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Watershed and Estuarine Controls Both Influence Plant Community and Tree Growth Changes in Tidal Freshwater Forested Wetlands along Two U.S. Mid-Atlantic Rivers

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Abstract: The tidal freshwater zone near the estuarine head-of-tide is potentially sensitive to both sea-level rise and associated salinity increases as well as changing watershed inputs of freshwater and nutrients. We evaluated the vegetation response of tidal freshwater forested wetlands (TFFW) to changes in nontidal river versus estuarine controls along the longitudinal gradient of the Mattaponi and Pamunkey rivers in the Mid-Atlantic USA. The gradient included nontidal freshwater floodplain (NT) and upper tidal (UT), lower tidal (LT), and stressed tidal forest transitioning to marsh (ST) TFFW habitats on both rivers. Plot-based vegetation sampling and dendrochronology were employed to examine: (1) downriver shifts in plant community composition and the structure of canopy trees, understory trees/saplings/shrubs and herbs, tree basal-area increment (BAI) and (2) interannual variability in BAI from 2015 dating back as far as 1969 in relation to long-term river and estuary monitoring data. With greater tidal influence downstream, tree species dominance shifted, live basal area generally decreased, long-term mean BAI of individual trees decreased, woody stem mortality increased, and live herbaceous vegetative cover and richness increased. *Acer rubrum*, *Fagus grandifolia*, *Ilex opaca*, and *Fraxinus pennsylvanica* dominated NT and UT sites, with *F. pennsylvanica* and *Nyssa sylvatica* increasingly dominating at more downstream tidal sites. Annual tree BAI growth was positively affected by nontidal river flow at NT and UT sites which were closer to the head-of-tide, positively influenced by small salinity increases at LT and ST sites further downstream, and positively influenced by estuarine water level throughout the gradient; nutrient influence was site specific with both positive and negative influences. The counterintuitive finding of salinity increasing tree growth at sites with low BAI is likely due to either competitive growth release from neighboring tree death or enhanced soil nutrient availability that may temporarily mitigate the negative effects of low-level salinization and sea-level increases on living TFFW canopy trees, even as overall plant community conversion to tidal marsh progresses.

Keywords: tidal freshwater wetland; tidal marsh; tidal forest; watershed; estuary; salinization; sea-level rise

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1. Introduction

Tidal freshwater forested wetlands (TFFW) are an important, yet relatively understudied ecosystem. In the United States, they predominantly occur in low-lying coastal areas along the Atlantic and Gulf coasts where they occupy at least 200,000 ha, likely more area than tidal freshwater marshes [1,2]. Ensign and Noe [3] recently calculated that tidal freshwater rivers, which support most TFFW, extend 2850 km along the U.S. Atlantic Coast, with a median length of 20 km among 127 rivers. Tidal freshwater forested wetlands also occur in the western United States, primarily limited to Oregon and Washington [4–6], where their area has been reduced by ~95% since European settlement, primarily as a result of diking and other land-use conversions [7,8]. These wetlands provide important ecosystem services, with high rates of C storage and sequestration [9], biotic diversity [10], denitrification [11,12], and sediment retention [13]. Given their hydrogeomorphic landscape position downstream of the head-of-tide along rivers, tidal freshwater wetlands are likely influenced by both watershed (e.g., nontidal river discharge and availability of nutrients and sediment) and estuarine controls (e.g., salinity and tidal inundation) [14,15]. Indeed, TFFW ecosystems are especially susceptible to sea-level rise, flood or drought stress, and saltwater intrusion [1,16,17]. However, the importance of these influences may depend on the temporal variability of ecosystem drivers and by location along longitudinal river gradients from head-of-tide to low salinity or oligohaline zones.

The vegetation communities of TFFW are known to change along hydrologic gradients of water depth and salinity along tidal rivers. The first published works on the vegetation of a tidal freshwater swamp did not start appearing until the mid-1980s [18,19]. Doumlele et al. [19] examined only a single site on the Pamunkey River in Virginia and described the dominant vegetation in TFFW and a nearby marsh community. Brinson et al. [18] was more descriptive of multiple sites and focused on change along a freshwater-to-low salinity transition within the Pamlico River Estuary, North Carolina. Stands with higher porewater salinity had reduced basal area and a higher proportion of dead trees along with dominant species shifts [18]. These initial studies began to identify that the stressors to TFFW composition and growth vary longitudinally downstream along rivers.

Vegetation studies of TFFW have increased in recent years. Rheinhardt [20] conducted a much more extensive survey of 23 tidal freshwater swamps along the Pamunkey River and found that they harbored two primary plant communities—downriver, wetter sites dominated by *Nyssa biflora* Walter and *Fraxinus* spp., and upriver, drier *Acer rubrum* L.-*Liquidambar styraciflua* L.-*N. biflora* dominated swamps. Subsequent studies of TFFW vegetation, primarily in Maryland [21,22], North Carolina [23], and South Carolina, Georgia, Louisiana, and Florida [24–29] expanded upon this initial work, culminating in the definition of four general community types ranging the southeastern United States by Duberstein et al. [30]: Water Tupelo (dominated by *Nyssa aquatica* L.); Swamp Tupelo (dominated by *N. biflora*); Dwarf Palmetto (dominated by *Sabal minor* (Jacq.) Pers.); and Cabbage Palm (with notable *S. palmetto* (Walter) Lodd. ex Schult. and Schult. f.) communities. In the Pacific Northwest of the United States, TFFW are often brackish (~8–10 ppt) during the summer dry season, resulting in a much less diverse tree community dominated by *Picea sitchensis* (Bongard) Carrière with the shrubs *Lonicera involucrata* (Richards) Banks ex. Spreng and *Malus fusca* (Raf.) C. K. Schneid. in the understory [4].

In addition to plant community studies, a few studies have focused on the effects of salinity and sea level rise on tree growth in TFFW. Some have examined the effects of these factors on growth indirectly, including sapflow and water use [31,32], chloride concentrations in stem tissue [33], and nutrient and water stress [34]. Other studies have assessed salinity and inundation impacts directly by measuring annual tree growth rings [27,35–38] or stem wood growth over time [29], but these studies were limited to investigation of a single species, *Taxodium distichum* (L.) Rich. In general, these and other findings from nontidal lowland habitats have shown that forest primary productivity exhibits a positive growth response to intermediate levels of flood duration but growth declines under prolonged or permanently flooded conditions [39]. Field studies have also identified the tolerance of *T. distichum* to low, chronic, or short acute salinization, but not to sustained levels beyond 2 ppt, and chronic or elevated saltwater presence inevitably results in decreased tree growth and ecophysiological stress [23,35,40]. Studies on tree growth in TFFW in relation to salinity and water level have, to our knowledge, not been undertaken on species other than *T. distichum*.

The objective of this study was to examine the extent to which watershed vs. estuarine controls influence TFFW vegetation along a longitudinal river gradient spanning from nontidal through the tidal freshwater zone on both the Mattaponi and Pamunkey rivers in eastern Virginia. We made the following predictions:

1. Estuarine water level and salinity negatively affect annual tree growth, and generate shifts in plant community composition and structure, with estuarine water level and salinity becoming increasingly important at driving vegetation assemblage in downriver locations within the tidal freshwater zone.
2. Watershed nutrient inputs and river flow positively affect annual growth in the tree community, becoming increasingly important along the upriver portions of the longitudinal tidal river gradient.

We employed plot-based vegetation sampling and dendrochronological analyses, and long-term watershed and estuarine monitoring data, to identify changes in vegetation composition and structure and tree growth along the longitudinal gradient of the two tidal rivers: (1) spatial changes along downriver gradients, and (2) interannual variability of tree growth in response to environmental controls over the past 31 years, the duration of long-term monitoring observations.

2. Materials and Methods

2.1. Study Sites

Our study sites comprised gradients of riparian forested wetland along the Mattaponi and Pamunkey tidal rivers in the Coastal Plain physiographic province of eastern Virginia. Each river gradient consisted of four floodplain sites spanning nontidal freshwater forested wetland (bottomland hardwood swamp), upper river TFFW, lower river TFFW, and stressed TFFW transitioning to tidal marsh (Mattaponi sites—MNT, MUT, MLT, and MST; Pamunkey sites—PNT, PUT, PLT, and PST; respectively; Figure 1). Nontidal sites were located near the head-of-tide with floodplain that was not directly tidally inundated, but the river channel was micro-tidal. The Mattaponi and Pamunkey rivers both have oligohaline marsh downstream of the ST sites before joining to form the York River, a tidal tributary of the Chesapeake Bay.

2.2. Vegetation Composition and Structure

Paired 20 × 20 m plots were installed at each site (Figure 1; however, the site MST could only fit one plot, for a total of 15 plots total), where all trees ≥5 cm in diameter at 1.3 m in height (diameter at breast height, DBH) were identified to species, tagged, and had their DBH and status (alive/dead) recorded. Two 5 × 5 m sapling and shrub subplots in opposing corners of each 20 × 20 m plot were also established where all woody species between 1 and 5 cm DBH were identified to species, tagged, and had their DBH and number of stems (if multiple) recorded. Lastly, three smaller, 1 × 1 m subplots (quadrats) were placed on the diagonal of the 20 × 20 m plot in which all woody species <1 cm DBH and <1.3 m tall, and all herbaceous species, were identified to either species or morphospecies (in the case of graminoids) and had their percent cover estimated visually. Taxonomic determinations followed the Flora of Virginia [41].

2.3. Tree Growth

Tree growth was assessed by collecting increment cores from up to 10 live, mature trees of at least the two dominant canopy species at each site. Increment cores were collected using 41 cm long, 5.2 mm diameter increment borers from approximately knee height (~0.5 m; above buttressing) on the tree trunk using standard procedures [42]. Cores were collected between May and July 2016 during the growing season. After air-drying in the laboratory, cores were mounted into wooden clamps, sanded successively with 120-grit, 320-grit, and 500-grit sandpaper and buffed with a lambswool pad on an electric drill press to prepare them for measurement. Annual growth ring widths of each core were measured to the nearest micrometer (µm) using a Velmex Unislide tree ring measuring system (Velmex, Inc., Bloomfield, NY, USA) and MeasureJ2X software (VoorTech Consulting, Holderness, HN, USA) to assess incremental growth. For each site, cores were cross-dated by identifying common narrow annual growth ring years across cores [43].

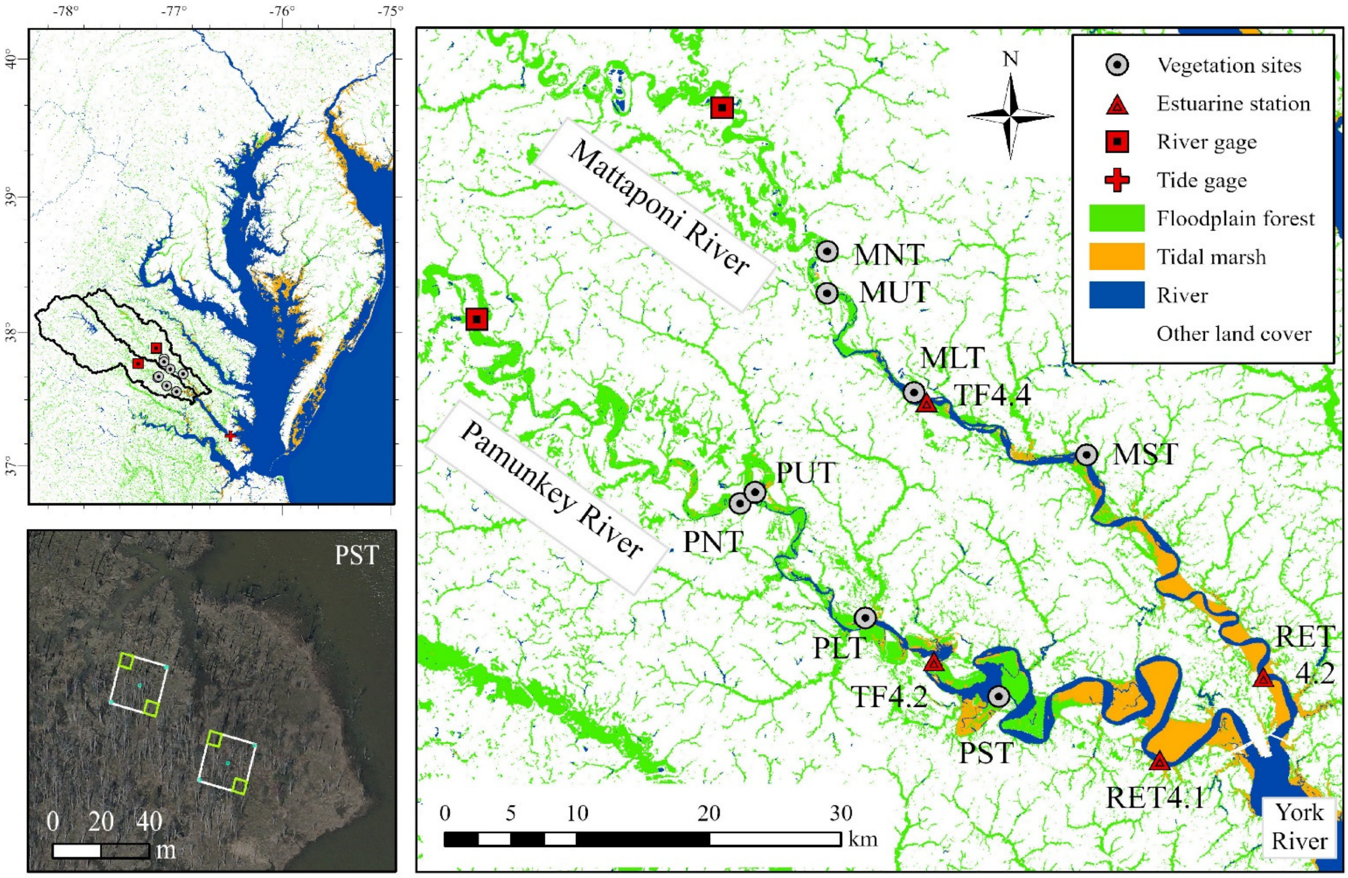

Figure 1. Location of study sites on the Mattaponi and Pamunkey rivers (**right**), location in the Chesapeake Bay watershed of the U.S. Mid-Atlantic (**left top**), and diagram of the vegetation sampling design within each site (**left bottom**; white = plot, green = sapling and shrub subplots, blue = seedling and herbaceous subplots). Vegetation sites: MNT and PNT, MUT and PUT, MLT and PLT, and MST and PST refer to Mattaponi River and Pamunkey River sites, respectively, for nontidal freshwater forested wetland, upper river TFFW, lower river TFFW, and stressed TFFW transitioning to tidal marsh.

Annual basal area increments (BAIs) of individual trees were calculated through 2015, the most recent full growing season captured in the tree cores. BAI values in square centimeters (cm^2) were calculated from annual ring widths (w), assuming circular tree trunks [44], and core radius length (R) for each year (t) with the formula:

$$\text{BAI}_t = \pi\,(R_t{}^2 - R_{t-1}{}^2),\ \text{where } R_{t-1} = R_t - w_t$$

Ring-width series were not temporally detrended because growth trends were the subject of our investigation; in addition, our restriction to the most recent 31 years of growth due to the temporal limitations of our environmental driver data precluded the need for detrending [44,45]. We calculated a mean annual individual tree BAI for each site by averaging all species annual BAIs by year, as well as mean annual BAIs for *Fraxinus pennsylvanica* Marshall and *A. rubrum*, the two tree species that were most commonly recorded across the study sites. We observed no evidence of emerald ash borer (*Agrilus planipennis* Fairmaire) infestation of *Fraxinus* trees at our sites to warrant analysis caution, and it had not been detected in the counties containing our study sites through 2018 [46].

2.4. Analyses

Basal area (BA) and importance value (IV; relative dominance + frequency + density [47]) were calculated for each woody species (trees and shrubs) recorded at each site, as well as total live and dead BA and stem density estimates per hectare, and mean BAI. Species richness (S), Shannon-Weiner diversity index (H'), and evenness (E) metrics were calculated for each site's woody and herbaceous plant community components, and average percent cover per species and total percent cover for each cover category type were calculated from each site's herbaceous layer plot data.

Datasets to examine the influence of watershed vs. estuarine controls on tree annual growth rates were compiled from several sources. Nontidal river annual mean freshwater discharge ($\mathrm{ft}^3\ \mathrm{s}^{-1}$) and flow-normalized total nitrogen (TN) and total phosphorus (TP) concentrations ($\mathrm{mg\ L}^{-1}$ N and $\mathrm{mg\ L}^{-1}$ P) over the period 1985–2015 were obtained from U.S. Geological Survey (USGS) stations located upriver of our sampling sites (Figure 1): on the Mattaponi River near Beulahville, Virginia (USGS 01674500) and the Pamunkey River near Hanover, Virginia (USGS 01673000) [48]. Flow-normalized concentrations were used to avoid covariation with river discharge, and therefore do not represent river load of nutrients. Monthly mean estuarine water level (m) relative to mean sea level (msl) at the Gloucester Point/Yorktown U.S. Coast Guard station tide gauge was extracted for the period 1969–2015 (https://tidesandcurrents.noaa.gov/map/index.html?id=8637689; accessed on 25 September 2017). Lastly, monthly surface water salinity (ppt) was downloaded for two stations with the longest data collection records for each tidal river (Figure 1; Mattaponi TF4.4 (1984–2010) and RET4.2 (1984–2015); Pamunkey TF4.2 (1984–2010,2012,2014) and RET4.1 (1984–2015)) from the Chesapeake Bay Program's water quality database website (https://www.chesapeakebay.net/what/downloads/cbp_water_quality_database_1984_present; accessed on 23 August 2017). For both estuarine water level and salinity, annual mean and maximum values were calculated. Finally, annual mean Palmer Drought Severity Index (PDSI) values at Walkerton, Virginia (adjacent to Mattaponi LT) were retrieved from the U.S. Drought Risk Atlas website (https://droughtatlas.unl.edu/Data.aspx; accessed on 21 December 2018).

Pearson correlation tests showed that mean and maximum annual estuarine salinity, as well as mean and maximum annual estuarine water level, were each highly correlated ($r \geq 0.75$). Therefore, we retained only the maximum annual salinity (as an indicator of acute salinity stress) and the mean annual estuarine water level variables from subsequent analyses. Maximum salinity and mean estuarine water level were uncorrelated at each of the long-term monitoring stations ($r \leq 0.28$). Flow-normalized river TP values obtained from the Mattaponi nontidal river station were nearly constant (0.052 ± 0.004, range 0.050–0.060 $\mathrm{mg\ L}^{-1}$ P) and were discarded from analyses. Although flow-normalized river TP and TN values from the Pamunkey nontidal river station were highly correlated (r = 0.857), both variables were retained in the analyses since TP had sufficient variability (0.079 ± 0.016, range 0.050–0.100 $\mathrm{mg\ L}^{-1}$ P) allowing the effects of both of these nutrients on annual BAI to be examined. Annual mean PDSI at Walkerton, Virginia, was not explanatory in any of the tree growth models (see next paragraph) and thus was not included as a final predictor variable. Final Mattaponi River annualized independent predictor variables included: mean river flow, flow-normalized river TN concentration, mean estuarine water level, and maximum estuarine salinity at the TF4.4 and RET4.2 stations. Final Pamunkey River annualized independent predictor variables included: mean river flow, flow-normalized river TN and TP concentrations, mean estuarine water level, and maximum salinity at the TF4.2 and RET4.1 stations. Based on overlapping records of these predictor variables, the common period of record was 1984 to 2015. We did not include estuarine salinity variables in regression models for the NT or UT sites on either river, as both were consistently freshwater and relevant nearby monitoring station data (TF4.0M and TF4.0P, upstream of TF4.4 and TF4.2) were only available for only portions of two years.

The relations between mean annual tree BAI and the potential watershed and estuarine controls for each site were analyzed using the all-possible-regressions multiple regression procedure in SAS 9.4 statistical software (SAS Institute, Cary NC). The best model for each site was selected by choosing the one that maximized the adjusted R^2 (R^2_{adj}) while minimizing the Akaike Information Criterion (*AIC*) and Mallows' Cp statistic (*Cp*) values. Model adequacy was assessed by the global F test for significance of the independent variables as a group to predict tree BAI, R^2_{adj} values, Coefficient of variation values (*CV*), and t-tests for significance of the individual independent variables in the model. Adherence to regression model assumptions was checked via examination of residual and partial residual plots, normal probability plots, and Durbin-Watson tests (d) to detect residual correlation. Box-Cox analyses were performed to determine the need for and type of data transformation. Pearson correlation coefficients were computed among all variables and in those instances showing high correlation, one of the variables was removed from the model. Variance inflation factors (VIFs) were also calculated to check for multicollinearity [49,50]. We tested for the effects of these watershed and estuarine controls on BAI in both the current year of growth and separately in the next growth year by analyzing for a 1-year lag effect.

3. Results

3.1. Longitudinal River Gradients

Along each river system, the NT, UT, and LT sites had higher species richness of canopy trees than ST sites. At the ST sites, the Mattaponi had slightly higher species richness than the Pamunkey. In contrast, LT sites of both rivers had the highest species richness of shrub and understory trees. Species evenness was fairly similar for canopy trees in the Mattaponi River study sites but increased from NT to ST in the understory shrub layer. No clear pattern was found in species evenness in the canopy tree layer at the Pamunkey River sites, though for the understory shrub layer the species evenness generally declined from NT to ST—contrary to the trend for the Mattaponi sites. Live tree basal area ranged between 20.9–29.6 m^2 ha^{-1} at most sites but was much lower (15.6m^2 ha^{-1}) at PST and much higher (44.4 m^2 ha^{-1}) at PUT. Similarly, shrub basal area was 1.0–1.9 m^2 ha^{-1} at most sites but was considerably lower at PNT (0.22 m^2 ha^{-1}) and PUT (0.79 m^2 ha^{-1}; Table 1). Species richness, diversity, and evenness of the herbaceous layer did not have consistent trends across sites or rivers, but mean percent herbaceous cover increased consistently from NT to ST along the downriver gradients, except at MST (Table 1, Figure 2).

Examination of woody plant mortality across the study sites showed that dead tree basal area increased consistently from PNT to PST along the downriver gradient, but changed inconsistently along the Mattaponi with substantial dead tree basal area at MNT and MLT but negligible at MUT and MST (Figure 2). Mortality in the shrub community was better assessed in terms of stem density, where dead shrubs were more abundant at MUT and MST, generally increased from PNT to PLT, but then were less common at PST, which had dead tree stems predominating. Shrub live stem density increased substantially from NT to ST on both rivers.

Average annual BAI of all species from 1979 to 2015, the longest period of tree-ring record in common across all sites, generally decreased downstream along both tidal rivers (Kruskal-Wallis test: Mattaponi $p = 0.005$; Pamunkey $p = 0.001$; Table 1). Trees along both rivers had smaller BAI at their ST sites (59% and 57% reduction, respectively) compared with their UT sites. Overall, trees of all species sampled along the Pamunkey River had 4x greater BAI than trees along the Mattaponi River ($p = 0.001$). The same downstream trend existed for each of the two dominant species along both rivers, *A. rubrum* and *F. pennsylvanica*, but the Pamunkey River had 7x and 6x greater BAI, respectively.

Table 1. Species richness (S), Shannon-Weiner diversity index (H'), Evenness (E), basal area (BA), basal area increment (BAI, 1979–2015), and mean herbaceous percent cover values for live canopy trees, understory woody species and herbaceous layer species at the study sites. The '*' indicates only one 20 × 20 m plot for trees, two 5 × 5 m plots for shrubs and three 1 × 1 m herbaceous layer plots were installed and surveyed at site MST.

			TREES		
Site	**S**	**H'**	**E**	**Live BA (m^2 ha^{-1})**	**Mean BAI of Individual Trees (cm^2 yr^{-1}) ± 1 SD**
MNT	14	1.89	0.72	26.18	2.4 ± 1.2
MUT	10	1.87	0.81	20.88	1.6 ± 1.5
MLT	10	1.68	0.73	26.06	1.8 ± 1.9
MST *	3	0.90	0.82	20.95	0.7 ± 0.1
PNT	9	1.33	0.61	22.10	10.6 ± 6.8
PUT	7	1.58	0.81	44.43	11.3 ± 8.1
PLT	8	1.64	0.79	29.61	3.4 ± 1.9
PST	6	1.43	0.80	15.57	4.6 ± 2.9
			SHRUBS		
Site	**S**	**H'**	**E**	**Live BA (m^2 ha^{-1})**	
MNT	6	1.16	0.65	1.02	
MUT	7	1.08	0.56	1.19	
MLT	9	1.78	0.81	1.27	
MST *	6	1.67	0.93	1.88	
PNT	5	1.61	1.00	0.22	
PUT	6	1.00	0.56	0.79	
PLT	8	1.50	0.72	1.56	
PST	3	0.64	0.58	1.38	
			HERBACEOUS LAYER		
Site	**S**	**H'**	**E**		**Mean Vegetative % Cover ± 1 SD**
MNT	25	1.41	0.44		40.2 ± 28.6
MUT	36	2.37	0.66		62.0 ± 36.1
MLT	27	1.87	0.57		90.5 ± 14.3
MST *	19	1.65	0.56		34.3 ± 7.7
PNT	29	2.25	0.67		45.2 ± 24.0
PUT	27	2.45	0.74		73.5 ± 17.5
PLT	37	2.23	0.62		67.0 ± 27.8
PST	31	2.62	0.76		88.8 ± 8.8

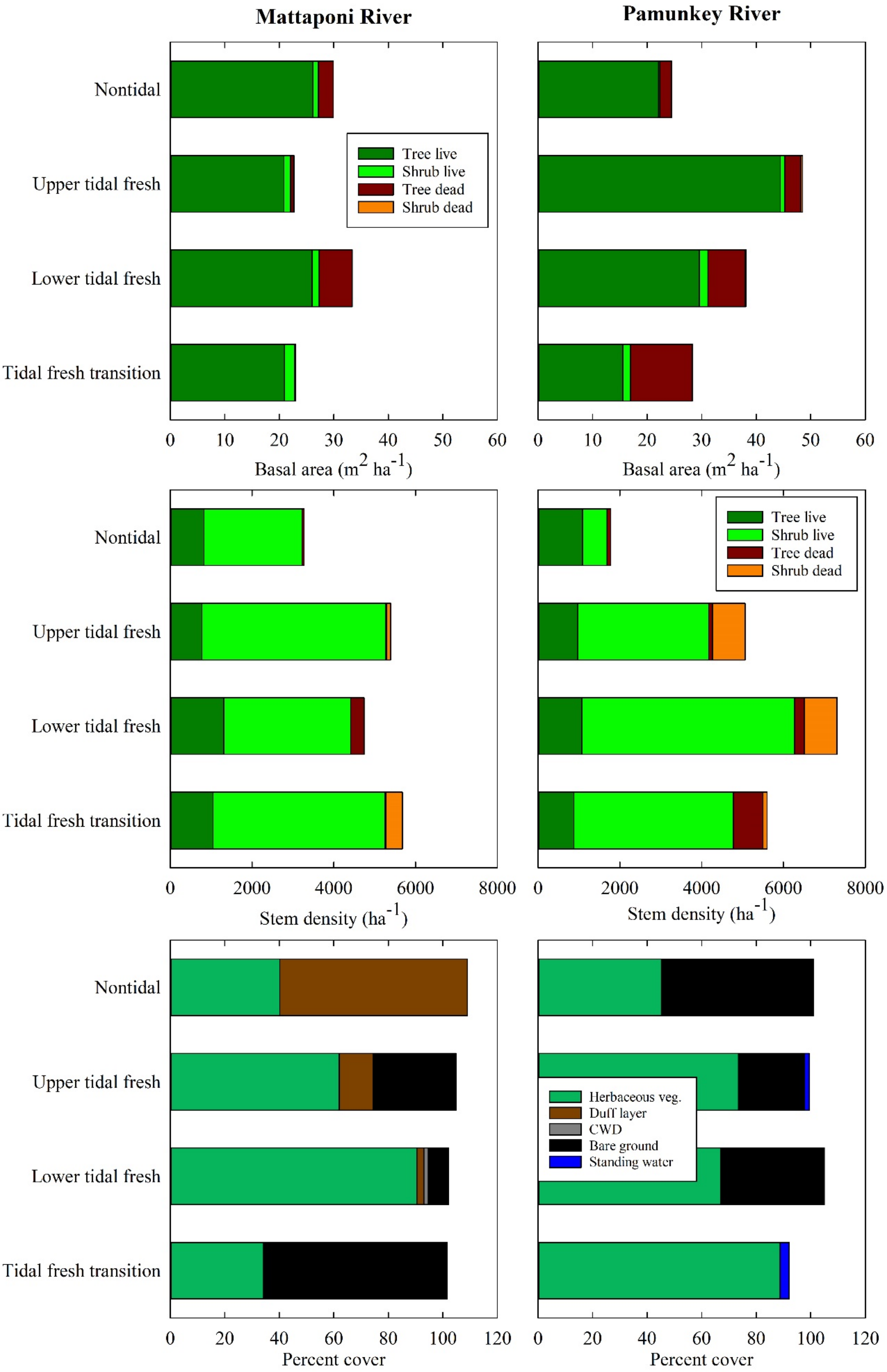

Figure 2. Mean basal area (**top**) and stem density (**middle**) for live and dead trees and shrubs, and percent herbaceous cover (**bottom**) at each of the study sites on the Mattaponi (**left**) and Pamunkey rivers (**right**) in 2016.

Species-level analyses of BA, percent cover, and IV (Table 2) showed that Mattaponi NT and UT sites are dominated by *Fagus grandifolia* Ehrh., *Nyssa sylvatica* Marshall and *A. rubrum* in the canopy, *Ilex opaca* Aiton and *Carpinus caroliniana* Walter in the subcanopy and *Clethra alnifolia* L., and *Murdannia keisak* (Hassk.) Hand.-Maz. in the herb layer, while the more tidally influenced sites are heavily dominated by *F. pennsylvanica* and *N. sylvatica* in the canopy, and *M. keisak*, *Persicaria sagittata* (L.) H. Gross, and *Viburnum nudum* L. seedlings in the herb layer. Pamunkey River NT and UT have canopies dominated by *A. rubrum* and *F. pennsylvanica*, whereas LT and ST sites mainly support *Nyssa biflora* Walter, *F. pennsylvanica,* and *N. sylvatica* in the canopy. The herb layer at all Pamunkey sites tended to have a more diverse composition of common herbs, with *M. keisak*, *Saururus cernuus* L., and *Peltandra virginica* (L.) Schott being particularly abundant. The shrub and understory tree layers were more variable across sites, with each site supporting one primary, often highly dominant species (*I. opaca* at MNT, *Alnus serrulata* (Aiton) Willd. at MUT, *Magnolia virginiana* L.at MLT, and *A. rubrum* at MST; *C. caroliniana* at PNT, *Ilex verticillata* (L.) A. Gray at PUT, *A. serrulata* at PLT, and *Morella cerifera* (L.) Small at PST).

3.2. Interannual Variation in Tree Growth

The 1-year lag regression analyses of mean BAI of all trees in a site, in relation to the prior year river and estuarine controls, did not perform substantially better than BAI in relation to the current year controls (Table 3). All-possible linear regression analyses on contemporaneous growth rates of the mean BAI of all species combined within a site identified a best model with statistical significance for all study sites (range of p: 0.027 to <0.0001, R^2_{adj}: 0.26–0.75; Table 3). Mean annual estuarine water level was the most consistently significant predictor of mean BAI of all tree species across most study sites. It had a significant positive effect at MUT, MST, PNT, and PST and a significant negative and borderline significant negative effect at MNT and PUT, respectively, but had no effect at the LT sites on either river. Mean annual river flow had a significant positive effect at MNT and PUT, whereas it was included in the best model but had a nonsignificant negative influence at PNT. Flow-normalized mean annual river TN also had a significant negative effect on tree mean BAI at MNT and MLT, while flow-normalized mean annual river TP had a nonsignificant positive influence at PLT and a significant negative effect at PST. Maximum annual estuarine salinity had a positive but nonsignificant effect at LT and ST on both rivers, approaching significance ($p = 0.0547$) only at the PST site (Figure 3).

Table 2. The most common species based on basal area and importance value (IV) at each study site in the canopy tree (top) and shrub and understory tree layers (middle), and the herbaceous layer species (bottom) with ≥5% average percent cover at one or more sites, along with their IVs. Bold fonts indicate high values.

TREES

Species	**MNT**		**MUT**		**MLT**		**MST**		**PNT**		**PUT**		**PLT**		**PST**	
	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV
Acer rubrum	3.90	30.3	2.22	21.5	1.94	27.8	2.00	67.9	**11.61**	**92.6**	**17.76**	**79.7**	3.23	46.9	2.22	51.6
Betula nigra	0.20	7.6	0.44	13.0					**6.34**	**100.6**						
Carpinus caroliniana	1.35	20.5	**2.92**	**59.8**					0.64	13.5	2.21	46.3			0.39	28.1
Carya cordiformis	2.50	24.9														
Fagus grandifolia	**6.69**	**50.6**	**4.89**	**36.1**	0.71	10.3										
Fraxinus pennsylvanica			1.44	30.4	**7.64**	**87.4**	**9.47**	**141.1**	1.37	25.9	**16.42**	**76.7**	**7.47**	**72.0**	**4.56**	**97.5**
Ilex opaca	**2.14**	**65.5**	**2.01**	**44.3**	0.07	14.5							0.35	15.5		
Ilex verticillata											0.07	19.6				
Liquidambar styraciflua	0.33	8.1			1.61	26.5			0.45	11.2	0.30	10.4				
Magnolia virginiana					1.39	30.7										
Nyssa biflora					A								**11.87**	**83.3**	**6.55**	**73.5**
Nyssa sylvatica	0.44	11.8	**4.86**	**57.9**	**8.84**	**56.3**	**9.48**	**91.1**			7.64	57.6	**6.45**	**52.9**	**1.53**	**23.3**
Platanus occidentalis			0.05	9.2					1.20	17.5						
Quercus phellos	4.18	29.3	1.00	13.8	1.61	18.3										
Ulmus rubra									0.35	19.9						

SHRUBS

Species	**MNT**		**MUT**		**MLT**		**MST**		**PNT**		**PUT**		**PLT**		**PST**	
	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV
Acer rubrum							**0.83**	**79.9**								
Alnus serrulata			**0.90**	**173.4**	0.06	11.8							**1.03**	**135.6**		
Betula nigra									0.02	51.0						
Carpinus caroliniana	0.08	24.1	0.02	18.2					**0.15**	**106.6**		19.8				
Campsis radicans									0.01	45.2	0.02	27.4				
Celtis occidentalis															0.06	39.5
Cornus sp.					0.05	22.5	0.05	31.1					0.2	46.9		
Diospyros virginiana									0.01	45.2			0.12	21.6		
Fraxinus pennsylvanica			0.05	20.3	0.11	22.3	0.59	67.2					0.03	13.2		
Ilex opaca	**0.68**	**167.1**			0.15	22.6	0.15	29.5					0.06	26.2	0.02	36.2
Ilex decidua			0.08	26.6												

Table 2. *Cont.*

TREES																
Species	**MNT**		**MUT**		**MLT**		**MST**		**PNT**		**PUT**		**PLT**		**PST**	
	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV
Ilex verticillata							0.22	69.0			**0.57**	**186.1**	0.06	15.2		
Lindera benzoin													0.04	27.8		
Lyonia ligustrina			0.03	19.0												
Magnolia virginiana					**0.57**	**97.4**										
Morella cerifera															**1.30**	**224.3**
Nyssa sylvatica	0.08	24.7			0.12	16.4										
Parthenocissus quinquefolia									0.03	52.1						
Rhododendron periclymenoides			0.10	24.5												
Vaccinium corymbosum	0.01	17.6														
Vaccinium stamineum	0.16	49.1														
Viburnum prunifolium											0.09	26.5				
Vitis sp.											0.05	21.2				

HERBACEOUS LAYER																
Species	**MNT**		**MUT**		**MLT**		**MST**		**PNT**		**PUT**		**PLT**		**PST**	
	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV	Mean Cover (%) ± 1 SD	IV
Boehmeria cylindrica									**5.0 ± 7.6**	**26.0**	1.7 ± 3.7	6.4				
Carex sp. 1					0.8 ± 1.9	3.4			3.7 ± 7.3	20.1			**11.7 ± 14.6**	**39.0**	2.5 ± 5.6	6.8
Chasmanthium latifoilum											**11.8 ± 16.4**	**37.9**	0.5 ± 1.1	4.5		
Cicuta maculata					3.2 ± 3.5	**13.4**							0.02 ± 0.04	1.5	8.0 ± 8.2	23.9
Clethra alnifolia	**25.0 ± 26.3**	**129.9**	**14.2 ± 13.7**	**54.6**	0.2 ± 0.4	3.6										
Cyperaceae sp. fine-leaved			**5.4 ± 11.1**	**22.6**												
Liquidambar styraciflua	1.1 ± 1.8	13.9	0.2 ± 0.4	6.1	0.8 ± 1.9	3.4										
Mitchella repens	**5.0 ± 7.1**	**33.5**	2.0 ± 3.6	11.9												
Murdannia keisak			**13.4 ± 29.8**	**46.5**	**43.7 ± 21.5**	**105.9**	0.4 ± 0.5	8.8	0.9 ± 1.9	7.7	**14.2 ± 23.9**	**42.3**	21.7 ± 21.9	70.3	**12.9 ± 9.9**	**36.1**
Persicaria sagittata			0.2 ± 0.4	4.2	**11.5 ± 9.5**	**35.0**	3.7 ± 4.5	27.9	0.2 ± 0.4	2.7	4.4 ± 9.2	17.6	6.2 ± 9.1	24.2	4.5 ± 2.8	17.2

Table 2. *Cont.*

TREES																
Species	**MNT**		**MUT**		**MLT**		**MST**		**PNT**		**PUT**		**PLT**		**PST**	
	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV	BA (m^2 ha^{-1})	IV
Peltandra virginica			0.02 ± 0.04	1.9	3.7 ± 3.9	12.9	3.0 ± 2.9	24.0	2.0 ± 3.7	12.8	**9.3 ± 11.6**	**33.0**	11.0 ± 7.1	41.5	**17.5 ± 8.0**	**46.6**
Poaceae sp. 1			0.2 ± 0.4	2.4			0.7 ± 0.9	14.2	**5.0 ± 7.6**	**26.0**			0.02 ± 0.04	1.5	0.8 ± 0.7	6.6
Ptilimnium capillaceum															**7.5 ± 11.5**	**19.3**
Saururus cernuus			3.3 ± 7.5	12.5	**6.7 ± 4.9**	**22.8**	3.3 ± 4.7	22.6	**15.0 ± 16.8**	**76.0**	**5.8 ± 10.9**	**21.6**	1.3 ± 1.4	8.4	1.3 ± 1.8	6.5
Typha latifolia					1.7 ± 3.7	5.3									**12.5 ± 18.1**	**34.1**
Viburnum nudum							**7.7 ± 8.7**	**54.3**					0.8 ± 1.9	3.9		

Table 3. Best model results from all-possible regression analyses of the effects of watershed and estuarine variables on the mean basal area increment (BAI) growth of trees at study sites on the Mattaponi and Pamunkey rivers. Significance of individual terms in models: ˆ = $p < 0.075$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; **** = $p < 0.0001$. N/A = no significant model possible. Grey-shaded cells indicate the regression included 1-year lagged (prior year) effects of predictors on BAI.

	Nontidal		**Upper Tidal**		**Lower Tidal**		**Stressed Tidal**	
	Terms	**Sign and Sig.**	**Terms**	**Sign and Sig.**	**Terms**	**Sign and Sig.**	**Terms**	**Sign and Sig.**
Mattaponi mean BAIs: all species	River TN River flow Estuarine Water Level ($n = 31$, $p = 0.0085$, $R^2 = 0.35$, Adj. $R^2 = 0.27$)	- ** + * - *	Estuarine Water Level ($n = 31$, $p < 0.0001$, $R^2 = 0.69$, Adj. $R^2 = 0.68$)	+ ****	River TN Max Salinity TF4.4 ($n = 26$, $p < 0.0001$, $R^2 = 0.77$, Adj. $R^2 = 0.75$)	- **** +	Estuarine Water Level Max Salinity RET4.2 ($n = 26$, $p = 0.006$, $R^2 = 0.53$, Adj. $R^2 = 0.48$)	+ * +
Pamunkey mean BAIs: all species	Estuarine Water Level River Flow ($n = 31$, $p = 0.0002$, $R^2 = 0.56$, Adj. $R^2 = 0.53$)	+ *** -	River Flow Estuarine Water Level ($n = 31$, $p = 0.027$, $R^2 = 0.31$, Adj. $R^2 = 0.26$)	+ ** - ˆ	River TP Max Salinity RET4.1 River Flow ($n = 28$, $p = 0.006$, $R^2 = 0.53$, Adj. $R^2 = 0.47$)	+ + +	Estuarine Water Level River TP Max Salinity TF4.2 ($n = 28$, $p = 0.005$, $R^2 = 0.49$, Adj. $R^2 = 0.43$)	+ *** - * +ˆ
Mattaponi mean BAIs: *F. pennsylvanica*	N/A		River TN ($n = 31$, $p = 0.27$, $R^2 = 0.09$, Adj. $R^2 = 0.06$)	+	River TN Estuarine Water Level Max Salinity TF4.4 ($n = 26$, $p = 0.024$, $R^2 = 0.45$, Adj. $R^2 = 0.37$)	- ** - ** -	Estuarine Water Level Max Salinity RET4.2 ($n = 26$, $p = 0.007$, $R^2 = 0.49$, Adj. $R^2 = 0.44$)	+ * +
Pamunkey mean BAIs: *F. pennsylvanica*	River TP Estuarine Water Level River Flow ($n = 15$, $p < 0.0001$, $R^2 = 0.90$, Adj. $R^2 = 0.87$)	- *** + +	Estuarine Water Level River TP River Flow ($n = 31$, $p < 0.0001$, $R^2 = 0.74$, Adj. $R^2 = 0.71$)	- ** - ** + *	River Flow River TP Max Salinity RET4.1 ($n = 28$, $p = 0.007$, $R^2 = 0.53$, Adj. $R^2 = 0.47$)	+ * + +	Estuarine Water Level Max Salinity TF4.2 ($n = 28$, $p = 0.25$, $R^2 = 0.25$, Adj. $R^2 = 0.19$)	+ˆ -
Mattaponi mean BAIs: *A. rubrum*	N/A		Estuarine Water Level ($n = 31$, $p = 0.0489$, $R^2 = 0.23$, Adj. $R^2 = 0.20$)	-	River Flow ($n = 16$, $p = 0.62$, $R^2 = 0.22$, Adj. $R^2 = 0.16$)	-	Estuarine Water Level River TN Max Salinity RET4.2 ($n = 26$, $p = 0.042$, $R^2 = 0.38$, Adj. $R^2 = 0.30$)	+ * + * +
Pamunkey mean BAIs: *A. rubrum*	Estuarine Water Level River Flow River TP ($n = 31$, $p < 0.0001$, $R^2 = 0.62$, Adj. $R^2 = 0.58$)	+ ** - +	River Flow River TP ($n = 31$, $p = 0.031$, $R^2 = 0.31$, Adj. $R^2 = 0.26$)	+ * +ˆ	Max Salinity RET4.1 River TP ($n = 28$, $p = 0.023$, $R^2 = 0.46$, Adj. $R^2 = 0.41$)	+ˆ +	Max Salinity RET4.1 Estuarine Water Level River TN ($n = 28$, $p = 0.020$, $R^2 = 0.45$, Adj. $R^2 = 0.38$)	- * + +

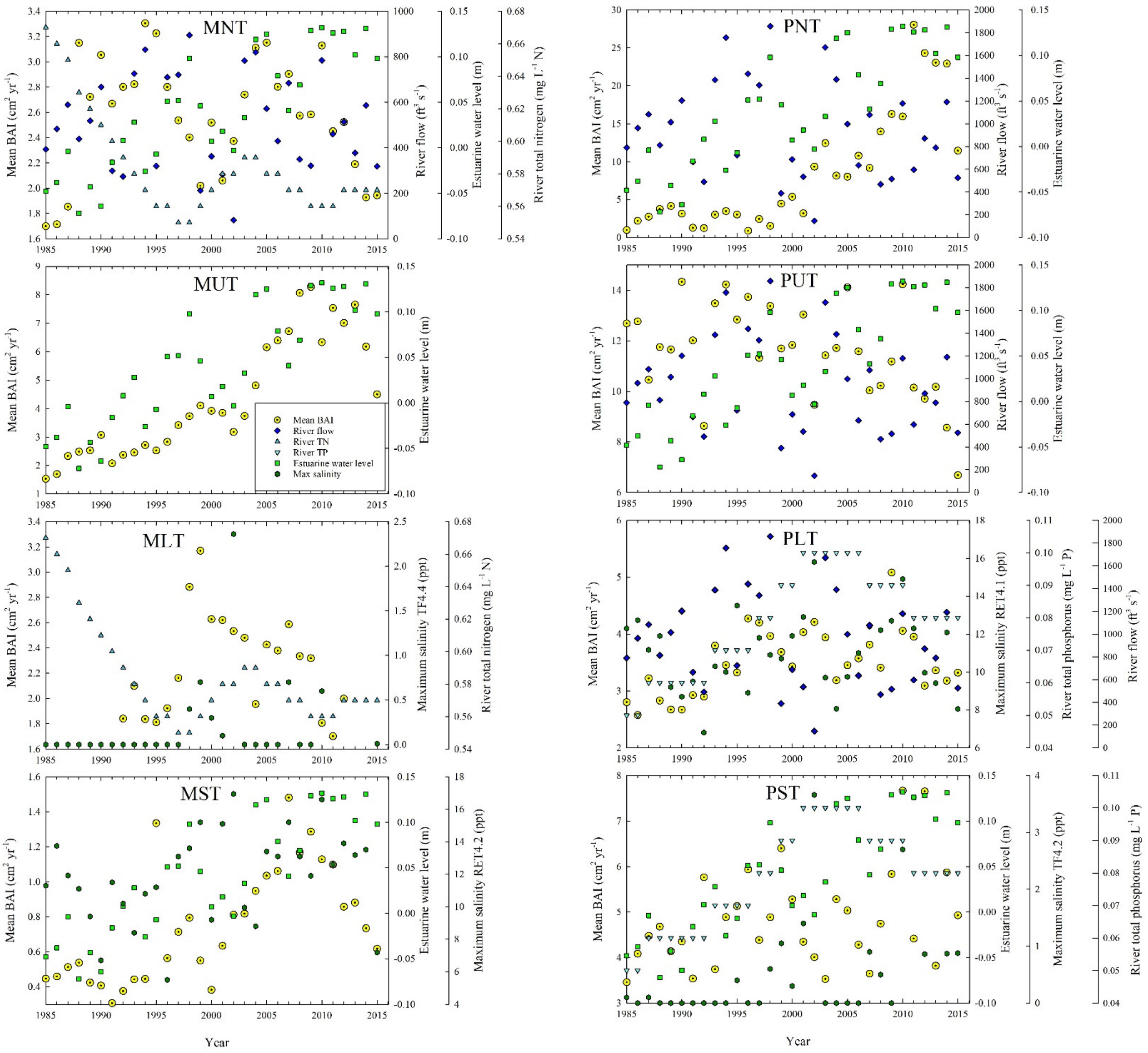

Figure 3. Changes in mean individual tree BAI and estuarine and watershed variables appearing in regression models of the Mattaponi River study sites (**left**) and Pamunkey River study sites (**right**). NT = nontidal, UT = upper tidal, LT = lower tidal, and ST = stressed tidal.

The same analyses on the species-specific growth rates of the two dominant tree species (*A. rubrum* and *F. pennsylvanica*) present at most of the study sites yielded somewhat similar results, with examination of current-year (contemporary) effects producing better regressions than 1-year lag analyses, except for *F. pennsylvanica* at MLT and for *A. rubrum* at MST, although these models were not strong ($R^2_{adj} = 0.37$ and 0.30 respectively; Table 3). Significant regression models were obtained for contemporary *F. pennsylvanica* growth at PNT, PUT, and PLT, with particularly strong results found at PNT ($p < 0.0001$, $R^2_{adj} = 0.87$) and PUT ($p < 0.0001$, $R^2_{adj} = 0.71$). Flow-normalized mean annual river TP had a highly significant negative influence on mean *F. pennsylvanica* BAI at both UT sites, while mean annual estuarine water level had a significant negative effect and mean annual river flow showed a significant positive effect at PUT. Mean annual river flow had a significant positive effect in the PLT regression model (Prob > F = 0.007, $R^2_{adj} = 0.47$), with mean river TP and annual maximum estuarine salinity at RET4.1 also included as positive but nonsignificant factors. No significant regression model for *F. pennsylvanica* growth was obtained for PST. Along the Mattaponi, a significant 1-year lag regression model for *F. pennsylvanica* BAI was found at MLT, where significant negative effects of flow-normalized annual river TN and mean annual estuarine water level were found for the next year's BAI. Mean annual estuarine water level had a significant positive effect and annual maximum estuarine salinity at RET4.2 and a nonsignificant but positive effect on contemporaneous mean BAI at MST. No regression models were significant at MUT, and *F. pennsylvanica* was not present at MNT.

For *A. rubrum*, significant regression models for effects on contemporaneous growth were found at all Pamunkey River sites (Table 3). Mean annual estuarine water level had a significant positive effect on *A. rubrum* mean BAI at PNT, mean annual river flow and flow-normalized river TP had significant positive and borderline significant positive (p = 0.051) effects respectively at PUT, and annual maximum estuarine salinity at RET4.1 had a nonsignificant positive influence (p = 0.065) and significant negative effect at PLT and PST, respectively. At Mattaponi River sites, a significant regression model with a negative effect of mean annual estuarine water level on *A. rubrum* mean BAI was obtained for MNT, and a significant 1-year lag model with significant positive effects of annual maximum salinity at RET4.1 and flow-normalized mean TN on the next year's *A. rubrum* mean BAI was derived for MST. No *A. rubrum* BAI regression model was significant at MLT, and *A. rubrum* was not present at MNT.

4. Discussion

4.1. Plant Communities and Structure

Along both river systems, we found that forested wetland vegetation structure and composition changed along the gradient going from the upper reaches of tidal influence downstream to tidal freshwater sites impacted by salinity. Patterns of forest structure and plant community composition across our gradient of study sites were consistent with findings from other studies of salinity and sea level effects on tidal freshwater forested wetlands (TFFW). Canopy tree species more characteristic of Coastal Plain riparian forest dominated our nontidal sites, with *Betula nigra* L. abundant on the Pamunkey, *F. grandifolia* and *I. opaca* most important on the Mattaponi, and *A. rubrum* being of secondary importance at both sites. Our lower river and transitioning TFFW sites on both rivers were dominated by *F. pennsylvanica* and *N. sylvatica*, also including *Nyssa biflora* on the Pamunkey River, and compared generally well with prior studies of TFFW on the Pamunkey River [19,20,51,52]; however, our sites fit more closely into only one of the two tidal swamp community types identified by Rheinhardt [20], namely the ash-blackgum (*Fraxinus* spp., *N. biflora,* and *A. rubrum*) swamp type. *Liquidambar styraciflua* occurred at two of our sites on each river (MNT, MLT, PNT, and PUT), however, it was only a minor component in terms of both basal area and importance value, and therefore our study did not include the drier, less extensive maple-sweetgum (*A. rubrum*, *L. styraciflua*, *N. biflora*, and *Fraxinus* spp.) community type identified along the Pamunkey River [20]. Vegetation of TFFW along the Mattaponi and Pamunkey rivers also was similar to the nearby Nanticoke River along the Chesapeake Bay in the U.S. Mid-Atlantic [21]. Slightly farther south, TFFW along the Pocomoke River had similar woody vegetation except for the co-dominance of *T. distichum* [22]. The Mattaponi and Pamunkey river TFFW were also similar to Duberstein et al.'s [30] Swamp Tupelo community type of the eastern United States.

Unique dominant species in the subcanopy and shrub layer at each site might be explained by the fact that the woody subcanopy did not segregate into the same communities as the canopy layer, and perhaps this is a sign that resources are being partitioned differently based on natural succession [20] or, more likely, in response to different drivers of vegetation change affecting the understory than the forest canopy. Our analysis suggested that flood depth was one of those potential drivers as these sites experienced sea-level rise of approximately 18 cm over the three decades of tree growth measured in this study (Yorktown, Virginia, tide gage). Our sites also had species such as *I. opaca* restricted to the more upriver sites, and *C. caroliniana* trees most abundant at TFFW just below the head-of-tide, and *I. verticillata* tending to be found at wetter sites more downriver, generally concurring with Rheinhardt [20]. However, neither *Lindera benzoin* (L.) Blume nor the vine community were prevalent in our study, and *M. cerifera* dominated the subcanopy in transitioning forest along the lower Pamunkey River, in contrast with Rheinhardt [20]. Liu et al. [29] also documented increases in *M. cerifera* dominance as salinity rose above roughly 1 ppt in South Carolina TFFW, potentially foreshadowing the eventual spread of this salt-tolerant shrub in TFFW of the Mattaponi and Pamunkey rivers. Furthermore, while flooding does stress *M. cerifera*, that stress may be partially ameliorated by less N demand by this N-fixing species, creating a competitive advantage for *M. cerifera* over regenerating conspecifics of overstory trees as soil N availability fluctuates with salinization until herbaceous plants respond to the higher N concentrations at lower tidal freshwater and stressed sites [53].

The herbaceous layer composition conformed well with those of other ash-blackgum community descriptions in the TFFW of the Pamunkey River [19,20,51,52], with species such as *P. virginica*, *S. cernuus*, and *M. keisak* being common and widespread throughout our sites except MNT. Two minor differences were that *Carex* spp. were less common and *P. sagittata* rather than *Persicaria arifolia* (L.) Haraldson was among the most common herbaceous species. Of the three main vegetation strata we sampled, the herbaceous layer was most dissimilar to that of the drier maple-sweetgum community type and most similar to that of the wetter ash-blackgum type described by Rheinhardt [20], again possibly due to sea-level rise that occurred between the two studies.

Species richness was somewhat lower than that documented by Rheinhardt [20,52] along the Pamunkey River, however Rheinhardt used more sampling plots than we did. Nevertheless, the most important species and their abundances in the present study were generally representative of those recorded by Rheinhardt [20,52]. Canopy tree basal area was typically inversely associated with herbaceous species richness and cover, implying that locations with lower tree basal area had more open canopies and hence higher richness and abundance in the herb layer. Rheinhardt [20] posited a link between wetness, hollow coverage, and canopy openness based on trees being spatially restricted to hummocks and canopy sparseness due to increasing inundation. This occurred at our lower TFFW sites where hummock-hollow topography (or microtopographic highs and lows, [54]) is more developed, but also at transitioning TFFW sites where tree mortality led to a more open tree canopy.

Tree growth rates in our Mid-Atlantic sites also changed downriver along both rivers. Our study sites that are transitioning from TFFW to oligohaline marsh (MST and PST) had long-term, chronic reductions in BAI compared with most upriver sites with consistent freshwater conditions (MUT, MLT, and PUT). Similarly, tree growth rate reductions occur along coastal rivers in the south-Atlantic U.S. due to increases in salinity and inundation at the lower end of the tidal freshwater zone [27,29,37]. We also found much larger BAI along the more alluvial, redwater, and N- and P-enriched Pamunkey River compared with the more blackwater Mattaponi River, similar to *T. distichum* BAI differences among river regimes in the south-Atlantic U.S. TFFW [35].

4.2. Annual Basal Area Increment Changes

Changes in annual tree growth over time occurred in tandem with temporal variation in both watershed and estuarine drivers. Statistical models identified the effects of watershed river controls (e.g., freshwater flow and nutrient concentrations) and estuarine controls (e.g., sea-level and salinity) on mean annual tree growth over 31 years at all sites spanning the longitudinal river gradients of the two tidal rivers. The spatial scope of the influence of the watershed or estuarine drivers largely matched the hypothesis that these coastal rivers are longitudinal river gradient-based systems of diminishing watershed influence and growing estuarine influence moving downriver, although exceptions occurred. Watershed riverine freshwater discharge was predictive of changes in tree growth of the all-species average as well as the two dominant species over time at the nontidal, upper TFFW, and lower TFFW of the rivers, but never at the most downriver transitioning-stressed TFFW sites (most estuarine) at the salinization front. Estuarine salinity was predictive of tree growth (all-species average and the two dominant species) at both the transitioning-stressed TFFW site near the oligohaline zones of the rivers, as well as at the lower TFFW somewhat further upstream; only these two sites along each river had salinity assessed in the regressions testing among the potential predictors because appreciable salinity (i.e., >0.5 ppt) was not present at the more upstream locations. Conversely, estuarine water level was included in the best BAI models along the entire longitudinal gradient of forested floodplain for either all trees average or one of the two dominant species. In contrast, watershed river TN and TP flow-normalized concentrations were sometimes predictive at a subset of sites that showed no longitudinal pattern. Thus, in general, estuarine controls extended upstream to the nontidal floodplain, whereas watershed controls did not extend all the way downstream to the oligohaline transition.

Although the expected spatial patterning of watershed and estuarine controls was mostly confirmed, the directionality of how the drivers influence tree growth was often counterintuitive with inconsistent directionality and influence. When considering the mean annual BAI of all individual trees in a site, the most consistently positive influence on interannual variation in tree growth was maximum monthly salinity (typically less than 1 ppt, see below). Years with greater estuarine salinity pulses were associated with greater BAI production at all four downriver sites, even though long-term BAI was reduced at these sites. Along both rivers, estuarine salinity and water level were uncorrelated and the regressions identified independent salinity and water level effects at the TFFW sites transitioning to marsh. Our finding of pulses of greater salinity enhancing BAI is contradictory with other studies of the salinity tolerance of tidal freshwater tree species that have found that time periods with greater salinity decreased annual growth [27,33,37]. The positive responses to salinity in this study are most likely due to the generally low salinity along portions of the Mattaponi and Pamunkey rivers where TFFW is transitioning to marsh. The estuarine long-term salinity stations just upstream of the transitioning TFFW on both rivers rarely recorded maximum annual salinity values above 1.0 ppt, with TF4.4 on the Mattaponi having only one year and TF4.2 on the Pamunkey having just four years above this threshold in the 26 and 28 years of data available for each river, respectively. The large water volume of the downstream Chesapeake Bay can moderate salinity fluctuations in the York River and its two tributaries [55]. Sustained annual porewater salinity greater than 2 ppt is needed to cause a transition from TFFW to oligohaline marsh [23,56], although individual TFFW tree species can be affected at lower salinities to yield a change in tree community composition [30,40]. Hackney and Avery [57] later asserted that flooding by >1 ppt for more than 25% of the total inundation period would also be sufficient to begin to convert TFFW (dominated by *T. distichum*) to oligohaline marsh. We have little doubt that this lower salinity concentration and exposure duration has begun and will continue to impact the growth and survival of the dominant *F. pennsylvanica*, *Nyssa* spp., and *A. rubrum* trees along our two Chesapeake Bay rivers.

Another possible explanation for the unexpected direction of salinity effects is that the moderate salinization at the transitioning TFFW led to increased growth by the surviving trees due to less competition as forest canopies thinned due to dieback and mortality of some trees. Our transitioning TFFW sites appear to be in the early stages of saltwater intrusion impacts on the forest community. Yet at these and the other TFFW, living trees still present on the elevated hummocks may be benefitting from the reduced competition due to gap creation [52] and ability to obtain fresher water using deeper roots [58,59]. Finally, salinization increases inorganic N and P availability within tidal freshwater soils and sediments [53,60], which potentially stimulates primary production [61].

In contrast, we found that years with greater estuarine salinity in the oligohaline zone had significantly decreased growth of *A. rubrum* at the transitioning TFFW along the Pamunkey River. Of our two study rivers, the Pamunkey River has larger tidal river cross-section to transport estuarine salinity pulses farther upstream, which may allow estuarine salt to impact the stressed site on the Pamunkey River more than the stressed site on the Mattaponi River. From 2014–2019, our measurements of porewater salinity occasionally exceeded 1.5 ppt at PST but only 0.5 ppt at MST. In addition, *A. rubrum* is less tolerant of salinity and water level increases than the dominant *F. pennsylvanica* and *Nyssa* spp. at the site [30,52].

Watershed nontidal river flow had a uniformly positive influence on yearly BAI in downstream TFFW when it was a significant factor in the regression models. The sites with positive effects of river flow were well upstream of the limits of salinization (i.e., MNT, PUT, and PLT) on both river systems. Thus, the mechanism behind river flow's influence was not related to changes in salinity. Similarly, flow-normalized nutrient concentrations were also evaluated by the regression modeling and river flow's influence was independent of changes in nutrient availability. Similar to watershed river flow, estuarine water level mostly had positive influence on yearly BAI. The effects of estuarine water level were detected at locations including the nontidal floodplain sites where the river channel tidal range is attenuated to microtidal. The nontidal floodplain sites are inundated by watershed-derived flooding that may be hydraulically elevated in years when estuarine base level is raised, rather than being directly inundated by tide. Superimposed on the 18 cm increase in annual mean estuarine water level (Yorktown, VA, USA) are annual fluctuations of about 5 cm.

Thus, the mostly positive influences of both watershed nontidal river flow and estuarine water level suggest that tree growth in these forested riverine wetlands in and around the upper estuary is stimulated by wetter conditions. This finding is surprising given the frequent inundation of the TFFW and nontidal floodplain near the head-of-tide in this study, where mean water levels range from 10 cm below to 10 cm above the soil surface. In the UT and LT TFFW, however, trees grow on small hummocks that are elevated 10–20 cm above the surrounding soil surface. Locations with a greater water level within wetlands typically have decreasing floodplain forest aboveground productivity, but only where mean water level is above the soil surface during the growing season [39]; wetland tree diameter growth is reduced by either drought or flood stress, making wet soils optimal [36]. However, the growth of individual trees can be greater at locations with more flooding that reduces stand density [62]. Years with higher precipitation and hence higher river flow and reliably wet soils can also have both direct effects on alleviating soil moisture limitation of floodplain tree growth [38,63] as well as indirect effects that would enhance tree growth, such as increased cloudiness yielding decreased temperature and heat stress and increased dissolved oxygen content in surface waters [64].

The influence of watershed-derived river nutrients, as reflected in the flow-normalized total nitrogen (TN) and total phosphorus (TP) concentrations, on changes in tree growth rates over time also was unexpectedly a mixture of negative and positive relationships. In most cases where river TP appeared as a significant factor in the regression models, the effect was negative, decreasing wood production. Although counterintuitive at first consideration, there are several potential explanations. First, TFFW have among the lowest rates of long-term sedimentation and associated particulate nutrient deposition of any riparian wetlands [65,66], particularly in their lower reaches due to depletion of the watershed sediment load by deposition in upstream wetlands [13,21,22,67]. Therefore, river nutrient loads measured well upstream of the head-of-tide, especially P that is predominantly attached to suspended sediment [68], may not have much predictive relevance to tree growth in lower TFFW much farther downstream from the nontidal river gages. Second, although the nontidal and upper TFFW sites should receive their sediment and nutrient inputs mainly from the watershed, implying that river nutrient concentrations should be important, these sites may not be uniformly nutrient limited. Similarly, Anderson and Lockaby [61] documented much less nutrient limitation in nontidal forested wetlands located above the head-of-tide compared with strong P limitation in downstream TFFW.

5. Conclusions

Vegetation communities and structure changed, and long-term tree growth decreased, in forested wetlands along a downriver gradient from nontidal through tidal freshwater forested wetlands to tidal forests transitioning to marsh near the oligohaline zone of two tidal rivers. Interannual variability in tree BAI growth switched from predominantly controlled by river inputs of freshwater to estuarine salinity along the downstream river-estuarine gradient. However, counter to expectation, tree growth typically increased in years with greater estuarine salinity and water level. As canopy trees thin and die due to chronic stress from low-level salinization and inundation, surviving trees may undergo competitive release and are able to survive and temporarily slightly increase their growth rate due to the decreased density, increased sunlight, and potential for increased nutrient availability at sites with acute low-level salinization near or below 1 ppt. This positive response in the TFFW tree canopy to salinization may occur for several years, at least on a decadal scale in some situations, before sea-level rise and its corresponding salinity intrusion gradually but inexorably increase stress to TFFW trees. Shifts in plant community composition, especially in the shrub and herbaceous layer, suggest an early indicator of conversion of TFFW to oligohaline marsh along the downstream tidal gradient, prior to the substantial decline and eventual loss of longer-lived trees. This finding calls for greater attention to the subcanopy components of TFFW and dynamics of individual canopy trees during salinization to better forecast their transitioning to marsh and inform mitigation actions for their conservation.

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