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

Ajinkya G. Deshpande[1], Thomas W. Boutton[1], Ayumi Hyodo[1], Charles W. Lafon[2], Georgianne W. Moore[1]

[1]Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX 77843, USA

[2]Department of Geography, Texas A&M University, College Station, TX 77843, USA

Correspondence to: Ajinkya G. Deshpande (ajinkyagd@tamu.edu)

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 radial growth using tree-ring width analysis, (ii) assess the magnitude of physiological stress inflicted by extreme hydroclimatic conditions using tree-ring Δ^{13}C measurements as a proxy, and (iii) evaluate the relationship between tree-ring width and Δ^{13}C values. Radial growth across the landscape was influenced most strongly by mid-growing season climate, while early-growing season climate had the strongest effect on Δ^{13}C. Growth inhibition was minimal and tree-ring Δ^{13}C values were not affected in trees at the wetter site under extreme hydrological conditions such as droughts or floods. In addition, trees at the wet site were less sensitive to precipitation and showed no response to

27 higher temperatures. In contrast, trees of the three drier sites experienced growth inhibition and

28 had lower tree-ring $\Delta^{13}C$ values during dry periods. Our results indicate more favorable growing

29 conditions and lower stress in trees growing under wetter hydrological conditions. Management

30 and conservation strategies dependent on site-specific conditions are critical for the health of these

31 wetland forests under a rapidly changing hydroclimate. This study provides the first

32 dendrochronological baseline for this region and a better understanding of favorable conditions for

33 the growth and health of these forests which can assist management decisions such as streamflow

34 regulation and conservation plans.

35 **1. Introduction**

36   Wetland forests are subjected to drought and floods, both of which can alter productivity

37 and cause physiological stress in plants (Miao et al., 2009; Vivian et al., 2014). These climate

38 extremes and warming are predicted to increase in the 21st century across southern North America

39 (Seager et al., 2007). Bottomland hardwood forests, a common wetland forest type, cover a

40 significant proportion of the floodplains of the rivers and bayous in coastal regions of the

41 southeastern USA. Along the upper Texas Gulf coast, the lower basins of the Brazos River, San

42 Bernard River and Colorado River combine to form the Columbia bottomland hardwood forests,

43 an area of high biodiversity with a critical role in regional hydrology. Large portions of the

44 Columbia basin forest have been cleared and land cover is now a mix of isolated forest patches,

45 cropland, and pasture (Griffith, 2004), with only a few larger forest patches remaining (Fig. 1A).

46 The pre-settlement distribution of these forests was >283,000 ha along a 150 km long corridor

47 inland from the coast, but has since been reduced to about 72,000 ha (USFWS, 1997; Barrow and

48 Renne, 2001; Barrow et al., 2005). In the last few decades, this ecosystem has been experiencing

49 dramatic hydrologic variation caused by severe droughts (Schmidt and Garland, 2012; Hoerling et

50 al., 2013; Moore et al., 2015) as well as floods (van Oldenborgh et al., 2017; Sebastian et al., 2019),

51 altering hydrologic conditions over short temporal scales. Annual precipitation amounts have been

52 highly variable with up to 61% more rainfall than average during some years, while up to 53%

53 deficit during others, in addition to at least five major tropical storms and hurricanes. Rapid

54 urbanization caused by the proximity to the city of Houston and increasing agricultural activity in

55 the area have likely altered water cycling significantly in these forests (Kearns et al., 2015; TWDB,

56 2017). Similar forcing factors have altered the state of most wetland forest types in southeastern

57 USA.

58   Dendrochronology, the study of tree-rings, has been extensively used to understand the

59 response of forest growth to changing environmental conditions (Babst et al., 2013; Charney et al.,

60 2016; Tei et al., 2017). Additionally, tree-ring carbon isotopic composition is an indirect record of

61 internal leaf CO_2 concentration, which is controlled by a balance between stomatal conductance

62 and photosynthetic rate in response to environmental conditions (Farquhar et al., 1989; McCarroll

63 and Loader, 2004; Gessler et al., 2014), such as temperature, vapor pressure and precipitation

64 (Robertson et al., 1997; Leavitt et al., 2002). As tree rings are distinguished by their high temporal

65 (annual or sub-annual) and spatial resolution, regional tree-ring chronologies and carbon isotopic

66 values have the potential to identify a wide range of growth and stress response of vegetation to

67 hydroclimatic variability. However, carbon isotopic composition of tree-rings ($\delta^{13}C$) is also

68 influenced by the changing carbon isotopic composition of atmospheric CO_2. The increase in

69 atmospheric CO_2 concentration mainly due to fossil fuel combustion has led to a significant

70 decrease in $\delta^{13}C$ of atmospheric CO_2 over the last century (Graven et al., 2017). Although this

71 change is relatively small over short temporal scales, this signal should be removed from tree-ring

72 records when using tree-ring $\delta^{13}C$ to understand plant physiological responses to local conditions.

73 Changes in carbon isotopic composition of atmospheric CO_2 can be accounted for by converting

74 tree-ring carbon isotope ratio ($\delta^{13}C$) to carbon isotope discrimination ($\Delta^{13}C$) (Farquhar, 1983).

75 Tree-ring $\delta^{13}C$ values are inversely related to $\Delta^{13}C$ values as higher discrimination results in a

76 lower $\delta^{13}C$ ratio.

77   Studies conducted across the globe demonstrate growth inhibition signals in the form of

78 narrow tree-rings in response to drought (Fang et al., 2011; Au and Tardif, 2012; Wang et al.,

79 2017; Gao et al., 2018; Mikac et al., 2018; Szejner et al., 2020). Through these studies, a strong

80 positive relationship between growth rates and precipitation has been well-established. However,

81 tree growth is also known to be affected by waterlogging and flooded soils (Astrade and Bégin,

82 1997; Kozlowski, 1997; St. George, 2014). These effects are more difficult to detect in tree-ring

83 patterns and therefore very few studies have evaluated growth responses to flooding (Ballesteros-

84 Canovas et al., 2015; Therrell and Bialecki, 2015; Meko and Therrell, 2020), particularly in

85 southeastern USA (LeBlanc and Stahle, 2015).

86   Lower $\Delta^{13}C$ values of tree-ring cellulose usually reflect stress caused by low

87 environmental moisture at the time of carbon fixation, while higher $\Delta^{13}C$ values are indicative of

88 non-stressful growing conditions (Ehleringer et al., 1993; Saurer et al., 1995). Thus,

89 dendroisotopic approaches combine the advantages of precisely dated and annually resolved tree

90 rings with the sensitivity of carbon isotopic composition governed by ecophysiological responses

91 to the environment (Gessler et al., 2009; Gessler et al., 2014). However, trees growing in wetland

92 settings may not respond solely to moisture deficit. Excessive levels of precipitation and prolonged

93 inundation or saturation in wetland ecosystems can also result in reduced stomatal conductance in

94 trees, resulting in low discrimination values; however, this effect is highly variable across species

95 (Stuiver et al., 1984; Ewe and Sternberg, 2002; Ewe and Sternberg, 2003; Anderson et al., 2005;

96 Buhay et al., 2008; Voelker et al., 2014). These studies in wetlands attribute this positive

97   relationship between tree-ring carbon isotopes and precipitation to excess water stress. Although

98   debatable, a number of possible mechanisms have been suggested with significant evidence to

99   support this relationship. These include disruption of water and nutrient uptake due to anoxic

100 conditions in the root zone (Jackson and Drew, 1984), lowered root hydraulic conductivity (Davies

101 and Flore, 1986), increased abscisic acid concentrations (Kozlowski and Pallardy, 1984) and

102 accumulation of metabolic toxins from flooding (Jackson and Drew, 1984). Additionally, higher

103 evaporation rates at wetland sites where ponding is common can reduce vapor pressure deficit in

104 the canopy, resulting in lower canopy conductance (Oren et al., 2001) and subsequently lower

105 discrimination rates. Anaerobic conditions at waterlogged sites can also lead to isotopically

106 depleted methane production from the soils and affect the ambient $\delta^{13}C$ in the canopy (Fisher et

107 al., 2017). If these conditions that are specific to wetland ecosystems persist over a longer period

108 during the growing season, carbon isotopic composition of tree-rings can be influenced.

109   In this study, we investigated how bottomland hardwood wetland forests of eastern Texas,

110 USA respond to hydroclimatic variation and extremes under different edaphic conditions. The

111 study was conducted at four sites, of which one was a frequently flooded wet site, while at the

112 other three sites waterlogging and surface flooding were much less frequent and more ephemeral.

113 Our first objective was to understand how radial growth is affected by hydroclimatic variation

114 using tree-ring width analysis in water oak (*Quercus nigra* L.*)*, a dominant species in the Columbia

115 bottomland hardwood forest. We hypothesized that at relatively drier sites, trees have lower growth

116 rates on average over long time scales compared to wetter sites. Periods of higher rainfall will be

117 associated with increases in growth. However, in extremely wet conditions, at the frequently

118 waterlogged site, trees will show a decline in growth caused by flooding and hypoxic conditions.

119 Our second objective was to assess tree-ring $\Delta^{13}C$ as an indicator of physiological stress inflicted

120   by hydroclimatic conditions on these forests. We hypothesized that tree-ring $\Delta^{13}C$ in trees growing

121   under relatively drier soil conditions will increase during periods of higher rainfall. In contrast, the

122   opposite trend is expected at the wetter site where increasing moisture would induce flooding

123   stress. In addition, we hypothesized that trees growing where waterlogging is common are less

124   stressed during dry periods than those at the drier sites because of slower depletion of soil water

125   reserves. Our third objective was to evaluate the relationship between physiological stress and

126   growth inhibition. Although a positive relationship between tree-ring $\Delta^{13}C$ and growth (tree-ring

127   width) is expected in this study, the strength of this relationship could vary with site conditions.

128   Given that water oaks are moderately tolerant of flooding, and dry conditions are also common in

129   this ecosystem, we hypothesized that drought stress had a stronger effect on growth than flooding

130   stress. Thus, we expected a stronger negative effect of physiological stress on growth at drier sites.

131   **2. Materials and Methods**

132   **2.1 Study Area Description**
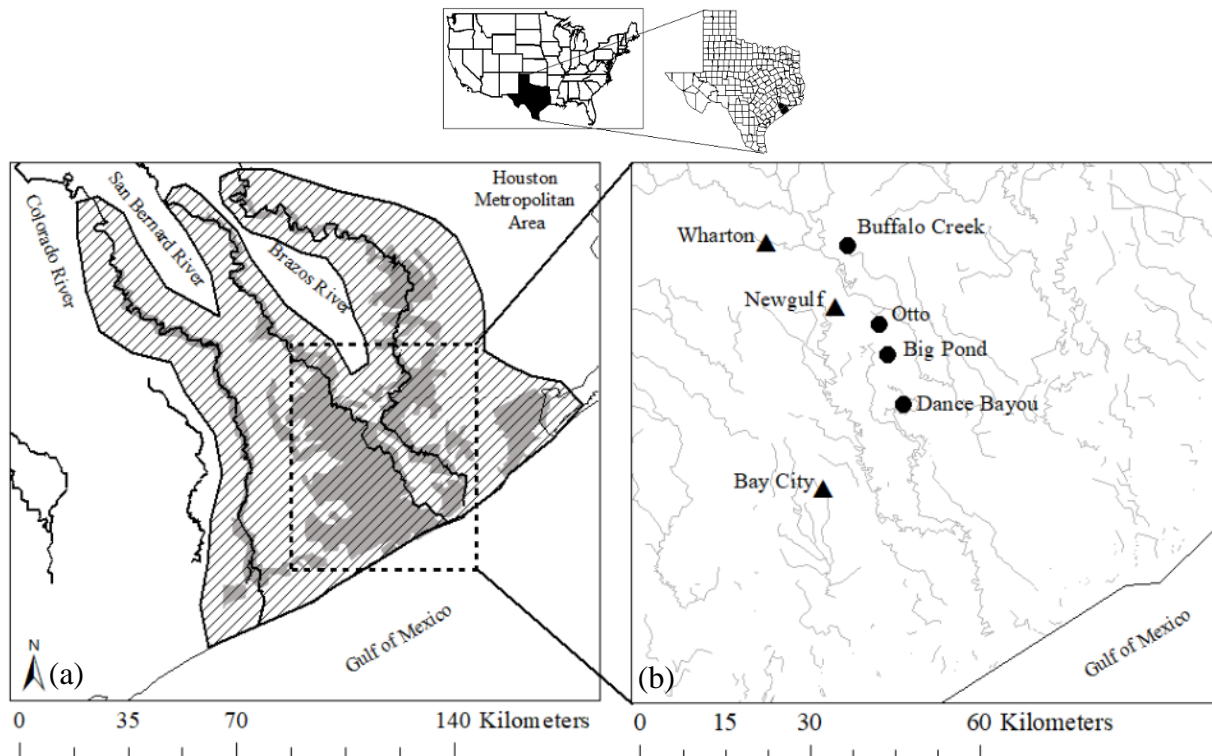
Figure 1. a) Current distribution of Columbia Bottomlands (grey) and historic extent shown by the slanted parallel lines (USFWS, 1997; Houston Wilderness, 2007; Rosen et al., 2008). The area in which the study sites are located is shown by the dashed box. b) Locations of study sites (circles) and weather 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, 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 $^{\circ}$C and the average minimum monthly temperature is approximately 15 $^{\circ}$C. Mean annual rainfall is 1143 mm, with an average relative humidity of ~70% (NOAA, 2018a). 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

158   complexity to the hydrology of Columbia Bottomlands in addition to an already fluctuating

159   hydroclimate.

160   Soils are mainly vertisols and alfisols dominated by clay, loam and sandy loam texture (NRCS,

161   2020). The soils series include Aris fine sandy loam, Bacliff clay, Edna loam, Leton loam, Pledger

162   Clay and Churnabog clay. In an Earth Resistivity Tomography study conducted by Guerra (2020)

163   at sites DB, BP and OT, the wetter site DB had more conductive soil in the root zone as compared

164   to the other two drier sites (Table 1). As all three sites had similar soil salinity, the more conductive

165   soils at site DB are attributed to higher soil moisture.

166   **Table 1.** Site description with basic soil properties (NRCS, 2020) and resistivity measurements
167   averaged over the top 100 cm depth (Guerra, 2020).
168

Site	Elevation (m)	Coordinates	Tree DBH (cm) (mean ± SE)	Clay %	Silt %	Sand %	Soil pH	Bulk Density (g/cm^3)	Organic Matter (%)	Resistivity (Ω•m) (mean)
DB	13	29°7'9.56" N 95°47'4.24" W	48.3 ± 5.6	33	58	9	7.4	1.37	1.7	9.9
BP	16	29°9'56.66"N 95°49'43.34"W	58.5 ± 3.2	71	28	1	7.1	1.12	4.8	16.2
OT	17	29°10'47.76"N 95°50'28.65"W	56.4 ± 4.7	71	28	1	7.1	1.12	4.8	12.2
BC	26	29°19'21.75"N 95°51'47.01"W	51.7 ± 3.8	55	34	11	7.8	1.20	2.2	N/A

169   **2.2 Tree core sampling**

170   We sampled eight mature *Q. nigra* trees at each site in May 2017. Healthy individuals with

171   no obvious injuries like cavities, scars or diseases were selected. Preference was given to trees

172   with larger diameters at breast height (>40 cm) and uniform girth (Stokes and Smiley, 1968). Three

173   cores were extracted at breast height from every tree spaced equally around the circumference.

174   Two cores were processed and used for ring-width measurements and the third core was used for

175    $\delta^{13}C$ analysis after cellulose extraction.

176   **2.3 Dendrochronology**

177   Tree cores were dried to constant weight at 60 ^{o}C and mounted on 9.5 x 9.5 mm grooved

178   core mounts. The mounted cores were sanded using a hand sander with progressively finer grades

179   of sandpaper (60 to 400 grit) (Speer, 2012). Tree-ring widths were visually crossdated and then

180   measured using MeasureJ2X linked to a sliding-stage microscope (2.5X). To verify and refine the

181   crossdating, tree-ring widths were statistically assessed using the COFECHA program (Holmes,

182   1983). Site-level series intercorrelation between individual cores and mean sensitivity obtained

183   from COFECHA were used to determine the quality of crossdating (Grissino-Mayer, 2001; Speer,

184   2012). Series intercorrelation indicates chronology-to-chronology variation in annual growth

185   within a given chronology group, while mean sensitivity indicates if the variation in annual growth

186   from year-to-year is sensitive enough for dendroclimatology analyses. As series intercorrelation

187   can be a useful metric to interpret variations in growth between cores from the same tree, trees

188   within a given site, cores across different sites and trees across different sites, we calculated all

189   four of these parameters separately (Bunn et al., 2020). To calculate series intercorrelation between

190   trees within and across sites, we first averaged corresponding annual ring widths from multiple

191   cores sampled from the same tree. The final standardized ARSTAN (A) chronology (ring-width

192   index (RWI)) was generated for each site using the ARSTAN program, which mathematically

193   standardizes tree-ring series by controlling the autocorrelation component in the time series and

194   maximizes the climate signal (Cook and Holmes, 1984; Speer, 2012). Additionally, we also

195   employed the Regional Curve Standardization (RCS) detrending method to generate site-level

196   RWI using the RCS function (Biondi and Qeadan, 2008) in dplR R package (Dendrochronology

197   Program Library in R) (Bunn et al., 2020). In the RCS detrending method, raw ring-width

198   measurements of multiple trees from the same site are aligned by cambial age to calculate the

199   average ring width for each annual ring. An age-related declining curve is then fit through the

200 measurements and ratio of each measurement to the RCS curve value (expected growth) is then

201 calculated to generate a RWI (Erlandsson, 1936; Briffa et al., 1992; Briffa and Melvin, 2011).

202 Unlike in the ARSTAN method in which RWI is generated by aligning ring widths by calendar

203 year, in the RCS detrending method, ring widths are aligned by cambial age. We also calculated

204 basal area increment (BAI) for each tree using the inside-out method (Biondi, 1999) in dplR R

205 package (Bunn et al., 2020). Site-level BAI was obtained by averaging BAI of all trees from the

206 site for each year.

2.4 Climate Data

208 Daily climate summaries for 1950-2016 from three weather stations (Bay City, Newgulf

209 and Wharton, Texas, USA, Fig. 1B) were obtained from the NOAA NCEI database (NOAA,

210 2018a) and Palmer Drought Severity Index (PDSI) measurement for the Texas Upper Coast

211 Division was collected from the NOAA NESDIS database (NOAA, 2018b). Monthly and annual

212 averages were used for analyses. As the three weather stations are located at equal distances from

213 the sites (<25 km) and the measurements are highly correlated, an average of the three records was

214 used for dendroclimatology analyses.

2.5 Tree-ring δ^{13}C analysis

216 Tree cores not utilized for ring-width analyses were hand-sanded using a sandpaper (220

217 grit) to enhance ring-visibility. Tree-rings were selected from years with a wide range of

218 precipitation to cover the maximum breadth of the dry-wet hydroclimatic spectrum (235-1120

219 mm/year). Selected tree-rings were precisely excised using an X-Acto knife. For δ^{13}C analysis, α-

220 cellulose was extracted from the tree-rings using a slightly modified version of the Jayme-Wise

221 Method (Green, 1963), in which a Soxhlet extraction assembly is used (Leavitt and Danzer, 1993;

222 Cullen and Macfarlane, 2005). δ^{13}C in tree-ring α-cellulose was analyzed using a Costech ECS

223 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA) interfaced with

224 a Delta V Advantage isotope ratio mass spectrometer (Delta V, ThermoFisher Scientific, Waltham,

225 MA, USA) operating in continuous flow mode in the Stable Isotopes for Biosphere Science (SIBS)

226 Lab, Texas A&M University (College Station, TX, USA). Tree-ring $\delta^{13}C$ was calculated in δ

227 notation using the following equation:

228 $\delta = \left[\frac{R_{SAMPLE} - R_{STD}}{R_{STD}}\right] * 10^3$ (1)

229 where R_{SAMPLE} is the $^{13}C/^{12}C$ ratio of the cellulose sample and R_{STD} is the $^{13}C/^{12}C$ ratio of the V-

230 PDB (Vienna Pee Dee Belemnite) standard (Coplen, 1995). Duplicate measurements taken after

231 every 10 measurements yielded a precision of ±0.1‰.

232   Atmospheric $\delta^{13}C$ depletion trend over the study period was removed from the tree-ring

233 carbon isotopic record by converting carbon isotope ratios ($\delta^{13}C$) to carbon isotope

234 discrimination values ($\Delta^{13}C$) (Farquhar, 1983):

235 $\Delta^{13}C = (\delta^{13}C_{atm} - \delta^{13}C_{plant})/(1 + \delta^{13}C_{plant})$ (2)

236 Average annual atmospheric $\delta^{13}C$ values from La Jolla Pier, CA, USA (Keeling and Keeling,

237 2017) were obtained to calculate $\Delta^{13}C$ (Table 2).

238 **Table 2:** Annual average atmospheric $\delta^{13}C$ values from La Jolla Pier, CA, USA.

Year	$\delta^{13}C$	Year	$\delta^{13}C$	Year	$\delta^{13}C$
1986	-7.70	1997	-8.02	2008	-8.34
1987	-7.77	1998	-8.11	2009	-8.32
1988	-7.87	1999	-8.13	2010	-8.36
1989	-7.87	2000	-8.10	2011	-8.38
1990	-7.89	2001	-8.11	2012	-8.43
1991	-7.92	2002	-8.14	2013	-8.47
1992	-7.91	2003	-8.23	2014	-8.51
1993	-7.89	2004	-8.24	2015	-8.51
1994	-7.95	2005	-8.26	2016	-8.59
1995	-8.01	2006	-8.33		
1996	-8.03	2007	-8.34		

239
240 **2.6 Statistical Analyses**

241   To evaluate differences in mean Δ^{13}C values between sites, we used one-way ANOVA.

242   Levene's test was used to check for equal variances, normality was tested using Shapiro-Wilk test

243   and post-hoc analysis was conducted using Tukey HSD. Total monthly precipitation was

244   calculated from daily summaries. Daily maximum temperatures for each day of the month were

245   used to compute mean monthly maximum temperature. Monthly PDSI values were used directly

246   as obtained (NOAA, 2018b). To identify the portion of the growing season that has the strongest

247   influence on growth and tree-ring Δ^{13}C, we used simple linear regressions between site-wise

248   annual ring-width index and Δ^{13}C against monthly precipitation, mean monthly maximum

249   temperature and monthly PDSI for all months of the same year as well as the previous year.

250   Additionally, to estimate the multi-month influence of early, late and overall growing season

251   climate on growth and tree-ring Δ^{13}C, we averaged monthly climate data over progressively longer

252   periods of up to 8 months within the growing season. We conducted additional linear regression

253   on these calculated means against annual ring-width index and Δ^{13}C. The time interval during

254   which climate was found to be most strongly influencing growth and tree-ring Δ^{13}C (maximum

255   coefficient of determination) was used for dendroclimatology analyses. To understand the

256   relationship between growth and stress, we also used linear regression between site-wise annual

257   ring width index and Δ^{13}C. All statistical analyses were conducted in R (R Core Team, 2012).

258   **3. Results**

259   **3.1 Site chronologies**

260   Site-level tree-ring width chronologies (ARSTAN and RCS) were closely related to

261   precipitation trends. Patterns of RWI and BAI were similar between sites for much of the 40-year

262   period, except a few wet years (1983, 1991, 1992, 1997, 2001, 2003 and 2007) (Fig. 2 a,b,c),

263   whereas, tree-ring Δ^{13}C patterns were more variable, with values from site DB being higher in

264   general (Fig. 2d). All site-level chronologies were found to be sensitive enough for

265   dendroclimatological analyses as mean sensitivity, which is a measurement of year-to-year

266   variability in annual growth, fell within an acceptable range (Table 3). Forest stands at sites DB

267   and OT were found to be younger (24 and 27 years, respectively) than the other two sites as

268   indicated by the mean series lengths (Table 3). High series intercorrelations for the drier sites

269   indicate lower within and between tree differences at these sites, as compared to the wettest site,

270   DB (Table 4). Series intercorrelations across and within sites were slightly lower when

271   calculated using tree-level means (Table 4). Ring-width indices calculated using the RCS and

272   ARSTAN detrending methods were strongly correlated for all four sites (DB: $p<0.0001$;

273    $R^2=0.71$; BP: $p<0.0001$; $R^2=0.93$; OT: $p<0.0001$; $R^2=0.82$; BC: $p<0.0001$; $R^2=0.92$) (Fig. 3).

274   BAI at all four sites increased at a slow rate until the year 2000, after which an increasing shift

275   was observed. At site DB, BAI increased more sharply possibly due to the stand being relatively

276   younger, while at site BP, which had the most mature stand, change in BAI over time was less

277   variable (Fig. 2c).

278
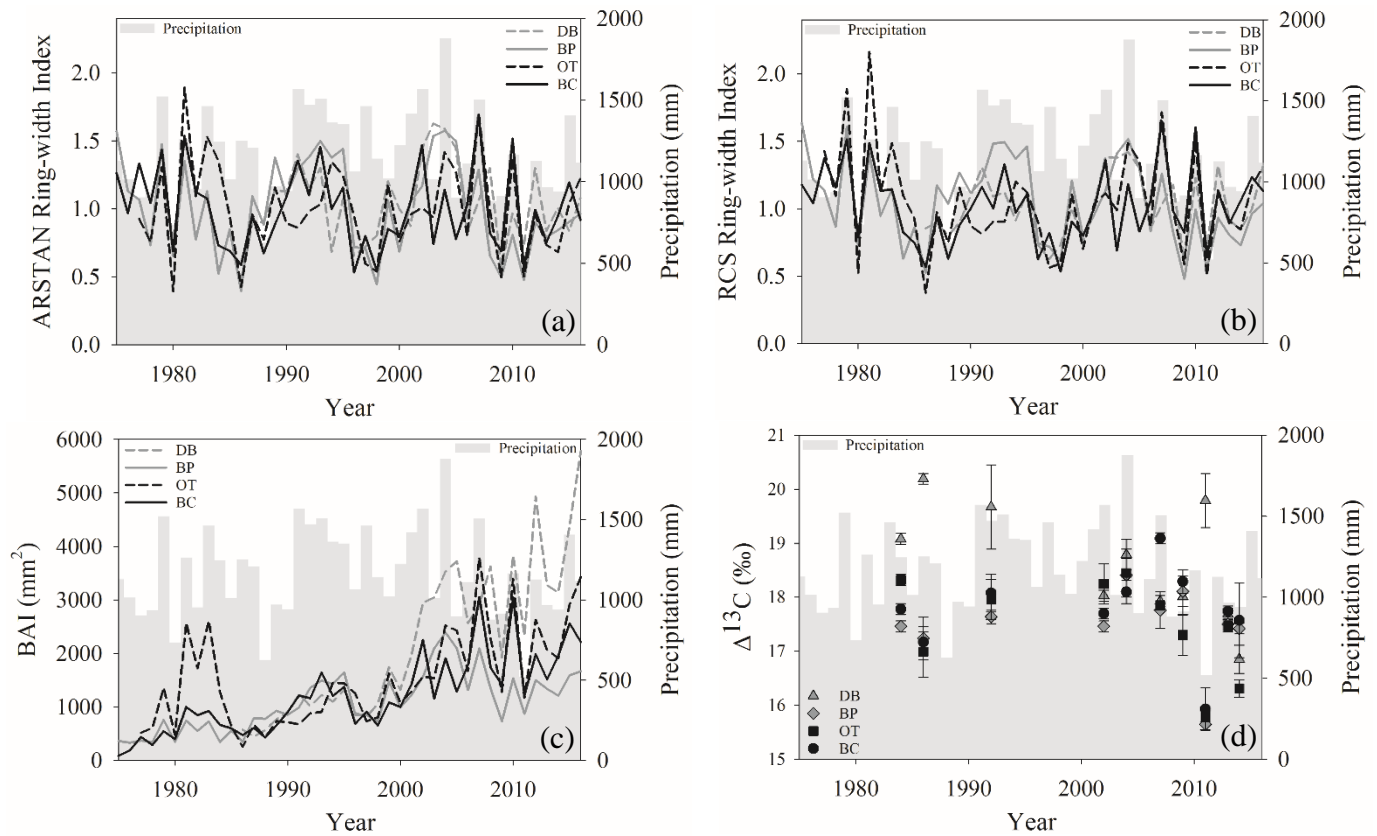
Figure 2. Temporal variation in a) ARSTAN ring-width index, b) RCS ring-width index, c) basal area increments and d) tree-ring $\Delta^{13}C$ values of *Quercus nigra* in the Brazos-Colorado Coastal Basin of Texas. Total annual precipitation is shown by grey shading.
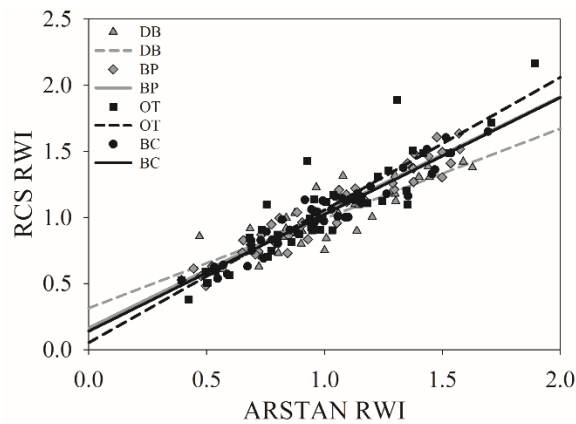
Figure 3. Relationship between site-level ring-width indices calculated using RCS detrending and using ARSTAN.

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

Chronology	Number of trees	Number of dated series	Mean Sensitivity	Mean Series Length
All sites	32	64	0.37	32 years
DB	8	16	0.35	24 years
BP	8	16	0.36	40 years
OT	8	16	0.42	27 years
BC	8	16	0.37	38 years

Table 4. Series intercorrelation values calculated using chronologies from individual cores and tree-level means across all sites and within each site.

Chronology	Across all sites (individual cores)	Across all sites (tree means)	Within site (individual cores)	Within site (tree means)
All sites	0.64	0.59	-	-
DB	-	-	0.61	0.51
BP	-	-	0.70	0.65
OT	-	-	0.79	0.67
BC	-	-	0.68	0.66

3.2 Differences in site-level tree-ring Δ^{13}C values

Comparison between site-level mean tree-ring Δ^{13}C measurements averaged over the entire 40-year study period supports our second hypothesis. Tree-ring Δ^{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 Δ^{13}C signal over the 40-year period. Post hoc analysis indicates that the wet site, DB, had a higher mean tree-ring Δ^{13}C value as compared to two drier sites, BP (p=0.03) and OT (p=0.02) (Fig. 4).
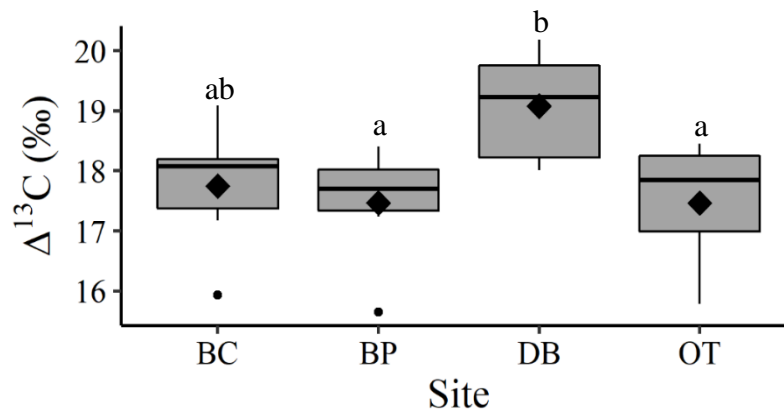
Figure 4. One-way ANOVA and Tukey post hoc analysis (denoted with letters) for mean difference in site-level tree-ring $\Delta^{13}C$ averaged over the 40-year period. Black diamonds indicate mean values, horizontal black lines indicate median values, black circles indicate outliers and grey boxes show values lying between the upper and lower quartiles.

3.3 Dendroclimatology analyses

Comparisons between ring-width indices 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 RWI 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 RWI and precipitation even at the wet site (Table 5, 6; Fig. 5a). We had hypothesized that for the wettest site, radial growth would decline due to flood stress, however, no such decline was observed even during extremely wet phases (Fig. 5a). Drought conditions and maximum temperatures during the mid-growing season resulted in decreasing RWI at the drier sites, but not at the wet site, as expected (Table 5, 6; Fig. 5b, c). Climatic variables had similar relationships with ring-width indices calculated using both the ARSTAN and RCS detrending methods (Table 5, 6). BAI overall had a much weaker relationship with climatic variables. BAI at the drier sites had weak positive relationship with precipitation, while at the wetter site, BAI was independent of precipitation (Table 7). Maximum temperature and PDSI did not affect BAI at any of the sites (Table 7).

Table 5. Relationships between ARSTAN ring-width index and mid-growing season climatic conditions ($\alpha=0.05$).

Site	Precipitation (May-July)		Temperature (May-July)		PDSI (July)	
	p value	R^2	p value	R^2	p value	R^2
DB	<0.05	0.13	ns	-	ns	-
BP	<0.001	0.39	<0.001	0.25	<0.001	0.49
OT	<0.001	0.42	<0.01	0.17	<0.001	0.31
BC	<0.001	0.44	<0.001	0.27	<0.001	0.47

325 **Table 6.** Relationships between RCS ring-width index and mid-growing season climatic
326 conditions (α=0.05).

327

Site	Precipitation (May-July)		Temperature (May-July)		PDSI (July) 328	
	p value	R^2	p value	R^2	p value	R^2 329
DB	<0.05	0.19	ns	-	ns	-
BP	<0.001	0.43	<0.01	0.22	<0.001	0.50
OT	<0.001	0.35	<0.01	0.15	<0.001	0.27
BC	<0.001	0.39	<0.01	0.24	<0.001	0.39

330 **Table 7.** Relationships between basal area increment and mid-growing season climatic conditions
331 (α=0.05).

Site	Precipitation (May-July)		Temperature (May-July)		PDSI (July)	
	p value	R^2	p value	R^2	p value	R^2
DB	ns	-	ns	-	ns	-
BP	<0.05	0.15	ns	-	ns	-
OT	<0.01	0.18	ns	-	ns	-
BC	<0.05	0.10	ns	-	ns	-
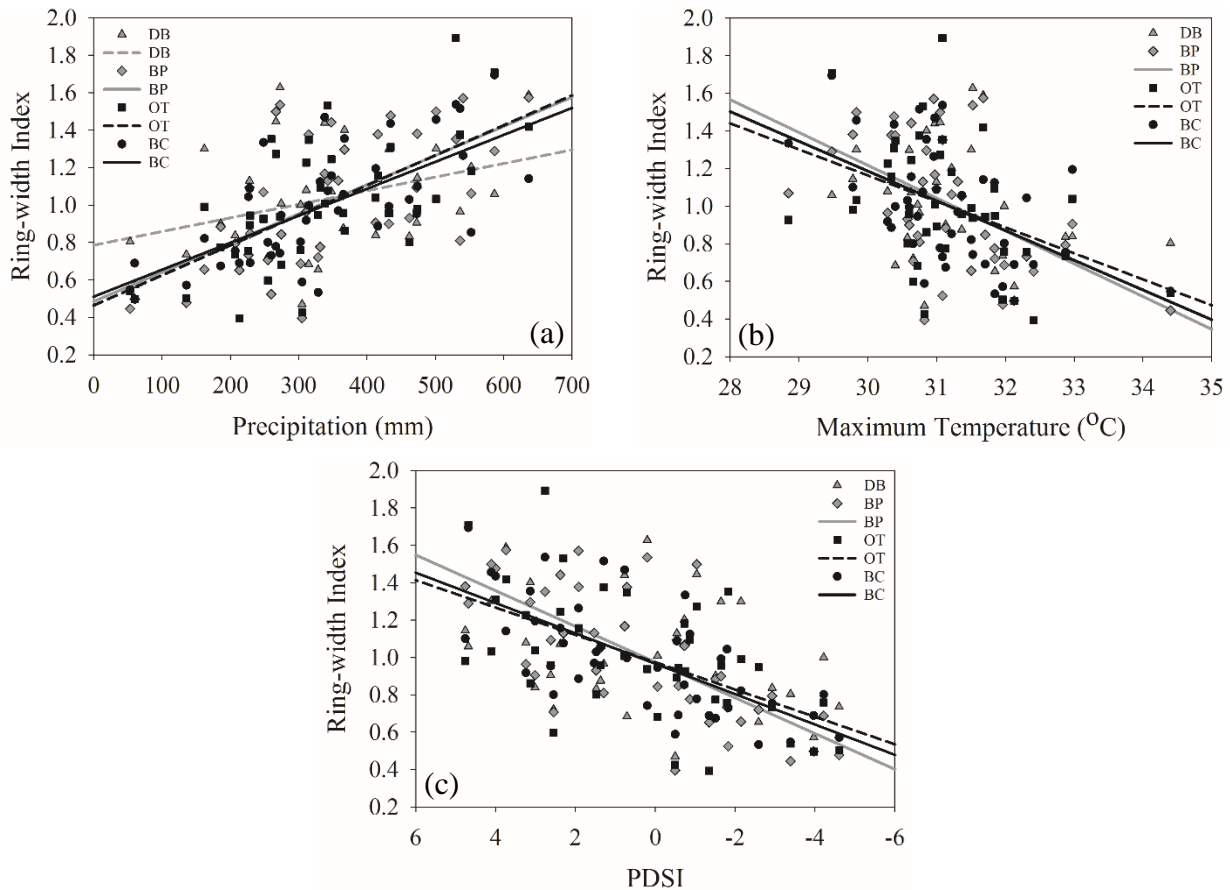
Figure 5. a) Relationship between ARSTAN ring-width index and mid-growing season precipitation (a), temperature (b) and PDSI (c). Site DB is represented by grey triangles, BP by grey diamonds, OT by black squares and BC by black circles. Regression lines are shown only for statistically significant relationships.

In line with our second hypothesis, we observed an increase in tree-ring Δ^{13}C values with increase in early-growing season precipitation at the drier sites (Table 8, Fig. 6a). We had hypothesized that high precipitation at the wet site will reduce carbon isotopic discrimination as a result of physiological stress caused by possible flooding stress. However, we found no relationship between tree-ring Δ^{13}C and precipitation at the wet site (Table 8). Higher maximum temperatures resulted in lower tree-ring Δ^{13}C values only at one of the drier sites (BC) (Table 8, Fig. 6b). PDSI did not have any effect on tree-ring Δ^{13}C values from all four sites (Table 8). 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 of the four sites.

Table 8. Relationships between tree-ring $\Delta^{13}C$ values and early-growing season climatic conditions ($\alpha=0.05$).

Site	Precipitation (April)		Temperature (April)		PDSI
	p value	R^2	p value	R^2	p value
DB	ns	-	ns	-	ns
BP	<0.05	0.70	ns	-	ns
OT	<0.05	0.68	ns	-	ns
BC	<0.05	0.59	<0.001	0.94	ns
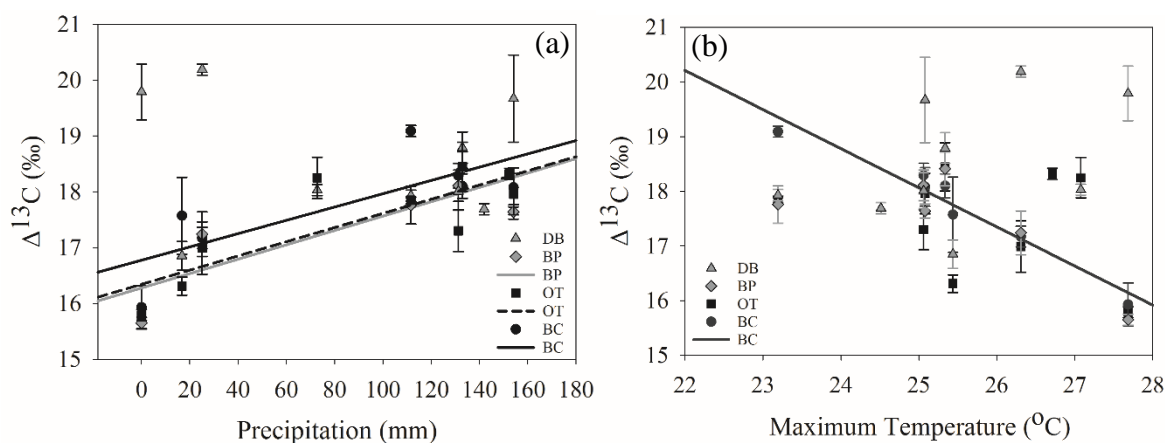
Figure 6. Relationship between tree-ring $\Delta^{13}C$ values and early-growing season (a) precipitation and (b) temperature. Site DB is represented by grey triangles, BP by grey diamonds, OT by black squares and BC by black circles. Regression lines are shown only for statistically significant relationships.

3.4 Relationship between RWI and tree-ring $\Delta^{13}C$

The comparison between tree-ring $\Delta^{13}C$ values and tree-ring width indices from corresponding years supports our third hypothesis only at the drier sites. ARSTAN as well as RCS ring-width indices were correlated with $\Delta^{13}C$ values only at sites OT (ARSTAN: $p<0.05$; $R^2=0.53$; RCS: $p<0.05$; $R^2=0.45$) and BC (ARSTAN: $p<0.05$; $R^2=0.58$; RCS: $p<0.05$; $R^2=0.62$). Tree-ring $\Delta^{13}C$ values were not correlated with annual growth at the wet site DB, which indicates that trees at this site were able to minimize growth inhibition during stressful conditions as compared to trees at the drier sites (Fig. 7). Tree-ring $\Delta^{13}C$ values were not correlated with BAI at any of the sites.
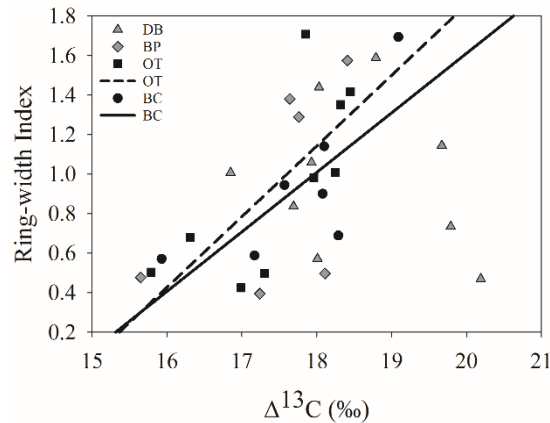
Figure 7. Relationship between ARSTAN ring-width index and tree-ring $\Delta^{13}C$. Site DB is represented by grey triangles, BP by grey diamonds, OT by black squares and BC by black circles. Regression lines are shown only for statistically significant relationships.

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 land use change and river regulation (Wear and Greis, 2002; Blann et al., 2009; Dahl, 2011) and the alteration is exacerbated by hydroclimatic anomalies such as droughts and floods (Ferrati et al., 2005; Erwin, 2008). These disturbances coupled with topographic heterogeneity cause some portions of these riverine wetland forests to be drier than others.

Contrary to our first hypothesis, similar annual radial growth 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

379   tables are more independent of climatic conditions than their drier counterparts. It has been

380   repeatedly observed across southeastern US that in wetter and hydrologically well-connected parts

381   of wetland forests, vegetation experiences lower stress during non-favorable growing conditions

382   (Clawson et al., 2001; Anderson et al., 2005; Gee et al., 2014; Allen et al., 2016).

383   Consistent with our second hypothesis, mean tree-ring $\Delta^{13}C$ values from the wetter site

384   were significantly higher than those from the drier sites over a longer temporal scale, suggesting

385   lower stomatal constraints on leaf gas exchange at the wet site as compared to those at the drier

386   sites. Also supporting our second hypothesis, reduced stomatal conductance in trees from the drier

387   site during drought years, clearly indicates prolonged stress caused by soil moisture deficit. This

388   relationship between tree-ring $\Delta^{13}C$ and drought conditions (low precipitation and high

389   temperatures) has been extensively observed across different ecosystems such as boreal forests

390   (Brooks et al., 1998; Au and Tardif, 2012), wetlands (Anderson et al., 2005; Buhay et al., 2008),

391   lowland rain forests (Schollaen et al., 2013), deserts (Lipp et al., 1996), etc. Generally, forested

392   wetlands are not known to be drought stressed because of ample soil moisture availability.

393   However, it is important to note that in parts of Columbia Bottomlands, depending on site-level

394   hydrologic conditions, vegetation does experience drought stress during some years when dry

395   climatic conditions persist over a longer period.

396   Our third hypothesis that tree-ring $\Delta^{13}C$ would have a positive relationship with radial

397   growth holds true under dry edaphic conditions, where drought stress restricts plant growth.

398   Whereas in trees growing in wetter soils, tree-ring $\Delta^{13}C$ and radial growth were largely decoupled.

399   Similar differences in the relationship between tree-ring $\Delta^{13}C$ and radial growth of the ring-porous

400   bur oak (*Quercus macrocarpa* M.) have been observed across continental gradients where tree-

401   ring $\Delta^{13}C$ correlates positively with radial growth at drier sites, while the relationship is negative

402 under wetter conditions (Voelker et al., 2014). These differences have been attributed to indicators

403 of site aridity (VPD, precipitation:evapotranspiration). A similar relationship has also been

404 observed in pond cypress trees in the southeastern Everglades, Florida, USA (Anderson et al.,

405 2005). While we did not observe a negative relationship between tree-ring Δ^{13}C and radial growth

406 at the wet site, no correlation between the two highlights the beneficial effect of wetter

407 hydrological conditions on vegetation at the flooded site. Consequently, the absence of drought-

408 related stress signals at the wet site is possibly due to supplemental soil moisture availability from

409 flooding. At the drier sites, drought-related lower tree-ring Δ^{13}C values are correlated with slower

410 radial growth, which indicates that moisture deficit causes physiological stress in these trees,

411 reducing stomatal conductance and eventually inhibits growth. Additionally, tree-ring Δ^{13}C and

412 radial growth at the wet site were uncorrelated especially during years when growing-season

413 precipitation was more erratic (dry spring followed by a wet summer and vice versa). The drought

414 effect of drier hydroclimatic conditions is ephemeral and less intense at the wet site due to slower

415 depletion of soil water reserves. Therefore, seasonal dry spells slightly reduce tree-ring Δ^{13}C but

416 do not always result in growth inhibition in wetter parts of this landscape due to sufficient moisture

417 availability. We had expected to observe lower tree-ring Δ^{13}C values during extremely wet

418 growing seasons due to flooding stress, but the absence of these signals indicates adaptation to

419 excessive wetness. It has been suggested that wetland species that experience frequent flooding

420 develop adaptive traits that enable rapid reopening of stomata with the recession of flood waters

421 as oxygen availability in the root zone increases (Crawford, 1982; Kozlowski and Pallardy, 1984;

422 Kozlowski, 2002). Consistent with this, our observations signify that trees growing in drier

423 conditions do have a more distinct tree-ring Δ^{13}C-growth relationship as compared to those

424 growing in wet conditions.

425   We found that mid-growing season precipitation (from May to July) is most critical for

426   growth in this landscape. Similarly, high temperatures during the same period were associated with

427   suppressed growth. Therefore, adequate precipitation and moderate temperatures during this

428   period are important controls over tree growth. However, due to changing climatic conditions and

429   altered hydrology of this region, change in the seasonal moisture availability during this period

430   can result in reduced productivity. Unlike the trees growing in drier conditions, the ones at the wet

431   site are not affected by temperature and drought severity throughout the growing season possibly

432   because of residual soil moisture availability despite evaporation caused by higher temperatures.

433   It is important to consider seasonal variation in precipitation because flood conditions in the

434   dormant winter season do not necessarily help sustain growth throughout the summer in drier sites,

435   especially if summers have below normal precipitation. On the other hand, trees at the wet site

436   may benefit from access to soil moisture reserves from waterlogging caused by winter

437   precipitation.

438   While the growth-climate relationship is more amplified during mid-growing season, tree-

439   ring $\Delta^{13}C$ is more prominently dependent on early-growing season precipitation. Lack of

440   precipitation early in the growing season (April) results in substantial physiological stress caused

441   by reduced stomatal conductance in trees at the drier sites. This is an indication that although dry

442   conditions early in the growing season cause stress in trees, most growth is attained during the

443   mid-growing season. Therefore, trees can recover from the stress and attain normal growth rates

444   if adequate precipitation occurs during the mid-growing season. The prominent dependence of

445   physiological stress on spring precipitation could be the result of more energy and resource

446   allocation during leaf out. However, this holds true only under dry edaphic conditions. Such

447   seasonal variations have been observed across different biomes and have been attributed to

448   formation of wood using previous or current growing season assimilates (Schollaen et al., 2013).

449   It is apparent that if wood at the very beginning of the growing season is formed using assimilates

450   from the previous growing season, earlywood tree-ring Δ^{13}C does not have a correlation with

451   early-growing season precipitation from the current year (Helle and Schleser, 2004; Porter et al.,

452   2009; Schollaen et al., 2013). In our study, tree-ring Δ^{13}C is well-correlated with early-growing

453   season precipitation from the current growing season. Although this indicates that majority of

454   annual wood is formed using assimilates from the current growing season, it needs to be noted that

455   earlywood portions of ring-porous oaks like those of *Q. nigra* have lower wood density (Gasson,

456   1987; Lei et al., 1996; Rao, 1997). Therefore, by using entire annual ring composites, the relatively

457   small signal from the previous year could be present but not distinctly detected. Hence, comparing

458   our ring-width indices and tree-ring Δ^{13}C values with previous years' climate yields no correlation

459   ($p > 0.05$) indicating its relatively weak effect.

460   Climate models have predicted a significant decrease in growing season precipitation and

461   increase in temperature throughout Texas (Jiang and Yang, 2012) and especially in the Brazos

462   River basin (Awal et al., 2016) where our study area is located. This region occurs at the extreme

463   southwestern edge of the bottomland hardwood forest type (Bray, 1906; Putnam et al., 1960),

464   which is also the southwestern edge of the distribution of *Q. nigra* and many other wetland tree

465   species. Edges of distribution ranges usually experience environmental conditions that are less

466   favorable (drier and warmer) to the species as compared to the range core (Rehm et al., 2015),

467   which makes them more resilient and better adapted to survive in stressful conditions relative to

468   core populations (Gutschick and Hormoz, 2003). Therefore, as climate changes, these native

469   wetland tree populations will play key roles in helping the species maintain their geographic

470   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 hydrologically wetter portions of this landscape experience less stress and subsequently lower growth inhibition in response to hydroclimatic changes as compared to drier areas. 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. Ayumi Hyodo provided laboratory protocols for cellulose extraction, provided laboratory equipment/materials for stable carbon isotope analysis and analyzed the samples for isotopic composition. 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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