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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Evidence that higher [CO_2] increases tree growth sensitivity to temperature: a comparison of modern and paleo oaks

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Abstract To test tree growth sensitivity to temperature under different ambient CO_2 concentrations, we determined stem radial growth rates as they relate to variation in temperature during the last deglacial period, and compare these to modern tree growth rates as they relate to spatial variation in temperature across the modern species distributional range. Paleo oaks were sampled from Northern Missouri, USA and compared to a pollen-based, high-resolution paleo temperature reconstruction from Northern Illinois, USA. Growth data were from 53 paleo bur oak log cross sections collected in Missouri. These oaks were preserved in river and stream sediments and were radiocarbon-dated to a period of rapid climate change during the last deglaciation (10.5 and 13.3 cal kyr BP). Growth data from modern bur oaks were obtained from increment core collections paired with USDA Forest Service Forest Inventory and Analysis data collected across the Great Plains, Midwest, and Upper Great Lakes regions. For modern oaks growing at an average [CO_2] of 330 ppm, growth sensitivity to temperature (i.e., the slope of growth rate versus temperature) was about twice that of paleo oaks growing at an average [CO_2] of 230 ppm. These data help to confirm that leaf-level predictions that photosynthesis and thus growth will be more sensitive to temperature at higher [CO_2] in mature trees—suggesting that tree growth forest productivity will be increasingly sensitive to temperature under projected global warming and high-[CO_2] conditions.

Keywords Carbon dioxide · NPP · GPP · Photosynthesis · Forest productivity

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Introduction

As global atmospheric [CO_2] continues to rise over the next centuries, many regions across the globe are projected to undergo a phase of anthropogenically driven climate change that will cause key forest physiological functions to be impacted by warmer temperatures (IPCC 2013). Given the importance of forests to the global carbon cycle (Pan et al. 2011) and the unknown magnitude to which temperature × [CO_2] interactions may affect forest productivity, there is a need for a keen understanding of whether tree growth responds in the direction and magnitude predicted by the theory embedded within large-scale models (Hickler et al. 2008; Medlyn et al. 2011; Anderson-Teixeira et al. 2013; Rogers et al. 2017).

CO_2 enrichment studies of trees and forests (e.g., Norby and Zak 2011; Bader et al. 2013; Dawes et al. 2015; Terrer et al. 2016) have yielded inferences for CO_2 effects on

growth but formal testing for interactions with thermal conditions have not been possible, because these experiments operated over a relatively modest range of inter-annual variation in temperature at each site and have not been replicated within a species across a strong temperature gradient. Likewise, cross-species and within-species tree growth or forest productivity has often been related to temperature in a linear or quasi-linear manner (Lieth 1973; Gholz 1982; Naurzbaev et al. 2004; Anderson et al. 2006; Voelker 2011), but these studies have not addressed potential interactions with CO_2. Tests of temperature × $[CO_2]$ interactions have been conducted at small scales; on tree branches (Teskey 1997) or on seedlings or saplings grown within an enclosure (Norby and Luo 2004; Ghannoum et al. 2010; Ameye et al. 2012; Bauweraerts et al. 2013). Meta-analytical approaches of these small-scale temperature × $[CO_2]$ experiments have reported, on average, that interactive effects could not be discerned from the null hypothesis of no interaction (Wang et al. 2012a, b; Baig et al. 2015). Therefore, representing this interaction in large-scale models has been challenging due to inconsistent experimental results and no robust assessments of how the growth of mature trees, growing in situ, will respond to $[CO_2]$ and temperature gradients.

A recent survey of contemporary large-scale models of terrestrial C_3 vegetation productivity indicates that photosynthetic responses to temperature and $[CO_2]$ and associated canopy uptake of $[CO_2]$ are built upon a similar scaffolding of underlying theory (Farquhar et al. 1980; von Caemmerer and Farquhar 1981), but with substantial differences in how the theory is applied and the models are parameterized (Rogers et al. 2017). Within these large-scale models, photosynthetic rates are generally limited through the minimum value of either the maximum carboxylation rate of 1,5-bisphosphate carboxylase/oxygenase (Rubisco) or the maximum rate of electron transport that drives ribulose-1,5-bisphosphate (RUBP) regeneration—both of which are dependent on temperature (Collatz et al. 1991; Bernacchi et al. 2001; Kattge and Knorr 2007). These various approaches to capturing temperature effects on photosynthetic rates can result in substantial differences among models (Ali et al. 2015). C_3 photosynthesis generally peaks at higher temperatures at progressively greater $[CO_2]$, because photorespiration is reduced at high $[CO_2]$ (Berry and Björkman 1980; Farquhar et al. 1980; Long 1991; Long and Bernacchi 2003). This response is largely driven by the solubility of O_2 versus CO_2 with temperature as well as a differential affinity of Rubisco towards O_2 versus CO_2 as temperature changes (Ku and Edwards 1977; Monson et al. 1982; Jordan and Ogren 1984; Sage and Sharkey 1987). Importantly, these photosynthetic responses are embedded within large-scale models, which results in predictions that the productivity of mature forests will become increasingly sensitive to temperature at high $[CO_2]$ (Medlyn et al. 2011) despite little to no direct evidence from mature trees.

Studies of tree-ring carbon isotope discrimination have documented how increasing $[CO_2]$ has caused tree-level, canopy integrated photosynthetic rates and water use efficiency to rise (Feng 1998; Andreu-Hayles et al. 2011; Peñuelas et al. 2011; Leonardi et al. 2012; Silva and Anand 2013; Lévesque et al. 2014; Saurer et al. 2014; van der Sleen et al. 2015; Voelker et al. 2016). Evidence from across the last glacial maximum to the present indicates that water use efficiency of woody species became more variable as $[CO_2]$ and temperatures rose (Gerhart et al. 2012). The conventional wisdom suggests that rising $[CO_2]$ and temperatures, in the absence of non-linear effects associated with greater drought stress or extraordinary heat waves, will increase photosynthetic rates and carbon storage in woody tissues of trees (Salzer et al. 2010; Medlyn et al. 2011; Büntgen et al. 2014). In contrast, studies from a wide array of ecosystems suggest that increasing $[CO_2]$ may not have increased the stem radial growth rates of mature trees (Andreu-Hayles et al. 2011; Peñuelas et al. 2011; Bader et al. 2013; Lévesque et al. 2014; Silva and Anand 2013; van der Sleen et al. 2015). In some of these studies, rising temperatures have been implicated in increasing evaporative demand and drought stress, which would override any effects of rising $[CO_2]$ on growth, since cell division and expansion are more closely regulated by water potentials than are photosynthetic rates (Hsiao 1973; Muller et al. 2011). Indeed, similar conclusions were drawn from a process model run for many sites and species across the Mediterranean region (Gea-Izquierdo et al. 2016). Moreover, dendrochronological methods employed by a study on tropical trees (van der Sleen et al. 2015) may have masked what would otherwise be increasing growth trends in a number of the species (Brienen et al. 2016). Therefore, additional integrated data-modeling integrations (sensu Gea-Izquierdo et al. 2016) that carefully incorporate the effects of water use efficiency and drought stress on cambial activity and allocation will be necessary before conclusive evidence will be gained on how recent trends in tree-ring growth have been modified by temperature × $[CO_2]$ interactions.

Studies of acclimation, migration, and adaptation responses to the past variation in $[CO_2]$ and/or rapid climate change events can yield important insights for predicting ecosystem responses to novel conditions of the future when this evidence is placed in the context of knowledge gained from observations of modern ecosystems, modeling, and experimentation (Williams and Jackson 2007; Voelker et al. 2016). To address the hypothesis that tree growth rates have depended upon a strong interaction between temperature and $[CO_2]$, we determined the temperature sensitivity of

(1) stem radial growth in modern bur oaks (*Quercus macrocarpa* Michx.) sampled across much of their wide distributional range (Fig. 1; Burns and Honkala 1990) and (2) stem radial growth of paleo oak logs radiocarbon dated to the last deglacial period (e.g., Voelker et al. 2012) and matched to a high resolution (i.e., 100-year resolution) temperature proxy for the region (Gonzales et al. 2009). The collection sites for the paleo oaks and the temperature proxy record are located between the northerly centered modern distributional range of bur oaks and the southerly displaced distribution of the oak genus during the last glacial maximum (Fig. 1).

Across central and eastern North America, the last glacial maximum to the early Holocene was defined by temperatures rising between 3 and 10 °C, depending on the location and seasonal resolution of the individual proxy records (Webb and Bryson 1972; Shane and Anderson 1993; Yu and Eicher 1998; Viau et al. 2006; Nordt et al. 2008; Gonzales et al. 2009; Grimley et al. 2009; Shuman et al. 2009; Voelker et al. 2012). The paleo oak and paleo temperature proxy record collection areas are both located near the Laurentide ice sheet margins during the last glacial maximum, thus experiencing the greatest climate change velocity since that time (Sandel et al. 2011). The range of [CO_2] from approximately 230 ppm for the paleo trees to 330 ppm for the modern trees would also be expected to provide greater leaf gas exchange responses compared to CO_2 enrichment studies, because the response of leaf gas exchange to increasing [CO_2] is steepest at low [CO_2] (Voelker et al. 2016). Thereby, the potential for contrasting trees that grew across a wide range of temperatures but at different and non-overlapping [CO_2] affords an opportunity to address whether tree growth sensitivity to temperature is increased at higher ambient [CO_2] levels as predicted at the leaf level by theory and empirical evidence.

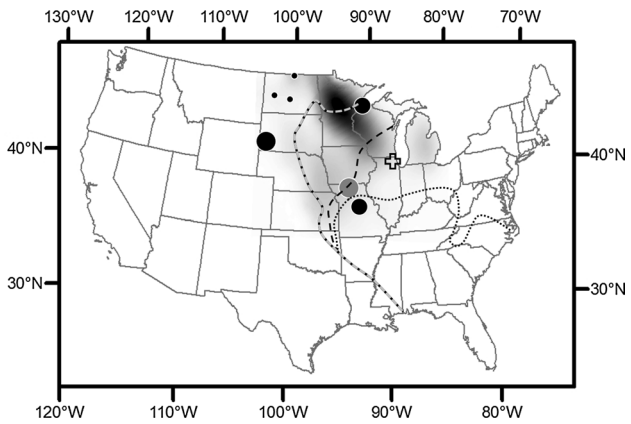

Fig. 1 Locations for modern and paleo oak sampling sites and paleo oak range edges overlaid on kriged values of relative sampling frequency of bur oak site trees from USDA Forest Service Forest Inventory data. For the kriged data, greater bur oak frequencies are indicated by darker shading. Oak tree-ring collection sites are shown by *circles*, with symbol size representing the proportional size of each collection. *Black circles* indicate that only modern oaks were sampled and the *gray circle* is the region, where modern and paleo oaks were sampled. The collection site for the palynology-based paleotemperature record is shown with a *cross*. The *gray/black-dashed*, *dashed black* and *dotted black lines* indicate the western/northern range edge for all oak taxa at 10, 14, and 18 cal kyr BP. Redrawn after Williams et al. (2004)

Materials and methods

Modern and paleo wood collections

For modern bur oaks, we used 373 cross-dated increment cores from 279 trees at collections spread across the central and western range of bur oaks (Fig. 1). The collections included locations in central Missouri, northern Wisconsin, and the Black Hills of South Dakota (Voelker et al. 2014) as well as northern MO (Stambaugh et al. 2011) and North Dakota (Sieg et al. 1996). Data from Sieg et al. (1996) were downloaded from the International Tree-Ring Data Bank (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring), and the tree cores were inspected, where they were archived at the University of Arizona Laboratory for Tree-Ring Research. For all increment cores, the number of tree rings to the pith that were missing due to off-center borer alignment was estimated and growth increments for those rings empirically modeled. Tree-ring measurements and cross-dating procedures have been described previously (Sieg et al. 1996; Stambaugh et al. 2011; Voelker et al. 2014).

Paleo oak log cross sections were collected from streams and stream banks in northern Missouri, USA, using a chainsaw as detailed elsewhere (Guyette et al. 2008 Stambaugh et al. 2011; Voelker et al. 2012). Composed of alluvial sediments, the stream channels and banks in northwestern Missouri are conducive to the frequent burial and excavation of wood (Guyette et al. 2008). Paleo oaks were distinguished from other species by their distinctive ring-porous anatomy, extensive radial cracks that follow bands of ray parenchyma cells and black to gray coloration of the heartwood that occurs after hundreds of years of burial. In general, only samples with more than about 100 rings were collected, which even for a tree with very low growth rates (Fig. 2), corresponds to a minimum diameter of about 20 cm. This minimum size would have been similar for the modern bur oaks sampled.

Radiocarbon dating

Procedures, analytical laboratory, raw data, and uncertainty associated with radiocarbon dating of paleo oaks were published previously (Voelker et al. 2012) and are freely

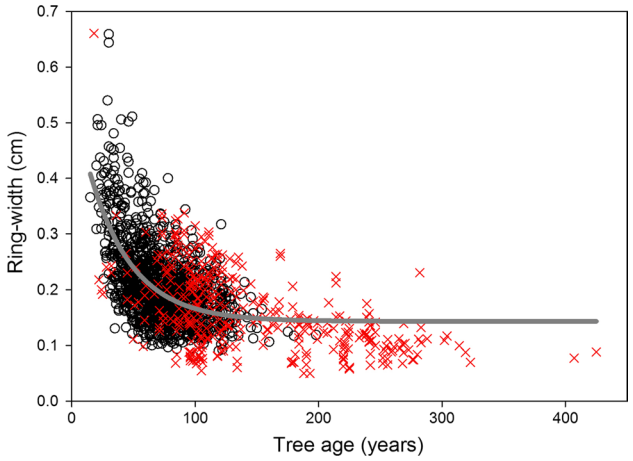

Fig. 2 Lifetime averaged ring width plotted versus tree age for modern bur oak trees across their range in the United States. Data were provided by the USDA Forest Service FIA program (*open circles*, see "Methods and materials") and combined with tree core data sampled for this research (*red crosses*). The regression relationship used as an index of modern growth was: ring-width $= 0.1435 + 0.4077e^{(-0.0288\text{tree age})}$. A color version of this figure is available online

available (http://esapubs.org/archive/mono/M082/006/suppl-1.htm). Briefly, for radiocarbon dating, small blocks removed from the outer edge of each log cross section underwent acid-alkali-acid treatment to remove mobile compounds and impurities before radiometric measurements of ^{14}C content. To calibrate radiocarbon ages, we used the CALIB Version 6.0 software (Stuiver and Reimer 1993) with the INTCAL13 data set (Reimer et al. 2013). Since the radiocarbon dates were from the outer edge of each tree, the dates assigned to younger cambial ages (i.e., number of rings from the tree center) were adjusted earlier in time to account for radiocarbon ages identified from the last ~20 years of growth.

Comparisons of tree growth

Tree growth was quantified for modern bur oaks using the increment core collections noted above, and the results were merged with data from >1800 bur oak "site index trees" downloaded from the USDA Forest Service Forest Inventory and Analysis (FIA) program (http://apps.fs.fed.us/fiadb-downloads/datamart.html). The reason for using these data is that they present a comprehensive record of spatial variation in the growth of modern trees than could be obtained from any individual study. Although the increment cores have [unfortunately] not been archived in most regions of the United States, the Interor West FIA program has made greater use of these data by measuring individual tree rings, archiving the samples and making these data available to the public (DeRose et al. 2013, 2016). The FIA data used here were collected from trees growing across 11 states (IL, IN, IA, KS, MI, MN, MO, NE, ND, SD, WI) representing a wide array of environmental and temperature conditions. We used data from site index trees rather than the standard FIA data, because only site index trees have age estimates, as counted from increment cores. There is expected to be some error in ring-count derived ages of site index trees, but this should be small, because ring-porous species generally do not have missing rings. The number of rings missing to the pith would have been visually estimated for off-center cores from site index trees. This process would be expected to include some increased level of error compared to estimates from a trained dendrochronologist. Therefore, the site index trees likely included slightly greater variation among trees in growth rate estimates, but should include little directional bias. As such, the lifetime average radial growth rate for each tree was estimated by dividing the tree diameter inside bark by two and then dividing by tree age. Like most tree species, radial growth shows a negative exponential relationship to tree age (Fig. 2).

To compare the growth rates of trees across space or time, we needed to account for the effects of age on growth rate because trees sampled may have been young (i.e., apparently fast growing) or old (i.e., apparently slow-growing) (Fig. 2). To adjust for tree age, the lifetime average ring width for each modern oak was divided by that predicted by the regression relationship fitted to the age of each tree and multiplied this ratio by 100 to yield an index of modern growth with an average of 100% (i.e., growth rate %, see Fig. 2). No paleo oaks were included in the calculation of the regression relationship in Fig. 2.

The potential impact of gradients in aridity/wetness across the species range this potential signal were removed from the FIA data set to ensure that the effect of temperature on tree growth rates obtained from the modern oaks was did not include drought effects and could thereby be more accurately compared to leaf-level predictions of photosynthetic responses to temperature and $[CO_2]$. This included regressing growth rate % data from individual FIA trees against the estimated 1960–1990 normal June–August average of climatic moisture deficit (CMD), which is defined as precipitation minus potential evapotranspiration (see the "Climate data"). The resulting polynomial relationship (growth rate $\% = -0.0152\text{CMD}^2 + 1.7871\text{C}$ MD $+ 52.376$, $R^2 = 0.113$, $P < 0.001$) was used to predict and remove the impacts of CMD on growth rate % for each tree in the FIA data set.

The raw ring-width growth rates of the 53 paleo oaks investigated here were measured as part of previous wood anatomical analyses (Voelker et al. 2012) but have not been published. The total number of oaks with ^{14}C dates during the deglacial and early Holocene periods was 79, but some

trees were not measured for the growth analyses because of difficulty in preparing highly degraded samples for measurements that would be comparable to modern oaks. For growth measurements on each cross section, we measured between 5 and 15 rings from inner, middle, and outer sampling locations, providing growth rates for three cambial ages spaced apart by 20–50 years on average. The cambial ages of each measurement zone were noted as part of the sampling. We avoided measuring bands of growth suppression, indicative of shading or injury, as well as anomalously large rings characteristic of reaction wood. Ring widths of paleo oaks were measured without letting the wood dry out (i.e., at wood moisture contents >30%) to prevent shrinkage of samples.

For paleo oaks, we calculated growth rate % using the same approach described above for modern oaks. However, before doing so, we had to account for two factors. The first of these is the difference between cambial age-specific growth rates of the paleo oaks versus the lifetime-averaged growth rates of the modern oaks and how these variables differ with cambial age. For this purpose, a correction factor was estimated by comparing both types of growth calculations as applied to each cambial age of the 279 modern bur oak trees for which increment cores had been sampled (Figure S1). The correction factor varies with tree age, because at progressively younger tree ages, the correction factor must necessarily approach one, whereas at older ages, the lifetime growth rates will include fast-growing younger periods that the age-specific growth rates do not. For bur oaks, the correction factor for ages >100 years approaches a value of 1.29 and can be highly variable, where sample sizes are low at progressively older ages. Therefore, we fitted an asymptotic relationship to the age-related correction factor (Figure S1), and applied the correction to each of the three age-specific growth rate measurements made for each paleo oak.

Comparing growth rates of trees from a single region (i.e., paleo oaks) to trees encompassing many different growing conditions across the species range, the second factor to account for is regional variation in growth rate. To determine the correction necessary for the environmental and soil conditions present at the paleo sampling sites, we used increment cores from 73 of the 279 modern oaks sampled from the Northern Missouri region, where paleo oaks were also collected (see gray dot in Fig. 1, and for detailed site information, see Stambaugh et al. 2011). From these data, we calculated an initial growth rate % equal to 133.2%, whereas the expected value across all oaks for the ~23 °C summer mean air temperature of June, July, and August (hereafter T_{air}) of this region is 112.7% (see "Results"). The locally greater growth rate % reflects the deep and highly productive loess soils of this region, which are dominated by intensive agricultural land uses. To accurately compare paleo oaks from a single region known to have higher than expected growth rates for a given T_{air} to the overall growth trends across all oaks, each raw paleo oak growth rate % was multiplied by the ratio of predicted to regional growth rate % (i.e., 112.7/133.2).

Climate data

Reconstructed summer paleo T_{air} were obtained from a high-resolution pollen record from Crystal Lake, Illinois (IL) (Gonzales et al. 2009). For our analyses, summer paleo temperatures were adjusted upward by 2.2 °C, to reflect the differences in T_{air} between the Missouri collection sites for paleo oak wood and the site, where sediment cores were collected in Illinois (Figure S2). These comparisons of modern T_{air} data were from monthly estimates of minimum and maximum temperatures since 1895, as obtained from the PRISM climate group (http://www.prism.oregonstate.edu/).

Modern T_{air} and climatic moisture deficit values were obtained for each tree using estimates of the latitude, longitude, and elevation data as inputs for ClimateNA v5.30, which is an extension of the Climate WNA software described by Wang et al. (2012a, b). Upon our initial investigation, paleo oaks were found to occur across a temperature range of about 10 °C, while modern oaks only occurred across an 8.5 °C range. We, therefore, used the original estimates of paleo T_{air} from Gonzales et al. (2009) as well as a scenario in which paleo T_{air} was constrained to a 8.5 °C range while maintaining the same mean paleo T_{air} by employing the following relationship: paleo constrained $T_{air} = \text{paleo } T_{air}^{0.9314} + 3.251$.

Statistical analyses

Regression coefficients and their significance were established with ordinary least squares (OLS) techniques using the SigmaPlot software (Systat Software, Inc., San Jose, CA, USA).

The program SMATR version 2.0, (standardized major axis tests and routines, Warton et al. 2006) was used with OLS methods to test whether the slopes of growth rate % versus T_{air} differed among modern and paleo wood collections.

Results

Our paleo oak wood collections dated to the Younger-Dryas (i.e. 12.9–11.5 cal kyr BP) likely grew near the northwest margin for bur oak, because the pollen record for the oak genus shows a northerly range boundary across the same region and time period (Fig. 1). During this period and

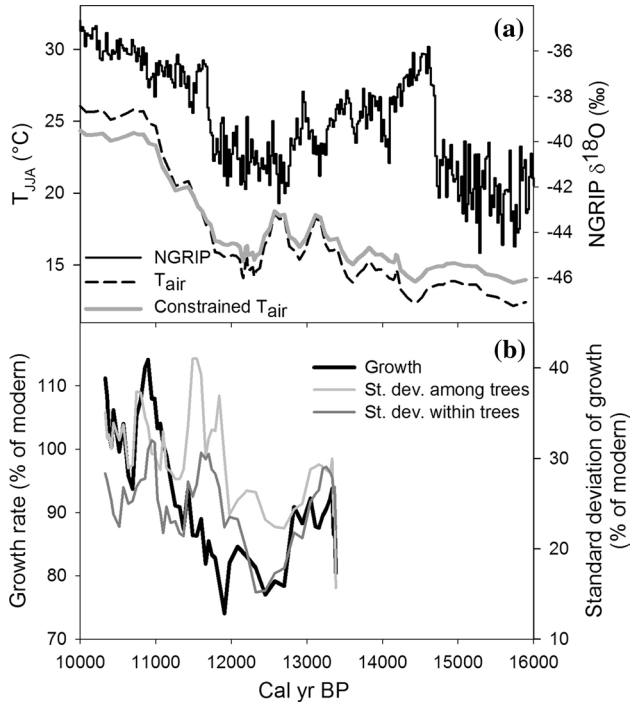

Fig. 3 Time-related trends in Greenland ice core $\delta^{18}O$ (NGRIP) and summer temperatures (T_{air}, after Gonzales et al. 2009) and constrained T_{air} (see "Methods and materials") (**a**), percentage radial growth rates, 9-point moving standard deviation among trees and a 9-point moving average of the standard deviation within each tree (**b**). Paleo T_{air} data in **a** were smoothed with a 3-point moving average. The standard deviations in **b** were smoothed using a first degree polynomial loess relationship. Among tree standard deviations are indicative of multi-decadal to centennial scale variability in growth, whereas within-tree standard deviations are indicative of decadal to multi-decadal variation in growth

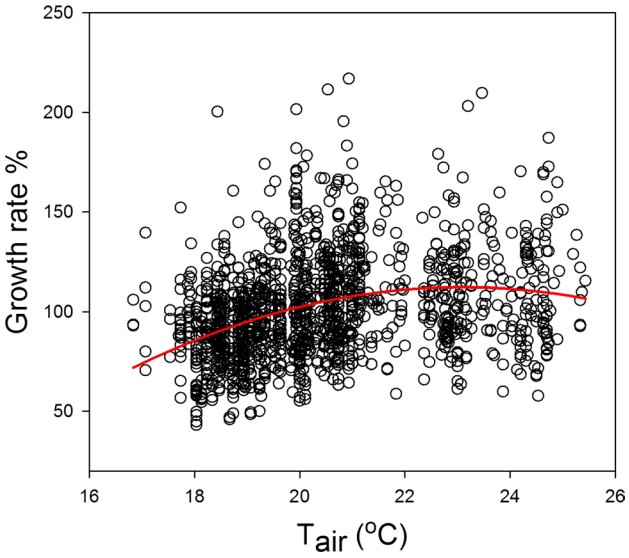

Fig. 4 Radial growth rates of modern oaks from the FIA data set (each data point is one tree) plotted versus the summer mean temperatures (T_{air}). Note the non-linear response to growth rate % that peaks at approximately 23 °C. A color version of this figure is available online

into the early Holocene, this region underwent dramatic changes in T_{air}. The pollen record employed here estimated a T_{air} range of approximately 10 °C (Fig. 3a). We also present a scenario in which the range of paleo T_{air} is constrained to only 8.5 °C (Fig. 3a). This constrained T_{air} scenario helped assess the potential incongruence between the 10 °C T_{air} range (13–23 °C) for the Midwest during the last deglacial period compared to the 8.5 °C T_{air} range (17–25.5 °C) for the core species distribution of modern bur oaks that excludes widespread refugia.

Close inspection of Fig. 3 reveals a multi-centennial lag between the pollen-based T_{air} record and either of the NGRIP ice core record or variation in oak growth rates and growth variability. As noted previously (Voelker et al. 2015), climate variability inferred from the pollen record for this region probably reflects a lagged response compared to the North Atlantic event stratigraphy due to the time it takes for a dominant species to decline in abundance and the time it takes a newly colonizing species to migrate and establish in response to rapid climate change. This differs from the alternate hypothesis that there was a multi-century lag in the climatic response of the region compared to North Atlantic events. A shift of T_{air} data to 200 years earlier maximized the correlations between paleo T_{air} and the dependent variables, as shown in Fig. 3b (data not shown). After shifting the paleo T_{air} data, there were strong correlations between T_{air} and the moving averages of growth rate % ($r = 0.86$, $P < 0.001$) and standard deviations of growth among trees ($r = 0.59$, $P = 0.001$) and within trees ($r = 0.49$, $P = 0.013$). Correlations with constrained paleo T_{air} yielded similar results ($r = 0.86$, 0.59, and 0.50, respectively).

The changes in T_{air} during the last deglacial corresponded closely to shifts in average tree growth rates, within-tree variation in growth, and among tree variation in growth (Fig. 3a, b). These patterns generally agree with modern growth rate % data from the FIA data set that exhibits a positive trend at lower T_{air} and a broad peak that is maximized at approximately 23 °C (Fig. 4). It is well known that high temperatures can decrease net photosynthesis, even in plants or trees adapted to warm growing conditions (Berry and Björkman 1980; Vårhammar et al. 2015; Way et al. 2015). To minimize the potential impact of these non-linear T_{air} responses, we removed any growth rate % data from modern or paleo oaks, where T_{air} exceeded 23 °C in further analyses comparing linear slopes of T_{air} effects on growth rate %. Across temperatures equal to or below 23 °C, modern oaks increased their growth rates by about 5.7% for each degree Celsius

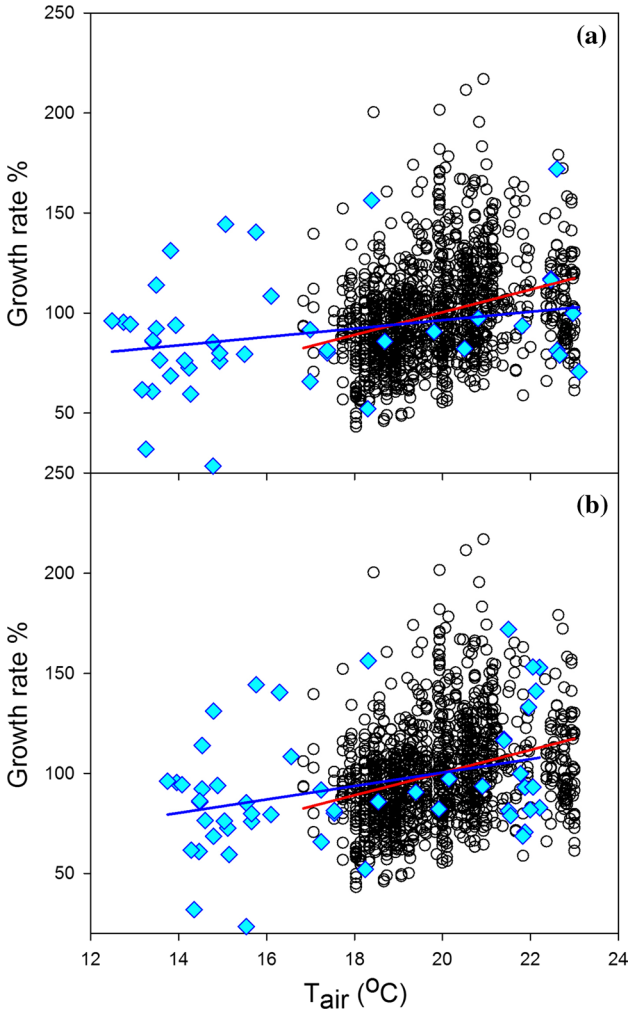

Fig. 5 Radial growth rates of modern (*black open circles* and *red regression line*) and paleo oaks (*blue diamonds* and *blue regression line*) plotted versus the summer mean temperatures (T_{air}). Each data point is one tree. Paleotemperature data in **a** are after Gonzales et al. (2009) and adjusted upwards by 2.2 °C for differences between Missouri and Illinois. Paleotemperature data in **b** were constrained to a range of 8.5°, which matches the range of T_{air} spanned by the modern FIA data set. Due to non-linear growth rate % responses to T_{air} (Fig. 4), any growth rate % data associated with T_{air} exceeding 23 °C were excluded from these figures and subsequent analyses. A color version of this figure is available online

in growing season T_{air} (growth rate % $= 5.65T_{air} - 12.60$, $R^2 = 0.097$, $P = 0.001$). In contrast, paleo oaks exhibited growth rate increases of only 2.1% per degree celsius (growth rate % $= 2.10T_{air} + 54.55$, $R^2 = 0.065$, $P = 0.100$, Fig. 5a) or 3.36% per degree Celsius for a range of paleo T_{air} constrained to 8.5 °C (growth rate % $= 3.36$ constrained $T_{air} + 33.24$, $R^2 = 0.117$, $P = 0.013$, Fig. 5b). The 200-year lag between paleo T_{air} and paleo oak growth rate % resulted in essentially no change to growth sensitivity to T_{air} of the paleo oaks (data not shown).

Discussion

Temperature and CO_2 both strongly affect the physiological functioning, allocation, productivity, and biogeochemical cycling of forests. As a result, temperature impacts have been studied extensively (Lieth 1973; Gholz 1982; Anderson et al. 2006; Way and Oren 2010; Voelker 2011; Larjavaara and Muller-Landau 2011; De Frenne et al. 2013; Reich et al. 2014). Meanwhile, CO_2 effects on forests have also been intensively studied in observational settings (Voelker et al. 2006; Andreu-Hayles et al. 2011; Peñuelas et al. 2011; Bader et al. 2013; Gerhart et al. 2012; Lévesque et al. 2013; Silva and Anand 2013; van der Sleen et al. 2015) as well as in experiments (Ainsworth and Long 2005; McCarthy et al. 2010; Norby and Zak 2011; Bader et al. 2013; Hungate et al. 2013; Dawes et al. 2015; Terrer et al. 2016). Despite massive research efforts on T_{air} and [CO_2]-effects on forests, testing of interactions between these factors on the growth of mature trees is, to our knowledge, non-existent.

The lack of studies designed to address mature trees is even more alarming considering that most models used to project forest productivity on regional to global scales have a positive $T_{air} \times [CO_2]$ interaction embedded within them (Medlyn et al. 2011). Essentially, elevated CO_2 increases the optimum temperature for C_3 photosynthesis. At the leaf-scale, C_3 photosynthesis is constrained by Rubisco, which has a stronger affinity for CO_2 but at higher temperatures has a stronger affinity for O_2. As atmospheric [CO_2] increases, and thereby, leaf internal [CO_2]) increases (Voelker et al. 2016), the temperature at which Rubisco has a stronger affinity for O_2 also increases (Ku and Edwards 1977; Monson et al. 1982; Jordan and Ogren 1984; Sage and Sharkey 1987; Long 1991; Long and Bernacchi 2003). As a result, higher [CO_2] should lead to photosynthetic rates being more sensitive to temperature. Our results help fill the $CO_2 \times T_{air}$ knowledge gap; they indicate that oak trees exposed to low [CO_2] during the last deglacial were characterized by growth sensitivity to T_{air} (i.e., slope of growth rate % versus T_{air}) that was 37–59% of modern trees exposed to high [CO_2]. This difference in sensitivity depended upon whether we used the original paleo T_{air} estimates of Gonzales et al. (2009) (Fig. 5a) or a scenario, where paleo T_{air} estimates constrained to equal the range of temperatures observed for modern oaks (Fig. 5b). Compared to the paleo oaks, the two-fold enhancement of growth-sensitivity to T_{air} of modern trees exposed to [CO_2] suggests that trees growing in a high-CO_2 future will be even more sensitive to variability in T_{air}, where drought stress, heat waves, and/or nitrogen limitation do not preempt these effects from being fully manifested.

Despite the lack of T_{air} × [CO_2] studies on mature trees, evidence from studies on seedlings and saplings may yield pertinent insights for comparison to our own results. Some studies have observed that the theoretical predictions of a T_{air} × [CO_2] interaction on photosynthesis are not observed (Tjoelker et al. 1998; Lewis et al. 2001; Luomala et al. 2003; Tingey et al. 2007; Ghannoum et al. 2010), whereas positive evidence was observed in another recent study (Quentin et al. 2015). In the latter, trees underwent factorial enriched [CO_2] and warming treatments and were grown to 10 m height, but no T_{air} × [CO_2] effects were found for tree growth. Further studies of T_{air} × [CO_2] effects on trees grown to canopy closure and beyond are needed. A review and meta-analysis by Wang et al. (2012a, b) found that the growth of small woody plants was not significantly affected by elevated T_{air} and [CO_2] compared to elevated [CO_2] alone. Experiments on young red oak (*Quercus rubra* L.) confirmed an interactive effect of T_{air} and [CO_2] on both net photosynthesis and biomass; the moderating effects of CO_2 having been greater for intermittent but not strong heat waves compared to only moderate heating that was uniformly applied (Ameye et al. 2012; Bauweraerts et al. 2013). These results highlight that for real-world applications, T_{air} × [CO_2] interactions may be best assessed using variability in heating to understand non-linear responses to T_{air}. A second, and more recent meta-analysis of seedling or sapling growth responses to experimental modifications of T_{air} and [CO_2] found a wide array of growth responses, some of which supported the existence of a T_{air} × [CO_2] interaction (Baig et al. 2015). The same study found that in situ testing of CO_2 effects across studies, where both species and temperature differed also provided some support for a T_{air} × [CO_2] interaction. As noted by Quentin et al. (2015), perhaps the divergent results among these many studies could be reconciled if there were knowledge of phylogenetic and/or functional group-variation in T_{air} impacts not only photosynthetic capacity, but also CO_2 photo-compensation point, mesophyll conductance, and stomatal conductance. Finally, plant- microbe interactions are an important aspect of plant responses to environmental change (Becklin et al. 2016). Indeed, plants that associate with ectomycorrhizal fungi appear to be able to better avoid nitrogen limitation of growth during CO_2 enrichment, whereas those that associate with arbuscular mycorrhizal fungi were less able to capture CO_2 in growth due to nitrogen limitation (Terrer et al. 2016). Oaks associate with a number of ectomycorrhizal fungi, which probably helps explain the strong T_{air} × [CO_2] interaction documented here that may not be present in other species that associate with arbuscular mycorrhizae.

Uncertainties in estimating growth-sensitivity to temperature

Although the T_{air} range of FIA bur oak data is only 8.5 °C, the range in paleo T_{air} of about 10 °C estimated by Gonzales et al. (2009) may very well be accurate, because bur oaks often survive in colder and warmer refugia based on the disturbance and resource regime of the rivers like those occurring in northern Missouri. For example, on the cold end of the modern T_{air} gradient, bur oaks occur along rivers as far northeast as New Brunswick, Canada (McPhee and Loo 2009), along rivers or streams within the lake-effect zone of Lake Superior west of Port Wing, WI and south of Sault St. Marie, MI (S. Voelker, Pers. Obs.), along rivers in the vicinity of Winnipeg, Canada (St. George and Nielsen 2002) and along headwater streams at the high elevation limit of the species in the Black Hills of South Dakota (~1630 m, S. Voelker, Pers. Obs.). Bur oaks also grow in much warmer climates compared to that delineated by FIA data, occurring sporadically along rivers across Texas, and as far south as Brazos Bend State Park (i.e., about 50 km from the Gulf of Mexico). FIA data from bur oaks are largely absent at these isolated locations at the cold edges of the species range, so the modern data used to compare to the paleo data do not overlap for the cooler temperature range (Fig. 4). Expanded analyses of oak growth sensitivity to T_{air} across these refugia and the 300+ paleo oaks our group has ^{14}C-dated across the entire Holocene could be beneficial to understanding a larger, non-linear range of temperature responses.

Both scenarios for paleo T_{air}, were considered in part because of the potential impact of plant species changes and no-analog species assemblages, meaning that there were combinations of species that occurred regularly in the past that rarely or never occur together under modern climate conditions. These vegetation dynamics are thought to have resulted from differential migration speeds among tree species, trophic cascade responses to the mass extinction of mega-herbivores at the end of the last glacial maximum, and no-analog climatic conditions (Shane and Anderson 1993; Yu and Wright 2001; Shuman et al. 2009; Williams et al. 2004; Grimm and Jacobson 2004; Gill et al. 2009; Voelker et al. 2015). Therefore, the no-analog conditions noted above as well as differential species competitive effects (Wright et al. 2015) would have contributed some unknown level of uncertainty to our estimates of growth sensitivity to T_{air}.

Differences in sampling protocols between modern and paleo oaks resulted in little bias for growth sensitivity to T_{air}. The FIA oaks were selected as site index trees, indicating that they were dominant or co-dominant trees of an important species for that entire forest inventory plot that were also free from apparent stem or crown damage. Trees

sampled for dendrochronological studies were selected, because they were dominant or co-dominant, lacking obvious stem, or crown damage and located next to streams or rivers, so they would have been growing under conditions comparable to those experienced by the paleo oaks. Despite the difference in tree selection criteria (i.e., near rivers or randomly sampled across the landscape), once tree age was accounted for, the growth rates of FIA trees differed very little from those of trees sampled for dendrochronological studies (Fig. 2; FIA and trees cored for dendroecological purposes had growth rate % means of 99.5 and 103.5%, respectively).

The allometry of woody plants can be modified by a number of environmental gradients; the strongest of these are wind-induced bending stresses and drought (Gartner 1991; Voelker et al. 2011; Lines et al. 2012). Paleo oaks in this study were sampled opportunistically after being exposed from streambank and in-stream sediments—so we were not able to determine the approximate height of the tree or the relative vertical location within the main stem, where the cross section was taken. However, inspection of the FIA data revealed that the height-to-diameter ratio, after accounting for the effects of drought (i.e., CMD), had a weak negative relationship with T_{air} ($R^2 = 0.030$, $P < 0.001$, data not shown). This was driven by gains in diameter growth having been greater relative to gains in height growth at warmer T_{air} (data not shown). Meta-analyses of C_3 plants growing at ambient versus enriched [CO_2] have found no general evidence for changes in above to below-ground allocation (Curtis and Wang 1998; Poorter and Nagel 2000), nor $T_{air} \times [CO_2]$ interactions (Wang et al. 2012a, b). Soil N-availability and ectomycorrhizal relationship does modify above- to below-ground allocation responses of plants, but for trees alone, too few data were available to confidently assess how allocation may have been modified by interactions among mycorrhizal type, soil N-availability, and CO_2 (Terrer et al. 2016). A meta-analysis of tree allocation responses to T_{air} did find that height growth was favored over stem radial increment and root growth, which is part of a larger trend of root:shoot ratio having been reduced by warming (Way and Oren 2010). Clearly, more research is needed to understand how allocation and other factors affecting forest productivity may change due complex $T_{air} \times [CO_2]$ interactions across species and ecosystems (Way et al. 2015; Fatichi et al. 2016). Once enough data are available, it seems reasonable that allocation responses of trees will respond to $T_{air} \times [CO_2]$ interactions, as modified by soil N and mycorrhizal association. Therefore, although we consider it likely that the stem growth sensitivity to $T_{air} \times [CO_2]$ documented here was modified to some extent by changes in allocation, it is not yet possible to estimate the magnitude or even the direction of such effects.

By most accounts, the hydroclimate conditions during the deglacial period were relatively wet, while the early Holocene was characterized by drying that resulted in the climate being comparable to that of the modern period (Voelker et al. 2015; Mason et al. 2008; Gonzales et al. 2009; Williams et al. 2010). Hence, it is possible that rapid deglacial changes in T_{air} (Fig. 3A) could have resulted in long-lived oaks having been poorly adapted to novel thermal conditions, leading to growth sensitivity to T_{air} being apparently lower compared to modern oaks. However, bur oaks should be resilient to rapid climate change because of their capacity for phenotypic plasticity. For example, bur oak FIA data show a strong negative relationship between height growth and latitude (*data not shown*), yet when 26 provenances of bur oak from across the species distributional range were grown in a common garden over nine years, height growth showed no detectable trend associated with latitude of origin (Dicke St and Bagley 1980).

Conclusions

Tree stem radial growth rates and growth variability were driven by rapid changes in T_{air} during the last deglacial period as well as by spatial variation in T_{air} across the north central United States. Growth of modern oaks was more responsive to T_{air}, attributable to [CO_2] having been ~100 ppm greater compared to the last deglacial period. Our findings suggest that when moisture is abundant, many temperate forest species will also become more productive a result of rising [CO_2] and temperatures. The magnitude of the changes in growth sensitivity to T_{air} documented here cannot be simply scaled from our study to future levels of [CO_2] that may exceed 500 ppm because of the non-linear effects of CO_2 on leaf gas exchange (Voelker et al. 2016). Climate change is widely expected to cause more extreme weather events (IPCC 2013) that may induce heat- or drought-related stress that mediates the potential for higher [CO_2] to stimulate forest productivity in many regions. Therefore, we conclude that $T_{air} \times [CO_2]$ interactions will cause future tree growth and forest productivity to become increasingly variable across space and time, and this will be imprinted upon the already looming prospect of tree growth being impacted by climates with more extreme weather events.

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Author contribution statement SLV, MCS, and RPG collected the data. SLV conceived the study design. SLV and MCS analyzed the data. SLV wrote the manuscript and other authors provided editorial advice.

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