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Research

Demographic shifts in eastern US forests increase the impact of late-season drought on forest growth

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While forest communities are changing as a result of global environmental change, the impacts of tree species shifts on ecosystem services such as carbon storage are poorly quantified. In many parts of the eastern United States (US), more xeric-adapted oak-hickory dominated stands are being replaced with mesic beech-maple assemblages. To examine the possible impacts of this ongoing change in forest composition, we investigated how two wide-ranging and co-occurring eastern US species – *Acer saccharum* (sugar maple) and *Quercus alba* (white oak) – respond to interannual climate variability. Using 781 tree cores from 418 individual trees at 18 locations, we found late-growing season drought reduced *A. saccharum* growth more than that of *Q. alba*. A gradient in the growth reduction across latitude was also found in *A. saccharum*, where southern populations of *A. saccharum* experienced greater reductions in growth during drought. Drought had a legacy effect on growth for both species, with drought occurring later in the growing season having a larger legacy effect. Consequently, as forests shift from oak to maple dominance, drought in the later part of the growing season is likely to become an increasingly important control on forest productivity. Thus, our findings suggest that co-occurring species are responding to environmental conditions during different times in the growing season and, therefore, the timing of drought conditions will play an important role in forest productivity and carbon sequestration as forest species composition changes. These findings are particularly important because the projected increases in potential evapotranspiration, combined with possible changes in the seasonality of precipitation could have a substantial impact on how tree growth responds to future climatic change.

Keywords: carbon sequestration, compositional shifts, mesophication, species-specific responses, tree rings, water use strategies

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Introduction

Forests sequester anthropogenic carbon (C) emissions (Bonan 2008) and thereby slow the pace of climate change. However, extreme climate events (e.g. severe drought and heat extremes) reduce the degree to which forests perform this vital ecosystem service. Extreme events diminish C uptake and storage by reducing C assimilation (Ciais et al. 2005) and inducing large-scale tree die-off (Allen et al. 2010, Anderegg et al. 2015, Choat et al. 2018). Such events can cause forests to shift from C sinks to C sources (Phillips et al. 2009). Even in mesic forests that have higher water availability, drought often limits tree growth and consequently constrains C exchange (Roman et al. 2015, Novick et al. 2016, Yi et al. 2019). Improved understanding of drought sensitivity of various forest components is critically important to predicting future C feedbacks under more frequent and intense climate extremes.

Tree species differ in their strategies for minimizing the impacts from drought stress. Predictions of how drought will impact forest productivity in the future require knowledge of species-specific sensitivities to water stress. Such responses are especially important in the highly productive and diverse forests of the eastern United States (US). These ecosystems currently sequester ~40% of regional carbon emissions (Pan et al. 2011), but ongoing shifts in species composition may influence future carbon uptake rates (Brzostek et al. 2014, Roman et al. 2015). Specifically, in recent decades, the species composition of eastern US forests has shifted from more fire-adapted species (e.g. *Quercus* spp.) to more shade-tolerant species such as maples (*Acer*) due to multiple drivers, including fire suppression, nitrogen deposition and climate change (Abrams 2003, McEwan et al. 2011, Jo et al. 2019). Decline in oak population is expected to cause detrimental impacts on forest ecosystems as oak acorns provide primary food sources for many species such as deer, weevils, birds and rodents (McEwan et al. 2011). Given that maples are believed to be less tolerant of drought than oaks owing to their frequent occurrence on more mesic sites, future forests of the region may be less able to buffer and withstand the impacts of drought due to losing diversity (Anderegg et al. 2018).

The shift from oak- to maple-dominated forests, or 'mesophication' (Nowacki and Abrams 2008, Knott et al. 2019), has taken place during a period of unusual hydrologic conditions. Several studies have found the last several decades in the midwestern and northeastern regions of the US to be the wettest (in terms of mean annual precipitation) in the observed record (Mishra and Cherkauer 2010, Horton et al. 2011, Seager et al. 2012, Fei et al. 2017). Paleoclimatic reconstructions also have shown that the recent period is the wettest in the last several centuries (McEwan et al. 2011, Pederson et al. 2013, Ford 2014, Shuman and Marsicek 2016, Maxwell and Harley 2017). However, even as moisture inputs to the ecosystem have increased, rising temperatures have driven an increase in the demand for water by the atmosphere, often expressed as the vapor pressure deficit (VPD, Ficklin and Novick 2017). Increasing VPD owing to rising temperatures accelerates moisture return to the air and represents an independent (from soil moisture) source of stress for plants, which close their stomates as VPD rises. The background increase in VPD is a contributing factor for predictions of more frequent and intense drought in the future (Huntington 2006, Ford et al. 2011, Ficklin and Novick 2017). Thus, despite the relatively wet conditions of the past 50–60 yr, there are many reasons to expect that eastern US forests will experience a more drought-prone future and the impacts of drought on forests under the ongoing compositional shift need further study.

While tree growth is strongly sensitive to climate variability, site conditions such as soil type, aspect and stand density (Hurteau et al. 2007), can also influence growth as well as the distribution of species across the landscape (Kannenberg et al. 2019). Thus, it can be difficult to disentangle species- versus site factors when examining growth responses. We confront this challenge by analyzing growth time series from species that co-occur across the landscape. While very few studies examined responses of multiple co-occurring tree species (Lévesque et al. 2014), it is necessary and fundamental to minimize the impacts of geographical location on tree growth responses so that proper interspecific climate responses comparison can be determined. To better understand how the changing species makeup of eastern US forests affects drought response, we focus on recent climate–growth relationships for two common tree species from the maple and oak genera, *Acer saccharum* (sugar maple) and *Quercus alba* (white oak), that are growing in the same forest stands and are a major part of forest compositional shifts in eastern North America. Specifically, we test the hypothesis that the more mesic species (*Acer saccharum*) has a stronger growth reduction than *Quercus alba* under water stress. Understanding species-specific drought responses can provide insight into how future climate may impact eastern forests and corresponding carbon sequestration. With ongoing changes in forest demographics and climate, a species-specific understanding of drought response is needed.

Material and methods

Study area and species

Our study sites are located across the eastern US, including Illinois, Indiana, Michigan, Missouri, New York, New Hampshire and Pennsylvania (Fig. 1). At each of the 18 sites, we sampled co-occurring *A. saccharum* and *Q. alba*, with the exception of Meltzer Woods (MW) where we sampled *Quercus macrocarpa* (bur oak) instead of *Q. alba* (white oak). However, both *Q. macrocarpa* and *Q. alba* belong to the white oak group, so they are expected to have similar responses (Woodcock 1989, Robertson 1992). At each of our study sites, we sampled 6–22 trees (11–44 total increment cores) for each species at breast height. We also gathered *Q. alba* ring-width data from the International Tree Ring Data Bank (Copenheaver 2012) and unpublished co-occurring *A. saccharum* from Lake Raystown in Entriken, Pennsylvania (Copenheaver unpubl.). We sampled trees that appeared

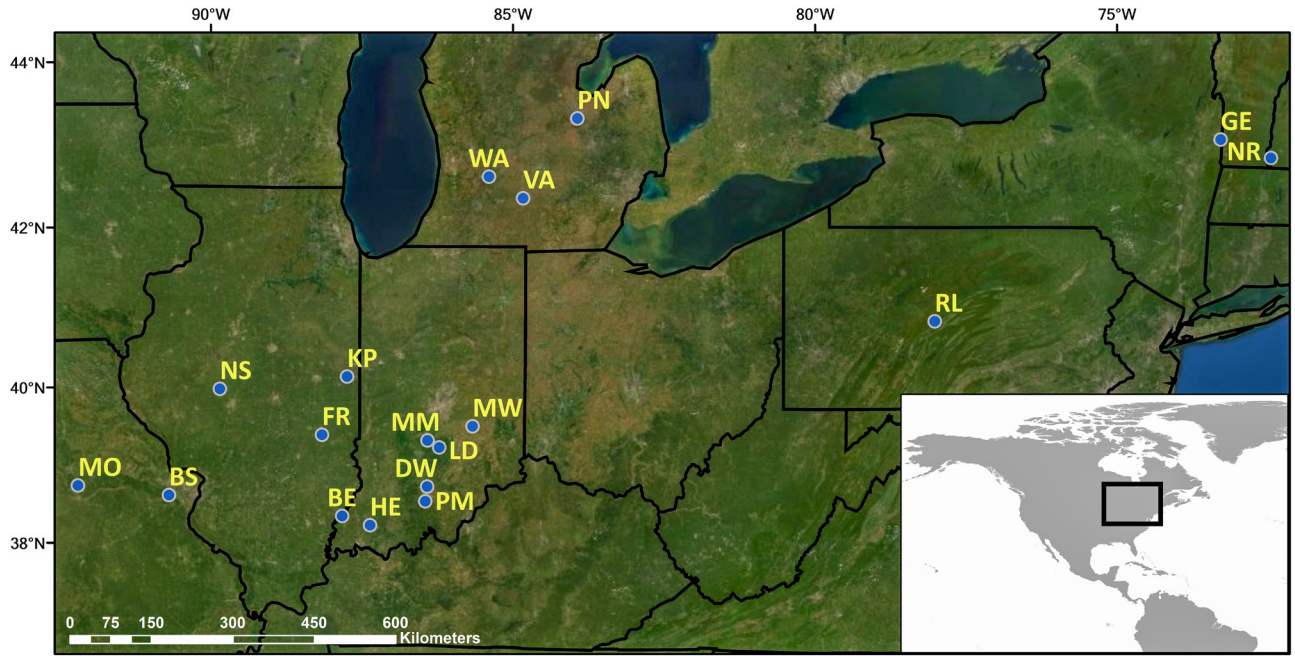


Figure 1. Location of 18 study sites across the eastern US where cores of co-occurring *Acer saccharum* and *Quercus alba* trees were analyzed. Site abbreviations are listed in Supplementary material Appendix 1 Table A1.

to be healthy and were canopy dominants to minimize the influence of forest dynamics and disturbance on the climate signals contained in the tree rings. Larger canopy-dominant trees are generally considered more sensitive to drought than sub-canopy trees (Alexander et al. 2018), account for more biomass and have higher rates of carbon sequestration (Bennett et al. 2015). Overall, we used 781 cores from 418 individual trees in the analysis.

Sampling and chronology development

Following standard dendrochronological techniques (Stokes and Smiley 1968), tree cores were mounted in wooden boards, air dried and polished progressively with finer sandpaper until growth rings were visible under a microscope. Tree cores were then visually crossdated and each ring width was measured to 0.001 mm precision using a Velmex measuring system (Velmex, Bloomfield, NY, USA) and cores from Price Nature Center, Voorhees Audubon Sanctuary and Warner Audubon Sanctuary were measured in program CooRecorder (ver. 9.0.1, Cybis Elektronik and DATA AB, Saltsjöbaden, Sweden) based on digital images which were made by scanning the cores at a resolution of at least 1200 dots per inch. The COFECHA program was used to statistically validate the accuracy of visual cross-dating and ring width measurement (Holmes 1983). The raw measurements of individual tree ring cores were standardized with a smoothing spline of two-thirds of the length of each series (i.e. a two-thirds spline; Cook and Peters 1981) using the ARSTAN program (Cook and Holmes 1986) to preserve growth variations reflecting climate variability and removing biological trends and growth associated with forest dynamics so that trees with different ages can be compared. The final species chronologies at each site were calculated using a bi-weight average of individual samples.

Climate data

Monthly climate data were obtained from the PRISM climate group at Oregon State Univ. (<http://prism.oregonstate.edu/>). The climate variables obtained were monthly means of daily maximum temperature (T_{max}), minimum temperature (T_{min}), precipitation (P) and maximum vapor pressure deficit (VPD_{max}) for the period 1895–2015 at the closest 4 km grid point for each of our sites (Supplementary material Appendix 1 Table A1). Although temperature may not limit tree growth during the growing season in the eastern US, T_{max} can represent water demand during the warm season. Similarly, VPD_{max} was chosen to represent the atmospheric water demand experienced by trees. The influence of water supply on tree growth was represented by P. Inclusion of T_{min} allows broader coverage of the temperature demand that potentially influences tree growth. To combine the effects of these climate variables, we calculated monthly potential evapotranspiration (PET) via the Hargreaves method using the 'SPEI' package in R (Beguería et al. 2017). PRISM mean monthly T_{max} and T_{min}, along with PRISM monthly P to account for cloudiness, were used in the PET calculation. We then calculated the climatic water balance as the difference between P and PET (i.e. P-PET). Lastly, to include a relative index of water availability that is more comparable across sites, we derived the monthly standardized precipitation evapotranspiration index (SPEI) from the same climate variables using the 'spei' function in the SPEI package in R (Beguería et al. 2017).

Climate–growth relationship

To identify the months with the strongest climate–growth relationships, we used Pearson's correlation coefficient on current and lagged year radial growth with monthly T_{max}, T_{min}, VPD_{max}, P and SPEI from previous-year April to current-year October. The correlation analysis was performed for the common period (1947–2006) of the climate variables and the 'arstan' standardized chronologies with at least five tree core samples available across all species and sites. To identify what portion of the growing season the two species were the most responsive to climate, we compared unweighted and optimally weighted June–July–August (JJA, wJJA respectively) correlation coefficients for T_{max}, P, SPEI and VPD_{max} across 18 study sites during 1947–2006. We created the optimal weighting by examining all possible linear combinations of each month in the JJA average separately to determine the weighting that maximized correlation with standardized tree growth. Whereas an equal weighting of 1/3 for the three months is nearly always used, our analysis could produce an optimal weighting of ½, ¼, ¼, which suggests that climate during June is more influential than during July and August (Supplementary material Appendix 1 Fig. A1). Because there was a lack of response to T_{min} during the period examined (Supplementary material Appendix 1 Fig. A2), we did not calculate seasonal averages for this variable.

Relationship between climatic water balance (P-PET) and tree growth

We used a linear mixed model (LMM) to investigate how drought impacts tree growth across our study sites and between our two species. As the growth of both *A. saccharum* and *Q. alba* had the highest correlation to wJJA water availability (Fig. 2d), we used this variable as a predictor in the model. We also included JJA drought effects and JJA 1-yr legacy effects as predictors. Lastly, we included interaction terms between species (*Q. alba*) and all of our predictors. The LMM was conducted over the common period of all our species chronologies 1947–2006. The model was computed using the 'lme4' package in R (Bates et al. 2015). The equation of the model is as follows:

$$\begin{aligned} \mathrm{SRW} = {} & \mathrm{A} + \beta(\mathrm{CWB}) + \beta(\mathrm{DE}) + \beta(\mathrm{DL}) + \gamma(\mathrm{Species} \times \mathrm{CWB}) \\ & + \gamma(\mathrm{Species} \times \mathrm{DE}) + \gamma(\mathrm{Species} \times \mathrm{DL}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \\ & + \varepsilon(\mathrm{Site} \times \mathrm{Species}) \end{aligned}$$

where SRW is the standardized radial width, A is overall intercept, β are the slopes for the fixed effects, γ are the slopes for interaction terms, CWB is wJJA climatic water balance, DE is JJA drought effect, DL is JJA 1-yr legacy effects, ε are the random effects with the number of sites (n = 18), the number of species (n = 2) and sites crossed with species (n = 36). We quantified the percentage of growth reduction of *A. saccharum* compared to *Q. alba* using the γ coefficients of the interaction terms between species and climatic water balance divided by the β coefficients of climatic water balance.

Drought effects and legacy

Drought effects on the species were defined as the difference of averaged standardized ring width (SRW) between drought years and non-drought years (i.e. $SRW_{drought} - SRW_{non\text{-}drought}$) for each site. We identified the drought years as being 1 standard deviation below the mean of P-PET (Kannenberg et al. 2019) where all drought years identified had a negative P-PET (Supplementary material Appendix 1 Table A2, A3). This analysis was performed for the individual months of May, June, July, August as well as the seasonal average of JJA and May–June–July–August (MJJA) for the current growing season. We used one sample t-tests to determine whether the mean growth suppression induced from drought conditions on SRW was different from zero for *A. saccharum* and *Q. alba* respectively. We further used two sample t-tests to determine whether the mean SRW reduction of each species was different from one another.

The species-specific drought legacy effects were calculated as the difference between predicted and observed SRW (i.e. $SRW_{predicted} - SRW_{observed}$). To obtain $SRW_{predicted}$, we applied a linear regression model between P-PET and SRW to estimate the SRW based on the climate conditions (Kannenberg et al. 2019) during the month of May, June, July, August, JJA and MJJA to determine species-specific drought legacy effects 1-yr and 2-yr after drought. We used one sample t-tests to determine whether the mean SRW legacy was different from zero for both species and used two sample t-tests to test whether the mean SRW legacy of each species was different from one another.

Latitudinal and longitudinal drought effect and SPEI responses

Our co-occurring *A. saccharum* and *Q. alba* network covered a wide geographical extent, therefore, the climatic responses of both species may vary along geographical gradients (Martin-Benito and Pederson 2015). We examined both the drought effect and SPEI correlation coefficient of co-occurring *A. saccharum* and *Q. alba* at the 18 sites during the growing season (i.e. June, July, August and JJA for drought effect and June, July, August and wJJA for SPEI correlation coefficient) across latitude and longitude respectively. We used linear regression to determine the strength of drought effect and SPEI responses along latitudinal and longitudinal gradients respectively. We also applied multiple linear regression models with latitude and longitude as the predictors to examine the interactive effects on both drought effect and SPEI responses.

Individual series responses to June SPEI

Correlation analysis revealed that tree growth was most strongly correlated with June climate throughout the study range. Thus, we calculated the regression slope coefficient

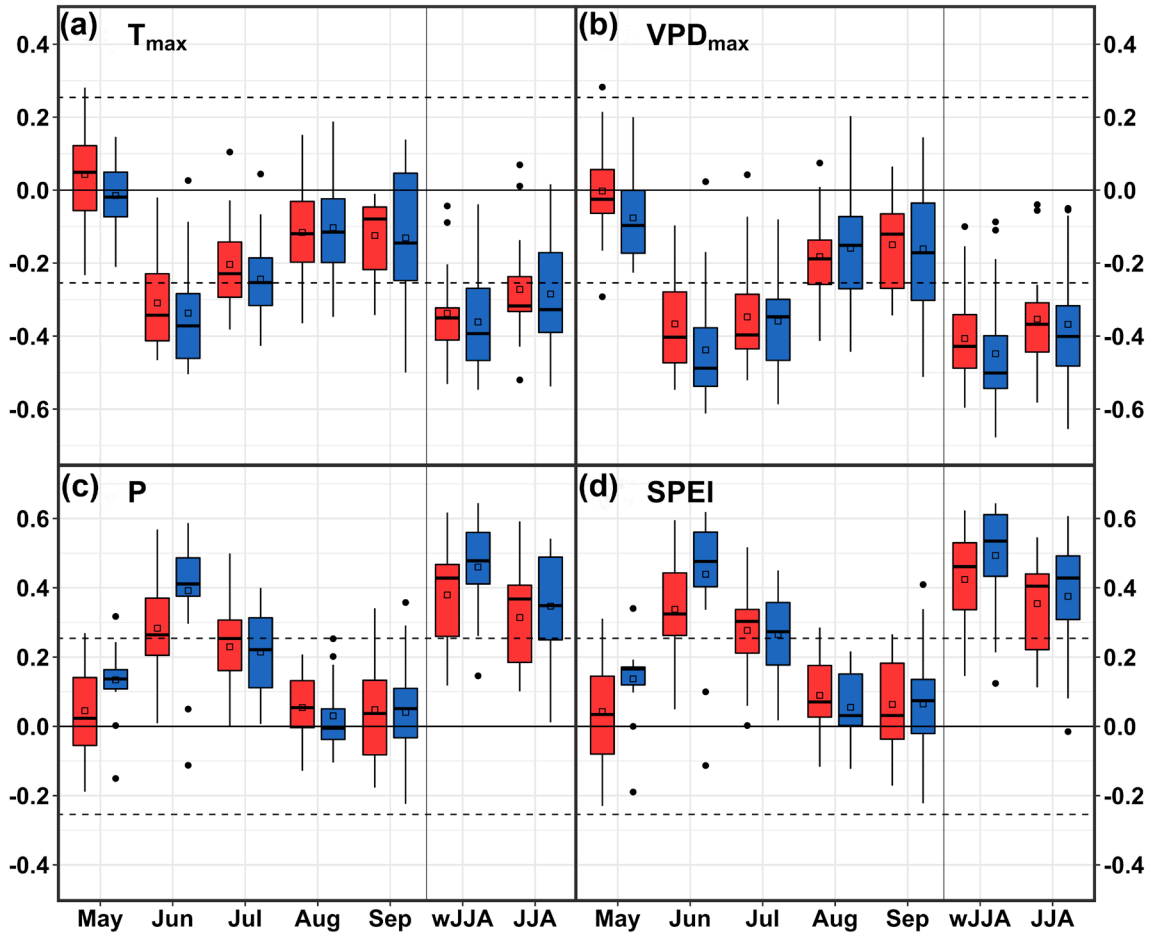


Figure 2. Boxplots of Pearson's correlation coefficients of *Acer saccharum* (red) and *Quercus alba* (blue) chronologies with climate variables across 18 sites: (a) maximum temperature (T_{max}), (b) maximum vapor pressure deficit (VPD_{max}), (c) precipitation (P) and (d) standardized precipitation evapotranspiration index (SPEI). Monthly values are used from current May to September as well as optimally weighted June–July–August (wJJA) and equally weighted JJA during the common period of 1947–2006. The upper and lower whiskers of boxplots are defined as the third quartile +1.5* inter-quartile range (IQR) and the first quartile −1.5*IQR respectively. Data beyond the upper and lower whiskers are considered outliers and represented as individual dots. The bold line in the boxplot represents the median while the open square represents the mean. Vertical lines separate individual months and seasonal averages for comparison. Dashed lines indicate the correlation coefficient associated with the critical type-I error ($\alpha = 0.05$).

between individual trees and June SPEI by averaging regression slope coefficients of the tree cores from the same tree. We then examined if the mean regression slope coefficients are different between species within individual sites by two sample t-test. When using the individual tree series in the correlation and regression analysis, we only used climate data from 1947 to 2006, as that period allowed us to have at least five cores available at all sites for both species to ensure the climate response was not overly influenced by one tree.

Interspecific temporal stability

We assessed the similarity of standardized chronologies of the two co-occurring species at each site using running correlations. We determined the period of appropriate sample depth using the year with at least five tree cores as a threshold shared between co-occurring species. For the common period of the standardized chronologies at each site, we calculated 21-yr running correlations between the two co-occurring species at sites that had sufficient data (~60 yr), with the correlation coefficients being reported for the center (11th year) of each window.

Age-dependent responses

Age-dependent radial growth responses have been reported for many hardwood species (Carrer and Urbinati 2004, Li et al. 2012, Primicia et al. 2015), including *Q. alba*. In order to determine whether differences in species climate–growth relationship could be related to differences in tree age, we first estimated the approximate age of every individual where possible (i.e. cored to the pith). We then calculated the average tree age of each species at each site so as to calculate the difference in mean tree age between the two species.

Next, we calculated the differences of correlation coefficients between the two species during the month of June and using the optimally weighted JJA value for each climate variable. We also calculated the differences of drought effects between the two species over the months of the growing season and seasonal average. We used R^2 to determine the extent to which the linear fits explain the relationship between differences in tree age with correlation coefficients and drought effects.

Results

Descriptive statistics of the chronologies

Inter-series correlations of the 36 chronologies ranged from 0.46 to 0.74, indicating that trees were statistically crossdated and responded similarly to environmental influences within each site (Supplementary material Appendix 1 Table A1). *A. saccharum* were generally younger (age range 61–153 yr) than the co-occurring *Q. alba* (age range 73–216 yr), but there were some exceptions, such as Morgan-Monroe State Forest, Missouri Flux Tower, Price Nature Center and Voorhees Audubon Sanctuary (Supplementary material Appendix 1 Table A1).

Climate–growth correlation analysis

At most sites, radial growth of both *A. saccharum* and *Q. alba* responded to climate variability within the current growing season of a given year (Supplementary material Appendix 1 Fig. A2). June was particularly important for both species. The growth of both maple and oak was positively correlated with June P and SPEI as well as negatively correlatied with June T_{max} and VPD_{max} ($p < 0.05$, Fig. 2). May and June climate had a higher correlation with the growth of *Q. alba* with all four climate variables compared to *A. saccharum*. On the other hand, the growth of *A. saccharum* was more correlated with July and August climate drivers, particularly for P and SPEI. The correlation coefficients of SPEI improved by 0.011 to 0.238 when we optimized the weighting during JJA (wJJA) (Fig. 2). This optimized scheme resulted in a higher June weighting for *Q. alba*, while *A. saccharum* had a higher weighting in July and August (Fig. 3).

Relationship between climatic water balance (P-PET) and tree growth

The linear mixed model confirmed that the climatic water balance (P-PET) had a strong influence on the standardized growth of *A. saccharum* and *Q. alba* ($p < 0.001$; Table 1). We further found a significant species-specific difference in the P-PET response ($p < 0.05$; Table 1) with *Q. alba* being less sensitive than *A. saccharum*. For every 100 mm decrease in the climatic water balance (P-PET), the growth of *A. saccharum* was reduced by 0.65 ± 0.04 while the reduction for *Q. alba* was 0.53 ± 0.06 (Table 1). Therefore, *A. saccharum* has a 18.5% more reduction than *Q. alba*. The species-specific drought effect and legacy effect had minimal impact on the standardized growth (Table 1).

Drought effects and drought legacy

Growth reductions in response to drought (or drought effects) for both species were significant during the months of the growing season and when averaged across the growing season months ($t_{17} = -3.63$ to -18.02, $p < 0.01$, Fig. 4a).

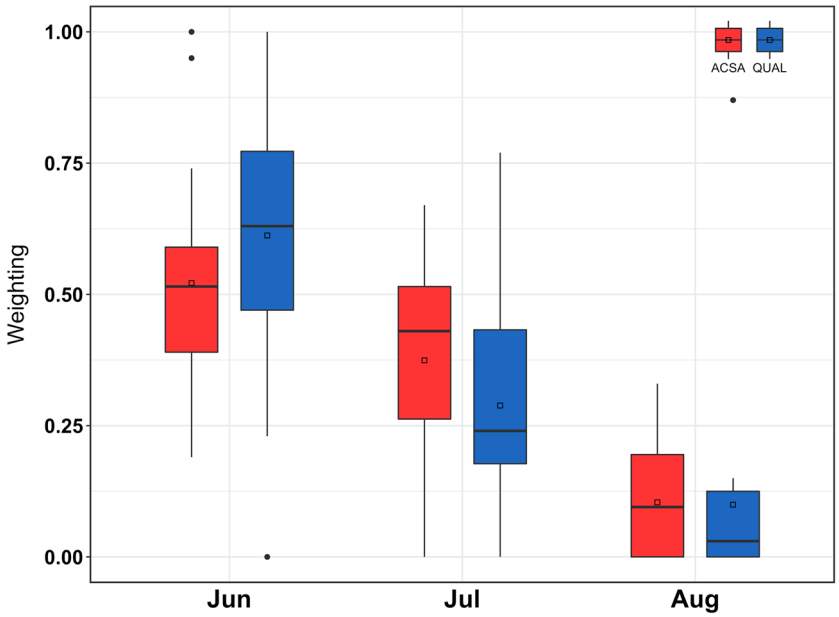


Figure 3. Boxplots of monthly weighting for SPEI that maximizes June–July–August (JJA) correlation coefficients with *Acer saccharum* (ACSA) and *Quercus alba* (QUAL) series at 18 sites. The traditional (equal) weighting of JJA uses a weight of 1/3 for each month.

Table 1. Fixed effect estimates, standard error (SE) and degree of freedom (df) of the linear mixed model used to predict the standardized growth of *Acer saccharum* and *Quercus alba* in response to site- and species-specific optimally weighted June–July–August (wJJA) climate water balance (P-PET), JJA drought effects and JJA drought legacy effects during 1947–2006 across 18 study sites.

Variables	Estimate ± SE	df	t value	p value
Intercept	1.16 ± 0.03	32.58	45.429	< 0.001
wJJA P-PET	0.0065 ± 0.0004	1465	15.522	< 0.001
JJA drought effect	0.145 ± 0.1	26.84	1.324	0.1967
JJA drought legacy	−0.03 ± 0.1	25.4	−0.303	0.7643
wJJA P-PET: species QUAL	−0.0012 ± 0.0006	734.4	−2.112	0.0351
JJA drought effect: species QUAL	0.076 ± 0.09	39.48	0.823	0.4156
JJA drought legacy: species QUAL	0.031 ± 0.27	28.01	0.117	0.9076

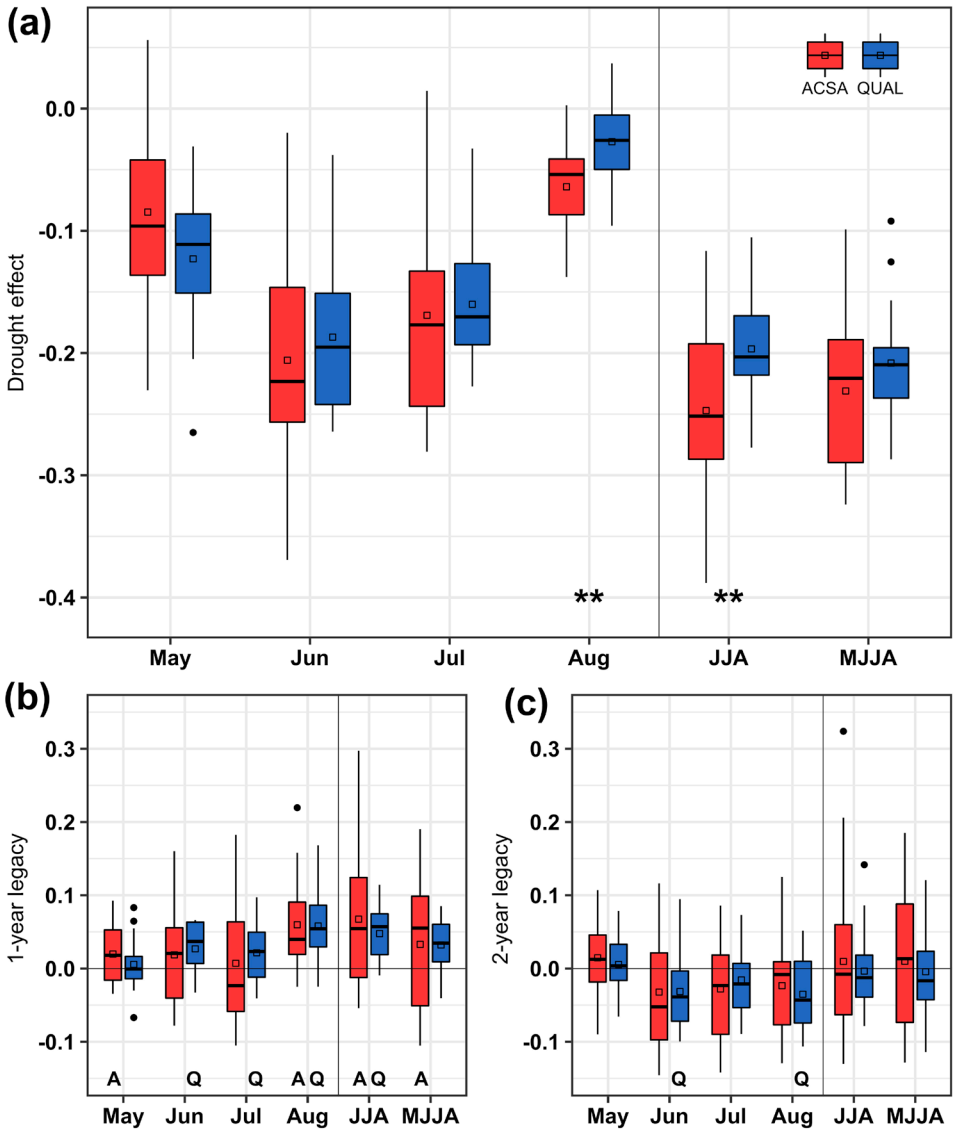


Figure 4. The (a) drought effect, (b) 1-yr legacy and (c) 2-yr legacy for *Acer saccharum* (ACSA, red boxes) and *Quercus alba* (QUAL, blue boxes) during the months of May, June, July, August, June–July–August (JJA) and May–June–July–August (MJJA). For drought effect, mean values of *A. saccharum* and *Q. alba* are significantly different from zero across all months ($\alpha = 0.05$). Asterisks indicate that means of *A. saccharum* and *Q. alba* are significantly different ($\alpha = 0.05$). For legacy effects, letter abbreviations for the species at the bottom (A for *A. saccharum*, Q for *Q. alba*) indicate the mean values are significantly different from zero ($\alpha = 0.05$). Vertical line separates individual months and seasonal averages for comparison. Mean values are reported in Supplementary material Appendix 1 Table A4.

Drought induced larger growth reductions for *A. saccharum* compared to *Q. alba* in August ($t_{34} = -3.30$, $p < 0.01$) and JJA ($t_{34} = -2.45$, $p < 0.05$). On the other hand, drought had a stronger effect in reducing the growth of *Q. alba* than *A. saccharum* in May, although the effect was weak ($t_{34} = 1.69$, $p = 0.101$). For the months of June and July, drought had a slightly stronger growth reducing effect in *A. saccharum* compared to *Q. alba* but both species were equally sensitive to drought during these two months (Supplementary material Appendix 1 Table A4).

Both species had significant legacy effects one year after drought occurrence (Fig. 4b). The mean legacy effects were strong in August and during JJA for *A. saccharum* (Aug: $t_{17} = 4.158$; JJA: $t_{17} = 2.945$, $p < 0.01$, Supplementary material Appendix 1 Table A4) and *Q. alba* (Aug: $t_{17} = 5.184$; JJA: $t_{17} = 5.649$, $p < 0.01$, Supplementary material Appendix 1 Table A4). There were no interspecific differences between the species for any months or season. The radial growth of both species returned to normal two years after drought occurrence (Fig. 4c) where *Q. alba* had a significant but weak increase of growth two years post drought for June ($t_{17} = 2.645$, $p = 0.017$) and August ($t_{17} = 2.818$, $p = 0.012$).

Latitudinal and longitudinal drought effect and SPEI responses

For *A. saccharum*, we found stronger drought effects at lower latitudes (and consequently weaker at higher latitudes) in June and August (Fig. 5a, c). Similarly, drought effects changed across longitude, with western sites having larger effects and eastern sites weaker effects in June, July and August (Supplementary material Appendix 1 Fig. A3a–c). For *Q. alba*, drought effects along latitudinal and longitudinal gradient were weak across all months (Fig. 5, Supplementary material

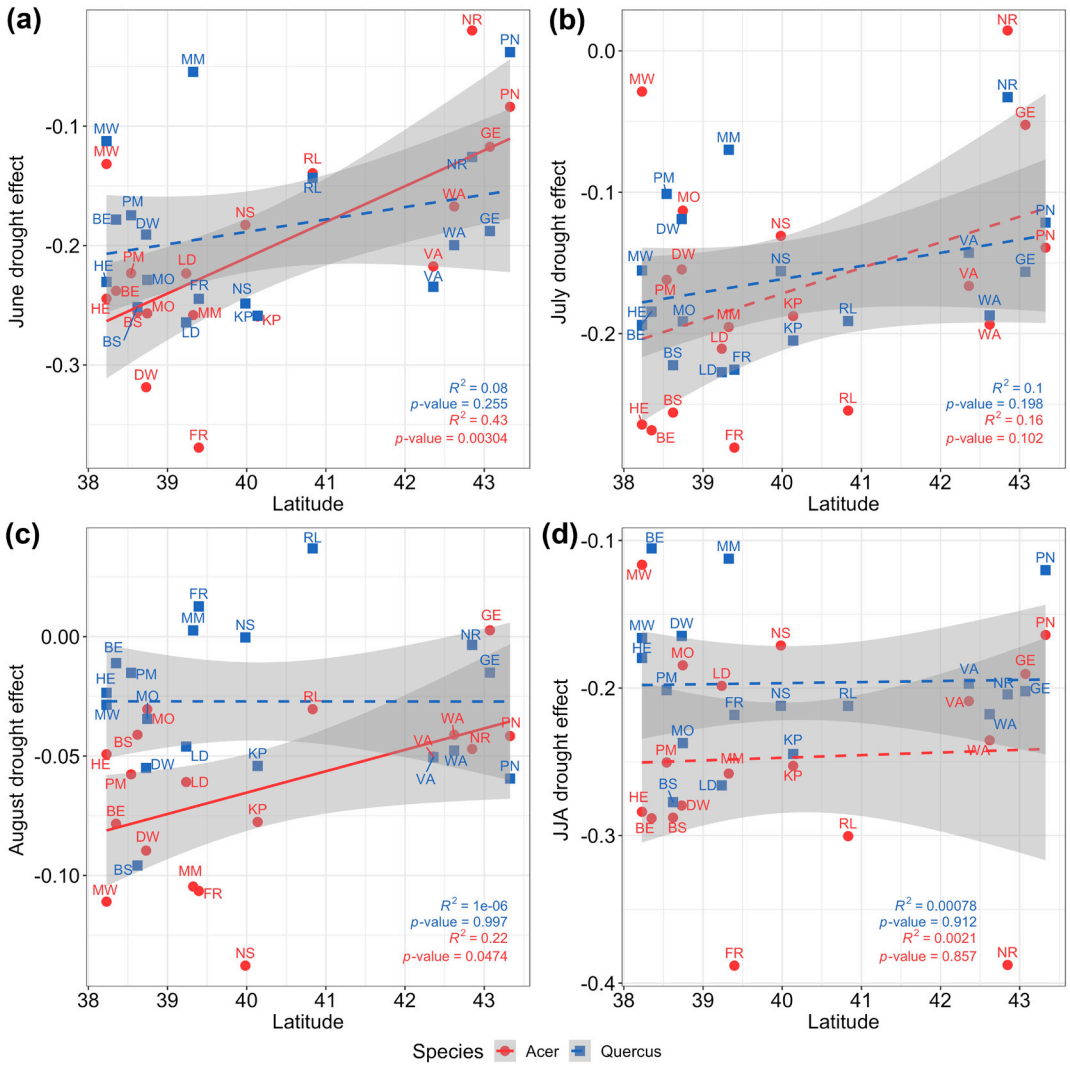


Figure 5. The drought effect of (a) June, (b) July, (c) August and (d) JJA across 18 sites along latitude gradient for *Acer saccharum* (red) and *Quercus alba* (blue). Solid regression lines indicate a significant latitudinal relationship with drought effect ($\alpha = 0.05$) while dashed lines indicate an insignificant latitudinal relationship.

Appendix 1 Fig. A3, Table A5) with a weak longitudinal response in July (Supplementary material Appendix 1 Fig. A3b). When we considered the combined influence of latitude and longitude on drought effects, stronger drought effects at lower latitudes still remained in June for *A. saccharum* (Adj. R^2: 0.48, $p < 0.01$; Supplementary material Appendix 1 Table A6).

We also found a strong influence of latitude and longitude on the SPEI responses. The SPEI response of *A. saccharum* was stronger in the southern sites compared to the northern sites in June and during JJA (Supplementary material Appendix 1 Fig. A4a, d). Along the longitudinal gradient, the SPEI response of *A. saccharum* was the stronger in the western sites than that of the eastern sites in June and during JJA (Supplementary material Appendix 1 Fig. A5a, d). In contrast, *Q. alba* had a weak trend in the SPEI response during June and JJA for latitude (Supplementary material Appendix 1 Fig. A4a, d) and longitude (Supplementary material Appendix 1 Fig. A5a, d). Weak latitudinal and longitudinal trends were observed in July and August for both *A. saccharum* and *Q. alba* (Supplementary material Appendix 1 Fig. A4, A5, Table A5). The combined influence of latitude and longitude on SPEI responses remained strong in June and JJA for *A. saccharum* (Adj. R^2: 0.48 and 0.30, $p < 0.01$ and $p < 0.05$; Supplementary material Appendix 1 Table A6).

Individual tree series responses to June SPEI

The response of individual tree growth to June SPEI across the 18 sites (Supplementary material Appendix 1 Fig. A6) was mixed. *A. saccharum* had higher mean regression slope coefficients than *Q. alba* at some sites, such as Babler State Park (BS) (0.029, $p < 0.1$), Donaldson Woods (DW) (0.036, $p < 0.1$), Fox Ridge (FR) (0.056, $p < 0.05$) and Morgan Monroe State Forest (MM) (0.08, $p < 0.05$), suggesting *A. saccharum* was more sensitive to June SPEI than *Q. alba* at these sites (Supplementary material Appendix 1 Fig. A6). At Hemmer Woods (HE), *Q. alba* was more sensitive to June SPEI (-0.034, $p < 0.05$). In general, individual *A. saccharum* trees had larger variability in June SPEI regression slope coefficients than *Q. alba*.

Interspecific temporal stability

Radial growth from both species was similar throughout the common period (Supplementary material Appendix 1 Fig. A7). Some sites, such as Donaldson Woods (DW), Fox Ridge (FR), Missouri Flux Tower (MO), Lincoln's New Salem (NS), Pioneer Mothers (PM) and Warner Audubon (WA), displayed relatively stable correlations through time. Other sites, such as North Round Pond Pisgah (NR) and Voorhees Audubon Sanctuary (VA), had fluctuating correlation coefficients between species, suggesting that the two species might adopt differential growth strategies only during certain environmental or climatic conditions. The remaining sites expressed stable but lacked a strong linear relationship between the two species.

Age-dependent responses

We did not find any significant linear relationships between age and any of the four climate variables in terms of optimally weighted JJA (wJJA) correlation coefficient and drought effect over the growing season (Supplementary material Appendix 1 Fig. A8, A10). However, we found a significant relationship between age and the difference of June P for the two species ($R^2 = 0.30$, $p < 0.05$, Supplementary material Appendix 1 Fig. A9). Although relative age-dependent correlation strength with P was significant, correlations with other climate variables, including SPEI, as well as age-dependent drought effect were not significant (Supplementary material Appendix 1 Fig. A8–A10), indicating that the relative difference in age between the two species did not strongly affect our conclusions about their drought response and sensitivity.

Discussion

Maples are becoming a dominant species in the canopy of the eastern United States forests. Our comparison of canopy dominant maples and oaks allows us to examine species-specific differences in the portion of the forests that accounts for a substantial amount of carbon sequestration. We expected that the mesic-adapted species, *A. saccharum*, would be more sensitive to water stress than the more xeric-adapted species *Q. alba*. Our conclusion about whether or not this hypothesis is correct depends on how we define sensitivity. If sensitivity was defined as the strength of the correlation between growth and the climate variable (hereafter the correlation sensitivity), which many dendroecological studies use, then we would conclude that both species are sensitive to water availability and infer that the timing of the highest sensitivity to water availability is the month of June for both species (Fig. 2). The seasonality of the correlation between growth and water availability was different across the two species (Fig. 3). *Quercus alba* exhibited stronger correlation coefficients during May and June compared to *A. saccharum*, suggesting a stronger climate–growth relationship during the early growing season (Fig. 2, Fig. 3). *Acer saccharum*, in contrast, displayed stronger correlation coefficients than *Q. alba* during the later portion of growing season, which indicated climate conditions in the later growing season are more important for its annual growth (Fig. 2, 3).

However, if drought sensitivity was based on the growth reduction in response to drought (hereafter the drought effect), we come to a much different conclusion. While correlation between climate conditions and growth is a widely used tool for detecting tree-drought responses, especially in dendrochronology, the size of the correlation coefficient alone does not convey the *magnitude* of drought response on tree growth. Although *A. saccharum* had lower correlation coefficients with SPEI than *Q. alba*, the magnitude of growth reductions were more profound in *A. saccharum* over the growing season (Fig. 4), suggesting that *A. saccharum* was more sensitive to drought than *Q. alba*. Further, when

examining growth reductions acorss all of out 18 sites using the LMM, *A. saccharum* has an 18.5% greater reduction in growth compared to *Q. alba* during drought (Table 1). We posit that variation in species-specific traits such as wood anatomy, differential water-use strategies and rooting depth may underlie the different seasonally-dependent growth sensitivities of the two species.

Wood anatomy

The seasonal climate–growth relationship can likely be related to the distinctive wood anatomy and the timing of xylem vessel formation of the two tree species. *Quercus alba* is a ring-porous species and forms new xylem only during the early part of the current growing season (Fritts 1962). Consequently, the early-season climate is a key limiting factor of radial growth. In contrast, *A. saccharum* has diffuse-porous xylem and vessel formation happens throughout the entire growing season (Zimmermann 1983, Taneda and Sperry 2008). Although *A. saccharum* also forms new xylem during the early growing season, it recruits xylem formed during the previous year and grows additional xylem after June (Zimmermann 1983). Therefore, the climate–growth relationship of *A. saccharum* is not as closely linked to the early growing season as that of *Q. alba*.

Water-use strategies

The different responses to drought of *A. saccharum* and *Q. alba* may relate to the different hydraulic strategies of these species. Maples (*Acer*) in the eastern US exhibit a more isohydric behaviour than oaks by closing stomates at the first signs of drought, which reduces transpiration and allows trees to maintain stable leaf-water potential during droughts (Oren and Pataki 2001, Meinzer et al. 2013, Roman et al. 2015, Maxwell et al. 2019). As a result, carbon uptake and assimilation are limited, which may explain the stronger growth reduction to drought in *A. saccharum*. In contrast, most ring-porous oak species (*Quercus*) have less sensitive stomatal responses to drought (i.e. are more anisohydric) than diffuse-porous species (Oren and Pataki 2001, Meinzer et al. 2013, Roman et al. 2015, Maxwell et al. 2019). The less conservative stomatal control in oak trees in the eastern US permits higher rates of photosynthesis during drought for oaks relative to their neighbors, including *A. saccharum* (Hinckley et al. 1979, Bahari et al. 1985, Abrams 1990, Roman et al. 2015). Given more static gas exchange and photosynthesis in *Q. alba* during drought, *Q. alba* had less growth reduction than *A. saccharum*.

Rooting depth

The differences in drought sensitivity and radial growth reduction also are partially attributable to different rooting depths between *A. saccharum* and *Q. alba* (Abrams 1990). *Acer saccharum* is reported to have a shallower root system (~1 m) than *Q. alba* (~4 m) (Hinckley et al. 1981, Abrams 1990). Predawn leaf water potential measurement can indirectly indicate rooting depth. *Acer saccharum* shows lower predawn leaf water potential than *Q. alba*, indicating that *A. saccharum* has relatively shallower roots (Hinckley et al. 1979, Gu et al. 2015). The extensive root system of oak allows access to deeper and more stable water sources while the shallow root system typical of maple shows larger reliance on near-surface soil moisture (Taneda and Sperry 2008). Therefore, *Q. alba* has greater resilience to drought, better adaptation to xeric sites and can better buffer against water deficit than other tree species (Hinckley et al. 1979, Abrams 1990).

Significance of co-occurring species network

Early-season droughts have been shown to cause radial growth reduction in eastern North America, while species traits were not significantly related to tree growth (D'Orangeville et al. 2018). D'Orangeville et al. (2018) examined multiple species from different sites across eastern North America where *Q. alba* generally had larger growth reductions than *A. saccharum* in response to drought. However, the majority of *A. saccharum* used in that study came from the northeastern part of US and Canada while *Q. alba* had a broader spatial coverage in the eastern US. Here, we controlled for site differences by using co-occurring species to compare drought responses in forest stands across 18 sites. Although *A. saccharum* and *Q. alba* share similar climate–growth relationships, the more mesic species, *A. saccharum*, was more sensitive to drought conditions than the more xeric species, *Q. alba*, in terms of the magnitude of growth reduction. The apparent differences in species-specific drought effects between our findings and D'Orangeville et al. (2018) are likely to be attributed to the influences of site characteristics and the differences of latitudinal and longitudinal locations of sites (Fig. 5, Supplementary material Appendix 1 Fig. A3–A5). We, therefore, stress the benefit of using a co-occurring species network of tree rings for deepening our understanding of forest responses to climate change.

Potential future drought impacts on forest ecosystems of eastern US

Drought timing and duration will give rise to species-specific responses to drought and such differential responses are likely attributable to species-specific traits and physiology. However, the drought response of tree species can also be impacted by geographical locations where latitudinal variations might be a stronger limiting factor in influencing the drought effects of *A. saccharum* than that of *Q. alba* (Fig. 5). Temperatures are projected to increase at higher latitude regions (Vose et al. 2017) along with a projected increase in potential evapotranspiration and summer drought frequency and intensity in many parts of the eastern US (Swain and Hayhoe 2015, Ficklin and Novick 2017). These results indicate that the southern populations in the future could be vulnerable to climatic conditions that *A. saccharum* has

not experienced, while the northern populations are likely to experience climate conditions similar to those of the southern populations. Forest composition in the eastern US is shifting from more xeric adapted species such as oak and hickory to more mesic species such as maple and beech (Nowacki and Abrams 2008, McEwan et al. 2011, Pederson et al. 2015, Knott et al. 2019). Such shifts will result in changes in the overall sensitivity of the ecosystem to drought and resilience for forests where drought over the growing season will cause larger reductions in growth and the corresponding carbon sequestration of mesic maple compared to more xeric oak. In the future, the combination of increased drought and shifting in forest composition indicates that future drought could have a profound impact on carbon sequestration.

Data availability statement

The tree ring chronologies are archived at the International Tree-Ring Data Bank (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>).

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References

Abrams, M. D. 1990. Adaptations and responses to drought in Quercus species of North America. – Tree Physiol. 7: 227–238.
Abrams, M. D. 2003. Where has all the white oak gone? – BioScience 53: 927–939.
Alexander, M. R. et al. 2018. Relative influences of multiple sources of uncertainty on cumulative and incremental tree-ring-derived aboveground biomass estimates. – Trees 32: 265–276.
Allen, C. D. et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. – For. Ecol. Manage. 259: 660–684.
Anderegg, W. R. et al. 2015. Tree mortality from drought, insects and their interactions in a changing climate. – New Phytol. 208: 674–683.
Anderegg, W. R. et al. 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. – Nature 561: 538–541.
Bahari, Z. et al. 1985. Photosynthesis, water relations and drought adaptation in six woody species of oak-hickory forests in central Missouri. – For. Sci. 31: 557–569.
Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.
Beguería, S. et al. 2017. Package 'SPEI'. – <https://cran.r-project.org/web/packages/SPEI/index.html>.
Bennett, A. C. et al. 2015. Larger trees suffer most during drought in forests worldwide. – Nat. Plants 1: 15139.
Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks and the climate benefits of forests. – Science 320: 1444–1449.
Brzostek, E. R. et al. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. – Global Change Biol. 20: 2531–2539.
Carrer, M. and Urbinati, C. 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. – Ecology 85: 730–740.
Choat, B. et al. 2018. Triggers of tree mortality under drought. – Nature 558: 531–539.
Ciais, P. et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. – Nature 437: 529–533.
Cook, E. R. and Peters, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. – Tree-Ring Bull. 41: 45–53.
Cook, E. R. and Holmes, R. L. 1986. Users manual for program ARSTAN. – Laboratory of Tree-Ring Research, Univ. of Arizona, Tucson, USA.
Copenheaver, C. A. 2012. NOAA/WDS Paleoclimatology – Copenheaver – Raystown Lake – QUAL – ITRDB PA015. [Raw Measurements]. – NOAA National Centers for Environmental Information, <https://doi.org/10.25921/kc7d-g806>, accessed 9 April 2018.
D'Orangeville, L. et al. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. – Global Change Biol. 24: 2339–2351.
Fei, S. et al. 2017. Divergence of species responses to climate change. – Sci. Adv. 3: e1603055.
Ficklin, D. L. and Novick, K. A. 2017. Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere. – J. Geophys. Res. Atmos. 122: 2061–2079.
Ford, C. R. et al. 2011. Can forest management be used to sustain water-based ecosystem services in the face of climate change? – Ecol. Appl. 21: 2049–2067.
Ford, T. W. 2014. Precipitation anomalies in eastern-central Iowa from 1640 to present. – J. Hydrol. 519: 918–924.
Fritts, H. C. 1962. The relation of growth ring widths in American beech and white oak to variations in climate. – Tree-Ring Bull. 25: 2–10.
Gu, L. et al. 2015. Drought-influenced mortality of tree species with different predawn leaf water dynamics in a decade-long study of a central US forest. – Biogeosciences 12: 2831–2845.
Hinckley, T. et al. 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. – Am. Midl. Nat. 102: 307–316.
Hinckley, T. et al. 1981. Temperate hardwood forests. – Water Deficit Plant Growth 6: 153–208.
Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measurement. – Tree-Ring Bull. 43: 69–78.

Horton, R. M. et al. 2011. Climate hazard assessment for stakeholder adaptation planning in New York City. – J. Appl. Meteorol. Clim. 50: 2247–2266.
Huntington, T. G. 2006. Evidence for intensification of the global water cycle: review and synthesis. – J. Hydrol. 319: 83–95.
Hurteau, M. et al. 2007. Species-specific response to climate reconstruction in upper-elevation mixed-conifer forests of the western Sierra Nevada, California. – Can. J. For. Res. 37: 1681–1691.
Jo, I. et al. 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. – Sci. Adv. 5: eaav6358.
Kannenberg, S. A. et al. 2019. Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US. – Ecol. Lett. 22: 119–127.
Knott, J. A. et al. 2019. Shifts in forest composition in the eastern United States. – For. Ecol. Manage. 433: 176–183.
Lévesque, M. et al. 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in central Europe. – Agric. For. Meteorol. 197: 1–12.
Li, X. et al. 2012. Age dependence of xylogenesis and its climatic sensitivity in Smith fir on the south-eastern Tibetan Plateau. – Tree Physiol. 33: 48–56.
Martin-Benito, D. and Pederson, N. 2015. Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. – J. Biogeogr. 42: 925–937.
Maxwell, J. T. and Harley, G. L. 2017. Increased tree-ring network density reveals more precise estimations of sub-regional hydroclimate variability and climate dynamics in the Midwest, USA. – Clim. Dyn. 49: 1479–1493.
Maxwell, J. T. et al. 2019. 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 USA. – J. Geophys. Res. Biogeosci. 124: 3798–3813.
McEwan, R. W. et al. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. – Ecography 34: 244–256.
Meinzer, F. C. et al. 2013. Above- and belowground controls on water use by trees of different wood types in an eastern US deciduous forest. – Tree Physiol. 33: 345–356.
Mishra, V. and Cherkauer, K. A. 2010. Retrospective droughts in the crop growing season: implications to corn and soybean yield in the Midwestern United States. – Agric. For. Meteorol. 150: 1030–1045.
Novick, K. A. et al. 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. – Nat. Clim. Change 6: 1023–1027.
Nowacki, G. J. and Abrams, M. D. 2008. The demise of fire and 'mesophication' of forests in the eastern United States. – BioScience 58: 123–138.

Supplementary material (available online as Appendix ecog-05055 at <www.ecography.org/appendix/ecog-05055>). Appendix 1.

Oren, R. and Pataki, D. E. 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. – Oecologia 127: 549–559.
Pan, Y. et al. 2011. A large and persistent carbon sink in the world's forests. – Science 333: 988–993.
Pederson, N. et al. 2013. Is an epic pluvial masking the water insecurity of the greater New York City region? – J. Clim. 26: 1339–1354.
Pederson, N. et al. 2015. Climate remains an important driver of post-European vegetation change in the eastern United States. – Global Change Biol. 21: 2105–2110.
Phillips, O. L. et al. 2009. Drought sensitivity of the Amazon rainforest. – Science 323: 1344–1347.
Primicia, I. et al. 2015. Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate. – For. Ecol. Manage. 354: 77–86.
Robertson, P. A. 1992. Factors affecting tree growth on three lowland sites in southern Illinois. – Am. Midl. Nat. 128: 218–236.
Roman, D. et al. 2015. The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought. – Oecologia 179: 641–654.
Seager, R. et al. 2012. The 1960s drought and the subsequent shift to a wetter climate in the Catskill Mountains region of the New York City watershed. – J. Clim. 25: 6721–6742.
Shuman, B. N. and Marsicek, J. 2016. The structure of Holocene climate change in mid-latitude North America. – Quat. Sci. Rev. 141: 38–51.
Stokes, M. and Smiley, T. 1968. An introduction to tree-ring dating. – Univ. of Chicago Press.
Swain, S. and Hayhoe, K. 2015. CMIP5 projected changes in spring and summer drought and wet conditions over North America. – Clim. Dyn. 44: 2737–2750.
Taneda, H. and Sperry, J. S. 2008. A case-study of water transport in co-occurring ring-versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. – Tree Physiol. 28: 1641–1651.
Vose, R. et al. 2017. Temperature changes in the United States. Publications, agencies and staff of the U.S. Department of Commerce, 587. – In: Wuebbles, D. J. et al. (eds), Climate science special report: a sustained assessment activity of the U.S. Global Change Research Program. U.S. Global Change Research Program, Washington, DC, USA, pp. 267–300.
Woodcock, D. 1989. Climate sensitivity of wood-anatomical features in a ring-porous oak (*Quercus macrocarpa*). – Can. J. For. Res. 19: 639–644.
Yi, K. et al. 2019. Linking variation in intrinsic water-use efficiency to isohydricity: a comparison at multiple spatiotemporal scales. – New Phytol. 221: 195–208.
Zimmermann, M. H. 1983. Xylem structure and the ascent of sap. – Springer.