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Key Points:

- Recent weakening of the relationship between climatic water balance and radial growth and C isotopes was species specific
- Water availability is the dominant factor influencing long-term radial growth even when considering the simultaneous influence of other factors such as increasing atmospheric CO₂ and decreasing acidic deposition
- Increasing atmospheric CO₂ concentrations increased water-use efficiency but not growth of most tree species

Supporting Information:

- Supporting Information S1

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Higher CO₂ Concentrations and Lower Acidic Deposition Have Not Changed Drought Response in Tree Growth But Do Influence iWUE in Hardwood Trees in the Midwestern United States

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Abstract Several important environmental influences of tree growth and carbon sequestration have changed over the past several decades in eastern North America, specifically, more frequent pluvial conditions, increased carbon dioxide (CO₂) concentrations, and decreased acidic deposition. These factors could lead to changes in the relationship between tree growth and water availability, and perhaps even decouple the two, having large implications on how future climate change will impact forest productivity and carbon sequestration. Here, we examine the concurrent influence of the climatic water balance (precipitation minus potential evapotranspiration), CO₂ concentrations, and sulfate and nitrogen deposition on radial tree growth, carbon isotopes, and intrinsic water-use efficiency (iWUE) for several hardwood tree species in the Midwestern United States. We found that when considering the simultaneous influence of these factors, the climatic water balance is the dominant influence on annual growth. Therefore, the recent pluvial period is the primary cause of the weakening relationship between radial growth and water availability. Even during pluvial periods, water availability is the primary control on growth, with increasing CO₂ concentrations and decreased SO₄ deposition being secondary factors. Importantly, the weakening in the climate-growth relationship is species specific, with *Acer* species having stable relationships with the climatic water balance, *Liriodendron tulipifera* showing a strengthening relationship, and *Quercus* species and *Populus grandidentata* exhibiting weakening. Thus, interannual variations in soil moisture unevenly impact tree growth and carbon sequestration. Our findings suggest that, despite recent pluvial conditions, increasing CO₂ concentrations and decreasing acidic deposition have not buffered the impact of water availability on tree growth and carbon sequestration.

Plain Language Summary In recent decades, many factors that influence tree growth have changed across the Midwestern United States, including more precipitation, higher carbon dioxide concentrations in the atmosphere, and fewer pollutants. Changes in these environmental factors could result in tree growth being less sensitive to water availability. While a weakening relationship between water availability and tree growth is present, it is difficult to determine the cause. Here, we examine the simultaneous influence of a wetter climate, higher carbon dioxide concentrations, and a decrease in pollutants deposition on tree growth and how efficiently trees use water. We found that when considering all three variables, increased moisture was the leading influence on tree growth. Therefore, the recent wet period is behind trees being less sensitive to soil moisture, not increases in carbon dioxide or decreases in pollutants. It is important to note that some species such as oak and aspen did become less sensitive to soil moisture, other species such as maple and tuliptree did not. This is important because when drought conditions return to the region, trees will still be sensitive despite higher carbon dioxide concentrations or decreases in sulfate and nitrate deposition.

1. Introduction

Tree rings in mesic, temperate forests are a useful tool for estimating past climatic conditions, including water availability (Cook, 1991; Cook & Jacoby, 1977; Maxwell et al., 2011; Pederson et al., 2013; Stahle & Cleaveland, 1992). To accommodate and survive extreme hydroclimatic variability, trees alter their stomatal conductance and photosynthetic assimilation rates, resulting in changes in primary and secondary tree growth (Bréda et al., 2006) and the stable isotopic composition of annual tree rings (Belmecheri et al., 2014; Gagen et al., 2011; Levesque et al., 2019; Lévesque et al., 2014; Loader et al., 2007; Yi et al., 2019). Therefore, radial growth and stable isotopes within tree rings can provide long-term information on the influence of seasonal and interannual changes in climate and environmental conditions on forest productivity. Water availability is an important driver of forest productivity and carbon sequestration even in the mesic Midwestern United States (hereafter Midwest) and is likely to become more influential in the future due to ongoing increases in air temperature and associated increases in vapor pressure deficit (VPD) and potential evapotranspiration (Allen et al., 2015; Choat et al., 2012; Choat et al., 2018; Clark et al., 2016; McDowell & Allen, 2015; Novick et al., 2016). In the Midwestern United States, radial growth from multiple species has been shown to be responsive to water availability (Maxwell, 2016; Maxwell et al., 2015). However, the last several decades have been the wettest in recorded history in the Midwest (Andersen et al., 2012; Karl et al., 1996; Mishra et al., 2010) and potentially the wettest in the last several centuries (Ford, 2014; Maxwell & Harley, 2017; McEwan et al., 2011). The recent pluvial period could be causing tree growth across the Midwest to appear less sensitive to soil moisture (Maxwell et al., 2016).

However, many other factors that influence tree growth have changed over the last several decades in the Midwest, making the attribution of a weakening relationship difficult. Pollution such as acidic deposition can negatively influence tree growth and the ability of trees to tolerate climatic stress (Cook et al., 1987; Johnson et al., 1988; LeBlanc et al., 1987). Acidic deposition has decreased in recent decades in the Midwest and this could have resulted in an increase in tree growth (Engel et al., 2016; Kosiba et al., 2018; Mathias & Thomas, 2018; Thomas et al., 2013), although other studies have shown little to no impact on growth (Bishop et al., 2015; Schaberg et al., 2014). Further, nitrogen deposition can act as a fertilizer to increase carbon storage of trees (Horn et al., 2018; Thomas et al., 2010). However, the ability of nitrogen deposition to increase growth appears modest (Caspersen et al., 2000; Hyvönen et al., 2008; Ollinger et al., 2002; Walker et al., 2019). Increasing atmospheric CO₂ concentrations may also increase tree growth (Ainsworth & Long, 2005; Graumlich, 1991; Soulé & Knapp, 2006), however, the relationship is not spatially uniform (Peñuelas et al., 2011) and complexities arise when multiple factors interact to influence growth (McCarthy et al., 2010; Norby & Zak, 2011; Zhu et al., 2016). When examining the simultaneous impacts of climate variability, CO₂ concentrations, and pollutants, Levesque et al. (2017) found the primary driver of tree growth at one site in the Northeast United States to be water availability. However, it is unclear if water availability is driving the documented weakening relationship between tree rings and soil moisture in the Midwest (Maxwell et al., 2016).

Moreover, the response of trees to these multiple drivers may vary from one species to the next. It is increasingly clear that key species growing in eastern United States forests adopt different approaches to respond to drought. For example, oaks (*Quercus*)—a keystone ecological species—tend to adopt an “anisohydric” drought response strategy that is characterized by relatively high rates of stomatal conductance and photosynthesis, at the expense of excessive water loss and potential damage to the tree's hydraulic system (Meinzer et al., 2013; Thomas et al., 2013; Brzostek et al., 2014; Roman et al., 2015). On the other hand, more “isohydric” species such as tulip poplar (*Liriodendron tulipifera*) close stomates quickly during drought stress, thereby limiting carbon uptake (Yi et al., 2019). However, we still have much to learn about how these leaf-level strategies translate into long-term growth responses (Kannenberg et al., 2019) and know very little about the interactions between drought response strategies and variation in atmospheric CO₂ or nitrogen deposition.

The recent pluvial period has been identified as a potential cause of the weakening relationship between tree rings and soil moisture (Maxwell et al., 2016). However, changes in CO₂ concentrations and nitrogen and sulfate deposition in recent decades could also independently enhance tree growth. In this paper, we examine the concurrent impacts of changes in moisture availability, CO₂ concentrations, and nitrogen and sulfate

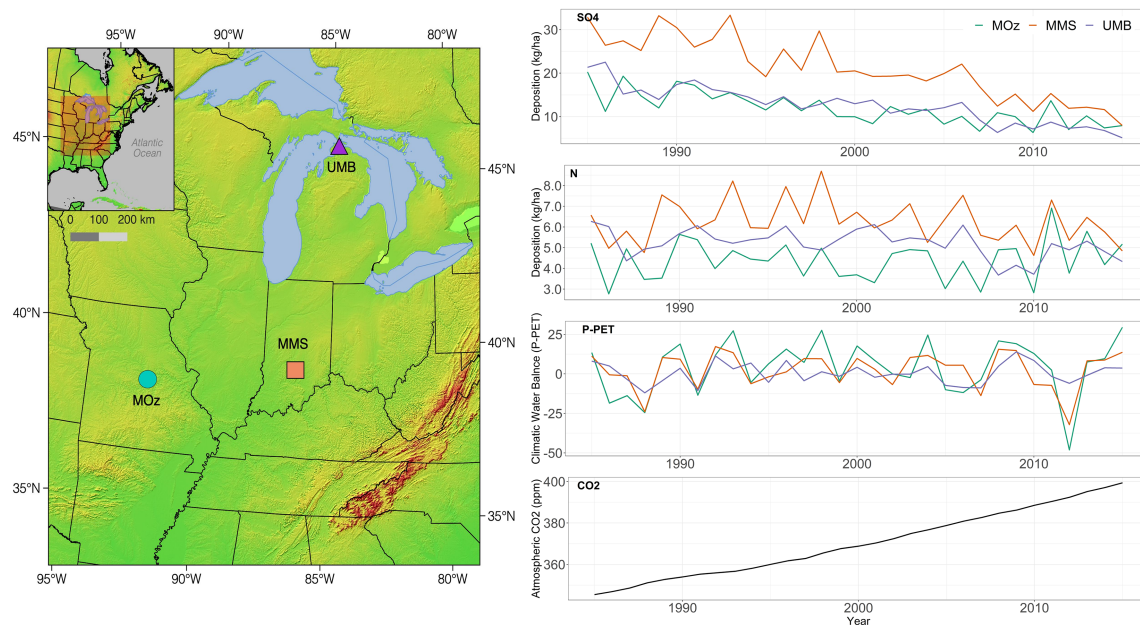


Figure 1. Map of study site location (left), where stars represent sites. For each site, a time series of sulfate (SO₄) deposition (top right), nitrogen (N) deposition (second right), climatic water balance (P-PET) (third right) is shown, along with the global average CO₂ concentrations (bottom right).

deposition on tree growth and stable carbon isotopic composition across three sites in the Midwest. We target important canopy-dominant species across the Midwest to test the hypothesis that water availability is the driving factor influencing radial growth when considering the simultaneous influence of other variables. We also test a secondary hypothesis: Trees that employ a more conservative isohydric water-use strategy will be more sensitive to water availability than those that use a more anisohydric strategy.

2. Data and Methods

2.1. Study Sites

We studied a variety of broadleaf tree species at three sites across the central hardwood region in the Midwest (Figure 1, left). Each site exists as a secondary to tertiary forest (i.e., forests that have regrown after timber harvest) and includes an Ameriflux tower: the Missouri Ozark Site (US-MOz), the Morgan-Monroe State Forest (US-MMS), and the University of Michigan Biological Station (US-UMB). Many tree species occur at each site, but we focused our sampling efforts to the two to three most common species with the criteria of having a relatively anisohydric species (i.e., *Quercus* species) and more isohydric codominants (i.e., *Acer* species, *Liriodendron tulipifera*). We sampled *Acer saccharum* and *Quercus alba* at MOz; *A. saccharum*, *Q. alba*, and *Liriodendron tulipifera* at MMS; and *A. rubrum*, *Q. rubra*, and *Populus grandidentata* at UMB. Generally, there was a gradient of drought occurrence across the sites. MOz experienced the most severe drought conditions, MMS experienced intermediate drought, and UMB was absent of recent drought, while all sites experienced similar CO₂ concentrations and nitrogen and sulfate deposition (Figure 1).

2.2. Dendrochronological Analyses

At each study site, we extracted cores from 5–15 trees of each species using a 4.3 mm diameter handheld increment borer. We targeted healthy canopy-dominant trees within each Ameriflux tower footprint and extracted two cores on opposite sides, parallel to the slope to help reduce the effect of asymmetric growth. Although sampling biases from only selecting canopy-dominant trees can arise, these are typically minimized when examining growth responses to environmental variability (Nehrbass-Ahles et al., 2014). Tree cores were air dried, glued to wooden mounts, and sanded using progressively finer sandpaper until the ring structure was visible under 10X magnification. For each species, we visually crossdated the growth rings from each sample core using the list method (Yamaguchi, 1991). We then statistically confirmed the

Table 1
Summary of Tree Characteristics and Crossdating Statistics

Site name	Species	n of trees (cores)		Mean age	Interseries correlation
		Ring width	Isotopes		
Missouri Ozarks (MOz)	<i>A. saccharum</i>	8(15)	4	102	0.50
	<i>Q. alba</i>	10(20)	4	92	0.68
Morgan-Monroe State Forest (MMS)	<i>A. saccharum</i>	9(17)	4	87	0.49
	<i>Q. alba</i>	12(21)	4	69	0.58
	<i>L. tulipifera</i>	10(20)	4	65	0.62
University of Michigan Biological Station (UMB)	<i>A. rubrum</i>	5(9)	4	81	0.64
	<i>Q. rubra</i>	5(9)	4	88	0.56
	<i>P. grandidentata</i>	6(10)	4	71	0.45

visual crossdating using the program COFECHA (Holmes, 1983), which calculates correlation coefficients of ring widths between a given sample and the remaining samples from different trees. To remove the age-related growth trend and the nonclimatic growth related to forest dynamics, we used a two thirds length spline with a frequency cutoff point of 50% (Cook, 1981) using the “dplR” package (Bunn, 2008) in R (R Core Team, 2017). We used the standardized chronology as it has been shown to retain the strongest climate signal in the Midwest, including this study region (Cook, 1985; Maxwell et al., 2015).

To ensure that the variance in growth is not influenced by sample size, we restricted the analysis of tree rings to the period where at least five trees (10 sample cores) are represented. To determine to what degree this standardization procedure could impact results, we also converted ring width to basal area increment (BAI) and removed only age-related trends using a Regional Curve Standardization approach (Peters et al., 2015). For each species, we calculated the regional curve, which is the average ontogenetic growth curve, by assigning the raw BAI measurements of each tree to the appropriate biological age. Each individual raw BAI series was then divided by the average regional curve to get the Regional Curve Standardization residual BAI series and then averaged across samples to get the standardized BAI chronology for each species (Briffa et al., 1992; Cook & Briffa, 1990).

2.3. Isotopic Analyses

We used tree ring $\delta^{13}\text{C}$ to calculate the carbon isotope discrimination ($\Delta^{13}\text{C}$) from the latewood of each annual ring from 1970–2015. We used only the latewood portion of the annual tree ring because this portion is more responsive to environmental factors (Battipaglia et al., 2009; Belmecheri et al., 2014; Lipp et al., 1991; Livingston & Spittlehouse, 1996). For the species with ring porous wood type (e.g., *Q. alba*), we sliced the latewood portion of the growth ring from each year (e.g., post vessel element rows) and for the diffuse porous species, we sliced the last third of the growth ring due to the lack of a distinction between earlywood and latewood (cf. Levesque et al., 2017; Levesque et al., 2019; Yi et al., 2019). We combined the latewood samples from the two radial cores for each tree for $\delta^{13}\text{C}$ analysis. For each tree ($n = 4$; Table 1), α -cellulose was extracted using a modified Soxhlet method (Loader et al., 1997). Using an elemental analyzer (ECS4010; Costech, Valencia, CA, USA) coupled to an isotope-ratio mass spectrometer (Finnigan DELTAplusXP; ThermoFisher Scientific, Waltham, MA, USA), we measured the isotopic signature of the CO_2 produced by α -cellulose composition to obtain $\delta^{13}\text{C}$ from 1970–2015.

During photosynthesis, ^{12}C atoms are used preferentially over ^{13}C atoms and therefore calculating carbon isotope discrimination ($\Delta^{13}\text{C}$) from tree rings allows us to look at the impacts of changes in photosynthetic carbon fixation over time. $\Delta^{13}\text{C}$ is calculated by taking the difference between the $\delta^{13}\text{C}$ of the air ($\delta^{13}\text{C}_{\text{air}}$) and $\delta^{13}\text{C}$ in tree ring ($\delta^{13}\text{C}_{\text{tree}}$). We obtain $\Delta^{13}\text{C}$ with the following equation:

$$\Delta^{13}\text{C} = \frac{(\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{tree}})}{\left(1 + \frac{\delta^{13}\text{C}_{\text{tree}}}{1000}\right)} \quad (1)$$

where $\delta^{13}\text{C}_{\text{air}}$ is the atmospheric $\delta^{13}\text{C}$ obtained from the Mauna Loa observatory (Keeling et al., 2005) and $\delta^{13}\text{C}_{\text{tree}}$ is the $\delta^{13}\text{C}$ from the α -cellulose tree ring samples. We estimated intercellular CO_2 concentration (c_i) by inverting the Farquhar et al. (1982) model of $\Delta^{13}\text{C}$ in C_3 plants:

$$\Delta^{13}\text{C} = a + (b-a) \frac{c_i}{c_a} \quad (2)$$

where a is a constant of 4.4‰ for the fractionation during CO₂ diffusion through the stomata (O'Leary 1981), b is a constant of 27‰ for the fractionation by ribulose 1,5-biphosphate carboxylase (Farquhar & Richards, 1984), and c_a are the ambient CO₂ concentrations. The intercellular CO₂ concentration was then used to calculate intrinsic water-use efficiency (iWUE), which is the ratio of net photosynthesis and conductance to water vapor:

$$iWUE = \frac{A}{g_s} = \frac{(c_a - c_i)}{1.6} \quad (3)$$

where A is the rate of CO₂ assimilation and g_s is the rate of leaf stomatal conductance to water. As the ratio of photosynthesis to stomatal conductance, intrinsic water-use efficiency is a useful indicator of how drought-driven declines in stomatal function (e.g., due to declining soil moisture) ultimately impact carbon uptake. Because the relationship between photosynthesis and conductance is nonlinear and tends to plateau when conductance is high, reduction to conductance (i.e., from unfavorable climatic water balance) should promote increases in iWUE while photosynthetic capacity itself is unaltered (Yi et al., 2019). At the same time, increase in photosynthesis that is not accompanied by reduction in stomatal conductance will also increase iWUE (Guerrieri et al., 2019). We show time series of the raw tree ring and isotopic data in supporting information Figure S1.

2.4. Climate and Deposition Data

We gathered mean monthly minimum and maximum temperature (Tmin and Tmax), maximum VPD, and total monthly precipitation (P) for the period 1895–2015. For each site, data for the nearest 4 × 4 km grid point from the PRISM data sets were used (<http://prism.orgonstate.edu>). Using the PRISM monthly mean minimum and maximum temperatures, we calculated potential evapotranspiration (PET) according to the Hargreaves formula (Hargreaves, 1994) using the “SPEI” package in R (Begueria et al., 2014; Vicente-Serrano et al., 2010). We then represented the climatic water balance as the difference between monthly precipitation and monthly potential evapotranspiration (i.e., P-PET). We gathered values of annual global average CO₂ concentrations ([www.columbia.edu/~mhs119/GHGs/](http://www.columbia.edu/~mhs119/GHG/)), and the water year (previous October to current September) total wet deposition of SO₄ and inorganic N from the National Atmospheric Deposition Program (Schwede & Lear, 2014) for the three 12 × 12 km grid points closest to our tree ring sampling sites.

2.5. Statistical Analyses

To examine the seasonal responses of the standardized growth metrics (i.e., standardized tree ring width and standardized BAI) and the isotopic metrics ($\Delta^{13}\text{C}$ and iWUE) to the monthly climate variables, we used Pearson's correlation analysis with bootstrapped estimates of significance using the R package “treeclim” (Zang & Biondi, 2015) for the common period between the climate data and the standardized growth and isotopic metrics (i.e., 1970–2015). The months of June, July, and August had the strongest correlations with the standardized growth and isotopic metrics and we, therefore, created a seasonal average over these months (hereafter: JJA). To examine potential differences in early and late portions of the growing season, we also created averages for May–June (MJ) and August–September (AS). All standardized growth and isotopic metrics and climate variables were prewhitened to remove the first-order autocorrelation before the correlation analysis. To determine if these species show a weakening relationship with water availability, we conducted a 40-year moving window correlation analysis between the standardized tree ring widths and BAI and the JJA P-PET for the period of overlap between the growth metrics and the climate data. Because all trees sampled were younger than the full length of the instrumental record, the common period was limited by the growth metrics and determined by only using growth data for the period were at least five trees were represented. However, using the longer growth metrics allows the assessment of a longer period due to the limited record of isotopic data.

Interpretation of moving correlation analysis can vary depending on the window size. Therefore, to evaluate the robustness of a potential change in the response of climate variability, we also used a state-space model with time varying parameter regression (Durbin and Koopman, 2001) and the Kalman filter (Kalman, 1960) to examine the time dependence of the relationship between tree growth and JJA P-PET using the R package

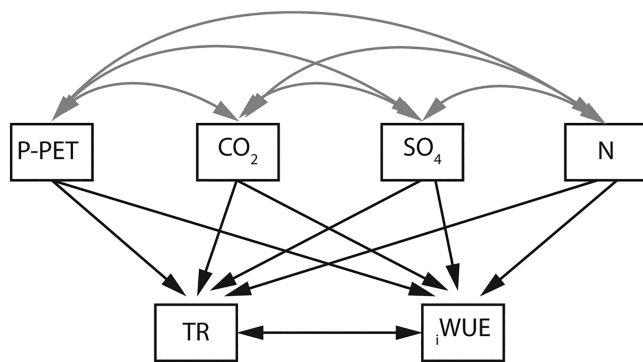


Figure 2. Hypothetical example of the structural equation model used to simultaneously assess the influence of climatic water balance, atmospheric CO₂ concentrations, SO₄ and N wet deposition on tree growth (standardized tree rings and basal area increment), and gas exchange inferred by $\Delta^{13}\text{C}$ and intrinsic water-use efficiency from tree rings. Double-headed black lines represent covariance relationship between response variables, and single-headed black lines indicate a causal relationship. Gray double-headed lines represent covariance between explanatory variables.

isotopic measurements (Figure 2). Because we have two growth metrics (tree ring width and BAI) and two isotopic metrics ($\Delta^{13}\text{C}$ and $i\text{WUE}$), we created piecewise SEMs for all possible combinations of the four metrics to determine if the results were sensitive to the metrics that were used. In any given SEM, we had one growth and one isotopic metric, resulting in a total of 32 models (four combinations of paired responses over eight species models). We used a linear mixed effects model (Zurr et al., 2009) to assess both the fixed effects (P-PET, CO₂, SO₄, and N) and random effects (individual trees) for each species at each site using the function *lme* in the “nlme” package (Pinheiro, 2013). All SEMs were fit for the period of overlap between all variables of 1985–2015. We used Fisher’s C statistic and Akaike’s information criterion (AIC) to assess model fit.

We also included Tmax as a variable in the SEMs to see if the inclusion would increase variance explained in the SEMs. We found that some of the models included Tmax as a possible explanatory variable, but in every one of these models Tmax replaced P-PET (i.e., T and P-PET were never both included in the same model). In the models that retained Tmax, we compared the AIC and R^2 of the two models and found that the AIC and R^2 indicated that the model with P-PET was a better fit. Thus, the Tmax response is more closely linked to increasing water demand and therefore we only included P-PET.

3. Results

3.1. Climate Analyses

All eight species chronologies statistically crossdated and produced interseries correlation values of 0.45–0.65, indicating that radial growth from individual trees for each species is responding similarly to environmental variability (Table 1). The months JJA had the highest correlation values with both the growth and isotopic metrics (Figure 3 and supporting information Figures S2–S10). However, the exception is with maximum temperatures, where the isotopic metrics had higher correlations in the earlier and later growing season (i.e., MJ and AS) compared to JJA (Figure 3). Generally, the early portion of the growing season (MJ) was more important to both growth and isotopic metrics than the later portion (AS), with the exceptions of maximum temperature and VPD. Interestingly, P and P-PET had stronger correlations with the growth metrics, while Tmax and VPD had a stronger influence on the isotopic metrics (Figure 3), potentially reflecting the importance of atmospheric water demand on stomatal conductance.

To evaluate the influence of water balance on both growth and isotopic metrics, we calculated the JJA average of the climatic water balance (P-PET). Moving correlations between the growth metrics and JJA P-PET suggested that the strength of the relationship between growth and climatic water balance for most species had become weaker with time (Figure 4). In contrast, *A. saccharum* at MOZ had a consistent correlation through time as did *Q. alba* at MMS, albeit weak, while *L. tulipifera* at MMS had an increasing correlation through time (Figure 4). In addition to general patterns in the correlations, the differences in correlation

“dlm” (Petris, 2010). The time varying method with the Kalman filter has been successfully used to examine the temporal variability of climate-growth relationships of tree rings (Bishop et al., 2015; Cook & Johnson, 1989; Visser et al., 2010). The Kalman filter relaxes the least squares assumption that assumes that growth rate is consistently determined by the most limiting factor, allowing the detection of changes in the responses of radial growth to a particular climate variable. We applied the Kalman filter to the standardized tree ring widths and BAI chronologies and JJA P-PET for the overlapping period between growth and climate data. We found nearly identical results and therefore present only those for the tree ring widths.

To determine how simultaneous changes in P-PET, CO₂ concentration, and SO₄ and N deposition could be interacting to influence tree growth or isotopic composition, we performed piecewise structural equation modeling (SEM) using the R package “piecewiseSEM” (Lefcheck, 2016). Piecewise SEMs are ideal for small sample sizes. For each species at each site, we developed a piecewise SEM model (i.e., eight models) in order to assess the combined impacts of changing P-PET, atmospheric CO₂ concentrations, and SO₄ and N deposition on the standardized growth and

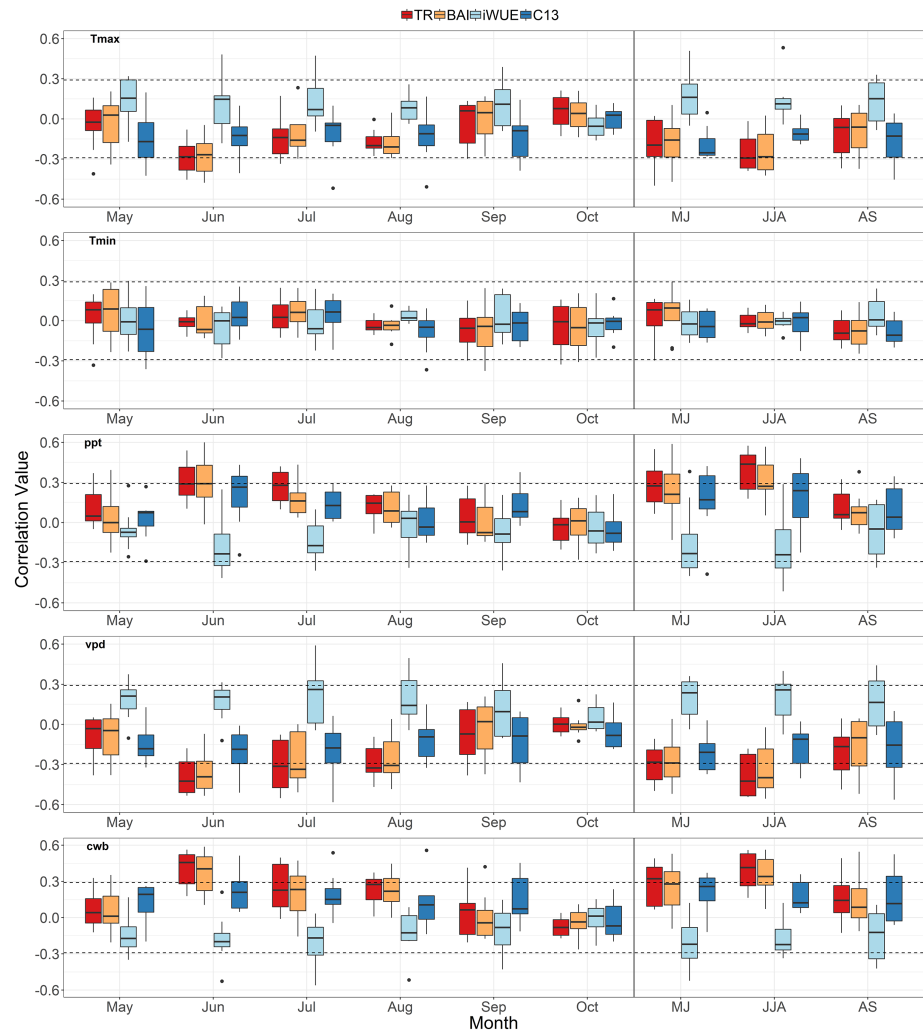


Figure 3. Boxplots of the correlation values of standardized tree rings (red), standardized basal area increment (orange), intrinsic water-use efficiency (light blue), and stable carbon isotopes (blue) pooled across study sites with climate variables for all eight species for current year May to October and the seasonal averages of May–June (MJ); June, July, and August (JJA); and August–September (AS).

values varies across sites and species. Generally, the *Acer* genus had less variance with the exception of MMS ACSA (*Acer saccharum*) (Table 2). The Kalman filter approach confirmed the overall declining relationships found in the moving correlation analysis, with the only difference being *A. rubrum* at UMB displayed a significant and stable relationship over the entire common period (Figure 5).

When examining the moving correlations between the growth metrics and P-PET for the early (MJ) and late (AS) portions of the growing season, we found that most species were temporally stable in the early portion but species at MMS had larger variances (Figure 6). Moving correlations of the later season showed both site- and species-specific differences. Correlation values increased through time for both species at MOz, while all other species at UMB and MMS decreased, with the exception of MMS LITU (Figure 6).

3.2. SEM

When examining the potential factors influencing growth simultaneously in the piecewise SEMs, we found that P-PET was the dominant influence (i.e., it had the highest standardized coefficients) of both metrics of growth for the majority of species at MOz and MMS, except for MOz *Q. alba*, where CO₂ was slightly stronger than P-PET (Figure 7 and supporting information Figures S10–S12). The SEMs generally explained between 15% to 50% of variance for the species at MOz and MMS with *L. tulipifera* being the most sensitive. In that

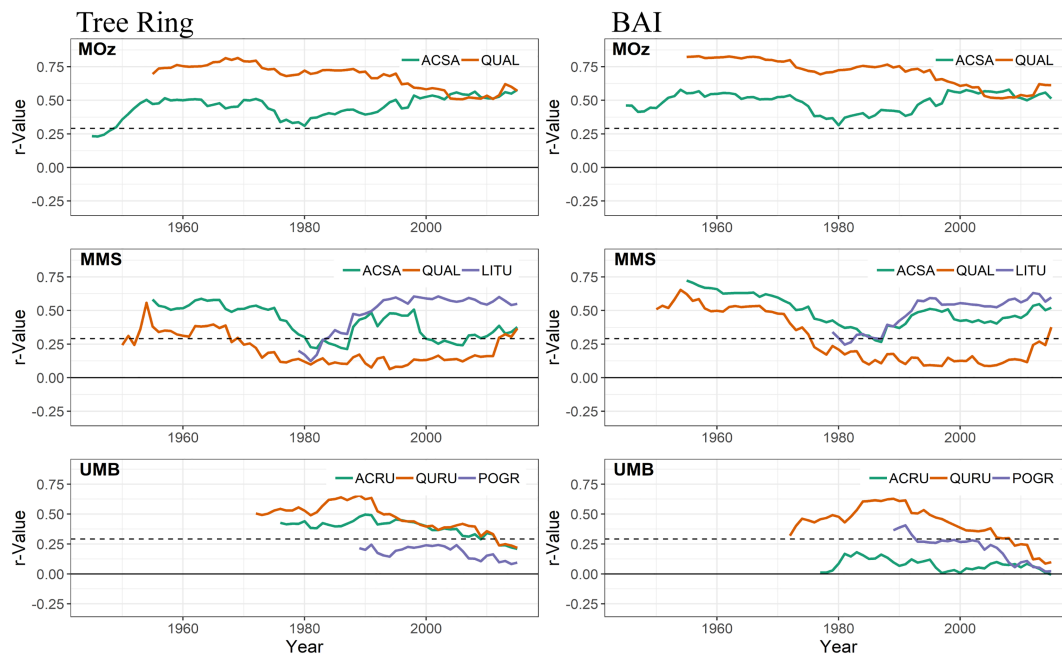


Figure 4. Moving correlations of JJA P-PET with standardized tree rings (left column) and standardized basal area increment (right column). Correlations were done in 40-year moving windows with the year on the x axis representing the last year of the interval. The length of the time series was determined by the expressed population signal values of >0.85. ACSA = *Acer saccharum*; QUAL = *Quercus alba*; LITU = *Liriodendron tulipifera*; ACRU = *Acer rubrum*; QURU = *Quercus rubra*; POGR = *Populus grandidentata*.

case, SEMs explained >30–60% of the variance (Figure 7). However, for UMB, all the variables had a weak influence on growth with SEMs explaining <20% of the variance, with the exception of POGR BAI. Further, only one species at UMB (*P. grandidentata*) had a P-PET as a variable that significantly influenced any of the growth metrics, while SO₄ and CO₂ were significant variables for *P. grandidentata* and *Q. rubra*, respectively, and CO₂ was significantly related to tree ring width for *A. rubrum* (Figure 7 and supporting information Figures S10–S12). In general, climatic water balance, CO₂, and SO₄ were the most consistent variables retained in the SEMs in UMB although the variance explained was generally low. The variables influencing iWUE were not consistent across species except CO₂ concentration, which was present in the majority of the SEMs (Figure 7 and supporting information Figures S10–S12). Moreover,

Table 2
Summary of the Range of Correlation Values From the Moving Correlation Analysis

Species	Metric	Maximum correlation	Minimum correlation	Difference (Max – Min)
MOz <i>A. saccharum</i>	BAI	0.58	0.32	0.26
	Tree Ring	0.58	0.23	0.35
MOz <i>Q. alba</i>	BAI	0.83	0.41	0.42
	Tree Ring	0.82	0.23	0.59
MMS <i>A. saccharum</i>	BAI	0.72	0.24	0.48
	Tree Ring	0.59	0.21	0.38
MMS <i>Q. alba</i>	BAI	0.65	0.09	0.56
	Tree Ring	0.63	0.06	0.57
MMS <i>L. tulipifera</i>	BAI	0.63	0.25	0.38
	Tree Ring	0.61	0.12	0.49
UMB <i>A. rubrum</i>	BAI	0.18	–0.006	0.18
	Tree Ring	0.49	0.21	0.28
UMB <i>Q. rubra</i>	BAI	0.63	0.09	0.54
	Tree Ring	0.66	0.22	0.44
UMB <i>P. grandidentata</i>	BAI	0.51	0.02	0.49
	Tree Ring	0.24	0.08	0.16

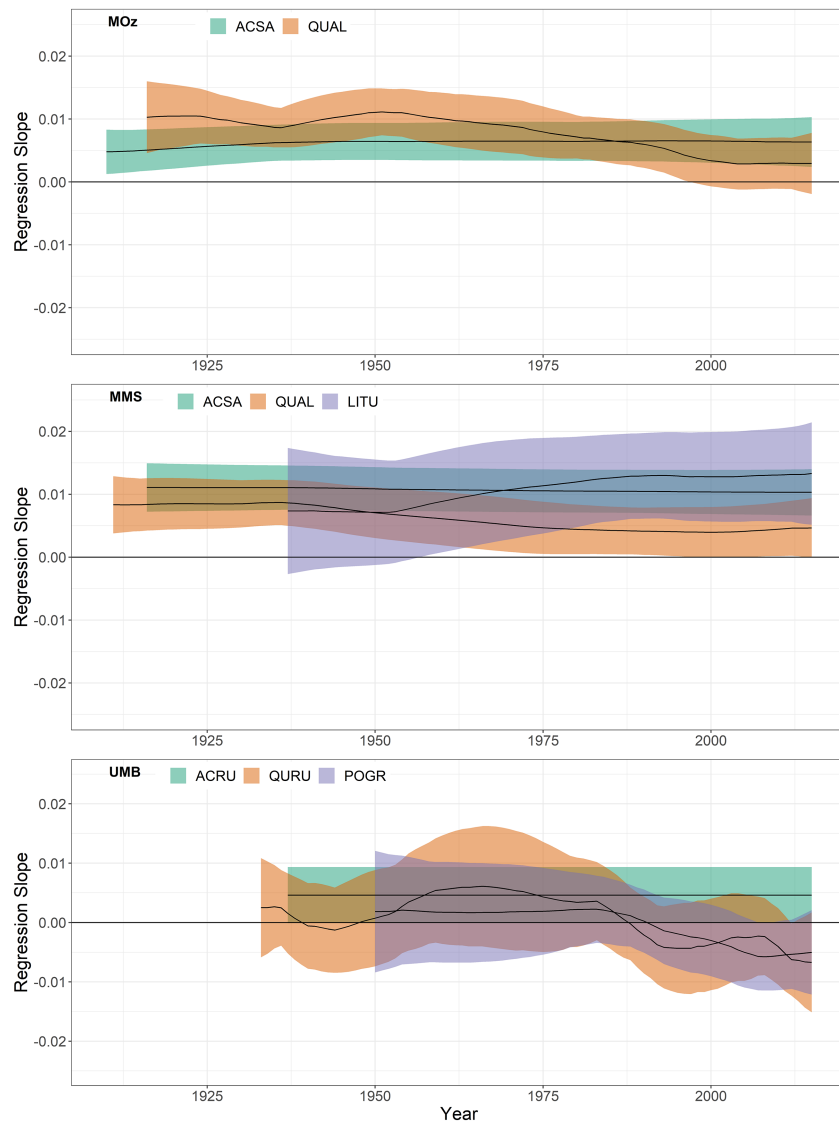


Figure 5. Time-varying parameter regression slope estimates (black line) of the relationship between standardized tree growth and June, July, and August climatic water balance (P-PET), colored shading representing the 95% confidence interval. ACSA = *Acer saccharum*; QUAL = *Quercus alba*; LITU = *Liriodendron tulipifera*; ACRU = *Acer rubrum*; QURU = *Quercus rubra*; POGR = *Populus grandidentata*.

the influences among the variables was not consistent across the isotopic metrics ($\Delta^{13}\text{C}$ and $i\text{WUE}$) within a given species. Climatic water balance was a significant predictor in three species SEMs, having a very strong influence on *L. tulipifera* $\Delta^{13}\text{C}$ and $i\text{WUE}$ at MMS and influencing *P. grandidentata* and *Q. rubra* $\Delta^{13}\text{C}$ at UMB (Figure 7 and supporting information Figures S10–S12). Both variables for pollution had limited influence on the isotopic metrics, with SO_4 and N deposition only impacting *A. rubrum* at UMB and *A. saccharum* at MOz, respectively (Figure 7 and supporting information Figures S10–S12). However, the inclusion of SO_4 improved model fit for another four species SEMs and N deposition improved three species SEMs (supporting information Figures S10–S12).

4. Discussion

4.1. Temporal Changes in Climate

While tree growth in the mesic eastern and Midwestern United States is sensitive to drought (Cook & Jacoby, 1977; Graumlich, 1993; Pederson et al., 2012, 2013; Rollinson et al., 2016; D’Orangeville et al., 2018; Canham

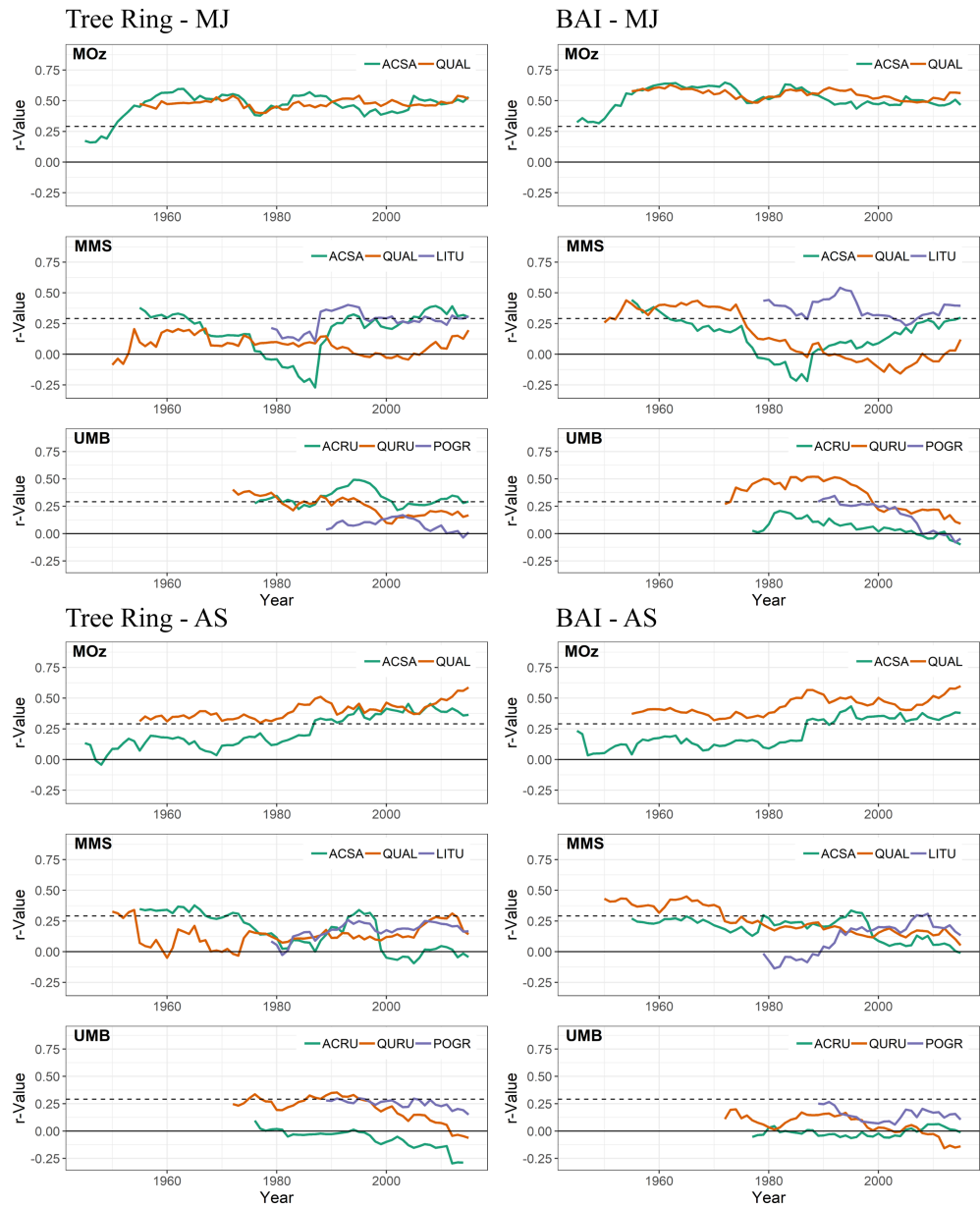


Figure 6. Time series of moving correlations of the early portion (May–June [MJ]; top six panels) and the later portion (August–September [AS]; bottom six panels) of the growing season P-PET with standardized tree rings (left column) and standardized basal area increment (right column). Correlations were done in 40-year moving windows with the year on the x axis representing the last year of the interval. ACSA = *Acer saccharum*; QUAL = *Quercus alba*; LITU = *Liriodendron tulipifera*; ACRU = *Acer rubrum*; QURU = *Quercus rubra*; POGR = *Populus grandidentata*.

et al., 2019), recent work showed a weakening relationship between radial growth and soil moisture starting in the early 1980s across sites and species in the Midwest (Maxwell et al., 2016). Our findings supported the recent weakening in response to water availability, with all *Quercus* species and *P. grandidentata* exhibiting a weakening relationship (Figures 4 and 5). However, by adding species not included in Maxwell et al. (2016) and by examining younger trees, we found that both *A. saccharum* and *A. rubrum* had stable relationships across our study region and *L. tulipifera* had become more sensitive to water availability (Figures 4 and 5). These results were well aligned with the relative degree of isohydricity of these species (i.e., *Quercus* are more anisohydric and *L. tulipifera* is very isohydric). Our findings suggested that all trees are sensitive to water availability when very dry conditions are included in the analysis. Even the anisohydric *Quercus* species responded to variations in P-PET when the drier 1950s were included. However, during periods where

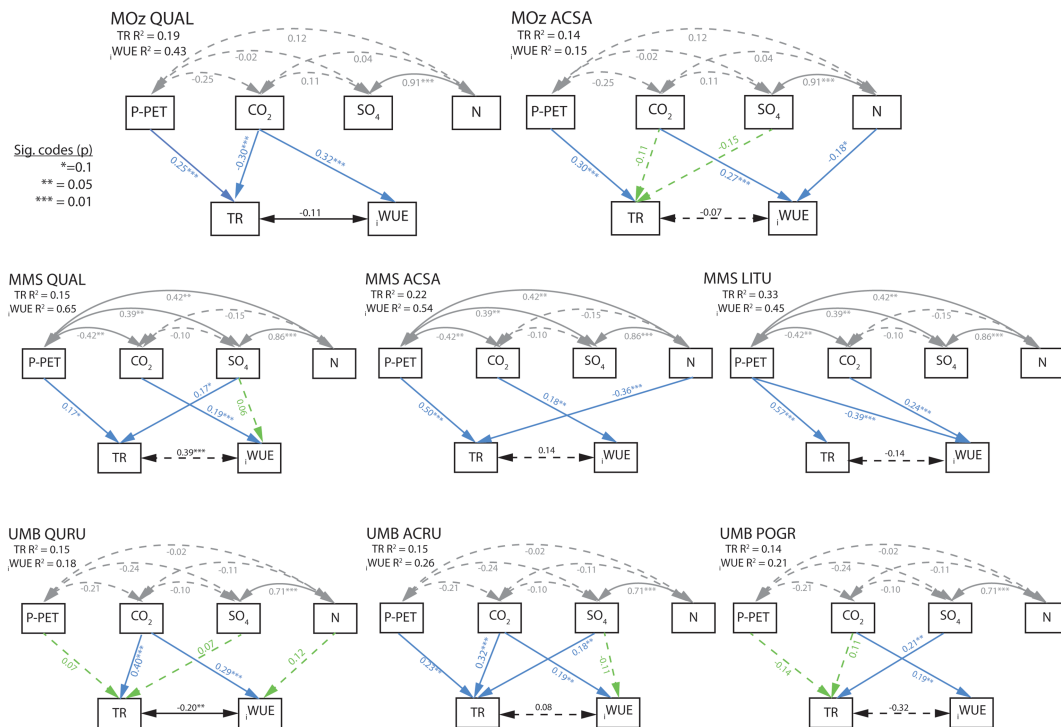


Figure 7. Relative influence of climatic water balance, atmospheric CO₂ concentrations, and SO₄ and N wet deposition on the standardized tree rings and intrinsic water-use efficiency using fitted piecewise structural equation models for the period 1985–2015. Single-headed arrows represent causal relationship while double-headed arrows indicate covariance between variables. Solid line represents a coefficient that was significant in the SEM, while dotted lines represent coefficients that were not significant but improved model fit. Blue solid lines represent significant causal relationship, green dashed lines represent insignificant influence of variable but improved fit of the model, and gray lines represent the covariation of the explanatory variables. ACSA = *Acer saccharum*; QUAL = *Quercus alba*; LITU = *Liriodendron tulipifera*; ACRU = *Acer rubrum*; QURU = *Quercus rubra*; POGR = *Populus grandidentata*.

droughts are lacking or infrequent, radial growth of anisohydric *Quercus* can become insensitive to water availability compared to periods of drought. We posit that during wetter periods, *Quercus* are less sensitive to water availability compared to other species because they have relatively deeper roots (Abrams, 1990; Hinckley et al., 1981) and therefore have continuous access to water, allowing for a more aggressive water-use strategy. Conversely, species that have shallower roots, such as *Acer* and *L. tulipifera* (Abrams, 1990; Hinckley et al., 1981) will have inconsistent access to water during short periods of dryness within the general wet conditions and therefore employ a more conservative water-use strategy. Wood anatomy (i.e., ring porous versus diffuse porous) is another species trait that aligns with our results. We found that species with diffuse porous wood anatomy (e.g., *Acer* species and *L. tulipifera*), tended to remain more sensitive to water availability during the ongoing pluvial, an intuitive finding given recent evidence that indicates radial growth in diffuse porous species wood anatomy are more sensitive to drought (Elliott et al., 2015; Kannenberg et al., 2019; Yi et al., 2019). While wood anatomy is not directly aligned with water-use strategy, differences between diffuse and ring porous wood results in different xylem architecture and therefore are related to stomatal regulation (Elliott et al., 2015).

Generally, we found a more widespread and consistent weakening of the signal at sites that have not experienced drought recently and saw more stable relationships at the sites that have had recent drought (Figures 4 and 5). Interestingly, tree growth and carbon isotope metrics at UMB were not correlated strongly with climate variables including JJA P-PET for the period of 1970–2015 (supporting information Figures S7–S9), indicating the most recent decline in sensitivity to P-PET may not be representative of the long-term growth responses at this location. The relatively more stable correlations in the early portion of the growing season (MJ) compared to the later portion (AS), indicates that conditions during AS are more influential to the overall weakening in the JJA relationship (Figure 6). While the correlations are generally weaker than the JJA season, the changing correlations in AS season are important due to this being a relatively drier portion of the growing season. However, firm conclusions on how the conditions in AS are contributing to the JJA

relationship are difficult to draw due to some sites (e.g., MOZ and MMS LITU) increasing in correlation, while species at other sites (UMB, MMS ACSA, and MMS QUAL) are decreasing (Figure 6).

4.2. Importance of Water Availability

Our results showed that while CO₂ concentrations, and to a lesser extent SO₄ and N deposition, influence the isotopic composition of tree rings, these variables resulted in a negligible influence on tree growth across species and sites over the timescale of our analysis. While increases in CO₂ concentrations have been shown to increase iWUE (Guerrieri et al., 2019), there is less support for growth enhancement from CO₂ due to lags between carbon allocation and stem growth and stand competition (Levesque et al., 2019; Giguere-Croteau et al., 2019). Further, the disagreement of the magnitude of the CO₂ fertilization effect on growth across data sources (e.g., Norby et al., 2005; Peñuelas et al., 2011, 2017) suggest that our understanding of how elevated CO₂ will impact tree growth and carbon sequestration when simultaneously being impacted by other pollutants and climate remains poorly understood. Our findings supported the work suggesting increases in atmospheric CO₂ influence iWUE but have weak if any influence on actual tree growth (Levesque et al., 2017; Peñuelas et al., 2011, 2017).

Considering that the period of analysis (1985–2015) is one of the wettest periods in the last several centuries (Ford, 2014; Maxwell & Harley, 2017), the continued importance of water availability on tree growth (while considering the simultaneous influence of CO₂ concentrations and SO₄ and N deposition) is particularly striking (Figure 7). CO₂ concentrations were more consistently related to the isotopic metrics than to the tree growth metrics (Figure 7), but that is partially explained by the inclusion of CO₂ in the calculation of iWUE (equation (3)). Regardless, the small influence of CO₂ concentrations on growth metrics indicates that increases in CO₂ are not contributing to the weakening relationship between tree rings and the climatic water balance. Similarly, the lack of influence of SO₄ and N deposition suggested that the decrease in pollutants is not contributing to a decrease in sensitivity of tree growth to water availability. Importantly, examining the variables simultaneously explains little of the variance (often <20%) in the growth and isotopic metrics at the site that has not experienced a drought recently (UMB). However, radial growth from both *Q. rubra* and *A. rubrum* had stronger correlations pre-1980 (Figures 4 and 5). These results indicate that while UMB is generally a wet site, trees have only recently become less sensitive to water availability and that decrease did not correspond to an increase in sensitivity in any other variable in the SEMs (Figure 7).

Finally, the inconsistent influence of climatic water balance on isotopic metrics across species (Figure 7) demonstrates the importance of understanding species-specific water-use strategies and how they relate to carbon uptake. The highly contrasting responses of *L. tulipifera* and *Q. alba* at MMS to climatic water balance is also supported by previous studies (Roman et al., 2015; Yi et al., 2019), which together suggest that the stomates of *L. tulipifera* are particularly sensitive to both changing water supply (P) and variable demand (PET), where *Q. alba* is largely insensitive to variation in water supply. If photosynthetic capacity is not directly affected by hydrologic stress, then stomatal closure in response to both reduced P and increased PET will tend to increase iWUE, since the relationship between photosynthesis and conductance is non-linear, and tends to saturate at relatively high conductance rate that characterize species growing in energy-limited environments (Yi et al., 2019). Our findings also provide further evidence of the usefulness of isotopic metrics to understand species-specific responses. It is important to note that while tree growth is one aspect of the forest carbon cycle, global change drivers could impact multiple aspects beyond just tree growth. As time series of flux towers and remote sensing products increase in length, we should be able to extend our hypotheses past tree rings and into other carbon cycle processes and quantify the extent to which the responses of tree rings to climate variability impact forest carbon uptake (Kannenberg et al., 2019).

5. Conclusions

We examined the simultaneous influence of climatic water balance (P-PET), CO₂ concentrations, and SO₄ and N depositions on tree growth and stable C isotopic composition from tree rings. We found that water availability was the most important driver of radial tree growth, although the SEMs at the site that has not experienced drought explained little variance. Generally, isohydric species were more sensitive to drought than anisohydric species and had a more stable and consistent relationship with water availability through time. CO₂ concentrations influenced the variability of $\Delta^{13}\text{C}$ and iWUE but not growth, suggesting

that the documented weakening in the relationship between tree growth and water availability is not due to increases in CO₂ concentrations. Similarly, both SO₄ and N deposition had little to no influence on tree growth, indicating that the recent pluvial period in the Midwest is likely causing the recent weakening relationship. With water availability being the dominant limitation of growth, a period absent of drought has resulted in trees being generally less sensitive to variation in the availability of water. However, the lack of influence of CO₂ concentrations and pollutant deposition on growth indicates that changes in these factors will unlikely offset growth reductions when drought returns in these regions. Therefore, future increases in the frequency and severity of drought will likely continue to be a limiting factor of both tree growth and carbon sequestration even with increased concentrations of CO₂ and lower levels of pollutants.

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