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SILVICULTURE IN FORESTED WETLANDS

Growth Rates of Atlantic White Cedar Depend on Hydrologic Regimes at Two Time Scales

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Abstract
Atlantic white cedar (AWC) stands form peat substrates in association with a seasonally flooded, saturated hydrologic regime. Less than 2% of the AWC swamp land area present during the pre-colonial era remains, and most of the current area now exhibits a temporarily flooded hydrologic regime. The purpose of this study was to quantify radial AWC growth at time scales that were cumulative (throughout ~60-year lifespans) and annual to clarify the relationship with hydrologic regime and climate in drained and undrained stands. Two 60-year-old stands having either drained or undrained conditions were selected in national wildlife refuges in Virginia and North Carolina, USA. Shallow groundwater wells fitted with continuous recorders measured depth-to-water-table during the 1999 calendar year to verify hydrologic regimes, and tree ring widths were evaluated from 54 trees per site. Cumulative time scale growth of individual tree stems was strongly suppressed by high water tables in the undrained stand. Annual growth rates among climate variables also diverged such that wetter months were positively correlated with tree ring width in the drained stand. Results suggest that AWC tree ring growth patterns can provide natural resource managers with insights into historic hydrologic conditions that influence ecosystem services and biodiversity.

Keywords Carbon sequestration · Hydrology · Water table · Tree ring chronology · Basal area increment · Peatland

Introduction

Atlantic white cedar (AWC, *Chamaecyparis thyoides* L. (B.S.P.)) is an obligate hydrophyte (USDA Plants Database 2018) that is the sole dominant tree species in a globally threatened type of forested peatland which was once a common swamp type (Noss et al. 1995). The species occurs along the outer US coast from Maine to Mississippi. AWC tolerates nutrient poor, highly acidic, and anoxic substrates classified as histosols and consisting of deep peat accumulations in some locations; the largest stands originally occurred in Virginia and North Carolina (Laderman 1989). Of the <2% of this ecosystem type that remains since the pre-colonial era, some stands are undrained and exhibit a seasonally flooded, saturated hydrologic regime (FGDC 2013) which protects a seed refugium that supports regeneration following fire or harvest (Little Jr 1950; Wurst et al. 2015). Other remnant stands are effectively drained and exhibit a temporarily flooded or similar hydrologic regime (FGDC 2013, Fred Wurster personal communication) which facilitates microbial oxidation of peat (Reddy and Patrick 1975). Growth parameters may be positively correlated to water availability as reported for forested floodplain species such as black walnut, *Juglans nigra* (L.) (Dudek et al. 1998) and oaks, e.g., *Quercus robur* (L.) (Gricar et al. 2013).

Cumulative growth of individual AWC trees is affected by a wide array of ecological conditions which include landscape position and the effect of peat on water tables. AWC swamps typically occur in a somewhat isolated hydrogeomorphic setting on the landscape and most swamps in this setting do not receive nutrients from overbank flooding (Brinson 1993). As peats develop, site conditions are further modified via increasing water holding capacity and the capillary fringe, a saturated layer of water under tension which can rise more than 60 cm above the phreatic water table (Verry 1997). The cumulative, negative effect of soil saturation on growth of various peatland tree species is evidenced by low tree height and circumference, and many northern countries with vast peatlands have developed extensive drainage plans to support silviculture goals since late in the twentieth century (Trettin et al. 1997).

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In the mid-Atlantic region of the US, drainage of AWC stands occurred by the mid-nineteenth century where peat accumulations were shallow, and extended to areas with deep peat by the mid-twentieth century (Lilly 1981). Several ecosystem services are associated with a seasonally flooded, saturated hydrologic regime (FGDC 2013) in natural peatlands. However, where ditches have been effective, temporarily flooded hydrologic regimes develop and most ecosystem services are negatively impacted.

Drainage can also alter water relations within peat. Long-drained peats exhibit biochemical and physical changes resulting in hydrophobic surfaces (Valet et al. 1991) that severely limit capillary rise (Lilly 1981), resist rewetting (Dolman and Buol 1967; Michel et al. 2001), and increase risk of peat-burning fire. In the Dismal Swamp, a 320-km ditching network drained most of the 400,000-ha swamp (USFWS 2018) and exerted cumulative effects on various ecological functions (e.g., Megonigal and Day Jr 1992) including tree growth which was demonstrated using basal area increment of tree rings (BAI_t) in loblolly pine, *Pinus taeda* L. (Phipps et al. 1978). Most of the last 1200 ha of AWC stands were destroyed by fires in 2008 and 2011 (Hutchins 2011, Bryan Poovey personal communication) and growth rates have not been reported.

Annual growth of AWC can be assessed through creation of unitless tree ring indices, which have successfully modeled ring response to annual climatic conditions in other species (Fritts 1976; Cook 1985), but rings may be complacent where moisture limitation to growth is infrequent (Dudek et al. 1998; Copenheaver et al. 2007) and where peatland soils retain moisture. Effects of precipitation also may be limited in AWC since roots can develop deeper according to water level (Korstian and Brush 1931; Little Jr 1950; Laderman 1989; Burns and Honkala 1990), and extensive microptopographic variation within AWC swamps influences oxygen distribution and availability (Ehrenfeld 1995; Atkinson et al. 2003).

Annual rings may be insensitive to temperature in the mid-Atlantic region located near the center of the species' distribution. Conversely, AWC found in Maine and thus at the northern extent of the range, exhibits temperature sensitivity which exceeds that of precipitation (Hopton and Pederson 2005; Pearl et al. 2017). Raney et al. (2016) suggested that high water tables in peatlands buffer some temperature responses among conifers, which could also limit ring sensitivity.

Hydrologic conditions and climate correlations have been reported for bald cypress (*Taxodium distichum* (L.) Rich.) (Stahle and Cleaveland 1992; Keim and Amos 2012; Stahle et al. 2012); however, similar studies are lacking for AWC. Natural resource managers may seek characterization of hydrologic regimes given the links to ecosystem services and biodiversity, as well as restoration planning. The purpose of this study was to characterize AWC tree ring growth responses at time scales that are cumulative (~60-year lifespan terminated by a hurricane in 2003) and annual (20-month climate model of annual growth) in stands representing disturbed (drained) and undisturbed (undrained) hydrologic regimes.

Site Descriptions

Alligator River National Wildlife Refuge (Alligator River), and the Great Dismal Swamp National Wildlife Refuge and North Carolina Dismal Swamp State Park (Dismal Swamp) represent the northernmost reaches of what Shaler (1890) refers to as swamp country in the Outer Coastal Plain Province. After reviewing historical logging records and aerial photos with refuge personnel, a ~60-year-old AWC stand in Alligator River and in Dismal Swamp were selected.

Alligator River

Alligator River is located in the Albemarle Peninsula of eastern North Carolina and was established in 1984 (35°50'N, 75°53'W). It contains about 61,600 ha of forested land, bordered on the west by the Alligator River, the east by Croatan and Pamlico Sounds, and to the north by Pamlico Sound (Laderman 1989) (Fig. 1). Elevation ranges from sea level to 3.7 m (Laderman 1989).

In addition to AWC, woody species representing ≥10% relative importance value (RIV) include swamp tupelo (*Nyssa biflora* Walt.) in the canopy and sweet pepperbush (*Lyonia lucida* (Lam.) K. Koch), holly (*Ilex coriacea* (Pursh) Chapman), and red bay (*Persea borbonia* (L.) Spreng.) in the subcanopy (Shacochis et al. 2003). Soils on the peninsula contain layers of silt, clay, sand, and shells beneath deep peat accumulations (Heath 1975). Organic matter, bulk density, and pore water pH was 97%, 0.10 SE 0.01 g/cc, and 3.5 to 3.6, respectively (Thompson et al. 2003).

Dismal Swamp

Dismal Swamp is located on the Virginia/North Carolina border about 250 km east of the coast (36°32'N, 76°28'W). The refuge contains 45,300 ha and is bordered by an escarpment (the Suffolk Scarp) to the west and the Atlantic coast to the east. The swamp ranges in elevation from 4.6 to 7.6 m and decreases in elevation approximately 0.2 m/km towards the east (Carter 1987; Laderman 1989).

Woody species representing ≥10% RIV include red maple (*Acer rubrum* L.) and red bay in the canopy and sweet pepperbush (*Clethra alnifolia* L.), fetterbush (*Lyonia lucida* C. Koch), and red bay the subcanopy (Shacochis et al. 2003). The soil is a deep histosol (2 m deep) that formed since the most recent glacial retreat (Whitehead and Oaks 1979), is classified as a Typic Medisaprist (Reber et al. 1981), and overlaying a clay layer (USDA 1974). The clay layer slows water

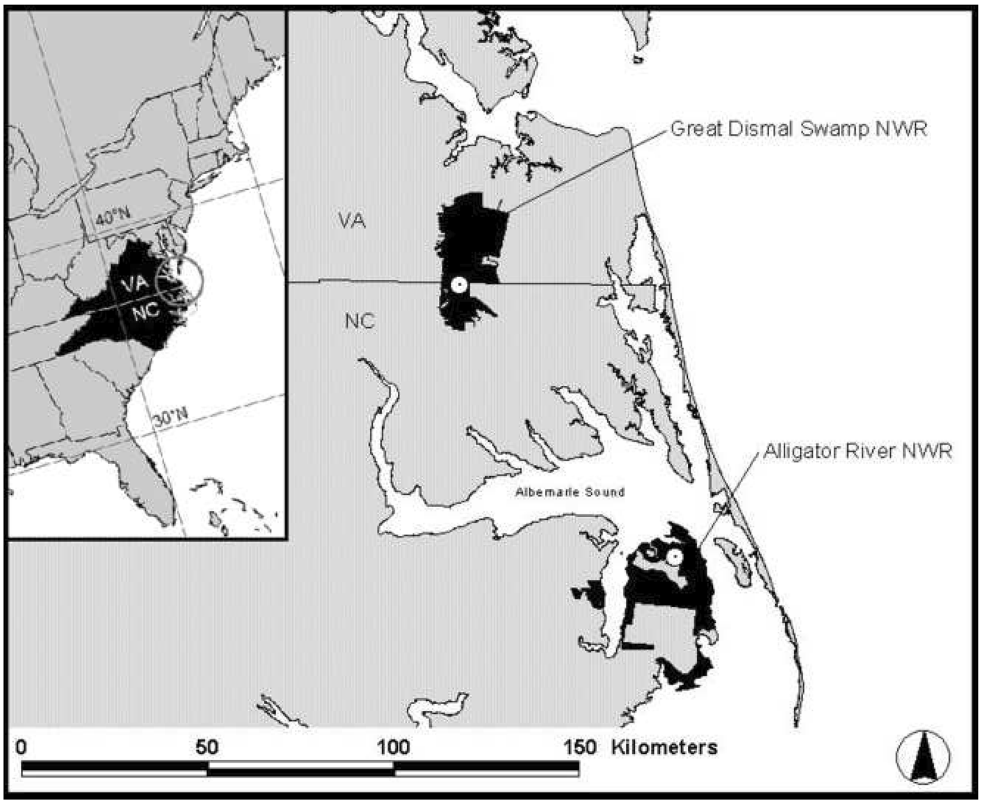

Fig. 1 Location of study sites in the Great Dismal Swamp National Wildlife Refuge in Virginia and North Carolina, and Alligator River National Wildlife Refuge in North Carolina. With permission from DeBerry and Atkinson (2014)

penetration which increases water retention within the peat. Organic matter content, bulk density, and stand pore water pH in Dismal Swamp was 93%, 0.16 SE 0.03 g/cc, and 3.3 to 3.6, respectively (Thompson et al. 2003). Although the growing season can be characterized as continuous in Dismal Swamp (Burdt et al. 2006), the growing season in Suffolk, VA, set forth by USDA NRCS (March 29 to November 7) was used in this study (Reber et al. 1981).

Methods

In each site, nine study plots were established, and shallow groundwater monitoring wells were installed within swales (aka pools) since thick roots beneath mounds prohibited well establishment. In 1998, one well at each site was fitted with a continuous recorder (Remote Data Systems™ WL-Series) and monitored for 14 months which included the 1999 calendar year, a year in which normal precipitation was recorded near both sites. Six AWC were cored at each study plot at both sites ($n = 54$ trees per site) during fall and winter, 2003 and 2004. Trees were cored at least twice through the entire diameter using a 4.33-mm-diameter bit with a 41-cm-long barrel. Cores were mounted on grooved pieces of wood and were sanded with progressively finer sandpaper (100 to 2500 grit) following Fritts (1976) and Stokes and Smiley (1996) until the tree rings were visible and clear (Merry 2005). Series were measured using a stereo boom microscope (Stokes and Smiley 1996) and a sliding stage connected to a computer with the software MeasureJ2X (VoorTech Consulting, Holderness, NH), which recorded the width of each ring with a precision of 0.001 mm. The series were visually cross-dated and statistically verified using the dplR package in R Studio version 3.2.2 (R Studio Team, Boston, MA 2018, Bunn 2010, Bunn et al. 2018). Phipps et al. (1978) suggested that for investigations of tree growth, tree ring widths should be converted to basal area increments for individual trees (BAI_t), which when quantified annually, provides a measure of cumulative growth (i.e., throughout the life of a tree). Similarly, Babst et al. (2014) distinguished between basal area increment of stands which those authors used for predicting forest carbon accumulation, versus BAI_t which they used as a measure of individual tree growth as employed in the current study. Basal area increment of each tree (BAI_t) was calculated in Excel (2016) using the formula:

$$BAI_t = \pi R_t^2 - \pi R_{t-1}^2$$

where R = radius of tree bole at a certain year (t). When pith was not reached during coring, the arc of the innermost ring of the tree was measured using a digital caliper to determine the missing area and ultimately obtain the radius of the initial year at 1.4 m above ground.

For the shorter, annual time scale, climatic response was accomplished using standardized tree-ring chronologies following Johnson and Abrams (2009) and Dennelar et al.

(2010). The tree-ring series were visually cross-dated, then cross-dated and checked for errors using the COFECHA program, Version 6.06p (Holmes 1983). The series were detrended to remove age related growth trends using a smoothing spline equal to 67% of stand age and were standardized to remove individual tree anomalies in favor of stand-wide trends (Cook 1985) using the dplR package. Signal-noise-ratio (SNR) values, a measure of series quality based on mean correlation of each ring width series compared to the master series, were quantified. Monthly Palmer Drought Severity Index (PDSI) and temperature data were obtained from the State Climate Office of North Carolina (2018). PDSI quantifies monthly precipitation incorporating previous monthly precipitation and temperature (Heddinghause and Sabol 1991) and was found to provide optimal prediction of AWC climatic response in Dismal Swamp by Patterson (2011). PDSI and mean monthly temperature were used to create a 20-month model consisting of 8 months in the previous year and 12 months in the current year to predict standardized tree-ring index values via Pearson Correlation tests.

Results

Hydrographs generated from continuously-recorded water levels within shallow groundwater monitoring wells detected a 60-cm difference in water tables at Alligator River and Dismal Swamp during a major portion of the growing season (Fig. 2). Based on climate station data, the total annual precipitation at Alligator River (146.8 cm; Cape Hatteras Climatological Station, 69 km distant) and Dismal Swamp study sites (140.6 cm; Wallaceton-Drummond Climatological Station, 8 km distant) was similar; however, median depth to water table during the 1999 growing season was considerably different among the study sites when hurricane-influenced events were excluded. Depth to water tables for Alligator River (Median − 0.41 cm, SD 5.76 cm) were closer to the surface than in Dismal Swamp (Median − 50.13 cm, SD 15.53 cm, $n = 155$ days, $P < 0.001$, Fig. 2, Table 1). Depth to water table

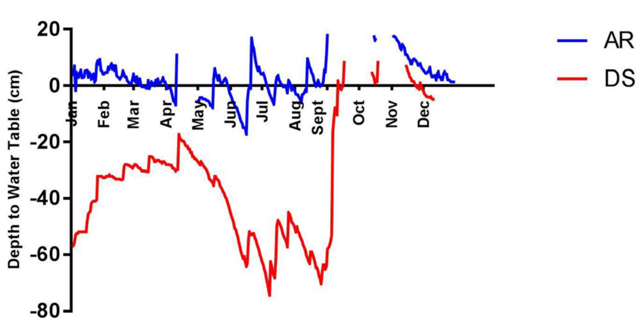

Fig. 2 Hydrograph representing depth to water table (cm) during 1999 in the Alligator River NWR (blue) and Great Dismal Swamp NWR (red) study sites

as a percentage of the growing season was calculated and was ≥20 cm below the soil surface for 0% at Alligator River and 68.8% at Dismal Swamp (Table 1, Atkinson et al. 2003).

Cumulative growth (Fig. 3) for individual trees over the 54 to 60-year period, expressed as BAI_t was smaller at Alligator River (239.78 mm^2, CI = 18.78 mm^2, $n = 54$) than at Dismal Swamp (1092.72 mm^2, CI = 74.38 mm^2, $n = 54$) ($P < 0.001$). For annual time scale assessment (Table 2), expressed population signals (EPS) at Alligator River (0.987) and at Dismal Swamp (0.984) were above the standard significance value of 0.85 suggesting that individual trees did not exert a divergent effect on the series (Wigley et al. 1984; Speer 2010); and SNR at Alligator River (0.530) and at Dismal Swamp (0.470) were above the threshold value of 0.328 suggested by Holmes (1983).

Monthly PDSI correlation values during the current year were not significant but tended to be negative at Alligator River (Fig. 4a), and at Dismal Swamp were mostly positive and were significantly positive for 4 months (September through December, Fig. 4b). Both sites tended to exhibit significant negative correlations with previous year monthly PDSI values.

Monthly temperature correlation values during the current and previous year were less often significant for both sites than were the correlations with PDSI. At Alligator River, current year temperature tended to be negatively correlated, especially in the months just prior to or at the start of the growing season (January, February, March, and April) which exhibited significant negative correlations (Fig. 5a). The tendency at Dismal Swamp was less pronounced but was significantly negative in June and December of the current year (Fig. 5b). Previous year temperature correlations at both sites tended to be negative but no monthly temperatures were significantly correlated with growth.

Discussion

Tree Rings at Annual Time Scale

Tree rings in the two study sites exhibited a somewhat divergent response to current-year monthly precipitation. The most statistically significant correlations were positive associations between precipitation (higher PDSI) and growth at the Dismal Swamp site where water tables were ~60 cm lower and were below the soil surface for a few months during the growing season (i.e., a temporarily flooded hydrologic regime). Similar growth responses have been reported for sugarberry (*Celtis laevigata* Willd.) and overcup oak (*Quercus lyrata* Walter) (Allen 2016) and for black walnut (*Juglans nigra* L.) (Dudek et al. 1998) in floodplain forested wetlands, indicating that trees are more sensitive to climatic variables when occurring on drier sites.

Table 1 Water Table (WT) characteristics during the 1999 growing season (GS, March 29–November 7) for Alligator River NWR (AR) and Great Dismal Swamp NWR (DS) AWC swamps based on continuous-recording wells. Hurricanes raised water tables above well recording range beginning on August 31 (at AR) and September 16 (at DS); depth to water table calculations exclude readings (*) that were obtained after August 30

Site	Inundation	WT ≥10 cm below surface as % of GS	WT ≥20 cm below surface as % of GS	Median WT (cm)*	WT variability
Standard Deviation*					
AR	62.1%	3.9%	0.0%	−0.41 cm	5.76 cm
DS	24.6%	72.8%	68.8%	−50.13 cm	15.53 cm

The positive response to PDSI at Dismal Swamp may result from drought sensitivity at this drier site. AWC typically exhibit shallow rooting (Pinchot 1899; Korstian and Brush 1931) which increases sensitivity to drought (Pallardy et al. 1995), and working in these same two sites, Rodgers et al. (2003) reported increased rate of AWC root mortality during periods of low water tables in Dismal Swamp, which these authors did not observe in the seasonally flooded, saturated site. The low water tables may have been further exacerbated by the condition of the peat as described above and may have resulted in frequent water limitations to growth that were not substantially reversed by high rates of precipitation (Verdonck 1983).

In the seasonally flooded, saturated site in Alligator River, growth and current year PDSI correlations were mostly negative though were not statistically significant. High water tables and the water holding capacity of the peat may have prevented draw down and resulted in persistent anoxic soil conditions which are commonly associated with reduced growth (Keeland and Sharitz 1997; Megonigal et al. 1997; Trettin et al. 1997).

Trees in both study sites exhibited lower response to temperature than to PDSI. Climate response is typically more complex at the center of a species' range relative to range margins (Hughes 2002). Pearl et al. (2017) studied AWC in New England, near the northern range limit of the species, and found that temperature effects on tree growth were greater than PDSI, opposite the findings of this study.

Significant negative correlations of growth and temperature were detected at both sites, including Alligator River (current year months of January, February and March) and at Dismal Swamp (current year months of June and December) (Figs. 5a, b). Higher temperatures may be associated with increased microbial and plant physiological processes at Alligator River, simultaneously increasing plant oxygen demand while reducing soil oxygen concentrations, particularly in winter months. At Dismal Swamp, cooler temperatures in June could delay early growing season growth that precedes summer water deficit stresses there.

Previous growing season conditions can influence growth rates in the current growing season (Fritts 1976). Trees in both sites in the current study exhibited negative associations between current year growth and previous growing season climate variables, particularly PDSI. Conifers use stored carbohydrates primarily for early-season growth (Gower et al. 1995; Kozlowski and Pallardy 1997) whereas diameter growth later in the growing season develops from current-year carbohydrates (Luxmoore et al. 1995). In addition, drought and cold temperatures may limit decomposition and nutrient availability in peatlands, further reducing growth the

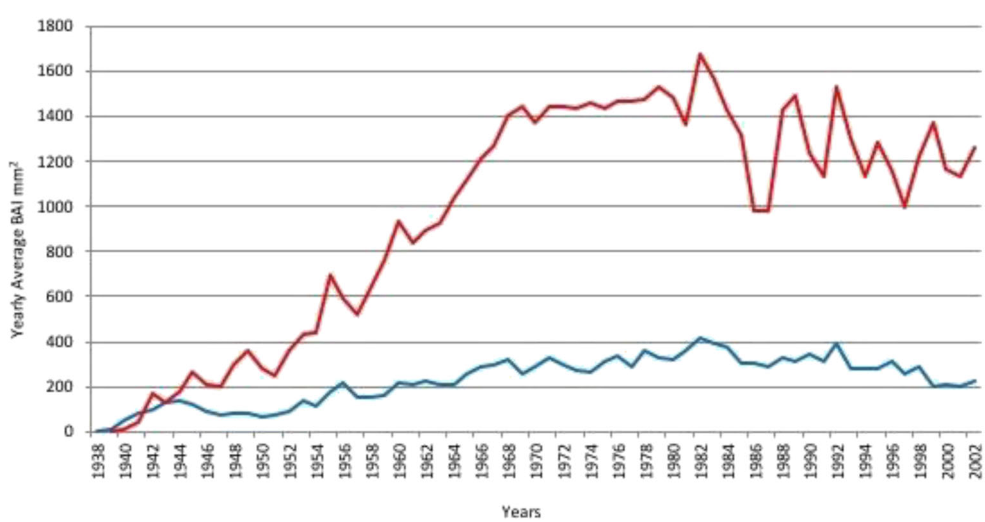

Fig. 3 Yearly average BAI_t for Alligator River NWR (blue) and Great Dismal Swamp NWR (red) study sites

Table 2 Final chronology description including sample size, time interval, age structure, total rings, averaged residual EPS, SNR, and averaged detrended ring indices r-bar for Alligator River (AR) and Dismal Swamp (DS)

Site	Trees sampled (count)	Tree cores (count)	Chronology interval	Mean age (min/max)	Rings in series	EPS	SNR	Mean rbar
AR	54	227	1938–2002	60 (49/65)	13,620	0.987	0.530	0.315
DS	54	231	1939–2002	54 (38/64)	12,474	0.984	0.470	0.267

following year. However, Day et al. (1988) reported that peat in one site in the Dismal Swamp retained sufficient root-zone moisture during drought conditions such that microbial activity was not limited.

Hydrologic Regimes

In Alligator River, long hydroperiods similar to that recorded for 1999 (Fig. 2) may be common. The Federal Geographic Data Committee (FGDC 2013) classifies such a hydrologic regime as "seasonally flooded, saturated" and Brinson (1993) described such sites as biogenic because persistent anoxia supports functions that form and maintain peat. However, the presence of ditches, such as are present at the Dismal Swamp, can lower the water table and establish a "temporarily flooded" hydrologic regime as classified by FGDC (2013).

Soil saturation differences between the study sites may be greater than that predicted by continuous-recording wells and could contribute to observed differences in AWC growth. The low topographic position of AWC stands in Alligator River

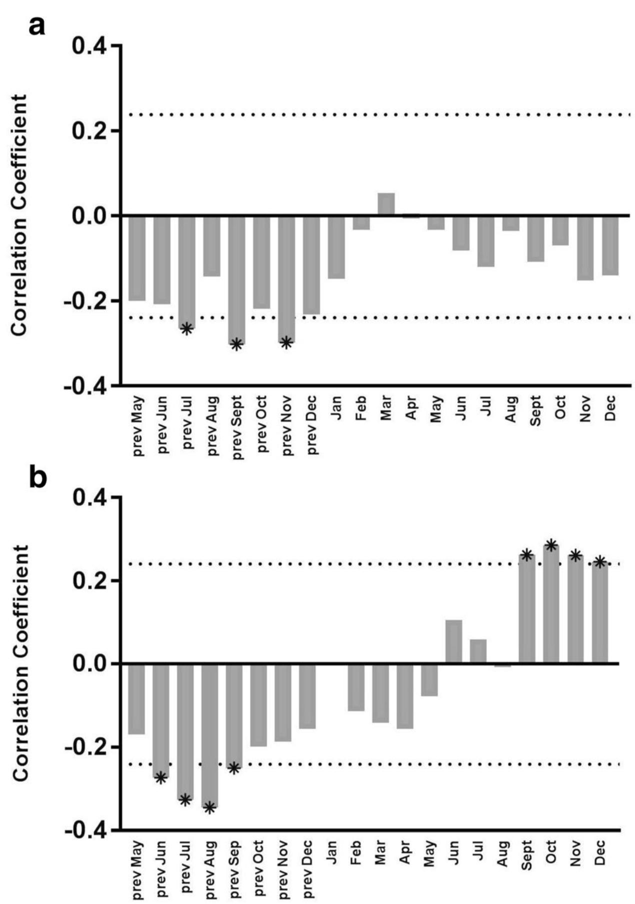

Fig. 4 **a** Alligator River National Wildlife Refuge site ring width correlation with current and previous year Palmer Drought Severity Index. Shaded bars represent significant correlation ($P < 0.05$). **b** Great Dismal Swamp National Wildlife Refuge site ring width correlation with current and previous year Palmer Drought Severity Index. Shaded bars represent significant correlation ($P < 0.05$)

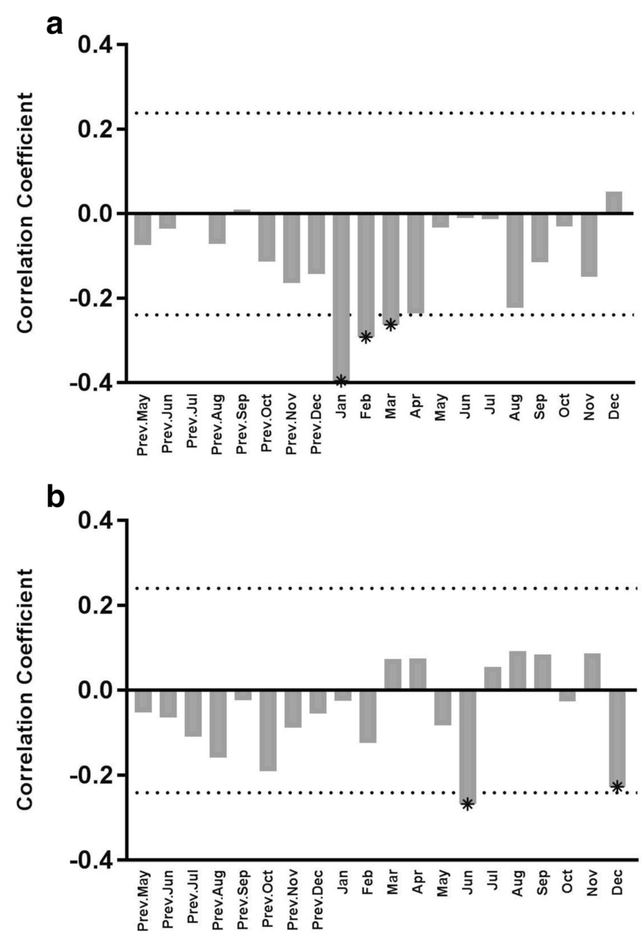

Fig. 5 **a** Alligator River National Wildlife Refuge site ring width correlation with current and previous year monthly temperature. Shaded bars represent significant correlation ($P < 0.05$). **b** Great Dismal Swamp National Wildlife Refuge site ring width correlation with current and previous year monthly temperature. Shaded bars represent significant correlation ($P < 0.05$)

(<1 m above sea level) precludes drainage and protects peat hydrologic functions such as high water holding capacity (Verdonck 1983), quick rise of water table following precipitation (Gillham 1984), and extensive capillary fringe which can saturate a soil profile by more than 60 cm above the water table in undrained peatlands (Verry 1997). In contrast, Dismal Swamp is ~5 m above sea level and ditches date to earlier than 1960 (some were first installed in the eighteenth century) and have effectively drained peats beneath AWC stands there. When drained for such long periods of time, normally hydrophilic peat surfaces have been shown to become strongly hydrophobic (Michel et al. 2001), particularly woody peats (Valet et al. 1991) which predominate in Virginia and North Carolina (Lilly 1981). As a result, capillary fringe may become severely restricted after drainage (Dolman and Buol 1967; Lilly 1981). Furthermore, shrinkage of drained peats can form cracks that allow rapid dewatering after rain events which was detected in December by continuously-recording wells (Fig. 2) and confirmed by manually-read wells following heavy rains in September through November (Atkinson et al. 2003).

Tree Rings at Cumulative Time Scale

Throughout the 60-year chronology, mean annual growth rate remained lower at Alligator River than at Dismal Swamp (Fig. 3). Anoxic soil conditions may be persistent and more stressful for AWC in Alligator River, but Dismal Swamp periods of anoxia may be of shorter duration and allow for greater growth over cumulative time scales. Anoxia has been found to limit growth in studies of myriad tree species in various settings including conifers in boreal peatlands (Trettin et al. 1997); bald cypress, an obligate wetland tree in floodplains (Conner and Day 1982; Megonigal and Day Jr 1992; Messina and Conner 1998); and several species planted in restored floodplain sites (Roquemore et al. 2014). AWC trees possess mechanisms to tolerate anoxic soils such as ethanol production (Kelsey et al. 2011) and exhibit elevated rates of root respiration when soil is saturated (Kalnins 2000). Under these conditions, AWC can out-compete other species, but the metabolic energy demands may slow growth of individual trees and reduce intra specific competition, resulting in dense stands that characterize the ecosystem as described by Laderman (1989) and DeBerry and Atkinson (2014).

Kozlowski and Pallardy (1997) suggested that, in addition to these stresses, nutrient availability may also be lower where soil saturation persists. Furthermore, tree growth in hydrologically isolated peatland forests may be constrained by the lack of connectivity to nutrient sources such as rivers that may strongly influence ecological functions of floodplain forests (Conner and Day Jr 1976; Conner et al. 2011). Nutrient limitations to growth may be less severe where temporarily flooded hydrologic regimes allow for peat mineralization.

Hydrologic regime effect on growth reported here are similar to those reported for <5-year-old planted AWC and other species and settings. Several studies of recently-planted AWC report that while inundation is often a major source of mortality, soil saturation is tolerated but inhibits growth of AWC among planted (Harrison et al. 2003; Cook et al. 2015; Foster et al. 2015) and naturally-regenerated stands (Wurst et al. 2015), i.e., young AWC trees in temporarily flooded sites grow faster than those grown in seasonally flooded, saturated hydrologic regimes.

Implications for Ecosystem Services

Carbon Sequestration Carbon sequestration results when primary production (carbon gain) exceeds peat oxidation (carbon loss); and tree rings have been used to help quantify these functions (Babst et al. 2014). Results of the current study add to the evidence that seasonally flooded, saturated hydrologic regimes are considerably more effective in carbon sequestration than are temporarily flooded AWC stands. In Alligator River, slower growth of individual trees reported in this study was offset by higher stem density such that standing biomass was equivalent (Alligator River = 199,844 kg/ha; Dismal Swamp = 207,649 kg/ha) at these same-aged stands (DeBerry and Atkinson 2014), and annual litter production at Alligator River was 125% of that at Dismal Swamp. These primary production patterns further illustrate the divergent response of this obligate hydrophyte to hydrologic regimes, but do not distinguish carbon sequestration rates. Rather, this key ecosystem service may be profoundly influenced by altered peat oxidation patterns that also can be predicted using AWC tree rings.

Peat oxidation can be chronic in the form of microbial decomposition, and acute as during peat-burning fires, and both processes are facilitated in temporarily flooded hydrologic regimes. Higher microbial decomposition rates in temporarily flooded peatlands have been reported globally (Moore and Dalva 1997; Holden 2005), in mixed hardwood forests within Dismal Swamp (Weiser 2014), and from soils within AWC swamps including the current study sites that were conducted in situ (Kalnins 2000) and in laboratory microcosms (Duttry et al. 2003). Dramatic, acute carbon loss during fire was reported in temporarily flooded AWC stands in the Dismal Swamp (Hutchins 2011). These functional differences point towards a need for natural resource managers to restore a seasonally flooded, saturated hydrologic regime.

Water Quality and Biodiversity Low water tables at Dismal Swamp may have facilitated decomposition (Bridgham and Richardson 1992; Hogg et al. 1992) and contributed to higher soil and water nutrient concentrations (Thompson et al. 2003) which can over-enrich receiving estuaries as described for peatlands by Macrae et al. (2013). Many peatlands also accumulate mercury, primarily from atmospheric deposition (Lodenius et al. 1987; Lavagnino et al. 2015), which can be released from temporarily flooded sites during peat oxidation (Turetsky et al. 2006).

AWC swamps contain a unique assemblage of species (Loomis et al. 2003) that includes endangered species (Laderman 1989) and enhances gamma diversity (Whittaker 1960); and, the ecosystem has been classified as a globally threatened (Noss et al. 1995). Saturated peat is essential for self-maintenance in AWC swamps which may live more than 600 years (Zimmermann and Mylecraine 2003). Stands regenerate when fire reaches the canopy and clears a stand, allowing sunlight to reach surficial peat layers which serve as a seed refugium. However, fire in a temporarily flooded hydrologic regime may allow a deep peat burn, e.g., recent fires is Dismal Swamp burned to a depth of more than 1 m, which eliminates the seedbank and results in an alternate successional direction. Longer periods of inundation may also threaten coastal swamps (Fernandes et al. 2018), and considerable acreage of AWC swamps is subject to loss via sea level rise, particularly in Alligator River National Wildlife Refuge.

Hydrologic Regime Classification and Management Recommendations

Characterizing Hydrologic Regime Using Tree Ring Growth Trends Cumulative growth at Alligator River was slow, such that average yearly increase in BAI_t (239.78 mm^2) was well below that at Dismal Swamp (1092.72 mm^2), and these growth rates may have been caused by hydrologic regime as described above. However, high stem density can also be associated with competition and slower growth rates (Ford 1975) which could confound interpretation of tree ring growth patterns unless annual growth is considered. Growth responses at the annual time scale were strongly correlated with monthly PDSI in models that diverged among the two stands, and serve to confirm characterization of hydrologic regimes at the two sites. In addition, variability in stem density and other disturbances associated with non-climatic events, e.g., blow downs, can weaken climate models; but in this study, both expressed population signal and signal-to-noise ratio were high (Table 2). Categorizing hydrologic regimes may be more difficult for stands in which cumulative time scales are interrupted by events such as selective logging, damming effects of road construction, or hydrologic modifications resulting from changes to ditches, as reported by Kowalski (2016) working in two AWC stands in Dismal Swamp.

Management Recommendations Globally, peatland forestry practices on privately held lands have favored soil drainage in order to increase tree growth (Trettin et al. 1997) and nearly all peatlands in the mid-Atlantic have been drained, either to increase tree growth or for conversion to agriculture. However, some wood products exhibit more valuable traits when growth is slower, which woodworking professionals term “tight grain” (Garland Wood personal communication). On publicly held peatlands, natural resource managers may value the array of ecosystem services described above. Fortunately, all are enhanced by restoration of a seasonally flooded, saturated hydrologic regime, and financial considerations also favor restoration given the high cost of extinguishing peat fires (USFWS 2019). Reestablishment of AWC would likely require water level control such that soils be saturated but would avoid inundation which is often lethal to young AWC.

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