Salinity Influences on Aboveground and Belowground Net Primary Productivity in Tidal Wetlands

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Abstract: Tidal freshwater wetlands are one of the most vulnerable ecosystems to climate change and rising sea levels. However salinification within these systems is poorly understood, therefore, productivity (litterfall, woody biomass, and fine roots) were investigated on three forested tidal wetlands [(1) freshwater, (2) moderately saline, and (3) heavily salt-impacted] and a marsh along the Waccamaw and Turkey Creek in South Carolina. Mean aboveground (litterfall and woody biomass) production on the freshwater, moderately saline, heavily salt-impacted, and marsh, respectively, was 1,061, 492, 79, and 0 $g\,m^{-2}\,year^{-1}$ versus belowground (fine roots) 860, 490, 620, and 2,128 $g\,m^{-2}\,year^{-1}$. Litterfall and woody biomass displayed an inverse relationship with salinity. Shifts in productivity across saline sites is of concern because sea level is predicted to continue rising. Results from the research reported in this paper provide baseline data upon which coupled hydrologic/wetland models can be created to quantify future changes in tidal forest functions. **DOI: 10.1061/(ASCE)HE.1943-5584.0001223.** *© 2015 American Society of Civil Engineers.*

Author keywords: River systems; Salinity; Wetlands; Marshes; Carbon; Nitrogen; Productivity; Baseline data for modeling.

Introduction

Tidal freshwater forested wetlands form as ecotones at the terrestrial–aquatic interface of freshwater rivers and saline estuaries, and support large lateral exchange of solutes and solids from the neighboring nontidal and oceanic systems (Megonigal and Neubauer 2009). The topographic position of tidal wetlands allows provision of flood abatement, protection from storm surges, and nutrient transformation. However, the capacity for tidal wetlands to fulfill these vital services is in jeopardy as predicted sea-level rise and anthropogenic alterations to the landscape continue (Titus et al. 2009). Effects of salinity on biological drivers of wetland integrity, such as productivity and nutrient dynamics, remain unclear.

According to the intergovernmental panel on climate change (IPCC), sea level is predicted to rise 30–100 cm by Year 2100 (Meehl et al. 2007) with rise based upon emissions and warming (Church et al. 2013). Impacts to most coastal wetlands will likely differ depending on physiographic region and geology (Jelgersma 1996). Annual subsidence rates along the Atlantic coast show an increase from <0.8 $mm\,year^{-1}$ in Maine to 1.7 $mm\,year^{-1}$ in Delaware and decreasing to <0.9 $mm\,year^{-1}$ in the Carolinas, while sea-level rise rates increase from north to south (Engelhart et al. 2009). As a result, shifts in the extent of coastal systems are expected to occur. Craft et al. (2009) predicted declines of 38 and 24% in tidal freshwater marsh and swamps, respectively, on the coast of Georgia, whereas salt marshes were suggested to increase by 4%.

Salinification of coastal freshwater systems occurs as oceanic water extends farther up coastal rivers, and as freshwater discharge from the same rivers declines during drought (Attrill et al. 1996; Doyle et al. 2007). Salinification of freshwater tidal areas has resulted in contamination of municipal freshwater resources and, as a result, artificial neural network models have been developed to predict the impacts of climate change on tidal river hydrology (Conrads et al. 2013). Recent climate model projections for the southeastern United States predict that the region will have slightly decreased precipitation and undergo a rise in annual air temperature of approximately 3°C by the Year 2100 (McNulty et al. 2013). The region is also predicted to undergo continued urbanization which may increase water supply stress throughout the region (McNulty et al. 2013). Increased freshwater demand upstream may further decrease the frequency, magnitude, and duration of freshwater flood events within large tidal river systems, resulting in more frequent annual saline pulses. The predicted changes in temperature, water resource allocation, and tidal river hydrology over the next century may have long-lasting impacts on productivity, and associated functions and values, of coastal forested wetlands along the Atlantic Coastal Plain.

Salt stress is known to influence productivity through altered protein synthesis, photosynthesis, and lipid metabolism (Parida and Das 2005). Salinity has been shown to interfere with root uptake of essential ions such as phosphate and nitrate (Criddle et al. 1989). The accumulation of salt ions within the rhizosphere not only disrupts nutrient uptake, but also can cause water stress and toxicity when sodium (Na) and chloride (Cl) accumulates in the roots (Greenway and Munns 1980; Poljakoff-Mayber 1988). Krauss et al. (2009) found that water salinity >1.3 ppt within tidal swamps dominated by bald cypress [*Taxodium distichum* (L.) Richard] in coastal Louisiana, South Carolina, and Georgia had

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a strong influence on productivity. Additionally, species such as swamp tupelo [*Nyssa biflora* (Walter) Sargent] and some oaks (*Quercus* spp.) have demonstrated cessation of growth at 2.0 ppt (Conner et al. 1997; McCarron et al. 1998). Thus species-specific sensitivities to contrasting salinity levels is one of the major driving factors affecting species composition in coastal wetlands (Mitsch and Gosselink 2007; Baldwin 2007).

Assimilation of carbon (C) by plants is referred to as net primary productivity (NPP) and forms the energy base for growth and maintenance of biological processes. Accurate estimates of NPP are required to understand regulation of global C pools and fluxes, particularly in wetlands, which are important to global carbon pools (Eswaran et al. 1995; Gorham 1991). Data on belowground C allocation are insufficient due to the intensive labor and time needed to quantify belowground net primary productivity (BNPP; Clark et al. 2001). The BNPP is a significant portion of total annual productivity, with >50% occurring belowground in Douglas fir and Pacific silver fir stands (Keyes and Grier 1981; Fogel 1983). Because there are complications and difficulties associated with measuring BNPP such as irregular root distribution (Roy and Singh 1995), and time and expense in separating roots, many studies focus only on aboveground productivity.

Recent climate change studies on fine root dynamics have examined the influence of elevated CO_2 (Ferguson and Nowak 2011; Keller 2012) and subsidence versus soil accretion in coastal wetlands (Kirwan and Guntenspergen 2012). The effects of salinification on fine root growth and structure in tidal wetlands, especially tidal freshwater forested wetlands, has received little attention. One exception is Krauss et al. (2012), who found soil respiration to be strongly related to root biomass and root length in mesocosms and in the field, respectively.

The primary objectives of the research reported in this paper were the following: (1) document the effects of differing salinity on NPP in tidal forested wetlands, and (2) compare BNPP in tidal forested wetlands with those of an oligohaline marsh. To achieve these objectives, NPP [aboveground net primary productivity (ANPP; litterfall and woody biomass) and belowground (BNPP fine roots)] were quantified in three tidal freshwater forested wetlands and an oligohaline marsh along a salinity gradient.

Methods

Study Area

The Waccamaw River converges with the Sampit River in the Winyah Bay estuary near Georgetown, South Carolina. Both of these rivers are classified as blackwater with their origins in the southeastern coastal plain and are characterized by low nutrient loads. A longitudinal transect from the upper Waccamaw River to the lower Sampit River results in a tidal salinification gradient affecting the forested wetlands and marsh floodplains associated with the rivers. Research was conducted on this transect using four sites, ranging from (1) a continuously freshwater forested wetland on Richmond Island [low saline (LS)] along the Waccamaw River, (2) moderately salt-impacted (MS) forested wetland on Butler Island along the Waccamaw River, (3) highly salt-impacted (HS) forested wetland on Turkey Creek, and (4) oligohaline marsh (simply termed marsh) on Turkey Creek near the Lower Sampit River (Fig. 1). Continuous daily river stage and specific conductance data within the study area were collected by USGS gages (USGS Station 021108125, Waccamaw River, near Pawley's Island). Nontidal freshwater river stage data were also taken from USGS Station 02110500 in Longs, South Carolina, to evaluate freshwater inputs to the lower tidal river system.

Soils were mapped as Hobonny (Euic, thermic Typic Haplosaprists on the HS and marsh, http://soilseries.sc.egov.usda.gov, accessed April 9, 2014) and Levy (fine, mixed, acid, thermic Typic Hydraquents (USDA 2014; Stuckey 1982) on the LS and MS. Average soil pH (equivalent water) for the LS, MS, HS, and marsh,

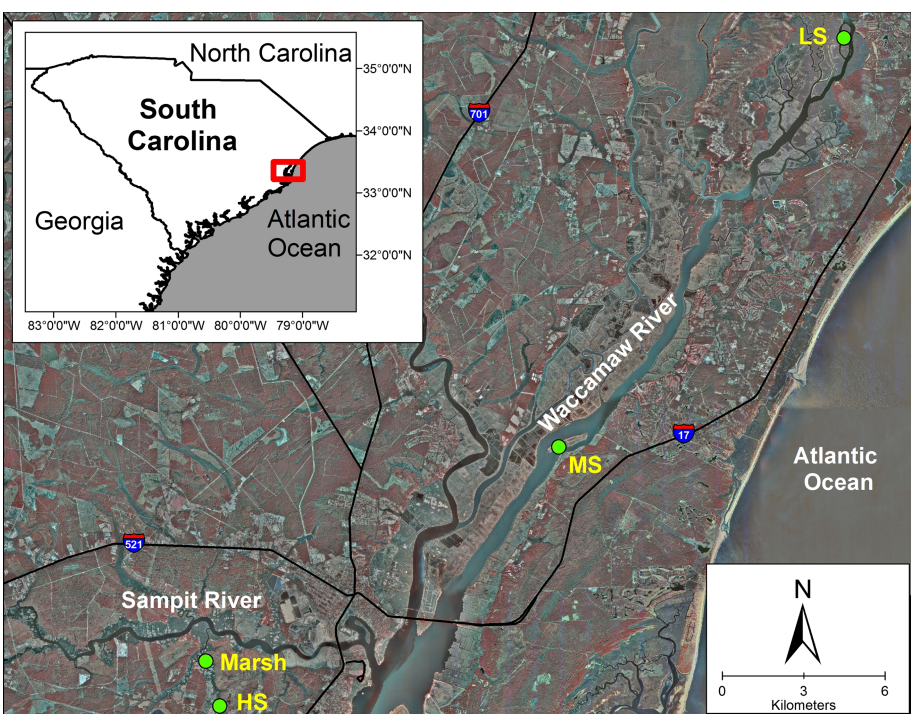

Fig. 1. Insert shows location of research plots along the Waccamaw River and Turkey Creek, South Carolina, United States; HS, heavily salt-impacted forested wetland; LS, freshwater forested wetland; MS, moderately saline forested wetland (reprinted from USDA et al. 2003)

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respectively were 5.53, 6.00, 6.34, and 6.18. Soil porewater salinity over the time period of the research reported in this paper was collected monthly from four different wells at each site. Average soil porewater salinities differed among the sites, as follows: (1) LS (0.09 ± 0.003 ppt), (2) MS (1.57 ± 0.13 ppt), (3) HS (2.61 ± 0.09 ppt), and (4) marsh (4.31 ± 0.27 ppt). During the collection period, precipitation (millimeters) varied from 30-year means with sites experiencing drought conditions from November 2010 through April 2012 (Fig. 2; South Carolina, Division 7, National Oceanic and Atmospheric Administration, National Climatic Data Center, http://www.ncdc.noaa.gov/temp-and-precip/, accessed April 14, 2014). Forests along the Waccamaw and Sampit reaches are dominated by bald cypress and tupelo (Conner et al. 2007). Mean basal area for the LS, MS, and HS, respectively, were 64.52 ± 4.25, 44.99 ± 0.25, and 15.24 ± 0.75 $m^2\ ha^{-1}$.

Aboveground Productivity

Litterfall was collected once per month from January 2010 to December 2012 from ten 0.25-m^2 litter traps on each site. Litter traps were raised 1 m to prevent flooding. Litterfall was oven-dried at 70°C to a constant mass and weighed. Monthly mean litterfall dry weights were summed to estimate annual litterfall at each site for Years 2010–2012. Woody biomass included changes in diameter at breast height (DBH) gathered from two 20×25 m plots, with measurements taken 2 m above ground level in order to compensate for butt swell. Trees ≥ 10 cm DBH contribute $\geq 90\%$ of vegetative biomass in large statue forests (Clark et al. 2001), therefore only trees >10 cm DBH were used for aboveground productivity analyses. Measurements of DBH were made in December 2009–2012. Dry weight for each tree was estimated from DBH based allometric equations for each tree species (Clark et al. 1985; Scott et al. 1985; Muzika et al. 1987). Woody productivity was estimated as change in biomass between sequential years. Aboveground productivity values for the herbaceous communities of the forested wetlands and marsh were taken from Ensign et al. (2013) and represent data collected between April 2011 and April 2012.

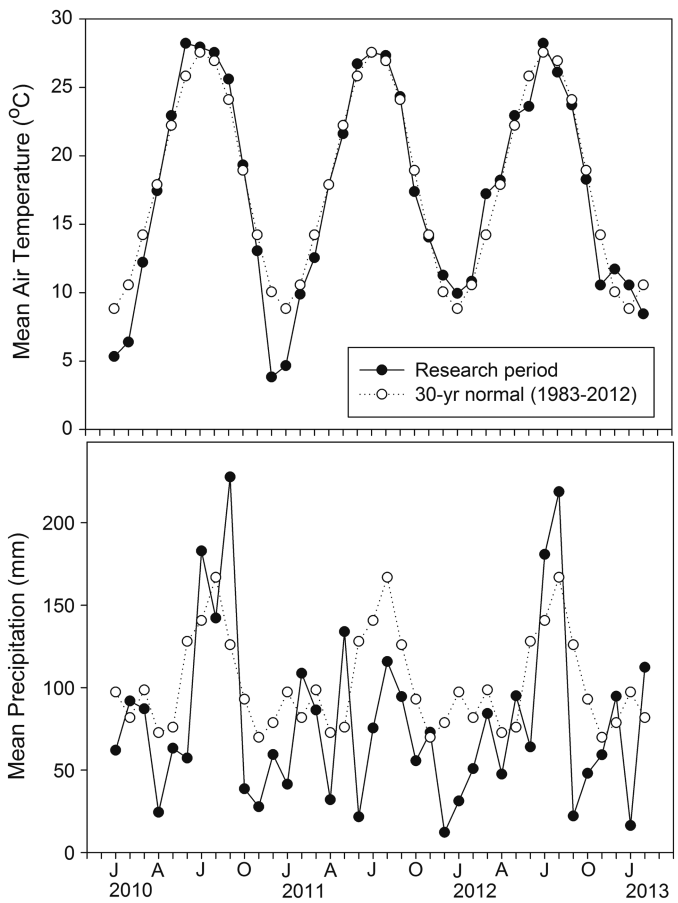

Fig. 2. Monthly average temperature (degrees Celsius) and precipitation (millimeters) on the study sites for the research period and 30-year normals (data from NOAA 2015)

Belowground Productivity

To determine BNPP, the sequential soil coring method of Vogt and Persson (1991) was used [i.e., summarized by Bledsoe et al. (1999)]. Root samples were collected at each site from three 4.57-m radius plots ($n = 9$ cores per site) which were representative of local vegetation and soil conditions. Samples were collected every 5–7 weeks between October 2010 and February 2013 at the three forested wetland sites. Those samples collected during December 2010–2012 were used to estimate BNPP (Years 2011 and 2012) so that annual production coincided with ANPP. The marsh site was added in April 2011 and these samples were then gathered in sequence with forested wetland sites, with marsh BNPP calculated from April 2011–2012. The BNPP was estimated as the sum of positive differences across collection dates, and root turnover as BNPP divided by mean root biomass. Root biomass data from the entire study period (October 2010–February 2013) were used to calculate turnover. During each collection, 8-cm diameter soil cores were taken randomly within each plot to a depth of 11 cm. This specific depth is based on previous studies that showed most fine and small root biomass in wet soils occurred within the top 10–15 cm of soil (Powell and Day 1991; Baker et al. 2001; Clawson et al. 2001). Samples were collected over a 1–2 day period, transported on ice in coolers, and stored at 4°C until processed. Roots were separated from the soil, rinsed, and oven-dried to a constant mass at 70°C for approximately 1 week and weighed. Tree roots were not separated from herbaceous species, due to the difficulty in identifying different species roots.

Statistical Analyses

Repeated-measures ANOVA was performed on ANPP, woody NPP, litterfall NPP, BNPP, and total NPP. ANOVA [Proc GLM; *SAS 9.2* (SAS 2004)] was used with Tukey's mean comparison, which used a Bonferonni adjustment to separate means in accordance with significant differences from ANOVA. Response variables included net primary productivity, standing crop values of litterfall, woody dry weight, and fine root dry weight. Relationships were considered significant at the 0.05 probability level. Data residuals were normally distributed with equal variance. Data transformations were not necessary.

Results and Discussion

In 2010, litterfall at the LS peaked in October and on the MS in November (Fig. 3), a pattern consistent with previous years (2005–2009) where maximum litterfall fell on all sites during October–December (Cormier et al. 2013). This is similar to the December timing for black gum (*Nyssa sylvatica* Marshall) and pond cypress (*Taxodium ascendens* Brongn.) reported by Watt and Golladay (1999). In 2011, both the LS and MS peaked in October. Peak litterfall on the HS in 2010 and 2011 fell in September before the other sites. Salt-impacted sites in North Carolina also

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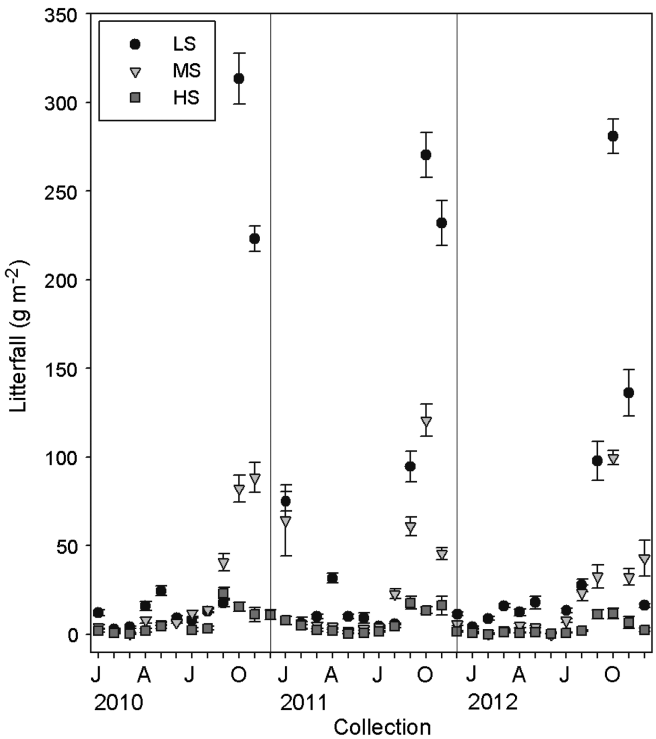

Fig. 3. Mean litterfall (grams per square meter) by collection for the LS, freshwater forested wetland; MS, moderately saline forested wetland; and HS, heavily salt-impacted forested wetland in South Carolina; vertical bars indicate standard errors

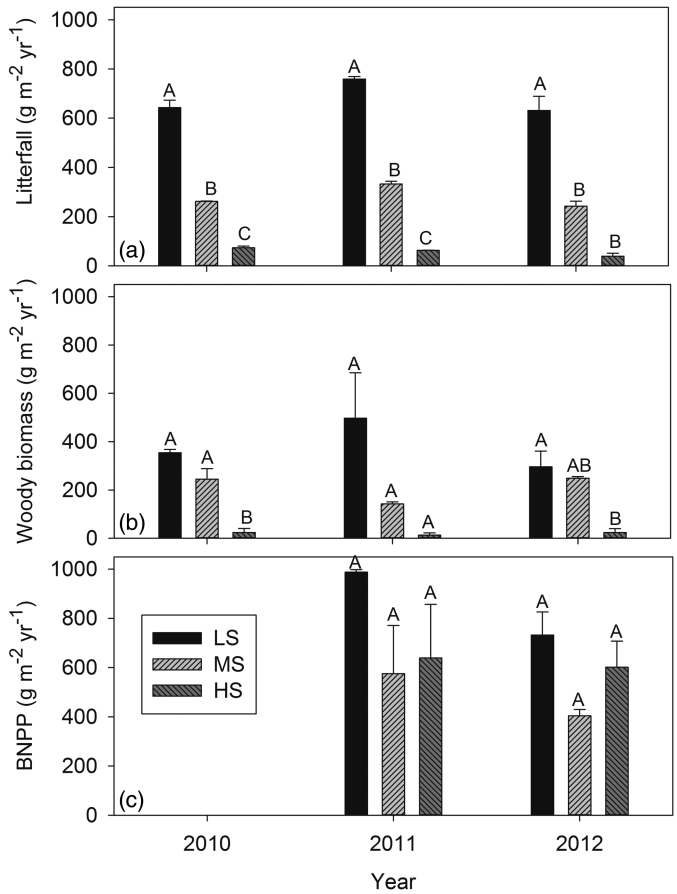

Fig. 4. Mean estimates by year for tidal forested wetland sites: (a) litterfall; (b) woody biomass; (c) BNPP ($g\,m^{-2}\,year^{-1}$); vertical bars indicate standard errors; means within each year with different capital letters are significantly different at $p < 0.05$; HS, heavily salt-impacted forested wetland; LS, freshwater forested wetland; MS, moderately saline forested wetland

Table 1. Repeated-Measures ANOVA of Site and Time for ANPP, Woody NPP, Litterfall NPP, BNPP, and Total NPP

Net primary productivity ($g\,m^{-2}\,year^{-1}$)	Source	Degrees of freedom	F statistic	P-value
Aboveground NPP	Site	2	47.4	0.0054
	Time	2	3.9	0.0830
	Time × site	4	4.6	0.0484
Woody NPP	Site	2	11.8	0.0377
	Time	2	0.2	0.8192
	Time × site	4	2.4	0.1651
Litterfall NPP	Site	2	265.1	0.0004
	Time	2	18.3	0.0028
	Time × site	4	4.1	0.0624
Belowground NPP	Site	2	3.0	0.1924
	Time	1	3.0	0.1833
	Time × site	2	0.5	0.6488
Total NPP	Site	2	30.7	0.0101
	Time	1	6.8	0.0795
	Time × site	2	2.6	0.2189

Note: Results were considered significant differences at $p < 0.05$.

dropped leaves slightly before freshwater sites (Brinson et al. 1985). In 2012, litterfall on all sites peaked in October. Litterfall variation among years has been suggested to be associated with annual climatic variability (Brantley 2008; Conner et al. 2011).

Repeated-measures ANOVA resulted in significant time by site interaction for total forest (tree) ANPP, whereas woody NPP, litterfall NPP, BNPP, and total NPP did not have significant time by site interactions (Table 1). Thus, differences between years did have a significant interaction for ANPP, and values for ANPP should only be interpreted by each year, not as a multiyear mean. Litterfall productivity across the salinity gradient showed significantly higher litterfall at the LS in 2010, F-statistic (2,3) = 272.6 $p < 0.0004$, in 2011 F-statistic (2,3) = 1,601.5 $p < 0.0001$, and in 2012 F-statistic (2,3) = 69.6 $p < 0.0031$ [Fig 4(a)] and reflected what was observed from 2005–2009 on these sites by Cormier et al. (2013). This inverse relationship between litterfall and increasing salinity was also observed in tidal swamps along the Savannah River (Cormier et al. 2013). The HS mean litterfall productivity for each of Years 2010–2012 (59 $g\,m^{-2}\,year^{-1}$) is comparable to Cormier et al. (2013) 5-year mean on the HS (88 $g\,m^{-2}\,year^{-1}$) as well as to that of a site in southeastern Louisiana (78 $g\,m^{-2}\,year^{-1}$) degraded by salinity (Shaffer et al. 2009). Although the previously mentioned means from salt-impacted stands are lower than some reported ranges of litterfall for bald cypress swamps, the LS (678.0 $g\,m^{-2}\,year^{-1}$) and MS (279.2 $g\,m^{-2}\,year^{-1}$) are within reported ranges in the southeastern United States (Burke et al. 1999; Conner et al. 2011; Megonigal et al. 1997; Watt and Golladay 1999).

Woody biomass productivity 3-year means also displayed an inverse relationship with salinity (LS, 382.5±63.8 $g\,m^{-2}\,year^{-1}$ > MS, 212.3±24.9 $g\,m^{-2}\,year^{-1}$ > HS, 20.2 ± 6.8 $g\,m^{-2}\,year^{-1}$) with productivity significantly less at the HS compared to LS in 2010 and 2012 [Fig. 4(b)]. Mean woody biomass productivity on the MS

for all years was comparable to estimates for a tidal freshwater island (175 $g\,m^{-2}year^{-1}$; Ozalp et al. 2007), blackwater floodplain (190 $g\,m^{-2}\,year^{-1}$; Schilling and Lockaby 2005), and sediment-stressed riparian area (229 $g\,m^{-2}\,year^{-1}$; Jolley et al. 2009), while the LS mean woody biomass estimate is comparable to wet and dry transitional zones in coastal South Carolina where woody productivity ranged between 420 and 570 $g\,m^{-2}\,year^{-1}$ (Burke et al. 1999). At the beginning of the study the LS, MS, and HS had 116, 58, and 35 total trees in all plots used for DBH and mortality calculations. Although a few trees from the LS and MS sites showed no increase, the HS site had a larger fraction that either died or showed no DBH growth. At the HS, mortality resulted in significant decreases of 38% in the number of live trees from 2009–2010 and an additional 24 and 3% in 2011 and 2012, respectively.

Fine root standing crop biomass for all sample collections was significantly higher at the marsh than on the forested wetland sites, F-statistic (3,230) = 21.4 $p < 0.0001$ (Fig. 5). The 2-year mean BNPP [Fig. 4(c)] for the LS ($860 \pm 83\ g\,m^{-2}\,year^{-1}$), MS ($490 \pm 95\ g\,m^{-2}\,year^{-1}$), HS ($620 \pm 100\ g\,m^{-2}year^{-1}$), and marsh ($2{,}128 \pm 212\ g\,m^{-2}\,year^{-1}$) was not in accordance with the same pattern observed with litterfall [Fig. 4(a)] or woody biomass [Fig. 4(b)]. Estimates for BNPP in the marsh were within ranges ($1{,}800 - 4{,}889\ g\,m^{-2}\,year^{-1}$) of published studies for cattail (*Typha* spp.) (Good and Good 1975; Sale and Wetzel 1983). Root turnover for all sites were 2.1, 1.8, 1.5, and 2.6 $year^{-1}$ for the LS, MS, HS, and marsh site, respectively, and was significantly different between the marsh and HS in 2011. In 2012 root turnover did not differ among forested wetland sites where values for the LS, MS, and HS were 2.3, 2.7, and 3.4 $year^{-1}$, respectively. Eissenstat and Yanai (2002) proposed that high-productivity sites should show higher root turnover since root growth is maximized in nutrient-rich areas and roots die when absorption is no longer efficient. Jolley et al. (2009) found indications that higher productivity was correlated with increased root turnover. The higher root turnover at the marsh in 2011 supports the general suggestion of increased root turnover associated with higher nutrient status.

Van Zandt et al. (2003) found Dixie iris (*Iris hexagona* Walter), a perennial endemic to brackish and freshwater wetlands, to allocate more production belowground as salinity approached 4 ppt. This trend was also noted for tidal marsh species in California (Pearcy and Ustin 1984). On the sites investigated in the research reported in this paper, Ensign et al. (2013) found that as overstory mortality increased with increasing salinity, the herbaceous components responded with increased growth. To get a better estimate of aboveground productivity, the herbaceous component from Ensign et al. (2013) was added to the estimates of this paper to calculate total NPP (litterfall, woody biomass, herbaceous, and BNPP) for the LS (2,025 $g\,m^{-2}\,year^{-1}$), MS (1,339 $g\,m^{-2}\,year^{-1}$), HS (1,129 $g\,m^{-2}\,year^{-1}$), and marsh (3,240 $g\,m^{-2}\,year^{-1}$; Table 2). The ANPP contribution from the herbaceous communities was insufficient to compensate entirely for the salinity-induced decreases in forest ANPP. The ANPP associated with trees declined from 52% of the system total at the LS to 7% at the HS (Table 2). Simultaneously, the proportion of system NPP derived from the herbaceous and fine root components increased from 5 and 43% at the LS to 38 and 55%, respectively, at the HS. Belowground productivity became particularly important in the marsh with 66% of total system NPP being associated with fine roots compared with 36–55% across the forested wetland sites (Table 2). Mean total NPP for the LS (2,025 $g\,m^{-2}\,year^{-1}$) is similar to the value found for NPP in a Florida cypress forest (2,278 $g\,m^{-2}\,year^{-1}$; Burns 1978), but both of these values are high compared to other published studies. In contrast, the total NPP values of the research reported in this paper for the MS (1,339 $g\,m^{-2}\,year^{-1}$) and HS (1,129 $g\,m^{-2}\,year^{-1}$) are less than those found across a wetness gradient within the Flint River floodplain forest ($1{,}523 - 1{,}728.9\ g\,m^{-2}\,year^{-1}$; Clawson et al. 2001) which is

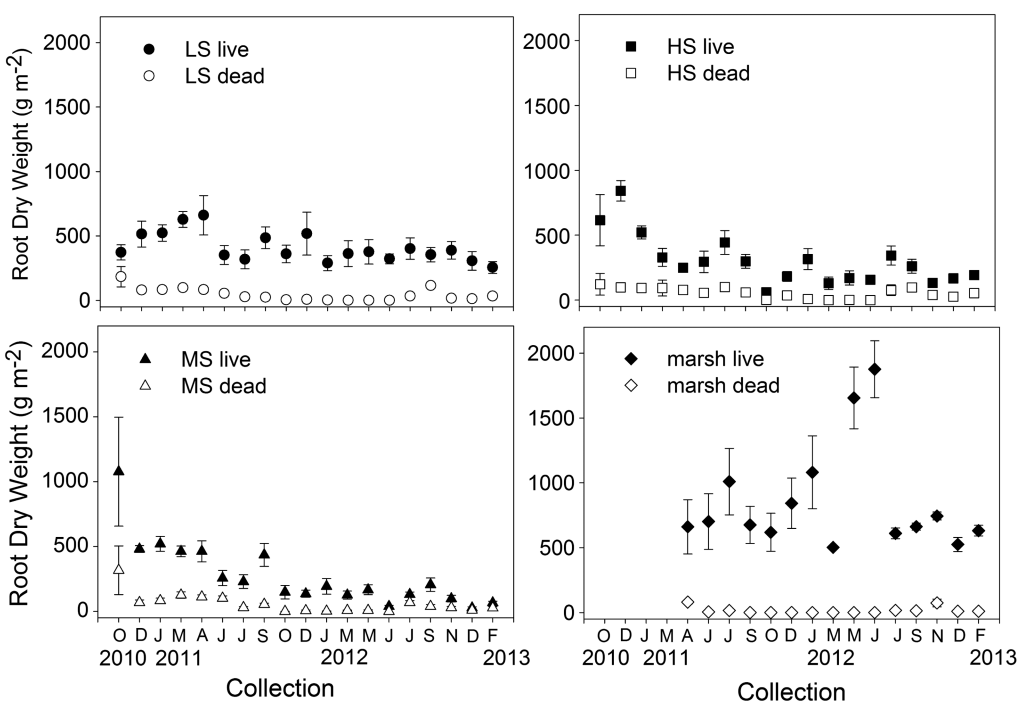

Fig. 5. Total live and dead fine mean root dry weight (grams per square meter) by collection for each site along the Waccamaw River and Turkey creek, South Carolina; HS, heavily salt-impacted forested wetland; LS, freshwater forested wetland; MS, moderately saline forested wetland; vertical bars indicate standard errors

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Table 2. Generalized Gradients in NPP Allocation with Increasing Salinities in Tidal Forest Wetlands and Adjacent Marsh

Ecosystem components	Sites[a]							
	LS		MS		HS		Marsh[b]	
Trees	1,061	52	492	37	79	7	0	—
Herbaceous[c]	104	5	357	27	430	38	1,112	34
Belowground NPP	860	43	490	36	620	55	2,128	66
Total	2,025	100	1,339	100	1,129	100	3,240	100

Note: The NPP allocation is given in units of grams per square meter per year (left-hand entries in each column) and in units of percent (right-hand entries in each column).

[a]HS, heavily salt-impacted forested wetland; LS, freshwater forested wetland; MS, moderately saline forested wetland. The LS includes looseflower water-willow, *Justicia ovata* (Walter) Lindau; green arrow arum, *Peltandra virginica* (L.) Schott; halberdleaf tearthumb, *Polygonum arifolium* L; the MS includes alligatorweed, *Alternanthera philoxeroides* (Mart.) Griseb.; spotted water hemlock, *Cicuta maculata* L.; softstem bulrush, *Schoenoplectus tabernaemontani* (C.C. Gmel.) Palla; and the HS includes eastern grasswort, *Lilaeopsis chinensis* (L.) Kuntze; bulltongue arrowhead, *Sagittaria lancifolia* L.; narrowleaf cattail, *Typha angustifolia* L; Marsh = big cordgrass, *Spartina cynosuroides* (L.) Roth; broadleaf cattail, *Typha latifolia* L.

[b]Marsh data reflects Years 2011–2012.

[c]Herbaceous component from Ensign et al. (2013) and authorities documented by the USDA Natural Resources Conservation Service plants database, accessed November 20, 2014, http://plants.usda.gov/java/.

expected since the Flint River floodplain is neither impacted by daily tides nor salinity.

Several studies have demonstrated that salinity can have adverse effects on bald cypress growth and physiology (Pezeshki et al. 1986, 1989; Allen et al. 1997; Krauss et al. 2009), with additional studies showing these effects are compounded with stress associated with flooding (Javanshir and Ewel 1993; Conner 1994; Allen et al. 1996). Hackney et al. (2007) suggested that 2.0 ppt is the brink for conversion of tidal swamps to oligohaline marsh and Krauss et al. (2009) found bald cypress growth greatly reduced at the same salinity. On the site investigated in the research reported in this paper that was below 2.0 ppt (MS), decreases in tree productivity were also observed. The influence of salinity is manifested through influences on many edaphic factors such as moisture availability and microbial populations, and consequently is a complex driver of plant productivity.

Conclusions

Total NPP for the tidal forested wetland sites was higher at the LS (2,025 $g\,m^{-2}\,year^{-1}$) compared to the HS (1,129 $g\,m^{-2}\,year^{-1}$). The LS also had the highest mean litterfall component (678 $g\,m^{-2}\,year^{-1}$) compared to both the MS (279 $g\,m^{-2}\,year^{-1}$), and HS (59 $g\,m^{-2}\,year^{-1}$), while the marsh had the highest fine root component (2,128 $g\,m^{-2}\,year^{-1}$) of all the sites. Comparisons among these sites suggest shifts in allocation of NPP among system components (trees, herbaceous, and roots) as salinity rises. As salinity induces tree mortality and canopy closure is diminished, the contributions of the herbaceous and belowground components to total NPP become more important.

Acknowledgments

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