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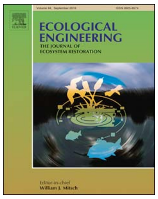

Tidal freshwater forests: Sentinels for climate change

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ABSTRACT

We measured plant community composition and productivity, soil accretion, and C, N, and P burial in a tidal freshwater forest of the Altamaha River, Georgia to gain a better understanding of the ecosystem services they deliver and their ability to keep pace with current and future rates of sea level rise. Ten species were identified in two 0.1 ha plots. *Nyssa aquatica* (Tupelo Gum) made up 50% of the density and 57% of the total basal area. *Nyssa biflora, Liquidambar styraciflua*, and *Fraxinus pennsylvanica* were the next dominant species, collectively accounting for 37% of the density and 26% of the total basal area. *Taxodium distichum* only accounted for 3% of the density, but 12% of the total basal area. Aboveground productivity, measured as litterfall and stem wood growth, averaged 927 and 1030 g/m^2 in 2015 and 2016, respectively, with litterfall accounting for 60% of the total. Tidal forest soils in the streamside and the interior (0–60 cm) contained 3–6% organic C, 0.20–0.40% N, and 270–540 µg/g P. Soil accretion based on ^{137}Cs was 4.0 mm/year on the streamside and 0.2 mm/year in the forest interior. The rate of accretion in the interior is considerably less than the current rate of sea level rise (3.1 mm/year) along the Georgia coast. Because the accretion rate was much higher on the streamside, rates of C sequestration, N and P accumulation, and mineral sediment deposition also were much greater. Low accretion rates in the interior of the forest that accounts for most of the acreage suggests that accelerated sea level rise is likely to lead to foreseeable death of tidal forests from saltwater intrusion and submergence.

1. Introduction

Tidal freshwater forests, situated in estuaries where the river meets the sea, cover approximately 200,000 ha of the southeastern United States (Field et al., 1999). Their proximity to the coast, valuable timber resources, and cultivation qualities make these unique systems ripe for human exploitation (Conner et al., 2007). In order to make the land more suitable for development and agriculture, the original hydrology and vegetation of tidal forests have been extensively altered through drainage and timber harvesting, leaving us with only remnant second and third growth forests. (Doyle et al., 2007).

In spite of this degradation and loss, tidal forests provide important ecosystem services, including carbon sequestration, nutrient storage, water quality improvement, and biodiversity (DeLaune et al., 1987; Duberstein 2004; Duberstein, 2011; Brittain and Craft, 2012; Craft, 2012, Noe et al., 2016). Little is known about how these systems will respond to the effects of climate change, manifested as sea level rise and saltwater intrusion. As climate change-driven sea level rise accelerates, the decline of tidal forests and expansion of oligohaline and brackish marshes will likely occur (Craft, 2012; Liu et al., 2017). This change may lead to an increase in the ability to deliver some ecosystem services such as carbon sequestration and sediment trapping, but hinder others such as denitrification and biodiversity. The ability of tidal forests to deliver ecosystem services faces an uncertain future as sea level continues to rise (DeLaune et al., 1987, Craft, 2012).

We studied a tidal forest on the Altamaha River in Georgia, USA to help predict how tidal forest ecosystem service provisioning will fare as sea level rises. We measured plant species composition, aboveground productivity, soil bulk density, and soil nutrient composition to estimate productivity and soil nutrient accumulation. We also measured ^{137}Cs to estimate vertical accretion rates and compare to the current rate of sea level rise.

2. Methods and materials

2.1. Site description

The Altamaha River watershed is about 36,260 square kilometers, making it the third largest contributor of freshwater from the U.S. into the Atlantic Ocean (Frangiamore and Gibbons, 2017). The study site is located on Lewis Island in MacIntosh County (31.3852° N, 81.5209° W). The site experiences twice daily tidal pulsing that reaches bankfull depth, but seldom is inundated except during upstream river flooding that usually occurs in spring. Vegetation of the site is dominated by

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deciduous broad- and needle-leaf trees, including bald cypress (*Taxodium distichum* (L.) Rich), tupelo gum (*Nyssa aquatica* L.), and black gum (*Nyssa sylvatica* var. *biflora* Walt.). Soils are classified as Swamp series fluvaquent (fluvial aquic Entisols; Natural Resource Conservation Service (NRCS), 2010).

2.2. Vegetation

We established two 0.1-ha plots in December 2013. In each plot, we identified and measured DBH (diameter at breast height) of every tree using standard diameter tapes. We also placed dendrometric bands on 40 trees (20 per plot) in December 2013. Bands were measured in December 2014 as baseline measurements and in December every year thereafter (2015, 2016). We used allometric equations from Megonigal et al. (1997) to estimate woody biomass, and thus annual stem wood growth, from the dendrometric band measurements.

Eight litterfall traps (0.25 m^2, 4 per plot) were established in fall 2014. Litterfall was collected monthly from October 2014 until October 2016. Litterfall was placed in a drying oven for 48 h after returning to the laboratory. Once dried, litterfall was weighed to the nearest 0.01 g. From October 2015 through December 2015 we sorted litterfall by the three dominant species (*T. distichum, N. biflora, and N. aquatica*). The remaining litter material was placed in the "other" category. Sorted leaf litter was then weighed and organic C, N, and total P were measured. Organic carbon and total nitrogen were determined using a Perkin Elmer 2400 CHN analyzer (Perkin-Elmer, Norwalk, CT, USA). Total P was measured as phosphate in HNO_3-$HClO_4$ digestions (Sommers and Nelson, 1972). Apple leaves were used as a standard with a 100% recovery rate for C, 98% for N, and 94.5% recovery rate for P.

2.3. Soils

We collected two 8.5 cm diameter by 60 cm deep soil cores, one from the natural streamside at the forest/river edge and one from the interior of the forest. Cores were sectioned in the field into 2-cm increments and transported to the lab where they were air-dried, weighed for bulk density, ground, and sieved.

Soil from each depth increment was packed into 50 mm diameter by 9 mm deep petri dishes and analyzed for ^{137}Cs and ^{210}Pb. ^{137}Cs was measured using gamma analysis of the 661.62 keV photopeak (Craft et al., 2003) to estimate accretion since 1964, the year of maximum deposition of atmospheric ^{137}Cs from aboveground nuclear testing. Total ^{210}Pb was measured using a gamma analysis of 46.5 keV photopeak (Craft et al., 2003). Excess ^{210}Pb was calculated using the difference between total and background ^{210}Pb, determined from constant ^{210}Pb from the deeper increments of the core. Accretion rates from ^{210}Pb were calculated using the constant activity model (Oldfield and Appleby, 1984) to estimate long-term (approximately 100 year) vertical accretion.

Each depth increment also was analyzed for bulk density, organic carbon, total nitrogen, and total phosphorus. Bulk density was calculated from the dry weight per unit volume for each depth increment (Blake and Hartge, 1986). Organic carbon and total nitrogen were determined using a Perkin Elmer 2400 CHN analyzer (Perkin-Elmer, Norwalk, CT, USA). Total P was measured as phosphate in HNO_3-$HClO_4$ digestions (Sommers and Nelson, 1972). Samples from Dean's Creek were used as an internal standard with a 96% recovery rate for C and N and 90.5% recovery rate for P. Rates of C, N and P accumulation were calculated using accretion rates, bulk density, and C, N, and P concentration data. Percent mineral matter was calculated as 100 - percent organic matter which was assumed to be 2 times organic C content (Craft et al., 1991).

Rates of carbon sequestration and nitrogen and phosphorus accumulation were calculated using ^{137}Cs- and ^{210}Pb-derived vertical accretion rates, bulk density, and concentrations down to and including the increment of maximum ^{137}Cs activity or extent of excess ^{210}Pb. Accumulation of mineral matter was calculated based on accretion, bulk density and mineral content.

Table 1
Species composition (density and basal area) of a tidal freshwater forest on the Altamaha River, Georgia.

Species	n	Density (#/ha)	Site richness (%)	Basal area (m^2/ha)	Basal area (%)
Nyssa aquatica	120	600	49.79	38.7	56.89
Nyssa biflora	30	150	12.77	7.9	11.66
Liquidambar styraciflua	33	165	13.69	4.9	7.19
Fraxinus pennsylvanica	26	130	10.79	5.0	7.38
Acer rubrum	11	55	4.56	1.4	2.01
Taxodium distichum	7	35	2.90	8.3	12.27
Magnolia virginiana	3	15	1.24	0.7	1.07
Quercus spp.	2	10	0.83	0.4	0.57
Quercus lyrata	2	10	0.83	0.6	0.90
Carpinus caroliniana	1	5	0.41	0.1	0.07
Total	241	1205		68.0	

3. Results

3.1. Species composition

Ten species were identified in the two plots (Table 1). The most abundant species was *Nyssa aquatica* which made up 50% of the density and 57% of the total basal area. *Nyssa biflora*, *Liquidambar styraciflua*, and *Fraxinus pennsylvanica* collectively accounted for 37% of the density and 26% of the total basal area. *Taxodium distichum* accounted for only 3% of the total density but 12% of the basal area. The other six species contributed the remainder, 10% of the density and 5% of the basal area.

3.2. Productivity

Litterfall during the two seasons ranged from 554 g/m^2 to 664 g/m^2. Stem wood growth was similar among the two years, 374 g/m^2 and 376 g/m^2. Total aboveground biomass (litterfall plus stem wood growth) for the 2014–2015 growing season was 927 g/m^2/yr and 1030 g/m^2/yr for 2015–2016 (Fig. 1). Litterfall accounted for 62% of the total aboveground biomass for the two growing seasons. *Nyssa aquatica*, *Nyssa biflora*, and *Taxodium distichum* collectively accounted for 45% of the total litterfall in 2014–2015. The remaining 55% of the leaf litter was composed of unidentifiable leaf material, twigs and fruits. Comparison of woody increment between *Nyssa aquatica* and *Taxodium*

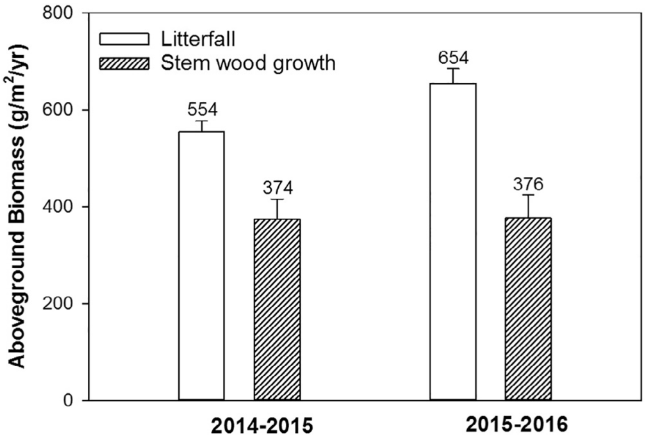

Fig. 1. Aboveground productivity (litterfall and stem wood growth) measured in 2015 and 2016.

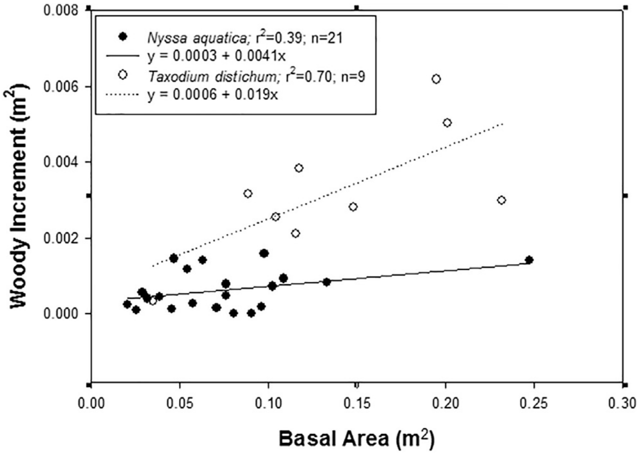

Fig. 2. Woody increment (increase in basal area) of *Nyssa aquatica* and *Taxodium distichum* during 2015.

Table 2

Litterfall C, N, and P concentrations, C:N:P ratios, and C, N, P returned annually to the forest floor by the three dominant species in 2015.

	Taxodium distichum	*Nyssa aquatic*	*Nyssa biflora*
Organic C (%)	53.7 (± 0.14)	52.1 (± 0.10)	51.9 (± 0.12)
N (%)	1.4 (± 0.03)	1.1 (± 0.04)	0.9 (± 0.02)
P (µg/g)	1150 (± 53.1)	780 (± 22.37)	700 (± 22.51)
C:N ratio	44	56	66
N:P ratio	28	33	30
C:P ratio	1239	1824	1973
Returned to Soil			
C (g/m²/yr)	53	47.2	31.6
N (g/m²/yr)	1.1	0.8	0.8
P (mg/m²/yr)	79.7	63.7	67.5

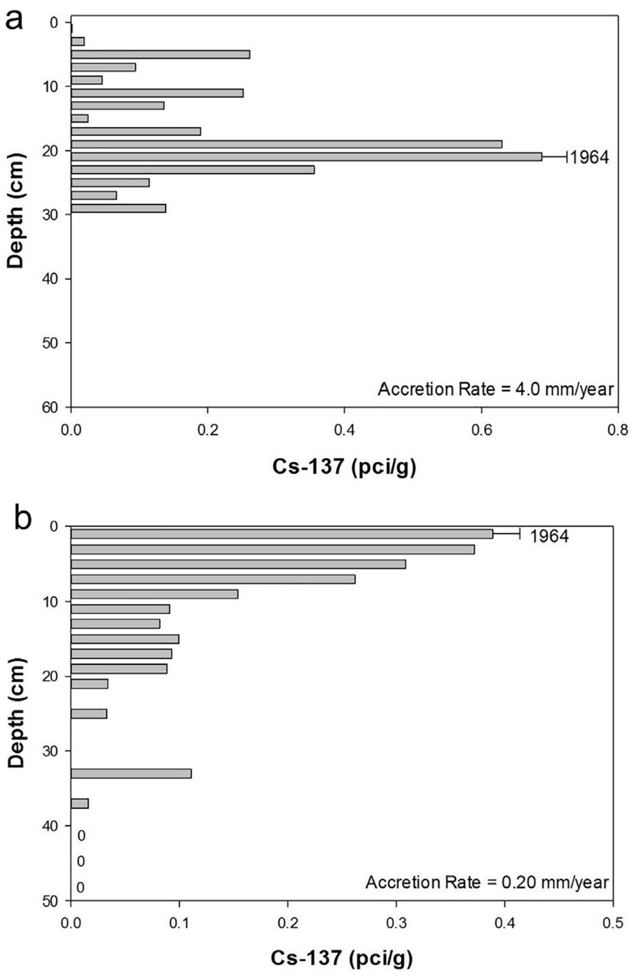

Fig. 3. Distribution of ^{137}Cs with depth in (a) streamside and (b) interior soil cores.

distichum (Fig. 2) revealed that *T. distichum* grew approximately twice as quickly as *N. aquatica*. These results may explain the relatively large contribution of *T. distichum* to the basal area of the forest in spite of its low density (Table 1).

Comparison of litterfall C, N, and P of the three dominant species revealed that *T. distichum* contained higher N (1.4%) and especially P (1140 µg/g) than *Nyssa* spp. (Table 2). As a result, C:N (44), N:P (28), and C:P (1239) were lower in *T. distichum* than the *Nyssa* spp. *Taxodium distichum* contributed 11% of the litterfall compared to 18% for *N. aquatica* and 16% for *N. biflora*. However, it returned more N (1.1 g/m²/yr) and P (g/m²/yr) to the soil than the *Nyssa* species (Table 2).

3.3. Soil properties

The tidal forest soil was minerogenic with moderate bulk density and relatively low percent organic C (Table 3). Soil organic C and N (0–60 cm) averaged 4.2% and 0.29% in the streamside and 5.8% and 0.40% in the interior. Soil P was 360 µg/g in streamside soil and 510 µg/g at the interior site. Interior soils exhibited relatively uniform bulk density and organic C between surface (0–30 cm) and subsurface (30–60 cm) soils. In contrast, bulk density decreased and organic C, N and P increased with depth in streamside soil. This was attributed to a large flooding event in winter 2015 that deposited a 4-cm-thick layer of sand on the streamside surface that was not deposited at the interior site (C. Craft personal observation). At both locations, soil P was greater in subsurface than surface soils (Table 3).

3.4. Soil accretion and accumulation

Soil cores collected from the streamside and interior sites had well defined ^{137}Cs peaks enabling the calculation of accretion rates for the past 50 years. Accretion was 4.0 mm/year in the streamside (Fig. 3a) and 0.2 mm/year in the interior (Fig. 3b). In the interior core, the distribution of total ^{210}Pb decreased exponentially with depth, reflecting the decay of atmospherically derived (excess) ^{210}Pb over time (Fig. 4a) and enabling us to calculate accretion for the past 100 years. Regression analysis of excess ^{210}Pb with depth (Fig. 4b) yielded an

Table 3

Soil bulk density, organic carbon, total nitrogen, and total phosphorus in surface (0–30 cm) and subsurface (30–60 cm) soils of streamside and interior locations.

		Bulk Density (g/cm³)	Organic Carbon (%)	Nitrogen (%)	Phosphorus (µg/g)
Streamside	0–30 cm	0.79 ± 0.10	3.3 ± 0.68	0.23 ± 0.04	270 ± 25.13
	30–60 cm	0.55 ± 0.05	5.0 ± 0.57	0.35 ± 0.03	444 ± 33.74
Interior	0–30 cm	0.36 ± 0.03	6.0 ± 0.54	0.41 ± 0.02	483 ± 20.93
	30–60 cm	0.43 ± 0.02	5.5 ± 0.14	0.38 ± 0.01	536 ± 60.18

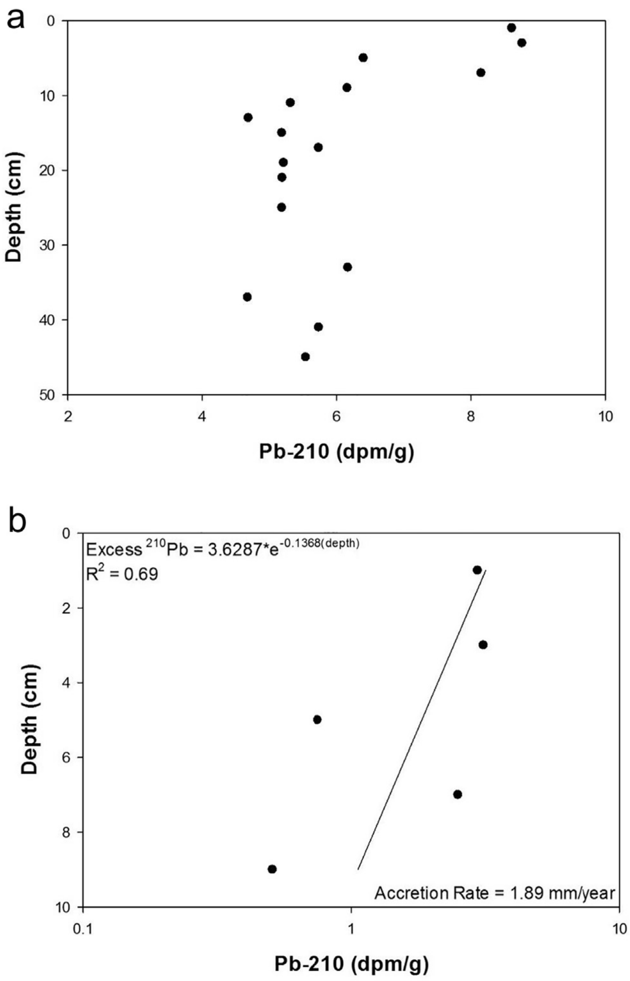

Fig. 4. Distribution of (a) total and (b) excess ^{210}Pb with depth in the core collected from the interior location.

Table 4
Vertical accretion and accumulation of organic carbon, total nitrogen, total phosphorus, and mineral sediment.

	Organic C ($g/m^2/yr$)	Total N ($g/m^2/yr$)	Total P ($g/m^2/yr$)	Sediment ($kg/m^2/yr$)	Accretion Rate (mm/yr)
Streamside (^{137}Cs)	117	8.0	0.87	2.39	4
Interior (^{137}Cs)	4	0.3	0.06	0.07	0.2
Interior (^{210}Pb)	42	2.9	0.56	0.65	1.89

Table 5
Basal area and density in other tidal freshwater forests.

Location	Basal Area (m^2/ha)	Density (stems/ha)	Reference
Altamaha & Savannah Rivers	70	7335	Duberstein et al. (2014)
Hobcaw Barony, SC	86.1	530	Krauss and Duberstein (2010)
Waccamaw River, SC	59.46	1190	Krauss et al. (2009)
Savannah River, GA	65.19	1220	Krauss et al. (2009)
Savannah River, GA	69	6425	Duberstein (2004)
Cohoke Swamp, VA	–	2433	Fowler and Hershner (1989)
Altamaha River, GA	68	1205	This study

accretion rate of 1.9 mm/yr which is substantially more than the ^{137}Cs-derived accretion rate for the interior location but much less than the streamside location.

Greater accretion on the streamside led to greater burial of organic carbon, nitrogen, and phosphorus. Using ^{137}Cs-based accretion rates, organic C and total N burial were 30 times greater and P burial was 15 times greater on the streamside than interior. Mineral sediment deposition was 30 times greater on the streamside (Table 4).

4. Discussion

4.1. Vegetation

Species composition of our site is comparable to other sites with similar dominant species, *Nyssa aquatica*, *Nyssa biflora,* and *Fraxinus pennsylvanica* (Duberstein 2004; Krauss et al., 2009; Krauss and Duberstein, 2010; Duberstein et al., 2014). Density is similar to some other studies (Fowler and Hershner, 1989, Krauss et al., 2009), but much less than what Duberstein (2004) and Duberstein et al., (2014) observed along the Savannah River (Table 5). Basal area is also comparable to other studies, falling within the range of 60–86 m^2/ha (Fowler and Hershner, 1989; Duberstein 2004; Krauss et al., 2009, Krauss and Duberstein, 2010, Duberstein et al., 2014; Table 5). Although *Taxodium distichum* only made up 3% of the overall density at our site, it made up 12% of the basal area (Table 1). *Taxodium distichum* was also observed to grow at a faster rate than *Nyssa aquatica* (Fig. 2).

4.2. Productivity

Averaged over both sampling years, litterfall accounted for 62% of total aboveground productivity while stem wood growth contributed the remaining 38% (Fig. 1). Ozalp et al. (2007) reported a similar contribution of litterfall (62%) and stem wood growth (38%) at a tidal forest in South Carolina, but their absolute measures of litterfall and stem wood growth were about 30% lower than ours (Table 6). This difference could be attributed to the longer growing season on the Altamaha River, GA than on Bull Island, SC which is about 150 miles north along the Atlantic coast. Our measure of aboveground productivity from litterfall was also about 50% higher than that found in a non-tidal cypress gum forest in Louisiana (Conner and Day, 1992). This difference could be because fruits and twigs were not removed from our litterfall traps before making measurements.

4.3. Soil properties

Rates of carbon, nitrogen, and phosphorus accumulation in the streamside were similar to those observed by Noe et al. (2016) who used feldspar markers to measure accretion rate (Table 7). In our study, C, N, and P accumulation rates were much lower in the interior than the streamside zone due to much lower soil accretion rate (0.2 mm/yr) in the interior compared to the streamside (4.0 mm/yr). The observed accretion rates in the interior are similar to those of other studies (Baldwin, 2007, Kroes and Hupp, 2010, Craft, 2012, Ensign et al., 2013a,b, Noe et al., 2016) based on feldspar markers and ^{137}Cs, but the accretion rate observed at the streamside is four times higher than those studies (Table 8). At our site, the accretion rate in the interior is not keeping up with the current rate of sea level rise (3.2 mm/yr, NOAA), so these systems may eventually convert to brackish marsh or open water in the future unless accretion increases to compensate.

5. Conclusion

Observed plant community composition and productivity in a tidal forest on the Altamaha River, GA are similar to those observed in other tidal freshwater forests on the southeastern coast. Low accretion rates in the interior indicate that tidal freshwater forests are not keeping pace

Table 6
Aboveground productivity in other tidal freshwater forests.

Litterfall (g/m^2/year)	Stem wood growth (g/m^2/year)	Location	Reference
463	279	Bull Island, SC	Ozalp et al. (2007)
405	–	Mississippi River, LA	Conner and Day (1992)
562	–	Savannah River, GA	Cormier et al. (2013)
470	427	Waccamaw River, SC	Liu et al. (2017)
678	382	Waccamaw River, SC	Pierfelice et al. (2015)
686	–	Waccamaw River, SC	Cormier et al. (2013)
554	374	Altamaha River, GA	This study, 2014–2015
654	376	Altamaha River, GA	This study, 2015–2016

Table 7
Soil nutrient content in other tidal freshwater forests.

Location	Sampling Depth (cm)	Bulk Density (g/cm^3)	C (%)	N (%)	P (mg/g)	Reference
Savannah River		0.24 ± 0.03	12.8 ± 2.2	0.74 ± 0.09	0.7 ± 0.09	Noe et al. (2016)
		0.18	49.8	–	0.1	Duberstein (2004)
		–	30.75*	1.79	–	Duberstein (2011)
		0.387 ± 0.032	–	–	–	Krauss et al. (2009)
		–	0.63 ± 0.1	10.1 ± 1.5		Cormier et al. (2013)
Waccamaw River		0.27 ± 0.12	17.0 ± 1.4	0.92 ± 0.08	0.92 ± 0.08	Noe et al. (2016)
		0.198 ± 0.009	–	–	–	Krauss et al. (2009)
		–	19.5 ± 1.6	1.26 ± 0.09	–	Cormier et al. (2013)
Altamaha River		–	21.8*	1.25	–	Duberstein (2011)
		0.26 ± 0.09	15.5 ± 5.4	0.9 ± 0.23	590 ± 120	Craft (2012)
Apalachicola River		–	12.5*	0.63	–	Duberstein (2011)
Ogeechee River		0.41 ± 0.12	10.4 ± 3.5	0.64 ± 0.15	750 ± 40	Craft (2012)
Satilla River		0.84 ± 0.12	2.9 ± 0.7	0.18 ± 0.04	160 ± 50	Craft (2012)
Suwanee River		–	33.9*	2.0	–	Duberstein (2011)
Altamaha River (interior)	0–30	0.36 ± 0.03	6.0 ± 0.54	0.41 ± 0.02	483 ± 20.93	This study
	30–60	0.43 ± 0.02	5.5 ± 0.14	0.38 ± 0.01	536 ± 60.18	This study
Altamaha River (streamside)	0–30	0.79 ± 0.10	3.3 ± 0.68	0.23 ± 0.04	270 ± 25.13	This study
	30–60	0.55 ± 0.05	5.0 ± 0.57	0.35 ± 0.03	444 ± 33.74	This study

* Calculated from% OM assuming OM is 50% C.

Table 8
Soil accretion and nutrient accumulation in other tidal freshwater forests.

Location	Accretion Rate (mm/year)	C (g/m^2/yr)	N (g/m^2/yr)	P (g/m^2/yr)	Sediment (g/m^2/yr)	Reference	Method
Savannah River	0.6 ± 0.1	180 ± 45	10.3 ± 2.8	0.94 ± 0.29	1407 ± 381	Noe et al. (2016)	Feldspar
	0.6	–	–	–	–	Ensign et al. (2013a)	Feldspar
Waccamaw River	0.6 ± 0.1	170 ± 32	9.2 ± 1.6	0.88 ± 0.2	973 ± 115	Noe et al. (2016)	Feldspar
	0.74	–	–	–	–	Ensign et al. (2013a)	Feldspar
Pocomoke River	8.4 ± 6.9	–	–	–	–	Ensign et al. (2013b)	Feldspar
	3.6	–	–	–	–	Kroes and Hupp (2010)	Feldspar
Nanticoke River	10.1 ± 3.4	–	–	–	–	Baldwin (2007)	Feldspar
Choptank River	16.7 ± 0.99	–	–	–	–	Ensign et al. (2013b)	Feldspar
Altamaha River	0.7–1.9	–	–	–	–	Craft (2012)	^{137}Cs
Ogeechee River	1.9–2.5	–	–	–	–	Craft (2012)	^{210}Pb
Altamaha River	4	117	8	0.87	2.39	This study	^{137}Cs
Altamaha River	0.2	4	0.3	0.06	0.07	This study	^{137}Cs
Altamaha River	1.89	42	2.9	0.56	0.65	This study	^{210}Pb

with sea level rise and the ecosystem services they provide will be lost unless they have room to migrate inland and upriver.

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