



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

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9 **Abstract.** Wetland forests around the world have been reduced to a small proportion of their
10 original expanse due to changing climatic conditions and intensification of human land use
11 activities. As a case in point, the Columbia bottomland hardwood forests along the Brazos-
12 Colorado Coastal Basin on the Gulf coast of Texas are currently threatened by an increasingly
13 erratic hydroclimate in the form of both extreme floods as well as droughts, and by urban
14 expansion. In this study, we use dendrochronology and tree-ring carbon isotopes to understand the
15 effect of changing hydroclimatic conditions on the functional attributes of these forests. We
16 examined tree-rings of *Quercus nigra* at four sites within the Columbia bottomlands, of which one
17 site experiences frequent and prolonged flooding, while the other three are less flood-prone. The
18 objectives of this study were to: (i) understand the impact of hydroclimatic variation on growth
19 rates using tree-ring width analysis, (ii) assess the magnitude of physiological stress inflicted by
20 extreme hydroclimatic conditions using tree-ring $\delta^{13}\text{C}$ measurements, and (iii) evaluate the
21 relationship between physiological stress and growth inhibition. Growth rates across the landscape
22 were influenced most strongly by mid-growing season climate, while early-growing season
23 climate inflicted the greatest physiological stress. Neither growth inhibition nor changes in $\delta^{13}\text{C}$
24 values were observed in trees at the wetter site under extreme hydrologic conditions such as
25 droughts or floods. In addition, trees at the wet site were less sensitive to precipitation and showed



26 no response to higher temperatures. In contrast, trees of the three drier sites experienced growth
27 inhibition and had higher tree-ring $\delta^{13}\text{C}$ 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.

33 **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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values have the potential to identify
64 a wide range of growth and stress response of vegetation to hydroclimatic variability. However,
65 tree-ring $\delta^{13}\text{C}$ is also influenced by the changing $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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; Kozłowski, 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 $\delta^{13}\text{C}$ values of tree-ring cellulose usually reflect stress caused by low
81 environmental moisture at the time of carbon fixation, while lower $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 (Kozłowski and Pallardy, 1984) and accumulation of
96 metabolic toxins from flooding (Jackson and Drew, 1984).

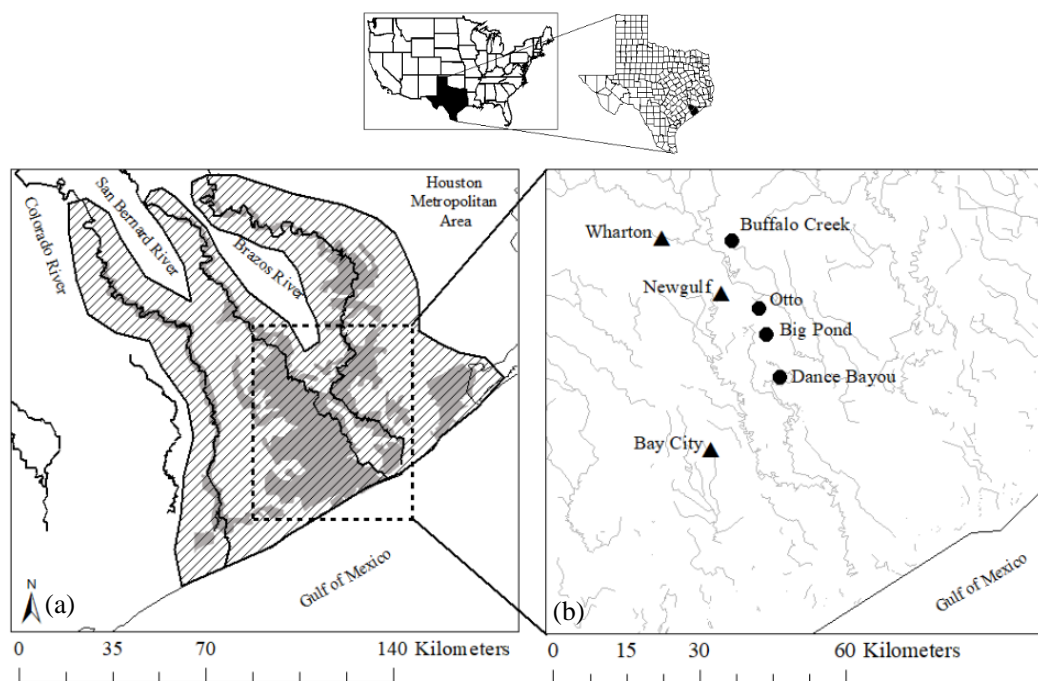
97 In this study, we investigated how bottomland hardwood wetland forests of eastern Texas,
98 USA respond to hydroclimatic variation and extremes under different edaphic conditions. The
99 study was conducted at four sites, of which one was a frequently flooded wet site, while at the
100 other three 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$) 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



118 stress. Thus, we expected a stronger negative relationship between growth and physiological stress
119 at drier sites.

120 2. Materials and Methods

121 2.1 Study Area Description



122 **Figure 1. a) Current distribution of Columbia Bottomlands (grey) and historic extent**
123 **shown by the slanted parallel lines (USFWS, 1997; Houston Wilderness, 2007; Rosen et al.,**
124 **2008). The area in which the study sites are located is shown by the dashed box. b)**
125 **Locations of study sites (circles) and weather stations (triangles) in the Brazos-Colorado**
126 **Coastal Basin.**

127
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 °C and the average minimum monthly temperature is approximately 15 °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.



152 **Table 1.** Site description with basic soil properties averaged over the top 100 cm depth (NRCS,
153 2020).
154

Site	Elevation (m)	Coordinates	Tree DBH (cm) (mean ± SE)	Clay %	Silt %	Sand %	Soil pH	Bulk Density (g/cm ³)	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

155 2.2 Tree core sampling

156 We sampled at least eight mature *Q. nigra* trees at each site in May 2017. Healthy
157 individuals with no obvious injuries like cavities, scars or diseases were selected. Preference was
158 given to trees with larger diameters at breast height (>40 cm) and uniform girth (Stokes and
159 Smiley, 1968). Three cores were extracted at breast height from every tree spaced equally around
160 the circumference. Two cores were processed and used for ring-width measurements and the third
161 core was used for $\delta^{13}\text{C}$ analysis after cellulose extraction.

162 2.3 Dendrochronology

163 Tree cores were dried to constant weight at 60 °C and mounted on 9.5 x 9.5 mm grooved
164 core mounts. The mounted cores were sanded using a hand sander with progressively finer grades
165 of sandpaper (60 to 400 grit) (Speer, 2012). Tree-ring widths were visually crossdated and then
166 measured using MeasureJ2X linked to a sliding-stage microscope (2.5X). To verify and refine the
167 crossdating, tree-ring widths were statistically assessed using the COFECHA program (Holmes,
168 1983). Series intercorrelation and mean sensitivity obtained from COFECHA were used to
169 determine the quality of crossdating (Grissino-Mayer, 2001; Speer, 2012). Series intercorrelation
170 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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). $\delta^{13}\text{C}$ 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:

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

200 where R_{SAMPLE} is the $^{13}\text{C}/^{12}\text{C}$ ratio of the sample and R_{STD} is the $^{13}\text{C}/^{12}\text{C}$ 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 $\pm 0.1\%$.

203 Atmospheric $\delta^{13}\text{C}$ depletion trend over the study period was removed from the tree-ring
204 $\delta^{13}\text{C}$ record by calculating the difference between average annual atmospheric $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$
207 values from corresponding years (McCarroll and Loader, 2004) (Table 2).

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

Year	$\delta^{13}\text{C}$	Δ	Year	$\delta^{13}\text{C}$	Δ	Year	$\delta^{13}\text{C}$	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



211 To evaluate differences in mean $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$, we used simple linear regressions between site-wise annual ring-width index and
218 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$, 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 $\delta^{13}\text{C}$. The time interval during which climate was found to be most strongly
224 influencing growth and $\delta^{13}\text{C}$ (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 $\delta^{13}\text{C}$. All statistical analyses
227 were conducted in R (R Core Team, 2012).

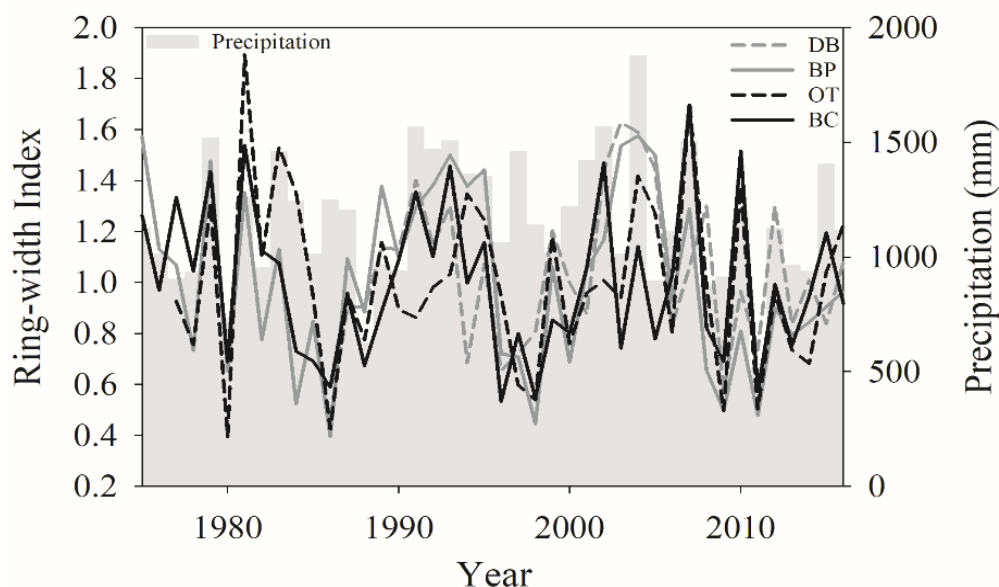
228 3. Results

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



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

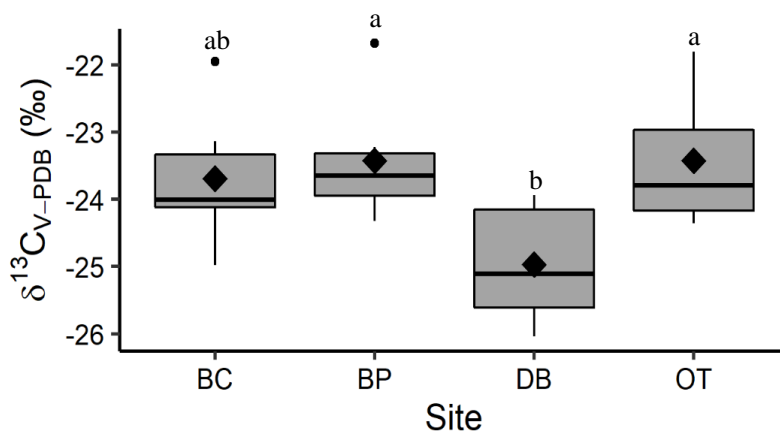
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248 3.2 Differences in site-level tree-ring $\delta^{13}\text{C}$ values

249 Comparison between site-level mean tree-ring $\delta^{13}\text{C}$ measurements averaged over the entire
250 40-year study period supports our second hypothesis. Tree-ring $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ signal over the
253 40-year period. Post hoc analysis indicates that the wet site, DB, had a lower mean tree-ring $\delta^{13}\text{C}$
254 value as compared to two drier sites, BP ($p=0.03$) and OT ($p=0.02$) (Fig. 3).

255



256 **Figure 3.** One-way ANOVA and Tukey post hoc analysis (denoted with letters) for mean
257 difference in site-level tree-ring $\delta^{13}\text{C}$ 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.

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 $\delta^{13}\text{C}$ measurements and climate



267 data indicate that climatic conditions early in the growing season (April) are critical for causing
268 physiological stress in these forests (Table S2).

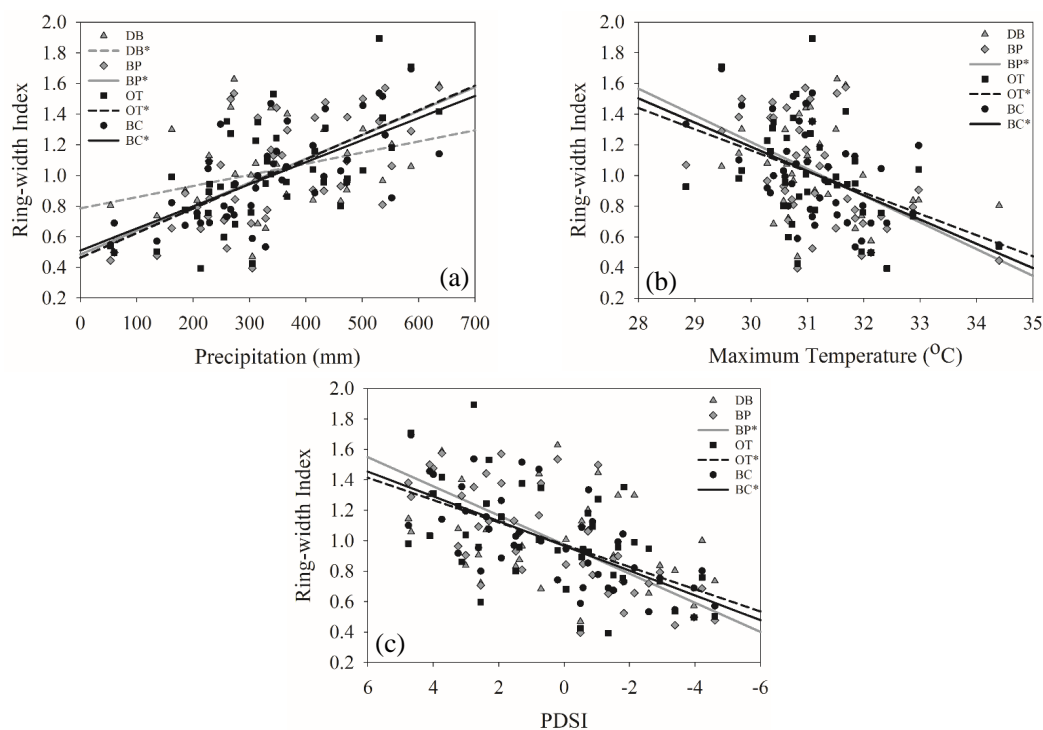
269 As hypothesized, we observed a strong increase in tree-ring widths with mid-growing
270 season precipitation. Although this positive relationship was expected for trees growing in drier
271 conditions, we observed a similar but weaker positive relationship between growth and
272 precipitation even 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



281 **Figure 4.** a) Relationship between ring-width index and mid-growing season precipitation (a),
282 temperature (b) and PDSI (c). Site DB is represented by grey triangles, BP by grey diamonds, OT
283 by black squares and BC by black circles. Statistically significant relationships are marked with
284 an asterisk (*).

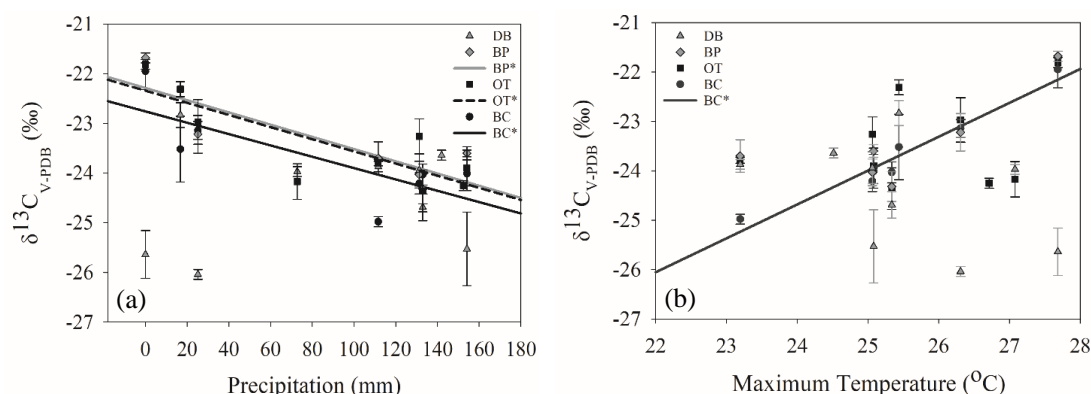
285 In line with our second hypothesis, we observed a depletion in tree-ring $\delta^{13}\text{C}$ values with
286 increase in early-growing season precipitation at the drier sites (Table 5, Fig. 5a). We had
287 hypothesized that high precipitation at the wet site will enrich tree-ring $\delta^{13}\text{C}$ values as a result of
288 physiological stress caused by possible flooding stress. However, we found no relationship
289 between tree-ring $\delta^{13}\text{C}$ and precipitation at the wet site (Table 5). Higher maximum temperatures
290 resulted in enriched tree-ring $\delta^{13}\text{C}$ values only at one of the drier sites (BC), indicating
291 physiological resistance to high temperatures in most parts of this wetland forest (Table 5, Fig.
292 5b). PDSI did not have any effect on tree-ring $\delta^{13}\text{C}$ values from all four sites (Table 5). Also,
293 previous year's climate did not have any statistically significant influence on either ring-width
294 index or tree-ring $\delta^{13}\text{C}$ measurements at any site.



295 **Table 5.** Relationships between tree-ring $\delta^{13}\text{C}$ values and early-growing season climatic conditions
 296 ($\alpha=0.05$).

Site	Precipitation (April)		Temperature (April)		PDSI p value
	p value	R ²	p value	R ²	
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

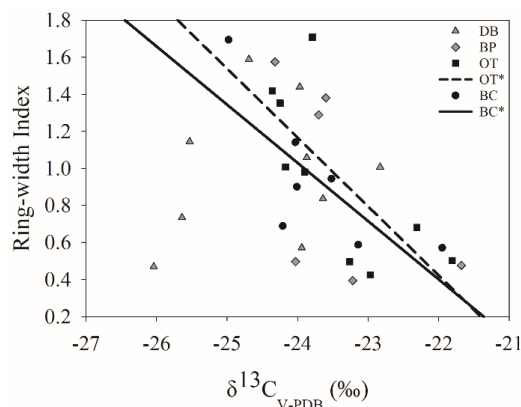
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298 **Figure 5.** Relationship between tree-ring $\delta^{13}\text{C}$ values and early-growing season (a) precipitation
 299 and (b) temperature. Site DB is represented by grey triangles, BP by grey diamonds, OT by black
 300 squares and BC by black circles. Statistically significant relationships are marked with an asterisk
 301 (*).

302 3.4 Relationship between growth and tree-ring $\delta^{13}\text{C}$

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



308

309 **Figure 6.** Relationship between ring-width index and tree-ring $\delta^{13}\text{C}$. Site DB is represented by
310 grey triangles, BP by grey diamonds, OT by black squares and BC by black circles. Statistically
311 significant relationships are marked with an asterisk (*).
312

312

313 4. Discussion

314 Bottomland hardwood forests in the southeastern United States have been reduced to a
315 small proportion of their original expanse. The hydrology of these wetland forests has been altered
316 due to expansion of agricultural and urban land uses, river regulation, drainage ditches,
317 impoundment from berms and poor drainage, and water table drawdowns (Wear and Greis, 2002;
318 Blann et al., 2009; Dahl, 2011). The ecological impacts of these disturbances are exacerbated by
319 hydroclimatic anomalies such as droughts and floods (Ferrati et al., 2005; Erwin, 2008). Changing
320 climatic conditions are not only resulting in increasingly drier conditions over time, but also more
321 intense storm events (Easterling et al., 2000; Seager et al., 2007; Knutson et al., 2010). Moreover,
322 fragmentation caused by anthropogenic pressures coupled with topographic heterogeneity causes
323 this **dry-wet transition** to not only be temporally but also spatially variable. As a result, portions of
324 these riverine wetland forests tend to be drier than others. These temporal and spatial variations
325 need to be considered while studying the impacts of changing hydroclimate and hydrology on
326 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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; Kozłowski and Pallardy, 1984; Kozłowski, 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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
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442

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449

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