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Bottomland hardwood forest growth and stress response to hydroclimatic variation: Evidence from dendrochronology and tree-ring δ13C 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 δ13C 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 δ13C 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

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26 no response to higher temperatures. In contrast, trees of the three drier sites experienced growth

27 inhibition and had higher tree-ring $\delta^{13}C$ values during dry periods. Our results indicate higher

28 physiological resilience in trees growing under wetter conditions. Management and conservation

29 strategies dependent on site-specific conditions are critical for the health of these wetland forests

30 under a rapidly changing hydroclimate. This study provides the first dendrochronological baseline

31 for this region and thresholds of optimum conditions for the growth and health of these forests

32 which can assist management decisions such as streamflow regulation and conservation plans.

1. Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

54   2017). Similar forcing factors have altered the state of most wetland forest types in southeastern

55   USA.

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

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

58   2016; Tei et al., 2017). Additionally, tree-ring $\delta^{13}C$ is an indirect record of internal leaf CO_2

59   concentration, which is controlled by a balance between stomatal conductance and photosynthetic

60   rate in response to environmental conditions (Farquhar et al., 1989; McCarroll and Loader, 2004;

61   Gessler et al., 2014), such as temperature, vapor pressure and precipitation (Robertson et al., 1997;

62   Leavitt et al., 2002). As tree rings are distinguished by their high temporal (annual or sub-annual)

63   and spatial resolution, regional tree-ring chronologies and $\delta^{13}C$ values have the potential to identify

64   a wide range of growth and stress response of vegetation to hydroclimatic variability. However,

65   tree-ring $\delta^{13}C$ is also influenced by the changing $\delta^{13}C$ value of atmospheric CO_2. The increase in

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

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

68   change is relatively small over short temporal scales, correction methods are available to remove

69   this signal from tree-ring records when using tree-ring $\delta^{13}C$ to understand plant physiological

70   responses to local conditions (McCarroll and Loader, 2004).

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

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

73   2017; Gao et al., 2018; Mikac et al., 2018; Szejner et al., 2020). Through these studies, a strong

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

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

76   1997; Kozlowski, 1997; St. George, 2014). These effects are more difficult to detect in tree-ring

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

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

79   southeastern USA (LeBlanc and Stahle, 2015).

80   Higher $\delta^{13}C$ values of tree-ring cellulose usually reflect stress caused by low

81   environmental moisture at the time of carbon fixation, while lower $\delta^{13}C$ values are indicative of

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

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

84   rings with the sensitivity of $\delta^{13}C$ values governed by ecophysiological responses to the

85   environment (Gessler et al., 2009; Gessler et al., 2014). However, trees growing in wetland settings

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

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

88   and/or increased assimilation rates in trees, resulting in high $\delta^{13}C$ values; however, this effect is

89   highly variable across species (Stuiver et al., 1984; Ewe and Sternberg, 2002; Ewe and Sternberg,

90   2003; Anderson et al., 2005; Buhay et al., 2008). These studies in wetlands attribute this positive

91   relationship between $\delta^{13}C$ and precipitation to excess water stress. Although debatable, a number

92   of possible mechanisms have been suggested with significant evidence to support this relationship.

93   These include disruption of water and nutrient uptake due to anoxic conditions in the root zone

94   (Jackson and Drew, 1984), lowered root hydraulic conductivity (Davies and Flore, 1986),

95   increased abscisic acid concentrations (Kozlowski and Pallardy, 1984) and accumulation of

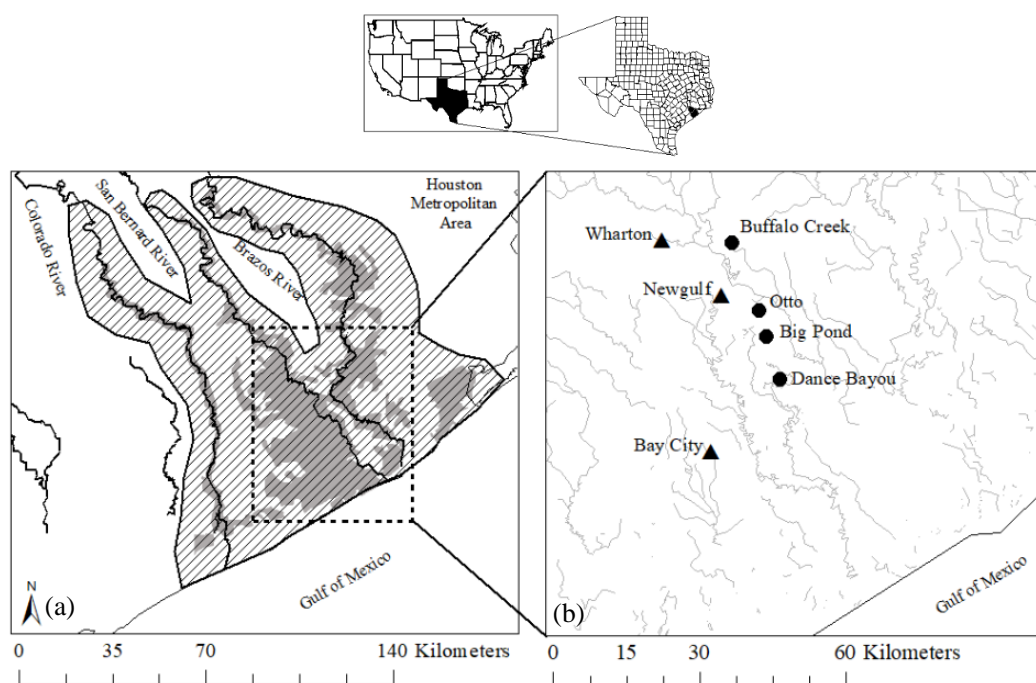96   metabolic toxins from flooding (Jackson and Drew, 1984).

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

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

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

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

101   Our first objective was to understand how growth rates are affected by hydroclimatic variation

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

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

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

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

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

107   Our second objective was to assess the magnitude of physiological stress inflicted by hydroclimatic

108   conditions on these forests. We hypothesized that tree-ring δ^{13}C in trees growing under relatively

109   drier soil conditions will decrease during periods of higher rainfall. In contrast, the opposite trend

110   is expected at wetter sites where increasing moisture would induce flooding stress. In addition, we

111   hypothesized that trees growing where waterlogging is common are less stressed during dry

112   periods than those at the drier sites because of slower depletion of soil water reserves. Our third

113   objective was to evaluate the relationship between physiological stress and growth inhibition.

114   Although a negative relationship between stress (tree-ring δ^{13}C) and growth (tree-ring width) is

115   expected in this study, the strength of this relationship could vary with site conditions. Given that

116   water oaks are moderately tolerant of flooding, and dry conditions are also common in this

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

5

118   stress. Thus, we expected a stronger negative relationship between growth and physiological stress

119   at drier sites.

2. Materials and Methods

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.

128   The study was conducted at four different sites located within the Brazos-Colorado Coastal

129   Basin in the San Bernard National Wildlife Refuge, Brazoria and Fort Bend Counties, Texas. The

130   four sites are Dance Bayou (DB), Big Pond (BP), Otto (OT) and Buffalo Creek (BC) (Fig. 1B;

131   Table 1). Site DB was observed to be flooded most frequently after significant rain events from

132   2016 to 2019. This site also remained waterlogged for prolonged periods, unlike the other three

133   sites. Therefore, we refer to this site as the "wet site". The sites are located in Ecoregion III Western

134   Gulf Coastal Plain and Ecoregion IV Floodplain and Low Terraces, dominated by mixed

135   bottomland hardwood forests (Griffith, 2004) at an elevation of about 16 m above MSL. Dominant

136   tree species at these sites include *Quercus nigra* L. (water oak), *Quercus fusiformis* Small (live

137   oak), *Celtis laevigata* Willd. (sugarberry) and *Triadica sebifera* (L.) Small (Chinese tallow). The

138   climate of this region is classified as Humid Subtropical (Cfa) under the Köppen–Geiger climate

139   classification system (Koppen, 1900). The average maximum monthly temperature is

140   approximately 26 $^{\circ}$C and the average minimum monthly temperature is approximately 15 $^{\circ}$C. Mean

141   annual rainfall is 1143 mm, with an average relative humidity of ~70% (NOAA, 2018). The sites

142   are located in the Linnville Bayou watershed of the San Bernard River Basin. As these forests are

143   situated in the floodplain, sloughs are a common occurrence and inundate significant parts of the

144   forest. Streamflow in Linnville Bayou and adjoining streams and sloughs that traverse the four

145   sites is driven by at least 7 dams on the San Bernard River with heights ranging from 2.5-7.5 m

146   (NID, 2020). Therefore, the presence of these dams and their varying discharge into Linnville

147   Bayou adds significant complexity to the hydrology of Columbia Bottomlands in addition to an

148   already fluctuating hydroclimate.

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

150   2020). The soils series include Aris fine sandy loam, Bacliff clay, Edna loam, Leton loam, Pledger

151   Clay and Churnabog clay.

Table 1. Site description with basic soil properties averaged over the top 100 cm depth (NRCS, 2020).

Site	Elevation (m)	Coordinates	Tree DBH (cm) (mean ± SE)	Clay %	Silt %	Sand %	Soil pH	Bulk Density (g/cm³)	Organic Matter (%)
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
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
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
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

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

2.3 Dendrochronology

Tree cores were dried to constant weight at 60 ^{o}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

171 sensitivity indicates if the variation in annual growth rates from year-to-year is sensitive enough

172 for dendroclimatology analysis. This crossdating was done separately for each site as well as on

173 pooled raw tree-ring widths from all sites. The final standardized (A) chronology (Ring-width

174 index) was generated for each site using ARSTAN, which mathematically standardizes tree-ring

175 series by controlling the autocorrelation component in the time series and maximizes the climate

176 signal (Cook and Holmes, 1984; Speer, 2012).

177 **2.4 Climate Data**

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

179 and Wharton, Texas, USA, Fig. 1B) and Palmer Drought Severity Index (PDSI) for the Texas

180 Upper Coast Division were collected from the NOAA NCEI database (NOAA, 2018). Monthly

181 and annual averages were used for analysis. As the three weather stations are located at equal

182 distances from the sites (<25 km) and the measurements are highly correlated, an average of the

183 three records was used for dendroclimatology analysis. Monthly average $\delta^{13}C$ values of

184 atmospheric CO_2 from La Jolla Pier, California, USA were obtained from the Scripps CO_2

185 Program and annual averages were calculated (Keeling and Keeling, 2017).

186 **2.5 Tree-ring $\delta^{13}C$ analysis**

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

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

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

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

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

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

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

194   4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA) interfaced with

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

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

197   Lab, Texas A&M University (College Station, TX, USA). Carbon isotope ratios are presented in

198   δ notation:

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

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

201   (Vienna Pee Dee Belemnite) standard (Coplen, 1995). Duplicate measurements taken after every

202   10 measurements yielded a precision of ±0.1‰.

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

204    $\delta^{13}C$ record by calculating the difference between average annual atmospheric $\delta^{13}C$ values

205   (Keeling and Keeling, 2017) and a standard value ('pre-industrial' value of -6.4‰) (Francey et

206   al., 2002). The difference is denoted by Δ. Yearly Δ values were then added to tree-ring $\delta^{13}C$

207   values from corresponding years (McCarroll and Loader, 2004) (Table 2).

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

Year	$\delta^{13}C$	Δ	Year	$\delta^{13}C$	Δ	Year	$\delta^{13}C$	Δ
1986	-7.70	1.30	1997	-8.02	1.62	2008	-8.34	1.94
1987	-7.77	1.37	1998	-8.11	1.71	2009	-8.32	1.92
1988	-7.87	1.47	1999	-8.13	1.71	2010	-8.36	1.96
1989	-7.87	1.47	2000	-8.10	1.70	2011	-8.38	1.98
1990	-7.89	1.49	2001	-8.11	1.71	2012	-8.43	2.03
1991	-7.92	1.52	2002	-8.14	1.74	2013	-8.47	2.07
1992	-7.91	1.51	2003	-8.23	1.83	2014	-8.51	2.11
1993	-7.89	1.49	2004	-8.24	1.84	2015	-8.51	2.11
1994	-7.95	1.55	2005	-8.26	1.86	2016	-8.59	2.19
1995	-8.01	1.61	2006	-8.33	1.93			
1996	-8.03	1.63	2007	-8.34	1.94			

209

210   **2.6 Statistical Analyses**

Biogeosciences
Discussions

EGU

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

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

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

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

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

216   as obtained. To identify the portion of the growing season that has the strongest influence on

217   growth and δ^{13}C, we used simple linear regressions between site-wise annual ring-width index and

218   δ^{13}C against monthly precipitation, mean monthly maximum temperature and monthly PDSI for

219   all months of the same year as well as the previous year. Additionally, to estimate the multi-month

220   influence of early, late and overall growing season climate on growth and δ^{13}C, we averaged

221   monthly climate data over progressively longer periods of up to 8 months within the growing

222   season. We conducted additional linear regression on these calculated means against annual ring-

223   width index and δ^{13}C. The time interval during which climate was found to be most strongly

224   influencing growth and δ^{13}C (maximum coefficient of determination) was used for

225   dendroclimatology analysis. To understand the relationship between growth and stress, we also

226   used linear regression between site-wise annual ring width index and δ^{13}C. All statistical analyses

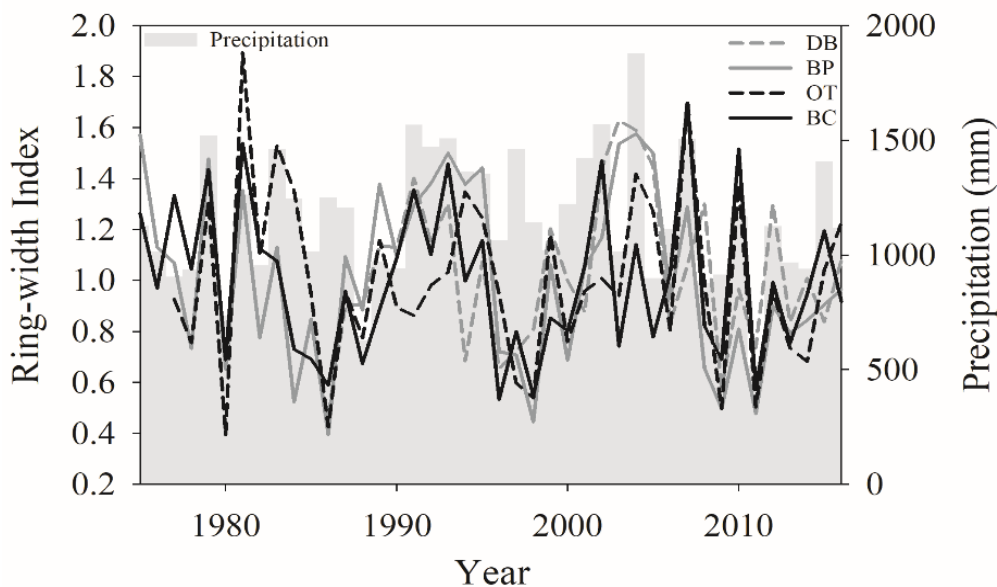227   were conducted in R (R Core Team, 2012).

228   **3. Results**

229   **3.1 Site chronologies**

230   Site-level tree-ring width chronologies were closely related to precipitation trends. Patterns

231   of annual growth rate were similar between sites for much of the 40-year period, except a few wet

232   years (1991, 1992, 1997, 2001, 2003 and 2007) (Fig. 2). The divergent responses to these wet

233   years apparently reduced the pooled series intercorrelation (Table 3). Hence, this multi-site

234   chronology was not used for further analyses. High series intercorrelation for the drier sites

11

235   indicates lower tree-to-tree differences at these sites, as compared to our wettest site, DB, which

236   had a slightly lower series intercorrelation (Table 3). All site-level chronologies were found to be

237   sensitive enough for dendroclimatological analysis as mean sensitivity, which is a measurement

238   of year-to-year variability in annual growth, fell within an acceptable range. Forest stands at sites

239   DB and OT were found to be younger (27 years) than the other two sites (40 years) as indicated

240   by the mean series lengths (Table 3).

241
242   **Figure 2.** Temporal variation in ring-width index of *Quercus nigra* within the Brazos-Colorado
243   Coastal Basin of Texas. Total annual precipitation is shown by grey shading.
244

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

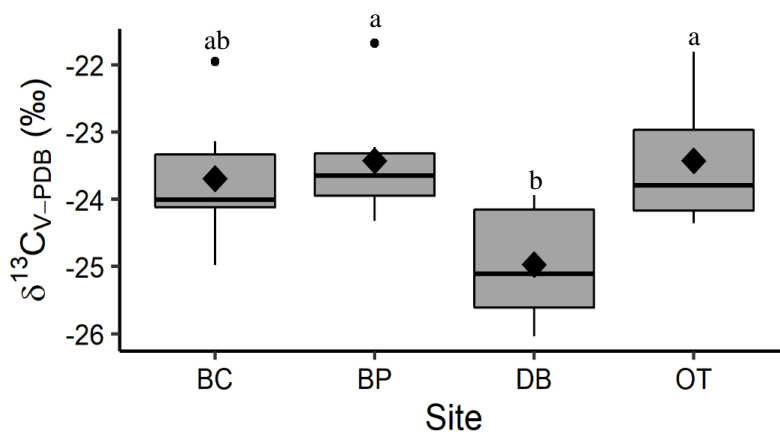| Chronology	Number of trees	Number of dated series	Series Intercorrelation	Mean Sensitivity	Mean Series Length
All sites	32	64	0.31	0.37	33 years
DB	8	16	0.52	0.35	27 years
BP	8	16	0.74	0.36	40 years
OT	8	16	0.78	0.42	27 years
BC	8	16	0.77	0.37	38 years

247

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

248

Comparison between site-level mean tree-ring δ^{13}C measurements averaged over the entire

249

250 40-year study period supports our second hypothesis. Tree-ring δ^{13}C measurements were different

251 between sites when averaged over the 40-year period [One-way ANOVA, F (3, 24) = 4.05, p =

252 0.01]. This indicates that at least one site has a significantly different mean δ^{13}C signal over the

253 40-year period. Post hoc analysis indicates that the wet site, DB, had a lower mean tree-ring δ^{13}C

254 value as compared to two drier sites, BP (p=0.03) and OT (p=0.02) (Fig. 3).

255

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

256

260
261 **3.3 Dendroclimatology analysis**

262 Comparisons between ring-width index and climate data reveal that growth rates are most

263 strongly influenced by mid-growing season climate (May-July precipitation and maximum

264 temperatures; July PDSI) (Table S1). Since a larger proportion of annual growth occurs during the

265 mid-growing season, higher rainfall and lower maximum temperatures during this period strongly

266 drive annual growth rates. Similar comparisons between tree-ring δ^{13}C measurements and climate

13

267   data indicate that climatic conditions early in the growing season (April) are critical for causing

268   physiological stress in these forests (Table S2).

269   As hypothesized, we observed a strong increase in tree-ring widths with mid-growing

270   season precipitation. Although this positive relationship was expected for trees growing in drier

271   conditions, we observed a similar but weaker positive relationship between growth and

272   precipitation even at the wet site (Table 4). We had hypothesized that at extremely wet conditions,

273   growth rates at the wet site would decline due to flood stress, however, no such decline was

274   observed even during extremely wet phases (Fig. 4a). Drought conditions and maximum

275   temperatures during the mid-growing season result in decreasing growth at the drier sites, but not

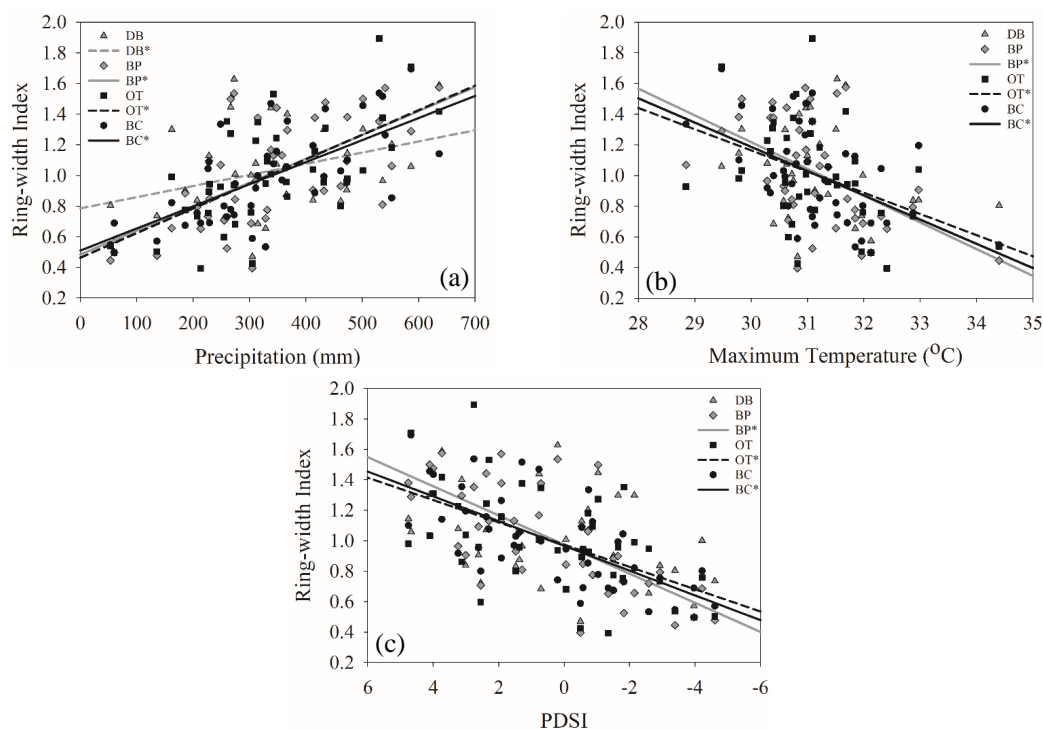276   at the wet site, as expected (Table 4; Fig. 4b, c).

277   **Table 4.** Relationships between ring-width index and mid-growing season climatic conditions
278   ($\alpha=0.05$).
279

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

280

Figure 4. a) Relationship between 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. Statistically significant relationships are marked with an asterisk (*).
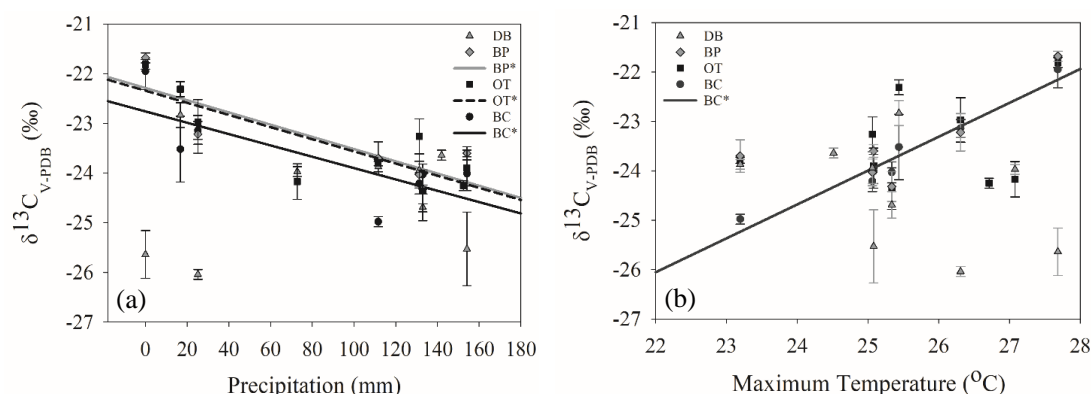
In line with our second hypothesis, we observed a depletion in tree-ring $\delta^{13}C$ values with increase in early-growing season precipitation at the drier sites (Table 5, Fig. 5a). We had hypothesized that high precipitation at the wet site will enrich tree-ring $\delta^{13}C$ values as a result 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 $\delta^{13}C$ 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 5. 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. Statistically significant relationships are marked with an asterisk (*).

3.4 Relationship between growth and tree-ring $\delta^{13}C$

The comparison between tree-ring $\delta^{13}C$ values and tree-ring width from corresponding years supports our third hypothesis only at the drier sites. Ring-width index was correlated with $\delta^{13}C$ values only at sites OT ($p<0.05$; $R^2=0.53$) and BC ($p<0.05$; $R^2=0.58$). 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 sustain their growth rates even during stressful conditions (Fig. 6).

Figure 6. Relationship between ring-width index and tree-ring δ^{13}C. 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 (*).

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.

327   Contrary to our first hypothesis, similar annual growth rates of trees at the wetter site and

328   the three drier sites during the past several decades suggests that trees at all sites have access to

329   moisture sufficient to sustain annual growth. Moreover, growth of trees at the wetter site was not

330   inhibited by excessive moisture during wet years, which may reflect adaptation by *Quercus nigra*

331   to the broad range of soil moisture conditions that occur in a floodplain forest (Gilman et al., 1994).

332   Within the wetter site, we observed more heterogeneity in growth rates, which could be attributed

333   to uneven waterlogging within the site. Although growth rates were correlated with rainfall across

334   all sites, the wet site had a much weaker dependence on rainfall and showed no negative response

335   to higher temperatures and drought severity. This suggests that wetland forests with high water

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

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

338   of wetland forests, vegetation is more physiologically resilient and experiences lower stress during

339   non-favorable growing conditions (Clawson et al., 2001; Anderson et al., 2005; Gee et al., 2014;

340   Allen et al., 2016).

341   Consistent with our second hypothesis, mean tree-ring δ^{13}C values from the wetter site

342   were significantly lower than those from the drier sites over a longer temporal scale, suggesting

343   lower physiological stress and higher resilience of trees at the wet site as compared to those at the

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

345   drier site during drought years, clearly indicates prolonged stress caused by soil moisture deficit.

346   This relationship between tree-ring δ^{13}C and drought conditions (low precipitation and high

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

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

349   lowland rain forests (Schollaen et al., 2013), deserts (Lipp et al., 1996), etc. It is important to note

350   that in parts of these forested wetlands, dry conditions can develop and cause stressful conditions

351   for the vegetation.

352   Our third hypothesis that physiological stress would have a negative relationship with

353   growth holds true under dry edaphic conditions, where stress restricts plant growth. Contrastingly,

354   in trees growing in wetter soils, stress and growth are largely decoupled. At the drier sites, drought-

355   related enriched tree-ring $\delta^{13}C$ values are correlated with slower growth rates, which indicates that

356   moisture deficit causes physiological stress in these trees, resulting in growth inhibition. The

357   absence of drought-related stress signals at the wet site is possibly due to supplemental soil

358   moisture availability from flooding and higher physiological resistance. Additionally, decoupling

359   between growth and stress signals from the wet site indicate that physiological stress does not

360   always result in growth inhibition in wetland trees, especially when optimum moisture is available.

361   A similar relationship has been observed in pond cypress trees in the southeastern Everglades,

362   Florida, USA (Anderson et al., 2005). This decoupling between stress signals and growth rates

363   seems to be more common in wetlands with prolonged waterlogging. It has been suggested that

364   wetland species that experience frequent flooding develop adaptive traits that enable rapid

365   reopening of stomata with the recession of flood waters as oxygen availability in the root zone

366   increases (Crawford, 1982; Kozlowski and Pallardy, 1984; Kozlowski, 2002). As a result, growth

367   may not be inhibited even though stress signals related to stomatal closure due to flooding are

368   detected in the same tree-ring. Consistent with this, our observations signify that trees growing in

369   drier conditions do have a more distinct stress-growth relationship as compared to those growing

370   in wet conditions.

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

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

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

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

375 altered hydrology of this region, change in the moisture availability during this period can be

376 severely detrimental to this ecosystem. Unlike the trees growing in drier conditions, the ones at

377 the wet site are not affected by temperature and drought severity throughout the growing season

378 possibly because of residual soil moisture availability despite evaporation caused by higher

379 temperatures. It is important to consider seasonal variation in precipitation because flood

380 conditions in the dormant winter season do not necessarily help sustain growth throughout the

381 summer in drier sites, especially if summers have below normal precipitation. On the other hand,

382 trees at the wet site may benefit from access to soil moisture reserves from waterlogging caused

383 by winter precipitation.

384   While the growth-climate relationship is more amplified during mid-growing season, stress

385 signals are more prominently dependent on early-growing season precipitation. Lack of

386 precipitation early in the growing season (April) results in substantial physiological stress in trees

387 at the drier sites. This is an indication that although dry conditions early in the growing season

388 cause stress in trees, most growth is attained during the mid-growing season. Therefore, trees can

389 recover from the stress and attain normal growth rates if adequate precipitation occurs during the

390 mid-growing season. The prominent dependence of physiological stress on spring precipitation

391 could be the result of more energy and resource allocation during leaf out. However, this holds

392 true only under dry edaphic conditions. Such seasonal variations have been observed across

393 different biomes and have been attributed to formation of wood using previous or current growing

394 season assimilates (Schollaen et al., 2013). It is apparent that if wood at the very beginning of the

395 growing season is formed using assimilates from the previous growing season, tree-ring $\delta^{13}C$ does

396   not have a correlation with early-growing season precipitation from the current year (Helle and

397   Schleser, 2004; Porter et al., 2009; Schollaen et al., 2013). However, like in our study, when tree-

398   ring δ^{13}C is well-correlated with precipitation from early-growing season, it indicates formation of

399   wood using assimilates from the current growing season. To confirm this relationship, we

400   compared our ring-width index and tree-ring δ^{13}C values with previous years' climate and found

401   no correlation.

402   Columbia bottomlands occur at the extreme southwestern edge of the bottomland

403   hardwood forest type (Bray, 1906; Putnam et al., 1960), which is also the southwestern edge of

404   the distribution of *Q. nigra* and many other wetland tree species. Consequently, the *Q. nigra*

405   populations examined in this study experience the driest and warmest conditions found throughout

406   its geographic range. Edges of distribution ranges usually experience harsher environmental

407   conditions as compared to the range core (Rehm et al., 2015). Therefore, range-edge populations

408   are more resilient and are better adapted to survive in stressful conditions relative to core

409   populations (Gutschick and Hormoz, 2003). Climate models have predicted a significant decrease

410   in precipitation and increase in temperature throughout Texas (Jiang and Yang, 2012) and

411   especially in the Brazos River basin (Awal et al., 2016) where this population occurs. As climate

412   changes, these native wetland tree populations will play key roles in helping the species maintain

413   their geographic distributions.

414   **5. Conclusion**

415   This study provides insights on hydroclimatic conditions that can provide suitable

416   conditions for better wetland forest productivity and health. Columbia bottomlands support a large

417   diversity of plants, mammals, birds, reptiles and insects. The knowledge of optimum growing

418   conditions for the vegetation in this region is critical for the survival and conservation of the

419 biodiversity that is dependent on this ecosystem. We provide evidence that wetter portions of this

420 landscape are more resilient to hydroclimatic changes than drier areas, as well as better adapted to

421 periods of flooding and waterlogging. Trees in drier areas grew more slowly during dry and warm

422 periods and were more sensitive to seasonal physiological stress. We observed variation in growth

423 and stress responses to climatic conditions during different phases of the growing season. Our

424 findings suggest that hydroclimatic changes to this ecosystem that alter the timing and frequency

425 of wet conditions can negatively impact forest health. This study also provides the first tree-ring

426 records from the Columbia bottomlands, which can act as a baseline for future ecological research

427 in the region.

428 *Data availability.* All data resulting from this study are available from the authors upon request
429 (ajinkyagd@tamu.edu).
430
431 *Competing interests.* The authors declare that they have no conflict of interest.
432
433 *Author contribution.* Ajinkya G. Deshpande conceptualized the study, developed the methodology,
434 collected field samples, conducted formal analysis including laboratory and statistical analysis and
435 wrote the original draft. Thomas W. Boutton contributed in conceptualization of the study,
436 provided laboratory equipment/materials for stable carbon isotope analysis and edited/reviewed
437 the original draft. Charles W. Lafon contributed in conceptualization of the study, provided all the
438 required equipment for dendrochronology and edited/reviewed the original draft. Georgianne W.
439 Moore was the investigator and supervisor of the study, played a major role in conceptualization
440 of the study, contributed in developing the methodology as well as statistical analyses, acquired
441 funds for the study and edited/reviewed the original draft.
442

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Biogeosciences
Discussions

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