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Changes within a South Carolina Coastal Wetland Forest in the Face of Rising Sea Level

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Abstract: Rising sea levels and increasing salinity are impacting coastal forests of the Southern U.S. Forest productivity and composition was studied from 2014 to 2020 in paired plots (20 × 25-m) along a porewater salinity gradient (0, 0.8, 2.6, 4.6 PSU). Aboveground net primary productivity was estimated by summing annual litterfall and woody growth. In addition, voucher specimens for each vascular plant species were collected. Productivity differed in forest communities across the salinity gradient averaging 1081, 777, 694, and 613 g m⁻² yr⁻¹ in fresh, low-salt, mid-salt, Freshwater forest communities and high-salt sites, respectively. The vascular flora consisted of 144 species within 121 genera and 57 families. Although salinity in Strawberry Swamp is currently declining, it hasn't reached levels low enough to reverse the loss of forested wetlands. With projections of continuing sea level rise and increasing salinity intrusions, tree regeneration and growth will continue to decline as the forest transitions into marsh.

Keywords: tidal freshwater forested wetlands; woody production; leaf production; forest productivity; vascular flora; Strawberry Swamp; South Carolina



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1. Introduction

Tidal freshwater forested wetlands (TFFWs) are unique forested wetland ecosystems whose structure is a result of flooding, salinity, and topographical gradients [1–4]. Aboveground net primary productivity (ANPP) of forested wetlands is greatest in areas with seasonal hydrology [5,6]. TFFWs also have relatively high primary productivity, likely due to the hydrological pulsing these systems experience from tides [7,8]. This productivity, combined with their broad distribution along the U.S. Gulf and Atlantic coasts [9], Europe, Central America, and the Amazon [10], means there is the potential for large amounts of carbon (C) to be stored in these areas [11]. Thus, it is important to understand how productivity of TFFWs is affected by tidal fluctuations, local precipitation, and freshwater inputs [12,13].

Global climate change has the potential to impact the ability of TFFWs to sequestration [14]. Greenhouse and field studies have documented the effects of increased salinity on freshwater systems (e.g., [15–17]), reporting decreases in productivity, tree death, and conversion to other community types [4,18–21]. It is forecast that climate change will cause sea level rise rates to increase, as well as cause changes in local precipitation and watershed runoff [22,23]. The greatest threat to TFFWs as sea level rises is increased flooding and decreased flushing.

In the Southeastern U.S., TFFWs are already experiencing increased saltwater intrusion, resulting in conversion of these forests to oligohaline marshes (e.g., [1,20,24,25]). However, these transformations are often less dramatic and occur slowly. For example, water tupelo (*Nyssa aquatica* L.) is typically replaced by swamp tupelo (*Nyssa biflora* Walt.) as salinity

increases above 0.5 ppt [26]. While the two species may be similar in their tolerance of prolonged flooding, the ecological services (e.g., rates of water use [27]) change as forest communities shift. Given the potentially long timeframe over which plant communities may take to change noticeably, detailed floristic inventories provide baseline data to assess community dynamics for future investigators.

There are a number of floristic and ecological studies of swamps in the Southeastern U.S. [28–31]. Typically, baldcypress (*Taxodium distichum* (L.) Rich) and water tupelo dominate in swamps flooded year-round, while swamp tupelo, Carolina ash (*Fraxinus caroliniana* Mill.), and red maple (*Acer rubrum* L.), along with baldcypress, are common in swamps that are seasonally flooded [32,33]. With minimal human disturbance, most swamps have few non-native taxa [34,35].

A detailed study of the flora on Hobcaw Barony near Georgetown, South Carolina was conducted by Barry [36] who mapped and described the vegetation on different soil associations. A floristic inventory and the ecology of marsh vegetation bordering the present study area was conducted on three abandoned rice fields (Alderly, Thousand Acre Marsh, and Air Port Marsh) by Baden [37]. The abandoned rice fields and coastal forested wetlands on the edges of Hobcaw Barony were severely damaged by a powerful storm surge from Hurricane Hugo in September 1989. Though many upland forests were blown down by Hurricane Hugo, the forested wetlands were relatively unaffected by the winds. Saltwater inundation did not cause widespread tree damage unless the water was deposited in depressions [38].

Liu et al. [39] studied three forest sites in Strawberry Swamp, from 2013 to 2015. In the current study, we continued monitoring the Liu et al. [39] plots from 2016 to 2020 and added a fresh site in the same watershed. Our objective was to document forest productivity variability along the porewater salinity gradient. In addition, we conducted a survey of the vegetation within the watershed that includes a complete listing of plants existing at this point in time, allowing researchers the ability to determine vegetation changes in the future (Supplementary Material, Tables S1 and S2).

2. Materials and Methods

2.1. Study Area

Three study sites were selected in Strawberry Swamp in June 2013 [39]. Because salinity was still a factor in all three of these sites, a fourth non-saline site was selected in 2016 further up the watershed to serve as a baseline. Strawberry Swamp is located on Hobcaw Barony, in Georgetown County, South Carolina (33°19′49″ N, 79°14′54″ W) (Figure 1). Numerous decaying stumps in the area indicate that the forests are at least second-growth stands. Sea level rise in the area has averaged 3–4 mm yr⁻¹ since 1920 [40], resulting in saltwater intrusion and flooding of the freshwater forest. Rainfall runoff from surrounding uplands is the major source of water to the swamp, with a seasonally intermittent groundwater flow. The swamp is 236 ha in area and discharges into the Winyah Bay estuary [41]. At the lower end of the swamp a road extends across the drainage basin. Since there is only one culvert, drainage of the basin could be restricted. Forest types in and adjacent to the swamp range from dry upland sites dominated by loblolly pine (*Pinus taeda* L.), sweetgum (*Liquidambar styraciflua* L.), southern red oak (*Quercus falcata* Michx.), and hickory (*Carya* spp.), to wet swamp where baldcypress, water tupelo, and swamp tupelo dominate. There has been considerable die-back of baldcypress trees in the lower reaches of the watershed during the past several decades due to increased salinity, and these areas are now occupied by oligohaline marsh [40]. Soils are of the Hobcaw series (fine-loamy, siliceous, thermic, Typic Umbraquults) [42]. The climate is classified as humid subtropical with hot summers and mild winters. Average high and low air temperatures are 27.6 °C in July and 8.2 °C in January, respectively. Average annual rainfall is 1330 mm (mean of 17 cm month⁻¹; from <https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/locations/ZIP:29440/detail#stationlist> (accessed on 9 September 2021); 33°21′56″ N, –79°16′43″ W).

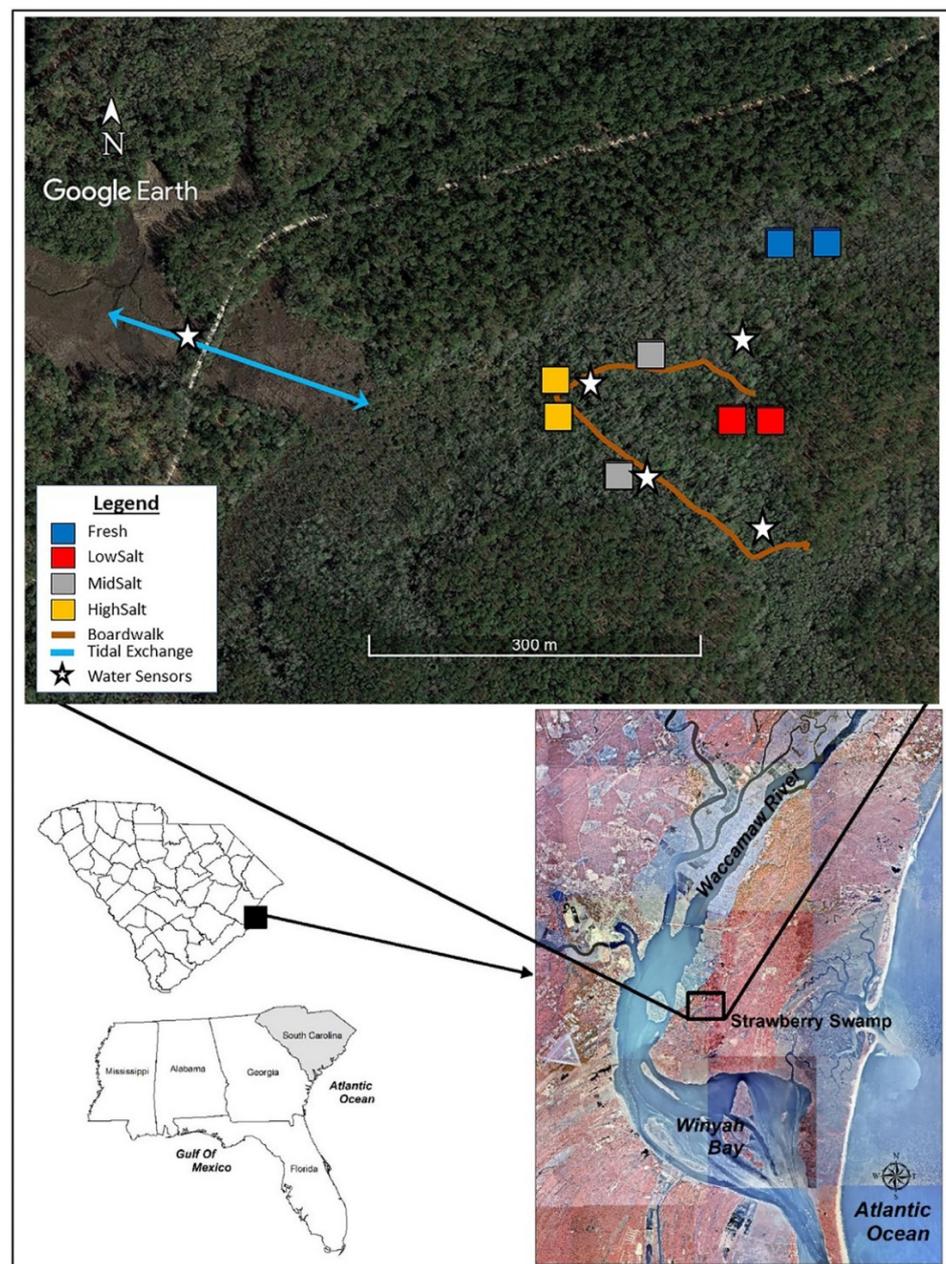


Figure 1. Location of study plots (upper) in Strawberry Swamp, Georgetown County, South Carolina across the salinity gradient. Salinity decreases as you move further from the area of tidal exchange.

2.2. Water Depth and Salinity

Water depth, temperature, and conductivity (CTD) sensors (Decagon CTD-10 Conductivity Temperature & Depth Sensor, Decagon Devices, Pullman, WA, USA) were used to measure conditions at the soil surface at 5 locations along the salinity gradient (Figure 1, stars). The CTD sensors allowed for consistent water depth and salinity measurements at 15-min intervals from January 2014 through December 2018. Based on CTD data, we quantified salinity level of the four study sites as: fresh (0.1 ppt), low-salt (~0.8 ppt), mid-salt (~2.6 ppt) and high-salt (~4.6 ppt). Porewater salinity was measured in each plot at a depth of 100 cm below the soil surface from shallow PVC wells that were regularly pumped of accumulated sediment prior to taking the measurement; this was done monthly using a handheld sensor (YSI Pro-30 Conductivity Meter, Yellow Springs, OH, USA) from January 2014 to December 2020. Precipitation data were downloaded from Georgetown, SC weather station US1SCGT0027 [43].

2.3. Woody Growth

Paired 20 × 25-m plots were established in 2013 along the salinity gradient that existed at the time, as determined with the use of CTD sensors (total of 8 plots; Figure 1). In the mid-salt area, the plots are not side by side as the others are but are still in the same salinity regime. This was done because of site variations (large openings) in the mid-salt area and the desire to have plots of the same forest community structure as possible as was the case for the other plots. Standard diameter tapes were used to measure diameter at breast height (DBH) at the end of each growing season from 2014–2020). DBH values were put into general allometric equations to estimate total tree woody biomass (stem, branch, and bark) for each year [44,45]. Though the equations are not specific to the Strawberry site, numerous studies in the Southeastern U.S. have used these equations to calculate tree biomass (e.g., [46–49]).

2.4. Litterfall and Aboveground Net Primary Production

Litterfall was collected monthly (January 2014 to December 2020) in each plot using five 0.25 m² wooden litter boxes with 1-m legs to prevent flooding. Litter traps were located near the four corners and centers of study plots. After litterfall was collected, it was returned to the laboratory and put into 70 °C ovens and dried at least 48 h to a constant weight. When dry, the litterfall was sorted into leaf litter (including leaves, seeds, and flowers) and non-leaf litter (including twigs, bark, lichens, moss), weighed to the nearest 0.01 g, and recorded as g m⁻² [50]. Annual aboveground net primary productivity represents the sum of monthly leaf litterfall and woody biomass growth estimates for each year [51,52].

2.5. Vascular Plant Collection

Plant collecting trips to Strawberry Swamp were initiated in 2015 and continued through 2019. Objectives for each trip included collection of voucher specimens of as many plant species as possible (see Supplementary Material, Tables S1 and S2). The boardwalk was used as a line transect to collect plants where the water table was above the ground. The boardwalk could be used by future investigators to sample plants 1 m on either side of the boardwalk as in this study. In the rarely flooded portion of the swamp, samples were collected by walking the area to gather as many plants as possible on each visit. Gordon Tucker (Eastern Illinois University: EIU) identified the sedges. Grasses were identified by John Nelson (A. C. Moore Herbarium, University of South Carolina: USCH). Eric Lamont (New York Botanical Garden) provided assistance with the Asteraceae. Native status and nomenclature at division, class, family, genus, and species follow Weakley [53]. All species names were confirmed using Weakley [53] and the Integrated Taxonomic Information System (<http://www.itis.gov>, accessed on 9 September 2021). One complete set of vouchers was deposited USCH. Duplicates of Cyperaceae were deposited at EIU.

2.6. Statistical Analysis

Repeated measures regressions were conducted to assess the influence of growing season monthly porewater salinity and year on ANPP and its components, regardless of plot designation using the mixed procedure in SAS software version 9.4 [54]. Response variables were log transformed to meet the model assumption that residuals are normally distributed. Monthly salinities from the wells located in the plots were averaged for the growing season (April to October). We constructed full models for ANPP, woody and litter production with salinity and year and their interaction using the repeated statement to account for the autocorrelation due to repeated measurements within the same plots and used a compound symmetry covariance structure. Only the litter production had a significant interaction effect of salinity and year ($F_{6,33} = 3.04$, $p = 0.0177$). Hackney and Avery [55] found that forests flooded 12–25% of the time with 1 ppt floodwater were in some state of transition from swamp to marsh. Therefore, to look at how ANPP and its

components respond to the 1 ppt threshold, correlations were run for productivity and year for salinity less than 1 and greater than or equal to 1 ppt.

3. Results

3.1. Water Depth and Salinity

Water depth was dynamic and sensitive to local precipitation in Strawberry Swamp. Depth fluctuated around 0.6 m, decreasing during summer months and spiking after precipitation events (Figure 2). Porewater salinity generally declined during years 2015–2020, with the largest decline of ~3 ppt occurring in the high-salt areas. This is largely due to heavy precipitation events during hurricanes. A large dip in salinity occurred in October 2015 from heavy rains from the remnants of Hurricane Joaquin, and a dip in salinity in October 2016 is the result of Hurricane Matthew that passed directly over Hobcaw. These dips also correspond to the peaks in daily water level (Figure 2).

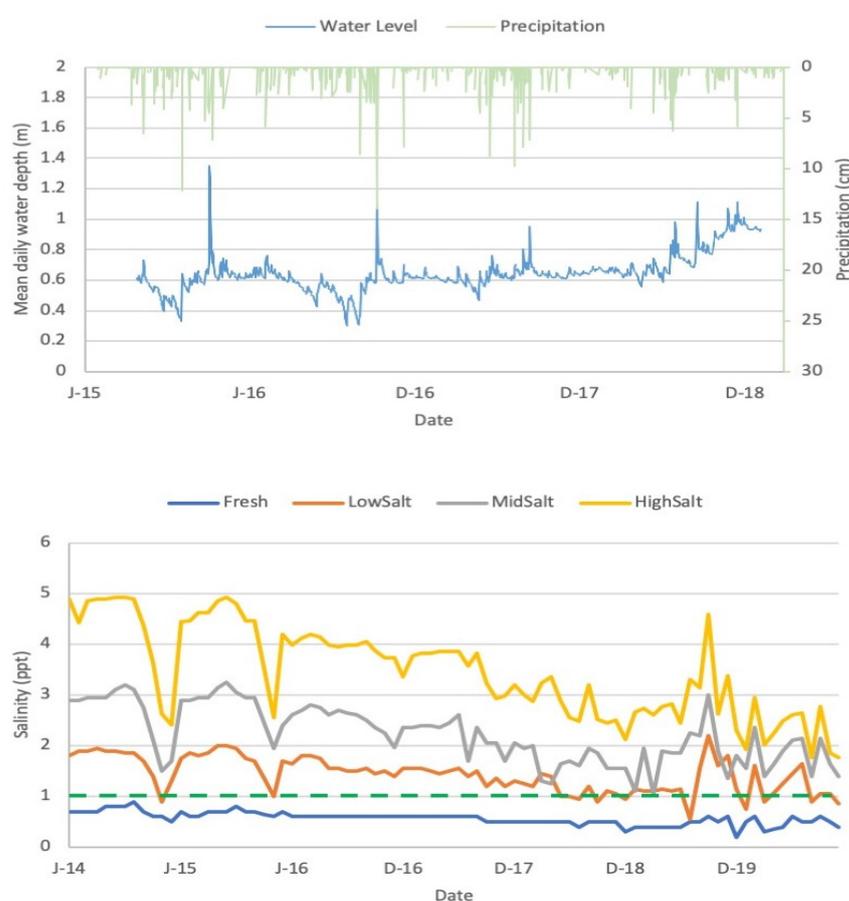


Figure 2. Mean daily water level and precipitation (parts per thousand: ppt) in Strawberry Swamp (**upper**) and porewater salinity across the established gradient (**lower**). The green line represents the salinity at which most trees begin to die.

3.2. Woody Growth, Litterfall, and Aboveground Net Primary Production

The overall composition of the forest vegetation is fairly similar across the salinity gradient (Table 1). Baldcypress, ash, swamp blackgum, and water tupelo are the dominant tree species in the low- to high-salt areas. Baldcypress and ash are also dominant in the fresh area, but red maple and sweetgum are also common. In the fresh area, there was very little change in mean dbh, density, and BA over the seven years of study except for the decline in red maple density (from 230 to 190 trees ha⁻¹). In the low-salt area there was an increase in baldcypress numbers as smaller individuals grew to tree size (>10 cm dbh) and a small decrease in ash and swamp blackgum numbers along with the introduction

of waxmyrtle and Dahoon holly. In the mid-salt area, there is a decline in numbers of all species except loblolly pine and red maple. There is a small decrease in baldcypress numbers in the high-salt area with a sharp decline in water tupelo numbers, along with the introduction of loblolly pine.

Table 1. Forest species composition of a South Carolina forested wetland across a water salinity gradient in 2014 and 2020.

Site	Species	Mean DBH (cm)		Density (# ha ⁻¹)		BA (m ² ha ⁻¹)	
		2014	2020	2014	2020	2014	2020
Fresh (0.1 ppt)	Ash	21.5	22.4	380	370	15.6	16.67
	Baldcypress	26.3	27.2	290	290	18.41	19.58
	Elm	31.5	31.5	10	10	0.78	0.78
	Red maple	22.8	23.3	230	190	10.61	9.2
	Swamp blackgum	46.4	46.4	20	20	3.68	3.68
	Sweetgum	16.2	16.7	150	150	3.56	3.78
	TOTAL			1080	1030	52.64	53.69
Low-salt (0.8 ppt)	Ash	25.5	27.1	60	50	3.54	3.3
	Baldcypress	28	26	290	320	23.58	25.12
	Swamp blackgum	24.7	25.1	250	240	13.34	13.23
	Water tupelo	36.8	37.2	140	140	16.5	16.8
	Waxmyrtle	–	11.6	–	20	–	0.21
	Dahoon holly	–	14.9	–	10	–	0.2
	TOTAL			740	780	56.96	58.86
Mid-salt (2.6 ppt)	Ash	54.4	–	10	–	2.32	–
	Baldcypress	45.4	46.5	260	240	42.74	42.73
	Swamp blackgum	20.2	20.6	170	160	5.81	5.7
	Water tupelo	34.6	33.6	130	110	15.43	12.76
	Waxmyrtle	12.2	12.9	30	20	0.39	0.2
	Loblolly pine	11.5	13.5	10	10	0.1	0.14
	Red maple	23	23.3	10	10	0.42	0.43
TOTAL			620	550	67.21	61.96	
High-salt (4.6 ppt)	Ash	10.15	11	10	10	0.08	0.1
	Baldcypress	47.45	47.38	250	230	46.99	43.08
	Swamp blackgum	17.49	18.32	130	130	3.49	3.78
	Water tupelo	23.9	16.3	140	40	7.42	0.86
	Waxmyrtle	10.95	11.65	70	30	0.73	0.31
	Loblolly pine	–	11.14	–	20	0.1	0.2
	TOTAL			600	460	58.81	48.33

Averaged over all plots across all years, ANPP ranged from 705 ± 101 (in 2020) to 870 ± 69 (in 2014) $\text{g m}^{-2} \text{yr}^{-1}$, decreasing by 19% from 2014 to 2020. Woody production averaged 44% of total ANPP across all years, with as little as 38% to as much as 54%. On average, litterfall was highest in the freshest sites ($540 \pm 7.7 \text{ g m}^{-2} \text{yr}^{-1}$) and ranged from 46 to 62% of ANPP. The overall contribution of baldcypress to total stem wood growth in each site increased with increasing salinity (32% in the fresh site, 47% in the low-salt site, 60% in the mid-salt site, and 85% in the high-salt site).

The freshest sites had the highest ANPP ($1081 \pm 54 \text{ g m}^{-2} \text{yr}^{-1}$), which declined with increasing salinity (proc mixed: salinity, $F_{1,33} = 18.57$, $p = 0.0001$). This seems to be driven by woody production of the surviving trees (proc mixed: salinity, $F_{1,35} = 14.94$, $p = 0.0005$), which in turn drives ANPP (Figure 3). Litter production also showed a decrease with salinity, but the response varied by year ($F_{6,33} = 3.04$, $p = 0.0177$). Correlations of ANPP and time indicate that plots with salinity greater than 1 ppt show decreased ANPP and woody production through time compared to plots with salinity less than 1 ppt. Leaf production is similar regardless of the 1 ppt threshold (Figure 4).

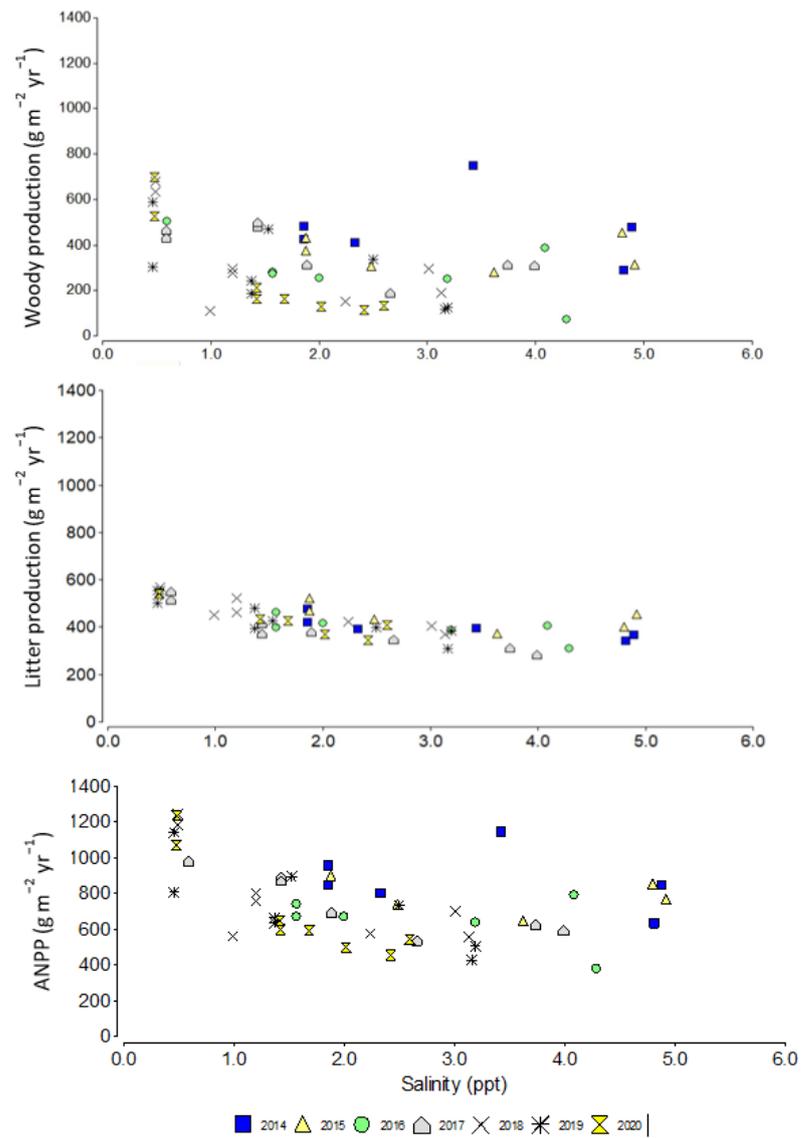


Figure 3. Annual wood production (**upper**), leaf litterfall (**middle**), and aboveground net primary productivity (**lower**) across the salinity gradient in Strawberry Swamp.

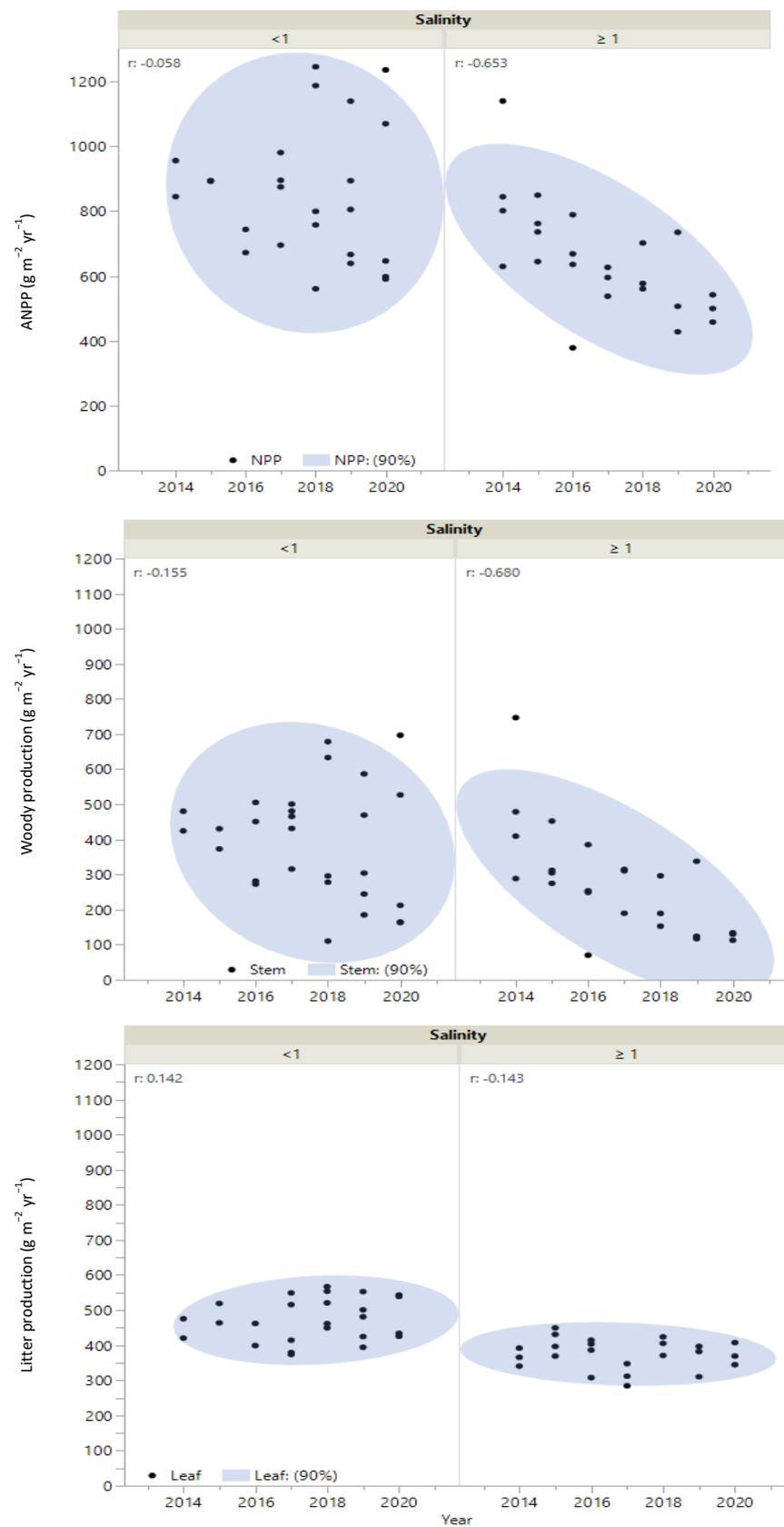


Figure 4. Correlation of annual net primary productivity (ANPP) and year when plots had salinity less than 1 ppt (left) or greater than or equal to 1 ppt (right). The grey circles represent 90% confidence ellipse.

3.3. Vascular Plant Collection

The vascular flora of Strawberry Swamp (Table S1) consists of 165 species in 127 genera and 72 families. The Cyperaceae (19 species) and Asteraceae (14 species) are the largest families in the flora (Table S2). *Carex* (9 species) and *Juncus* (5 species) are the largest genera in the flora. Non-native plants (9 species) are rare in the area and compose 5% of the floral diversity. One foreign taxon, common reed (*Phragmites australis* (Cav.) Trin. Ex Steud.), is a dominant component of the flora and is expanding its range locally. Common reed was first observed in South Carolina in 1974 near Rt. 17S and the Waccamaw River (very near Strawberry Swamp) by Stalter [56]. Common reed has replaced cattail (*Typha latifolia* L.) as the dominant herbaceous species in the zone of tidal exchange (Figure 1) at Strawberry Swamp and may eliminate additional vascular plant species onsite as sea level and water salinity rises.

Typical swamp taxa at Strawberry Swamp include baldcypress, Carolina ash, swamp tupelo, waxmyrtle, swamp loosestrife (*Decodon verticillatus* (L.) Ell.), dahoon (*Ilex cassine* L.), herb of grace (*Bacopa monnieri* L. Pennell), blue waterhyssop (*B. caroliniana* (Walt.) B.L. Robinson), bladderwort (*Utricularia* spp.), sedges (*Carex*, spp.), and rushes (*Juncus* spp.); additional southeastern swamp taxa are listed in Supplementary Material Table S1. Three orchids, nodding lady's tresses (*Spiranthes cernua* (L.) L.C. Richard), marsh lady's tresses (*S. odorata* (Nutt.) Lindl.), and crested fringed orchid (*Platanthera cristata* (Michx.) Lindley) are conspicuous components of the flora when in flower. No rare and endangered taxa were detected.

4. Discussion

Baldcypress and swamp tupelo are the most dominant canopy species in tidal freshwater forested wetlands of Southeastern U.S. [57]. Water tupelo also occurs in many TFFW areas throughout the Southeastern U.S. [10,26,58], but Celik et al. [49] found it to be restricted to more non-tidal areas where daily salinity was <0.2 ppt. Strawberry Swamp does not experience the effects of daily tidal fluctuations as other TFFW often do. However, it is subject to the same stress brought on by marine-derived salinity, while being ameliorated by local upland drainage (from rain events). Runoff waters tend to flush the porewaters of salts, resulting in lowered porewater salinities across the relatively small gradient in Strawberry Swamp [59]. Swamp tupelo and water tupelo generally die off when even low levels of porewater salinity (e.g., ~2 ppt) persist for multiple years [39] as seen in the high-salt area. However, baldcypress seems to be more resilient to flooding and salinity than many other freshwater tree species [24], but its growth rate decreases when salinity levels exceed 1 ppt [60].

William Bartram in 1791 was perhaps the first explorer to document a natural progression of cypress/tupelo swamp forest to salt marsh along the Atlantic coast in the Carolinas [61]. Mattoon [62] described the early death of baldcypress trees in coastal swamps being due to salt brought in by storm surges. Penfound and Hathaway [63] described areas of "ghost forests" of standing dead trees in Louisiana created by hurricane storm surges bringing in saltwater.

TFFW along the Atlantic and Gulf coasts occur in low lying areas which makes them susceptible to upland runoff, tidal flooding, saltwater intrusion, and other global climate change phenomena [64]. These forests are readily impacted by slight changes in salinity as a result of rising sea level [3,4,50,65–67]. While porewater salinity decreased during this study, it rarely fell below 1 ppt and only in the areas furthest from the where tidal exchange occurs (Figures 1 and 2). Overall ANPP decreased as salinity increased above 1 ppt, but woody production was variable across this gradient during the 7 years of this study (Figures 3 and 4). While leaf litter production is lower in higher salinities, there is not a dramatic shift in litter production over time.

By 2020, all sites with porewater salinity levels above 1 ppt showed reduced growth (Figures 3 and 4). As salinity increased, baldcypress became the dominant species as tupelo species tend to die off with sustained high porewater salinity. Whereas the fresh

plots had woody growth rates averaging $612 \text{ g m}^{-2} \text{ yr}^{-1}$, woody growth ranged from $129\text{--}188 \text{ g m}^{-2} \text{ yr}^{-1}$ across the salinity gradient. The low woody growth in salt impacted areas is comparable to the $144 \text{ g m}^{-2} \text{ yr}^{-1}$ reported by Shaffer et al. [49] in a Louisiana salt-impacted swamp, and higher than the $20 \text{ g m}^{-2} \text{ yr}^{-1}$ reported in a nearby high salinity TFFW in South Carolina [68].

Multiple studies of coastal baldcypress swamps have found that salinity reduces growth of baldcypress (e.g., [14,20,69–71]). We surmise that trees with long-term exposure to higher salinity conditions had inherently limited woody productivity because of individual tree structural changes that have occurred in these trees, in particular noticeably smaller individual tree canopies and fewer leaves on branches. The insignificant relationship between leaf productivity and salinity may be a reflection of plentiful rainfall during the study that caused an overall decrease in salinity in all study plots within Strawberry Swamp over the past 10 years. While structural changes cause long-term difference in leaf production, woody growth may be more dynamic and respond more quickly to lower salinity conditions.

Litterfall values from this study were relatively high as compared to other forested wetlands in the Southeastern U.S. Values of $540 \text{ g m}^{-2} \text{ yr}^{-1}$ at the Strawberry Swamp fresh sites are comparable to the $564\text{--}667 \text{ g m}^{-2} \text{ yr}^{-1}$ from a fresh TFFW site 25 km north on the Waccamaw River [7]. Other studies in unimpacted freshwater swamp forests have reported $627\text{--}902 \text{ g m}^{-2} \text{ yr}^{-1}$ at Ogeechee River, Georgia [72], $243\text{--}582 \text{ g m}^{-2} \text{ yr}^{-1}$ at Ichauway Ecological Reserve, Georgia [73], $554\text{--}664 \text{ g m}^{-2} \text{ yr}^{-1}$ at Altamaha River, Georgia [48], and $455\text{--}536 \text{ g m}^{-2} \text{ yr}^{-1}$ in the Great Dismal Swamp, Virginia [74]. Litterfall rates of $363\text{--}447 \text{ g m}^{-2} \text{ yr}^{-1}$ across the salinity gradient in Strawberry Swamp sites were higher than the 88 and $118 \text{ g m}^{-2} \text{ yr}^{-1}$ reported for high-salt impacted areas on the Savannah and Waccamaw rivers, respectively. Pierfelice et al. [68] reported litterfall values of $59 \text{ g m}^{-2} \text{ yr}^{-1}$ in salt-impacted TFFW along the nearby Waccamaw River, and Shaffer et al. [49] reported $78 \text{ g m}^{-2} \text{ yr}^{-1}$ in a Southeastern Louisiana salt-impacted site.

The Strawberry Swamp watershed experienced a 29% loss in forested wetland between 1949–2009 due to sea level rise and increasing salinity levels [40]. During the course of the present study, mortality of trees increased across the salinity gradient from 4% in fresh and low impacted plots, which is slightly higher than the 2% rate observed in healthy wetland forests that are not impacted by salinity [75], to 26% in the most saline plots. Mortality in these plots in Strawberry Swamp is higher than the 20% mortality reported by Shaffer et al. [48] for salt-impacted sites in Louisiana, yet lower than the 38% reported by Pierfelice et al. [68] for salt-impacted sites in South Carolina. Although salinity in Strawberry Swamp is currently declining as a result of increased precipitation and overland flow since 2015, it hasn't declined to levels low enough to reverse the trend of tree mortality. With projections of continuing sea level rise and increasing salinity intrusions, tree growth will continue to decline and transition from forests to marsh or open water areas, as has been reported by others in areas affected by salinity [4,18–20,49,65]. During the 5 yrs of plant collection, there were no temporal changes noted in species present or absent in the study area. The most conspicuous change in the herbaceous community is the spread of common reed. Prior to the initiation of this study, common reed had taken over the marsh area below the forest zone. It is now well established at the lower end of the study site and may eventually become a major contributor to a loss in species diversity within Strawberry Swamp as it has in other nearby sites [35].

5. Conclusions

Sites with higher porewater salinity had lower woody growth and reduced leaf litter fall, but the magnitude of the response depends on the year. Overall, ANPP is decreasing and shifting to domination by cypress trees. With continued sea level rise, forested wetlands in Strawberry Swamp will eventually be replaced by marshes. Strawberry Swamp is a unique forested wetland system with a compact salinity gradient, and is undergoing change as a result of saltwater intrusion. Strawberry Swamp's protected status and abundant

floristry and ongoing ecological studies provide a unique setting for comparative work in the future.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f13030414/s1>, Table S1: Checklist of Species, Strawberry Swamp, South Carolina. Table S2: Summary of the Vascular Flora at Strawberry Swamp, South Carolina.

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