

Point-by-point responses

Referee #1

The outstanding request I make, that will require more substantial work, is that your calculation (and associated analyses) be switched to using a conventional big delta D13C carbon isotope discrimination rather than reporting small delta d13C values that were corrected with a pseudo-discrimination value.

Authors' Response: We agree that switching our carbon isotope results from $\delta^{13}\text{C}$ to discrimination ($\Delta^{13}\text{C}$) is a more robust approach than the pseudo-correction method that we had used earlier. Consequently, we have now switched all our calculations and analyses to $\Delta^{13}\text{C}$ notation. Since the effect of declining atmospheric $\delta^{13}\text{C}$ signature is relatively small over the study period, the conversion of our isotope measurements to $\Delta^{13}\text{C}$ did not change the strength of relationships between tree-ring C isotope values and climate or ring-width index. However, we are now replacing the plots and related text with $\Delta^{13}\text{C}$.

Lines 173-174: ARSTAN produced three detrended chronologies (Standardized, Residual and ARSTAN). To be clear, please state that you used the ARSTAN chronology, correct?

Authors' Response: Edited to “*The final standardized ARSTAN (A) chronology (ring-width index (RWI)) was generated for each site using the ARSTAN program.*” (now line 191).

Line 181: Analyses, here and elsewhere unless referring to a single measurement or test.

Authors' Response: Changed to “analyses” at all relevant mentions.

Lines 203-208: It would help readers in biogeosciences to use the most common or conventional definition for big delta (D13C) and employed this in their analyses where $\text{D13C} = (\text{13C}_{\text{air}} - \text{13C}_{\text{plant}})/(\text{1} + \text{13C}_{\text{plant}})$. The original citation for carbon isotope discrimination is Farquhar 1983 (Aust J Plant Phys Mol Biol), but most often cited as the review paper by Farquhar, Ehleringer and Hubick 1989. Either one would be appropriate, in my view.

Authors' Response: Please refer to our first response. This paragraph now reads as: “*Atmospheric $\delta^{13}\text{C}$ depletion trend over the study period was removed from the tree-ring carbon isotopic record by converting carbon isotope ratios ($\delta^{13}\text{C}$) to carbon isotope discrimination values ($\Delta^{13}\text{C}$) (Farquhar, 1983):*

$$\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{plant}})/(1 + \delta^{13}\text{C}_{\text{plant}})$$

Average annual atmospheric $\delta^{13}\text{C}$ values from La Jolla Pier, CA, USA (Keeling and Keeling, 2017) were obtained to calculate $\Delta^{13}\text{C}$ (Table 2).” (now lines 232-237).

Lines 215-216: Obtained from where? Provide source.

Authors' Response: Source added (NOAA NESDIS, 2018) here and in section 2.4. (now line 246).

Lines 245-246: These series intercorrelation values are quite high. What is reported here is not incorrect but it would help readers get a truer sense of the shared variation among trees if you calculated the series intercorrelation after averaging ring-width values within each tree. You can report both values if you wish. Without doing so, calculating intercorrelation values across all series represents variation within and between trees with no viable means for readers to know which was more important.

Authors' Response: A new table with the suggested intercorrelation values has been added.

Line 323: What dry-wet transition? Be more specific.

Authors' Response: The first paragraph of the discussion section has been shortened and edited as follows: "*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 tend to be drier than others.*" The term dry-wet transition has been deleted.

Lines 327-329: I did not see evidence that fully tested this hypothesis. The detrending methods used are not incorrect for comparing climate responses, however, there may be very different raw tree growth rates among stands that could help shed light on the sufficiency of moisture availability for growth. This can be assessed using "RCS" type methods that detrends each site by the age-specific ring-width growth or age-specific basal area increment growth across all trees and stands. Controlling for cambial age is especially important when investigating growth rates of relatively young trees like those in this study. I am not saying to your or the editor that you should get rid of your current detrending methods -- I am saying that you should employ another set of analyses noting whether or not the raw growth rates among stands corresponds with the differences in climate sensitivity and carbon isotope results you show.

Authors' Response: Thank you for this very useful suggestion. After considering your suggestion about adding an age-specific ring-width index, we employed RCS detrending as given by Briffa et al. (1992) using the method specified by Biondi and Qeadan (2008), which controls for cambial age. We have now analyzed our growth-climate and growth- $\Delta^{13}\text{C}$ relationships using the new ring-width index generated by RCS detrending in addition to ARSTAN. We have added these methods and results to the revised version. However, it needs to be noted that our ring-width indices generated using both the methods were highly correlated. Additionally, we also calculated BAI and did the above-mentioned analyses using BAI as well.

Line 343: Water-logged soils also can impose physiological stress that is not well measured by stable isotopes, so this statement may be too broad. I think it would be more correct to say that the trees from the wetter sites had lower stomatal constraints on leaf gas exchange.

Authors' Response: Sentence rephrased as suggested (now line 385).

Line 343: The use of resilience here (and in most papers) is not supported by any sort of physiological definition. It would be more accurate to simply omit this statement.

Authors' Response: We agree with your and the other referees' comments about the use of the term "resilience" in this study and we acknowledge that defining resilience in this ecosystem would require a more detailed approach. Consequently, we have omitted the resilience narrative from this study and have explained our findings as a function of differences in physical/hydrological conditions between sites.

Lines 352-356: This part of the Discussion could be improved by framing these findings within that previously shown for tree growth and carbon isotopes in another riparian oak trees across a continental gradient in aridity (see Voelker et al. 2014 *Plant Cell & Environ* 37: 766-779). In that paper we demonstrated that the relationship between growth and carbon isotopes changes greatly and potentially switches in directionality depending on site aridity.

Authors' Response: Thank you for pointing us towards this study. It is very interesting to see how the relationship between RWI and $\Delta^{13}\text{C}$ varies over a large geographical area encompassing a wide distribution range of a species. The manner in which the relationship switches from positive to negative with wetter and cooler conditions is very intriguing. In case of our study, we can see the trend of this relationship change from positive to a flatter slope within the same landscape. We have cited Voelker et al. (2014) to improve this part of the discussion. (now lines 396 onwards).

Line 358: I am not sure what this means. Are you saying these trees are morphologically different and/or genetically different?

Authors' Response: We have omitted "physiological resistance" from this sentence as the absence of drought-related stress signals at the wet site can be attributed to hydrological differences and higher soil moisture availability.

Line 359: It seems you are referring to drought stress here, correct? Please be specific.

Authors' Response: Please see our response below.

Line 362: Again, do you mean drought stress?

Authors' Response: Please see our response below.

Line 363: Although, if you read Voelker et al. 2014, we found the same trend for trees growing under cool and wet conditions as compared to those trees at warmer and/or drier locations irrespective of waterlogging.

Authors' Response: Lines 352-370 (now lines 396-424) edited to: "*Our third hypothesis that tree-ring $\Delta^{13}\text{C}$ would have a positive relationship with radial growth holds true under dry edaphic conditions, where drought stress restricts plant growth. Whereas in trees growing in*

wetter soils, tree-ring $\Delta^{13}\text{C}$ and radial growth were largely decoupled. Similar differences in the relationship between tree-ring $\Delta^{13}\text{C}$ and radial growth of the ring-porous bur oak (*Quercus macrocarpa* M.) have been observed across continental gradients where tree-ring $\Delta^{13}\text{C}$ correlates positively with radial growth at drier sites, while the relationship is negative under wetter conditions (Voelker et al., 2014). These differences have been attributed to indicators of site aridity (VPD, precipitation:evapotranspiration). A similar relationship has also been observed in pond cypress trees in the southeastern Everglades, Florida, USA (Anderson et al., 2005). While we did not observe a negative relationship between tree-ring $\Delta^{13}\text{C}$ and radial growth at the wet site, no correlation between the two highlights the beneficial effect of wetter hydrological conditions on vegetation at the flooded site. Consequently, the absence of drought-related stress signals at the wet site is possibly due to supplemental soil moisture availability from flooding. At the drier sites, drought-related lower tree-ring $\Delta^{13}\text{C}$ values are correlated with slower radial growth, which indicates that moisture deficit causes physiological stress in these trees, reducing stomatal conductance and eventually inhibits growth. Additionally, tree-ring $\Delta^{13}\text{C}$ and radial growth at the wet site was highly uncorrelated especially during years when growing-season precipitation was more erratic (dry spring followed by a wet summer and vice versa). The drought effect of drier hydroclimatic conditions is ephemeral and less intense at the wet site due to slower depletion of soil water reserves. Therefore, seasonal dry spells slightly reduce tree-ring $\Delta^{13}\text{C}$ but do not always result in growth inhibition in wetter parts of this landscape due to sufficient moisture availability. We had expected to observe lower tree-ring $\Delta^{13}\text{C}$ values during extremely wet growing seasons due to flooding stress, but the absence of these signals indicates adaptation to excessive wetness. It has been suggested that wetland species that experience frequent flooding develop adaptive traits that enable rapid reopening of stomata with the recession of flood waters as oxygen availability in the root zone increases (Crawford, 1982; Kozłowski and Pallardy, 1984; Kozłowski, 2002). Consistent with this, our observations signify that trees growing in drier conditions do have a more distinct tree-ring $\Delta^{13}\text{C}$ -growth relationship as compared to those growing in wet conditions.”

Lines 395-396: This should be more specific than just "tree-ring $\delta^{13}\text{C}$ ". The $\delta^{13}\text{C}$ signature of initial radial growth in each year will not reflect spring conditions, but spring conditions could affect the $\delta^{13}\text{C}$ of wood that forms later.

Authors' Response: Please see our response below.

Lines 397-399: Yes, but it would help to be clear that these results are not evidence of an absence of a signal from the previous year, it just means that the signal from the previous year was likely relatively small compared to that of the current year. This would be expected because the earlywood portion of ring-porous oaks like those of *Q. nigra* have very low wood density compared to the latewood. Therefore, even if all early wood vessels had a $\delta^{13}\text{C}$ signature purely from the previous year, by compositing with the latewood (from young trees where latewood is a large proportion of the ring), the signal of the previous year would be too small to detect.

Lines 399-401: See previous comment.

Authors' Response: We completely agree with your point. Rephrased lines 394-401 (now lines 449-459) to: “It is apparent that if wood at the very beginning of the growing season

*is formed using assimilates from the previous growing season, earlywood tree-ring $\Delta^{13}\text{C}$ does not have a correlation with early-growing season precipitation from the current year (Helle and Schleser, 2004; Porter et al., 2009; Schollaen et al., 2013). In our study, tree-ring $\Delta^{13}\text{C}$ is well-correlated with early-growing season precipitation from the current growing season. Although this indicates that majority of annual wood is formed using assimilates from the current growing season, it needs to be noted that earlywood portions of ring-porous oaks like those of *Q. nigra* have lower wood density (Gasson, 1987; Lei et al., 1996; Rao, 1997). Therefore, by using entire annual ring composites, the relatively small signal from the previous year could be present but not distinctly detected. Hence, comparing our RWI and tree-ring $\Delta^{13}\text{C}$ values with previous years' climate yields no correlation ($p > 0.05$) indicating its relatively weak effect."*

Referee #2

(1) Other than soil moisture, the authors did not make any substantive effort to consider other differences between the wet and dry sites. The wet sites would have enhanced ET (more E) and therefore higher humidity in the canopy, this would affect VPD and evaporative demand on the leaves. The surface water would also lead to a different Bowen ratio and perhaps less extreme temperatures for the soils. The reduced heating at the soil surface would reduce convection and mixing into the canopy that might influence flushing of the canopy. My general concern is that while the broader regional meteorological conditions might be similar between sites, the actual conditions in the canopy could be very different. This could indeed modulate growth and $\delta^{13}\text{C}$ in a way that is not really about "physiological resilience" as the authors state but more simply that the trees are just experiencing different physical forcing.

Authors' Response: We agree with your concern about differences in site-level latent heat flux and higher evaporation as a result of ponding at the wet site. This can certainly result in lower VPD in the canopy and reduce canopy conductance. However, it needs to be noted that the wet site mainly gets flooded intermittently. Although this can result in higher overall soil moisture, surface water does not necessarily occur at this site throughout the growing season. Therefore, the effect of higher evaporation at this site would be more significant on short temporal scales. Our current setup in which the $\delta^{13}\text{C}$ measurements are annually resolved may not be suitable for detecting this effect. Additionally, if more evaporation and lower VPD in the canopy of the wet site were prominent over the entire growing season, it should have resulted in enriched $\delta^{13}\text{C}$ values during extremely wet years because of reduced canopy conductance, which we did not observe. However, we have made improvements to the introduction and discussion to acknowledge this effect.

(2) The authors should take a more mechanistic approach to interpreting their $\delta^{13}\text{C}$ data. This does not need to involve a highly sophisticated model but a simple approach that considers $\delta^{13}\text{C}$ as a function of atmospheric ^{13}C and A/g (as in the Farquhar model). While I think it is qualitatively fine to discuss $\delta^{13}\text{C}$ variability as merely a "stress indicator" this not necessarily true. Notably, the trees at the wet and dry sites have similar growth rates but very different $\delta^{13}\text{C}$ values. One question that I have is whether there is a source of depleted CO_2 that emitted from the waterlogged sites that influences the $\delta^{13}\text{C}$ of the cellulose there. For example, if these soils produce isotopically depleted methane that is oxidized to CO_2 , this could deplete the isotopic

ratio of the soils. The most interesting finding in the study is that $\delta^{13}\text{C}$ for the wet sites show their more depleted values when growth rates are lowest. This is a very unique and exciting result. A series of simple sensitivity tests with a $\delta^{13}\text{C}$ cellulose model could be very helpful.

Authors' Response: As per your second comment, we have converted our carbon isotope results to $\Delta^{13}\text{C}$ notation, which includes the effect of atmospheric $\delta^{13}\text{C}$. We have now also calculated iWUE as per your suggestion. However, iWUE values are very strongly correlated to $\Delta^{13}\text{C}$ values inversely, therefore, comparing either of the two values with climate data yields relationships that are similar in strength. Hence, it might be better to use either $\Delta^{13}\text{C}$ or iWUE instead of both. We were equally excited and intrigued to see depleted $\delta^{13}\text{C}$ values when growth rates were lowest at the wet site and we also modeled $\delta^{13}\text{C}_{\text{wet}} - \delta^{13}\text{C}_{\text{predicted}}$ from dry sites versus precipitation as you have recommended. However, the relationship was not significant and hence, it is difficult to draw conclusions. We think it would be more interesting to highlight that tree-ring $\delta^{13}\text{C}$ values at the wet site are not dependent on climatic conditions and do not affect growth rates as opposed to the drier sites, where these relationships are more prominent.

(3) The design of only measuring $\delta^{13}\text{C}$ during extreme years is not ideal with respect to understanding how a previous year influences $\delta^{13}\text{C}$. The authors would need to measure the isotopic ratio of the cellulose for the year following the extreme year as well to see if that signal shows up. It is too late to ask this, but the authors would have a more compelling argument regarding previous years if they had used this approach.

Authors' Response: We completely agree with your comment about assessing tree-ring $\delta^{13}\text{C}$ from years following extreme years but we were constrained by sample size limitations which prevented us from analyzing a more continuous tree-ring $\delta^{13}\text{C}$ record.

(4) This is a rather simple comment, but I was surprised to see the authors did not use VPD as an explanatory variable. Particularly as to whether the response of wet site to precipitation was a result not of soil moisture stress (i.e. precip.) but actually because drier years were associated with higher VPD.

Authors' Response: We wished to analyze the effect of VPD on growth and $\delta^{13}\text{C}$ but we could not do so because the weather stations closest to our sites did not have past relative humidity measurements. Also, since we are using past data from the nearest NOAA weather stations, the climate data used in the study represents regional-scale conditions. Therefore, we have not made interpretations about site-specific microclimatic conditions.

Small comments:

100: How was the frequency of flooding characterized between sites?

Authors' Response: Flooding frequency was characterized by visual assessment during our bi-weekly visits over the course of two years (2017-2019). Also, following major storm events such as Hurricane Harvey, we documented flooding depth but representing those sporadic measurements seem to be out of the scope of this study. In an Earth Resistivity Tomography

study conducted by researchers from the Department of Geology and Geophysics, Texas A&M University, soil resistivity was measured before and after multiple storm events. We have added their average site-level resistivity measurements to Table 1.

254: The actual number of $\delta^{13}\text{C}$ measurements and presentation of the data is sort of obscured. It would be nice to see a time series of all the $\delta^{13}\text{C}$ even if the time series is discontinuous.

Authors' Response: This is a very valid suggestion. We have added a sub-figure representing the $\Delta^{13}\text{C}$ chronology in Figure 2.

Fig 3: Were BC and DB not different as well?

Authors' Response: The difference between BC and DB was not statistically significant at $\alpha=0.05$ ($p=0.08$) because DB values were slightly more variable (now Figure 4).

269: The presentation of the actual correlation analyses would be nice to have in the main text even if the correlations were insignificant. This especially true for the lag analyses.

Authors' Response: The correlation analyses results are in supplementary tables 1 and 2. We added those tables to the supplementary material because of their large size but we can move them to the main content, if required.

272: "...that for the wettest site, growth rates would decline due to flood stress..."

Authors' Response: Sentence rephrased as suggested (now line 313).

285: With respect to previous season effect on $\delta^{13}\text{C}$, it would seem the biggest effect would be from the late growing season of the previous year.

Authors' Response: We analyzed the effect of previous season on $\Delta^{13}\text{C}$ using the same approach as we did for the current season (described in lines 249-253). We did not find a significant effect of previous year's August-October climate on tree-ring $\Delta^{13}\text{C}$. However, as referee-1 has also suggested, we have made changes to lines 449-459 acknowledging that there could be an effect of previous season in the low-density earlywood of *Q. nigra* tree-rings. The lower density of earlywood in these ring-porous oaks and as a result of using annual ring composites, a relatively smaller effect of previous year's conditions could have been present but was difficult to detect.

297: It is noted that $\delta^{13}\text{C}$ and precip. are not correlated for the wettest site. However, it is interesting that the distance between $\delta^{13}\text{C}$ at the wettest site and the regression between $\delta^{13}\text{C}$ and precip. for the driest sites increases as it gets drier. A potentially useful variable would be $\delta^{13}\text{C}_{\text{wet}} - \delta^{13}\text{C}_{\text{predicted}}$ defined as $\delta^{13}\text{C}_{\text{wet}} - \delta^{13}\text{C}_{\text{predicted}}$ from dry sites.

Authors' Response: This is a great observation. Following your suggestion, we ran the model as you have described but unfortunately, we could not find any significant correlation. However, as this trend is observed only during two specific years, we assessed the monthly

climatic measurements and observed that during those two years, spring had been much drier followed by sizeable precipitation in the summer. As a result, by sampling the tree-ring as a whole, $\Delta^{13}\text{C}$ values were enriched as a result of largely non-stressful mid- and late-growing seasons. Therefore, in Figure 6a, in which we have compared $\Delta^{13}\text{C}$ values with spring precipitation, enriched $\Delta^{13}\text{C}$ values for those two years correspond to low precipitation.

307: You say growth was sustained at wet sites even during dry years but it is also true that growth did decline somewhat during dry years, so there was some sensitivity.

Authors' Response: Sentence rephrased to: “*trees at this site were able to minimize growth inhibition during stressful conditions as compared to trees at the drier sites.*” (now line 357).

Figure 6: As mentioned above, the points on the lower left of the graph (low $\delta^{13}\text{C}$ and low ring width) are extremely interesting. I would like to see a more mechanistic approach to explain them. (now Figure 7).

Authors' Response: Two out of the three points on the lower left are the two years with drier spring seasons followed by relatively wetter summers, thus resulting in lower growth but enriched $\Delta^{13}\text{C}$. The third point corresponds to a year with a relatively wetter spring followed by a drier late-summer. Hence, these “outlier” points are results of more abrupt changes in seasonal climatic conditions from spring to summer during some years. We do not see such outlier data points at the drier sites because overall drier conditions at these sites result in $\Delta^{13}\text{C}$ depletion as opposed to the wetter site. We have added this explanation to the discussion section. Building a mechanistic modeling approach to explain these three points is proving difficult because of the large scattering and randomness in the $\Delta^{13}\text{C}$ measurements from the wet site.

314-326: The first paragraph of Discussion is too long. It is fine to revisit some of the context and motivation for the study here, but this can be shortened to 1-2 sentences and then jump into discussing the results.

Authors' Response: Paragraph rephrased and shortened to “*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 tend to be drier than others.*” (now lines 364-369).

333: I was a little confused about the comment of more heterogenous growth at waterlogged sites. I don't remember that result being presented and it is difficult to understand why. On the one hand, waterlogging does not have a big effect on growth but its presence or absence on the local scale does drive differences in growth. Please clarify.

Authors' Response: The presence or absence of waterlogging on a local scale causes variation in tree-to-tree growth rates at the wettest site. It does not affect site-level annual trends

in radial growth but causes some trees to grow a little slower than the others within the same site. This is interpreted from the lower series intercorrelation values for this site shown in Table 4. These lower series intercorrelation values indicate differences in tree-level growth rates within the wettest site.

338: As noted, there is an argument for physiological resilience at the wet site but also an argument that because of the site's hydrology, soil moisture changes persist across years and reduces the response to precipitation variability. This could therefore be a physical/hydrological not physiological process.

Authors' Response: We completely agree with this point and we think that our results are better indicative of physical/hydrological differences between sites rather than the interpretation that trees at the wettest site are more physiologically resilient. We have therefore omitted the resilience narrative from this study and have now explained our findings as a result of differences in physical/hydrological conditions between sites.

As noted, I think it is worth addressing whether there could be low $\delta^{13}\text{C}$ in the atmosphere of the waterlogged site.

Authors' Response: Although this site experiences waterlogging more often than the other three sites, which very rarely get flooded, it doesn't remain waterlogged throughout the growing season. Flooding occurs at the wet site at specific periods during the growing season and conditions transition from flooded to non-flooded and vice versa as the growing season progresses. Therefore, phenomena such as low VPD or the presence of depleted $\delta^{13}\text{C}$ in the canopy due to methane production would be ephemeral and difficult to detect in annual tree-rings. These effects can possibly be detected by employing a model like CANISOTOPE, which requires site-level eddy flux and micrometeorological measurements. It could also be possible to observe these effects in tree-ring cellulose by segregating earlywood and latewood. However, a large number of our sampled tree-rings were narrow with the earlywood-latewood distinction being barely visible. A more advanced ring-cutting method would be required as compared to the manual approach that we have used.

400: The role of previous season's conditions on $\delta^{13}\text{C}$ is not sufficiently established here for reasons described above. More attention and discussion needs to be paid as to why the analysis might be limited i.e. you would need to measure the $\delta^{13}\text{C}$ following an extreme year.

Authors' Response: We have rephrased lines 394-401 (now lines 449-459) to: "*It is apparent that if wood at the very beginning of the growing season is formed using assimilates from the previous growing season, earlywood tree-ring $\Delta^{13}\text{C}$ does not have a correlation with early-growing season precipitation from the current year (Helle and Schleser, 2004; Porter et al., 2009; Schollaen et al., 2013). In our study, tree-ring $\Delta^{13}\text{C}$ is well-correlated with early-growing season precipitation from the current growing season. Although this indicates that majority of annual wood is formed using assimilates from the current growing season, it needs to be noted that earlywood portions of ring-porous oaks like those of *Q. nigra* have lower wood density (Gasson, 1987; Lei et al., 1996; Rao, 1997). Therefore, by using entire annual ring composites, the relatively small signal from the previous year could be present but not distinctly*

detected. Hence, comparing our RWI and tree-ring $\Delta^{13}\text{C}$ values with previous years' climate yields no correlation ($p>0.05$) indicating its relatively weak effect."

It needs to be noted that we have not only used rings from extreme years but also moderate years to cover a wider range of hydroclimatic conditions. This will be clearer from the new $\Delta^{13}\text{C}$ chronology figure that we have added (Fig. 2d). However, we completely agree with your suggestion about assessing tree-ring $\delta^{13}\text{C}$ from years following extreme years but our sample size limitation prevented us from analyzing a more continuous tree-ring $\delta^{13}\text{C}$ record.

406: Not "harsher" conditions, per se, but conditions less favorable to the species.

Authors' Response: Edited as per suggestion (now line 465).

Referee #3

My primary concerns and suggestions are related to concepts that need to be further developed in the discussion (and sometimes other areas) that are not clear or clearly supported from the data presented. Specifically, the authors invoke soil moisture deficits as the mechanism to explain hydroclimate, stable isotope, and growth relationships. However, beyond the observations that the wet site floods more frequently, there is no measure of soil moisture status among these sites. While I believe the authors that there is variability among the sites, some form of estimation of soil moisture status would strengthen their arguments when invoking it as a mechanistic explanation for their findings. For example, how do the physical properties of the soil reported in table 1 relate to water holding capacity and plant available water (especially given the large difference in clay content).

Authors' Response: We have now cited a study conducted in 2018-19 at three of our sites (including the wet site) by researchers from the Department of Geology and Geophysics, Texas A&M University. In this Earth Resistivity Tomography (ERT) study, soil resistivity (and conductivity) was used as a proxy for soil moisture while controlling for other effects like soil salinity. After repeated seasonal ERT measurements, the top 1 m soil at the wet site was found to be more conductive as compared to the drier sites as a result of higher soil moisture. We have added the resistivity measurements to Table 1, which gives a more empirical estimate of differences in soil moisture between the sites (lines 162-165 and Table 1).

The other area that needs to be more clearly defined and developed is resilience. The authors refer to the resilience of these systems frequently throughout the paper, but resilience is not defined and it is unclear how the data presented fit into a predictive framework for resilience for these systems. For example, the authors do examine possible carry-over effects in ^{13}C from one year to the next, but did not find any relationship. How does this fit into a resilience conceptual framework? Given that the authors emphasize the importance of these ecotone systems, it will greatly improve the impact of the paper to have a concrete framework for resilience and to put their findings within that framework.

Authors' Response: We agree with your and the other referees' comments about the use of the term "resilience" in this study and we acknowledge that defining resilience in this

ecosystem would require a more detailed approach. Consequently, we have omitted the resilience narrative from this study and have explained our findings as a result of differences in physical/hydrological conditions between sites.

Specific comments by line number:

65-70: this is pretty standard methods and not necessary in the introduction

Authors' Response: We have edited and shortened this portion but we think a brief mention of these methods might be necessary because we have now converted our $\delta^{13}\text{C}$ values to $\Delta^{13}\text{C}$ notation, which is a function of atmospheric $\delta^{13}\text{C}$. The description in these lines provides justification for using $\Delta^{13}\text{C}$ instead of $\delta^{13}\text{C}$.

88: Most of your examples and the assumptions related to hypotheses are related to stress which would result in declines in stomatal conductance. Why invoke increased assimilation here? Is that a likely driver in this system?

Authors' Response: We agree with this suggestion. We have removed the use of the term 'assimilation' from line 88 (now line 93) as we are mainly concerned about reduction in stomatal conductance which is the stronger driver in this system.

156: Why does this say "at least eight" when table 3 indicates that there are only eight? All figures with regressions. It appears that regression lines are only include for significant relationships so it is not necessary to also indicate significance with a *

Authors' Response: Edited as per the suggestions. We had earlier mentioned "at least eight" because we had sampled more than eight trees at each site but some samples had to be discarded due to low ring visibility.

291: Physiological resilience is not defined. How is this different from another form of resilience? What do you mean by this term?

Authors' Response: Please refer to our response to comment #2.

302 – 307: What about the BP site? Anything to report?

Authors' Response: Growth at BP declined with $\delta^{13}\text{C}$ similar to that at the other two drier sites but the slope was not significant, hence we have not reported the numbers.

332 -333: It unclear where the reader was supposed to gather that growth was more heterogeneous in the wetter site. Did this play out in ^{13}C ? The relationship to waterlogging is highly speculative. What supports this interpretation?

Authors' Response: More heterogenous growth at the wet site is interpreted from the lower series intercorrelation values for this site shown in Table 4. These lower series intercorrelation values indicate differences in tree-level growth rates within the wet site.

349-351: this seems to be an incomplete line of discussion. Can you say more?

Authors' Response: Sentence rephrased: “*Generally, forested wetlands are known are not known to be drought stressed because of ample soil moisture availability. However, it is important to note that in parts of Columbia Bottomlands, depending on site-level hydrologic conditions, vegetation does experience drought stress during some years when dry climatic conditions persist over a longer period.*” (now lines 391-395).

353: how are dry edaphic conditions defined or measured?

Authors' Response: Resistivity measurements as a proxy for soil moisture from the ERT study mentioned in our earlier comment along with visual assessments are the parameters that we have used to characterize drier edaphic conditions.

376: “severely detrimental to this ecosystem”: I’m very unclear what data indicates what hydrologic change will be severely detrimental. Based on the RWI, all of these sites seem to be broadly growing in a similar way. Are there signs of mortality? In general, how is this statement supported?

Authors' Response: The statement is supported by Figure 4 (now Figure 5), which shows decline in growth during years with low precipitation, high temperatures and high drought severity during the mid-growing season at all sites. However, we understand your concern and we have rephrase this sentence by mentioning “reduced productivity” specifically instead of mentioning detrimental effects in general. (now line 430).

402-413: this paragraph needs organizational work. It is unclear from the topic sentence where is paragraph is going. The paragraph is difficult parse until you get to the end.

Authors' Response: Paragraph rephrased as per suggestion: “*Climate models have predicted a significant decrease in growing season precipitation and increase in temperature throughout Texas (Jiang and Yang, 2012) and especially in the Brazos River basin (Awal et al., 2016) where our study area is located. This region occurs at the extreme southwestern edge of the bottomland hardwood forest type (Bray, 1906; Putnam et al., 1960), which is also the southwestern edge of the distribution of Q. nigra and many other wetland tree species. Edges of distribution ranges usually experience environmental conditions that are less favorable (drier and warmer) to the species as compared to the range core (Rehm et al., 2015), which makes them more resilient and better adapted to survive in stressful conditions relative to core populations (Gutschick and Hormoz, 2003). Therefore, as climate changes, these native wetland tree populations will play key roles in helping the species maintain their geographic distributions.*” (now lines 460-470).

List of all relevant changes

4: Co-authors- Added Dr. Ayumi Hyodo from the Department of Ecology and Conservation Biology, Texas A&M University as a co-author.

Abstract:

19: 'Growth rates' changed to 'radial growth'.

21: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$. Added "as a proxy" at the end of the sentence.

21: Objective 3 edited to 'evaluate the relationship between tree-ring width and $\Delta^{13}\text{C}$ values.'

22: 'Growth rates' changed to 'radial growth'.

23: Sentence edited: 'early-growing season climate had the strongest effect on $\Delta^{13}\text{C}$.'

24: Sentence edited: 'Growth inhibition was minimal and tree-ring $\Delta^{13}\text{C}$ values were not affected in trees at the wetter site under extreme hydrological conditions such as droughts or floods.'

28: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

28: Sentence edited: 'Our results indicate more favorable growing conditions and lower stress in trees growing under wetter hydrological conditions.'

Introduction:

60: 'tree-ring $\delta^{13}\text{C}$ ' changed to 'tree-ring carbon isotopic composition'.

67: Sentence edited: 'However, carbon isotopic composition of tree-rings ($\delta^{13}\text{C}$) is also influenced by the changing carbon isotopic composition of atmospheric CO_2 .'

71: Sentence edited: 'this signal should be removed from tree-ring records'

73-76: Sentences added to introduce the need for conversion of $\delta^{13}\text{C}$ to $\Delta^{13}\text{C}$.

86: 'Higher $\delta^{13}\text{C}$ ' changed to 'Lower $\Delta^{13}\text{C}$ '.

87: 'lower $\delta^{13}\text{C}$ ' changed to 'higher $\Delta^{13}\text{C}$ '.

90: ' $\delta^{13}\text{C}$ values' changed to 'carbon isotopic composition'.

93: Removed the mention of assimilation rates.

94: 'high $\delta^{13}\text{C}$ ' changed to 'low discrimination'.

97: ' $\delta^{13}\text{C}$ ' changed to 'tree-ring carbon isotopes'.

102-108: Sentences added to acknowledge the effect of lower canopy conductance due to reduced VPD in the canopy from evaporation of ponded water and anaerobic methane emission on tree-ring carbon isotopic composition.

113: 'growth rates' changed to 'radial growth'.

119: Objective edited: ‘Our second objective was to assess tree-ring $\Delta^{13}\text{C}$ as an indicator of physiological stress inflicted by hydroclimatic conditions on these forests.’

120: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

121: ‘decrease’ changed to ‘increase’.

126: Sentence edited: ‘Although a positive relationship between tree-ring $\Delta^{13}\text{C}$ and growth (tree-ring width) is expected’.

Materials and Methods:

143: Removed ‘for prolonged periods’ because the flooding was more intermittent than prolonged.

162-165: Added results from an Earth Resistivity Tomography study conducted by Guerra (2020) which showed higher soil moisture (as indicated by higher soil conductivity) at site DB as compared to the drier sites. They accounted for other factors such as soil salinity that can influence conductivity measurements.

166: Table 1: Added a column showing resistivity measurements from Guerra (2020).

170: Deleted ‘at least’.

182: ‘Series intercorrelation’ changed to ‘Site-level series intercorrelation between individual cores’.

184: Sentence edited: ‘Series intercorrelation indicates chronology-to-chronology variation in annual growth within a given chronology group’.

186: ‘analysis’ changed to ‘analyses’.

186-191: Sentences added to describe the multiple series intercorrelation values calculated as suggested by Dr. Voelker.

191: Added ‘ARSTAN’.

194-203: Sentences added to describe the methods for calculating ring-width index using the RCS detrending method.

203-206: Sentences added to describe basal area increment calculation.

211: Added source of PDSI measurements.

212: ‘analysis’ changed to ‘analyses’.

214: ‘analysis’ changed to ‘analyses’.

232-237: Sentences added to describe the conversion of $\delta^{13}\text{C}$ values to $\Delta^{13}\text{C}$ using the equation given by Farquhar (1983).

238: Correction factor column removed from Table 2.

246: Added source of PDSI measurements.

247: ' $\delta^{13}\text{C}$ ' changed to 'tree-ring $\Delta^{13}\text{C}$ '.

248: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

251: ' $\delta^{13}\text{C}$ ' changed to 'tree-ring $\Delta^{13}\text{C}$ '.

253: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

254: ' $\delta^{13}\text{C}$ ' changed to 'tree-ring $\Delta^{13}\text{C}$ '.

255: 'analysis' changed to 'analyses'.

257: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

Results:

260: Added ARSTAN and RCS in parenthesis after chronologies.

261: 'Patterns of annual growth rate' changed to 'Patterns of RWI and BAI'.

263: Added description of annual variation in site-level tree-ring $\Delta^{13}\text{C}$ values.

268-271: Description of series intercorrelations.

271-273: Sentence describes the strong correlation between ring-width indices calculated using the ARSTAN and RCS detrending methods at all four sites.

274-277: Sentences describe BAI trends.

279: NEW FIGURES: Figure 2 now has four parts, each showing a different chronology. A) ARSTAN RWI, B) RCS RWI, C) BAI and D) $\Delta^{13}\text{C}$.

282: NEW FIGURE: Figure 3 shows the strong correlation between ring-width indices calculated using the ARSTAN and RCS detrending methods at all four sites.

284: Table 3: Series intercorrelation column removed.

287: NEW TABLE: Table 4 shows series intercorrelation values calculated using chronologies from individual cores and tree-level means across all sites and within each site.

291, 292, 294: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

295: 'lower mean tree-ring $\delta^{13}\text{C}$ ' changed to 'higher mean tree-ring $\Delta^{13}\text{C}$ '.

298, 307: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

310: 'tree-ring widths' changed to 'RWI'.

312: 'growth' changed to 'RWI'.

313: Sentence edited: 'We had hypothesized that for the wettest site, radial growth would decline due to flood stress'.

316: 'growth' changed to 'RWI'.

317: Sentences added to describe the relationship between climatic variables and ARSTAN RWI, RCS RWI and BAI.

325: NEW TABLE: Table 6: Relationships between RCS ring-width index and mid-growing season climatic conditions.

330: NEW TABLE: Table 7: Relationships between basal area increment and mid-growing season climatic conditions.

336: 'depletion in tree-ring $\delta^{13}\text{C}$ values' changed to 'increase in tree-ring $\Delta^{13}\text{C}$ values'.

338: 'enrich tree-ring $\delta^{13}\text{C}$ values' changed to 'reduce carbon isotopic discrimination'.

340: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

341: 'enrich tree-ring $\delta^{13}\text{C}$ values' changed to 'lower tree-ring $\Delta^{13}\text{C}$ values'.

342, 344, 345, 347, 352: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

352: 'tree-ring width' changed to 'tree-ring width indices'.

353-355: Sentences added to describe the relationship between ARSTAN and RCS RWI with tree-ring $\Delta^{13}\text{C}$ values'.

356: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

358: Sentence added: 'Tree-ring $\Delta^{13}\text{C}$ values were not correlated with BAI at any of the sites.'

359: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

Discussion:

364-369: Paragraph shortened as suggested by Referee #2.

381: Removed the term 'physiologically resilient'.

383: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

384: 'lower' changed to 'higher'.

385: 'physiological stress and higher resilience of trees' changed to 'stomatal constraints on leaf gas exchange'.

388: $\delta^{13}\text{C}$ changed to $\Delta^{13}\text{C}$.

391-395: Last part of the paragraph has been elaborated as suggested by Referee #3.

396: 'physiological stress' changed to 'tree-ring $\Delta^{13}\text{C}$ ', 'positive' changed to 'negative', 'growth' changed to 'radial growth'.

398: 'stress and growth' changed to 'tree-ring $\Delta^{13}\text{C}$ and radial growth'.

399-419: Edited as per Dr. Voelker's suggestions.

423: 'stress-growth relationship' changed to 'tree-ring $\Delta^{13}\text{C}$ -growth relationship'.

429: 'moisture availability' changed to 'seasonal moisture availability'.

430: 'severely detrimental to this ecosystem' changed to 'result in reduced productivity'.

438: 'stress signals' changed to 'tree-ring $\Delta^{13}\text{C}$ '.

440: Sentence edited: 'physiological stress caused by reduced stomatal conductance'.

450: 'tree-ring $\delta^{13}\text{C}$ ' changed to 'earlywood tree-ring $\Delta^{13}\text{C}$ '.

452-459: Edited as suggested by Dr. Voelker and Referee #2.

460-470: Paragraph restructured as suggested by Referee #3.

Conclusion:

476: 'wetter portions' changed to 'hydrologically wetter portions'.

477-478: Sentence edited to incorporated the overall changes made in the manuscript.

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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10 **Abstract.** Wetland forests around the world have been reduced to a small proportion of their
11 original expanse due to changing climatic conditions and intensification of human land use
12 activities. As a case in point, the Columbia bottomland hardwood forests along the Brazos-
13 Colorado Coastal Basin on the Gulf coast of Texas are currently threatened by an increasingly
14 erratic hydroclimate in the form of both extreme floods as well as droughts, and by urban
15 expansion. In this study, we use dendrochronology and tree-ring carbon isotopes to understand the
16 effect of changing hydroclimatic conditions on the functional attributes of these forests. We
17 examined tree-rings of *Quercus nigra* at four sites within the Columbia bottomlands, of which one
18 site experiences frequent and prolonged flooding, while the other three are less flood-prone. The
19 objectives of this study were to: (i) understand the impact of hydroclimatic variation on radial
20 growth using tree-ring width analysis, (ii) assess the magnitude of physiological stress inflicted by
21 extreme hydroclimatic conditions using tree-ring $\Delta^{13}\text{C}$ measurements as a proxy, and (iii) evaluate
22 the relationship between tree-ring width and $\Delta^{13}\text{C}$ values. Radial growth across the landscape was
23 influenced most strongly by mid-growing season climate, while early-growing season climate had
24 the strongest effect on $\Delta^{13}\text{C}$. Growth inhibition was minimal and tree-ring $\Delta^{13}\text{C}$ values were not
25 affected in trees at the wetter site under extreme hydrological conditions such as droughts or floods.
26 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 $\Delta^{13}\text{C}$ 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 CO₂ 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 ($\delta^{13}\text{C}$) is also
68 influenced by the changing carbon isotopic composition of atmospheric CO₂. The increase in
69 atmospheric CO₂ concentration mainly due to fossil fuel combustion has led to a significant
70 decrease in $\delta^{13}\text{C}$ of atmospheric CO₂ 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 $\delta^{13}\text{C}$ to understand plant physiological responses to local conditions.
73 Changes in carbon isotopic composition of atmospheric CO₂ can be accounted for by converting

74 tree-ring carbon isotope ratio ($\delta^{13}\text{C}$) to carbon isotope discrimination ($\Delta^{13}\text{C}$) (Farquhar, 1983).
75 Tree-ring $\delta^{13}\text{C}$ values are inversely related to $\Delta^{13}\text{C}$ values as higher discrimination results in a
76 lower $\delta^{13}\text{C}$ 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; Kozłowski, 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 $\Delta^{13}\text{C}$ values of tree-ring cellulose usually reflect stress caused by low
87 environmental moisture at the time of carbon fixation, while higher $\Delta^{13}\text{C}$ 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

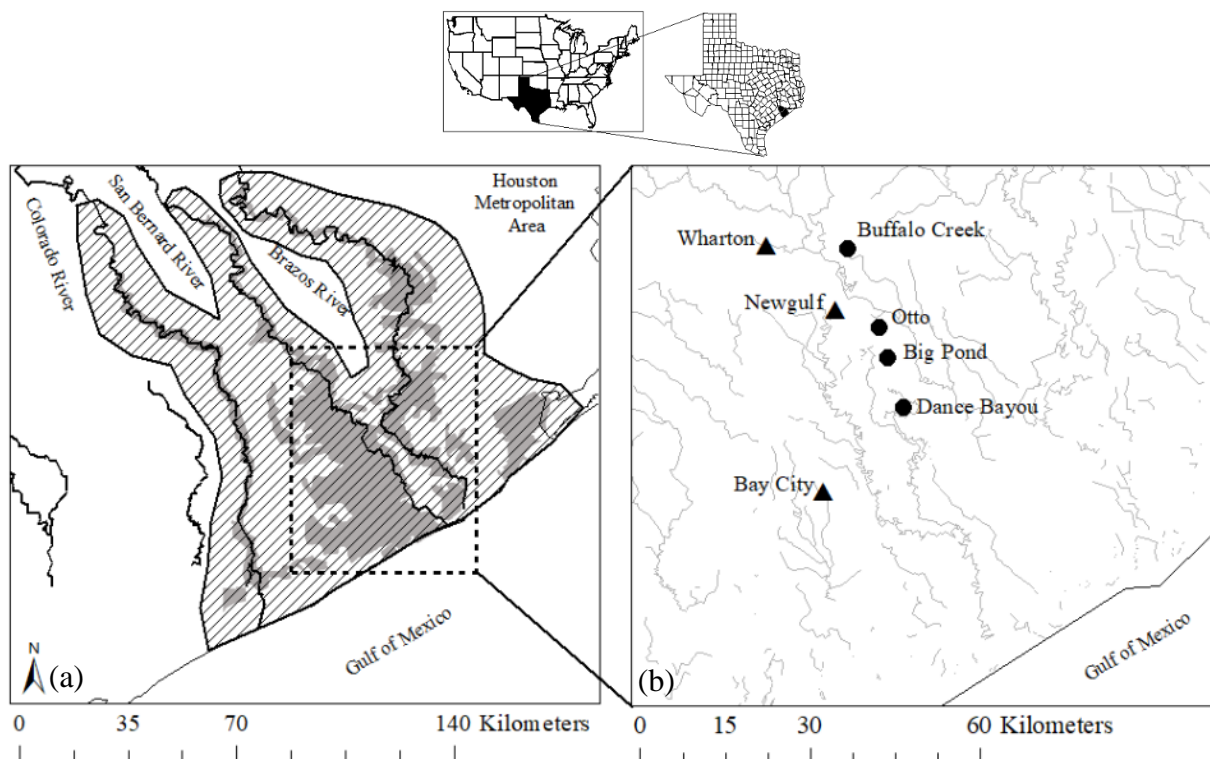
97 relationship between tree-ring carbon isotopes and precipitation to excess water stress. Although
98 debatable, a number of possible mechanisms have been suggested with significant evidence to
99 support this relationship. These include disruption of water and nutrient uptake due to anoxic
100 conditions 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 $\delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ as an indicator of physiological stress inflicted

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



133 **Figure 1. a) Current distribution of Columbia Bottomlands (grey) and historic extent**
134 **shown by the slanted parallel lines (USFWS, 1997; Houston Wilderness, 2007; Rosen et al.,**
135 **2008). The area in which the study sites are located is shown by the dashed box. b)**
136 **Locations of study sites (circles) and weather stations (triangles) in the Brazos-Colorado**
137 **Coastal Basin.**

138
139 The study was conducted at four different sites located within the Brazos-Colorado Coastal
140 Basin in the San Bernard National Wildlife Refuge, Brazoria and Fort Bend Counties, Texas. The
141 four sites are Dance Bayou (DB), Big Pond (BP), Otto (OT) and Buffalo Creek (BC) (Fig. 1B;
142 Table 1). Site DB was observed to be flooded most frequently after significant rain events from
143 2016 to 2019. This site also remained waterlogged, unlike the other three sites. Therefore, we refer
144 to this site as the “wet site”. The sites are located in Ecoregion III Western Gulf Coastal Plain and
145 Ecoregion IV Floodplain and Low Terraces, dominated by mixed bottomland hardwood forests
146 (Griffith, 2004) at an elevation of about 16 m above MSL. Dominant tree species at these sites
147 include *Quercus nigra* L. (water oak), *Quercus fusiformis* Small (live oak), *Celtis laevigata* Willd.
148 (sugarberry) and *Triadica sebifera* (L.) Small (Chinese tallow). The climate of this region is
149 classified as Humid Subtropical (Cfa) under the Köppen–Geiger climate classification system
150 (Koppen, 1900). The average maximum monthly temperature is approximately 26 °C and the
151 average minimum monthly temperature is approximately 15 °C. Mean annual rainfall is 1143 mm,
152 with an average relative humidity of ~70% (NOAA, 2018a). The sites are located in the Linnville
153 Bayou watershed of the San Bernard River Basin. As these forests are situated in the floodplain,
154 sloughs are a common occurrence and inundate significant parts of the forest. Streamflow in
155 Linnville Bayou and adjoining streams and sloughs that traverse the four sites is driven by at least
156 7 dams on the San Bernard River with heights ranging from 2.5-7.5 m (NID, 2020). Therefore, the
157 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).

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 δ¹³C analysis after cellulose extraction.

176 2.3 Dendrochronology

177 Tree cores were dried to constant weight at 60 °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.

207 **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.

215 **2.5 Tree-ring $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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). $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ was calculated in δ
 227 notation using the following equation:

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

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

232 Atmospheric $\delta^{13}\text{C}$ depletion trend over the study period was removed from the tree-ring
 233 carbon isotopic record by converting carbon isotope ratios ($\delta^{13}\text{C}$) to carbon isotope
 234 discrimination values ($\Delta^{13}\text{C}$) (Farquhar, 1983):

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

236 Average annual atmospheric $\delta^{13}\text{C}$ values from La Jolla Pier, CA, USA (Keeling and Keeling,
 237 2017) were obtained to calculate $\Delta^{13}\text{C}$ (Table 2).

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

<i>Year</i>	<i>$\delta^{13}\text{C}$</i>	<i>Year</i>	<i>$\delta^{13}\text{C}$</i>	<i>Year</i>	<i>$\delta^{13}\text{C}$</i>
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**

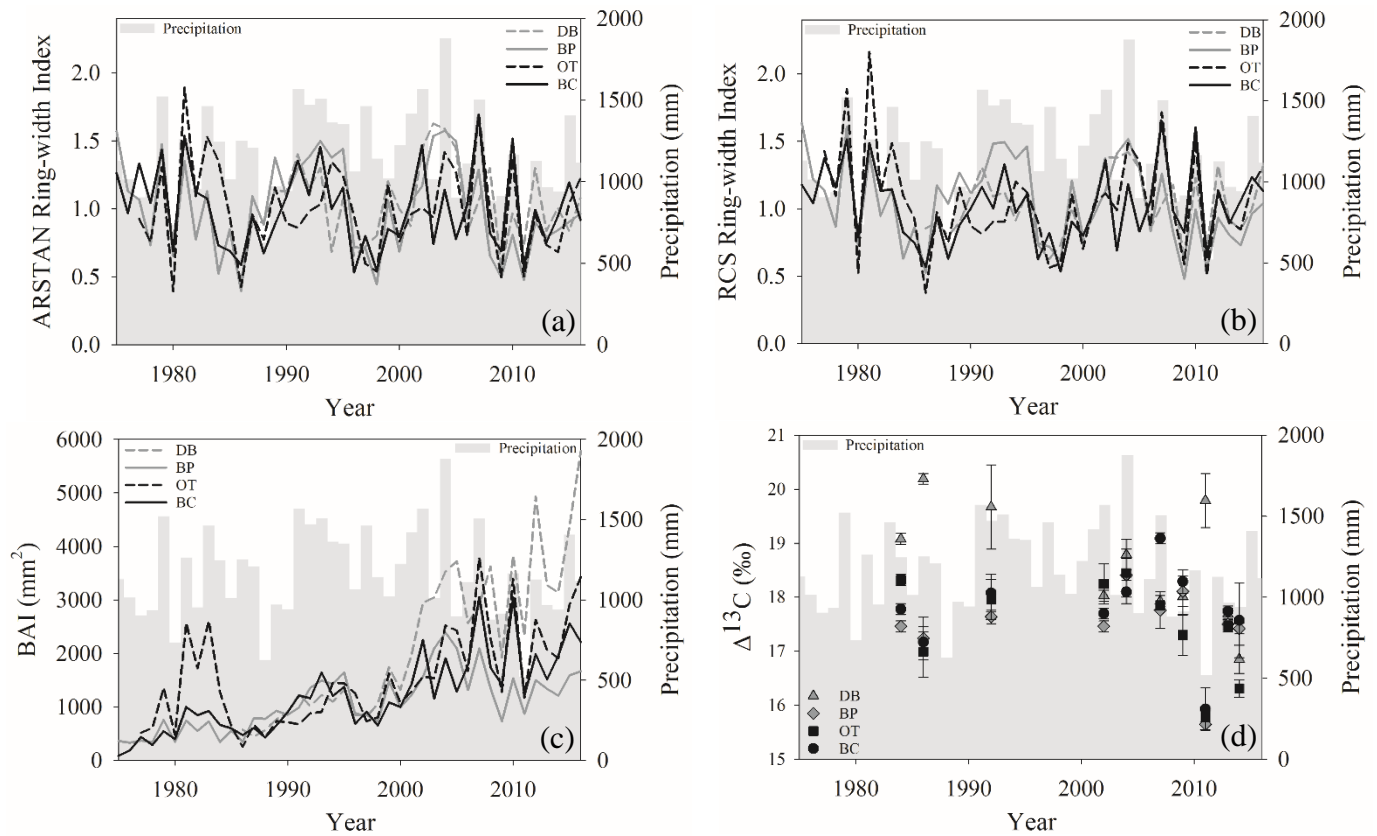
241 To evaluate differences in mean $\Delta^{13}\text{C}$ values between sites, we used one-way ANOVA.
242 Levene's test was used to check for equal variances, normality was tested using Shapiro-Wilk test
243 and post-hoc analysis was conducted using Tukey HSD. Total monthly precipitation was
244 calculated 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 $\Delta^{13}\text{C}$, we used simple linear regressions between site-wise
248 annual ring-width index and $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$, 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 $\Delta^{13}\text{C}$. The time interval during
254 which climate was found to be most strongly influencing growth and tree-ring $\Delta^{13}\text{C}$ (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 $\Delta^{13}\text{C}$. All statistical analyses were conducted in R (R Core Team, 2012).

258 3. Results

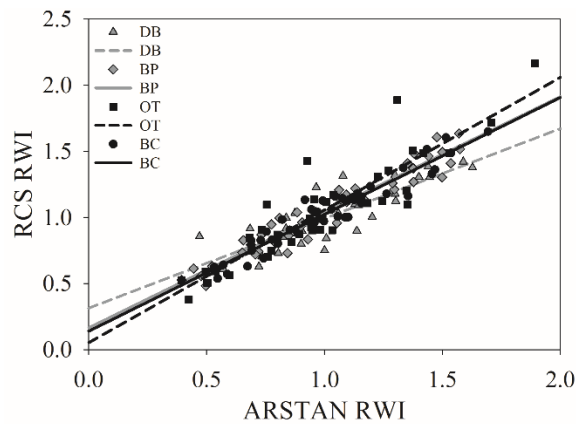
259 3.1 Site chronologies

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 $\Delta^{13}\text{C}$ 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).



279 **Figure 2.** Temporal variation in a) ARSTAN ring-width index, b) RCS ring-width index, c)
 280 basal area increments and d) tree-ring $\Delta^{13}\text{C}$ values of *Quercus nigra* in the Brazos-Colorado
 281 Coastal Basin of Texas. Total annual precipitation is shown by grey shading.



282 **Figure 3.** Relationship between site-level ring-width indices calculated using RCS detrending and
 283 using ARSTAN.

284 **Table 3.** Descriptive statistics of site-level as well as combined tree-ring chronologies generated
 285 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

286

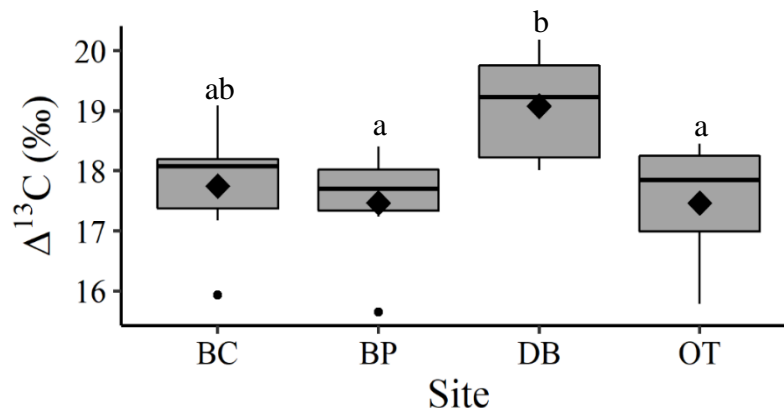
287 **Table 4.** Series intercorrelation values calculated using chronologies from individual cores and
 288 tree-level means across all sites and within each site.

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

289

290 **3.2 Differences in site-level tree-ring $\Delta^{13}\text{C}$ values**

291 Comparison between site-level mean tree-ring $\Delta^{13}\text{C}$ measurements averaged over the
 292 entire 40-year study period supports our second hypothesis. Tree-ring $\Delta^{13}\text{C}$ measurements were
 293 different between sites when averaged over the 40-year period [One-way ANOVA, $F(3, 24) =$
 294 4.05 , $p = 0.01$]. This indicates that at least one site has a significantly different mean $\Delta^{13}\text{C}$ signal
 295 over the 40-year period. Post hoc analysis indicates that the wet site, DB, had a higher mean tree-
 296 ring $\Delta^{13}\text{C}$ value as compared to two drier sites, BP ($p=0.03$) and OT ($p=0.02$) (Fig. 4).



297 **Figure 4.** One-way ANOVA and Tukey post hoc analysis (denoted with letters) for mean
298 difference in site-level tree-ring $\Delta^{13}\text{C}$ averaged over the 40-year period. Black diamonds indicate
299 mean values, horizontal black lines indicate median values, black circles indicate outliers and grey
300 boxes show values lying between the upper and lower quartiles.

301

302 **3.3 Dendroclimatology analyses**

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

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

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

324

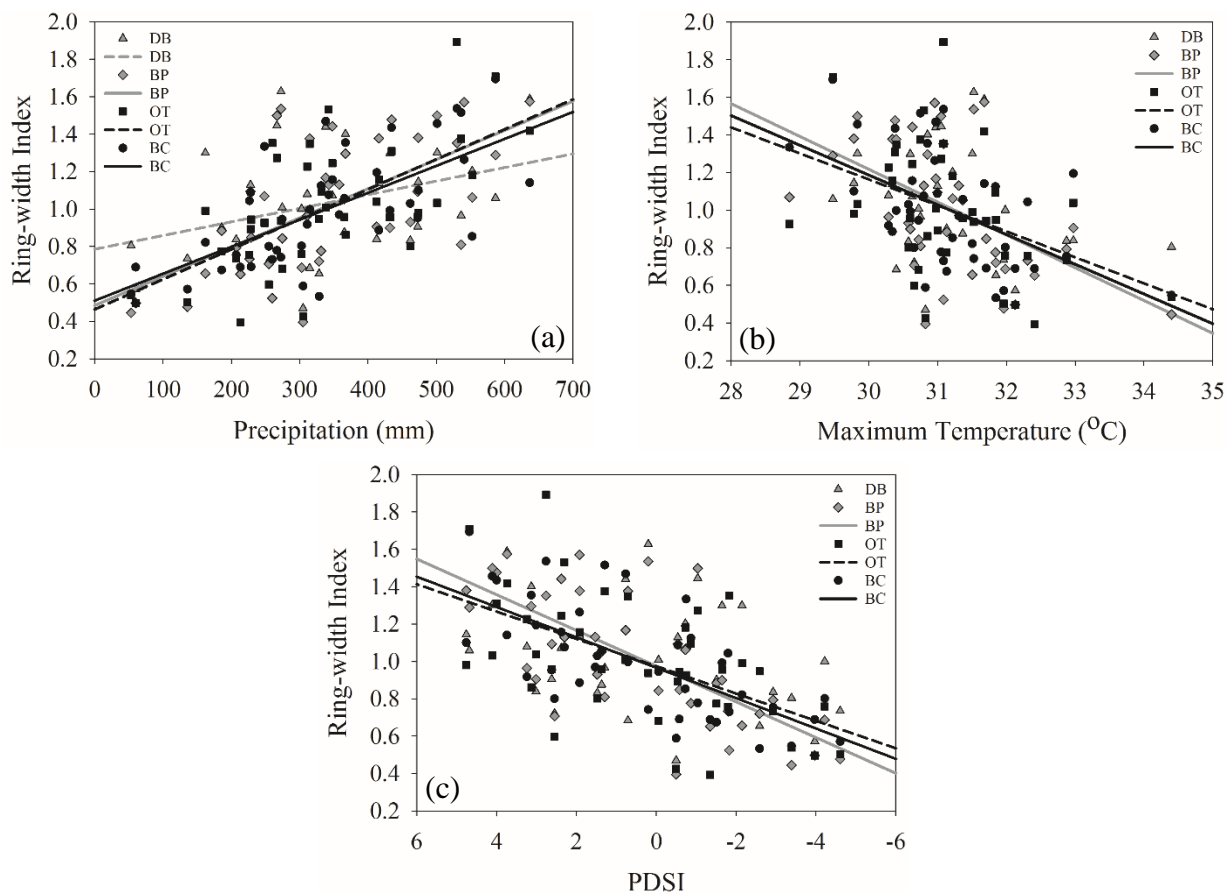
Site	Precipitation (May-July)		Temperature (May-July)		PDSI (July)	
	p value	R ²	p value	R ²	p value	R ²
DB	<0.05	0.13	ns	-	ns	-
BP	<0.001	0.39	<0.001	0.25	<0.001	0.49
OT	<0.001	0.42	<0.01	0.17	<0.001	0.31
BC	<0.001	0.44	<0.001	0.27	<0.001	0.47

325 **Table 6.** Relationships between RCS ring-width index and mid-growing season climatic
 326 conditions ($\alpha=0.05$).
 327

Site	Precipitation (May-July)		Temperature (May-July)		PDSI (July)	
	p value	R ²	p value	R ²	p value	R ²
DB	<0.05	0.19	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 ($\alpha=0.05$).
 328
 329

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	-



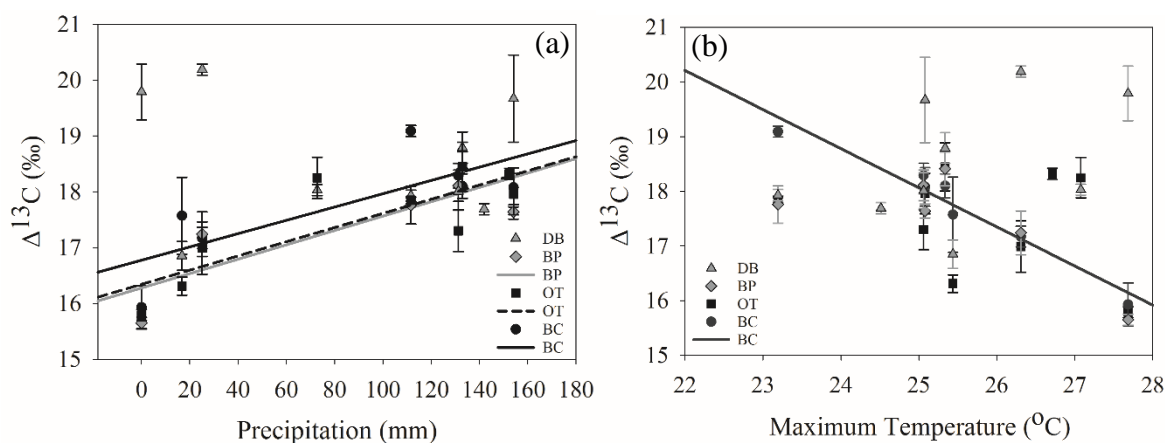
332 **Figure 5.** a) Relationship between ARSTAN ring-width index and mid-growing season
 333 precipitation (a), temperature (b) and PDSI (c). Site DB is represented by grey triangles, BP by
 334 grey diamonds, OT by black squares and BC by black circles. Regression lines are shown only for
 335 statistically significant relationships.

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

343 previous year's climate did not have any statistically significant influence on either ring-width
 344 index or tree-ring $\Delta^{13}\text{C}$ measurements at any of the four sites.

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

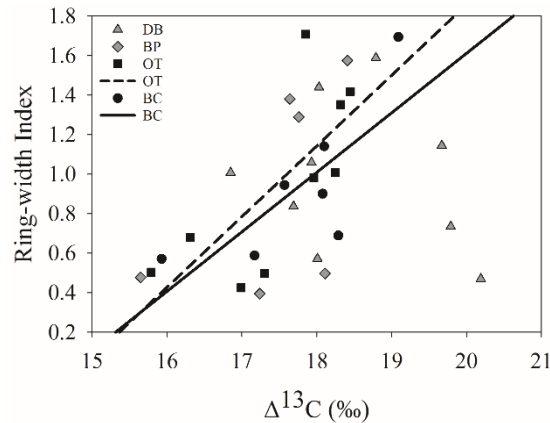
Site	Precipitation (April)		Temperature (April)		PDSI p value
	p value	R ²	p value	R ²	
DB	ns	-	ns	-	ns
BP	<0.05	0.70	ns	-	ns
OT	<0.05	0.68	ns	-	ns
BC	<0.05	0.59	<0.001	0.94	ns



347 **Figure 6.** Relationship between tree-ring $\Delta^{13}\text{C}$ values and early-growing season (a) precipitation
 348 and (b) temperature. Site DB is represented by grey triangles, BP by grey diamonds,
 349 squares and BC by black circles. Regression lines are shown only for statistically significant
 350 relationships.

351 3.4 Relationship between RWI and tree-ring $\Delta^{13}\text{C}$

352 The comparison between tree-ring $\Delta^{13}\text{C}$ values and tree-ring width indices from
 353 corresponding years supports our third hypothesis only at the drier sites. ARSTAN as well as RCS
 354 ring-width indices were correlated with $\Delta^{13}\text{C}$ values only at sites OT (ARSTAN: $p<0.05$; $R^2=0.53$;
 355 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
 356 $\Delta^{13}\text{C}$ values were not correlated with annual growth at the wet site DB, which indicates that trees
 357 at this site were able to minimize growth inhibition during stressful conditions as compared to trees
 358 at the drier sites (Fig. 7). Tree-ring $\Delta^{13}\text{C}$ values were not correlated with BAI at any of the sites.



359 **Figure 7.** Relationship between ARSTAN ring-width index and tree-ring $\Delta^{13}\text{C}$. Site DB is
 360 represented by grey triangles, BP by grey diamonds, OT by black squares and BC by black
 361 circles. Regression lines are shown only for statistically significant relationships.

362

363 4. Discussion

364 Bottomland hardwood forests in the southeastern United States have been reduced to a
 365 small proportion of their original expanse. The hydrology of these wetland forests has been altered
 366 due to land use change and river regulation (Wear and Greis, 2002; Blann et al., 2009; Dahl, 2011)
 367 and the alteration is exacerbated by hydroclimatic anomalies such as droughts and floods (Ferrati
 368 et al., 2005; Erwin, 2008). These disturbances coupled with topographic heterogeneity cause some
 369 portions of these riverine wetland forests tend to be drier than others.

370 Contrary to our first hypothesis, similar annual radial growth of trees at the wetter site and
 371 the three drier sites during the past several decades suggests that trees at all sites have access to
 372 moisture sufficient to sustain annual growth. Moreover, growth of trees at the wetter site was not
 373 inhibited by excessive moisture during wet years, which may reflect adaptation by *Quercus nigra*
 374 to the broad range of soil moisture conditions that occur in a floodplain forest (Gilman et al., 1994).
 375 Within the wetter site, we observed more heterogeneity in growth rates, which could be attributed
 376 to uneven waterlogging within the site. Although growth rates were correlated with rainfall across
 377 all sites, the wet site had a much weaker dependence on rainfall and showed no negative response
 378 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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 known are not known to be drought stressed because of ample soil moisture
393 availability. However, it is important to note that in parts of Columbia Bottomlands, depending on
394 site-level hydrologic conditions, vegetation does experience drought stress during some years
395 when dry climatic conditions persist over a longer period.

396 Our third hypothesis that tree-ring $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ and radial growth were largely decoupled.
399 Similar differences in the relationship between tree-ring $\Delta^{13}\text{C}$ and radial growth of the ring-porous
400 bur oak (*Quercus macrocarpa* M.) have been observed across continental gradients where tree-
401 ring $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ and
412 radial growth at the wet site were highly uncorrelated especially during years when growing-
413 season precipitation was more erratic (dry spring followed by a wet summer and vice versa). The
414 drought effect of drier hydroclimatic conditions is ephemeral and less intense at the wet site due
415 to slower depletion of soil water reserves. Therefore, seasonal dry spells slightly reduce tree-ring
416 $\Delta^{13}\text{C}$ but do not always result in growth inhibition in wetter parts of this landscape due to sufficient
417 moisture availability. We had expected to observe lower tree-ring $\Delta^{13}\text{C}$ values during extremely
418 wet growing seasons due to flooding stress, but the absence of these signals indicates adaptation
419 to 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 $\Delta^{13}\text{C}$ -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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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.

471 **5. Conclusion**

472 This study provides insights on hydroclimatic conditions that can provide suitable
473 conditions for better wetland forest productivity and health. Columbia bottomlands support a large
474 diversity of plants, mammals, birds, reptiles and insects. The knowledge of optimum growing
475 conditions for the vegetation in this region is critical for the survival and conservation of the
476 biodiversity that is dependent on this ecosystem. We provide evidence that hydrologically wetter
477 portions of this landscape experience less stress and subsequently lower growth inhibition in
478 response to hydroclimatic changes as compared to drier areas. Trees in drier areas grew more
479 slowly during dry and warm periods and were more sensitive to seasonal physiological stress. We
480 observed variation in growth and stress responses to climatic conditions during different phases of
481 the growing season. Our findings suggest that hydroclimatic changes to this ecosystem that alter
482 the timing and frequency of wet conditions can negatively impact forest health. This study also
483 provides the first tree-ring records from the Columbia bottomlands, which can act as a baseline for
484 future ecological research in the region.

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

487
488 *Competing interests.* The authors declare that they have no conflict of interest.

489
490 *Author contribution.* Ajinkya G. Deshpande conceptualized the study, developed the methodology,
491 collected field samples, conducted formal analysis including laboratory and statistical analysis and
492 wrote the original draft. Thomas W. Boutton contributed in conceptualization of the study,
493 provided laboratory equipment/materials for stable carbon isotope analysis and edited/reviewed
494 the original draft. Ayumi Hyodo provided laboratory protocols for cellulose extraction, provided
495 laboratory equipment/materials for stable carbon isotope analysis and analyzed the samples for
496 isotopic composition. Charles W. Lafon contributed in conceptualization of the study, provided all
497 the required equipment for dendrochronology and edited/reviewed the original draft. Georgianne
498 W. Moore was the investigator and supervisor of the study, played a major role in
499 conceptualization of the study, contributed in developing the methodology as well as statistical
500 analyses, acquired funds for the study and edited/reviewed the original draft.

501

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508

509 **References**

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