EFFECTS OF SALINITY ON PRODUCTIVITY AND BIOGEOCHEMICAL PROCESSES IN TIDAL FRESHWATER AND OLIGOHALINE WETLANDS OF SOUTH CAROLINA, USA

by

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Abstract

A principal threat to tidal freshwater and oligohaline wetlands in the Southeastern United States is salinity intrusion from sea level rise, which affects their structure, growth, and function. This study was designed to improve our understanding of nutrient cycling and growth dynamics in relation to increasing salinity within tidal freshwater and oligohaline wetlands near Georgetown, South Carolina. To achieve this goal, net primary productivity (NPP), nutrient dynamics, microbial biomass, and litter decomposition were quantified across a salinity gradient at three forested sites along the Waccamaw and Sampit rivers, and also a tidal oligohaline marsh. The gradient was comprised of an upper (freshwater; <0.1 ppt), middle (moderately salt impacted; 1.8 ppt), and lower (heavily salt impacted; 2.8 ppt) forested site, and an oligohaline marsh (5.4 ppt). We hypothesized that NPP will decrease as salinification increases in the forested sites due to inhibited ability of plants to take up key nutrients, thus decreasing the capacity for C assimilation and maintenance of effective nutrient pools. Additionally, at the forested sites we hypothesized that litter decomposition will slow as salinity influences the microbial community and litter breakdown, possibly facilitating nutrient limitations at the most saline, forested site undergoing active salinity-induced transition to marsh. In contrast, at the marsh we hypothesized that high belowground NPP would drive increased microbial biomass. Response variables for the forested sites included: NPP (both aboveground and belowground NPP for 2011); a 68-week foliar decomposition study; microbial biomass determined from soil samples taken every 6 weeks from December 2010-July 2012; foliar analyses completed in 2009; and two fertilized root ingrowth core studies from the spring and autumn of 2011. Those for the

marsh consisted of microbial biomass and root productivity estimates (April 2011-July 2012). Results supported portions of our hypotheses. For example, a significant decrease was seen in total NPP between the upper (2263 g m^{-2} yr^{-1}) and lower forested sites (634 g m^{-2} yr^{-1}) as salinities transitioned from 0.1 to 2.8 ppt. The marsh had the greatest mean live root biomass, which included an estimated 3.30 Mg ha^{-1} of C and 0.07 Mg ha^{-1} of N. Mass remaining of foliar litter at week 68 did not differ among sites. However, decreased P resorption proficiency at the lower site paired with no difference in soil extractable P between upper and lower forested sites suggest inhibited plant acquisition of P at the lower forested site. As salinity increases, tidal freshwater forested wetlands may have a reduced potential to cycle and utilize nutrients, thus leading to declines in productivity and C storage. However, belowground C storage and N pools possibly rebound after forest transitions to marsh. Information gained from this study is vital to our understanding of how global climate change affects biogeochemical fluxes of coastal wetlands and their ability to store C.

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Introduction

Structure and Function of Tidal Freshwater Wetlands in the Southeastern United States

Tidal freshwater wetlands are unique and productive ecosystems that fulfill vital services while being highly susceptible to ecological changes (Baldwin, 2007). Many of these wetlands are already threatened by a rise in sea level, and also by developmental practices affecting their hydrology; however, they have not been studied to the degree of other wetland types (Anderson and Lockaby, 2007). Tidal freshwater wetlands are characterized by the influence of tidal water and freshwater inputs, often from rivers (REF). Tides affect biogeochemical processes through not only salinity intrusion, but also by additional nutrients and particulates carried by tidal waters. Low river stages can drive salinity spikes during drought and carry varying loads of nutrients depending on the type of river. For example, redwater rivers originate in the Piedmont region and are generally nutrient rich, while blackwater rivers arise in the Coastal Plain and are characterized by low nutrients and high dissolved organic C content (Doyle et al., 2007b).

In the southeastern United States, tidal wetlands are often comprised of coastal marshes that shift into closed-canopy forested systems at the upper intertidal reaches of large rivers. The South Carolina coast has tides that are semidiurnal, yielding two similar high and low upper-microtidal (1-2 m range) (Doyle et al., 2007b). Aside from tides, hydrology fluxes in tidal systems include flooding and increased oceanic water incursion during major storm events (Doyle et al., 2007b).

Biogeochemical processes are affected by tides as chemical properties of water are altered through fluctuations in pH, redox potential, and nutrient content (Armstrong et al., 1985; Pennings and Callaway, 1992). This pattern can indirectly regulate C assimilation by plants (McHugh and Dighton, 2004; Wang et al., 2006), while also being a direct barrier to gas diffusion in the soil (Heinsch et al., 2004). Additionally, tidal pulses are a prominent driver in the lateral exchange of organic matter and inorganic nutrients into coastal zones, while exporting organic nutrients from these systems to the ocean (Teal and Howes, 2000). Within marshes, elevation has also been shown to influence plant zonation (Bertness and Pennings, 2000) and deposition of marine sediments (Gardner and Porter, 2001).

A major ecosystem service of wetlands is the large role played in terrestrial C sequestration and their importance in global C budgets (Schlesinger, 1997). Services also include abatement of storms, mitigation of floods, and provision of critical fish habitat and human recreational (Millennium Ecosystem Assessment, 2005). However, ecosystem services often vary among ecological and institutional scales as their benefits are interwoven into contrasting cultural, political, and environmental perspectives. Sustainability of these systems is important for ensuring these services, which can be easily compromised given their position at the aquatic-terrestrial interface. At the core of tidal freshwater forested wetland integrity are belowground biogeochemical processes, where little is known about the complexity of cycles occurring at the soil-root matrix.

Net Primary Productivity and Biogeochemical Processes in Tidal Wetlands

Wetlands, which serve as material sinks, sources, and transformers (Johnston, 1991; Mitsch and Gosselink, 1993), often contain numerous hotspots of high localized biogeochemical reaction rates compared to surrounding area (McClain et al., 2003). Hotspots, along with other

biogeochemical processes, control NPP, with significant interrelationships among water, nitrogen (N), phosphorus (P), and carbon (C) dynamics (Keyes and Grier, 1981; Nadelhoffer et al., 1985). Past productivity studies have mostly focused on aboveground data, so there is ample opportunity to research belowground processes, which is needed to provide an accurate view of total NPP and nutrient dynamics.

NPP in the Southeast ranges from 627-2278 g m^{-2} yr^{-1} (Burns, 1978; Clawson et al., 2001; Jolley et al., 2009), whereas ANPP and BNPP separately range between 200-2000 g m^{-2} yr^{-1} (Conner, 1994) and 56-1261 g m^{-2} yr^{-1} (Baker et al., 2001; Clawson et al., 2001; Cavalcanti and Lockaby, 2005; Brantley, 2008; Jolley et al., 2009), respectively. Salinity can impair plants by preventing nutrient uptake and causing water stress through buildup of salt ions in the root rhizosphere (Greenway and Munns, 1980; Poljakoff-Mayber, 1988). Krauss et al. (2009) found salinity negatively affected stand height and basal area in cypress dominated tidal swamps, although effects of salinity on total productivity are still unclear.

Soils of tidal freshwater wetlands contain a high organic matter and have the potential to serve as sinks for nutrients through sedimentation, sorption, and microbial immobilization (Anderson and Lockaby, 2007). Also, associated with increased organic matter is greater retention of pollutants and heavy metals (Simpson et al., 1983). Anderson and Lockaby (2007) reported that total nutrients in soils of tidal swamps were high compared to non-tidal floodplain wetlands, although tidal wetlands may exhibit higher nutrient limitations than non-tidal systems (Anderson and Lockaby, 2011).

Salinity intrusion in tidal systems can alter microbial pathways of organic matter mineralization (Weston et al., 2006), and salinity can reduce microbial biomass (Sardinha et al., 2003). Erkenbrecher and Stevenson (1975) found microbial biomass to decline during low tide in

salt marshes when salinity was highest. Laboratory experiments have suggested that salinity increases microbial decomposition (Craft, 2007; Weston et. al., 2011). However, a field study in Belize demonstrated salinity decreased cellulose decomposition (Rejmankova and Houdkova, 2006). Completing studies in-situ may be important in discerning how salinity intrusion will ultimately affect microbial and decomposition processes, since it is difficult in the laboratory trials to account for the complex pathways that exist in natural systems.

Environmental constraints of salinity and shifting hydrological regime in tidal freshwater wetlands have not been adequately studied in-situ, leaving large gaps in our understanding of how microbes and litter decomposition processes actually function in these contrasting conditions. Laboratory experiments offer good insight into potential processes; however, the goal is to understand if microbial processes are affected as hypothesized within the field. Given the susceptibility of tidal wetlands to climatic shifts and their importance in C storage and nutrient cycling, it is necessary to gain a more natural understanding of these processes. In turn, the information acquired from these studies is critical in forming accurate global C and nutrient budgets to improve our ability to adapt to future climate scenarios and preserve the services of tidal wetlands.

Objectives

Primary objectives of this study were to: i) quantify differences in biogeochemical transformations along a salinity gradient associated with a tidal freshwater forested wetlands to oligohaline marsh transition, ii) identify linkages between: NPP, nutrient limitations, microbial biomass, and litter decomposition, and iii) estimate potential implications of sea level rise on C storage along this gradient.

Hypotheses

The following hypotheses were tested:

1) In forested tidal freshwater wetlands, availability of nutrients decline as sites become increasingly salt impacted.
2) Declines in nutrient availability are driven by a combination of decreased decomposition and immobilization of N and P by microbes, leading to a decline in NPP.
3) Interactions among decomposition, microbial biomass, nutrient cycling, and NPP create a degraded ecosystem at the highly salt impacted forested tidal wetland, thus losing some ability to maintain effective C and nutrient pools.
4) Increased belowground production in the marsh will enhance nutrient availability through increased microbial activity.

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Chapter II

Trends in Net Primary Productivity and Fine Root Dynamics along a Salinity Gradient in Tidal Freshwater Wetlands

Abstract

Tidal freshwater wetlands are one of the most vulnerable ecosystems in the face of climate change and the influence of rising sea levels. However, little is known of the impact of salinification within these systems. Productivity, fine roots (<3.0 mm), and carbon (C) dynamics were examined on three forested sites along a salinity gradient on the Waccamaw River, South Carolina (continuously freshwater, moderately salt-impacted, and heavily salt-impacted) and an oligohaline marsh. Aboveground production, belowground production, and fine root analyses were examined at the three tidally forested sites (tidal swamps), and belowground processes were analyzed within the oligohaline marsh to add to available information from the same marsh. Total net primary productivity was determined for the tidal swamps by summing belowground and aboveground production. Total net primary productivity (NPP) was greater at the freshwater forested site than at the heavily salt-impacted forested site (2263 and 633 g m^{-2} yr^{-1}, respectively). Belowground, the marsh exhibited the highest production (3025.8 g m^{-2} yr^{-1}), exceeding combined aboveground and belowground components of all forest sites, with almost 98% of root biomass of the marsh allocated within very fine roots (<1.0 mm). Live fine root C concentrations were lowest in the forested sites with the highest salinity. However, N concentration and C/N ratios did not differ among the sites. The reduced capacity for the heavily

salt impacted site to be productive is of concern as sea level is predicted to continue rising and these systems are already undergoing decline. Our results suggest that belowground stocks of C may expand after severely salinity stressed forest systems transition to marsh, although impacts on nutrient cycling and loss of structural services associated with tidal swamps remain unclear.

Introduction

Tidal freshwater forested wetlands form as ecotones at the terrestrial-aquatic interface of freshwater rivers and saline estuaries, promoting lateral exchange of solutes and solids from the neighboring non-tidal 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 (e.g., dredging) continue. 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 2100 (Meehl et al., 2007). Impacts to most coastal wetlands will likely differ depending on physiographic region and geology (Jlgersma, 1996). Subsidence rates along the Atlantic coast show an increase from <0.8 mm a^{-1} in Maine to 1.7 mm a^{-1} in Delaware and decreasing to <0.9 mm a^{-1} in the Carolinas, while sea-level rise rates increase from north to south (Engelhart et al., 2009). As a result, shifts in extent and services 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. Salt stress is known to influence productivity through altering photosynthesis, protein synthesis, and lipid metabolism (Parida et al., 2004). Stress occurs as salt reduces water potential and causes ion imbalance, leading to growth suppression and, in extreme cases, plant death. Within ecosystems, 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 can cause water stress and toxicity when sodium (Na) and chloride (Cl) build up in the roots (Greenway and Munns, 1980; Poljakoff-Mayber, 1988).

Krauss et al. (2009b) found that water salinity >1.3 ppt within tidal swamps dominated by baldcypress (*Taxodium distichum*) in coastal Louisiana and South Carolina, had a stronger influence on productivity than flood duration or frequency. Additionally, species such as swamp tupelo (*Nyssa biflora*) and some oaks (*Quercus* spp.) have demonstrated cessation of growth at 2.0 ppt (Conner et al., 1998; McCarron et al., 1998). Species-specific sensitivities to contrasting salinity levels is one of the major driving factors affecting species composition in coastal wetlands (Mitsch and Gosselink, 2000; Baldwin, 2007).

Net Primary Productivity

Assimilation of C by plants is referred to as net primary productivity (NPP) and forms the energy base for growth and maintenance of biological processes. NPP therefore provides important links between fluxes of climate, hydrology, soil, and nutrients, and necessary for evaluating terrestrial C cycles. Accurate estimates of NPP are required to understand regulation of global C pools and fluxes, particularly in wetlands, which are suggested to contain 25% of the global non-oceanic C (Eswaran et al., 1995; Gorham, 1991). Data on belowground C allocation

are insufficient due to the intensive labor and time needed to quantify belowground NPP (BNPP, Clark et al., 2001). BNPP is a significant portion of total annual productivity, with >50% occurring belowground in some forests (Keyes and Grier, 1981; Fogel, 1985). However, there are complications and difficulties associated with measuring BNPP. Root distribution is often irregular and constrained by variability in microtopogophy and plant species (Roy and Singh, 1995). Due to these challenges, many studies focus only on above ground productivity. Consequently, lack of BNPP data can lead to inaccurate calculations and skew global C sequestration estimates.

Fine Root Dynamics

As a consequence of global climate change, recent studies on fine root dynamics have focused on the influence of elevated CO_2 (Ferguson and Nowak, 2012; Keller, 2012) and subsidence verses soil accretion in coastal wetlands (Kiwan 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), which explored the interrelationships of root biomass, salinity, hydrology and temperature in tidal swamps, with a focus on soil respiration.

Fine roots play an essential role in nutrient cycling (Raich and Nadelhoffer, 1989), and may act as sources, sinks, and transformers of N and P. For example, belowground contributions of N through root mortality may add quantities that are 15-85% more than that of aboveground litterfall (Meier et al., 1985; Vogt et al., 1986), whereas root construction and maintenance can represent a large proportion of the C cycled annually through a forest (Vogt et al., 1996). Alterations to roots driven by salinification have the potential to cause major alterations to

nutrient cycling and impact the structure and function of tidal wetlands, thus potentially redefining their placement in global biogeochemical budgets.

Root dynamics may be especially important in areas facing periodic inundation such as tidal wetlands, where impacts of salinification and hydroperiod likely differ between above- and belowground processes. For example, flooding can reduce the proportion of total biomass allocated belowground, while aboveground proportions remain the same or increased (Clawson et al., 2001). Consequently, belowground biomass may be more sensitive to changes in soil oxidation-reduction potential than aboveground (Day and Megonigal, 1993).

The primary goal of this study is to 1) quantify the effects of increasing salinity on NPP and fine root dynamics in tidal forested wetlands, and 2) compare belowground processes with an oligohaline marsh. To achieve this objective, we quantified NPP (above and belowground) and analyzed fine root dynamics in three tidal freshwater forested wetlands and an oligohaline marsh along a salinity gradient. We hypothesized that NPP will decrease as salinification increases in the forested sites due to the inhibited ability of plants to take up key nutrients, thus decreasing the capacity for C assimilation and maintenance of effective nutrient pools. In contrast, we proposed that an increase in marsh BNPP will increase microbial activity and nutrient pools.

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 and characterized by low nutrients with their origins in the southeastern coastal plain. A longitudinal transect from the upper Waccamaw River to the lower Sampit River results in a salinification and tidal

gradient affecting the forested and marsh floodplains associated with the rivers. Research was conducted on this transect with four sites ranging from a continuously freshwater forested wetland on Richmond Island (upper) along the Waccamaw River, a moderately salt-impacted forested wetland on Butler Island (middle) along the Waccamaw River, a highly salt-impacted forested wetland (Turkey Creek, lower) on the Lower Sampit River, and an oligohaline marsh (marsh) at the Lower Sampit River. Average porewater salinities differed drastically among the sites: upper (0.1 ppt), middle (1.8 ppt), lower (2.8 ppt), and marsh (5.4 ppt). Mean monthly salinity was acquired directly from US Geological Survey, from measurements taken with a salinity sensor at four different wells on each site.

Forests along the Waccamaw and Sampit reaches are dominated by baldcypress/tupelo (Conner et al., 2007). The oligohaline marsh site was dominated by cattail (*Typha latifolia*), which can also encroach on the lower forested site. At each site, three 4.57-m radius plots, representative of local vegetation were flagged and used to collect soil and root samples. Water table at each site fluctuates with semidiurnal tides. Two similar high and low tides a day occur each day with a tidal range of 1-2 m, thus being classified as upper-microtidal (Doyle et al., 2007).

Aboveground Productivity

Data for aboveground productivity were acquired from William H. Conner at the Baruch Institute of Coastal Ecology and Forest Science as part of the US Geological Survey's Global Climate Change (GCC) project. Data included dbh (diameter at breast height; ≥10 cm dbh) gathered from two 20 x 25 m plots, with measurements taken 2 m above ground level as compensation for butt swell. Measurements were made in December 2009, 2010, and 2011. Dry weight for each tree was estimated from dbh based on published allometric equations for each

tree species (Clark et al., 1985; Scott et al., 1985; Muzika et al., 1987). Woody production was estimated as change in biomass each year.

Litterfall was quantified monthly from January 2010- December 2011from ten randomly placed 0.25 m^2 litter traps. Litter traps were raised 1 m to prevent flooding. Litterfall was collected monthly and separated into leaves, wood, and reproductive parts, oven dried at 70°C to a constant mass, and weighed. Mean litterfall dry weights were summed at each site for 2010 and 2011. Total aboveground NPP (ANPP) was estimated as the sum of mean woody and leaf production per site.

Fine Roots and Belowground Productivity

To determine BNPP, the sequential soil coring method of Vogt and Persson (1991) and summarized by Bledsoe et al. (1999) was used. Samples were collected every 5-7 weeks between October 2010 and June 2012 at the 3 forested sites. However, only samples taken December 2010-December 2011 were used to estimate BNPP 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 sites, with marsh BNPP calculated from April 2011- April 2012. BNPP was estimated as the sum of positive differences across collection dates, and root turnover as BNPP divided by mean root biomass (Aerts et al., 1990). To analyze fine root biomass, length, and nutrient dynamics, samples from the entire study period (October 2010- June 2012) were used. Each sampling date consisted of three subsamples from each of the three plots per site for a total of nine samples per site during every collection.

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 occured 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 4^0C until processed.

Initial processing of root samples included manual separation and characterization of roots within cores. Roots were removed from the soil and classified according to live/dead fractions and diameter. Size classes for fine roots were 0.1-1.0 mm (very-fine), 1.1-2.0 mm (intermediate-fine), and 2.1-3.0 mm (coarse-fine). Fine roots were rinsed in a low-pressure wash over a .5 mm screen to remove any soil and minimize nutrient and very-fine root loss. Placement of roots into a life fraction was determined by visual criteria. Live roots were considered white or light brown and firm, whereas dead roots were brittle or limp, black or dark in color, and the sheaf slipping easily from the cortex (Bohm, 1979; Bledsoe et al., 1999).

Once roots were extracted from the soil core, washed, and classified, fine root length was estimated by the intersection method described by Bohm (1979). Fine roots were oven dried to a constant mass at 70^0C for at least 72 hs and weighed. Roots were ground through a Wiley mill to pass a 40-mesh screen before chemical analyses for C and N. C and N were determined by thermal combustion using a Perkin-Elmer 2400 series II CHNS/O analyzer (Perkin-Elmer Corp., Norwalk, CT). P analysis was completed on a subsample (n=3) of live roots from each site. These samples were dry-ashed, extracted, and read on a Spectronic 501 spectrophotometer (Milton Roy Co., Rochester, NY, USA).

Statistical Analyses

Statistical analyses utilized analysis of variance (ANOVA) [Proc GLM; SAS version 9.2 (SAS, 2004)], with Tukey's mean comparison used to separate means following any significant results from ANOVA. Response variables included: net primary productivity; standing crop values of litterfall and woody dry weight; and fine root dry weight along with fine root nutrient

contents and concentrations. Relationships were considered significant at the 0.05 probability level.

Results

Net Primary Productivity

Litterfall productivity significantly differed among sites for both 2010 and 2011 (Figure 1) with significant increases for both upper and middle sites between years. In both years, peak litterfall was in October and September for upper and lower sites, respectively, whereas peak litterfall at the middle site changed from November to October between 2010 and 2011. In 2011, upper and middle sites had a small peak in litterfall in January before declining again until April.

Woody productivity was significantly less at the lower site during 2010; however, in 2011 there were not significant differences despite numerical values declining from upper to lower sites (Figure 2). Although a few trees from upper and middle sites showed no growth, the lower site had a much larger fraction of its trees either dying or with no change in dbh. At the lower site, mortality resulted in a significant decreases of 38% in the number of growing trees from 2009 to 2010 with an additional 24% in 2011.

Litterfall contributed an average of 52% of ANPP across all sites for both years, with the lower site having the greatest percentage in 2010 and 2011 (76 and 84%, respectively). ANPP was significantly different among sites for 2010, and in 2011 only the upper site was significantly higher than the lower site (Figure 3). ANPP ranges across both years for the upper, middle, and lower sites were 954.3-1476.1, 461.9-552.3, and 74.1-121.2 g m^{-2} yr^{-1}, respectively.

In 2011 the upper and lower sites differed significantly in BNPP, with the middle site being numerically intermediate (Figure 4). For each site, BNPP peaked in summer; however, it was only significantly higher for the lower site compared to autumn and winter. Lowest

estimates of BNPP for the upper, middle, and lower sites occurred in spring (115.4 g m^{-2} yr^{-1}), autumn (103.1 g m^{-2} yr^{-1}), and winter (28.8 g m^{-2} yr^{-1}), respectively (Figure 5). Root turnover was not significantly different among sites.

ANPP and BNPP were summed for 2011 to determine total NPP during that year. The upper site had higher productivity than the lower site along the salinity gradient (Table 1). Interestingly, along this gradient ratio of ANPP and BNPP to total NPP changed. Significantly more productivity was allocated belowground at the lower site, where contributions to NPP from BNPP 43%< 57%< 88% at the upper, middle, and lower sites, respectively.

Fine Root Physiology and Nutrient Dynamics of Forested Sites

Live Fine Root Trends

Mean live root standing crop biomass and estimated lengths by diameter class for each site are shown in Table 2. Biomasses (all sites combined) of very-fine and coarse-fine roots were significantly higher than that of intermediate-fine roots, with values of 95.0, 69.4, and 32.3 g m^{-2} yr^{-1}, respectively. Very-fine roots had a mean length of 876.5 cm and were significantly greater than intermediate-fine or coarse-fine roots (80.9 and 40.5 cm, respectively).

Significant differences among mean root biomass estimates of each collection and size class are displayed in Table 4. Seasonal fluctuations in root biomass for size classes also were different among sites. At the upper site, with the exception of December 2010, very-fine root biomass was higher at each date and peaked in April 2011 (415.4 g m^{-2} yr^{-1}) and December 2011 (479.5 g m^{-2} yr^{-1}). Intermediate-fine and coarse-fine roots at the upper site followed similar patterns with peaks in December 2010 and March 2011. At the middle site, all size classes responded differently to temporal changes, except October of both years, where values increased and were similar among size classes. Very-fine root biomass reflected fluctuations across

collections, whereas intermediate-fine and coarse-fine roots were less variable and minimal after December 2011. Regarding coarse-fine roots, the lower site fluctuated widely with peaks of 386.9 and 239.9 g m^{-2} yr^{-1} in January and July of 2011, respectively. Very-fine roots at this site also rose in January 2012, approaching 260 g m^{-2} yr^{-1}, whereas intermediate roots exceeded 200 g m^{-2} yr^{-1} in only December 2010.

Total mean live root biomass for the entire sampling period was significantly higher at the upper compared to the lower site, with corresponding values for the upper, middle, and lower sites of 434.4, 338.2, 329.3 g m^{-2} yr^{-1}, respectively. Seasonal fluctuations in total root biomass were evident for all sites (Figure 6). Total root biomass ranged across all sites from 1.9-3294.4 g m^{-2} yr^{-1}.

Dead Fine Root Trends

Dead root length and biomass estimates for each diameter class and site are presented in Table 2. Mean root length by size class was significant, and ranked by size class as very-fine>intermediate-fine>coarse-fine with corresponding values of 117.5>59.4>18.1 cm, respectively. Mean dead root biomass by size class ranged from 0-1019 g m^{-2} yr^{-1}, with no significant differences among size classes.

Differences among sites in mean biomass of each diameter root class are shown in Table 4. Root biomass fluctuations occurred among collections for each size class within each site, with trends varying; however, during June 2012 all sites had no dead fine root biomass. Coarse-fine roots peaked in October 2010 and April 2011 at the upper site (69.1 and 40.7 g m^{-2} yr^{-1}, respectively), whereas very-fine roots also peaked in April (38.5 g m^{-2} yr^{-1}) and intermediate-fine roots peaked in December 2010 (34.7 g m^{-2} yr^{-1}). Over most collections at the middle site, there was higher biomass and more variability in coarse-fine and intermediate-fine roots than very-fine

roots, with all size classes peaking in spring 2011 (March-April). In contrast to the other sites, all three size classes at the lower site showed variable biomass trends across collections. Peak dead biomass of very-fine roots at the lower site occurred in July 2011, intermediate-fine in October 2010, and coarse-fine in March 2011 (46.4, 73.9, and 42.5 g m^{-2} yr^{-1}, respectively, Table 4).

Total fine root biomass did not differ significantly among sites with values of 44.3, 65.55, and 54.8 g m^{-2} yr^{-1} for upper, middle, and lower sites, respectively. Seasonal variation for total dead fine root biomass is illustrated in Figure 6.

Nutrient Trends of Live and Dead Fine Roots

C and N content of roots followed similar relationships as biomass with the upper site having significantly higher C and N content of live roots than other sites (Figure 7) and no difference among sites for dead fine roots (Figure 8). N concentration of live roots did not separate out by site; however, for dead roots, the middle site had significantly less than both upper and middle sites. In contrast, C concentrations of live roots were significantly different among sites upper (459,218 mg/kg)> lower (444,244 mg/kg) > middle (435,578 mg/kg)). This same pattern was apparent in dead roots except only the upper was significantly greater than both middle and lower sites. When total N and C concentrations were compared between live and dead fine roots, significant but contrasting differences were found. N concentrations were significantly greater in dead roots than live, while C concentrations were significantly greater in live roots compared to dead roots. Comparisons among sites showed no differences for C/N ratios for live roots (Figure 7). However, dead roots exhibited a decreased mass C/N ratio at the lower site (32.6) compared to the upper (36.6) (Figure 8).

C and N content of different diameter classes tracked biomass trends for both live and dead roots. Both live and dead root C and N content had a significant inverse relationship with

size class, whereas C concentration was significantly greater in coarse-fine than very-fine roots (Table 3). A clear and significant trend was seen for declining C/N ratios for both live and dead roots as diameter decreased (Table 3).

Concentration of P in live, fine roots for the upper, middle, and lower forested sites were 2207, 1975, and 895 mg/kg, respectively. The lower forested site had significantly less P concentration in live roots. Total live root P content closely followed root biomass trends and were 1.1, 0.6, and 0.4 g m^{-2}, for the upper, middle, and lower sites, respectively.

Carbon Allocation within Forested Sites

Total belowground root C pools were significantly higher at the upper site, and numerically decreased approaching the coast (1.99>1.49>1.46 Mg ha^{-1}), similar to belowground biomass trends. The least amount of C was allocated to intermediate fine roots (0.49 Mg ha^{-1}) with very fine roots exhibiting the highest C allocation, although not significantly different than coarse fine roots (0.80 and 0.76 Mg ha^{-1}, respectively).

Comparison of Oligohaline Marsh and Forested Sites

Comparisons with the forested sites show that the oligohaline marsh had greater total BNPP (3,025.8 g m^{-2} yr^{-1}) and seasonal BNPP for both spring and autumn of 2011 (856.8 and 843.9 g m^{-2} yr^{-1}, respectively) .The only significant difference among seasons within the marsh was winter (2012) where productivity was 1247 g m^{-2} yr^{-1} contrasted with summer (2011) productivity of 288.2 g m^{-2} yr^{-1} (Figure 9). Root turnover (2.6 yr^{-1}) in the marsh was significantly higher than the middle and lower sites, but not the upper site (1.8, 1.5, and 2.1 yr^{-1}, respectively). Total fine root live biomass peaked in June 2012 and dead roots peaked in April 2011 (Figure 11). Dead roots became negligible after June 2011 (Figure 10).

Fine roots >1.0 mm diameter were minimal in the live category and almost nonexistent in dead roots (13 and 8 g m^{-2}, respectively), in turn leading to live and dead very-fine roots having significantly greater biomass than intermediate-fine and coarse-fine roots. Values for live and dead very-fine, intermediate-fine, and coarse-fine were 889, 8, and 5 g m^{-2} and 83, 6, and 2 g m^{-2}, respectively. N concentration in dead roots for each diameter class were not different with values of 9,474, 10,579, and 9,751 mg/kg for very-fine, intermediate-fine, and coarse-fine roots, respectively. Coarse-fine was significantly less than very-fine and intermediate-fine live roots (5,838, 8,763, and 7,475 mg/kg, respectively). C concentrations in live were 382,606, 400,111, and 384, 678 mg/kg for very-fine, intermediate-fine, and coarse-fine roots. C concentrations in dead roots were 388,590, 379, 096, and 371,828 for very-fine, intermediate-fine, and coarse-fine roots. C and N content mirrored biomass trends for each diameter class. Total live root C and N pools were both significantly greater at the marsh than all forested sites (325.0 and 7.8 g m^{-2}, respectively); however, no significant differences were found in dead roots. Mass C/N ratios were greater at the marsh site than either the middle or lower site for dead roots, with no significant differences found for live roots. C belowground allocation in the marsh was significantly greater than any of the forested sites at 3.3 Mg ha^{-1} (Figure 11).

The marsh was significantly higher in live root P concentration (1652 mg/kg) than the lower forested site and significantly less than the upper or middle forested sites. The marsh had the highest amount of total P content (1.60 g m^{-2}), compared to the forested sites.

Discussion

Net Primary Productivity

Litterfall productivity showed a strong trend along the salinity gradient for 2010 and 2011. The clear inverse relationship of litterfall with increasing salinity has been documented

before at these sites and another salinity gradient on the Savannah River, where five year means ranged 88.3-686.3 g m^{-2} yr^{-1} (Cormier et al., 2012). The lower site mean of 65 g m^{-2} yr^{-1} is comparable to a degraded site (78 g m^{-2} yr^{-1}) in southeastern Louisiana, which was impacted by salinity exposure (Shaffer et al., 2006). Both values are much less than ranges for known baldcypress swamps. Our litterfall rates for the upper and middle sites were within ranges for reports in the Southeast. In South Carolina, rates ranged from 295-655 g m^{-2} yr^{-1} (Burke et al., 1999; Conner et al., 2011) and studies in Georgia reported ranges of 243-972 g m^{-2} yr^{-1} (Megonigal et al., 1997; Watt and Golladay, 1999). It is important to note that the upper site's 2011 mean litterfall was 782.1 g m^{-2} yr^{-1}, which is the highest litterfall rate documented on the Waccamaw River (Ratard, 2003; Cormier et al., 2012).

Litterfall increased significantly between 2010 and 2011 for both middle and upper sites. Climatic variables were not analyzed in this study, although interannual variation in litterfall has been suggested to be associated with climatic variability between years (Brantely, 2008; Conner et al., 2011). Seasonally, all three sites had different peaks of litterfall in both years with the lower site peaking the month (September) before the upper site (October). Brinson et al. (1985) also found that salt impacted sites in North Carolina drop leaves slightly before freshwater sites. Interestingly, the middle site dropped most its leaves last, in November; a pattern not consistent with previous litterfall reports on these sites (Cormier et al., 2012). The peak leaf litter drop at the middle site is closer to the December timing, reported by Watt and Golladay (1999) for black gum and pond cypress (*Taxodium ascendens*). A later litterfall peak also was reported by Conner et al. (2011) for intermediate wet sites. The results from this study suggest that at the lower site, litterfall drop is driven by primarily by salinity, while both middle and upper sites are most likely confounded by salinity and hydroperiod.

Woody biomass productivity often is affected by extreme hydroperiod events such as drought or wetness (Conner et al., 2011) and high stem density (Busbee et al., 2003). At the lower site, where woody production was 13.1 g m^{-2} yr^{-1}, the system had only black gum and baldcypress. These two species are known to often be the only overstory inhabitants of heavily salt-impacted systems as forests are transitioning to marsh (Krauss et al., 2009a). Diversity increases at the middle site, although woody productivity still was less than lowest estimates for a tidal freshwater island (175 g m^{-2} yr^{-1}; Ozalp, 2007), blackwater floodplain (190 g m^{-2} yr^{-1}; Schilling and Lockaby, 2005), and sediment-stressed riparian area (229 g m^{-2} yr^{-1}). In contrast, the upper site's biomass productivity estimate of 496.9 g m^{-2} yr^{-1} is comparable to wet and dry transitional zones in coastal South Carolina where woody production range between 420-570 g m^{-2} yr^{-1} (Burke et al., 1999). The decline in woody production along the salinity gradient is not surprising, as decreased basal growth, stand height, and mortality all have been documented to occur with increased salinity (Krauss et al., 2012).

Reports of BNPP in southeastern forested wetlands vary: Great Dismal Swamp, VA (59-989 g m^{-2} yr^{-1}; Powell and Day, 1991); Flint River floodplain, GA (56.2-211.1 g m^{-2} yr^{-1}; Clawson et al., 2001); Coosawatchie River floodplain, SC (90-180 g m^{-2} yr^{-1}; Baker et al., 2001); and riparian forests, Fort Benning, GA (82-1261 g m^{-2} yr^{-1}; Cavalcancti and Lockaby, 2005). Similar to ANPP trends, our upper site is on the higher end of ranges found for forested floodplains at 985.1 g m^{-2} yr^{-1}. At our lower site, 88% of production was allocated belowground (556.2 g m^{-2} yr^{-1}), and contrasting with allocation data, previously published for forested wetlands. Powell and Day (1991), Baker (1998), and Clawson et al. (2001) all reported less allocation to BNPP on their wetter, more frequently flooded sites. However, Van Zandt (2003) found *Iris hexagona,* a periennal endemic to brackish and freshwater wetlands, to allocate more

production belowground as salinity approached 4 ppt and with a similar trend reported for tidal marsh species in California (Pearey and Ustin, 1984). Therefore, allocation patterns at our lower site are most likely driven by salinity more so than hydroperiod.

Although fine root turnover was not significantly different among sites, values still decreased approaching the coast (2.1>1.8>1.5 yr^{-1}). Eissenstat and Yanai (2002) suggested 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. Our results do not support the general finding of root turnover associated with nutrient status, and are high compared to global results presented by Gill and Jackson (2000). In their study, wetland systems had a turnover rate of 0.6 yr^{-1} although they calculated turnover as BNPP divided by maximum biomass instead of mean biomass. Different methods of determining BNPP, fine root turnover, and varying field methods creates obstacles comparing values across studies. This disparity can be further compounded by the host of variables (i.e. soil morphology) that can influence fine root turnover.

Our total NPP estimate for the upper site (2263 g m^{-2} yr^{-1}) is similar to the value found for NPP of a Florida cypress forest (2278 g m^{-2} yr^{-1}; Burns, 1978), but both of these values are high compared to other published studies. In contrast, our values for the middle and lower site are less than those found across three wetness gradients in a floodplain forest (1523-1728.9 g m^{-2} yr^{-1}; Clawson et al, 2001), but close to a highly disturbed, sediment-laden site (672 g m^{-2} yr^{-1}; Jolley et al., 2009). These results suggest that NPP on our middle and lower sites are representative of stressed systems, while the upper site is a healthy wetland system.

Several studies have demonstrated that salinity can have adverse effects on baldcypress growth and physiology (Pezeshki et al., 1986; Allen et al., 1997; Krauss et al., 2009b), with additional studies showing these effects are compounded with combined stress of salinity and flooding (Javanshir and Ewel 1993; Conner et al., 1994; Allen et al., 1996). Our results from tidal freshwater forests, which are dominated by baldcypress and undergo salinity gradients, support these results. Results indicating that the upper site had higher NPP than the lower more salt-impacted site support our hypothesis that salinity adversely affects NPP; however, the threshold remains unclear. Hackney et al. (2007) suggested 2.0 ppt is the brink for conversion of tidal swamps to oligohaline marsh and Krauss et al. (2009b) found bald cypress growth greatly reduced at the same salinity. Our results conform to this expectation since the lower site's salinity was 2.8 ppt, well over the suggested threshold. Furthermore, the middle site data suggest indications of degradation as salinity approaches 2.0 ppt.

At the most heavily salt impacted site, we observed high mortality of trees throughout the study and encroachment of marsh at the fringes. This transition to marsh implies that regeneration is inhibited, and although this may be attributed to salinity, other variables have been suggested. For example, Myers et al. (1995) showed biotic factors such as herbivory and macronutrients were primarily responsible for lack of regeneration of baldcypress in southeast Louisiana. However, the interactions among various factors remain unclear.

Fine Roots

For all sites, live roots peaked in late summer 2011 (July/September) with declines in October 2011 and June 2012, and dead roots became scarce after January 2012. Salinity could be a driving force for these similarities; however, salinity data were not available for the entire study. Data acquired for 2011 show increases in mean monthly porewater salinity for the middle

and lower sites from summer into autumn (June-November). Large declines might be expected after prolonged periods of increased salinity, such as in October 2011. Peaks in live roots can be a product of temperature and soil moisture conditions, which, in turn, can cause seasonal variability among studies. As examples, Powell and Day (1991) reported summer and winter peaks, while Schilling and Lockaby (1999) observed peaks in spring and autumn, and Cavalcanti and Lockaby (2005) found peaks spring, spring/winter, and summer/winter.

In a review of 56 published studies, Gordon and Jackson (2000) found that roots <2.0 mm contained significantly more N and less C concentration then 2-5 mm roots, had a mean C/N ratio of 43:1, and did not exhibit any differences in N concentration between live and dead roots. Our results with fine roots <3.0 mm also show a mean C/N ratio of 43:1; however, in contrast, we found a higher N concentration in dead roots than live roots. Fluctuations in root nutrient concentrations have been suggested to be from retranslocation between live and dead roots (Nambiar, 1987), and may be impacted by retranslocation between shoots and roots (Brantley, 2008) or nutrient ratios (Gordon and Jackson, 2000). Higher N in dead roots in our study suggests microbial immobilization of N, similar to that often seen at the initial stages of leaf litter decomposition.

Mean live, root P concentration has been found to be 900 mg/kg for biomes across the globe (Gordon and Jackson, 2000). This value is comparable to our lower forested site. The upper and middle forested sites, however, are much higher. Root production and turnover are known to be important processes for cycling nutrients, and have been suggested to transfer more C and N to the soil than aboveground litterfall (Fogel, 1983; Heal and Anderson, 1997). The quantities of P found in live roots at the upper and middle forested sites suggest roots contribute to a substantial amount of P being stored and cycled to the soil.

Oligohaline Marsh

Estimates for BNPP in the marsh were within ranges (1800-4889 g m^{-2} yr^{-1}) of published studies for *Typha* spp. (Good and Good, 1975; Sale and Wetzel, 1983). The mechanism behind this high productivity is not well understood; however, Rocha and Goulden (2008) suggest that it associated with high C use efficiency (CUE), which is greater than that found in most other systems including the tropics. Also, the influence of the tidal pulsing, may play a role. Odum's (1980) outwelling hypothesis suggests tidal marshes are highly productive, and therefore export nutrients during tidal pulses, which, in turn, contribute an energy source to marine systems. This has been shown in South Carolina, where tidal pulses were found to be responsible for net fluxes outward of C, N, and P in a tidal marsh (Dam, 1986). However, it is unclear what role those tidal pulses might play in the redistribution of nutrient-laden sediment over vast marsh systems and if there are associations with marsh productivity.

Peak belowground biomass in our study occurred in July 2011, January 2012, and June 2012, whereas lowest estimates were in late spring and early summer (Figure 12). These results differ from a study on a tidal marsh in Georgia where belowground biomass peaked in February and December, but are similar to our study where the lowest estimate were in May (Schubaur and Hopkinson, 1984). Seasonality was also apparent in the N concentration of live and dead roots with peaks in spring and autumn, similar to that found in freshwater marshes in Florida (Bayley et al., 1985). An increase in live root P concentration between the lower forested site and marsh suggest the marsh is able to negate some of the effects of salinity on P cycling within the soil and root matrix.

Conclusions

Comparisons between the upper and lower forested sites demonstrate reduced capacity for tidal swamps to maintain C pools and productivity as they become severely stressed. In contrast, belowground C stock at the marsh implies no loss and possible enhancement of C storage and increased N and P pools in fine roots. This pattern indicates high nutrient acquisition capability and/or high availability. Lowest live root concentrations of N at the middle site, and P at the lower site partially support the possibility that reduced nutrient concentration in roots is a reflection of salinity inhibiting nutrient uptake. Differential trends in N and P demonstrate how uniquely salinity may impact N and P fluxes within tidal swamps. This biogeochemical enhancement of N, P, and C pools in marshes will likely compensate for some of the C sequestration lost from tidal swamps as sea levels continue to rise. It may also help to maintain tidal wetlands' role in global biogeochemical budgets. However, to what extent tidal swamps will transition to marsh and the true capacity of marsh systems to buffer C storage loss remains unclear**.**

Table 1. Mean estimate (± SE) of total NPP, ANPP, BNPP for 2011 and ANPP for 2010 of all forested sites. Different letters represent significant differences among sites for each variable at $p<0.05$.

NPP ($g\ m^{-2}\ yr^{-1}$)	Upper	Middle	Lower	Range	F	P
		2011				
Aboveground	1278.7(197.3)a	477.9(2)b	78.1(0.29)c	76.7-1476.1	135.7	0.0010
Woody	496.9(187.9)a	142.3(8.9)a	13.1(9.23)a	3.9-684.8	5.3	0.1034
Litterfall	782.1(20.3)a	335.6(29.3)b	65.0(12.8)c	1.0-884.7	272.9	<0.0001
Belowground	985.1(158.3)a	640.3(76.4)ab	556.2 (101.8)b	171.3-1666.2	3.7	0.0400
Total	2263.8(207.8)a	1118.2(194.3)ab	634.3(203.2)b	498.1-2474.0	15.6	0.0260
		2010				
Aboveground	997.8(43.5)a	507.1(45.2)b	97.6(23.5)b	74.1-1041.4	28.8	0.0100
Woody	354.4(14)a	245.5(43.2)a	23.9(16.5)b	7.5-368.4	36.4	0.0079
Litterfall	643.4(13.1)a	261.7(18.1)b	73.7 (13.2)c	9.5-696.9	375.1	<0.0001

Table 2. Dry weight and length (± SE) by size class for live and dead fine roots. Different letters represent significant differences among sites at $p<0.05$.

Variable	Upper	Middle	Lower	Range
		Live Fine Roots		
Very Fine				
Dry Weight (g m^{-2} yr^{-1})	272.3(20.9)a	137.1(38.7)b	143.8(11.4)b	1.7-1668
Length (cm)	1112.8(47.1)a	788(57.8)b	729.9(44.1)b	30-3210
Intermediate Fine				
Dry Weight (g m^{-2} yr^{-1})	84.8(8.9)a	84.2(12.4)a	81.9(10.2)a	0-1347
Length (cm)	69.4(4.6)b	65.6(4.7)b	109.3(9.8)a	0-459
Coarse Fine				
Dry Weight (g m^{-2} yr^{-1})	77(8.2)a	116.9(17.6)a	104.2(14.8)a	0-935
Length (cm)	34.8(2.9)b	39.1(3.1)ab	48.2(4.7)a	0-172
		Dead Fine Roots		
Very Fine				
Dry Weight (g m^{-2} yr^{-1})	16.8(5.9)a	38.7(13.4)a	17.9(3.3)a	0-953
Length (cm)	109.7(13.1)a	118(14.3)a	124.1(10.9)a	0-844
Intermediate Fine				
Dry Weight (g m^{-2} yr^{-1})	10.3(1.6)b	37.5(11.7)a	18.3(5.2)ab	0-1019
Length (cm)	36.9(3.4)b	54.3(9.3)ab	84.3(19.7)a	0-1399
Coarse Fine				
Dry Weight (g m^{-2} yr^{-1})	18(8.2)a	32.9(5.2)a	17(2.8)a	0-211
Length (cm)	15.7(1.7)a	22.1(2.3)a	15.9(2.3)a	0-99

Table 3. C and N content and concentration, and C/N ratio (±SE) for live and dead fine root diameter classes. Different letters represent significant differences among sites at $p<0.05$.

Variable	Very-fine	Intermediate-fine	Coarse-fine	Range	F	P
			Live Roots			
C content	78.9(3.9)a	47.3(3.1)b	74.2(5.1)a	0.0-713.7	19.1	<0.0001
N Content	2.5(0.1)a	0.9(0.1)b	1.2(0.1)b	0.0-25.8	69.5	<0.0001
C/N Ratio	33.2(0.3)c	51.8(0.7)b	65.1(1.6)a	19.9-60.6	368.2	<0.0001
C Concentration	436454.2(1594.9)b	456548.1(1798.1)a	458934.1(1675.8)a	369590.0-536150.0	56.1	<0.0001
N Concentration	13450.2(99.5)a	9257.2(109.2)b	7740.2(136.1)c	2140.0-18430.0	719.4	<0.0001
			Dead Roots			
C content	13.9(2.8)a	16.4(2.9)a	19.6(3.2)a	0-450.9	0.9	0.4132
N Content	0.4(0.1)a	0.4(0.1)a	0.4(0.1)a	0-6.8	0.2	0.8563
C/N Ratio	30.9(0.4)c	39.7(1.1)b	52.3(2.2)a	16.1-237.9	69.8	<0.0001
C Concentration	407683.8(2881.6)b	413948.9(3483.5)b	427547.6(3871.7)a	210370.1-519470.0	8.6	0.0002
N Concentration	13716.1(159.5)a	11614.9(214.3)b	9803.9(234.3)c	2050.0-22580.0	97.3	<0.0001

Table 4. Live and dead standing crop root biomass, by diameter class for each forested site. Significant differences among sites, within diameter class represented by different letters at $p<0.05$.

	0.1-1.0 mm			1.1-2.0 mm			2.1-3.0 mm		
	Very-fine			Intermediate-fine			Coarse-fine		
Time	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
				Live Fine Roots					
10/10	185.6a	394.4a	160.8a	36ab	288.7a	200.4b	123.4a	394.9a	254.2a
12/10	169.9ab	82.8b	203a	166a	130.5a	252.6a	178.5b	267.6ab	386.9a
1/11	209.7a	140.7a	202.6a	151.3a	166.5a	161a	161.9a	212.9a	158.9a
3/11	249.9a	128.1b	104.6b	196.1a	142.9a	81.2b	181.5a	191.9a	143.5a
4/11	415.4a	100.4a	110.4a	115.5ab	130.5a	63.3b	130.1a	231.8a	75.4a
6/11	236.9a	91.7a	143.8ab	42.9a	55.5a	67.6a	71.9a	109.7a	92.6a
7/11	211.2a	160.5a	103.1a	51.5ab	36.2b	100.6a	55.7b	32.5b	239.9a
9/11	274.3a	148.2ab	133.2b	115.9a	140.9a	84.5a	95.1a	146.4a	89.8a
10/11	222.7a	105.1b	47.8b	11.47a	16.8b	12.6a	26.5a	25.9a	0a
12/11	479.5a	99.9b	159.2a	27.6a	26.5a	14.8a	10.6a	9.7a	7.5a
1/12	207.9a	185.8a	258.6a	65.2a	7.29b	50.6ab	15.9a	0.0b	6.4b
3/12	293.7a	96.2a	118.9a	37a	19.9a	10.4a	32.1a	9.7a	0.0a
5/12	332.1a	147.5a	154.6a	43.9a	16.5a	12.8a	0.0a	2.7a	31.8a
6/12	322.3a	38.3b	122.1b	0.0a	0.0a	34.1a	0.0a	0.0a	0.0a
				Dead Fine Roots					
10/10	10.2a	11.2a	17.3a	14.2a	17.9a	73.9a	69.7a	18.1a	30.9a
12/10	10.9a	12.4a	37.6a	34.7a	24.9a	18.8a	34.2a	31a	41.9a
1/11	10.8a	21.5a	28.5a	21.5a	30.7a	34.1a	23.9a	31.2a	21.6a
3/11	38.4a	24.8ab	23.2b	27.6a	60.4a	27.4a	33.8a	40.9a	42.5a
4/11	38.5a	18.4a	24.9a	23a	41.9a	21.1a	40.7a	52.2a	32.7a
6/11	19.9a	18.8a	28.8a	16.1b	46.5a	27.4b	14.2a	37.2a	11.7a
7/11	23.6b	12.9b	46.4a	1.5b	7.2b	23.6a	16.2a	9.9a	30.1a
9/11	9.7a	17.4a	26.1a	3.1a	23.9a	24a	18.2a	17.2a	9.1a
10/11	2.8a	.22b	.88ab	0.0a	0.0a	0.0a	1.1a	0.0a	0.0a
12/11	3.3a	5.9a	28.9a	1.8a	0.2a	1.3a	0.0a	0.0a	5.1a
1/12	5.3a	1.5a	0.9a	2.2a	0.2a	4.2a	0.0a	0.0a	3.1a
3/12	0.2b	5.9a	0.0b	0.0a	1.5a	0.0a	0.0a	0.7a	0.0a
5/12	0.2a	7.5a	0.7a	0.0a	0.0a	0.0a	0.0a	0.0a	0.0a
6/12	0.0a	0.0a	0.0a	0.0a	0.0a	0.0a	0.0a	0.0a	0.0a

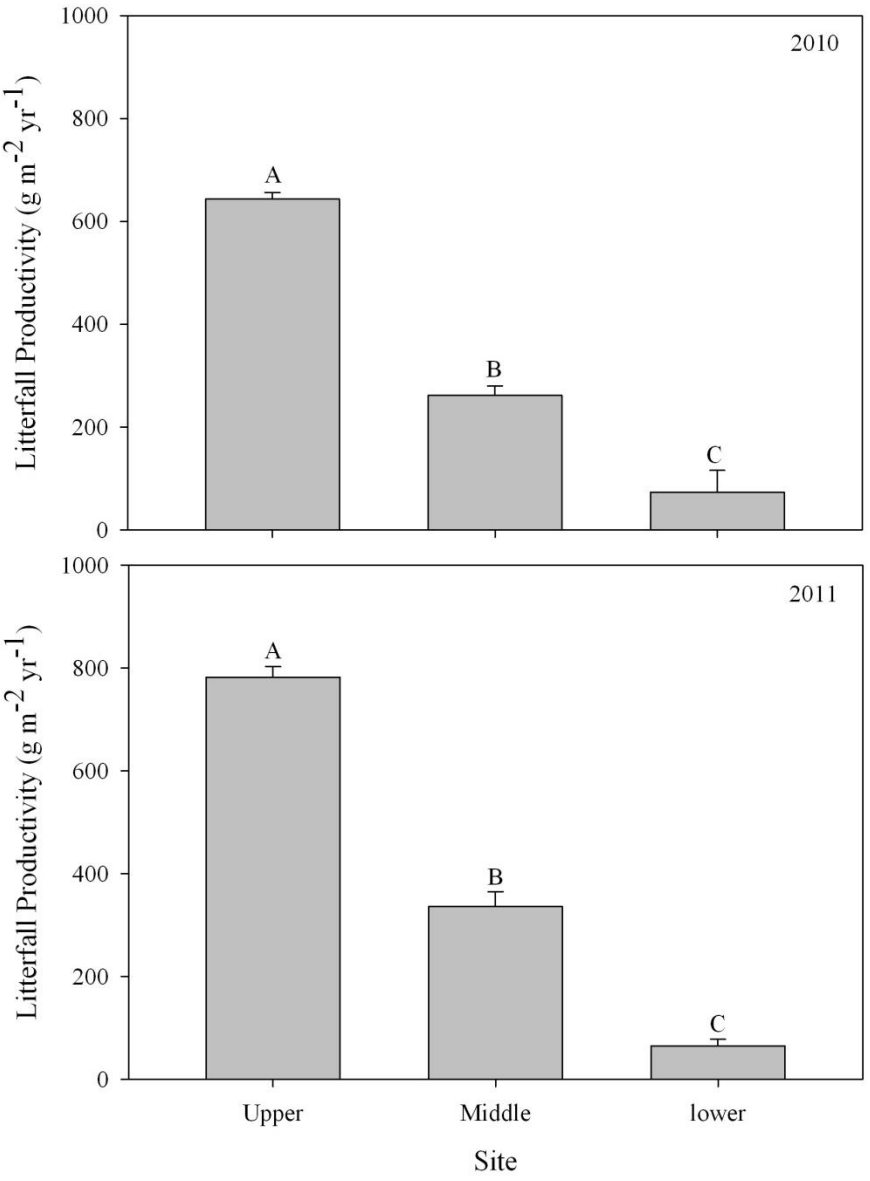

Figure 1. 2010 and 2011 litterfall productivity (g m^{-2} yr^{-1}) by site with significant differences among sites represented by different letters at $p<0.05$. Vertical bars indicate standard errors.

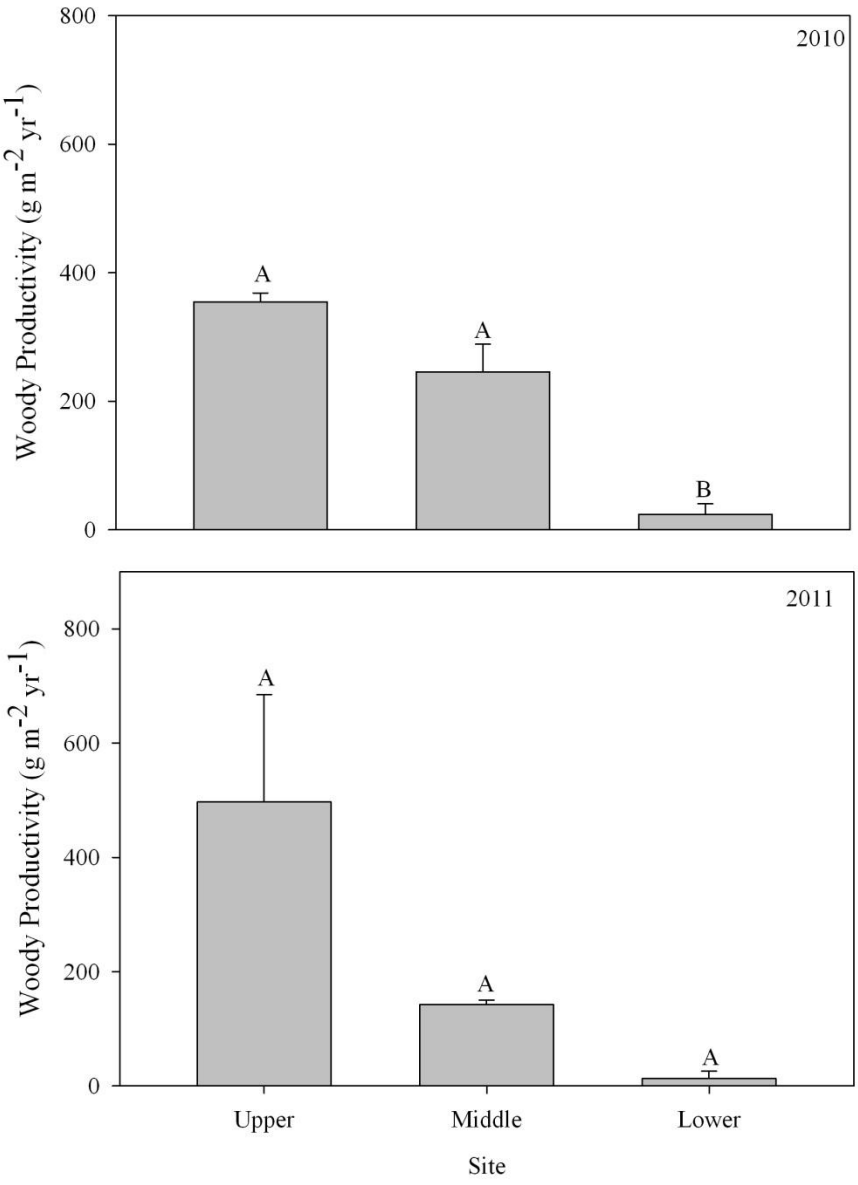

Figure 2. 2010 and 2011 woody productivity compared among sites, with different letters represent significant differences at $p<0.05$. Vertical bars indicate standard errors.

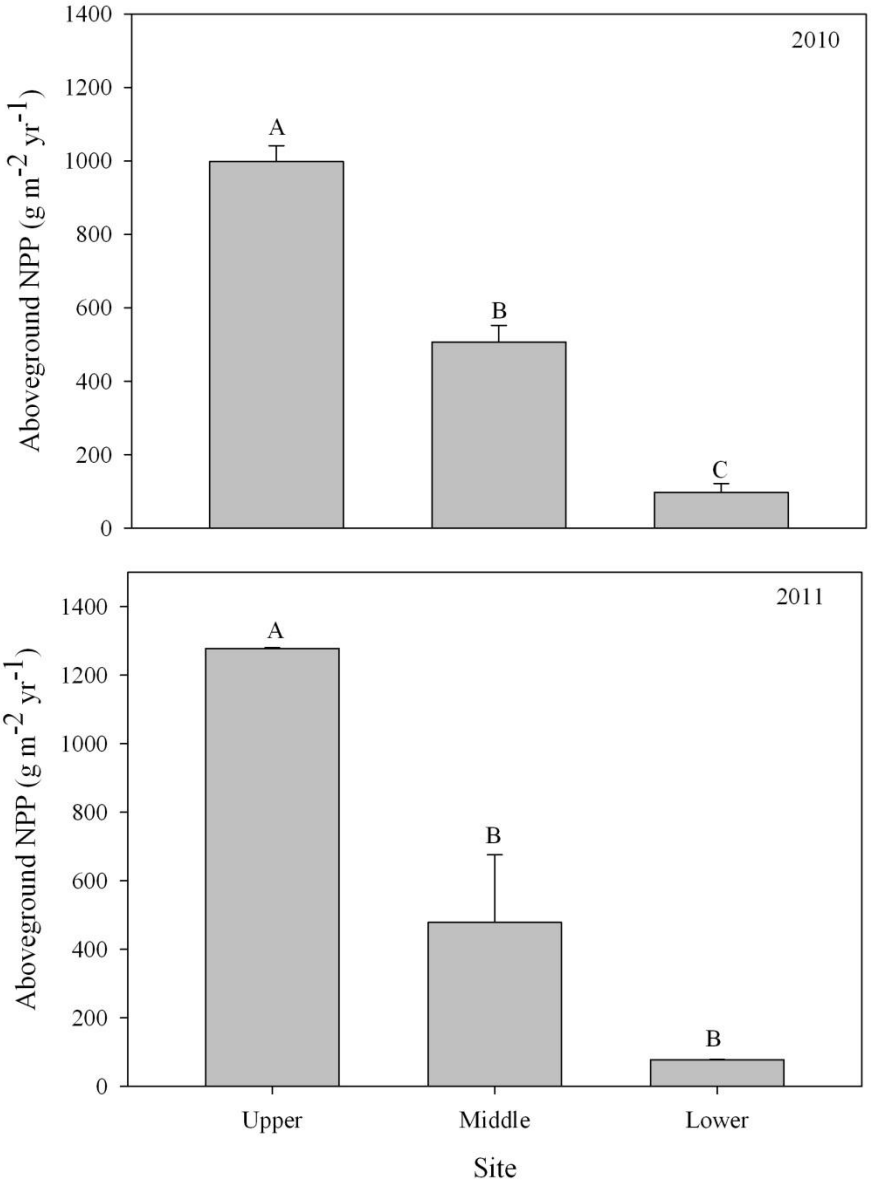

Figure 3. 2010 and 2011 ANPP with significant differences among sites represented by different letters at $p<0.05$. Vertical bars indicate standard errors.

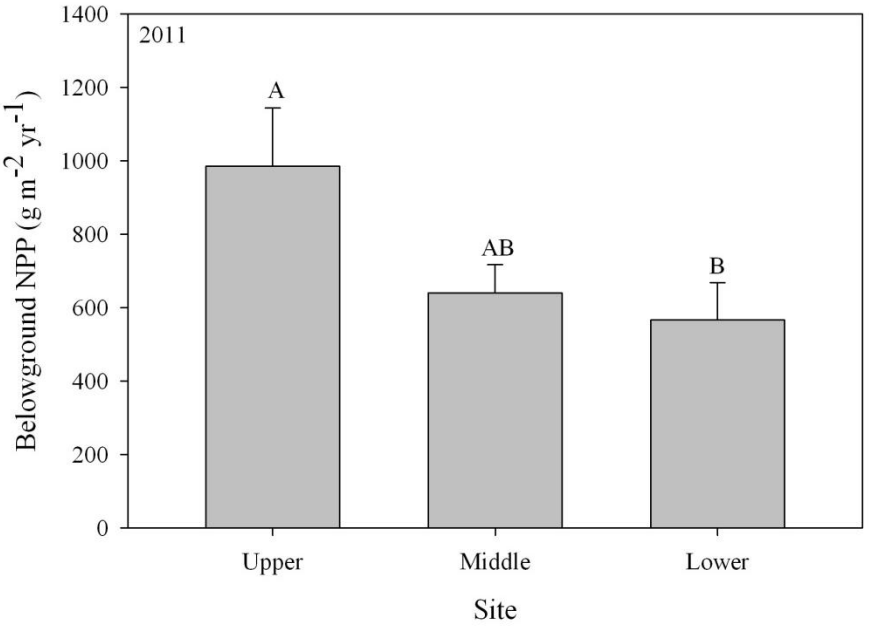

Figure 4. Estimates of BNPP for 2011, significant differences among sites are represented by different letters at $p<0.05$. Vertical bars indicate standard errors.

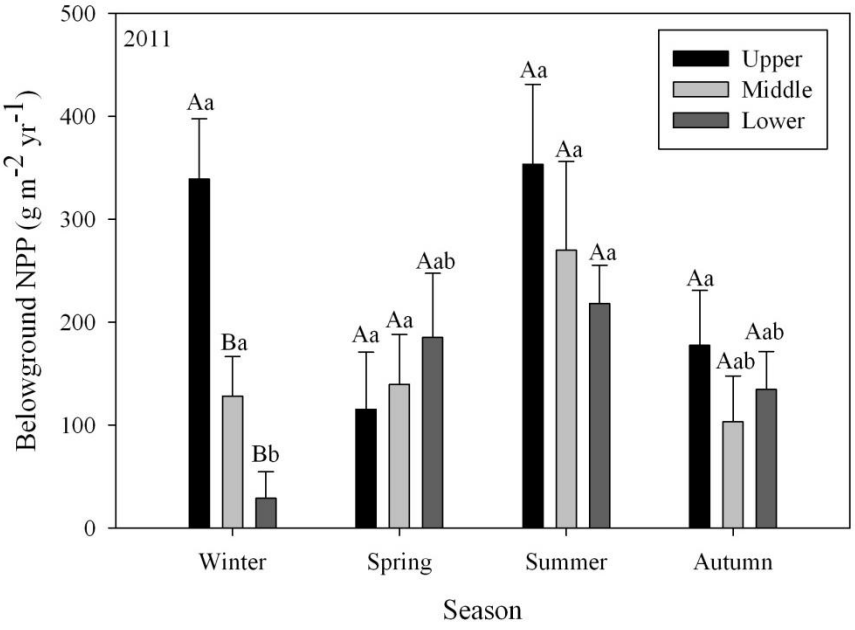

Figure 5. Seasonal belowground productivity for 2011, capital letters represent significant differences among sites within a season and lower case letters between sites across seasons at $p<0.05$. Vertical bars indicate standard errors.

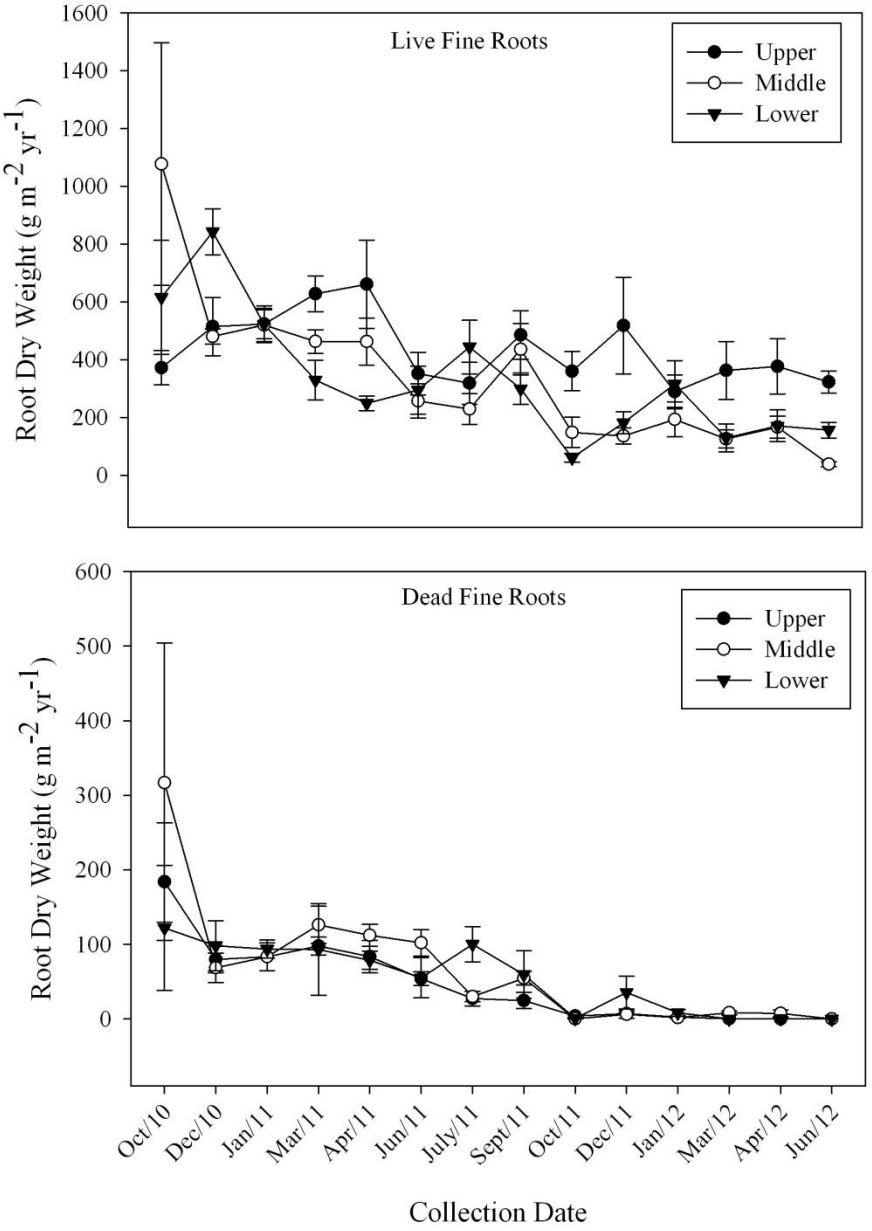

Figure 6. Total live and dead fine mean root dry weight (g m^{-2} yr^{-1}) by collection for each forested site. Vertical bars indicate standard errors.

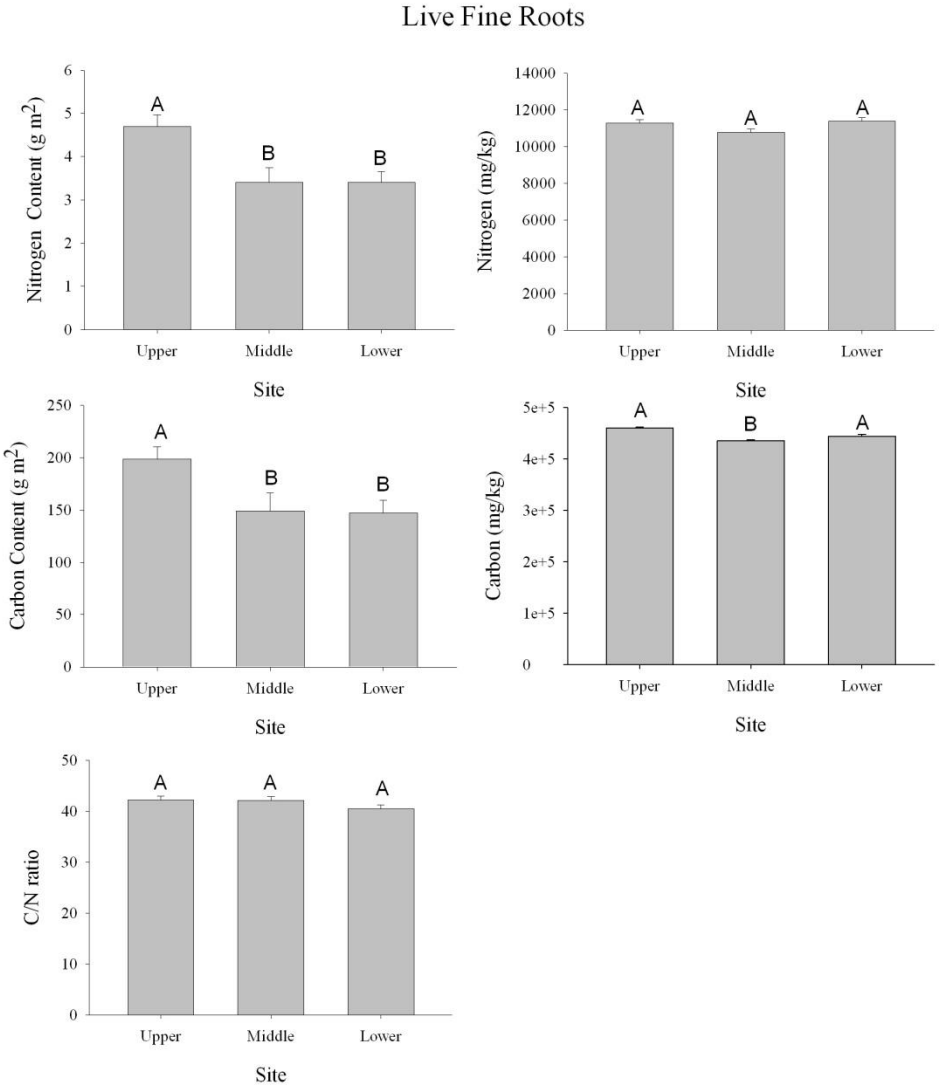

Figure 7. Live fine root C and N content (g m^{-2} yr^{-1}), concentration (mg/kg), and C/N ratio compared among sites with letters representing significant differences at $p<0.05$. Vertical bars indicate standard errors.

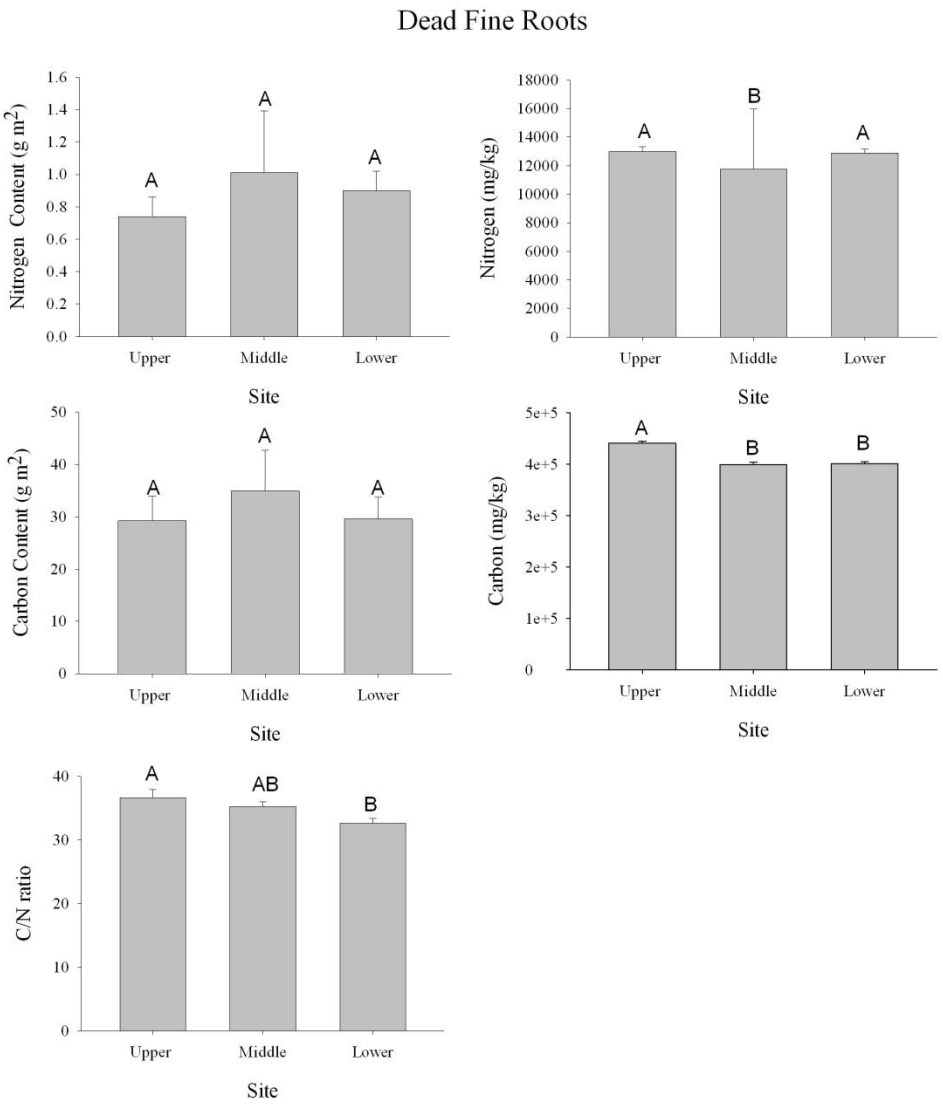

Figure 8. Dead fine root C and N content (g m^{-2} yr^{-1}), concentration (mg/kg), and C/N ratio compared among sites with letters representing significant differences at $p<0.05$. Vertical bars indicate standard errors.

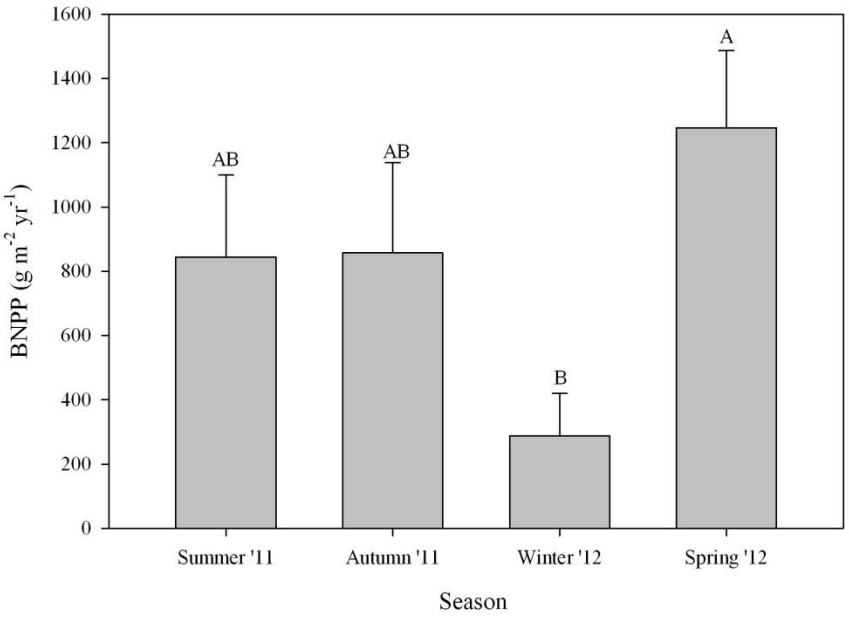

Figure 9. Seasonal BNPP for the oligohaline marsh site, with significant differences among seasons represented by different letters at $p<0.05$. Vertical bars indicate standard errors.

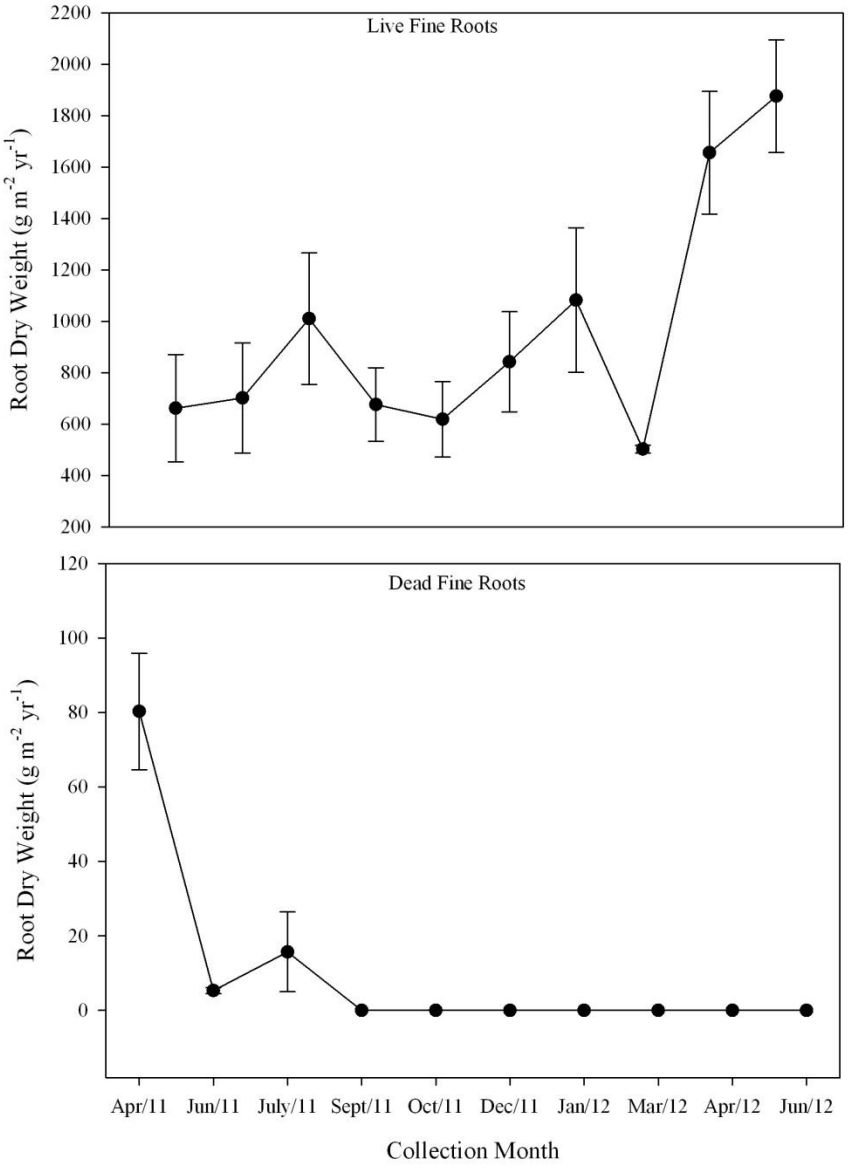

Figure 10. Total live and dead fine roots for the marsh site across collections. Vertical bars indicate standard errors.

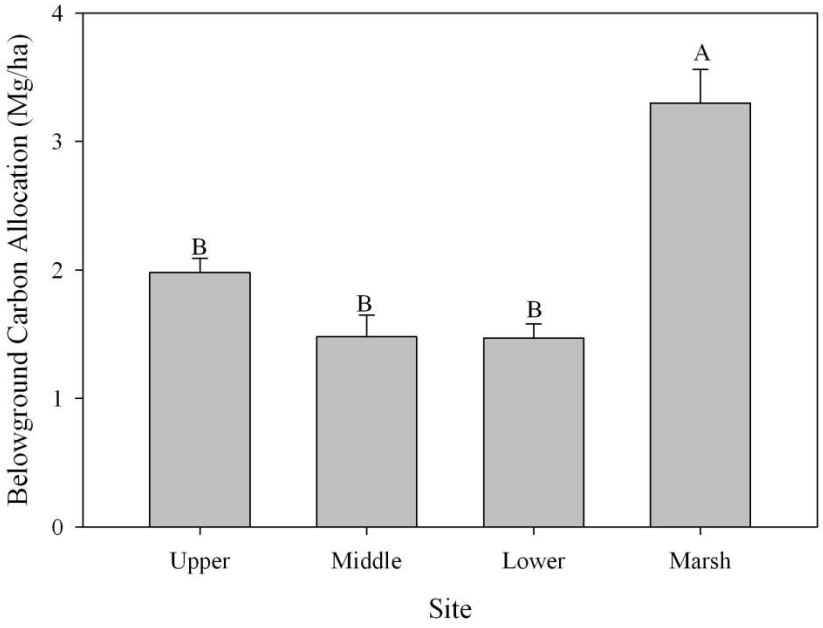

Figure 11. Belowground C allocation for all sites. Forested sampling dates were October 2010-July 2012, with the oligohaline marsh added in March 2011. Different letters represent significant differences at $p<0.05$. Bars indicate standard errors.

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CHAPTER III

Changes in Microbial Biomass and Litter Decomposition along a Salinity Gradient in Tidal Freshwater Forested Wetlands and an Oligohaline Marsh in South Carolina, USA

Abstract

The impact of salinification on the nutrient cycling and biogeochemistry of tidal freshwater wetlands was studied along a salinity gradient on the Waccamaw River, South Carolina. Three tidal forested sites of varying porewater salinity and an oligohaline marsh were included in the study. Sustainability of these systems relies on nutrients derived from the breakdown of organic matter by microbes. To study these processes, we assessed nutrient limitations through fertilized ingrowth cores and foliar analyses, determined rates of litter decomposition, and quantified microbial biomass C and N. Porewater salinity averaged <0.1, 1.8, 2.8, and 5.4 ppt at the upper, middle, and lower forested sites, and oligohaline marsh, respectively. Site position did not have a controlling effect on decomposition as there was no difference among rates or percent mass remaining among sites. Microbial N declined in proximity to the coast for the forested sites and then increased slightly between the lower forested site and marsh. Microbial C was significantly greater at the upper and middle sites compared to both the lower site and marsh. Although litter analyses exhibited lower N and P nutrient proficiency at the lower forested site, the fertilized ingrowth cores there did not show significant responses to N, P, or N+P fertilization treatments within or across sites. Decomposition does not appear to be inhibited by salinity; however, lower P concentrations in foliage and decreased microbial biomass C and N suggest changes in

nutrient accessibility and/or reduced availability for tree uptake in the highly salt impacted, lower forested site.

Introduction

Located at the mouth and lower reaches of coastal rivers, tidal wetlands occupy a unique niche between marine and terrestrial systems. Due to the geographic position of tidal wetlands, one of the principal threats to these systems is salinity intrusion from sea level rise and persistent land use change (e.g., river dredging, upstream dams, etc.). Salinification of these ecosystems may affect their structure, growth, and function. In spite of recent attention, large knowledge gaps still remain, especially regarding nutrient cycling. Complexity of these systems arises from interactions among river stages, tidal fluctuations, and storm surges, factors that create variation in salinity gradients. At the upper reaches of these transects are tidal freshwater forested wetlands (tidal swamps), which change in composition before transitioning into tidal marshes near the mouth of rivers. Driving this transformation are hydrology and nutrient processes in the soil, which involve soil organisms and decomposition of organic matter.

Leaf litter production rates in southeastern floodplain forests have been reported as high as 972 g m^{-2} yr^{-1} (Megonigal et al., 1997), representing a significant transfer of nutrients within the system. This litter is then broken down and used for energy by soil microorganisms and macroinvertebrates. Within decomposing litter, nutrients are leached, mineralized, and immobilized (Brinson et al., 1985; Lockaby and Walbridge, 1998). Decomposition has been found to be controlled by litter quality, moisture, and temperature and is heavily influenced by hydroperiod (Sharitz and Mitsch, 1993; Ozalp et al., 2007). Due to the high variability of hydroperiod and opportunity for confounding effects, the hydroperiod influence on decomposition remains unclear (Mitsch and Gosselink, 1993). However, some studies provide a

better understanding of hydroperiod dynamics. For example, a controlled field experiment by Lockaby et al. (1996), analyzed different flooding regimes and determined that temporary, aerobic flooding stimulated mass and C loss from decomposing litter to the greatest extent.

In the southeastern United States, tidal wetlands often experience prolonged inundation from tidal flooding, which changes on daily, weekly, and seasonal scales (Day et al., 2007; Anderson and Lockaby, 2011b). Fluctuations in porewater salinity of tidal swamps are determined by saltwater intrusion (e.g., storms) and salinity stress from droughts, sea level rise, and land use change. Although, tidal freshwater forests are usually limited to salinities <0.5 ppt, species such as baldcypress (*Taxodium distichum*) show tolerance to levels >2.0 ppt (Conner et al., 1997; McLeod et al., 1996; Krauss et al., 2007). At the coastal terminus of these forests are the oligohaline marshes, which may exhibit salinities of 5.0 ppt (Crain et al., 2002).

Salinity or associated factors related to salinity have been shown to decrease decomposition, demonstrating that microenvironmental factors have a stronger influence than litter quality in marsh grasses (Rejmankova and Houdkova, 2006). Decreases in decomposition due to salinity are often attributed to limited microbial activity, although microbes may not be directly inhibited by salinity, but rather by soil fertility (Mendelssohn et al., 1999).

Nutrient limitations in forested systems have implications spanning influence on microbial populations to controls on C allocation and net primary productivity (NPP) (Keyes and Grier, 1981; Nadelhoffer et al., 1985). It is known that N and P are two of the most limiting nutrients to plant productivity globally (Vitousek and Howarth, 1991), with studies supporting more limitation by N in temperate areas (Reich and Oleksyn, 2004) and a shift to P in some tropical areas (Walker and Syers, 1976). However, patterns of N and P limitation are often complex, and while N has been shown to be globally distributed (LeBauer and Tresder, 2008),

areas such as blackwater floodplains have been found to be limited more by P (Schilling and Lockaby, 2005).

Nutrient patterns have been demonstrated to shift across narrow spatial gradients (Feller et al., 2002). Exploring how nutrient resources change across ecological gradients is essential to understanding future impacts on particular systems. In tidal wetlands, small changes in annual sea level have the potential to alter porewater salinity to an extent that may drive ecological changes significantly. In turn, influences of these fluctuations can affect species composition, microbial processes, and, ultimately, NPP.

Studies have suggested that symptoms of nutrient limited systems include higher NUE (Vitousek, 1982), decreased nutrient concentration in leaves (Binkley, 1986), threshold N:P ratios (Koerselman and Mueleman, 1996; Lockaby and Conner, 1999), and increased response to fertilization treatments (Shaver and Chapin, 1980). Although some of the parameters such as threshold ratios alone may not be conclusive, a compilation of several analyses lends itself to a strong assessment of nutrient limitations.

When discussing limiting nutrients, primary focus is given to N and P, and sometimes K, Ca, and Mg. Also essential to plant nutrition are micronutrients, which are required in lower quantities than macronutrients (Mengel and Kirkby, 1987). Generally, micronutrients are thought to only limit forest production under special conditions (Binkley, 1986), and previous research has focused on agricultural areas where micronutrient dynamics are well known (Barker and Pilbeam, 2006). In this study, micronutrients are reported and discussed because few reports of micronutrient biogeochemistry exist in the wetland literature.

To determine whether changes occur in nutrient cycling, we studied three forested wetlands and a tidal oligohaline marsh. Our objectives were to: (i) quantify litter decomposition

in tidal freshwater forested communities of differing salinities; (ii) examine how microbial populations change in response to salinity and the impacts of such changes on nutrient cycling; and (iii) discern how salinity may alter nutrient availability. We hypothesized that the most salt-impacted forested site would have the lowest microbial biomass and slowest decomposition due to inhibition of microbial processes and higher degree of nutrient limitation. We also hypothesized that increased belowground productivity at the marsh would stimulate microbial populations, especially when compared to the lower forested site.

Methods

Study Site

Our study was done along the reaches of the Waccamaw and lower Sampit rivers near Georgetown, South Carolina. Both of these rivers arise on the Coastal Plain and therefore are blackwater systems characterized by low sediment and nutrient loads (Doyle et al., 2007). Our study sites were arranged at the lower reaches of these rivers where tidal freshwater forests occupy a salinity gradient that transforms to marsh at its coastal limit. The canopy is dominated primarily by baldcypress and swamp tupelo (*Nyssa biflora*), while the marsh hosts mostly cattails (*Typha latifolia*) and bull tull (*Scirpus robustus*).

Salinity intrusion within the Waccamaw and Sampit rivers is likely the combination of land-use change, geographic features, and sea level rise. Sites along the salinity gradient were comprised of an upper (<0.1 ppt) and middle (1.8 ppt) forested site along the Waccamaw River and a lower forested site (2.8 ppt) and marsh site (5.4 ppt) on the lower Sampit River. All sites are classified as upper microtidal, having two similar high and low tides per day with a range of 1-2 m (Doyle et al., 2007). For sampling purposes, three 4.57 m (radius) circular plots were delineated at each site.

Green Foliage and Soil Analyses

Nutrient limitations for the three forested sites were determined utilizing ingrowth fertilized cores during Spring and Fall 2011, along with foliar analyses completed in 2009. Treatments for ingrowth cores consisted of a control (CTRL), N fertilization, P fertilization, and an N/P combination. Nitrogen in the form of urea and P as triple phosphate were used for fertilization treatments, with amounts equal to 300 and 50 kg/ha, respectively.

Each ingrowth core was formed by removing a soil core to a depth of 11 cm with a diameter of 8 cm. This soil core was placed directly into a mesh cylinder of the same size, and inserted into the soil. Each soil core received one of the four treatments, with fertilizers mixed into the top 5 cm of soil with sand used as a carrier, and sand without fertilizer mixed into the CTRL cores. Sets of these four treatments at each site were placed in a randomized block experiment. In the spring, three sets of cores were placed at each site, and a second sampling of five sets in the autumn.

Soil cores were left in the field for 8 weeks during both spring and autumn. Excess soil was removed from the exterior of the core upon removal, and roots were cut flush with the wire mesh. Cores were transported to Auburn University, and kept in a cooler at 4°C until processed. Initial processing of each core included a fine pressure rinse over a screen and separation of live from dead roots. Placement of roots into a life class was determined by visual criteria outlined by Bohm (1979) and Bledsoe et al. (1999). Live root length was determined by the line-intersection method (Bohm, 1979), and then live fine roots were oven-dried at 70°C for 72 hs and ground through a Wiley mill to pass a 40-mesh screen. Live roots from each core were then weighed to calculate total standing crop biomass.

For assessment of green tree foliar nutrients, leaves were sampled from representative canopy trees in July 2009. Leaves were acquired from the mid to upper canopy by shooting branches, with at least 3 trees sampled per forested site. Species of trees sampled included baldcypress, swamp tupelo, and red maple (*Acer rubrum*). Leaves were placed in paper bags and returned to the laboratory, where they were dried at 60°C, and ground to pass a 1-mm sieve.

Two soil samples were collected from each plot for all forested sites in September 2010. This step was repeated in March 2012 to also include the oligohaline marsh. Soil was oven-dried to a constant mass at 70°C and sieved through a 2-mm screen. Chemical and additional laboratory analyses were performed after roots, green foliage, and soil were dried and sieved (see laboratory analyses).

Microbial Biomass

Microbial biomass was sampled at 5-7 wk intervals from October 2010 to July 2012 for the three tidal forested sites and from April 2010 and July 2012 for the tidal oligohaline marsh. Three random samples of 1.9 L of soil were taken from each plot, transported on ice, and stored at 4°C until processed, which was typically within 24 hs. Debris and any large organic matter were removed from the soil and the samples sieved through 2-mm mesh before further analysis.

Litter Decomposition

The litter bag approach (Swift et al., 1979) was used to determine decomposition rates and nutrient dynamics of decomposing litter. Senesced foliar litter was collected in raised 0.25 m^2 traps (n=10 per site) during fall 2010 and early winter 2011, air-dried for 2 wk, and sorted by species for each site. Litterbag composition was determined according to the relative contribution to mass by species for each site, thus generating different species compositions among sites. This step resulted in 78% baldcypress and 12% hardwood for the upper, 99%

baldcypress and 1% hardwood for the middle, and 83% baldcypress, 15% hardwood, and 2% pine at the lower site. Dominant species included baldcypress, swamp tupelo, and red maple.

Nylon mesh bags measuring 13 x 13 cm, with a 5-mm mesh on top and a 2-mm mesh on bottom, were filled with 10 g of air-dried leaf litter from each site. Three sets of 10 litterbags were placed at each plot for the upper and middle forested sites. Due to a lack of leaf litter present the lower site had only 2 plots receiving 2 sets of 10 litterbags. Wooden popsicle sticks measuring 15.5 cm in length by 1.7 cm wide and made of birch (*Betula* sp.) were placed at all sites for a standardized assessment of microenvironment influences on a common substrate. Popsicle sticks were placed in small nylon bags (5 x 5 cm), with mesh corresponding to the litter bags, attached in sets of 10, and one set placed at each plot that had litterbags. Popsicle sticks and litterbags were collected at intervals of 0, 2, 4, 8, 12, 16, 30, 36, and 68 wk from April 2011 to July 2012.

Litter bags and popsicle sticks were transported to the laboratory in plastic bags, where they were cleaned of soil and debris, and then oven-dried at 70°C for 72 h. Popsicle sticks were used to evaluate mass loss trends among sites, but were not used for nutrient dynamics. Litterbag samples were dried and weighed, sieved through 20-mesh screen, and analyzed for nutrients.

Laboratory Analyses

Soil pH was determined using an automated LabFit AS-3000 pH analyzer on a 1:1 soil:0.01 M $CaCl_2$ suspension. Soluble salts (SS) were analyzed using an Orion model 162A conductance-resistance meter in a 1:2 soil:water extract. For soil, extractable phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), zinc (Zn), copper (Cu), iron (Fe), sodium (Na), lead (Pb), and cadmium (Cd) were determined on a Mehlich-1 extraction solution with elemental analysis determined on an inductively coupled plasma spectrograph

(ICAP). Green foliage nutrients were analyzed the same, except for P. Total P for green foliage and leaf litter was determined using the vanadomolybdate procedure (Jackson, 1958), which consisted of dry-ashing and extraction with acid digestion, followed by colorimetric analysis. C and N for soil and plant tissue (green foliage and leaf litter) were determined using a Perkin-Elmer 2400 series II CHNS/O analyzer (Perkin-Elmer Corp., Norwalk, CT).

At time 0, leaf litter lignin and cellulose concentrations were determined with acid detergent fiber and neutral detergent fiber methods (Goering and Van Soest, 1970). The lignin-cellulose index (LCI) was determined from the equation: LCI= lignin/(lignin + cellulose) (Melillo et al., 1982). Mean nutrient concentration of litterfall at time 0 was also used to calculate resorption proficiency (Killingbeck, 1996).

Microbial biomass analysis was based on the chloroform-fumigation technique (Vance et al., 1987; Brooks et al., 1985). For this method, fumigated and non-fumigated subsamples of 18.5 g were analyzed. After fumigated samples were placed in a vacuum desiccator with chloroform for 24 h, they were extracted with 125 mL of 0.5 M potassium sulfate. This extraction also was used on non-fumigated samples, and then both solutions were shaken for 30 min and filtered. Organic C and N were measured using a Shimadzu TOC-V and total N combustion analyzer and Apollo 9000 combustion TOC analyzer with TN module. Estimations of microbial C and N were calculated as the difference between organic C and N contents of fumigated and unfumigated samples (Vance et al., 1987; Brooks et al., 1985).

Statistical Analyses

All statistical analyses were completed using SAS version 9.2 (SAS, 2004). Analysis of variance (ANOVA) (Proc GLM with Tukey's HSD) was used to determine differences among sites for microbial biomass values, C, N, and P concentration, and mass remaining in

decomposing litter, and litter decomposition rates. Repeated-measures ANOVA was used to determine significant interactions of site and season for microbial biomass C and N.

The NLIN procedure in SAS was used to determine decomposition rates (k) following Olson's (1963) model, $X_1/X_0=e^{-kt}$, where X_1 is original mass, X_0 is mass remaining, k is decay rate, and t is time. Independent linear comparisons were made for the fertilization treatments utilizing paired comparisons. This analysis was completed so we could see significant differences in rank among the pairs. These comparisons aimed to understand nutrient limitations that spanned the whole salinity gradient. The following pairs were tested: P vs. N, P vs. CTRL, P vs. N+P, P and N vs. CTRL, P and N vs. N+P, P and N+P vs. CTRL, P and N vs. CTRL, N vs. CTRL, N and N+P vs. CTRL, N and N+P vs. P, and N+P vs. CTRL. Relationships were considered significant at the 0.05 probability level; however, differences at the 0.10 probability level are discussed.

Results

Nutrient Limitations and Soil Analyses of Forested Sites

Foliar P concentrations were significantly different among forested wetland sites and were ranked: middle >upper>lower (Table 1). Other macronutrients were not significantly different among sites, except for Ca, which was highest at the upper site (Table 1). Only foliar micronutrients Na and Cu exhibited differences among sites. Mean foliar Na concentration at the middle site was 10861 mg/kg, and was significantly greater than that of the upper site (396 mg/kg). The middle site also had greater foliar Cu concentrations compared to the lower site. All N/P foliar mass ratios were <6 and did not differ among sites. Leaf litter nutrient proficiency was significantly lower at the lower site for both N and P (7970 and 800 mg/kg, respectively).

Within each site, in both spring and autumn, there were no significant differences among fertilization treatments for mass or root length density. Figure 1 shows responses of fertilization treatments compared to control. Because of high within-site variation, pairwise comparisons across all sites did not exhibit any significant differences among nutrients. For both spring and autumn, total N, total C, and root length were not significant within and among sites.

Soil micro- and macronutrients, pH, base saturation (%), and soil conductivity (mmhos/cm) for forested and marsh sites are displayed in Table 2. Generally, the upper site had greater macronutrient concentrations of total C and N, and extractable Ca except for extractable P, which was highest at the middle site. Soil pH, base saturation, and salinity were greatest at the lower site, where soil concentrations of Cu, Fe, and Zn were lowest (Table 2).

Litter Decomposition

Due to vandalism, the lower site only retained a sufficient number of decomposition bags to proceed through week 36 and popsicle bags through week 30, whereas both upper and middle sites collections continued through week 68. Litter quality at time 0 is presented in Table 3.

Percent P, C, N, and mass remaining did not exhibit significant differences among sites except for P remaining at week 8, which was significantly greater at the middle site compared to the upper. As expected, complete decomposition was not achieved at any of the sites within the 68 week study (Figure 2). Mass remaining at week 36 for the upper, middle, and lower sites was 24.6, 20.6, and 14.9%, respectively. The relationship between mass remaining at the upper and middle sites shifted at week 68 with the upper site concluding at 13.4% and the middle site being slightly higher at 16.9%, but was not significant. Percent P and N remaining followed similar trends among the sites as mass remaining for weeks 36 and 68, with the exception of N

remaining at week 36. At that time, the lower site had more N remaining (35.3%) than the middle site (32.3%), even though there was less mass remaining (Figure 2).

Immobilization patterns of N and P were similar among sites, with immobilization of both nutrients occurring before week 12 (Figure 2). Over the entire study, ratios of C/N, N/P, and C/P for all sites ranged from 23-65, 4-16, and 127-840, respectively. Higher litter C/P ratios were found for each collection on the lower compared to the middle and upper sites, with the exception of week 36. Also, the lower site exhibited significantly higher N/P ratios compared to the upper and middle site until week 30. C/N ratios were less consistent, with the lower site showing a significantly greater ratio compared to the upper and middle sites for weeks 0, 1, 2, 12, and 30, and being slightly greater than the upper site for week 16.

Decay constant *k* values were 0.71, 0.55, and 0.77 for the upper, middle, and lower sites, respectively. All *k* rates were not significantly different among sites. Similar to leaf litter, mass remaining and *k* values for popsicle sticks were not significantly different among sites.

Microbial Biomass

Microbial biomass N resulted in significant site-season interaction (Table 4); therefore, differences among sites for total mean microbial N should be interpreted with caution. Site and season did not have a significant interaction for microbial biomass C. Mean microbial C was significantly less at the lower site (353.4 μg g^{-1} dry $soil^{-1}$) than that of both the upper and middle sites (637.9 and 594.1 μg g^{-1} dry $soil^{-1}$, respectively) (Figure 3). Mean microbial N was significantly different among all sites with a rank of upper>middle>lower and corresponding values of 69.8>50.7>28.4 μg g^{-1} dry $soil^{-1}$ (Figure 4). These patterns were also observed seasonally for both microbial C and N, with a few exceptions (Figure 5 and Figure 6). The lower site had significantly less microbial C than both the upper or middle sites for most seasons, with

the exception of fall (2010), summer (2011), and winter (2011-12). For every season, microbial N at the sites ranked upper>middle>lower, with significant differences among sites during winter (2010-11), spring (2011), summer (2011), and summer (2012). Mean microbial C/N ratio was significantly less at the upper site than both the middle and lower site (Figure 7). Microbial C and N biomass did not exhibit definitive seasonal trends (Figure 5 and 6).

The olighaline marsh exhibited a mean microbial N of 41.7 μg g^{-1} dry $soil^{-1}$, which was significantly different than the three forested sites, and ranked between the middle and lower site values. In contrast, marsh microbial C was ranked lowest among the forested sites at 276.5 μg g^{-1} dry $soil^{-1}$, but was only significantly less than the upper and middle forested sites. Microbial C/N ratios were significantly less at the marsh compared to the forested sites. Unlike the forested sites, marsh microbial C and N biomass peaked in spring (2011).

Discussion

Nutrient limitations

Foliar, Leaf Litter, and Soil Analyses

Anderson and Lockaby (2011a) found lower foliar nutrient concentrations and high N/P and C/P ratios in tidal swamps compared to non-tidal swamps, thus suggesting higher P limitation in tidal swamps. Foliar N concentrations at the middle (10,037 mg/kg) and lower (7,098 mg/kg) sites in the present study were low compared to some other studies of baldcypress in non-tidal and tidal wetlands where values for foliar total N included 15,000 mg/kg (non-tidal; Effler et al., 2006), 12,000-17,400 mg/kg (non-tidal; Messina et al., 1986), and12,000 mg/kg (tidal; Anderson and Lockaby, 2011a). In contrast, mean foliar P concentrations ranged from 1,266-2,885 mg/kg at our sites, and were comparable at both the middle and upper sites to means previously published for baldcypress in tidal and non-tidal swamps (2,600 mg/kg; tidal and 2,200

mg/kg; non-tidal, respectively) (Bandle and Day, 1985; Messina et al., 1986; Anderson and Lockaby, 2011a). Lockaby and Conner (1999) proposed that N/P ratios <12 were N limited and >16 were P limited. Our N/P ratios were narrow (< 6), falling well within the N-limitation range.

Foliar K and Mg did not differ among sites; however, K was lower and Mg higher than in some tidal swamps of Georgia (Anderson and Lockaby, 2011a). Lower mean Na at the upper site may reflect reduced effects of salt-water intrusion. A higher concentration of Cu at the middle site is unexpected since salt and frequent flooding is known to increase mobility of Cu from soils. It is possibly the result of soil characteristics such as organic matter constituents which heavily affect mobility of Cu in riverine floodplain soils (Laing et al., 2009).

Nutrient resorption by plants from senescing leaves is an important mechanism for nutrient conservation (Bleeker, 1998; Aerts and Chapin, 2000). At nutrient-poor sites, efficient resorption would be expected to evolve and be reflected as lower nutrient proficiencies in leaf litter (decreased nutrient concentration) (Killingbeck, 1996). The present study showed that increased salinity decreases N and P proficiencies in leaf litter, suggesting these trees have adapted to reduce N and P loss (Killingbeck, 1996). Anderson and Lockaby (2011a) found low P resorption proficiencies and high N/P ratios (>21) in tidal swamps, thus suggesting P limitation. However, our N limitation data contrasted with those results. Rather, our results suggest salinity may be creating a slightly more severe N and P limitation at the lower forested sites despite consistent N limitation demonstrated by N/P ratios in green foliage. In a study on P and N mineralization at the same sites, Noe et al. (2012) reported a peak in N mineralization and N turnover rates at the lower site, which could have driven P limitation.

Middle and lower site means for soil TN were within the range Jun et al. (2012) found on the Ogeechee River (8,900-10,400 mg/kg), with the upper site being similar to values recorded

by Kelly et al. (1993) at the White Oak River estuary North Carolina (12,000-19,200 mg/kg). Interestingly, soil TN and TC for these same sites taken in 2005 and reported by Krauss et al. (2009) and Cormier et al. (2012) showed the lower site being numerically greater compared to middle and upper sites. In contrast, TN and TC of our study decreased numerically in value as salinity increased, with the upper site being significantly greater than other sites. Since depth increments and number of samples varied between the two time periods, differences must be interpreted with caution. Soil extractable P at our sites was well above those of tidal sites near Apalachicola, FL (Anderson and Lockaby, 2011a) and redwater floodplains in GA (Schilling and Lockaby, 2005).

Fertilized Ingrowth Cores

Several studies have used fertilized ingrowth cores as bioassays for nutrient limitation (Raich et al., 1994; Peterjohn et al., 1999; Stewart, 2000; Gleeson and Good, 2003; Gress et al., 2007). This method is based on the potential of root proliferation into nutrient rich patches (Hodges, 1999). There were no significant differences among ingrowth core treatments within or across sites. The lack of significant differences is likely due to high variability among samples, due to microtopographic differences.

Wetlands often have highly variable microtopography, which in turn influences microscale hydrology, species composition, and biogeochemistry. Tidal sites are often characterized by hummock and hollow topography, creating concave and convex microsites that differ 15-20 cm in elevation (Duberstein and Conner, 2009). This condition causes high spatial variability and requires large sample size to offeset heterogeneity of the soils and roots. In the spring, results showed consistent numeric, although not significant, responses to fertilization treatments. We, therefore, increased the sampling from n=3 to n=5 per treatment, in an attempt to

overcome variability. However, there remained a nonsignificant response to fertilization treatments. Additionally, we used soil directly taken from the sites and not manipulated in the laboratory, unlike studies such as Cuevas and Medina (1988), Raich et al. (1994), and Stewart (2000), which utilized foreign plant growth mediums. We choose to use soils from the sites, to insure proper representation of current soil characteristics of each site.

Litter Decomposition

At the end of the study, percent mass remaining in the upper and middle sites (68 wk) and lower site (36 wk) were similar to dry sites on the Coosawatchie River, SC after 100 wk (Baker et al., 2001) and lower than a site on a blackwater floodplain, which at 68 wk had 68% mass remaining (Lockaby et al., 1997). In comparison, our decomposition at all sites was rapid, which, along with temperature and litter quality, could be a product of tidal influence. Ozalp et al. (2007) found complete decomposition of tupelo leaves within 1 y on a SC tidally influenced island, with faster decomposition of the island side most exposed to tides. In addition to the tide creating periodic, aerobic flooding that favors decomposition (Lockaby et al., 1996), it also has the potential to increase the physical export of litter from the bag after initial breakdown occurs.

Litter quality has been found to be the most important factor regulating litter decomposition across large scales (Zhang et al., 2008). In our study, the lower site exhibited reduced litter quality represented by high ratios at time=0 of lignin/cellulose, lignin/N, C/P, C/N, and N/P. Despite these initial differences in litter quality, decomposition did not differ among the sites. Furthermore, decomposition has been shown to be inhibited by soil salinity (Mendelssohn et al., 1999), which we would expect to see reflected along this gradient. Instead, we found similar decomposition among sites, suggesting the process is mostly being driven by

microenvironmental characteristics, such as hydroperiod and temperature (Lockaby and Walbridge, 1998).

Similar N and P mineralization and immobilization patterns in litterbags suggest little difference in N or P availability. Mineralization of both nutrients occurred after week 12, at which time C/N ratios among the sites ranged from 29-36. Mineralization of N occurs after an optimum C/N ratio is achieved, and N is no longer immobilized in an effort to use C (Bowden, 1987). The threshold for C/N ratio is not clear, but has been suggested to be <50 (Paul and Clark, 1989) or <25 (Heal et al., 1997). In the Southeast, N mineralization can begin at C/N ratios as high as 43.7 (Ozalp et al., 2007). Litterbag N/P ratios were narrow throughout our study (<14), which is typically indicative of N-limitation. However, Guswell and Freeman (2005) found that at these low ratios, decomposition can be limited by N, P, N+P, or not limited at all.

Microbial Biomass

Microbial C and N on the upper and middle sites are comparable to those of the Satilla floodplain, a blackwater system in GA (661 and 54.8 $\mu g\ g^{-1}$ dry $soil^{-1}$, respectively; Schilling and Lockaby, 2005). These values are lower than ranges of microbial C and N reported by Schilling et al. (1999) on the Pearl River floodplain, a brown water (nutrient rich) system in MS (1403-2511 and 95.2-158 ug g^{-1} dry $soil^{-1}$, respectively). Comparison of the lower site's microbial C and N show similarities to those of sediment stressed catchments at Fort Benning, GA (Lockaby et al., 2005), and woodland swamps and maple pools reported by Groffman et al. (1996) in NY.

Typically, porewater salinity will spike in coastal freshwaters during summer when freshwater input from the river is reduced. Microbial biomass in coastal soils has been shown to diminish at this time, with highest values recorded in winter (Tripathi et al., 2006). Over the eight data seasons, there are few consistencies among the same seasons from year to year for

microbial C or N (Figure 5 and Figure 6). These sites are prone to a variety of influences that can alter microenvironmental properties and drive microbial fluctuations such as, precipitation of upland watersheds, sea level rise, and temperature.

Cleveland and Liptzin (2007) suggested microbial element ratios could be useful in defining possible nutrient limitations in terrestrial systems. The upper site had significantly lower microbial C/N ratios than both the middle and lower site. C/N ratios for the upper, middle, and lower sites were 9.4, 13.4, and 14.5, respectively (Figure 7). Allen and Schlesinger (2003) found lower microbial C/N ratios after addition of N to the soil. If high microbial C/N ratios are indicative of a N-limited system, then our results would suggest that the upper site is the least N-limited along the forested gradient. However, due to limited knowledge of microbial stoichiometry in relation to terrestrial nutrient limitations, our results are not conclusive.

Although microbial C and N followed patterns similar to those of other wetlands, microbial N exhibited the strongest effect of site and was significantly different along the gradient, while microbial C was only significantly less at the lower site (Figure 4 and Figure 5). Higher soil concentrations of C at the upper site could be contributing to higher microbial biomass C. The decreases in microbial N along the gradient suggest less immobilization of N at the lower site. This is a possible product of the microbes not being limited by N, less N available, or less microbial activity. At these same sites, Noe et al. (2012) found N mineralization to peak at the lower site, although not significantly, attributing it to increased detritus from dying trees and encroaching marsh grass. Therefore, greater N mineralization would support a lack of N limitation at the lower site.

Comparison of Marsh Microbial Biomass and Soil with Forested Sites

The oligohaline marsh had higher extractable P and exchangeable Mg and K, along with lower exchangeable Zn and Ca soil values than the forested sites. Soil extractable P concentration in the marsh averaged 45.38 mg/kg, which was well above values for forested sites. Increased extractable P concentrations in the marsh could be a product of enhanced retention of P from the river or increased deposition from marine deposits. Oligohaline marshes have been shown to retain through sediment burial up to 81% of P that would otherwise be cycled or exported (Merrill and Cornwell, 2002). Wong et al. (2008) suggest that, at increasing salinity, soil substrate is easily decomposable, thus releasing more C and surface area for microbes. Our data did not support this finding, as microbial C at the marsh (most salinity-influenced site) was lower than the middle and upper sites. Interestingly, there was an increase of microbial N between lower forested site and marsh, along with a decrease in microbial C/N ratio. This pattern suggests that the microbial populations may be N limited, which would increase the amount of N incorporated, and drive changes in microbial N biomass and microbial C/N ratios.

Conclusions

Narrow live foliar N/P ratios imply that aboveground production is limited by N along the salinity gradient. However, mineralization and immobilization patterns in litter between P and N were similar, suggesting co-limitations. Patterns of foliar and litter concentrations along the gradient indicate slightly more severe limitation by N and P at the lower site. Although microbial populations are mostly stimulated by N availability, the high C/N ratio at the lower site suggests less N limitation compared to the upper site. Our data suggest that limitations along this gradient include both N and P. Additionally, peaking P and N resorption proficiencies at the

lower site, low litter quality, reduced microbial C and N, and decreased total soil C and N show a tendency for salinity to inhibit nutrient pools and fluxes.

Table 1. Green foliar macronutrient concentrations (mg/kg) of baldcypress, swamp tupelo, and red maple for each forested site. Standard errors are in parentheses. Different letters across rows represent significant differences at $p<0.05$.

Foliar Variable	Site		
	Upper	Middle	Lower
P	2169 (150)b	2588 (291)a	1393 (132)c
C	472530 (10500)a	477360 (1750)a	486880 (13000)a
N	12100 (4104)a	10036 (1585)a	7098 (152)a
Ca	10525 (1107)a	5733 (290)b	5400 (750)b
K	4975 (1231)a	5233 (617)a	3350 (580)a
Mg	7200 (488)a	6766 (548)a	6825 (487)a

Table 2. Mean concentrations (± SE) for chemical soil properties of three forested sites and the marsh. Standard errors are in parentheses. Different letters across rows represent significant differences at $p<0.05$.

Soil parameter	Site					
	Upper	Middle	Lower	Marsh	F value	P value
C (mg/kg)	225509 (5796)a	178210 (4357)b	176108 (7419)b	160460 (1197)b	19.77	<0.0001
N (mg/kg)	14332 (438)a	10305 (227)b	9491 (351)b	8797 (139)b	46.00	<0.0001
Ca (mg/kg)	5167.7(236)a	2940.8 (118)bc	3592.4 (216)b	2059.3 (98)c	29.30	<0.0001
Cd (mg/kg)	0.16 (0.02)a	0.11 (0.01)ab	0.07 (0.01)b	--	6.91	0.0047
Cu (mg/kg)	2.24 (0.32)a	2.40 (0.24)a	1.30 (0.14)b	--	5.81	0.0088
Fe (mg/kg)	413.1 (43)a	398.8(44)a	129.2(16)b	--	19.17	<0.0001
K (mg/kg)	233.9 (13)c	298.1 (7)b	213.3(13)c	492.7 (4)a	40.89	<0.0001
Mg (mg/kg)	797.2 (29)a	2069.4 (67)b	1599.1 (113)a	1979.3 (84)ab	49.73	<0.0001
Mn (mg/kg)	171.4 (23)a	155.1 (23)a	91.3 (10)a	106.6 (10)a	3.33	0.2790
Na (mg/kg)	244.1 (11)b	1372.2 (95)a	1716.7 (213)a	--	32.72	<0.0001
Ni (mg/kg)	1.38 (0.08)a	1.09 (0.05)a	1.37 (0.18)a	--	1.77	0.1980
P (mg/kg)	14.29 (1.01)c	23.60 (2.03)b	14.17 (1.46)c	45.38 (3.51)a	28.32	<0.0001
Pb (mg/kg)	1.31 (0.15)a	1.46 (0.19)a	1.60 (0.10)a	--	0.72	0.4950
Zn (mg/kg)	18.4 (1.2)a	14.7 (0.5)a	9.9 (0.9)b	14.6 (0.4)ab	14.95	<0.0001
pH ($CaCl_2$)	4.88 (0.04)c	5.29 (0.03)b	5.62 (0.05)a	5.58 (0.05)a	59.24	<0.0001
Base Saturation (%)	75.56 (1.54)c	88.85 (0.99)b	93.02 (0.56)a	--	67.79	<0.0001
SS (mmhos/cm)	0.51 (0.03)c	1.59 (0.21)bc	2.79 (0.42)b	6.23 (0.12)a	30.86	<0.0001

Table 3. Litter quality at time=0 for each forested site. Standard errors are in parentheses. Different letters across rows represent significance at p<0.05.

Variable	Site				
	Upper	Middle	Lower	F value	P value
Lignin (%)	23.4 (1.9) a	23 (1.3) a	21 (2.2)b	3.2	0.0820
Cellulose (%)	15.8 (0.6)ab	17.1 (1.2)a	15 (0.6)b	5.0	0.0280
Lignin/Cellulose	0.57 (0.02)b	0.59 (0.01)ab	0.61 (0.01)a	3.3	0.0750
Lignin/N	22.7 (1.2)b	26 (1.6)ab	28.9 (1.2)a	10.3	0.0030
C/P	339.3 (8)b	368.7 (19)b	624.7 (65)a	34.5	0.0001
C/N	53.4 (1)b	55.4 (1)ab	53.4 (3)a	5.6	0.0210
N/P	6.4 (0.01)b	6.7 (0.40)b	10.0 (0.60)a	19.4	0.0002

Table 4. Repeated-measures ANOVA for microbial biomass C and N for site and season Significance at p<0.05.

Microbial Type	Source	DF	F value	P value
C	Site	2	14.2	<0.0001
	Season	8	5.6	<0.0001
	SitexSeason	16	1.4	0.1456
N	Site	2	68.8	<0.0001
	Season	8	11.2	<0.0001
	SitexSeason	16	2.0	0.0157

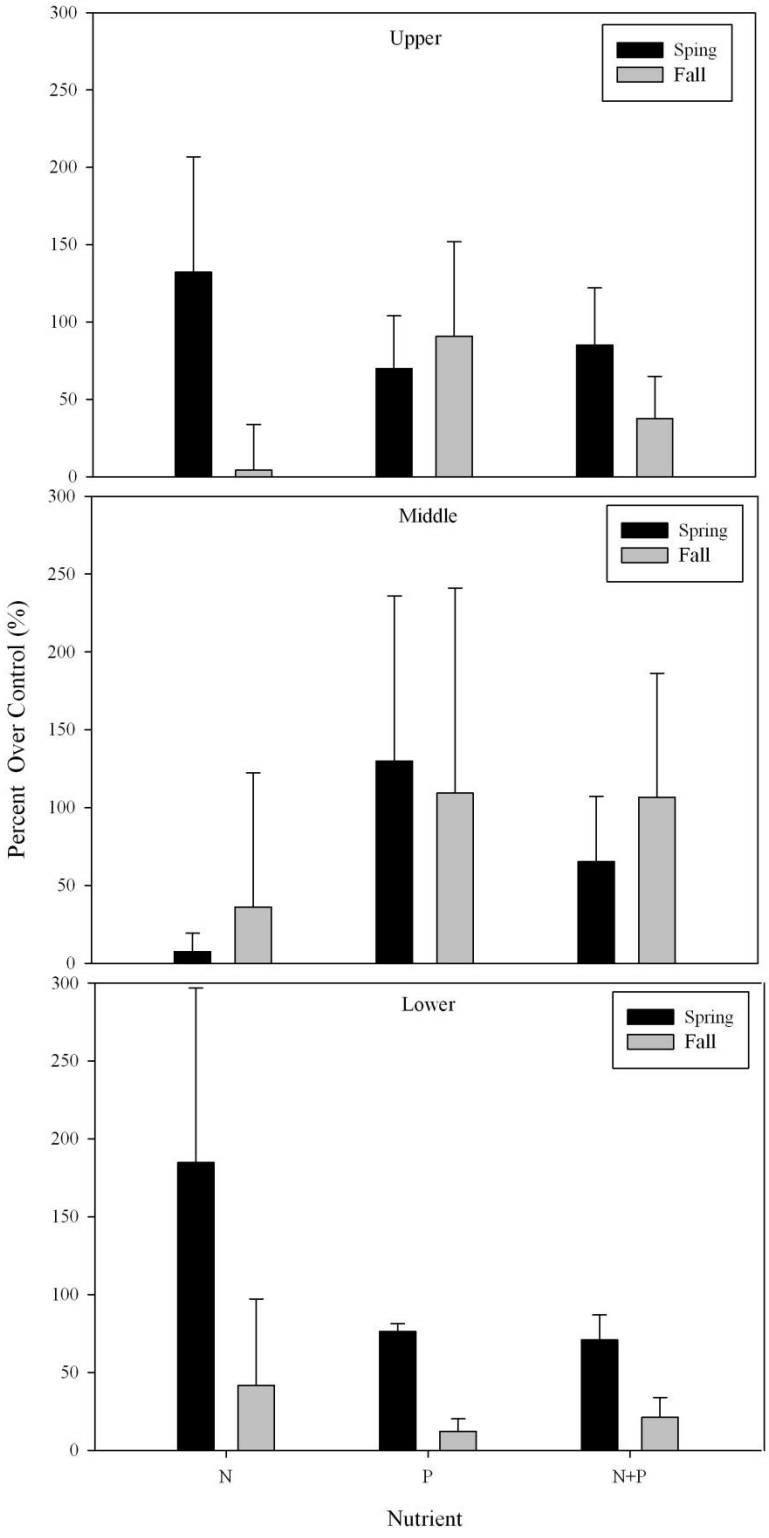

Figure 1. Percent over control for root ingrowth cores subjected to N, P, and N+P fertilization treatments. Vertical bars indicate standard errors.

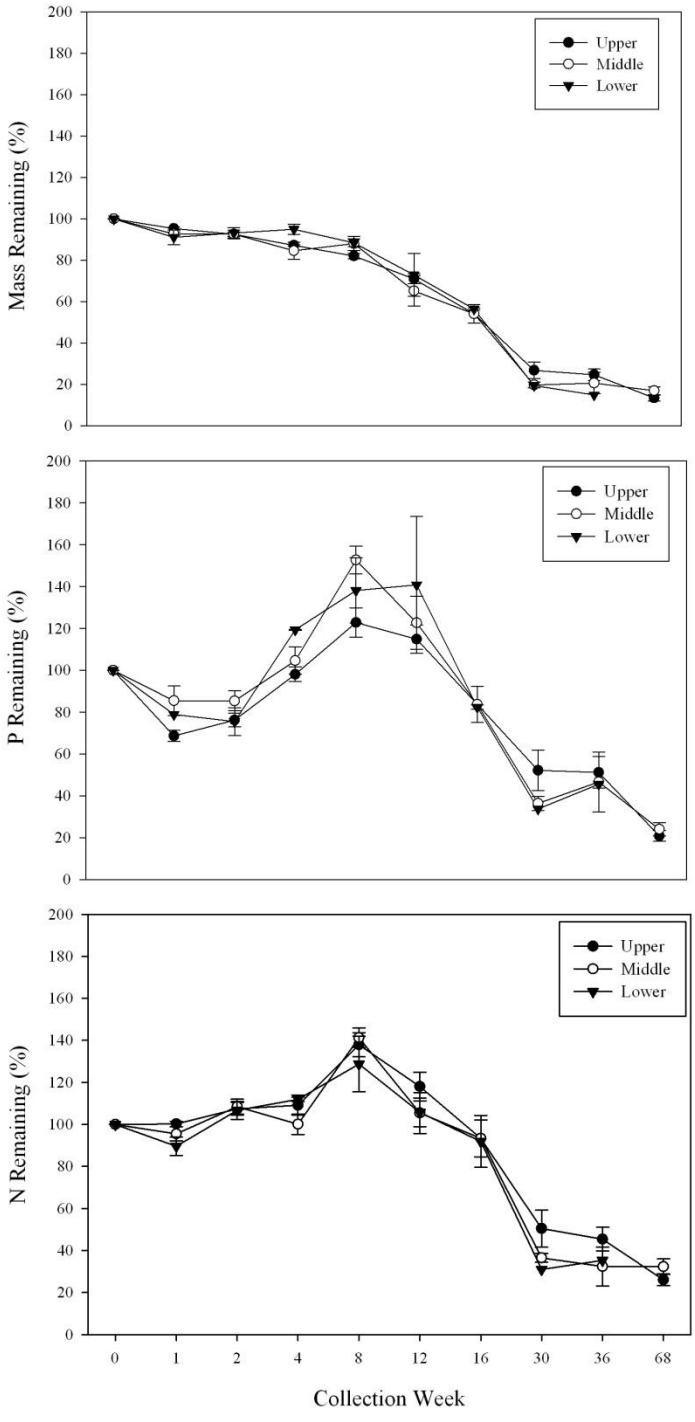

Figure 2. Percent mass, P, and N remaining in litter bags over 68 weeks for each forested site. Vertical bars indicate standard errors.

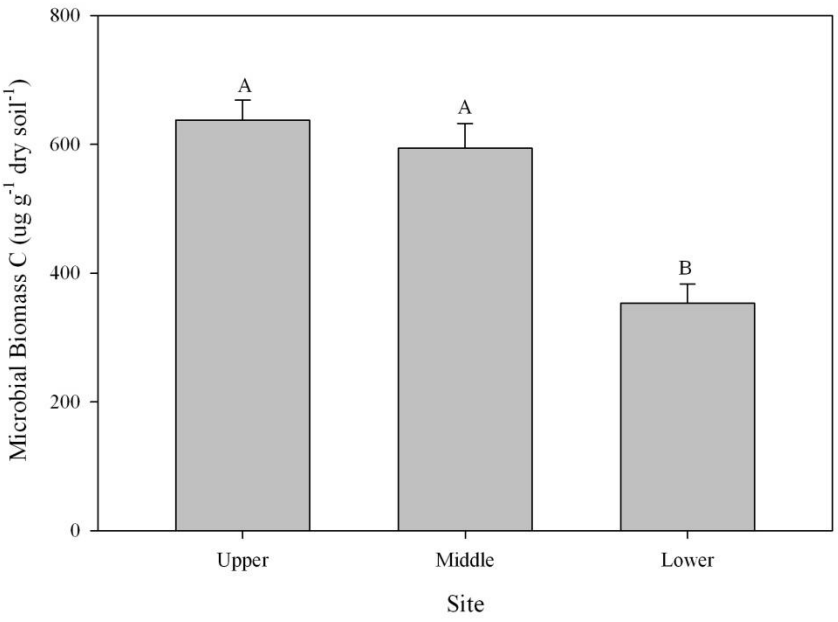

Figure 3. Mean microbial biomass C for the forested sites. Letters represent significant differences at $p<0.05$. Vertical bars indicate standard error.

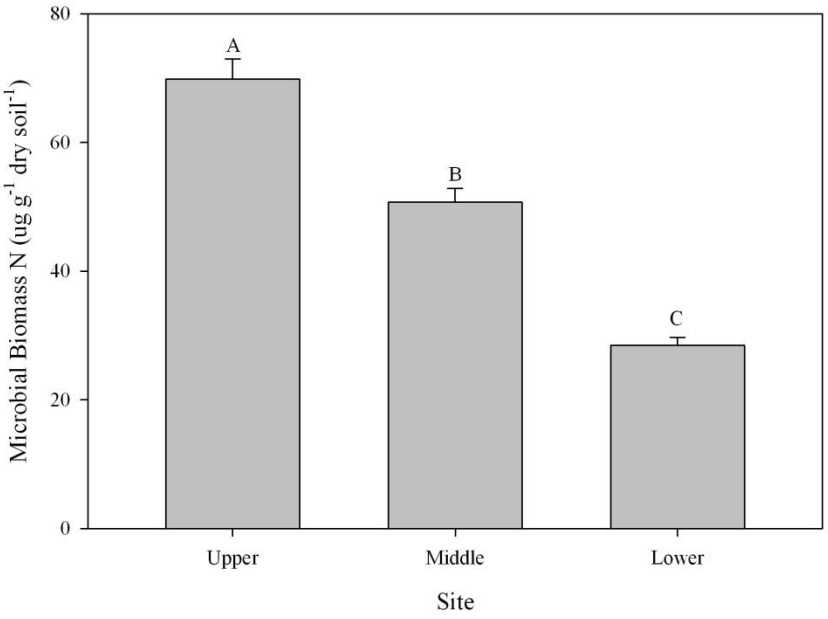

Figure 4. Mean microbial biomass N for the forested sites. Letters represent significant differences at $p<0.05$. Vertical bars indicate standard errors.

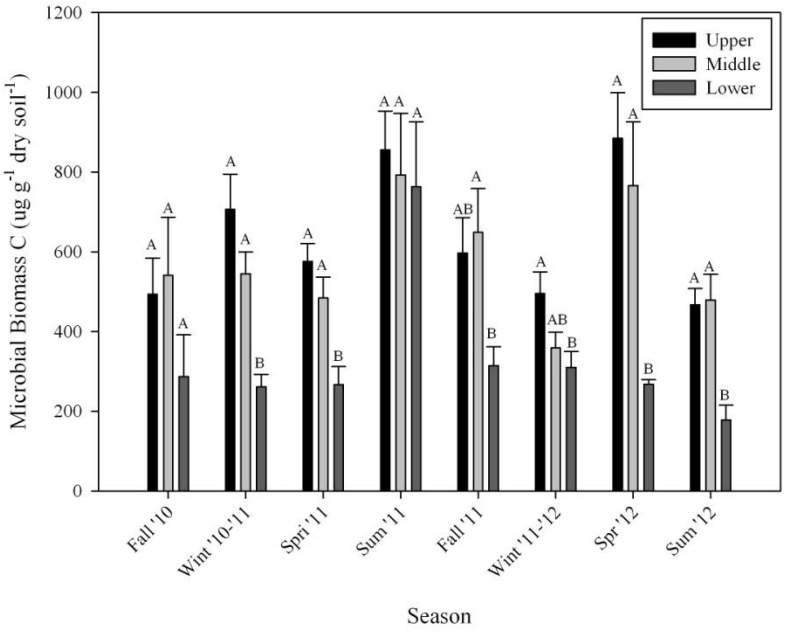

Figure 5. Microbial biomass C for each forested site compared among seasons. Different letters represent significant differences among sites within season at $p<0.05$. Vertical bars indicate standard errors.

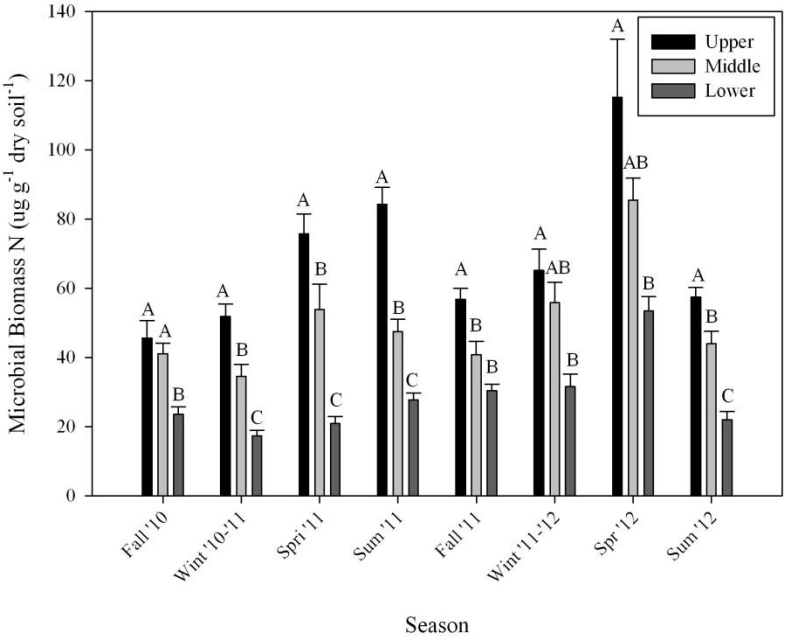

Figure 6. Microbial biomass N for each forested site compared among seasons. Different letters represent significant differences among sites within season at $p<0.05$. Vertical bars indicate standard errors.

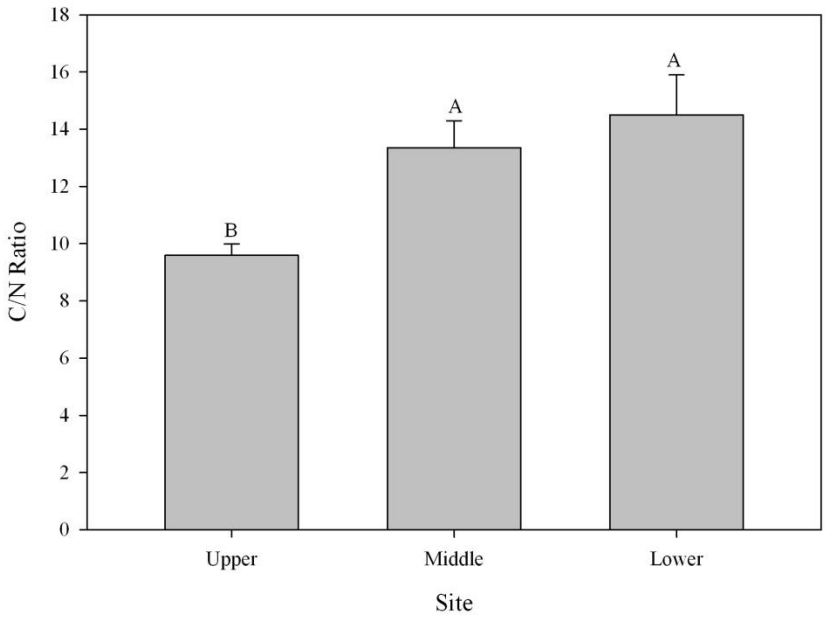

Figure 7. Mean microbial C/N ratios for each forested site over the study period. Different letters represent significant differences at $p<0.05$. Vertical bars indicate standard error.

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Chapter IV

Conclusions

Study Objectives

This study was aimed at understanding the effects of sea level rise on NPP and biogeochemical processes in tidal freshwater wetlands. To achieve this goal, we quantified NPP, fine root growth and nutrient dynamics, nutrient limitations, litter decomposition, and microbial biomass in tidal freshwater forested wetlands and an oligohaline marsh along a salinification gradient. Our objectives were to: i) quantify differences in biogeochemical transformations along a salinification gradient in tidal freshwater wetlands, ii) identify linkages between these biogeochemical indices: NPP, nutrient limitations, microbial biomass, and litter decomposition, and iii) determine implications of sea level rise on C storage and allocation in tidal freshwater wetland ecosystems.

Carbon Storage and Productivity

Effects of salinity on belowground C storage and productivity in tidal freshwater wetlands are dependent on ecosystem type (forested vs. marsh) and degree of salinification. Among forested sites, total NPP is drastically reduced at porewater salinity of 2.8 ppt. Reduction in NPP is demonstrated by the severely stressed lower site having significantly less total NPP, ANPP, and BNPP than the upper forested site. Also, higher salinity was associated with larger portions of production to be allocated belowground among the forested sites. The lack of aboveground production on the lower forested site can most likely be attributed to the high

mortality of trees there. BNPP increased at the marsh, resulting in significantly greater C pools compared to the forested sites. These data suggest that tidal freshwater forested wetlands are at risk of reduced belowground C storage at increasing salinities although C pools may rebound as the community transitions to marsh. After this point, there is evidence for recovery and possible enhancement of C storage in roots.

Fine Root Dynamics

Standing crop biomass of live fine roots closely followed BNPP trends, thus the lower forested site had significantly less BNPP than the upper site. Comparisons of forested sites with the marsh indicated that the greatest amount of live fine root biomass occurred at the marsh. For all sites, live very-fine root biomass was significantly greater than that of live intermediate-fine or coarse-fine roots. These trends were not evident for dead roots. Instead, the only significant difference among sites was the middle forested site being greater in terms of very-fine dead root biomass than the lower forested site. Salinity did not appear to have a regulatory effect on dead roots, but appeared to drive live standing crop biomasses. Similar to BNPP, a shift from forest to a marsh community may mitigate some effects of salinity.

N and P content of live roots mimicked biomass trends, and was significantly less for both nutrients at the lower compared to the upper forested site. As a result, the lower forested site had significantly less N and P available to cycle from the roots to the soil. Among the forested sites, N and P concentrations in live roots were significantly lower at the middle and lower sites, respectively. Lower P concentrations at the lower site combined with the diminished root biomass may further reflect the negative effects of salinity on belowground P cycling.

Nutrient Cycling

Lack of differences in decomposition rates among the sites suggest that nutrient transfer from leaf litter in tidal swamps does not appear to be heavily influenced by salinity. However, total litter N and P at time=0 was significantly less at the lower forested site compared to both the upper and middle sites. Reduction in litter quality results in lower nutrient transfer through decomposition. Microbial biomass N declines significantly with salinity among forested sites, before rebounding slightly at the marsh. Microbial C biomass also shows differences among sites with the upper and middle sites being significantly greater than the lower site and marsh. This demonstrates that microbial populations decline at higher salinities.

Leaf litter resorption proficiencies suggest limitation of both N and P at the lower forested site, while all sites have green, foliar N/P ratios suggestive of N limitation (<6) (Lockaby and Conner, 1999). Among the forested sites, soil extractable P was highest at the middle site, with no difference between the upper and lower sites. These data could suggest less acquisition of P and N at the lower site, possibly due to decreased root biomass or disruption of uptake. Likely, the increase in soil extractable P at the middle site is due to the alluvial (redwater) Pee Dee River that joins the Waccamaw in close proximity to this island. Alluvial rivers are known to carry higher amounts of nutrients than blackwater rivers such as the Waccamaw River (Doyle et al., 2007). It is possible the Pee Dee is dropping P loaded sediment onto the middle site as it joins the Waccamaw River and driving P soil values.

Synthesis

Among the forested sites, our data demonstrate that salinity reduces total NPP, belowground C storage, microbial C and N biomass, and influences cycling of N and P. These sites appear to be characterized by N limitation, with salinity further enhancing a N and P

limitation. Site position along the gradient does not appear to be the major controlling force on decomposition; therefore, rates of nutrient transfer from the forest floor may not be influencing productivity trends. However, belowground N and P pools are reduced at the lower site due to decreased litter quality and reduced N and P root content. Compared to the lower forested site, the marsh exhibited higher belowground C storage, BNPP, N and P pools, and microbial N biomass. It is apparent among the forested sites that salinity negatively impacts productivity, C storage, and nutrient cycling. However, the marsh may play a role in mitigating some of those changes as it encroaches on tidal swamps.

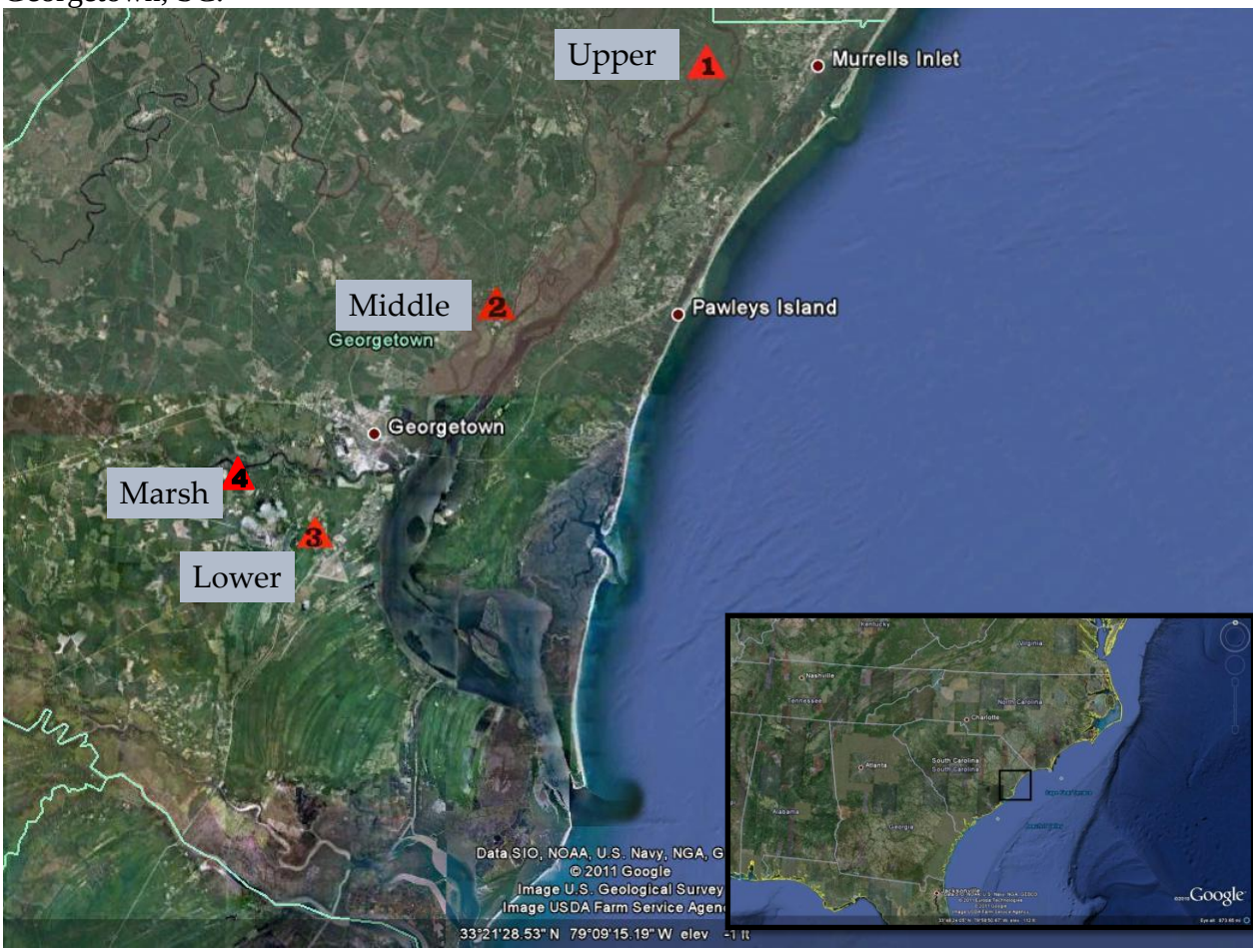
Despite the societal importance of tidal wetlands, there continues to be a disparity in our knowledge of these systems compared to other wetland types. Our data demonstrate impacts of increased salinity intrusion on productivity and biogeochemical processes in tidal swamps; however, more research is still needed. Sea levels are predicted to continue rising, and the extent and rate of these changes are unclear. Furthermore, tidal swamps occur all across the Southeast and the vast diversity of these systems warrants studies in other geographical areas. Additionally, due to the complexity and variability associated with biogeochemical processes, long-term studies are needed to capture the entirety of change that tidal swamps are expected to undergo.

References

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: W.H. Conner, T.W. Doyle, and K.W. Krauss (eds) Ecology of tidal freshwater forested wetlands of the southeastern United States. Springer. The Netherlands. pp. 1-28.

Lockaby, B.G., and W.H. Conner. 1999. N:P balance in wetland forests: Productivity across a biogeochemical continuum. Bot. Rev. 65:171-185.

Appendix I. Map displaying all study sites along the Waccamaw and Sampit rivers near Georgetown, SC.



Appendix II. C concentrations (± SE) in green foliage, fine roots, and soil for each site. Significant differences among sites are indicated by different letters at $p<0.05$.

C(mg/kg)	Site					
	Upper	Middle	Lower	Marsh	F	P
Leaves	472537(5237)a	477356(1010)a	486880(6653)a	--	1.9	0.2036
Roots	453849(1870)a	424123(2402)b	432171(2986)b	382681(4190)c	98.3	<0.0001
Soil	225509(5796)a	178210(4357)b	176108 (7419)b	160460(1197)b	19.7	<.0001

Appendix III. Allometric equations for calculating woody production. Equations were developed from trees sampled in bottomland hardwood and swamp forests. The form of each equation is $M=f(D)$ where M is in mass in pounds or kilograms, D is diameter at breast height (dbh) in inches or centimeters, and f is a parameterized function of D.†

Species‡	Mass	Function	dbh range (cm)
Acer rubrum[1]	M	$2.39959\ (D^2)^{1.20036}$	10-28
Fraxinus spp.[1]	M	$2.66900\ (D^2)^{1.16332}$	>10
Myrica cerifera[1]	M	$2.54671(D^2)^{1.20138}$	>10
Nyssa aquatica[2]	$\log_{10}M$	$-0.919 + 2.291 \log_{10}D$	>10
Nyssa sylvatica[1]	M	$2.43427(D^2)^{1.16974}$	10-28
		$1.30697(D^2)^{1.29943}$	>28
Taxodium distchium[3]	$\log_{10}M$	$-0.97 - 2.34 \log_{10}D$	>10

†Source: Megonigal et al. 1997.

‡Sources of equations and units: 1 = Clark et al. 1985, pounds and inches; 2 = Muzika et al. 1987, kg and cm; Scott et al. 1985, kg and cm.