Bottomland hardwood forest growth and stress response to hydroclimatic variation: Evidence from dendrochronology and tree-ring $\delta^{13}C$ values

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Abstract. Wetland forests around the world have been reduced to a small proportion of their original expanse due to changing climatic conditions and intensification of human land use activities. As a case in point, the Columbia bottomland hardwood forests along the Brazos-Colorado Coastal Basin on the Gulf coast of Texas are currently threatened by an increasingly erratic hydroclimate in the form of both extreme floods as well as droughts, and by urban expansion. In this study, we use dendrochronology and tree-ring carbon isotopes to understand the effect of changing hydroclimatic conditions on the functional attributes of these forests. We examined tree-rings of Quercus nigra at four sites within the Columbia bottomlands, of which one site experiences frequent and prolonged flooding, while the other three are less flood-prone. The objectives of this study were to: (i) understand the impact of hydroclimatic variation on growth rates using tree-ring width analysis, (ii) assess the magnitude of physiological stress inflicted by extreme hydroclimatic conditions using tree-ring $\delta^{13}C$ measurements, and (iii) evaluate the relationship between physiological stress and growth inhibition. Growth rates across the landscape were influenced most strongly by mid-growing season climate, while early-growing season climate inflicted the greatest physiological stress. Neither growth inhibition nor changes in $\delta^{13}C$ values were observed in trees at the wetter site under extreme hydrologic conditions such as droughts or floods. In addition, trees at the wet site were less sensitive to precipitation and showed...
no response to higher temperatures. In contrast, trees of the three drier sites experienced growth inhibition and had higher tree-ring δ¹³C values during dry periods. Our results indicate higher physiological resilience in trees growing under wetter conditions. Management and conservation strategies dependent on site-specific conditions are critical for the health of these wetland forests under a rapidly changing hydroclimate. This study provides the first dendrochronological baseline for this region and thresholds of optimum conditions for the growth and health of these forests which can assist management decisions such as streamflow regulation and conservation plans.

1. Introduction

Wetland forests are subjected to drought and floods, both of which can alter productivity and cause physiological stress in plants (Miao et al., 2009; Vivian et al., 2014). These climate extremes and warming are predicted to increase in the 21st century across southern North America (Seager et al., 2007). Bottomland hardwood forests, a common wetland forest type, cover a significant proportion of the floodplains of the rivers and bayous in coastal regions of the southeastern USA. Along the upper Texas Gulf coast, the lower basins of the Brazos River, San Bernard River and Colorado River combine to form the Columbia bottomland hardwood forests, an area of high biodiversity with a critical role in regional hydrology. Large portions of the Columbia basin forest have been cleared and land cover is now a mix of isolated forest patches, cropland, and pasture (Griffith, 2004), with only a few larger forest patches remaining (Fig. 1A). The pre-settlement distribution of these forests was >283,000 ha along a 150 km long corridor inland from the coast, but has since been reduced to about 72,000 ha (USFWS, 1997; Barrow and Renne, 2001; Barrow et al., 2005). In the last few decades, this ecosystem has been experiencing dramatic hydrologic variation caused by severe droughts (Schmidt and Garland, 2012; Hoerling et al., 2013; Moore et al., 2015) as well as floods (van Oldenborgh et al., 2017; Sebastian et al., 2019), altering hydrologic conditions over short temporal scales. Annual precipitation amounts have been
highly variable with up to 61% more rainfall than average during some years, while up to 53% deficit during others, in addition to at least five major tropical storms and hurricanes. Rapid urbanization caused by the proximity to the city of Houston and increasing agricultural activity in the area have likely altered water cycling significantly in these forests (Kearns et al., 2015; TWDB, 2017). Similar forcing factors have altered the state of most wetland forest types in southeastern USA.

Dendrochronology, the study of tree-rings, has been extensively used to understand the response of forest growth to changing environmental conditions (Babst et al., 2013; Charney et al., 2016; Tei et al., 2017). Additionally, tree-ring δ¹³C is an indirect record of internal leaf CO₂ concentration, which is controlled by a balance between stomatal conductance and photosynthetic rate in response to environmental conditions (Farquhar et al., 1989; McCarroll and Loader, 2004; Gessler et al., 2014), such as temperature, vapor pressure and precipitation (Robertson et al., 1997; Leavitt et al., 2002). As tree rings are distinguished by their high temporal (annual or sub-annual) and spatial resolution, regional tree-ring chronologies and δ¹³C values have the potential to identify a wide range of growth and stress response of vegetation to hydroclimatic variability. However, tree-ring δ¹³C is also influenced by the changing δ¹³C value of atmospheric CO₂. The increase in atmospheric CO₂ concentration mainly due to fossil fuel combustion has led to a significant decrease in δ¹³C of atmospheric CO₂ over the last century (Graven et al., 2017). Although this change is relatively small over short temporal scales, correction methods are available to remove this signal from tree-ring records when using tree-ring δ¹³C to understand plant physiological responses to local conditions (McCarroll and Loader, 2004).

Studies conducted across the globe demonstrate growth inhibition signals in the form of narrow tree-rings in response to drought (Fang et al., 2011; Au and Tardif, 2012; Wang et al.,
Through these studies, a strong positive relationship between growth rates and precipitation has been well-established. However, tree growth is also known to be affected by waterlogging and flooded soils (Astrate and Bégin, 1997; Kozlowski, 1997; St. George, 2014). These effects are more difficult to detect in tree-ring patterns and therefore very few studies have evaluated growth responses to flooding (Ballestros-Canovas et al., 2015; Therrell and Bialecki, 2015; Meko and Therrell, 2020), particularly in southeastern USA (LeBlanc and Stahle, 2015).

Higher δ¹³C values of tree-ring cellulose usually reflect stress caused by low environmental moisture at the time of carbon fixation, while lower δ¹³C values are indicative of non-stressful growing conditions (Ehleringer et al., 1993; Saurer et al., 1995). Thus, dendroisotopic approaches combine the advantages of precisely dated and annually resolved tree rings with the sensitivity of δ¹³C values governed by ecophysiological responses to the environment (Gessler et al., 2009; Gessler et al., 2014). However, trees growing in wetland settings may not respond solely to moisture deficit. Excessive levels of precipitation and prolonged inundation or saturation in wetland ecosystems can also result in reduced stomatal conductance and/or increased assimilation rates in trees, resulting in high δ¹³C values; however, this effect is highly variable across species (Stuiver et al., 1984; Ewe and Sternberg, 2002; Ewe and Sternberg, 2003; Anderson et al., 2005; Buhay et al., 2008). These studies in wetlands attribute this positive relationship between δ¹³C and precipitation to excess water stress. Although debatable, a number of possible mechanisms have been suggested with significant evidence to support this relationship. These include disruption of water and nutrient uptake due to anoxic conditions in the root zone (Jackson and Drew, 1984), lowered root hydraulic conductivity (Davies and Flore, 1986),
increased abscisic acid concentrations (Kozlowski and Pallardy, 1984) and accumulation of metabolic toxins from flooding (Jackson and Drew, 1984).

In this study, we investigated how bottomland hardwood wetland forests of eastern Texas, USA respond to hydroclimatic variation and extremes under different edaphic conditions. The study was conducted at four sites, of which one was a frequently flooded wet site, while at the other three sites waterlogging and surface flooding were much less frequent and more ephemeral.

Our first objective was to understand how growth rates are affected by hydroclimatic variation using tree-ring width analysis in water oak (*Quercus nigra* L.), a dominant species in the Columbia bottomland hardwood forest. We hypothesized that at relatively drier sites, trees have lower growth rates on average over long time scales compared to wetter sites. Periods of higher rainfall will be associated with increases in growth. However, in extremely wet conditions, at frequently waterlogged sites, trees will show a decline in growth caused by flooding and hypoxic conditions.

Our second objective was to assess the magnitude of physiological stress inflicted by hydroclimatic conditions on these forests. We hypothesized that tree-ring δ¹³C in trees growing under relatively drier soil conditions will decrease during periods of higher rainfall. In contrast, the opposite trend is expected at wetter sites where increasing moisture would induce flooding stress. In addition, we hypothesized that trees growing where waterlogging is common are less stressed during dry periods than those at the drier sites because of slower depletion of soil water reserves. Our third objective was to evaluate the relationship between physiological stress and growth inhibition. Although a negative relationship between stress (tree-ring δ¹³C) and growth (tree-ring width) is expected in this study, the strength of this relationship could vary with site conditions. Given that water oaks are moderately tolerant of flooding, and dry conditions are also common in this ecosystem, we hypothesized that drought stress had a stronger effect on growth than flooding.
stress. Thus, we expected a stronger negative relationship between growth and physiological stress at drier sites.

2. Materials and Methods

2.1 Study Area Description

![Map of study area](https://example.com/map.png)

Figure 1. a) Current distribution of Columbia Bottomlands (grey) and historic extent shown by the slanted parallel lines (USFWS, 1997; Houston Wilderness, 2007; Rosen et al., 2008). The area in which the study sites are located is shown by the dashed box. b) Locations of study sites (circles) and weather stations (triangles) in the Brazos-Colorado Coastal Basin.

The study was conducted at four different sites located within the Brazos-Colorado Coastal Basin in the San Bernard National Wildlife Refuge, Brazoria and Fort Bend Counties, Texas. The four sites are Dance Bayou (DB), Big Pond (BP), Otto (OT) and Buffalo Creek (BC) (Fig. 1B; Table 1). Site DB was observed to be flooded most frequently after significant rain events from 2016 to 2019. This site also remained waterlogged for prolonged periods, unlike the other three...
sites. Therefore, we refer to this site as the “wet site”. The sites are located in Ecoregion III Western Gulf Coastal Plain and Ecoregion IV Floodplain and Low Terraces, dominated by mixed bottomland hardwood forests (Griffith, 2004) at an elevation of about 16 m above MSL. Dominant tree species at these sites include *Quercus nigra* L. (water oak), *Quercus fusiformis* Small (live oak), *Celtis laevigata* Willd. (sugarberry) and *Triadica sebifera* (L.) Small (Chinese tallow). The climate of this region is classified as Humid Subtropical (Cfa) under the Köppen–Geiger climate classification system (Koppen, 1900). The average maximum monthly temperature is approximately 26 °C and the average minimum monthly temperature is approximately 15 °C. Mean annual rainfall is 1143 mm, with an average relative humidity of ~70% (NOAA, 2018). The sites are located in the Linnville Bayou watershed of the San Bernard River Basin. As these forests are situated in the floodplain, sloughs are a common occurrence and inundate significant parts of the forest. Streamflow in Linnville Bayou and adjoining streams and sloughs that traverse the four sites is driven by at least 7 dams on the San Bernard River with heights ranging from 2.5-7.5 m (NID, 2020). Therefore, the presence of these dams and their varying discharge into Linnville Bayou adds significant complexity to the hydrology of Columbia Bottomlands in addition to an already fluctuating hydroclimate.

Soils are mainly vertisols and alfisols dominated by clay, loam and sandy loam texture (NRCS, 2020). The soils series include Aris fine sandy loam, Bacliff clay, Edna loam, Leton loam, Pledger Clay and Churnabog clay.
Table 1. Site description with basic soil properties averaged over the top 100 cm depth (NRCS, 2020).

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation (m)</th>
<th>Coordinates</th>
<th>Tree DBH (cm) (mean ± SE)</th>
<th>Clay (%)</th>
<th>Silt (%)</th>
<th>Sand (%)</th>
<th>Soil pH</th>
<th>Bulk Density (g/cm³)</th>
<th>Organic Matter (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DB</td>
<td>13</td>
<td>29°7'9.56&quot; N 95°47'4.24&quot; W</td>
<td>48.3 ± 5.6</td>
<td>33</td>
<td>58</td>
<td>9</td>
<td>7.4</td>
<td>1.37</td>
<td>1.7</td>
</tr>
<tr>
<td>BP</td>
<td>16</td>
<td>29°9'56.66&quot;N 95°49'43.34&quot;W</td>
<td>58.5 ± 3.2</td>
<td>71</td>
<td>28</td>
<td>1</td>
<td>7.1</td>
<td>1.12</td>
<td>4.8</td>
</tr>
<tr>
<td>OT</td>
<td>17</td>
<td>29°10'47.76&quot;N 95°50'28.65&quot;W</td>
<td>56.4 ± 4.7</td>
<td>71</td>
<td>28</td>
<td>1</td>
<td>7.1</td>
<td>1.12</td>
<td>4.8</td>
</tr>
<tr>
<td>BC</td>
<td>26</td>
<td>29°19'21.75&quot;N 95°51'47.01&quot;W</td>
<td>51.7 ± 3.8</td>
<td>55</td>
<td>34</td>
<td>11</td>
<td>7.8</td>
<td>1.20</td>
<td>2.2</td>
</tr>
</tbody>
</table>

2.2 Tree core sampling

We sampled at least eight mature Q. nigra trees at each site in May 2017. Healthy individuals with no obvious injuries like cavities, scars or diseases were selected. Preference was given to trees with larger diameters at breast height (>40 cm) and uniform girth (Stokes and Smiley, 1968). Three cores were extracted at breast height from every tree spaced equally around the circumference. Two cores were processed and used for ring-width measurements and the third core was used for δ¹³C analysis after cellulose extraction.

2.3 Dendrochronology

Tree cores were dried to constant weight at 60 °C and mounted on 9.5 x 9.5 mm grooved core mounts. The mounted cores were sanded using a hand sander with progressively finer grades of sandpaper (60 to 400 grit) (Speer, 2012). Tree-ring widths were visually crossdated and then measured using MeasureJ2X linked to a sliding-stage microscope (2.5X). To verify and refine the crossdating, tree-ring widths were statistically assessed using the COFECHA program (Holmes, 1983). Series intercorrelation and mean sensitivity obtained from COFECHA were used to determine the quality of crossdating (Grissino-Mayer, 2001; Speer, 2012). Series intercorrelation indicates core-to-core variation in annual growth rates within a given chronology, while mean
sensitivity indicates if the variation in annual growth rates from year-to-year is sensitive enough for dendroclimatology analysis. This crossdating was done separately for each site as well as on pooled raw tree-ring widths from all sites. The final standardized (\(A\)) chronology (Ring-width index) was generated for each site using ARSTAN, which mathematically standardizes tree-ring series by controlling the autocorrelation component in the time series and maximizes the climate signal (Cook and Holmes, 1984; Speer, 2012).

### 2.4 Climate Data

Daily climate summaries for 1950-2016 from three weather stations (Bay City, Newgulf and Wharton, Texas, USA, Fig. 1B) and Palmer Drought Severity Index (PDSI) for the Texas Upper Coast Division were collected from the NOAA NCEI database (NOAA, 2018). Monthly and annual averages were used for analysis. As the three weather stations are located at equal distances from the sites (<25 km) and the measurements are highly correlated, an average of the three records was used for dendroclimatology analysis. Monthly average \(\delta^{13}C\) values of atmospheric CO\(_2\) from La Jolla Pier, California, USA were obtained from the Scripps CO\(_2\) Program and annual averages were calculated (Keeling and Keeling, 2017).

### 2.5 Tree-ring \(\delta^{13}C\) analysis

Tree cores not utilized for ring-width analyses were hand-sanded using a sandpaper (220 grit) to enhance ring-visibility. Tree-rings were selected from years with a wide range of precipitation to cover the maximum breadth of the dry-wet hydroclimatic spectrum (235-1120 mm/year). Selected tree-rings were precisely excised using an X-Acto knife. For \(\delta^{13}C\) analysis, \(\alpha\)-cellulose was extracted from the tree-rings using a slightly modified version of the Jayme-Wise Method (Green, 1963), in which a Soxhlet extraction assembly is used (Leavitt and Danzer, 1993; Cullen and Macfarlane, 2005). \(\delta^{13}C\) in tree-ring \(\alpha\)-cellulose was analyzed using a Costech ECS
4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA) interfaced with a Delta V Advantage isotope ratio mass spectrometer (Delta V, ThermoFisher Scientific, Waltham, MA, USA) operating in continuous flow mode in the Stable Isotopes for Biosphere Science (SIBS) Lab, Texas A&M University (College Station, TX, USA). Carbon isotope ratios are presented in δ notation:

\[
\delta = \left( \frac{R_{\text{SAMPLE}} - R_{\text{STD}}}{R_{\text{STD}}} \right) \times 10^3
\]  

(1)

where \(R_{\text{SAMPLE}}\) is the \(^{13}\text{C}/^{12}\text{C}\) ratio of the sample and \(R_{\text{STD}}\) is the \(^{13}\text{C}/^{12}\text{C}\) ratio of the V-PDB (Vienna Pee Dee Belemnite) standard (Coplen, 1995). Duplicate measurements taken after every 10 measurements yielded a precision of ±0.1‰.

Atmospheric δ\(^{13}\text{C}\) depletion trend over the study period was removed from the tree-ring δ\(^{13}\text{C}\) record by calculating the difference between average annual atmospheric δ\(^{13}\text{C}\) values (Keeling and Keeling, 2017) and a standard value (‘pre-industrial’ value of -6.4‰) (Francey et al., 2002). The difference is denoted by Δ. Yearly Δ values were then added to tree-ring δ\(^{13}\text{C}\) values from corresponding years (McCarroll and Loader, 2004) (Table 2).

**Table 2:** Annual average atmospheric δ\(^{13}\text{C}\) values and yearly correction factor (Δ).

<table>
<thead>
<tr>
<th>Year</th>
<th>δ(^{13}\text{C})</th>
<th>Δ</th>
<th>Year</th>
<th>δ(^{13}\text{C})</th>
<th>Δ</th>
<th>Year</th>
<th>δ(^{13}\text{C})</th>
<th>Δ</th>
</tr>
</thead>
<tbody>
<tr>
<td>1986</td>
<td>-7.70</td>
<td>1.30</td>
<td>1997</td>
<td>-8.02</td>
<td>1.62</td>
<td>2008</td>
<td>-8.34</td>
<td>1.94</td>
</tr>
<tr>
<td>1990</td>
<td>-7.89</td>
<td>1.49</td>
<td>2001</td>
<td>-8.11</td>
<td>1.71</td>
<td>2012</td>
<td>-8.43</td>
<td>2.03</td>
</tr>
<tr>
<td>1993</td>
<td>-7.89</td>
<td>1.49</td>
<td>2004</td>
<td>-8.24</td>
<td>1.84</td>
<td>2015</td>
<td>-8.51</td>
<td>2.11</td>
</tr>
<tr>
<td>1995</td>
<td>-8.01</td>
<td>1.61</td>
<td>2006</td>
<td>-8.33</td>
<td>1.93</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>-8.03</td>
<td>1.63</td>
<td>2007</td>
<td>-8.34</td>
<td>1.94</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

2.6 Statistical Analyses
To evaluate differences in mean δ^{13}C values between sites, we used one-way ANOVA. Levene’s test was used to check for equal variances, normality was tested using Shapiro-Wilk test and post-hoc analysis was conducted using Tukey HSD. Total monthly precipitation was calculated from daily summaries. Daily maximum temperatures for each day of the month were used to compute mean monthly maximum temperature. Monthly PDSI values were used directly as obtained. To identify the portion of the growing season that has the strongest influence on growth and δ^{13}C, we used simple linear regressions between site-wise annual ring-width index and δ^{13}C against monthly precipitation, mean monthly maximum temperature and monthly PDSI for all months of the same year as well as the previous year. Additionally, to estimate the multi-month influence of early, late and overall growing season climate on growth and δ^{13}C, we averaged monthly climate data over progressively longer periods of up to 8 months within the growing season. We conducted additional linear regression on these calculated means against annual ring-width index and δ^{13}C. The time interval during which climate was found to be most strongly influencing growth and δ^{13}C (maximum coefficient of determination) was used for dendroclimatology analysis. To understand the relationship between growth and stress, we also used linear regression between site-wise annual ring width index and δ^{13}C. All statistical analyses were conducted in R (R Core Team, 2012).

3. Results

3.1 Site chronologies

Site-level tree-ring width chronologies were closely related to precipitation trends. Patterns of annual growth rate were similar between sites for much of the 40-year period, except a few wet years (1991, 1992, 1997, 2001, 2003 and 2007) (Fig. 2). The divergent responses to these wet years apparently reduced the pooled series intercorrelation (Table 3). Hence, this multi-site chronology was not used for further analyses. High series intercorrelation for the drier sites...
indicates lower tree-to-tree differences at these sites, as compared to our wettest site, DB, which had a slightly lower series intercorrelation (Table 3). All site-level chronologies were found to be sensitive enough for dendroclimatological analysis as mean sensitivity, which is a measurement of year-to-year variability in annual growth, fell within an acceptable range. Forest stands at sites DB and OT were found to be younger (27 years) than the other two sites (40 years) as indicated by the mean series lengths (Table 3).

**Figure 2.** Temporal variation in ring-width index of *Quercus nigra* within the Brazos-Colorado Coastal Basin of Texas. Total annual precipitation is shown by grey shading.

**Table 3.** Descriptive statistics of site-level as well as combined tree-ring chronologies generated using COFECHA.

<table>
<thead>
<tr>
<th>Chronology</th>
<th>Number of trees</th>
<th>Number of dated series</th>
<th>Series Intercorrelation</th>
<th>Mean Sensitivity</th>
<th>Mean Series Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>All sites</td>
<td>32</td>
<td>64</td>
<td>0.31</td>
<td>0.37</td>
<td>33 years</td>
</tr>
<tr>
<td>DB</td>
<td>8</td>
<td>16</td>
<td>0.52</td>
<td>0.35</td>
<td>27 years</td>
</tr>
<tr>
<td>BP</td>
<td>8</td>
<td>16</td>
<td>0.74</td>
<td>0.36</td>
<td>40 years</td>
</tr>
<tr>
<td>OT</td>
<td>8</td>
<td>16</td>
<td>0.78</td>
<td>0.42</td>
<td>27 years</td>
</tr>
<tr>
<td>BC</td>
<td>8</td>
<td>16</td>
<td>0.77</td>
<td>0.37</td>
<td>38 years</td>
</tr>
</tbody>
</table>
3.2 Differences in site-level tree-ring $\delta^{13}C$ values

Comparison between site-level mean tree-ring $\delta^{13}C$ measurements averaged over the entire 40-year study period supports our second hypothesis. Tree-ring $\delta^{13}C$ measurements were different between sites when averaged over the 40-year period [One-way ANOVA, F (3, 24) = 4.05, p = 0.01]. This indicates that at least one site has a significantly different mean $\delta^{13}C$ signal over the 40-year period. Post hoc analysis indicates that the wet site, DB, had a lower mean tree-ring $\delta^{13}C$ value as compared to two drier sites, BP (p=0.03) and OT (p=0.02) (Fig. 3).

![Figure 3](https://doi.org/10.5194/bg-2020-131)

**Figure 3.** One-way ANOVA and Tukey post hoc analysis (denoted with letters) for mean difference in site-level tree-ring $\delta^{13}C$ averaged over the 40-year period. Black diamonds indicate mean values, horizontal black lines indicate median values, black circles indicate outliers and grey boxes show values lying between the upper and lower quartiles.

3.3 Dendroclimatology analysis

Comparisons between ring-width index and climate data reveal that growth rates are most strongly influenced by mid-growing season climate (May-July precipitation and maximum temperatures; July PDSI) (Table S1). Since a larger proportion of annual growth occurs during the mid-growing season, higher rainfall and lower maximum temperatures during this period strongly drive annual growth rates. Similar comparisons between tree-ring $\delta^{13}C$ measurements and climate
data indicate that climatic conditions early in the growing season (April) are critical for causing physiological stress in these forests (Table S2).

As hypothesized, we observed a strong increase in tree-ring widths with mid-growing season precipitation. Although this positive relationship was expected for trees growing in drier conditions, we observed a similar but weaker positive relationship between growth and precipitation even at the wet site (Table 4). We had hypothesized that at extremely wet conditions, growth rates at the wet site would decline due to flood stress, however, no such decline was observed even during extremely wet phases (Fig. 4a). Drought conditions and maximum temperatures during the mid-growing season result in decreasing growth at the drier sites, but not at the wet site, as expected (Table 4; Fig. 4b, c).

Table 4. Relationships between ring-width index and mid-growing season climatic conditions (α=0.05).

<table>
<thead>
<tr>
<th>Site</th>
<th>Precipitation (May-July) p value</th>
<th>R²</th>
<th>Temperature (May-July) p value</th>
<th>R²</th>
<th>PDSI (July) p value</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>DB</td>
<td>&lt;0.05</td>
<td>0.13</td>
<td>ns</td>
<td>-</td>
<td>ns</td>
<td>-</td>
</tr>
<tr>
<td>BP</td>
<td>&lt;0.001</td>
<td>0.39</td>
<td>&lt;0.001</td>
<td>0.25</td>
<td>&lt;0.001</td>
<td>0.49</td>
</tr>
<tr>
<td>OT</td>
<td>&lt;0.001</td>
<td>0.42</td>
<td>&lt;0.01</td>
<td>0.17</td>
<td>&lt;0.001</td>
<td>0.31</td>
</tr>
<tr>
<td>BC</td>
<td>&lt;0.001</td>
<td>0.44</td>
<td>&lt;0.001</td>
<td>0.27</td>
<td>&lt;0.001</td>
<td>0.47</td>
</tr>
</tbody>
</table>
In line with our second hypothesis, we observed a depletion in tree-ring $\delta^{13}$C values with increase in early-growing season precipitation at the drier sites (Table 5, Fig. 5a). We had hypothesized that high precipitation at the wet site will enrich tree-ring $\delta^{13}$C values as a result of physiological stress caused by possible flooding stress. However, we found no relationship between tree-ring $\delta^{13}$C and precipitation at the wet site (Table 5). Higher maximum temperatures resulted in enriched tree-ring $\delta^{13}$C values only at one of the drier sites (BC), indicating physiological resistance to high temperatures in most parts of this wetland forest (Table 5, Fig. 5b). PDSI did not have any effect on tree-ring $\delta^{13}$C values from all four sites (Table 5). Also, previous year’s climate did not have any statistically significant influence on either ring-width index or tree-ring $\delta^{13}$C measurements at any site.
Table 5. Relationships between tree-ring δ\textsuperscript{13}C values and early-growing season climatic conditions (α=0.05).

<table>
<thead>
<tr>
<th>Site</th>
<th>Precipitation (April)</th>
<th>Temperature (April)</th>
<th>PDSI</th>
<th>p value</th>
<th>R\textsuperscript{2}</th>
<th>p value</th>
<th>R\textsuperscript{2}</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>DB</td>
<td>ns</td>
<td>-</td>
<td>ns</td>
<td>-</td>
<td>ns</td>
<td>-</td>
<td>ns</td>
<td>-</td>
</tr>
<tr>
<td>BP</td>
<td>&lt;0.05</td>
<td>0.70</td>
<td>ns</td>
<td>-</td>
<td>ns</td>
<td>ns</td>
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<td>BC</td>
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Figure 5. Relationship between tree-ring δ\textsuperscript{13}C values and early-growing season (a) precipitation and (b) temperature. Site DB is represented by grey triangles, BP by grey diamonds, OT by black squares and BC by black circles. Statistically significant relationships are marked with an asterisk (*).

3.4 Relationship between growth and tree-ring δ\textsuperscript{13}C

The comparison between tree-ring δ\textsuperscript{13}C values and tree-ring width from corresponding years supports our third hypothesis only at the drier sites. Ring-width index was correlated with δ\textsuperscript{13}C values only at sites OT (p<0.05; R\textsuperscript{2}=0.53) and BC (p<0.05; R\textsuperscript{2}=0.58). Tree-ring δ\textsuperscript{13}C values were not correlated with annual growth at the wet site DB, which indicates that trees at this site were able to sustain their growth rates even during stressful conditions (Fig. 6).
4. Discussion

Bottomland hardwood forests in the southeastern United States have been reduced to a small proportion of their original expanse. The hydrology of these wetland forests has been altered due to expansion of agricultural and urban land uses, river regulation, drainage ditches, impoundment from berms and poor drainage, and water table drawdowns (Wear and Greis, 2002; Blann et al., 2009; Dahl, 2011). The ecological impacts of these disturbances are exacerbated by hydroclimatic anomalies such as droughts and floods (Ferrati et al., 2005; Erwin, 2008). Changing climatic conditions are not only resulting in increasingly drier conditions over time, but also more intense storm events (Easterling et al., 2000; Seager et al., 2007; Knutson et al., 2010). Moreover, fragmentation caused by anthropogenic pressures coupled with topographic heterogeneity causes this dry-wet transition to not only be temporally but also spatially variable. As a result, portions of these riverine wetland forests tend to be drier than others. These temporal and spatial variations need to be considered while studying the impacts of changing hydroclimate and hydrology on plants in such ecosystems.
Contrary to our first hypothesis, similar annual growth rates of trees at the wetter site and the three drier sites during the past several decades suggests that trees at all sites have access to moisture sufficient to sustain annual growth. Moreover, growth of trees at the wetter site was not inhibited by excessive moisture during wet years, which may reflect adaptation by *Quercus nigra* to the broad range of soil moisture conditions that occur in a floodplain forest (Gilman et al., 1994). Within the wetter site, we observed more heterogeneity in growth rates, which could be attributed to uneven waterlogging within the site. Although growth rates were correlated with rainfall across all sites, the wet site had a much weaker dependence on rainfall and showed no negative response to higher temperatures and drought severity. This suggests that wetland forests with high water tables are more independent of climatic conditions than their drier counterparts. It has been repeatedly observed across southeastern US that in wetter and hydrologically well-connected parts of wetland forests, vegetation is more physiologically resilient and experiences lower stress during non-favorable growing conditions (Clawson et al., 2001; Anderson et al., 2005; Gee et al., 2014; Allen et al., 2016).

Consistent with our second hypothesis, mean tree-ring δ¹³C values from the wetter site were significantly lower than those from the drier sites over a longer temporal scale, suggesting lower physiological stress and higher resilience of trees at the wet site as compared to those at the drier sites. Also supporting our second hypothesis, reduced stomatal conductance in trees from the drier site during drought years, clearly indicates prolonged stress caused by soil moisture deficit. This relationship between tree-ring δ¹³C and drought conditions (low precipitation and high temperatures) has been extensively observed across different ecosystems such as boreal forests (Brooks et al., 1998; Au and Tardif, 2012), wetlands (Anderson et al., 2005; Buhay et al., 2008), lowland rain forests (Schollaen et al., 2013), deserts (Lipp et al., 1996), etc. It is important to note
that in parts of these forested wetlands, dry conditions can develop and cause stressful conditions for the vegetation.

Our third hypothesis that physiological stress would have a negative relationship with growth holds true under dry edaphic conditions, where stress restricts plant growth. Contrastingly, in trees growing in wetter soils, stress and growth are largely decoupled. At the drier sites, drought-related enriched tree-ring $\delta^{13}$C values are correlated with slower growth rates, which indicates that moisture deficit causes physiological stress in these trees, resulting in growth inhibition. The absence of drought-related stress signals at the wet site is possibly due to supplemental soil moisture availability from flooding and higher physiological resistance. Additionally, decoupling between growth and stress signals from the wet site indicate that physiological stress does not always result in growth inhibition in wetland trees, especially when optimum moisture is available. A similar relationship has been observed in pond cypress trees in the southeastern Everglades, Florida, USA (Anderson et al., 2005). This decoupling between stress signals and growth rates seems to be more common in wetlands with prolonged waterlogging. It has been suggested that wetland species that experience frequent flooding develop adaptive traits that enable rapid reopening of stomata with the recession of flood waters as oxygen availability in the root zone increases (Crawford, 1982; Kozlowski and Pallardy, 1984; Kozlowski, 2002). As a result, growth may not be inhibited even though stress signals related to stomatal closure due to flooding are detected in the same tree-ring. Consistent with this, our observations signify that trees growing in drier conditions do have a more distinct stress-growth relationship as compared to those growing in wet conditions.

We found that mid-growing season precipitation (from May to July) is most critical for growth in this landscape. Similarly, high temperatures during the same period were associated with
suppressed growth. Therefore, adequate precipitation and moderate temperatures during this period are important controls over tree growth. However, due to changing climatic conditions and altered hydrology of this region, change in the moisture availability during this period can be severely detrimental to this ecosystem. Unlike the trees growing in drier conditions, the ones at the wet site are not affected by temperature and drought severity throughout the growing season possibly because of residual soil moisture availability despite evaporation caused by higher temperatures. It is important to consider seasonal variation in precipitation because flood conditions in the dormant winter season do not necessarily help sustain growth throughout the summer in drier sites, especially if summers have below normal precipitation. On the other hand, trees at the wet site may benefit from access to soil moisture reserves from waterlogging caused by winter precipitation.

While the growth-climate relationship is more amplified during mid-growing season, stress signals are more prominently dependent on early-growing season precipitation. Lack of precipitation early in the growing season (April) results in substantial physiological stress in trees at the drier sites. This is an indication that although dry conditions early in the growing season cause stress in trees, most growth is attained during the mid-growing season. Therefore, trees can recover from the stress and attain normal growth rates if adequate precipitation occurs during the mid-growing season. The prominent dependence of physiological stress on spring precipitation could be the result of more energy and resource allocation during leaf out. However, this holds true only under dry edaphic conditions. Such seasonal variations have been observed across different biomes and have been attributed to formation of wood using previous or current growing season assimilates (Schollaen et al., 2013). It is apparent that if wood at the very beginning of the growing season is formed using assimilates from the previous growing season, tree-ring \( \delta^{13}C \) does
not have a correlation with early-growing season precipitation from the current year (Helle and Schleser, 2004; Porter et al., 2009; Schollaen et al., 2013). However, like in our study, when tree-ring $\delta^{13}C$ is well-correlated with precipitation from early-growing season, it indicates formation of wood using assimilates from the current growing season. To confirm this relationship, we compared our ring-width index and tree-ring $\delta^{13}C$ values with previous years’ climate and found no correlation.

Columbia bottomlands occur at the extreme southwestern edge of the bottomland hardwood forest type (Bray, 1906; Putnam et al., 1960), which is also the southwestern edge of the distribution of Q. nigra and many other wetland tree species. Consequently, the Q. nigra populations examined in this study experience the driest and warmest conditions found throughout its geographic range. Edges of distribution ranges usually experience harsher environmental conditions as compared to the range core (Rehm et al., 2015). Therefore, range-edge populations are more resilient and are better adapted to survive in stressful conditions relative to core populations (Gutschick and Hormoz, 2003). Climate models have predicted a significant decrease in precipitation and increase in temperature throughout Texas (Jiang and Yang, 2012) and especially in the Brazos River basin (Awal et al., 2016) where this population occurs. As climate changes, these native wetland tree populations will play key roles in helping the species maintain their geographic distributions.

5. Conclusion

This study provides insights on hydroclimatic conditions that can provide suitable conditions for better wetland forest productivity and health. Columbia bottomlands support a large diversity of plants, mammals, birds, reptiles and insects. The knowledge of optimum growing conditions for the vegetation in this region is critical for the survival and conservation of the
biodiversity that is dependent on this ecosystem. We provide evidence that wetter portions of this landscape are more resilient to hydroclimatic changes than drier areas, as well as better adapted to periods of flooding and waterlogging. Trees in drier areas grew more slowly during dry and warm periods and were more sensitive to seasonal physiological stress. We observed variation in growth and stress responses to climatic conditions during different phases of the growing season. Our findings suggest that hydroclimatic changes to this ecosystem that alter the timing and frequency of wet conditions can negatively impact forest health. This study also provides the first tree-ring records from the Columbia bottomlands, which can act as a baseline for future ecological research in the region.

Data availability. All data resulting from this study are available from the authors upon request (ajinkyagd@tamu.edu).

Competing interests. The authors declare that they have no conflict of interest.

Author contribution. Ajinkya G. Deshpande conceptualized the study, developed the methodology, collected field samples, conducted formal analysis including laboratory and statistical analysis and wrote the original draft. Thomas W. Boutton contributed in conceptualization of the study, provided laboratory equipment/materials for stable carbon isotope analysis and edited/reviewed the original draft. Charles W. Lafon contributed in conceptualization of the study, provided all the required equipment for dendrochronology and edited/reviewed the original draft. Georgianne W. Moore was the investigator and supervisor of the study, played a major role in conceptualization of the study, contributed in developing the methodology as well as statistical analyses, acquired funds for the study and edited/reviewed the original draft.

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