

Effects of Coastal Flooding on the Growth of Trees in Low-Lying Forests along the St. Jones River, Delaware

Report

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Introduction

Accelerating sea level rise, and the increase of associated environmental stressors such as increasing flood intensity, is a major concern along the Mid Atlantic coast. Along the coast of Delaware, long-term sea level rise, exacerbated by geologic subsidence (forebulge collapse; Engelhart et al. 2011), is increasing locally by 4-5 mm yr^{1} (NOAA). This rate may exceed 10 mm yr^{1} by the end of this century (Callahan et al. 2017). Additionally, recent reports show that nuisance high tide flooding is becoming more frequent (Sweet et al. 2018). Given that one third of the United States population resides in coastal areas (NOAA 2013), tracking how sea level rise will continue to shape coastal environments and their resilience, or the capacity to recover from change, is integral to the well-being of millions of citizens and the health of their local economies.

As sea levels rise, flooding in low-lying forests will become more frequent. Intertidal marshes are already experiencing increased inundation (Haaf et al. *submitted manuscript*). Low-lying forests (elevations above MHW but less than 2 m NAVD88) likely flood semi-regularly and during storm events. Flood frequencies will become more recurrent as water levels rise and coastal storms become stronger. As many low-lying trees have limited tolerance to flooding, salt, or both, increased saltwater flooding will eventually lead to tree mortality and forest retreat. The precise mechanisms of ecological change, however, are not well understood due to variability among geographies and tree species.

We can discern how coastal flood exposure affects tree growth through studying patterns in annual growth rings. Previous studies have found that storm surge impacted low-lying loblolly pine (*Pinus taeda*) growth for three years after the event (Fernandes et al. 2018). Storm surge was also implicated in slash pine (*Pinus elliottii*) growth reductions up to 6 years following tropical storm flooding along the Gulf coast (Tucker et al. 2018). Thus, tree ring chronologies can provide the necessary information to discern how coastal floods affect low-lying forests.

Sap flow may provide essential context to study tree responses to saltwater flooding as it occurs. Typically, transpiration potential drives rates of sap flow in xylem tissues, but if water loss rates are too high, or if respiration rates at the roots decline, sap flow rates respond accordingly. In this sense, tree vulnerability to flooding and sea level rise can be assessed by monitoring how sap flow changes in response to flood events. For instance, Krauss and Duberstein (2009) found that bald cypress trees reduced sap flow rates to adapt to perennial salinity intrusion, which might act to reduce salt-driven mortality. Reduced sap flows limit the transport of nutrients, so these reductions likely have consequence to tree growth. The relationships between salt exposure, sap flow reductions, and resultant deficient growth convey the susceptibility of a tree to mortality after coastal flooding.

As storm surge and sea level rise become more challenging issues, understanding the effects of salt water inundation in low lying uplands is critical to management decision making. Studying tree exposure and responses to coastal flooding will help managers identify forests with the highest risk of impacts due to surge or sea level rise. The objectives of this study were to i) create growth chronologies of red cedar (*Juniperus virginiana*) and American holly (*Ilex opaca*) in low-lying, frequently flooded forests; ii) investigate climatic and flood exposure (by elevation proxy) influences in tree growth records; iii) monitor sap flow in a frequently flooded red cedar; and iv) map low-lying forests in the St. Jones River watershed to help define coastal flood exposure.

Methods

Study Location and species

Coastal Forests at the Delaware National Estuarine Research Reserve

Our study site was within the Delaware National Estuarine Research Reserve's (DNERR) St. Jones Reserve located in Kent County, DE. We sampled trees at the DNERR headquarters property, near Kitts Hummock, DE, as well as at the Ted Harvey Conservation Area, which is another site along the St. Jones River (Figure 1). We selected red cedar (*Juniperus virginiana* L. var. *virginiana*) and American holly (*Ilex opaca* Aiton) for this study for their abundance and exposure to flooding at the site.

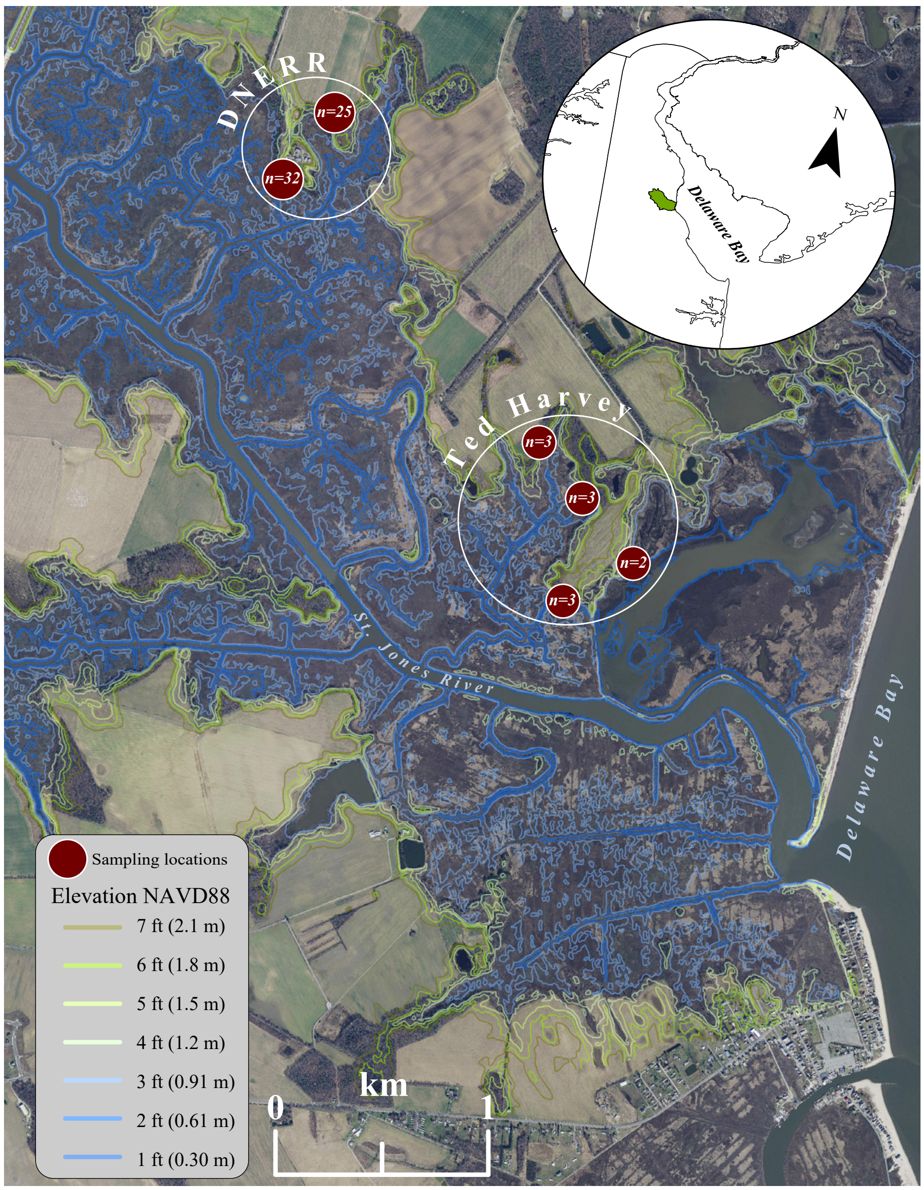

Figure 1. Map of the DNERR study area with elevation isolines. Red circles show locations of core extractions with sample numbers for both species.

Autecology of red cedars and American holly

American holly trees (*Ilex opaca* Aiton) are slow-growing, shade-tolerant evergreen angiosperms. It is commonly distributed along the coast from Massachusetts to Delaware and as far south as mid-Florida and west to eastern Texas (Dersal and William, 1938; Grelen, 1990). A mature tree can reach 50' (15 m) in height with a mature spread of equal size and a typical trunk diameter of 20" (50 cm)(Ferdinand, 1950). American holly is tolerant of a wide variety of soil types but grows best in moist, slightly acidic, well-drained or sandy soils. The growing season ranges from 150 days in its northeastern limit to yearlong in central Florida (Grelen, 1990). Growth rate is slow at 12" to 24" of height increase per year. American hollies are dioecious, so trees bear either flowers (males) or fruit (female; Figure 2A). Flowering begins around May-June in its northern range and, on female trees, berries ripen from September through December. Flowers are pollinated by insects, but seeds are distributed by birds and other small wildlife. Seed germination is very slow and can take upwards of 3 years to occur naturally (Bonner, 1974). American holly is resistant to salt spray (Martin, 1959) and although the tree has some degree of flood tolerance, it will not survive if soils are saturated for more than 17% of its growing season (Teskey and Hinckley, 1977). The wood of the American holly is pale, close-grained, dense yet not strong (Grelen, 1990). American holly has subtle, diffuse porous growth rings with abrupt latewood formation and prominent rays.

Easter red cedar (*Juniperus virginiana* L. var. *virginiana*) is an aromatic, early successional, frost hardy coniferous evergreen tree. Its distribution extends from southeastern Canada to northern Florida, west to Ontario, south through the Great Plains to the Gulf of Mexico (Anderson, 2003). Mature trees, living to be hundreds of years old, can grow to 70' (21 m) tall with a trunk diameter up to 67" (1.7 m). Eastern red cedar thrives best in moist, well-drained alluvial soils deeper than 24" (61 cm). High foliar calcium content typically changes the pH of underlying acidic or alkaline soils (Ferguson et al, 1968). Eastern red cedars are dioecious, with females bearing small blue cones (Figure 2B). Pollen is wind dispersed February through May depending on the location (Convers, 2003). Eastern red cedars pioneer open fields and rugged upland areas. Its growing season ranges from 120 days in the north to 250 days in the south. They grow under a

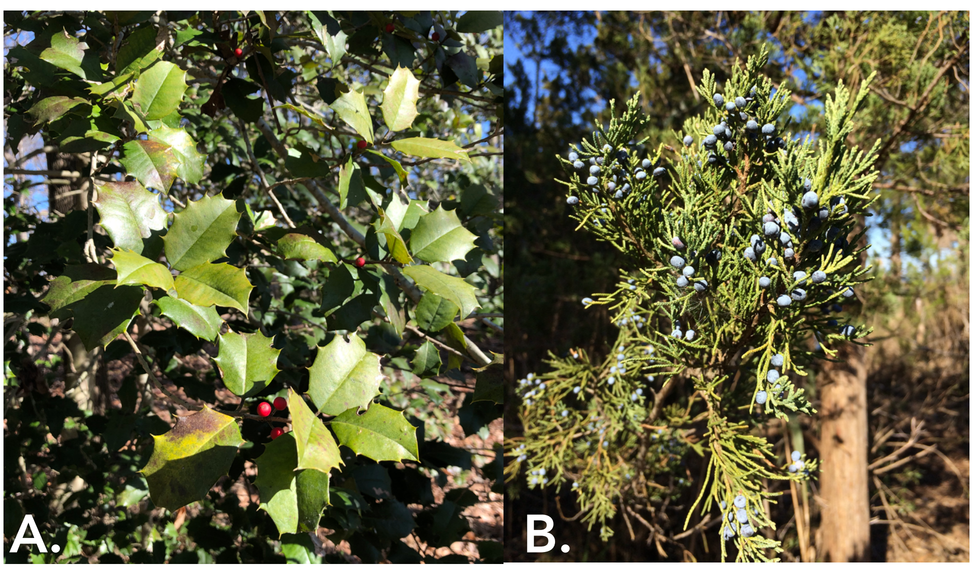

Figure 2. American holly with red berries (A; *Ilex opaca*) and eastern red cedar with blue cones (B; *Juniperus virginiana*).

broad range of climate conditions where average precipitation ranges from 15 to 60" (38 to 152 cm) and average annual temperatures range from -45 to 115°F (-42 to 68°C). Red cedars are considered resistant to salt spray (Martin, 1959). The wood of the eastern red cedar is relatively soft and heartwood coloration ranges from deep pinks or reds to dark purples. Eastern red cedar has prominent growth rings with well developed latewood. Growth patterns in this species are notably sensitive to environmental conditions (Grissino-Mayer 1993).

Although eastern red cedar and the American holly are distributed across the eastern United States, their presence in coastal maritime forests of the Delaware Bay is particularly unique. Unlike forests further inland, maritime forests are exposed to stressors such as rising tides, hurricanes, salt spray, and saltwater intrusion. These factors influence ecological succession, gap regeneration processes, and species composition through the alteration of soil salinity and composition (Forrester and Leopold, 2005). Coastal forests may retreat upslope as shorelines erode, sand buries lower elevation areas , or if trees succumb to saltwater exposure. Land use changes can limit forest retreat, resulting in forest mortality, saltwater intrusion into the shallow groundwater supply, and changes to the balance of herbivory (Forrester et al 2007, Smith et al 1997). Additionally, forests that historically withstood droughts may experience accelerated mortality with the effects of sea-level rise (Williams et al. 2003; Desantis et al 2007).

Dendrochronology

Field sampling

Trees were sampled along a gradient of elevations (0.9-1.8 m North American Vertical Datum 1988 (NAVD88)) upslope from the neighboring salt marsh edge (MHHW is ~0.7 m NAVD88). Individual tree selection was based on their location, age, health and overall condition being free of evidence of disturbance and disease. Each tree's diameter at breast height (DBH; ~1.2 m from root crown) and GPS location was recorded. Cores were extracted using a 5 mm Haglöf increment borer, driven to a depth sufficient to extract or pass through pith (Figure 3). Samples were placed into plastic straws, labeled, extraction direction noted, and transported back to the lab for sample preparation and data analysis. Elevation surveys were conducted using real time kinematic (RTK) GPS to compare the accuracy of a existing LiDAR digital elevation model (DEM).

Figure 3. Coring an American holly with a Haglöf 5mm increment borer.

Sample preparation

Cores were placed in wooden vice racks to avoid warping and dried for 4 to 5 days. Once dry, the transverse surface of each core was hand-sanded with a series of progressively finer grade sandpaper (320, 800, 3000 grits) until a smooth and highly polished surface was obtained.

Ring-width measurements and chronology building

Tree-ring widths were measured to a precision of ±0.001 mm using a Velmex® unislide measuring table coupled with either Tellervo® or J2X® software. Measured values were verified by a second party for quality assurance, inconsistencies were evaluated, and a resultant chronology was established for each core. Cross-dating accuracy was tested in R statistical software with the "dplR" package (Bunn 2008; R Core Team 2019) or with COFECHA (Holmes 1983).

Individual tree chronologies were detrended using a modified Hugershoff growth model then converted to ring width indices (RWI). We estimated a common signal chronology (i.e. a mean chronology) using a biweight robust mean. Chronologies were built and prewhitened (a statistical procedure that reduces random variability and autocorrelation) in R statistical software with the "dplR" package (Bunn 2008; R Core Team 2019).

Tree ring correlation with environmental factors

Water level, temperature, and precipitation data

A long term water level chronology was developed by correcting the NOAA Lewes tide gage monthly maximum tidal water levels to those observed at the DNERR Scotton Landing gage over a matching period of record (August 2008 - August 2019). A linear regression of maximum water levels between Lewes and Scotton Landing was used to hind-cast water levels observed at the DNERR study site for a longer record (ca. 1955). We assumed that this relationship was stationary through time and used these regressed, hind-casted values to identified months/years where flood levels exceeded 0.89 m NAVD88 at Scotton Landing.

We obtained average temperature, precipitation, and 3-month average Palmer Drought Severity Index (PDSI-Z, which isolates previous time period dependencies) values for the state of Delaware from NOAA's NCDC regional climate dataset (https://www.ncdc.noaa.gov/cag/statewide/time-series). We then averaged temperature and precipitation values over 3-month seasonal periods: January-February-March (JFM), April-May-June (AMJ), July-August-September (JAS), and October-November-December (OND or pOND[1]).

Data analysis

We used Pearson's product-moment correlation test, or simply Pearson's test, to identify correlations among RWI, PDSI-Z, temperature, and precipitation values.

Using flood height information and the range of sampled American holly elevations, we selected a cut off elevation of 1.2 m NAVD88 by which to group trees into high or low flood exposure. This value was derived by adding 1 ft (0.3 m) of coastal flooding to the lowest American holly tree elevation. Chronologies were constructed separately for each group to illustrate the growth differences under different flood exposures.

We isolated high water episodes which were greater than 0.89 m NAVD88 by season (JFM, AMJ, JAS, OND). We used these event years to compare lagged suppression responses via superposed epoch analysis (SEA) ("burnr" package; Malevich et al. 2018; 3 years post event, bootstrap n=5000).

Sap flow and stem psychrometry

Monitoring equipment installation

We installed a sap flow meter (SFM-1 by ICT International® Armidale, NSW, Australia) and a stem psychrometer PSY-1 by ICT International® Armidale, NSW, Australia) to a red cedar on the DNERR property that was known to be regularly inundated during storm tide events. The sap flow meter measures the velocity of xylem fluids using the heat ratio method. The stem psychrometer measure xylem sap water potential, which is a proxy for sap conductivity or salinity. Both meters were installed for this study according to instructions developed by the manufacturer (see links above).

1. Environmental factors assigned to dated tree rings began in October of the previous calendar year. This better captures cumulative environmental effects of a 12-month period on tree growth. Growth ceases in ~October, so events between October-December affect the following calendar year's growth (i.e. pOND).

Data manipulation and analysis

Volumetric sap flow (kg hr^{-1}) was calculated by extrapolating mean daily sap velocity, which was monitored, across the sapwood basal area (ICT manual). We associated daily maximum volumetric sap flow with daily maximum meteorological variables (temperature, relative humidity, solar radiance, and wind speed/direction), daily high water levels, and daily maximum sap conductivity from stem psychrometry data (Pearson's product-moment correlation test).

To investigate whether flood events contributed to variability in sapflow, we identified outliers using the interquartile range rule. We compared the timing of these outliers to floods with elevations greater than the monitored tree's elevation (i.e. ≥0.86 m NAVD88).

Mapping

In April 2019, we surveyed random elevation points in focal elevation bands (Spartina dominated marsh, *Phragmites* dominated marsh, and uplands). We used these data to resolve errors (due to plant interference) associated with LiDAR DEMs of the St. Jones River watershed. DEM information was then used to extract the elevation of each sampled American holly. Elevation uncertainties (i.e. LiDAR errors) were derived from mean differences observed from LiDAR DEM and survey elevations.

We used an elevation value of 1.13 m NAVD88 to define flood frequency, such that higher elevation trees experience low frequency flooding compared to those of lower elevations. The cutoff value was determined by the estimated 1 ft (0.31 m) coastal flood depth, which is 1 ft above local MHW (~2.2 ft or 0.67 m NAVD88).

For watershed mapping, we used existing, publicly available coastal inundation maps (2017 update; firstmap.delaware.gov) to isolate low-lying forests (forest data available on firstmap.delaware.gov) with high (MHHW-1 ft depth; > 1.13 m NAVD 88) and low (1-3 ft depth; 1.13-1.65 m NAVD 88) inundation exposure.

Results

Dendrochronology

American holly

Of the 45 collected American holly cores, 43 (96%) were datable. Two undateable cores were from inosculated trees, so annual ring directionality was difficult to discern and rot marred the wood. Mean chronology spanned 118 years, from 1902-2019. Average series length was ~66 years (Figure 4). Mean series intercorrelation was 0.44. American holly growth correlated loosely with spring (AMJ) PDSI-Z (R=.13, p = 0.07), but no other associations with local climate were significant (Table 1).

We separated trees into flood exposure categories and constructed separate chronologies of each to determine how flood exposure affects growth (Figure 5 and 6). For the low flood exposure category (tree elevations >1.2 m NAVD88), there were 19 series, spanning 108 years, with an interseries correlation of 0.43. The high flood exposure group (tree elevations <1.2 m NAVD88) had 24 series, spanning 118 years, with an interseries correlation of 0.42. The difference in growth between these groups had a significant negative correlation with previous fall (pOND) temperatures (Table 2).

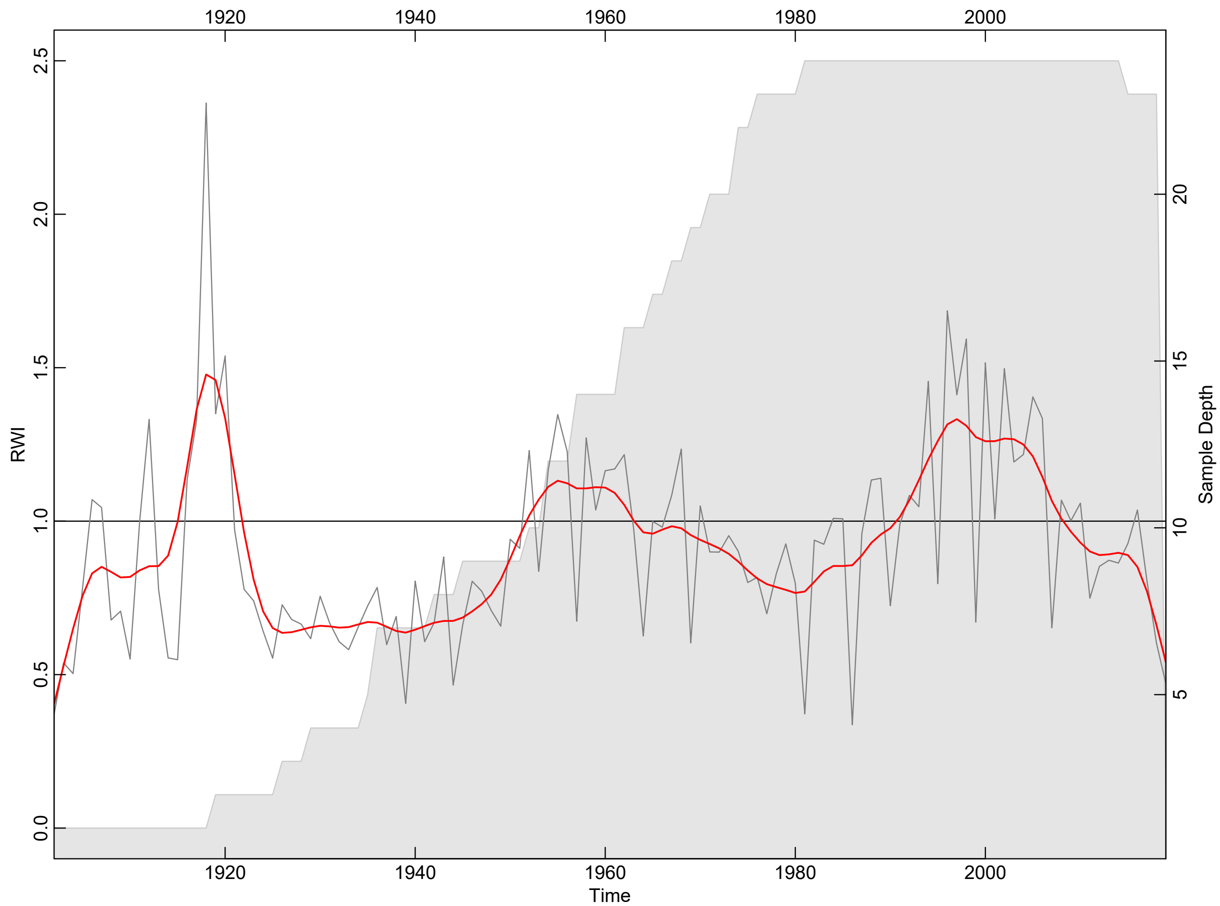

Figure 4. Mean ring width index (RWI) chronology of sampled American hollies; red line is a 5-year spline.

Table 1. Table of Pearson correlation results for American holly growth and climatic variables. Non-significant results are noted as "n. s." (i.e. α=0.05).

Season	Temperature	Precipitation	PDSI-Z
pOND (previous autumn)	n. s.	n. s.	n. s.
JFM (winter)	n. s.	n. s.	n. s.
AMJ (spring)	n. s.	n. s.	t=1.8, R=0.13, p=0.07
JAS (summer)	n. s.	n. s.	n. s.

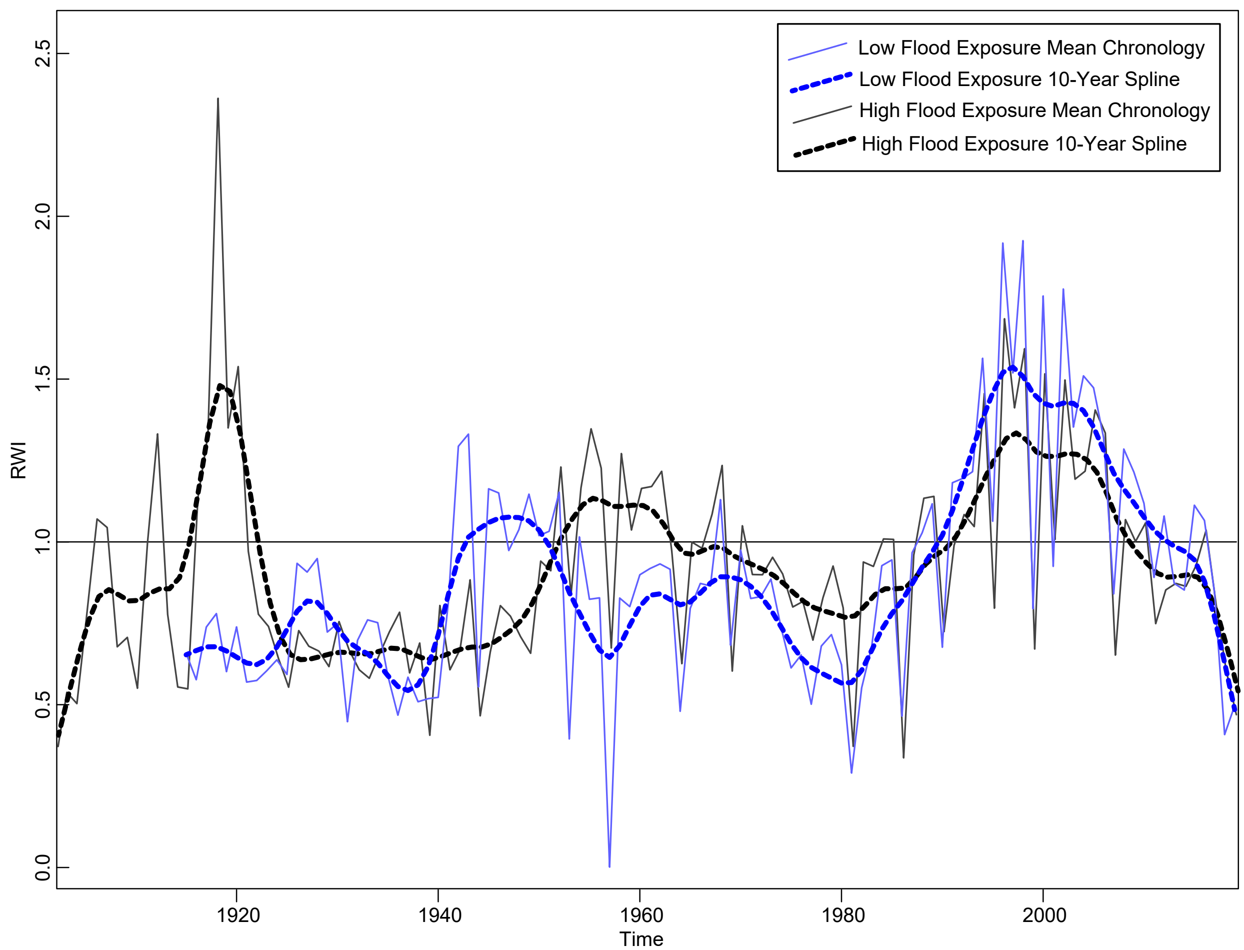

Figure 5. Chronologies for American hollies with high (black lines) and low (blue lines) flood exposure.

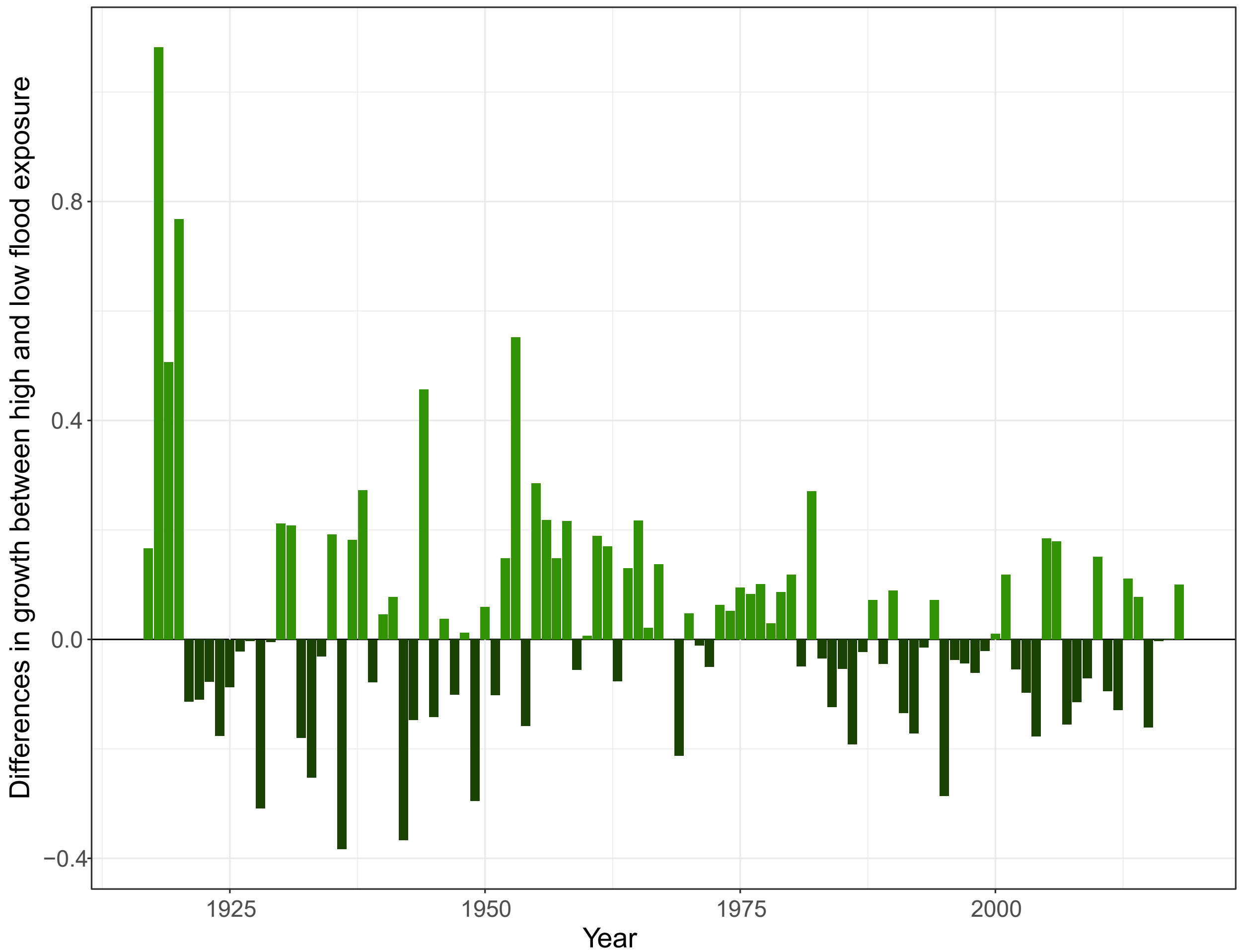

Figure 6. Annual differences between high and low flood exposed American hollies. Dark green bars are years that high elevation (low flood exposure) trees did comparatively better, whereas light green bars are years where low elevation (high flood exposure) trees did better.

Table 2. American holly Pearson correlation results for differences in flood exposure and climate. Non-significant results are noted as "n. s." (i.e. α=0.05).

Season	Temperature	Precipitation	PDSI-Z
pOND (previous autumn)	t=-4.1, R=-0.37, p<<0.001	n. s.	n. s.
JFM (winter)	n. s.	n. s.	n. s.
AMJ (spring)	n. s.	n. s.	n. s.
JAS (summer)	n. s.	n. s.	n. s.

Eastern red cedar

Of the 23 collected red cedar cores, 14 (61%) were datable. Undateable cores had questionable annual ring directionality and so were excluded from these analyses. The mean red cedar chronology spanned 52 years, from 1967-2018. Average series length was ~41 years (Figure 7). Mean series intercorrelation was 0.43. This dataset only includes trees with high flood exposure (tree elevations <1.2 m NAVD88). Red cedar growth correlated strongly with summer (JAS) PDSI-Z ($R=0.42$, $p<0.01$), summer precipitation ($R=0.30$, $p<0.05$), and, inversely, summer temperature ($R=-0.30$, $p<0.05$)(Table 3). Weaker correlations were observed for winter (JFM) and spring (AMJ) precipitation, as well as spring PDSI-Z.

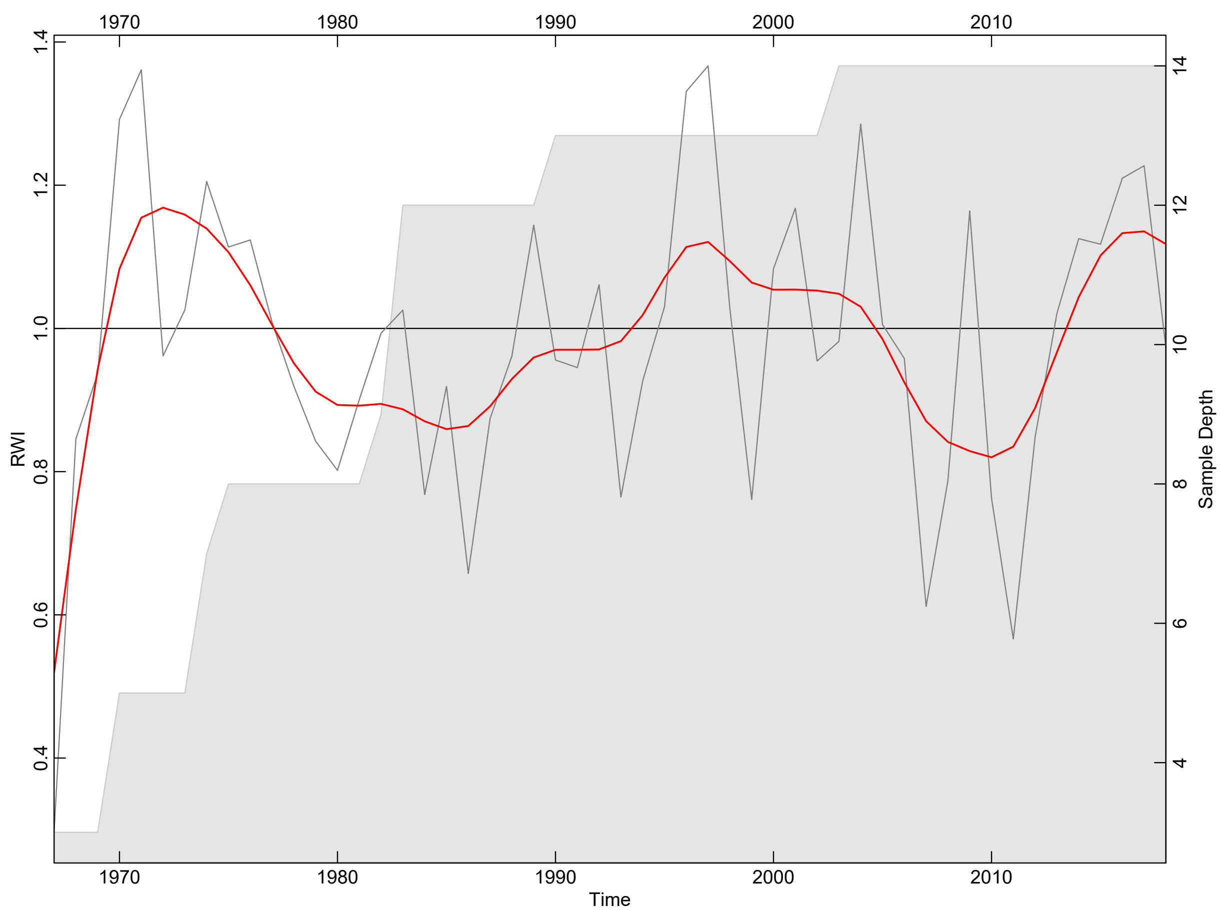

Figure 7. Mean ring width index (RWI) chronology of sampled eastern red cedars.

Table 3. Eastern red cedar Pearson correlation results for differences in flood exposure and climate. Non-significant results are noted as "n. s." (i.e. α=0.05).

Season	Temperature	Precipitation	PDSI-Z
pOND (previous autumn)	n. s.	n. s.	n. s.
JFM (winter)	n. s.	t=-1.73, R=-0.23, p=0.09	n. s.
AMJ (spring)	n. s.	t=1.73, R=0.23, p=0.09	t=1.8, R=0.25, p=0.07
JAS (summer)	t=-2.11, R=-0.30, p<0.05	t=2.24, R=0.30, p<0.05	t=3.2, R=0.42, p<0.01

Water levels

The linear relationship between tide gages at Lewes, DE water levels and Scotton Landing, DE from March 2008 to August 2019 was 0.5315x+0.3022 (R^2=0.4383). This equation was used to create a proxy water level record extending beyond 2008, to approximately 1960, at Scotton Landing (Figure 8). We split mean water levels by season. On average, water levels in winter (JFM) and autumn (OND) are higher than in spring (AMJ) and summer (JAS).

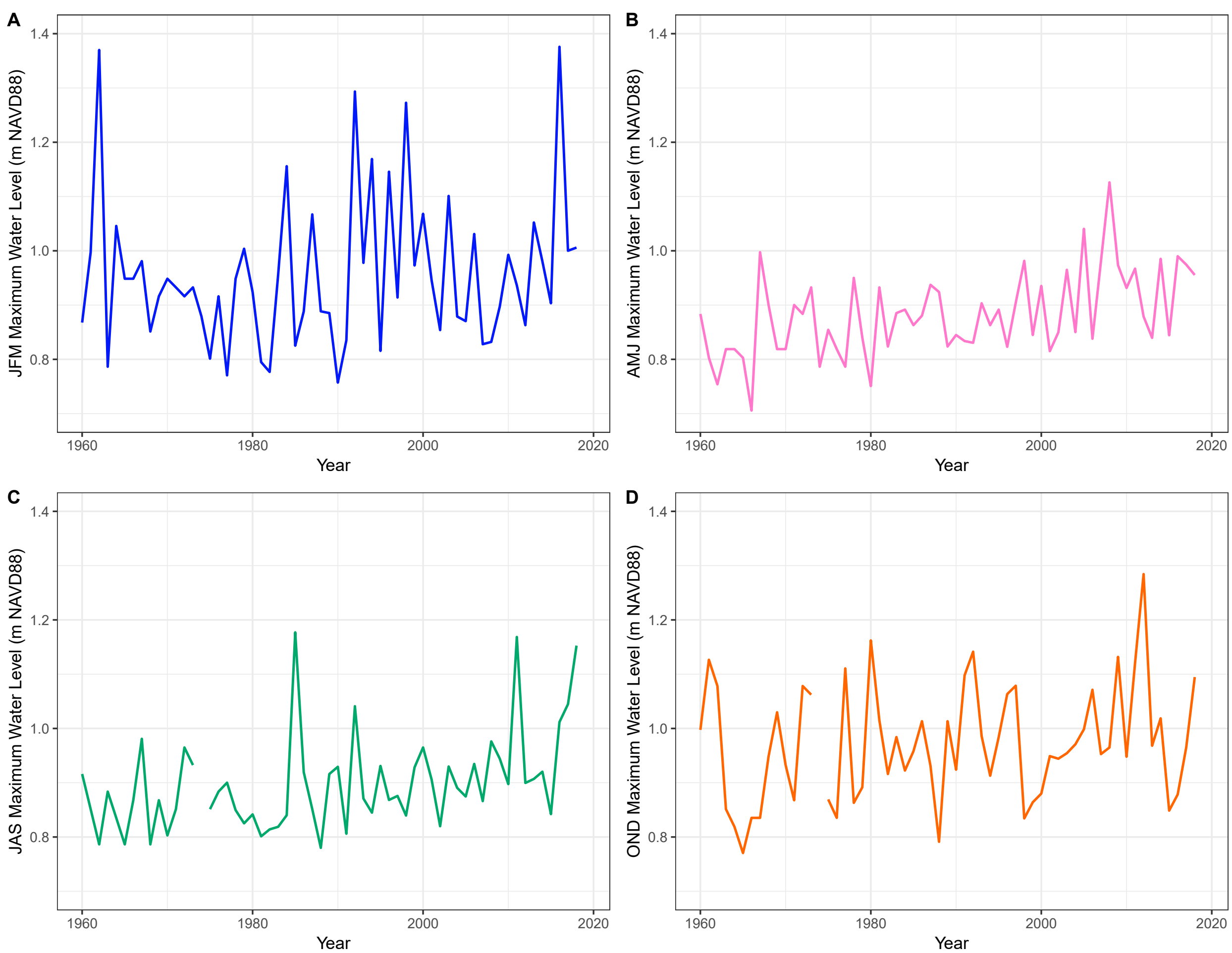

Figure 8. Historical maximum water levels at Scotton Landing in winter (A), spring (B), summer (C), and autumn (D).

We ran correlations between tree growth and seasonal water level patterns. We found that holly growth correlated with winter water levels but found no significant relationships for red cedar (Tables 4 and 5).

Superposed epoch analysis (SEA) results suggest significant negative growth responses and lags for both tree species following high water events. We identified 34 winter, 23 spring, 26 summer, and 41 autumn high water events using a 0.89 m NAVD88 cut-off (i.e. the lowest American holly elevation).

Winter high water events impacted holly growth at post-event years 0, 1, and 2; autumn high water events also impacted holly growth at post-event years 1 and 2 (so the previous year's autumn water levels affected current year's growth)(Table 6; Figure 9). In red cedar, winter high water events had detectable impacts up to 3 years post-event. Spring high water events impacted red cedar growth at post-event years 0 and 1 (Table 7; Figure 10).

Table 4. American holly Pearson correlation results for growth and three month maximum water levels. Correlation results from the master chronology are mean annual growth values, whereas High-Low Differences are differences in growth due to flood exposure. Non-significant results are noted as "n. s." (i.e. α=0.05).

Season	Master Chronology	High-Low Differences
pOND (previous autumn)	n.s.	n. s.
JFM (winter)	t = 2.5, R=0.32, p< 0.05	n. s.
AMJ (spring)	n. s.	n. s.
JAS (summer)	n. s.	n. s.

Table 5. Eastern red cedar Pearson correlation results for growth and three month maximum water levels. Correlation results from the master chronology are mean annual growth values. Non-significant results are noted as "n. s." (i.e. α=0.05).

Season	Master Chronology
pOND (previous autumn)	n.s.
JFM (winter)	n.s.
AMJ (spring)	n. s.
JAS (summer)	n. s.

Table 6. Superposed epoch analysis results for American holly. Lag years, or years after the event, begin when the event occurred at year 0. Seasonal values are given as departures from the mean chronology. Values in parenthesis are the lower 95% confidence interval. Mean departures that surpass the lower 95% confidence interval are considered significant (*) or very significant (**).

Lag Year	JFM (winter)	AMJ (spring)	JAS (summer)	OND (autumn)
0	-2.287 (-0.819)**	-1.249 (0.598)	-0.828 (1.126)	-1.237 (0.207)
1	-1.844 (-0.095)*	-0.903 (0.475)	-0.741 (0.687)	-1.188 (-0.0919)*
2	-1.994 (-0.982)**	-1.086 (-0.319)*	-0.643 (0.616)	-1.275 (-0.316)*
3	-1.545 (0.028)	-0.672 (1.273)	-0.413 (1.522)	-1.017 (0.5)

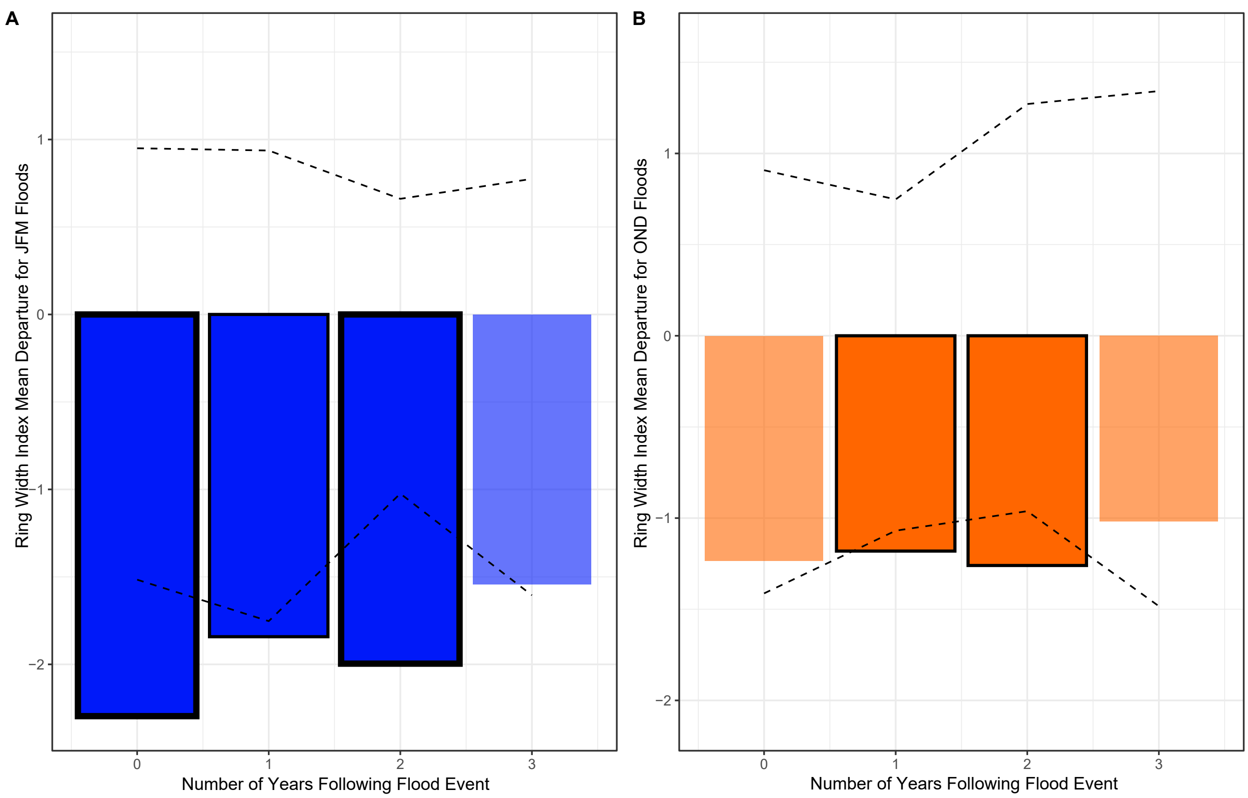

Figure 9. Notable superposed epoch analysis results for American holly for winter (A) and autumn (B) surge events. Lag years, or years after the event, begin when the event occurred at year 0. Bars are departures from the mean chronology. Black dashed lines are upper and lower 95% confidence intervals. Mean departures that surpass the 95% confidence interval are considered significant (dark colors, thin black outlines) or very significant (dark colors, thick black outlines).

Table 7. Superposed epoch analysis results for eastern red cedar. Lag years, or years after the event, begin when the event occurred at year 0. Seasonal values are given as departures from the mean chronology. Values in parenthesis are the lower 95% confidence interval. Mean departures that surpass the lower 95% confidence interval are considered significant (*) or very significant (**).

Lag Year	JFM (low 95% CI)	AMJ (low 95% CI)	JAS (low 95% CI)	OND (low 95% CI)
0	-1.274 (0.31)*	-1.161 (0.048)*	-0.439 (-0.696)	-0.501 (-0.406)
1	-1.371 (0.443)**	-1.247 (0.13)*	-0.54 (-0.543)	-0.501 (-0.378)
2	-1.176 (0.198)*	-0.911 (-0.16)	-0.35 (-0.736)	-0.295 (-0.605)
3	-1.09 (0.248)*	-0.886 (-0.129)	-0.423 (-0.583)	-0.457 (-0.334)

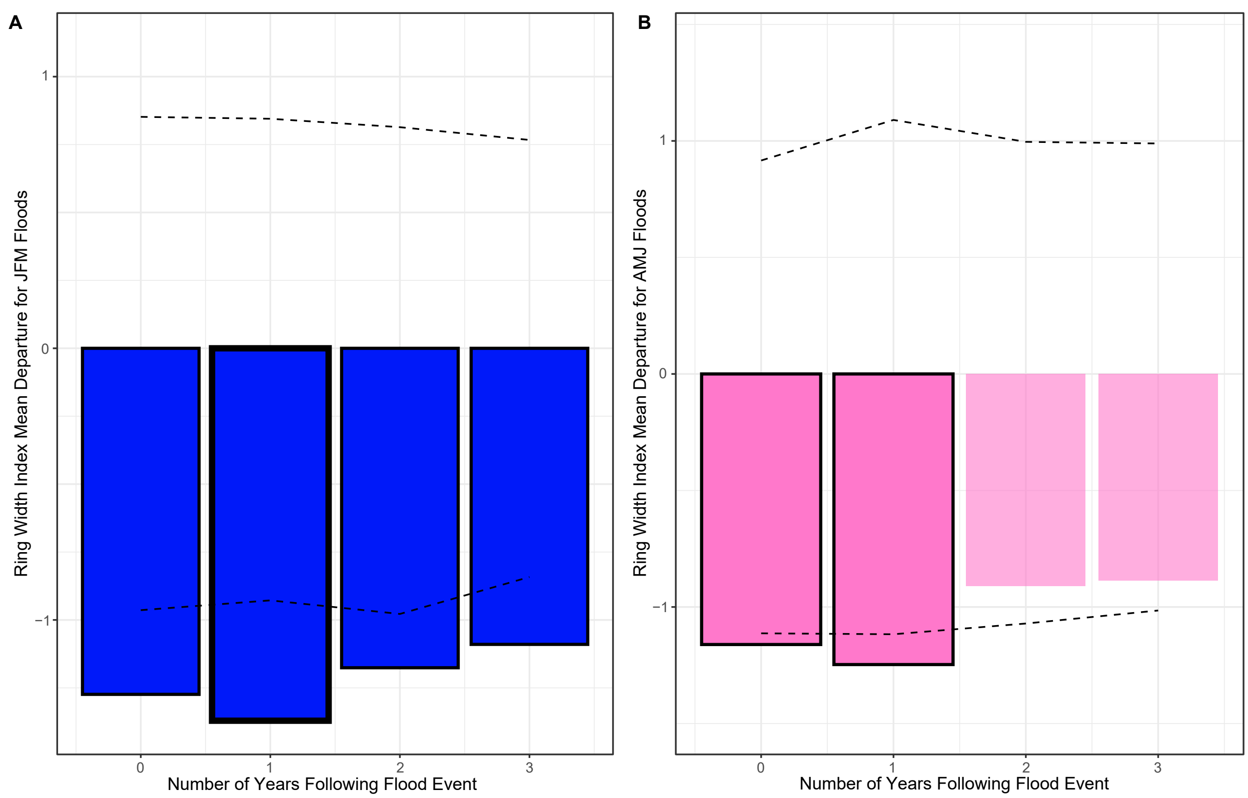

Figure 10. Notable superposed epoch analysis results for red cedar for winter (A) and spring (B) surge events. Lag years, or years after the event, begin when the event occurred at year 0. Bars are departures from the mean chronology. Black dashed lines are upper and lower 95% confidence intervals. Mean departures that surpass the 95% confidence interval are considered significant (dark colors, thin black outlines) or very significant (dark colors, thick black outlines).

Sapflow and stem psychrometry

Sap flow is tightly associated with meteorological conditions, specifically with factors that drive transpiration. As such, we found significant correlations with daily minimum relative humidity, daily maximum solar radiation, and daily maximum wind speed (Table 8A). Future statistical work should account for significant covariance between daily minimum relative humidity and daily maximum solar radiation (t =-11.5, *R*=-0.68, p<0.001).

We found significant correlations between maximum daily sap flow rates and daily mean high water level, as well as maximum daily sap water potential (a proxy for sap conductivity or salinity). Most correlations between sap water potential and environmental variables did not yield significant results, except daily maximum wind speed (Table 8B).

Table 8. Sap flow (A) and sap water potential (B) Pearson correlation results. Non-significant results are noted as "n. s." (i.e. α=0.05).

A. Sap Flow		B. Sap Water Potential	
Metric	**Result**	**Metric**	**Result**
Minimum relative humidity	t =-7.3, R=-0.51, p<< 0.01	Minimum relative humidity	n. s.
Solar radiance	t = 7.1, R=0.31, p<< 0.001	Solar radiance	n. s.
Wind speed	t = 3.5, R=0.27, p<< 0.001	Wind speed	t = -2.5, R=-0.19, p< 0.05
Maximum water level	t = -3.6, R=-0.28, p<< 0.01	Maximum water level	n. s.
Sap water potential	t = -4.1, R=-0.32, p<< 0.01	Wind direction	n. s.

From April to September, we also noted several large sap flow rate outliers (Figure 11). Sap flow rates tend to be higher in the spring as trees begin a stage of rapid water uptake and growth following the winter, so we isolated outliers by finding large deviations from a linear trend (i.e. IQR of linear residuals). High water events ≥0.86 m NAVD88 (i.e. the approximate tree elevation), only coincided with 6 of the 16 outliers (37.5%). Due to the potential complexity and requirement of other measured variables on the soil surface, we did not perform any additional analyses with outliers.

Maps

We developed a geodatabase map product of the St. Jones River watershed that contains subsets of publicly available data layers for flow-lying forests, surge risks, inundation height risks, and elevations. It is available for download here: https://delawareestuary.s3.amazonaws.com/DNERR+Wetlands/DNERR+Geodatabase/DNERR_Report.gdb.zip. As we continue to study tree species distributions and species-specific flood exposure sensitivities, this geodatabase can be updated to reflect new findings. No trees used in this report were within habitats of high associated error (*Phragmites* dominated fringe), so susceptibility maps were generated using publicly available DEMs (firstmap.delaware.gov).

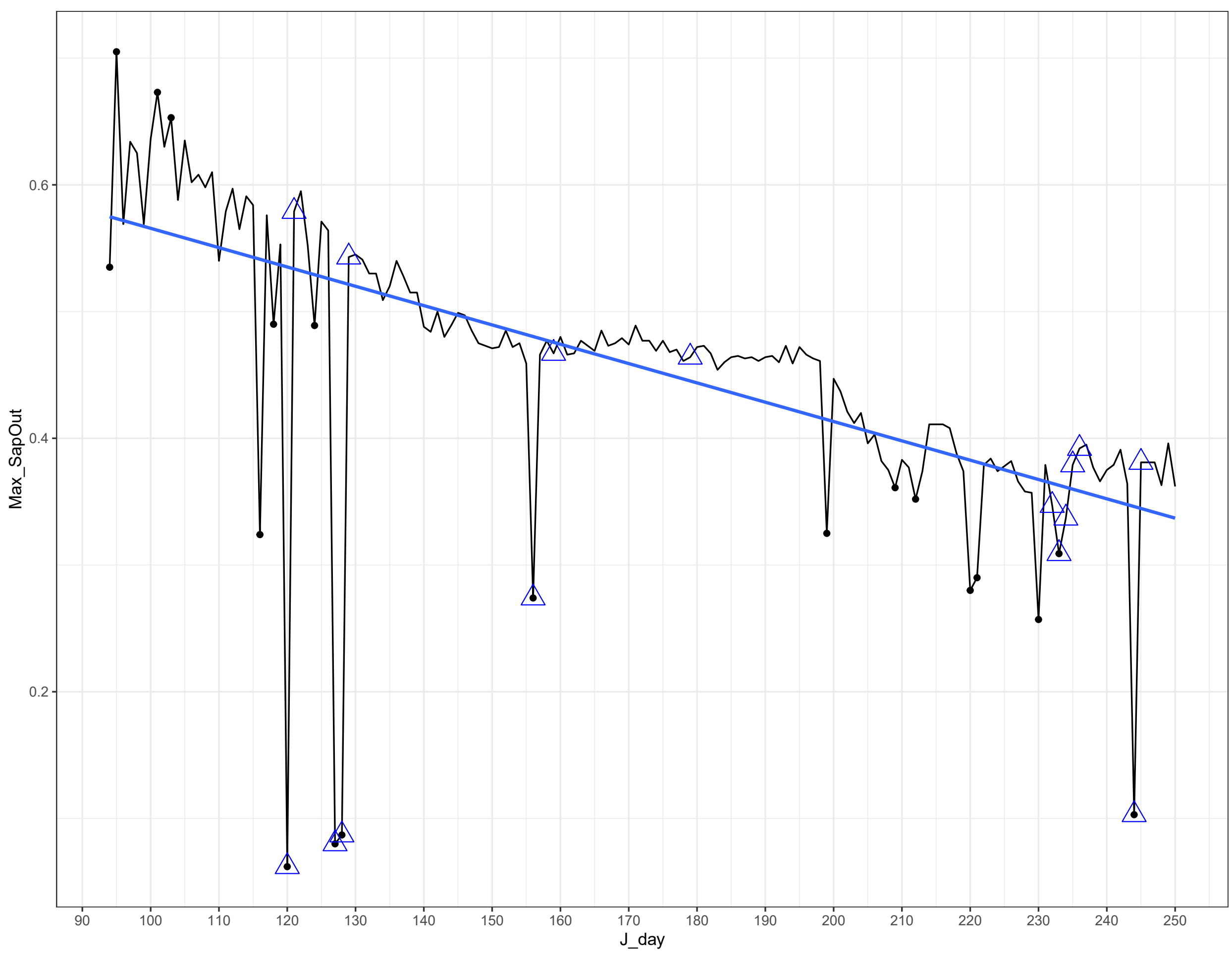

Figure 11. Maximum daily sap flow over study period (April-September 2019; J_day is the julian calendar date). Black dots are outliers and blue, hollow triangles are water levels ≥0.86 m NAVD88.

Table 9. LiDAR DEM errors associated with key habitats as derived from on site elevation surveys. Estimated mean errors are in meters and standard deviations of these values are given in parenthesis.

Habitat	Error
Spartina dominated salt marsh	-0.214 (0.074)
Phragmites australis dominated ecotone	-0.237 (0.11)
Uplands	-0.025 (0.099)

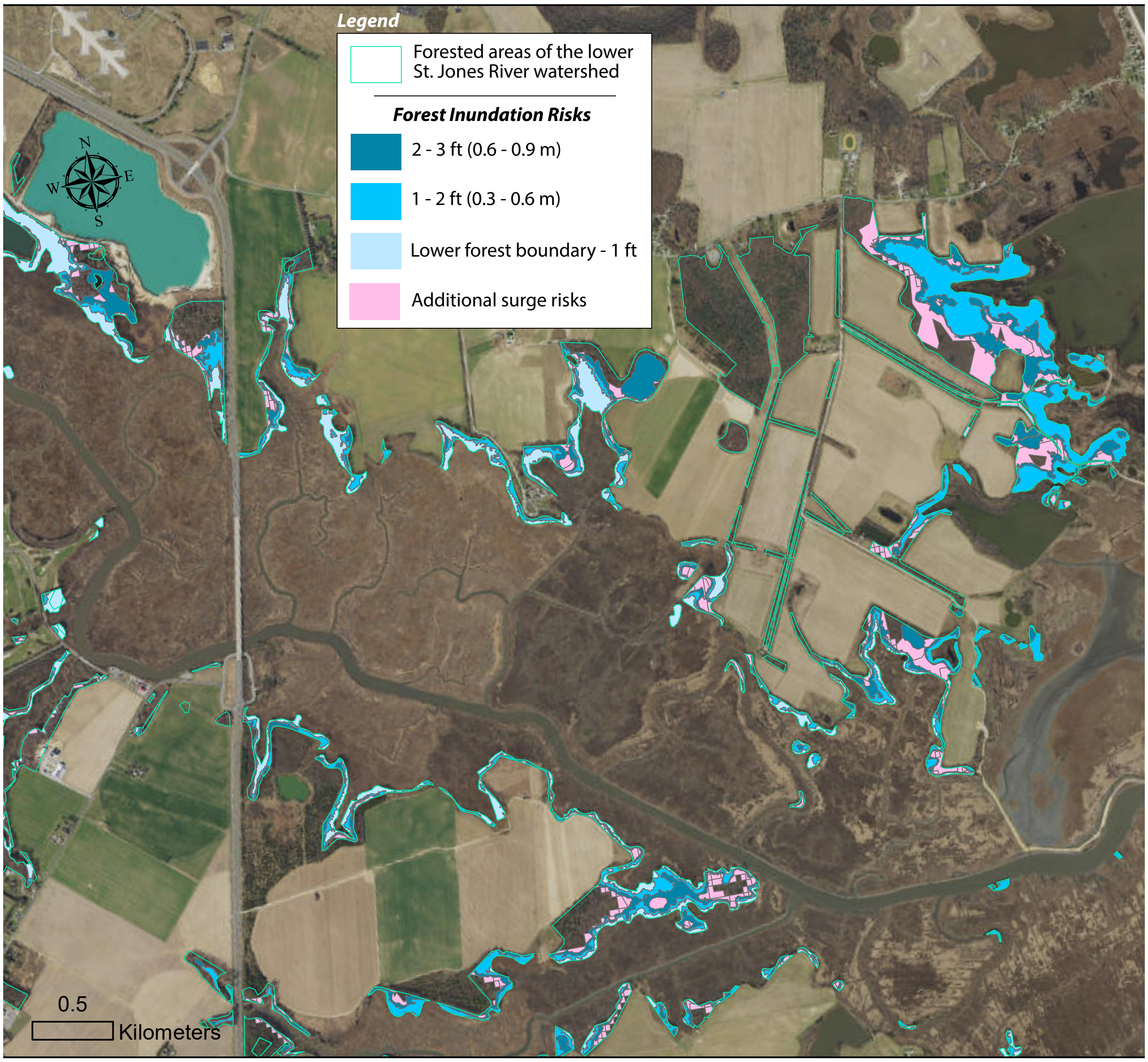

Figure 12. An example subset map of St. Jones tidal watershed with critical low-lying forest areas and associated inundation or surge risk. A geodatabase of these data layers are available for download online.

Discussion

Research on the effects of saltwater inundation in low-lying forests caused by rising sea levels and increasing storm surge intensity is a critical need to improve management decision making. To help resolve current knowledge gaps, this report proposed three objectives. The first objective was to construct growth chronologies of low elevation eastern red cedars and American hollies to investigate whether those trees have undergone growth declines that may be attributable to changing inundation patterns. The second objective investigated whether other factors, such as flood exposure and climatic variables, drove variation in tree growth, and how those drivers varied between species. To understand physiological responses to flood events better, we monitored sap flow in one frequently flooded red cedar. Lastly, we compiled relevant map information for the St. Jones River watershed as a baseline to gauge low-lying forest flood exposure.

American holly results suggested that spring droughts and winter tidal water levels effected growth overall, but few other associations appeared significant. The absence of other significant climatic associations support anecdotes about American holly hardiness under a wide range of environmental conditions (Grelen 1990). As with many other tree species, spring is an important developmental season for hollies. In a process sometimes referred to as "spring flush," many trees utilize warmer temperatures, higher light availability, and residual soil moisture to produce new wood, flowers, and leaves from April-May. This process requires a substantial draw of moisture, and so during droughts when moisture is limiting, trees generally do not grow as much through the remaining warm season. Additionally, hollies may not undergo full dormancy in winter months, as they are evergreen and adapted to handle water stress caused by colder temperatures (e.g. thick waxy leaf cuticles). If photosynthesis occurs, water uptake must also continue, thus moisture availability and sodicity (i.e. soil salt content) in winter becomes important. Furthermore, since winter water levels are usually highest, saltwater flood exposure for low-lying hollies during this season is high. Our results also suggested that autumn and winter surge events negatively affect holly growth. Given our surge and water level results, we hypothesize that hollies are likely disproportionately vulnerable to floods during cooler months, as those time periods may be important to their biological or ecological viability.

Another conspicuous result in our study is that low-elevation, and frequently flooded, American holly trees fared better than higher elevation trees during cooler autumns, which may be the result of cavitation resistance. Trees form smaller vessel sizes to manipulate water potential stress caused by drought, freezing, and source water salinity (Pfautsch 2016). During these conditions, smaller vessel sizes reduce the possibility of cavitation, a damaging phenomenon caused by air bubbles (emboli) that form when fluid potential change abruptly. Although smaller vessels increase cavitation resistance, it comes at a cost to hydraulic efficiency (Stiller 2009). Trees generally do not differentiate the cause of water potential stress, so as hollies respond morphologically to frequent saltwater flooding, they also inherently confer cavitation protection from freezing and/or drought. Although there is an abundance of literature on the mechanisms of cavitation resistance across many different tree species (see Stiller 2009 and references therein), the ecological role that cavitation resistance plays in the ecology and long-term viability of frequently flooded coastal forests in the Mid Atlantic is currently unclear.

Eastern red cedar results suggested that summer climatic conditions effected growth most. Summer heat negatively affected the growth of eastern red cedars, but precipitation in the winter, spring, and summer had positive effects. Although all of the sampled red cedars occurred at low elevations (<2.0 m NAVD88), we did not observe any patterns with seasonal water levels. From these results, and considering that they have very shallow root systems, we surmise that eastern red cedars are likely dependent on precipitation as a water source. Extreme summer temperatures may also exacerbate lower average rainfall observed in summer months. Summer saltwater floods are less likely to occur in months when low soil moisture becomes a notable stressor for the species (due to heat and low rainfall). This suggests that some perceived tolerance of red cedar to saltwater flooding may also be due, in part, to lack of exposure during the critical summer season. Our results suggest that spring and winter storm-surge events negatively affected eastern red cedars. Similar to hollies, eastern red cedars undergo a "spring flush" and they photosynthesize at a reduced rate during the winter so negative responses to surge during these months may either disrupt advantages of winter activity or increase sodicity.

Although American hollies and eastern red cedars have some similarities, we learned from our data that each species responds to seasonal conditions and flooding differently, which has implications for forest viability as sea levels rise. For instance, both species are evergreen, yet we found that hollies are sensitive to spring moisture availability whereas red cedars are more sensitive to summer conditions. We also found winter tidal water levels affects in hollies, but they had little or no effect on red cedars. These differences in species-specific sensitivity suggest that forest compositional changes will likely follow patterns of minimum seasonal water potentials caused by climate or seasonal flood frequencies (Bhaskar and Ackerly 2006). As such, in areas prone to saltwater flooding in winter, American hollies may experience increasing winter water potential stress as floods become more frequent. Stress ultimately leads to decline, and other species less negatively affected by winter flood exposure, like red cedar, may replace hollies in low-lying forests. Thus, trade-offs between each species' seasonal tolerance of minimum water potential and the extent of increasing saltwater flood exposure will likely have significant ecological effects (Williams et al. 2003; DeSantis et al. 2007). These ecological dynamics will be important for predicting forest compositional change and forests losses. These predictions will likely be critical for management decision-making as sea level rise increases flood frequencies in low-lying areas.

We monitored sap flow and sap water potential in a frequently flooded (i.e. low-lying) eastern red cedar for most of the growing season and found that the tree reduced sap flow during high water events, yet sap water potential (SWP; a proxy for sap salinity) was most influenced by high wind speeds. Transpiration potential mostly affects sap flow, but when water losses exceed potential uptake, trees limit transpiration through leaf stomatal closure. Flooding can inhibit root growth and respiration, so a tree may reduce potential transpirational water losses during floods by closing stomata, thus slowing sap flow. We found that sap flow rates were lower when water levels and SWP were high, which suggests that the monitored tree likely responded to saltwater floods by stomatal closure. Broadly, this may reduce water losses, as well as limit salt build up and toxicity. SWP correlated positively with wind speed, yet did not correlate with most other weather parameters or high water levels. This suggests that soil salt content and wind-driven evaporation that increases soil salinity affects sap conductivity, rather than the flood event itself. Thus, SWP may have a lagged response to high water levels, especially if the tree experiences sap flow rate reductions while inundated.

Lastly, we mapped low-lying forests that may be of critical management concern regarding their flood exposure. More research will be necessary to elucidate how seasonal flood exposure and species-specific tolerances, as may be surmised from cavitation-reducing morphological changes, affect forest viability and distribution, but these initial maps provide a baseline for continued investigation. Through our field elevation surveys, we found that existing LiDAR DEMs (from firstmap.delaware.gov) were suitable for uplands and forests, yet significant error was associated with tidal marsh and *Phragmites australis* margins.

As *P. australis* regularly occupies marsh-forest ecotones, accurate elevations and slope estimations in these high-error zones will be critical for determining future flood frequencies.

Next Steps

This project served as a critical baseline for research on how high water flooding affects low-lying forests in the Mid Atlantic. At least three graduate students were engaged in this project, and due to its success, we hope these students continue to provide essential context to our growing knowledge of tree responses to sea level rise. Additionally, this project has led to another graduate research project that will aim to develop difference chronologies (as was developed for American holly in this report) for eastern red cedar. A proposal has also been submitted to the Coastal Zone program to expand upon this project 's results by improving sample numbers for tree ring analyses and sap flow monitoring, as well as performing similar methods on other species (e.g. red maples - *Acer rubrum*). That proposal also considers important nutrient feedbacks, as more frequent high tide flooding may alter those dynamics.

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Appendix I: Notable disturbance events

Year	Description	Explanation
1918	Outlier	OND 1917 low temperatures
1957	Outlier	April-September drought
1961	Lewes Feb. tide gage missing	1960: December blizzard 1961: January-February blizzards (*n*=2)
1963	Lewes June – July tide gage missing	June T-storms and high winds
1964	Lewes March tide gage missing	F1 tornado in Kent Co.
1967	Lewes April tide gage missing	1966: December blizzard 1961: February-March blizzards (*n*=2)
1974	Lewes June – Dec tide gage missing	May heavy rain/hail Sept-Dec T-storms and high winds in .
1975	Lewes Jan., Feb., and April tide gage missing	1974: T-storms and high winds in Sept., and Dec. 1975: F1 tornado and T-storms in Apr.
1978	Lewes Feb. tide gage missing	January-February blizzards (*n*=3)
1986	Outlier	1985: (Aug) Hurricane Danny 7" rain in S. DE. 1985: (Sep) Tropical Storm Henri 1' rain near coast. 1985: (Sep) Hurricane Gloria winds, mod rain, significant beach erosion
1996	Outlier	Jul – Dec extreme moisture January-February blizzards (*n*=3)
1999	Outlier	1998: (Aug) remnants of Hurricane Bonnie, beach erosion, wind gusts 1998: (Dec) winter storm and winds 1999: Mar – May moderate drought 1999: March blizzard 1999: Jun – Aug extreme drought
2000	Lewes Oct tide gage missing	September remnants of Hurricane Gordon, heavy rain and flooding January blizzard