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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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Abstract:

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 ≥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.

Keywords: Tidal freshwater forested wetlands; Basal area; Litterfall; Aboveground net primary productivity; Overstory and understory composition

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; Sahile 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 et al., 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; Williams et al., 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 I and Thomas, 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-minute 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 $\leq$ DBH < 20 cm (small trees), 20 cm $\leq$ DBH < 30 cm (medium trees), 30 cm $\leq$ 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 events. Over the period of the study, water depths at the high-saline site gradually increased from 200 mm in January 2014 to about 400 mm in December 2015. There was also a large increase in water depths in the spring of 2015 that was not apparent at the other two sites including a large spike in water depth in April 2015.

As expected with daily freshwater flow and significant drop of water depth after storm events, water salinity decreased in all sites during 2014 and 2015, especially after the October storm in 2015 (Fig. 1). Measured salinity at the low-saline site remained around 0.8 PSU throughout the study. Salinity levels were highest during the high water depth periods of summer 2014 and 2015, and lowest during the low winter water depths. At the mid-saline site, salinity averaged around 2.6 PSU and appeared to show a weak association with water depths, with lower salinity associated with low water depths during the summer time and higher salinity corresponding to periods when water depths were generally high during the spring of 2014 and 2015. The absolute variation of salinity at the medium site was low, ranging from 1.6 to 3.5 PSU. At the high-saline site, the average salinity was 4.7 PSU over the period of study and ranged from 3.2 to 6.3 PSU. Similar to the mid-saline site, there appears to be a weak but positive association with water depth and salinity, with higher water depths associated with higher salinity.

3.2. Tree species composition

Six tree species were found at each site, with baldcypress, swamp blackgum, and water tupelo being dominant, making up 85.0%, 91.9%, and 85.2% growing in the low-saline, mid-saline, and high-saline site, respectively. Other tree species included ash (*Fraxinus* spp.; 7.5% of total stems), sweetgum (6.3%), and dahoon holly (*Ilex cassine* L.; 1.3%) at the low-saline site, wax myrtle (*Morella cerifera* (L.) Small; 4.8%), red maple (*Acer rubrum* L.; 1.6%), and loblolly pine (*Pinus taeda* L.; 1.6%) at the mid-saline site, and wax myrtle (11.5%), ash (1.6%), and redbay (*Persea borbonia* (L.) Spreng.; 1.6%) at the high-saline site. With increasing salinity, dahoon holly and sweetgum disappeared, swamp blackgum decreased significantly in mid-saline and high-saline sites, and wax myrtle increased in mid-saline and high-saline sites.

3.3. Tree density, Basal Area, and Importance Values

There were 800, 620, and 600 tree stems ha^{-1} in the low-saline, mid-saline, and high-saline sites, respectively (Table 1). Water tupelo was the largest tree in the low-saline site with an average DBH of 38.2 cm, while baldcypress was the largest tree in the mid-saline and high-saline sites, with an average DBH of 45.6 and 47.8 cm, respectively. While water tupelo and swamp blackgum were common in low-saline and mid-saline sites, they were not found in the high-saline site. Overall distribution of tree density by size class in the three sites is shown in Fig. 2. Across the salinity gradient, there were 340, 170, and 250 small tree-sized stems ha^{-1} found in the low-saline, mid-saline, and high-saline sites, respectively. The number of medium trees decreased from 170 to 150 to 90 stems ha^{-1} while medium-large trees decreased from 240 to 190 to 170 stems ha^{-1}

in the low-saline, mid-saline, and high-saline sites, respectively. Large trees increased from 50 stems ha^{-1} in the low-saline site to 110 stems ha^{-1} in the mid-saline site and 100 stems ha^{-1} in the high-saline site.

Tree density (stems ha^{-1}) by size class for each species in the three sites is presented in Table 1. In the low-saline site, 6 species were found in the small tree-size class, but only 2 of those species (baldcypress and water tupelo) make it to the large tree group. In the mid-saline site, wax myrtle appears in the small tree-size class; swamp blackgum numbers are greatest in the small and medium tree classes, but are not found in the larger size classes; baldcypress and water tupelo are the only species found in the medium-large and large size classes. In the high-saline site, wax myrtle and swamp blackgum are dominant species in the small tree-size class; water tupelo, swamp blackgum, and baldcypress are the only species in the medium and medium-large size classes, with only baldypress trees found in the largest size class.

Basal area was highest at the mid-saline site with 66.1 m^2 ha^{-1}, followed by the low-saline site (65.1 m^2 ha^{-1}) and high-saline site (58.7 m^2 ha^{-1}) (Table 1). Baldcypress represented 80% of the BA at the high-saline site (47.1 m^2 ha^{-1}) and 65% of the BA at the mid-saline site (42.7 m^2 ha^{-1}), while baldcypress, swamp blackgum, and water tupelo (23.3, 19.7 and 16.5 m^2 ha^{-1}, respectively) dominated in the mid-saline site. As with BA, the IV of swamp blackgum and water tupelo decreased as salinity increased, but IV of baldcypress increased with increasing salinity.

3.4 Stem wood growth

Average stem wood growth (SWG) during the study was 427 g m^{-2} yr^{-1}, 412 g m^{-2} yr^{-1} and 386 g m^{-2} yr^{-1} in low-saline, mid-saline, and high-saline sites, respectively (Fig. 3). Although there seems to be a general decline in average SWG with increasing salinity, the decline was not significant. There were distinct differences between the two study years. In 2014, the greatest SWG occurred in the mid-saline site (555 g m^{-2} yr^{-1}) followed by the low-saline site and the high-saline site. For 2015, the mid-saline site exhibited the lowest SWG (269 g m^{-2} yr^{-1}) followed by the low-saline and high-saline sites at approximately 400 g m^{-2} yr^{-1} each. The contribution of baldcypress to total SWG was significantly greater in the mid-saline and high-saline sites both years. The average contribution of baldcypress to total SWG over the course of the study was 44.3% in the low-saline site, 66.4% in the mid-saline site and 77.5% in the high-saline site.

3.5 Leaf litterfall

An examination of the monthly dynamics of leaf litterfall shows that there are two peaks in litterfall each year. Maximum monthly leaf litterfall occurs in the fall and winter (September, November to December) at all sites with a second smaller peak in the spring (April and early May) (Fig. 4). The fall peak was higher in the low-saline site than in the mid- and high-saline sites, probably due to the higher tree density in the low-saline site. However, the spring peak was highest in the high-saline site. There were no significant differences among salinity and years. On average, annual leaf litterfall production was 470 g m^{-2} yr^{-1} at the low-saline site. The mid-saline site produced the smallest amount of annual leaf litterfall (396 g m^{-2} yr^{-1}), with the high-saline site being intermediate between the other two sites at 428 g m^{-2} yr^{-1}.

3.6 Aboveground net primary productivity

Stem wood growth and annual leaf litterfall were summed for each forested wetland to yield total ANPP during 2014 and 2015 (Table 2). While the mid-saline site had the highest ANPP among sites in 2014 (948 g m^{-2} yr^{-1}), it had the lowest ANPP among sites in 2015 (669 g m^{-2} yr^{-1}). There was little difference in ANPP in the low-saline site between 2014 and 2015 (900 and 894 g m^{-2} yr^{-1}, respectively), while in the high-saline site ANPP increased from 765 to 864 g m^{-2} yr^{-1} in 2014 and 2015, respectively. Overall, the average ANPP between 2014 and 2015 was highest in the low-saline site (897 g m^{-2} yr^{-1}), lowest in the mid-saline site (808 g m^{-2} $yr^{-1),}$ and intermediate in the high-saline (814 g m^{-2} yr^{-1}). There were no significant differences in ANPP among the three water salinity sites.

3.7 Shrub composition

Understory species composition changes across the salinity gradient (Table 3). The number of shrub species ranged from 10 species in the low-saline site to 8 and 9 species in the mid- and high-saline sites, respectively. In the low-saline site, the main understory species are wax myrtle, fetterbush (*Lyonia lucida* (Lam.) K. Koch), dahoon holly, redbay, and baldcypress. American holly (*Ilex opaca* Aiton), sweetgum, water tupelo, and American elm disappeared as salinity increased, with loblolly pine and Virginia willow (*Itea virginica* L.) appearing in mid- and high-saline sites. The number of wax myrtle, fetterbush, dahoon holly and redbay significantly increased with higher salinity levels. Wax myrtle numbers were fairly equal in mid- and high-saline sites, with fetterbush and redbay numbers being highest in the mid-saline site, and dahoon holly numbers increasing tenfold in the high-saline site. Numerous baldcypress saplings (770 stems ha^{-1}) were found in the low-saline site, but few were found in the mid-saline (20 stems ha^{-1})

and high-saline site (10 stems ha^{-1}).

4. Discussion

Tidal freshwater forested wetlands of the southeastern United States are experiencing an increase in salinity intrusions as a result of rising sea level (Craft et al., 2009; Cormier et al., 2013; Anderson et al., 2013). In this study, low-saline and mid-saline sites had similar water depth, but the level was significantly lower than in the high-saline site. The water depth gradient influenced species richness, composition and productivity of tree species similar to that reported by Conner et al. (2011) from a nearby non-tidal freshwater forested wetland. Our study observed that salinity in Strawberry Swamp decreased with freshwater flow, and the greatest decreases in salinity occurring in the high-saline site. This is similar to salinity fluctuations in response to seasonal variations in freshwater inflow from rivers reported by Stoker (1992).

4.1 Effect of water salinity on overstory forest community

Coastal forests have been changed by increasing water depths, saltwater intrusion, or both (Anderson and Lockaby, 2011; Brinson et al., 1995; Williams et al., 1999). Tidal swamp forest vegetation killed by saltwater and chronic salinization, even under low salinity levels, reduces total ANPP (Pezeshki et al., 1987; Hackney et al., 2007; Krauss et al., 2009, 2012). Forest stands with higher salinity had lower BA, tree densities, stem wood production, and leaf litter fall (Cormier et al., 2013). Our study clearly found major changes occurring in forest communities and productivity along the salinity gradient. Water salinity did not change the dominance of tree species (baldcypress, swamp blackgum, and water tupelo) occurring in these wetlands, but baldcypress has become the dominant tree species occurring in the high-saline environment. The older and larger water tupelo and swamp blackgum generally died with increasing salinity, resulting in decreased BA, DBH, and IV. Wax myrtle seems to adapt to high salinity conditions better than swamp blackgum, dahoon holly, and sweetgum. Other studies have examined freshwater forested wetland communities and identified some of the same indicator species observed here. Light et al. (2002) found that baldcypress, swamp tupelo, and water tupelo were the most dominant canopy species in forested tidal sections of Suwannee River, FL. Duberstein and Kitchens (2007) and Pierfelice et al. (2015) examined the influence of tide on edaphic conditions showing it to be an important factor affecting species composition and productivity.

Saltwater intrusion can dramatically affect forest structure through mortality of seedlings, saplings, and trees (Smith et al., 1997; Conner and Inabinette, 2003)**.** In our study, increasing water salinity from 0.8 PSU to 4.6 PSU reduced the overstory tree density by 25%. Hackney et al. (2007) suggested that 2 PSU represents the point where tidal swamps begin converting to oligohaline marshes. Hackney and Avery (2015) go as far as saying that flooding by >1 PSU for more than 25% of the time is enough to start the conversion process. As trees become stressed and eventually die, there are more canopy gaps created in the forest. The creation of canopy gaps allows for greater light penetration (Rheinhardt, 2007) which could benefit understory vegetation growth. The surviving larger and older trees may escape salt stress by getting fresher water using deeper roots (William et al., 1999; Williams et al., 2007).

In our study, annual leaf litterfall (383-492 g m^{-2} yr^{-1}) was lower than the 464-850 g m^{-2} yr^{-1} reported for riverine forested wetlands (Conner and Buford, 1998; Xiong and Nilsson, 1997). ANPP values for freshwater forested wetlands in the southeastern United States can reach up to 2000 g m^{-2} yr^{-1} but more typically are around 1000 g m^{-2} yr^{-1} for healthy wetland forests (Conner, 1994; Conner and Buford, 1998; Conner and Day, 1976; Conner et al., 2011). The decline in water tupelo and swamp blackgum stem numbers during the study is one factor leading to reduced ANPP and may be related to the high water salinity and fluctuating water depth throughout the study. Previous studies have demonstrated that increased salinity reduced tree growth by 2% per year and vegetation coverage by 1.87% per year (Bompy et al., 2014, Dutta et al., 2004). Small increases in salinity (0-2 PSU) have been shown to reduce total biomass of water tupelo (McLeod et al., 1996) by inducing severe physiological dysfunctions and causing widespread direct and indirect harmful effects such as limiting vegetative and reproductive growth (Kozlowski, 1997; Shannon and White, 1994).

Baldcypress is the predominant tree species in the overstory layer in Strawberry Swamp, but small baldcypress trees were only found in the low-saline site. With increased water depths and the introduction of salinity, baldcypress regeneration will be more difficult and maybe impossible. Therefore, natural succession may be altered in these coastal freshwater forest wetlands.

4.2. Effect of water salinity on understory tree composition

Salinity significantly altered the density, DBH, BA, and IV of the understory species found in this study. Mid-saline and high-saline sites had significantly increased numbers of individuals, as well as greater DBH, BA, and IV for species like wax myrtle, fetterbush, dahoon holly, and redbay, but dramatically reduced values for baldcypress. Wax myrtle was the dominant understory shrub in mid-saline and high-saline sites and is on the way to forming an almost uniform mid-story canopy layer.

5. Conclusions

Baldcypress, swamp blackgum, and water tupelo are dominant tree species in coastal freshwater forested wetlands. Our study confirms the differing response of coastal freshwater forest productivity and understory shrubs composition to salinity in oligohaline environments. Higher salinity reduced the number of tree species and BA, but trees growing in those sites had significantly greater mean DBH ($p < 0.05$). Species like dahoon holly, sweetgum, red maple, loblolly pine, and ash are susceptible to salt intrusion. The introduction of salinity greater than 2.6 PSU resulted in the death of swamp tupelo and water tupelo trees in this study. Salinity reduced average ANPP due to the decline in average stem wood growth and litterfall. Baldcypress was the predominant canopy species with highest density, DBH, BA, and IV in higher salinity sites. The contribution of baldcypress to total SWG increased significantly with increasing salinity, although there was a moderately negative decline in annual BA growth across the salinity gradient. Mean DBH growth rates of the remaining baldcypress trees were greater than other tree species along the salinity gradient, but baldcypress growth also decreased with increasing salinity. Salinity decreased the number of shrub species, but there was a dramatic increase in the density of wax myrtle. Even low levels of salinity as found in this study affect forest health resulting in a decline in productivity and regeneration.

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Literature Cited

Anderson, C.J., Lockaby, B.G., 2011. Forested wetland communities as indicators of tidal influence along the Apalachicola River, Florida, USA. Wetlands 31, 895–906.

Anderson, C.J., Lockaby, B.G., Click, N., 2013. Changes in wetland forest structure, basal growth, and composition across a tidal gradient. Am. Midl. Nat. 170, 1–13.

Bompy, F., Lequeue, G., Imbert, D., Dulormne, M., 2014. Increasing fluctuations of water salinity affect seedling growth performances and physiology in three Neotropical mangrove species. Plant Soil 380, 399–413.

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

Busbee, W.S., Conner, W.H., Allen, D.M., Lanham, J.D., 2003. Composition and aboveground productivity of three seasonally flooded depressional forested wetlands in coastal South Carolina. Southeast. Nat. 2, 335–346.

Catchpole, W.R., Wheeler, C.J., 1992. Estimating plant biomass: A review of techniques. Austral. Ecol. 17, 121–131.

Clark, A., III, Phillips, D.R., Frederick, D.J., 1985. Weight, volume, and physical properties of major hardwood species in the Gulf and Atlantic coastal plains. USDA Forest Service, Southeastern Forest Experiment Station, Research Paper SE-250.

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

Conner, W.H., 1994. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. J. Coast. Res. 10, 1045–1049.

Conner, W.H., Brody, M., 1989. Rising water depths and the future of southeastern Louisiana swamp forests. Estuaries 12, 318–323.

Conner, W.H., Buford, M., 1998. Southern Deepwater Swamps. In: Messina, M.G., Conner, W.H., (Eds.), Southern Forested Wetlands: Ecology and Management. Boca Raton, FL: Lewis Publishers/CRC Press. pp. 261–287.

Conner, W.H., Day, J.W., 1976. Productivity and composition of a baldcypress-water tupelo site and a bottomland hardwood site in a Louisiana Swamp. Am. J. Bot. 63, 1354–1364.

Conner, W.H., Day, J.W., 1992. Diameter growth of *Taxodium distichum* (L.) Rich. and *Nyssa aquatica* L. from 1979-1985 in 4 Louisiana swamp stands. Am. Midl. Nat. 127, 290–299.

Conner, W.H., Inabinette, L.W., 2003. Tree growth in three South Carolina (USA) swamps after Hurricane Hugo: 1991-2001. For. Ecol. Manage. 182, 371–380.

Conner, W.H., Doyle, T.W., Krauss, K.W. (Eds.), 2007. Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States. Springer, Dordrecht.

Conner, W.H., Song, B., Williams, T.M., Vernon, J.T., 2011. Long-term tree productivity of a South Carolina coastal plain forest across a hydrology gradient. J. Plant Ecol. 4, 67–76.

Cormier, N., Krauss, K.W., Conner, W.H., 2013. Periodicity in stem growth and litterfall in tidal freshwater forested wetlands: influence of salinity and drought on nitrogen recycling. Estuaries and Coasts 36, 533–546.

Craft, C., Clough, J., Ehman, J., Jove, S., Park, R., Pennings, S., Guo, H., Machmuller, M., 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Front. Ecol. Environ. 7, 73–78.

DeLaune, R.D., Lindau, C.W., 1987. ^{13}C signature of organic carbon in estuarine bottom sediment as an indicator of carbon export from adjacent marshes. Biogeochemistry 4, 225–230.

Doyle, T.W., Conner, W.H., Ratard, M., Inabinette, L.W., 2007. Assessing the impacts of tidal flooding and salinity on long-term growth of baldcypress under changing climate and riverflow. In: Conner, W.H., Doyle, T.W., Krauss, K.W. (Eds.), Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States. Springer, Dordrecht, pp. 441–445.

Duberstein, J.A. and W.M. Kitchens. 2007. Community composition of select areas of tidal freshwater forest along the Savannah River. In: Conner, W.H., Doyle, T.W., Krauss, K.W. (Eds.), Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States. Springer, Dordrecht, pp. 321–48.

Dutta, A.K., Iftekhar M.S., 2004. Tree species survival in the Homestead forests of salt affected areas: A perception analysis for Bangladesh. J. Biol. Sci. 4(3), 309-313.

Go I, M.A., Thomas, K.A., 2000. Sources and transformations of organic matter in surface soils and sediments from a tidal estuary. Estuaries 548, 548–564.

Hackney, C.T., Avery, G.B., 2015. Tidal wetland community response to varying levels of flooding by saline water. Wetlands 35, 227–236.

Hackney, C.T., Avery, G.B., Leonard, L.A. Posey, M., Alphin, T., 2007. Biological, chemical, and physical characteristics of tidal freshwater swamp forests of the Lower Cape Fear River/Estuary, North Carolina. In: Conner, W.H., Doyle, T.W., Krauss, K.W. (Eds.), Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States. Springer, Dordrecht, pp. 183–221.

Hopkinson, C.S., Lugo, A.E., Alber, M., Covich, A., and van Bloem, S., 2008. Understanding and forecasting the effects of sea level rise and intense windstorms on coastal and upland ecosystems: the need for a continental-scale network of observatories. Frontiers in Ecology and Environment 6, 255-263.

Jayakaran, A.D., Williams, T.M., Conner, W.H., Hitchcock, D.R., Song, B., Chow, A.T., Smith, E.M., 2014. Monitoring water quality changes in a forested freshwater wetland threatened by salinity. Proceedings of the 2014 South Carolina Water Resources Conference, held October 15-16, 2014 at the Columbia Metropolitan Convention Center.

Kent, M., Coker, P., 1992. Vegetation description and analysis: A practical approach. CRC Press, Boca Raton.

Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. 1, 1–29.

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

Krauss, K.W., Whitbeck, J.L., Howard, R.J., 2012. On the relative roles of hydrology, salinity, temperature, and root productivity in controlling soil respiration from coastal swamps (freshwater). Plant Soil 358, 265–274.

Light, H.M., Darst, M.R., Lewis, L.J., 2002. Hydrology, vegetation and soils of riverine and tidal floodplain forests of the lower Suwannee River, and potential impacts of flow reductions. Professional Paper 1656-A. U.S. Geological Survey, Washington, DC.

McLeod, K.W., McCarron, J.K., Conner, W.H., 1996. Effects of flooding and salinity on photosynthesis and water relations of four Southeastern Coastal Plain forest species. Wetl. Ecol. Manage. 4, 31–42.

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

Mitsch, W.J., Taylor, J.R., Benson, K.B., 1991. Estimating primary productivity of forested wetland communities in different hydrologic landscapes. Landsc. Ecol. 5, 75–92.

Morris, J.T., Sundareshwar, P.V., Nietch C.T., Kjerfve B, Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. Ecology 83, 2869–2877.

Nicholls, R.J., Cazenave, A., 2010. Sea-level rise and its impact on coastal zones. Science 328, 1517–1520.

Pezeshki, S.R., DeLaune, R.D., Patrick, W.H., 1987. Response of *Spartina patens* to increasing levels of salinity in rapidly subsiding marshes of the Mississippi River Deltaic Plain. Estuar. Coast. Shelf Sci. 24, 389–399.

Pezeshki, S.R., Delaune, R.D., Patrick, W.H., 1990. Flooding and saltwater intrusion: Potential effects on survival and productivity of wetland forests along the U.S. Gulf Coast. For. Ecol. Manage. 33-34, 287–301.

Pierfelice, K.N., Lockaby, B.G., Krauss, K.W., Conner, W.H., Noe, G.B., Ricker, M.C., 2015. Salinity influences on aboveground and belowground net primary productivity in tidal wetlands. J. Hydrol. Engnr. DOI: 10.1061/(ASCE)HE.1943-5584.0001223.

Ratard, M.A., 2004. Factors affecting growth and regeneration of baldcypress in a South Carolina tidal freshwater swamp. Ph.D. thesis, Clemson University, Clemson, South Carolina.

Rheinhardt, R.D., 2007. Tidal freshwater swamps of a lower Chesapeake Bay subestuary. In: Conner, W.H., Doyle, T.W., Krauss, K.W. (Eds.), Ecology of Tidal Freshwater Wetlands of the Southeastern United States. Springer, Dordrecht, pp. 161–182.

Schile, L.M., Callaway, J.C., Parker, V.T., Vasey, M.C., 2011. Salinity and inundation influence productivity of the halophytic plant *Sarcocornia pacifica*. Wetlands 31, 1165–1174.

Schilling, E.B., Lockaby, B.G., 2006. Relationships between productivity and nutrient circulation within two contrasting southeastern U.S. floodplain forests. Wetlands 26, 181–192.

Shaffer, G.P., Wood, W.B., Hoeppner, S.S., Perkins, T.E., Zoller, J., Kandalepas, D., 2009. Degradation of baldcypress–water tupelo swamp to marsh and open water in Southeastern Louisiana, U.S.A.: An irreversible trajectory? J. Coast. Res. Special Issue 54, 152–165.

Shannon, R.D., White, J.R., 1994. A three-year study of controls on methane emissions from two Michigan peatlands. Biogeochemistry 27, 35–60.

Smith, G.F., Nicholas, N.S., Zedaker, S.M., 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. For. Ecol. Manage. 95, 275–283.

Stoker, Y.E., 1992. Salinity distribution and variation with freshwater inflow and tide, and potential changes in salinity due to altered freshwater inflow in the Charlotte Harbor estuarine system, Florida. U.S. Geological Survey Water-Resources Investigations Report 92-4062, Tallahassee, FL.

Stuckey, B.N. 1982. Soil Survey of Georgetown County South Carolina. Rep. Prepared for the Soil Conservation Service, USDA, Washington, DC.

Ungar, I.A., 1991. Ecophysiology of Vascular Halophytes. CRC Press, Boca Raton.

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

Williams, K., Ewel, K.C., Stumpf, R.P., Putz, F.E., Thomas, W., Workman, T.W., 2007. Sea-level rise and coastal forest retreat on the west coast of Florida, USA. Ecology 80, 2045–2063.

Williams, T., Chow, A.T., Song, B., 2012. Historical visualization evidence on forest-salt marsh transition in Winyah Bay, South Carolina: A retrospective study in sea level rise. Wetl. Sci. Pract. 29, 5-17.

Xiong, S., Nilsson, C., 1997. Dynamics of leaf litter accumulation and its effects on riparian vegetation: A review. Bot. Rev. 63, 240–64.

Table 1 Canopy tree species composition and character of a South Carolina forested wetland across a water salinity gradient

Salinity	Canopy Species	Density (Stems ha^{-1})	DBH (cm)	BA ($\text{m}^2\ \text{ha}^{-1}$)	IV
Low-Saline (0.8 PSU)	Ash (*Fraxinus* spp.)	60	24.6	3.5	7
	Baldcypress (*Taxodium distichum*)	290	28.5	23.3	37
	Dahoon holly (*Ilex cassine*)	10	13.7	0.3	21
	Swamp blackgum (*Nyssa biflora*)	250	24.6	19.7	30
	Sweetgum (*Liquidambar styraciflua*)	50	14.8	1.9	4
	Water tupelo (*Nyssa aquatica*)	140	38.2	16.5	21
	Total	800		65.1	100
Mid-Saline (2.6 PSU)	Baldcypress (*Taxodium distichum*)	250	45.6	42.7	52
	Loblolly pine (*Pinus taeda*)	10	11.2	0.2	1
	Red maple (*Acer rubrum*)	10	23.1	0.8	1
	Swamp blackgum (*Nyssa biflora*)	170	20.9	4.0	17
	Water tupelo (*Nyssa aquatica*)	150	34	18.0	26
	Wax myrtle (*Morella cerifera*)	30	12.6	0.4	3
	Total	620		66.1	100
High-Saline (4.6 PSU)	Ash (*Fraxinus spp.*)	10	10	0.2	1
	Baldcypress (*Taxodium distichum*)	250	47.8	47.1	61
	Redbay (*Persea borbonia*)	10	10.1	0.2	1
	Swamp blackgum (*Nyssa biflora*)	130	17.1	3.5	15
	Water tupelo (*Nyssa aquatica*)	140	18.1	7.4	15
	Wax myrtle (*Morella cerifera*)	70	11.4	0.5	7
	Total	610		58.7	100

Table 2 Leaf litterfall and ANPP for 2014-2015 in a South Carolina forested wetland across a water salinity gradient (Mean ± 1 S.E.)

Parameters	Year	Low-Saline	Mid-Saline	High-Saline
Stem Wood Growth (g m^{-2})	2014	452.5±28.0	555.5±164.6	381.5±97.3
	2015	401.9±28.7	268.5±6.7	391.0±80.0
	Average	427.2±0.4	412.0±85.7	386.3±8.7
Leaf Litterfall (g m^{-2})	2014	448.1±27.6	392.5±0.5	383.3±42.5
	2015	491.6±27.7	400.3±30.9	473.1±76.3
	Average	469.8±27.6	396.4±15.2	428.2±59.4
Aboveground Net Primary Productivity (g m^{-2} yr^{-1})	2014	900.5±55.5	948.0±165.1	764.8±139.8
	2015	893.4±1.0	668.7±24.1	863.0±3.6
	Average	897.0±27.3	808.3±70.5	813.9±68.1

Table 3 Understory species composition of a South Carolina forested wetland across a water salinity gradient

Salinity	Understory Species	Density (Stems ha^{-1})	DBH (cm)	BA (m^2 ha^{-1})	IV
Low-Saline (0.8 PSU)	American elm (*Ulmus americana*)	20	0.1	0.0001	<1
	American holly (*Ilex opaca*)	20	1.9	0.0422	1
	Baldcypress (*Taxodium distichum*)	770	3.9	1.2256	22
	Dahoon holly (*Ilex cassine*)	90	1.7	0.0499	1
	Fetterbush (*Lyonia lucida*)	900	0.5	0.0326	8
	Redbay (*Persea borbonia*)	80	0.8	0.0238	1
	Swamp blackgum (*Nyssa biflora*)	20	1.6	0.0627	1
	Sweetgum (*Liquidambar styraciflua*)	40	2.7	0.0972	1
	Water tupelo (*Nyssa aquatica*)	30	4.9	0.1061	1
	Wax myrtle (*Morella cerifera*)	4950	1.9	2.0904	63
	Total / Average	6920	2.0	3.7306	100
Mid-Saline (2.6 PSU)	American holly (*Ilex opaca*)	10	0.3	0.0011	<1
	Baldcypress (*Taxodium distichum*)	20	2.7	0.0558	<1
	Dahoon holly (*Ilex cassine*)	430	1.2	0.1321	3
	Fetterbush (*Lyonia lucida*)	2010	0.7	0.1011	10
	Loblolly pine (*Pinus taeda*)	300	1.7	0.1483	3
	Redbay (*Persea borbonia*)	250	2.6	0.2002	3
	Virginia willow (*Itea virginica*)	70	0.7	0.0019	<1
	Wax myrtle (*Morella cerifera*)	8680	2.2	4.7793	81
	Total / Average	11770	1.5	5.4198	100
High-Saline (4.6 PSU)	Baldcypress (*Taxodium distichum*)	10	0.3	0.0009	<1
	Dahoon holly (*Ilex cassine*)	1190	1.6	0.3558	8
	Eastern baccharis (*Baccharis halimifolia*)	10	0.1	0.0001	<1
	Fetterbush (*Lyonia lucida*)	1160	0.6	0.0483	6
	Loblolly pine (*Pinus taeda*)	110	2.5	0.1247	1

Figure Legends

Figure 1 Water depth (blue), water salinity (red), and rainfall (green) across a salinity gradient in a South Carolina freshwater forested wetland during 2014 and 2015

Figure 2 Tree density by DBH size class: 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)

Figure 3 Stem growth and contribution of baldcypress to total SWG for 2014-2015 across the salinity gradient (mean ± 1 SE)

Figure 4 Monthly and cumulative leaf litterfall for 2014-2015 across the salinity gradient (mean ± 1 SE)

Figure 1

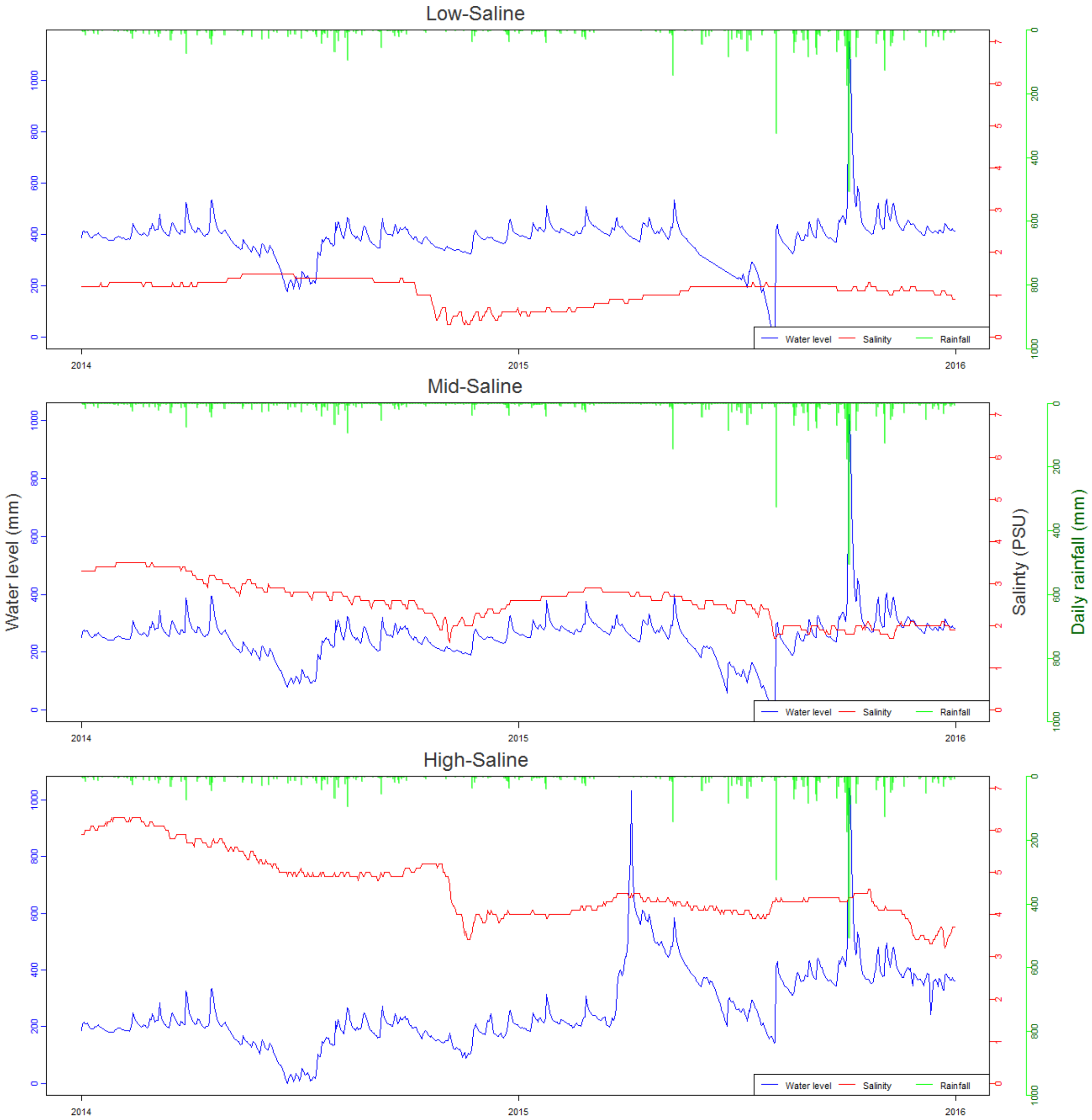

Low-Saline
Mid-Saline
High-Saline
Water level (mm)
Salinty (PSU)
Daily rainfall (mm)
0
200
400
600
800
1000
0
1
2
3
4
5
6
7
Water level
Salinity
Rainfall
2014
2015
2016

Figure 2

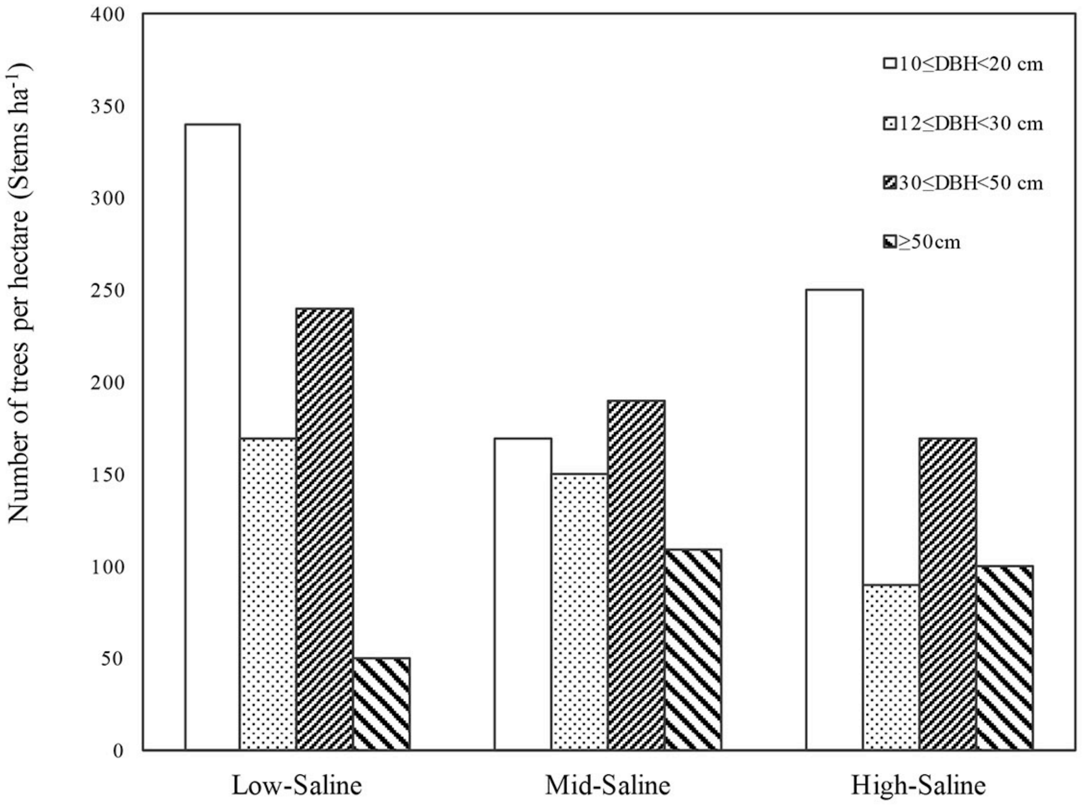

Number of trees per hectare (Stems ha^{-1})
400
350
300
250
200
150
100
50
0
10≤DBH<20 cm
12≤DBH<30 cm
30≤DBH<50 cm
≥50cm
Low-Saline
Mid-Saline
High-Saline

Figure 3

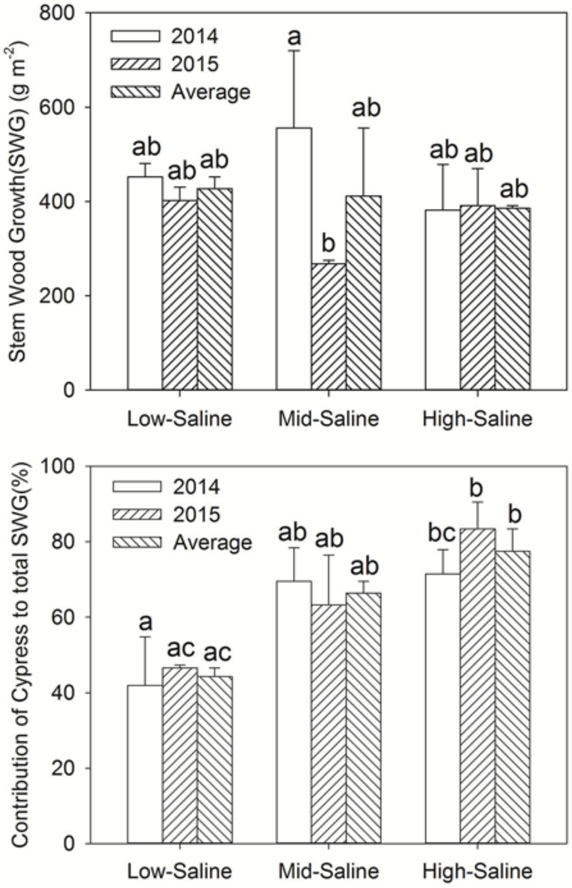
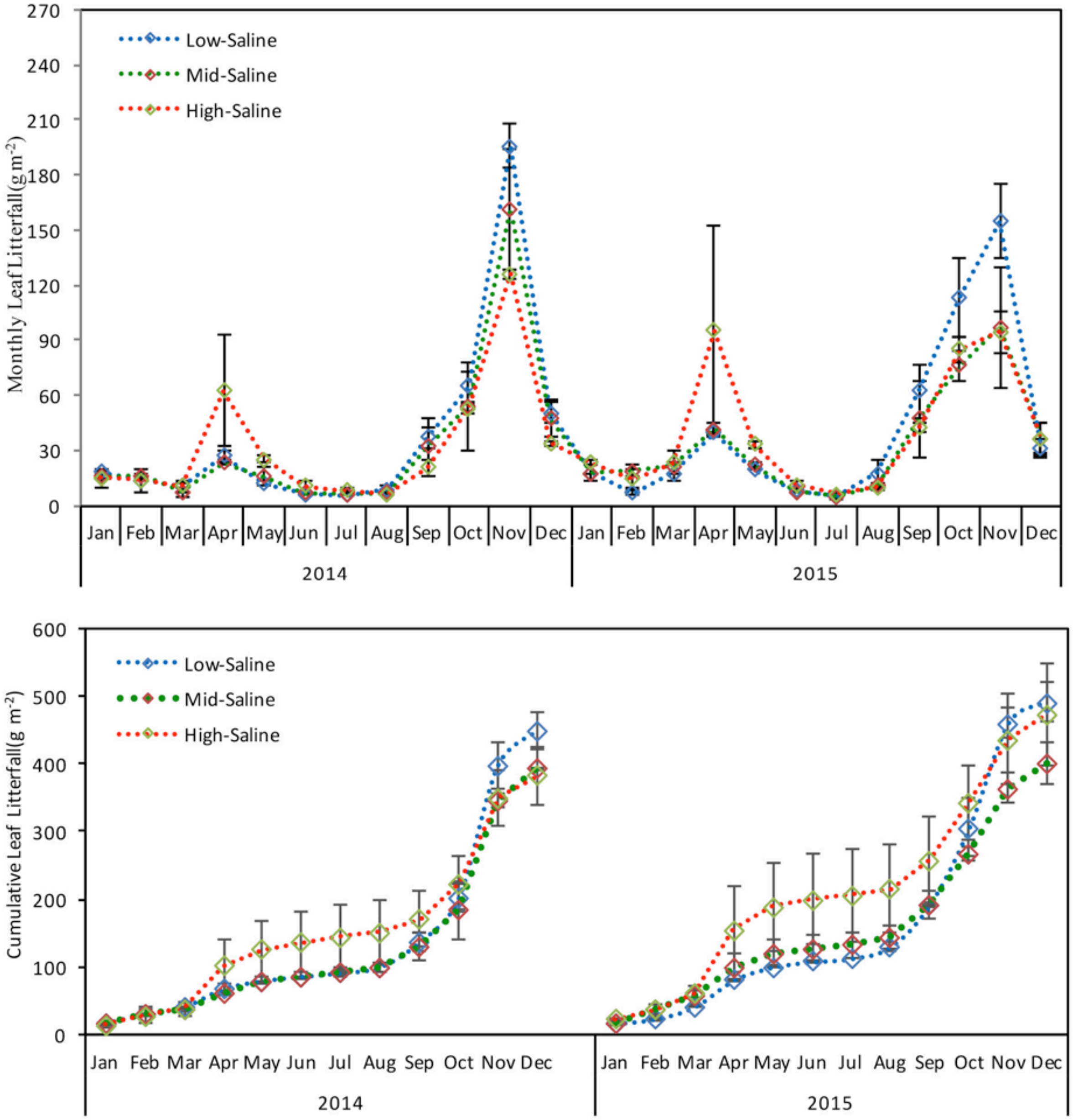

Stem Wood Growth(SWG) (g m^{-2})
800
600
400
200
0
2014
2015
Average
ab
ab
ab
a
b
ab
ab
ab
ab
Low-Saline
Mid-Saline
High-Saline
Contribution of Cypress to total SWG(%)
100
80
60
40
20
0
2014
2015
Average
a
ac
ac
ab
ab
ab
bc
b
b
Low-Saline
Mid-Saline
High-Saline

Figure 4


Low-Saline
Mid-Saline
High-Saline
Monthly Leaf Litterfall(g m^{-2})
0
30
60
90
120
150
180
210
240
270
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
2014
2015
Cumulative Leaf Litterfall(g m^{-2})
0
100
200
300
400
500
600