



Article

An Analysis of Atlantic White Cedar (*Chamaecyparis thyoides* (L.) B.S.P.) Tree Rings as Indicators of Ghost Forest Development in a Globally Threatened Ecosystem

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Abstract: Atlantic White Cedar (AWC) swamps are a globally threatened type of wetland ecosystem and are a new form of ghost forest in the mid-Atlantic region of the US. Hydrogeomorphic regimes foster peat formation, resulting in unique biodiversity and carbon sequestration services. Our sites include regimes that are exposed to sea-level rise and storm-driven seawater intrusion, yet other sites are protected by higher elevations. In this study, we evaluated climatic variables to discern differences in tree ring formation as an indicator of growth among nine stands including micro-tidal, oligohaline sites as well as other protected areas which served as a control. Standard dendrochronological techniques were used, and series were divided into two sub-chronologies, 1895 to 1971 (early) and 1972 to 2018 (recent). AWC growth in response to precipitation parameters, e.g., Palmer Drought Severity Index (PDSI), were largely non-significant but were somewhat reversed among sub-chronologies. Early correlations were primarily negatively correlated with PDSI, while recent correlations were mostly positive, which suggests that even though inundation may reduce photosynthate availability for growth, precipitation has begun to increase growth by alleviating osmotic and toxic stresses associated with seawater. Analysis of climatic variables and tree growth at the reference site found that other anthropogenic stressors associated with ditching exert a greater influence. Hurricane impacts on tree growth exhibited no lasting negative effects; however, an AWC ghost forest report from New Jersey connected mortality to a hurricane. Hydrogeomorphic regimes may delay rather than eliminate risks associated with sea-level rise and storm-driven seawater.

Keywords: dendrochronology; hydrogeomorphic regime; hurricanes; Palmer Drought Severity Index; sea level rise; salinity; tree rings

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1. Introduction

Climate change affects coastal ecosystems through sea-level rise (SLR) [1] and increased storm intensity, among other mechanisms [2], impacting plant communities [3] and altering ecosystem services [4,5]. In coastal wetlands, climatic variables interact with local hydrogeomorphic conditions [6] and influence inundation and salinity, which are critical environmental determinants of wetland functions. The effects may be lethal to vegetation, and when entire forested ecosystems are affected, the standing deadwood is termed a ghost forest [3,7]. The phenomenon occurs in drowned river estuaries within two hydrogeomorphic settings: microtidal hydrologic regimes behind coastal barrier islands, where water levels are primarily influenced by wind, and macrotidal regimes, where barrier islands are lacking [8]. Due to climate change, hydroperiods and salinity are increasing in both contexts, thus understanding the role of inundation and salinity in ghost forest formation is necessary for developing predictive models and adaptive management strategies. Concerns are greater for ecosystems such as Atlantic White Cedar (AWC), *Chamaecyparis thyoides* (L.) B.S.P.-dominated swamps.

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Within the Cupressaceae family, the genus *Chamaecyparis* is restricted to extreme environments but is globally distributed [9]. AWC was first described as endangered in 1748 [10] and occurs in the United States from Maine to Mississippi in a narrow coastal band [11]. The swamp exerts hydrologic control through the production of peat, resulting in acidic and anoxic soil conditions [12] and influencing primary production [13], soil respiration [14,15], and decomposition [16] functions, causing additional peat formation and carbon sequestration. The peat maintains soil saturation and acts as a seed refugium during fire. When fire kills the canopy, dense regeneration of AWC ensues such that a monoculture develops [17,18], but the ecosystem is otherwise characterized by unique biodiversity [19]. In the mid-Atlantic region, AWC extent has gradually declined due to ditching within higher elevation sites such as the Great Dismal Swamp (GDS; mean elevation 3 m above Mean Sea Level) (Figure 1). A large portion of the swamp forms the Great Dismal Swamp National Wildlife Refuge (GDSNWR), which serves as a reference site in this study. Currently, the largest remaining AWC stands occur in Alligator River National Wildlife Refuge (ARNWR) within Dare County, NC, where the low landscape position (<1 m above MSL) has protected AWC stands from drainage. However, the low elevation exposes AWC stands to inundation and seawater associated with climate change (Figure 1).

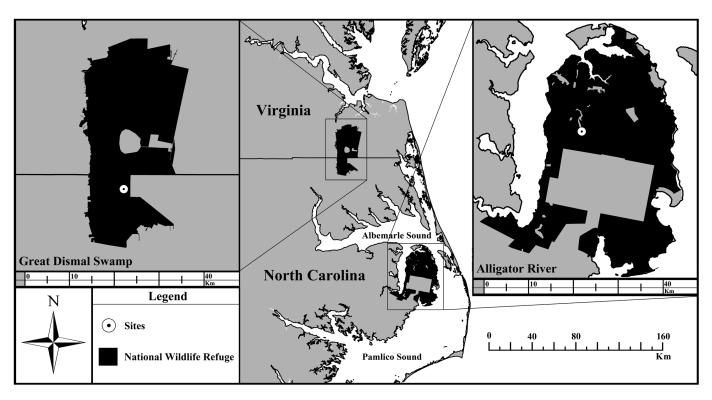


Figure 1. Location of Great Dismal Swamp National Wildlife Refuge (GDSNWR) and Alligator River National Wildlife Refuge (ARNWR). Alligator River forms the western boundary of the Albemarle-Pamlico Peninsula.

Soil saturation and inundation create anoxic soil layers to which wetland plants are variously adapted [20–23], and these stresses increase as a result of climate change [24]. Bald Cypress, *Taxodium distichum* (L.) Rich., and AWC historically were co-dominant species in our sites [25,26] and are classified as obligate wetland species [11], but the species diverge in their inundation tolerance. Bald Cypress persists where inundation is deep [27,28] and of long duration [29]; however, AWC is inundation-intolerant. Peatlands dominated by AWC are characterized by a micro-topography of hummocks and hollows with AWC establishing on hummocks. This pattern has been described in New Jersey [30] and in GDSNWR and ARNWR in Virginia and North Carolina [31]. Avoidance of the water table can also be achieved by shallow rooting, and Rodgers et al. [32], working within a subset

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of our stands, reported greater root biomass where water tables were higher. In addition, several authors have reported that young AWC exhibit reduced growth and increased mortality in response to inundation [33–36].

Seawater has osmotic and direct toxicological effects on non-halophytes [23] and enters coastal systems via chronic mechanisms such as salt wedges and tides, or more acutely as with storm-driven inputs where barrier islands otherwise protect estuaries [1,37]. Once seawater enters the sound system, dilution by watershed runoff creates a salinity gradient that is analogous to other drowned river valley estuaries, and both tidal and non-tidal wetlands plant communities are structured by the salinity gradient [38,39]. As sea level rises, the salt wedge progresses and species composition is altered [4,40]. In forested wetlands, other coniferous tree species exhibit reduced growth in response to seawater, including Loblolly Pine, Pinus taeda L. [41–43], and Red Spruce, Picea rubens Sarg. [44]. However, two other coniferous species in the Cupresaceae family appear to have some tolerance: Eastern Red Cedar, Juniperus virginiana, particularly J. virginiana var. silicicola ((Small) Silba) [11], although its occurrence in Virginia is not confirmed [45], and Bald Cypress, which accumulates salt in wood tissue [46] and can persist with salinity up to 3.4 ppt [47]. While no published studies of AWC salt tolerance were found, young AWC in a greenhouse study were shown to be sensitive to very low salt concentrations [48]. Early in the twentieth century, channelization of the Saint John River in Delaware decreased the growth of AWC, perhaps in response to increased salinity; however, growth rates among surviving trees recovered within 2 years [49]. AWC ghost forest formation was reported for mature AWC stands following Hurricane Sandy in New Jersey [50].

In addition to coastal peatlands along rivers, AWC swamps also occur in isolated hydrogeomorphic settings such as the Great Dismal Swamp in Virginia and North Carolina (Figure 1). These settings are not subject to sea-level rise or storm-driven seawater intrusion; however, unditched AWC peatlands were not available in the region. GDSNWR contains 254 km of ditches [51], and the lower water table allows for increased growth of conifers generally [52,53], and for AWC in GDSNWR [13] who found that growth between drained and undrained sites are similar; however, drained sites support fewer, albeit larger trees. In addition, while also working in GDSNWR [54], an evaluation of AWC tree ring growth correlated to water availability, which was modeled using the Palmer Drought Severity Index (PDSI), an indicator of monthly water availability as influenced by antecedent precipitation and temperature [55]. Correlation patterns diverged among drained and undrained stands, suggesting that PDSI can detect water stress in AWC in the mid-Atlantic region.

Extensive tree mortality in or near ARNWR has been linked to hurricane events [56], wind-driven water levels and salinity [1], local sea-level rise [3], and ditches [1,57]. AWC mortality was noted in patches of ARNWR as early as 2005 [58]. AWC tree ring growth has been found to correlate with PDSI and is influenced by ditches in GDSNWR [54] and by historic channelization in Delaware [49]. Objectives of this study were to (1) evaluate climate variables as indicators of AWC growth among 103 trees in 4 stands in the ARNWR, (2) contrast the ARNWR tree growth response with that of a reference site consisting of 42 trees in 5 stands in the GDSNWR that are not exposed to sea-level rise or storm-driven seawater, and (3) combine climatic analysis with the hydrogeomorphic setting of ARNWR in order to anticipate the response of the species to climate change.

2. Materials and Methods

2.1. Study Area

Alligator River National Wildlife Refuge (ARNWR) is located between the Albemarle Sound and Pamlico Sound about 16 km from the Atlantic Ocean on the Albemarle-Pamlico Peninsula (Figure 1). The ~61,600 ha refuge was established in 1984 [59]. ARNWR ranges in elevation above sea level from 3.8 m in the west to 0.3 m in the east [60] and water inputs in this hydrogeomorphic setting are primarily influenced by wind direction and wind tides [6]. The dominant habitat type in the refuge is pocosin wetlands and AWC stands comprise ~2700 ha, which have been considered among the largest continuous

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stands of AWC in the species' range [19]. The pocosin wetlands that the refuge contains are characterized by deep mucks and peats, predominantly Pungo Muck soil series [60], which has organic horizons to a depth of 1.83 m [61]. Site selection included AWC as the dominant canopy species and Swamp Tupelo, *Nyssa biflora* Walt., was commonly associated in the canopy [62]. Sample sites were along Milltail Creek, a water body that flows east to west across the peninsula (Figure 1).

Great Dismal Swamp National Wildlife Refuge (GDSNWR) is located on the border of Virginia and North Carolina about 50 km from the Atlantic Ocean and adjacent to the Suffolk Scarp [19] (Figure 1). The 44,500 ha refuge was established in 1974 [63]. Elevation varies across the refuge from 4.6 m to 7.6 m above sea level in the west and gradually slopes (2 m per km) to the east, and water inputs are primarily precipitation and runoff [6,64]. AWC acreage declined following the operation of the Dismal Swamp Canal in 1805, which began to lower the water tables. Drainage increased following enhanced ditching in the 1950s [65] and ditches total 224 km in length [51]. The last 1200 AWC disappeared after Hurricane Isabel (2003) and our lab removed stem cuts in concert with salvage logging. Two peat-burning fires ensued without substantial regeneration, and remnant stands were most recently surveyed by Duberstein and Krauss [66]. Large stands of Red Maple, Acer rubrum L., and Nyssa spp. Are dominant in the refuge [67], and Red Maple and Swamp Tupelo were commonly associated with AWC in our sites in GDSNWR [62]. Soil composition in the refuge is mostly organic [68], and the soil type in our sites was a Pungo muck, as in ARNWR. Sample sites were located in the southern portion of the refuge and Corapeake, Forest Line, Cross Canal, and South were the closest ditches [69] (Figure 1).

2.2. Wood Sample Collection and Preparation

In ARNWR, we collected two cores from 20 trees within each of three stands in 2018 and cores from 54 trees in a nearby stand in 2003 [70]. In GDSNWR reference sites, stem-cut samples were collected from a total of 42 trees from five stands during 2006–2008 [69] (Figure 1). All trees were sampled at breast height on north/south and east/west axes. Core samples were dried and mounted. All samples were sanded with progressively finer sandpaper [71].

2.3. Cross-Dating and Chronology Development

Tree rings were measured for each core, and for at least 4 radii per stem cut, using a binocular microscope fitted to a Velmex TA (Velmex Inc., Bloomfield, NY, USA) micrometer system and measured to the nearest 0.001 mm and recorded using Measure J2X Software (v5.0) [72]. Patterson and Merry dated rings by visual reinspection of core and use of marker years and employed COFECHA (v6.06 P) and ARSTAN (v6.05 P) to generate master series of growth and to perform detrending of master series [69,70]. The remaining site series (3 sites in ARNWR) were cross-dated in the Dendrochronology Program Library, dplR [73], in R [74] using R Studio [75]. Detrending was also conducted in dplR using a Friedman Super Smoother, and master chronologies for ARNWR and GDSNWR of Ring Width Indexes (RWI) were produced. Reliability of each chronology was verified using Effective Average Correlation between Series (RBAR.eff), Expressed Population Signal (EPS), Mean Subsample Signal Strength (SSS), and Signal-to-Noise Ratio (SNR) thresholds [76,77].

2.4. Climatological Data

Palmer Drought Severity Index (PDSI), Palmer Hydrological Drought Index (PHDI), and average monthly temperature were retrieved from the National Centers for Environmental Information (NCEI) [78] from NOAA North Carolina Division 7 for ARNWR and Virginia Division 1 for GDSNWR. Hurricane data were obtained from an NOAA database, "Historical Hurricane Tracks", which uses data from the NCEI International Best Track Archive for Climate Stewardship, IBTrACS, and the NOAA National Hurricane Center Best Track Data, HURDAT2 [79]. An area of interest including ARNWR with a range of 20 nautical miles (37 km) was constructed and named hurricanes passing through between

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1895 and 2018 were sorted for highest intensity. The most intense named hurricanes were Gloria (1985), Donna (1960), Connie (1955), Ione (1955), and Cleo (1964) [79]. Three additional hurricanes of regional importance were also identified including Isabel (2003) [51], Hazel (1954) [37], and Irene (2011) [56] (Table 1).

Table 1. Descriptive information for five major named hurricanes within the AOI, 20 nautical miles (37 km) of ARNWR during the study period (1895–2018), and an additional three of regional importance [37,51,56]. Maximum Sustained Windspeed in knots (kt) is reported. Percent Change is the deviation from 10-year running average of RWI prior to the current year. Lags are in the current year, one, two, and three years post-hurricane, all contrasting the same 10-year period for each hurricane.

Year	Hurricane Name	Max Wind Speed in AOI (kt)	10-Year Running Average RWI	Percent Change from 10-Year Average			
				+0	+1	+2	+3
1954	Hazel	80	0.926	28.269	-11.089	22.449	39.807
1955	Connie, Ione	85, 65	0.984	-7.929	26.801	44.776	3.944
1960	Donna	85	0.966	-1.622	13.918	6.107	6.929
1964	Cleo	40	1.010	-10.034	-14.378	0.434	5.218
1985	Gloria	90	1.021	2.273	-14.681	-10.487	-14.670
2003	Isabel	85	0.981	7.507	-5.390	-2.230	-4.045
2011	Irene	65	0.986	3.337	0.366	-5.243	-2.396

2.5. Data Analysis

To better isolate the trends of sea-level rise from the late twentieth century to the present, chronologies at ARNWR and GDSNWR were divided in half based on average series age (chronologies ranged from 1895 to 2018, average age was 62 years, and the midpoint year was 1972). Thus, dataset groupings include an "early period" from 1895 to 1971 and a "recent period" from 1972 to 2018 (Table 2). Reliability of each chronology was verified by RBAR.eff, EPS, SSS, and SNR thresholds [76,77].

Table 2. Descriptive statistics of ARNWR and GDSNWR chronologies during full, early, and recent periods.

	ARNWR			GDSNWR			
	Full	Early	Recent	Full	Early	Recent	
Number of Trees (number of time series)	103 (420)	102 (416)	103 (419)	42 stem cuts (≥168 radii)	42 stem cuts (≥168 radii)	42 stem cuts (≥168 radii)	
Chronology Length	1895-2018	1895-1971	1972-2018	1919-2003	1919-1971	1972-2003	
(years)	(123)	(76)	(46)	(84)	(52)	(31)	
Mean Age	62.25	28.88	33.69	81.26	49.26	32	
Median Age	61	30	32	81	49	32	
Signal-to-Noise Ratio (SNR)	31.147	38.57	28.341	43.888	64.379	28.565	
Mean Subsample Signal Strength (SSS)	0.8175	0.7859	0.9659	0.9943	0.9935	1	
Expressed Population Signal (EPS)	0.969	0.975	0.966	0.978	0.985	0.966	
Effective Average Correlation Between Series (RBAR.eff)	0.184	0.273	0.126	0.522	0.623	0.405	

Correlations of monthly climatological variables and standardized annual growth were evaluated using a 24-month climate window consisting of January in the previous year to December of the current year. Climate correlations were performed on both periods in the ARNWR and in the GDSNWR study sites.

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Most parameters failed normality tests both before and after transformation, so a Spearman Ranked Correlation test was used for all months in the 24-month window. Significance thresholds were evaluated using the Benjamini–Hochberg method with a false discovery rate of 20% [80].

3. Results

3.1. ARNWR and GDSNWR Ring Width Index Results for the Full Chronologies

The ARNWR full (undivided) chronology results were reliable based on EPS (0.969), SNR (31.147), RBAR.eff (0.184), and Mean SSS (0.8175; Table 2). Chronologies for each time period at ARNWR were similarly reliable regarding EPS (\geq 0.966), SNR (\geq 28.341), RBAR.eff (\geq 0.126), and Mean SSS (\geq 0.7859; Table 2). Mean RWI was 0.993 and ranged from 0.74 (in 1951) to 1.294 (in 1957) (Figure 2).

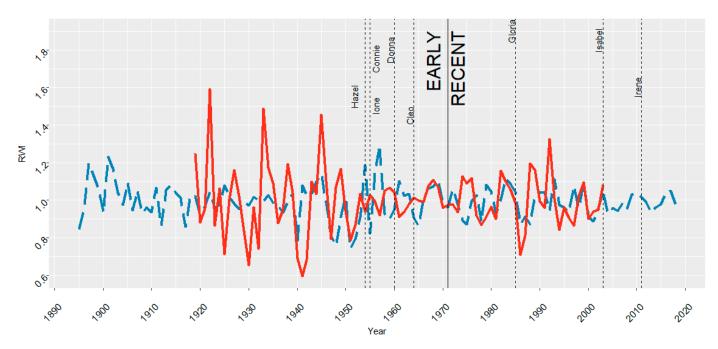


Figure 2. Ring Width Index (RWI) for the full study period, 1895–2018. ARNWR (dashed blue) spans 1895–2018 and GDSNWR (red) spans 1919–2003. Years 1971/1972 denote division of early and recent periods. The five most intense named hurricanes in ARNWR (based on wind speed in the area of interest) and three of regional importance from published studies are labeled. Higher names indicate greater relative intensity.

Major hurricane events in the early period generally increased growth at a lag of 1, 2, and 3 years but generally decreased growth for the year in which the hurricane occurred, based on comparison to a 10-year running average of RWI. Hurricane events in the recent period were generally associated with suppressed growth in 1, 2, and 3-year lags and increased growth in the year in which they occurred (Table 1).

The GDSNWR full (undivided) chronology results were reliable based on EPS (0.978), SNR (43.89), RBAR.eff (0.522), and Mean SSS (0.994; Table 2). Chronologies for each time period at GDSNWR were similarly reliable according to EPS (\geq 0.978), SNR (\geq 28.565), RBAR.eff (\geq 0.405), and Mean SSS (\geq 0.993; Table 2). Mean RWI was 0.997 and ranged from 0.595 in 1941 to 1.593 in 1922, which was considerably more variable than RWI in ARNWR (Figure 2).

3.2. Correlations of AWC Growth and PDSI at ARNWR and GDSNWR for Divided (Early and Recent) Chronologies

In ARNWR, correlations of growth and PDSI were not statistically significant but diverged sharply among recent and early periods. PDSI and growth in the previous year were consistently negative in the early period but became consistently positive in the recent

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period, particularly for the previous 12 months and continued through May of the current year (Figure 3a).

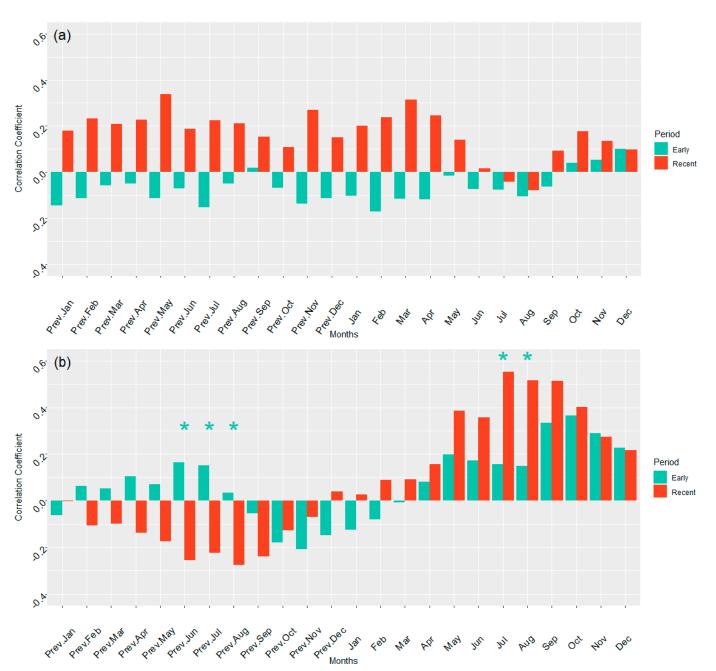


Figure 3. Spearman correlations in each month of 24-month window (12 months in current year and 12 in the previous year) based on standardized tree ring chronology and Palmer Drought Severity Index (PDSI) for ARNWR (a) and GDSNWR (b) sites. Each site is further divided into time periods including early (pre-1972, teal) and recent (post-1972, red). Significant correlations are denoted by "*", and colors correspond with periods.

In GDSNWR, correlations of growth and PDSI tended to be stronger during both periods (early and recent, maximum = 0.553) (Figure 3b), and correlations were generally higher than in ARNWR (maximum = 0.338) (Figure 3a). However, PSDI and growth correlation patterns did not diverge as they did in ARNWR. Patterns of correlations in early and recent periods were somewhat similar during the current year, and some significant correlations were detected during the previous year (early = negative; recent = positive) (Figure 3b). In the early period, the summer months of the previous year (June, July,

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and August) and two months of the current year (July and August) were significantly positively correlated.

3.3. Temperature Correlation with Growth in ARNWR and GDSNWR

ARNWR average monthly temperature for the early period had the highest correlation value in March ($r_s = 0.173$) and the lowest correlation value in previous January ($r_s = -0.198$) (Figure 4a). Correlation values between the previous and current year lacked a clear trend. The average monthly temperature for the recent period had the highest correlation value in previous December ($r_s = 0.197$) and the lowest correlation value in Previous March ($r_s = -0.262$). Correlation values between previous and current years lacked a clear trend.

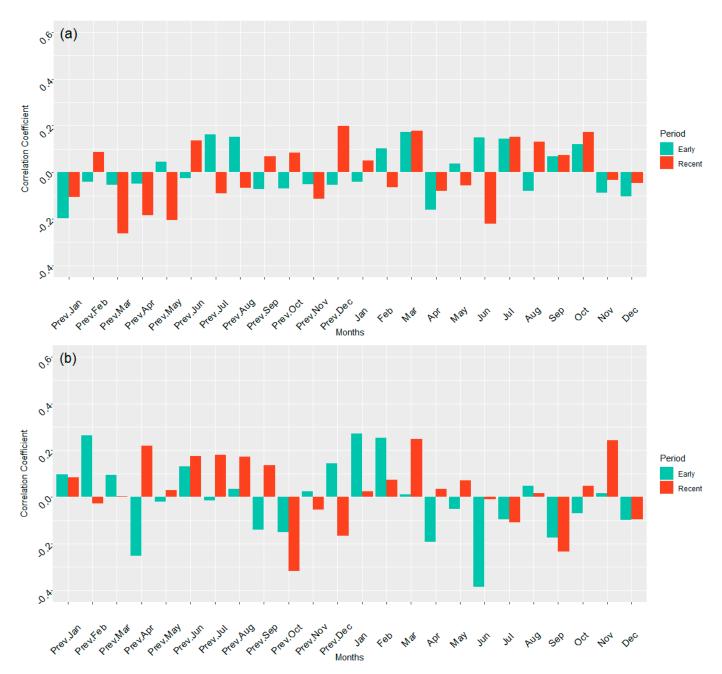


Figure 4. Spearman correlations in each month of 24-month window (12 months in the current year and 12 in the previous year) based on standardized tree ring chronology and average monthly temperature for ARNWR (a) and GDSNWR (b) sites. Each site is further divided into time periods including early (pre-1972, teal) and recent (post-1972, red). Significant correlations are denoted by "*" and colors correspond with periods.

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GDSNWR average monthly temperature for the late period had the highest correlation value in January ($r_s = 0.272$) and the lowest correlation value in June ($r_s = -0.384$) (Figure 4b). Correlation values between the previous and current year lacked a clear trend. Average monthly temperature and growth for the recent period had the highest correlation value in March ($r_s = 0.248$) and the lowest correlation value in previous October ($r_s = -0.316$), but no clear trend was detected among previous and current years with regard to temperature.

4. Discussion

4.1. Climate-Growth Relationships among Study Periods and Reference Sites

4.1.1. PDSI and Growth

The high values for EPS, interseries correlation (RBAR.eff), and mean SSS support evaluation of the four stands at ARNWR as a single chronology (Table 1). In contrast to the early period in this chronology (1908–1971), the recent period (1972–2013) exhibits a markedly different response of growth to PDSI. At ARNWR, PDSI and growth exhibited a non-significant, positive correlation in 12 of 12 months for the prior year and 9 of 12 months for the current year. We interpret the change as an indication that AWC is more sensitive to increasing seawater concentrations than to increasing inundation. Seawater intrusion into ARNWR is limited by the barrier island system and diluted by precipitation within the 4,755,000-ha Albemarle Sound watershed [37] and by the 141,000-ha Alligator River watershed [81], Goose Creek-Alligator River (HUC12: 030102050903), but salinity may have increased as a cumulative effect of SLR and storms during the 123-year tree-ring chronology. Precipitation (direct and via runoff from the watershed) dilutes salt and other soil toxins such as hydrogen sulfide [82] and alleviates these stresses on AWC. Stotts et al. [49] reported that growth was suppressed following the circa-1920 channelization of the Saint John River in Delaware, and the pattern of correlations of PDSI with growth is similar to the results reported here.

We found evidence that inundation inhibits AWC growth at ARNWR. In contrast to the ARNWR PDSI in the recent period, the early period ARNWR PDSI exhibited a non-significant, negative correlation with growth in 20 of 24 months. Inundation and soil anoxia associated with the seasonally saturated-flooded hydrologic regime [83] limit mineralization and reduce nutrient availability [84–86]. Furthermore, roots respire more when exposed to higher water tables in Loblolly Pine-dominated forest of the mid-Atlantic region [87], which has also been reported for our AWC stands [88]. AWC roots can tolerate long-term anoxic soil conditions [32], perhaps due to the species' ability to create aerenchyma through ethanol production [89], which would reduce the availability of photosynthate and result in the lower growth rate we observed.

In the reference site (GDSNWR), the AWC growth rate response to climate variables diverged from that of ARNWR, perhaps due to differences among hydrogeomorphic regimes. In the recent period, and to a lesser extent in the early period, growth rates of AWC in GDSNWR exhibited a stronger, positive correlation with PDSI during the current growing season (Figure 3b). The higher landscape position (~3 m above MSL), more inland location, and extensive ditching network in GDSNWR have been shown to lower the water tables there in comparison to ARNWR, which is generally <1 m above sea level [31] (Figure 1). GDSNWR growth patterns appear to confirm that reduced water availability can limit growth both above ground [54] and below ground [32] in GDSNWR, but not in ARNWR, where peat helps to maintain soil saturation. Root depth distribution represents a morphological adaptation to water table position [32], which complicates our comparison of the two sites, as deep rooting in GDSNWR prevents desiccation in late summer but exposes roots to excess saturation during early growing season months, resulting in root mortality at GDSNWR, but not at ARNWR. In addition, GDSNWR showed a weaker but still positive response to PDSI in the recent period, which may have been influenced by more extensive ditching efforts between 1955 and 1970 [90]. Ditching within GDSNWR

reduces the risk of anoxic stresses there, but lower elevation precludes drainage by ditching at ARNWR.

4.1.2. Temperature and Growth

Unlike PDSI, temperature was neither correlated with growth nor evidenced in seasonal trends in ARNWR or GDSNWR. Geographically positioned near the middle of the range for this species [19], temperature influences at both sites were expected to be minor [91] compared to sites near the northern limit of the range [92]; however, some environmental factors and responses merit discussion. During the current growing season, i.e., during early spring wood formation, growth in ARNWR is positively correlated with temperature (March of the current year) (Figure 3b), which is likely a response to extended growing seasons [93]. In addition, nutrient availability tends to be low due to sequestration within peat, and seasonal organic inputs reach a peak circa August within AWC swamps [13]. Mineralization of this more labile organic matter input may support subsequent growth.

4.2. Hurricane Responses for Both Periods in the Study Site

We found no major or lasting influence of hurricanes on AWC growth (Figure 2). Hurricanes may increase salinity through breaches in the barrier island system and by intensifying wind tides but can also lower salinity through watershed runoff [94]. Indeed, the greatest change we detected for the year after major hurricanes was positive (+26.8%, based on 10-year running average of ring width index) (Figure 2 and Table 1). Ury et al. [56] used remotely sensed data for ARNWR and found that hurricanes coincided with ghost forest formation, especially Hurricane Irene in 2011, which followed a drought. However, our trees showed no directional change in growth for 2011 or for the following 3 years, compared to a 10-year running average. Indeed, all three of the major hurricanes we considered occurred during the recent period, and all three coincided with negative trends in growth. Decreases were fairly minor except for Hurricane Gloria in 1985, after which growth declined by a total of $\sim 15\%$ within 3 years (Table 1). In the growth suppression analysis by Stotts et al. [49], hurricane-induced suppression of AWC was modest and persisted for less than 2 years. In contrast, AWC ghost forests formed following Hurricane Sandy in New Jersey [50,95], and the protection afforded AWC in the hydrogeomorphic regime at ARNWR may be limited.

4.3. Self-Maintenance Implications of Water Level and Salinity

For some wetlands, sediment accretion can keep pace with sea-level rise and maintain pre-disturbance inundation rates. Allochthonous mineral inputs accrete in response to local conditions in swamps [96] and both macro-tidal marshes [97] and micro-tidal marshes [98] and may offset relative sea-level rise, which is also locally variable [99]. Autochthonous organic inputs and peatland formation occur in some settings, and peat accumulation approached 10 m during the last 10,000–12,000 years in GDSNWR [100]. In the microtidal hydrogeomorphic setting at ARNWR, mineral sediment deposits are restricted to storm events [98], and AWC peat accumulation may be limited by seawater intrusion, which suggests that these stands may experience increased exposure to seawater intrusion as sea level continues to rise.

Ury [56] reported 11% of ARNWR forests have been converted into ghost forests, but those losses occurred on the eastern side of the peninsula and may have excluded AWC. Salinity decreases as one travels north and west on the peninsula and declines still further within the Alligator River, probably as a result of dilution by runoff from the 1479.50 km² watershed [101]. AWC stands are therefore protected by the hydrogeomorphic regime in which the barrier island system restricts tidal exchange in the sounds, the eastern half of the peninsula buffers storms, and salinity in the Alligator River is diluted by riverine discharges. However, Manda et al. [1] and Ferrell et al. [57] contend that sea water can extend from Alligator River to peatlands when wind-driven tides flow through natural

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and artificial ditches, and the change in monthly PDSI correlations with growth that we detected (Figure 2) supports their claim.

5. Conclusions

Water levels above those needed to saturate soil horizons are stressful to AWC, as detected in the early period (prior to 1972); however, we demonstrated a shift during the recent period, which implies a greater sensitivity to salt. In 2045, sea-level rise across North Carolina is expected to range from 6.1 to 13.7 cm [102], and storm intensity is expected to increase [2]. Given the projections for sea-level rise and probability of increasing storm intensity, it seems likely that geographic position and dilution provide little more than a delay in the loss of these stands and natural resource managers should plan for westward migration of species where higher elevations occur on Pocosin Lakes National Wildlife Refuge and Emily and Richardson Preyer Buckridge Coastal Reserve.

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