictable ways as salinity levels increase in TFFW. Our objective in this study was to document inter-annual and intra-annual variability in forest productivity along a water salinity gradient.

2. Methods

2.1. Study area

Strawberry Swamp is a coastal freshwater forested wetland located on Hobcaw Barony, in Georgetown County, SC (33°19′49″N, 79°14′54″W), that is being subjected to saltwater intrusion and flooding due to rising sea level which has averaged 3–4 mm yr^{-1} since 1920 (Williams et al., 2012). The swamp is 236 ha in area, dropping 6 m from its catchment ridge to its tidally influenced outflow into a tidal creek that discharges into the Winyah Bay estuary (Jayakaran et al., 2014). There is a seasonally intermittent groundwater flow through the swamp. Forests in the swamp range from very dry upland sites with forests of loblolly pine (*Pinus taeda* L.), scattered sweetgum (*Liquidambar styraciflua* L.), southern red oak (*Quercus falcata* Michx.), and hickory (*Carya* spp.) to permanently flooded swamp at its lowest reaches containing baldcypress (*Taxodium distichum* (L.) Rich.) with some water tupelo (*Nyssa aquatica* L.) and swamp blackgum (*Nyssa biflora* Walt.). Strawberry Swamp and surrounding areas are at least second-growth forests, as evidenced by numerous decaying stumps. Soils are of the Hobcaw series (fine-loamy, siliceous, thermic, Typic Umbraquults) (Stuckey, 1982). Surrounding forests contain 80% soil organic matter at 0–1 cm decreasing to 53% at 8–9 cm (Go et al., 2000). The climate is classified as humid subtropical climate with hot summers and mild winters. Air and water temperatures drop below 0 °C for only a few days in December and January with the lowest temperature being 2.5 °C. Average high and low air temperatures are 27.6 °C in July and 8.2 °C in January, respectively. Average annual rainfall is 1330 mm (mean of 17 cm $month^{-1}$; from National Climate Data Center). The swamp has experienced considerable die-back of baldcypress trees in the lower reaches during the past several decades as a result of rising sea level and increased salinity (Williams et al., 2012).

2.2. Water depth and salinity

Water depth, temperature, and conductivity (CTD) sensors (Decagon CTD-10 Conductivity Temperature & Depth Sensor, Decagon Devices, Pullman, WA) were installed at 3 locations along the salinity gradient in Strawberry Swamp. The CTD sensors allowed for the continuous measurement of temporal variations of water depth and salinity along this salinity gradient. All data were measured at 15-min intervals from January 2014 through December 2015. Based on water salinity and water depth, we quantified salinity level of the three study sites as: low-saline (~0.8 PSU), mid-saline (~2.6 PSU) and high-saline (~4.6 PSU). Microclimatic conditions were also measured using a weather station (Campbell Scientific, Logan, UT) installed within the watershed.

2.3. Forest productivity

Three study sites were selected in Strawberry Swamp in June 2013. Each site consisted of paired 20 × 25-m plots (six plots) along the salinity gradient. All trees in each plot were remeasured for diameter at breast height (DBH) at the end of each growing season (2014–2015) using standard diameter tapes. Total tree biomass (stem, branch, and bark) for each year were estimated from DBH using general allometric equations (Clark et al., 1985; Megonigal et al., 1997). While not specific to the site, these equations have been used by a number of researchers in the southeastern United States to calculate biomass of trees (e.g., Busbee et al., 2003; Clawson et al., 2001; Cormier et al., 2013; Megonigal et al., 1997; Schilling and Lockaby, 2006; Shaffer et al., 2009). Shrubs and sapling DBH (>1.3 m tall but <10 cm DBH) were measured with digital electronic calipers in 2015. Basal area (BA), stand density, and species composition for trees and shrubs were assessed for each plot. Importance values (IV), ranging from 0 to 100, were calculated based on the relative density and relative dominance of each species in each plot (Kent and Coker, 1992).

To assess the effect of water salinity on tree size, trees were separated into four DBH classes: 10 cm ⩽ DBH < 20 cm (small trees), 20 cm ⩽ DBH < 30 cm (medium trees), 30 cm ⩽ DBH < 50 cm (medium-large trees) and >50 cm (large trees). The four tree DBH class categorizations were calculated to identify the change of diameter classes within a species among salinities.

2.4. Litterfall and aboveground net primary production

Litterfall was collected monthly from January 2014 to December 2015 in each plot using five 0.25 m^{-2} wooden litter boxes with 1 mm mesh fiberglass screen bottoms. The litter traps were elevated to 1 m above ground to prevent inundation during flooding. Litterfall was oven-dried immediately upon returning to the laboratory for at least 48 h at 70 °C to a constant weight, then sorted into two categories: 1) leaf litterfall (including leaves, seeds, and flowers), and 2) non-leaf litterfall (including twigs, bark, lichens, moss). Sorted litter from each trap was then weighed to the nearest 0.01 g, and recorded as g m^{-2} (Cormier et al., 2013). Mean monthly leaf litterfall dry weights were summed to estimate annual litterfall at each site and added to stemwood increment to get aboveground net primary productivity (ANPP) (Catchpole and Wheeler, 1992; Mitsch et al., 1991).

Data were analyzed using one-way ANOVA in SPSS (Version 22.0) with a level of significance for all tests set at 0.05.

3. Results

3.1. Water depth and salinity

Water depth and salinity data in Strawberry Swamp show that water depth at all three sites were dynamic and responsive, driven by precipitation events that caused water depths to spike after rainfall events (Fig. 1). Water depth variations at the low-saline site and mid-saline site appear to vary similarly over the period of study. Perennial water depths at these sites were fairly constant between storm events except during the summer time when all three sites exhibit annual low levels in 2014 and 2015. Water depths at the start of the study period were similar to those measured at the end of 2015 at these three sites. All three sites showed a spike in water depth associated with a major storm event between 10/1/15 and 10/5/15 with 936 mm of rainfall measured in the watershed. Water depth variation at the high-saline site showed more variation compared to the other two sites with water depths appearing to be influenced by more than just precipitation