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Drought timing and local climate determine the sensitivity of eastern temperate forests to drought

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Abstract

Projected changes in temperature and drought regime are likely to reduce carbon (C) storage in forests, thereby amplifying rates of climate change. While such reductions are often presumed to be greatest in semi-arid forests that experience widespread tree mortality, the consequences of drought may also be important in temperate mesic forests of Eastern North America (ENA) if tree growth is significantly curtailed by drought. Investigations of the environmental conditions that determine drought sensitivity are critically needed to accurately predict ecosystem feedbacks to climate change. We matched site factors with the growth responses to

drought of 10,753 trees across mesic forests of ENA, representing 24 species and 346 stands, to determine the broad-scale drivers of drought sensitivity for the dominant trees in ENA. Here we show that two factors—the timing of drought, and the atmospheric demand for water (i.e., local potential evapotranspiration; PET)—are stronger drivers of drought sensitivity than soil and stand characteristics. Drought-induced reductions in tree growth were greatest when the droughts occurred during early-season peaks in radial growth, especially for trees growing in the warmest, driest regions (i.e., highest PET). Further, mean species trait values (rooting depth and ψ_{50}) were poor predictors of drought sensitivity, as intraspecific variation in sensitivity was equal to or greater than interspecific variation in 17 of 24 species. From a general circulation model ensemble, we find that future increases in early-season PET may exacerbate these effects, and potentially offset gains in C uptake and storage in ENA owing to other global change factors.

KEYWORDS

climate change, drought, evapotranspiration, forest ecology, phenology, temperate forest, tree-ring

1 | INTRODUCTION

Climate models project significant increases in the intensity and frequency of droughts—defined as periods of anomalously low water availability—for large land areas on earth during the 21st century (Cook, Ault, & Smerdon, 2015; Dai, 2011). Such changes are likely to be consequential for all forest ecosystems, including temperate mesic forests in Eastern North America (ENA; Dewes, Rangwala, Barsugli, Hobbins, & Kumar, 2017). Unlike western forests of the United States, droughts and drought-induced disturbances in ENA have not recently resulted in widespread mortality (Clark et al., 2016). However, tree growth may be substantially reduced by drought, resulting in large reductions in ecosystem C storage (Brzostek et al., 2014). Given that forests in ENA sequester up to 40% of eastern US carbon (C) emissions annually (Pan et al., 2011a; Xiao et al., 2011), drought-induced reductions in growth have the potential to be consequential for climate, and offset regional gains in C sequestration owing to longer growing seasons (Dragoni et al., 2011), land use change (Houghton, Hackler, & Lawrence, 1999), rising atmospheric CO₂ (Norby et al., 2005) and nitrogen fertilization (Ibáñez, Zak, Burton, & Pregitzer, 2018; Thomas, Canham, Weathers, & Goodale, 2010).

Predicting how forests differ in their sensitivity to drought (in terms of growth reduction) is critically important to predicting climate-C cycle feedbacks. While forest sensitivity depends in part on the identity of the dominant tree species and associated hydraulic traits (Bréda, Huc, Granier, & Dreyer, 2006; Clark et al., 2016), research is increasingly showing that trait effects vary with local conditions (Anderegg, 2015). Thus, models predicting forest

sensitivity to drought should also consider local adaptation of trees to factors such as precipitation and evaporative demand (McDowell & Allen, 2015; Williams et al., 2013), competition (D'Amato, Bradford, Fraver, & Palik, 2013), soil characteristics and microtopography (Buckland, Grime, Hodgson, & Thompson, 1997; Jung et al., 2014; West et al., 2012). Further, functional processes related to C allocation such as radial growth are typically less studied than hydraulic traits that control C assimilation rates through leaf-level gas exchanges during drought. Yet, the highly seasonal nature of C allocation to growth (i.e., wood cell division and differentiation), and its sensitivity to water availability (Foster, Schmalzer, & Fox, 2014; Gruber, Stöbl, Veit, & Oberhuber, 2010; Lempereur et al., 2015), suggest that the timing of drought may also have a decisive influence on the drought sensitivity of temperate forests.

Given emerging interest in modeling plant responses to changing conditions (van Bodegom, Douma, & Verheijen, 2014; Skelton, West, & Dawson, 2015), understanding the relative importance of environmental controls on forest sensitivity to drought will improve parameterizations of earth system models, and reduce uncertainty about the magnitude of climate-vegetation feedbacks (Prentice, Liang, Medlyn, & Wang, 2015). Most of what is known about tree growth responses to drought comes from field observations during naturally occurring droughts (Ciais et al., 2005), from experimental water manipulations (Beier et al., 2012; D'Orangeville, Côté, Houle, & Morin, 2013), or from tree-ring research where the goal is to target specific individuals, species, or conditions that would enable annually resolved reconstructions of hydroclimatic history (Cook, Meko, Stahle, & Cleaveland, 1999). While these approaches have yielded great insight, they typically include only a handful of tree species across a

limited range of sites. Consequently, empirical data on drought sensitivity (i.e., radial growth) from a larger number of species and locations spanning a larger environmental gradient across ENA is required to better assess the environmental control over assimilated C conversion into wood in times of water deficits.

Here, we tested the hypothesis that broad-scale tree sensitivity to drought varies with local environment (soil, tree characteristics, long-term climate), and the timing, duration and intensity of drought. To this end, we determined the relationship between dimensionless tree-growth indices (standardized growth) from 10,753 trees representing 24 temperate tree species, including 16 out of the 18 most abundant tree species of northeastern United States (Landscape Change Research Group, 2014), across 346 stands (Figure 1). Stands had a median age (120 ± 3 years, median \pm SE) that is similar with the average stand age in ENA (50–120 years; Pan et al., 2011b).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area spans the Eastern United States and Canada from 32° to 50°N and from 66° to 94°W, an area dominated by temperate continental and mountain systems. Climate over this area is humid continental to humid sub-tropical, with mean annual temperatures and precipitation for years 1970–2000 ranging between -0.3 and 16.7°C (mean 7.0°C) and 777 and 2054 mm (mean 1,136 mm), respectively. While temperatures decrease steadily with increasing latitude, precipitation displays a longitudinal gradient, with sites closer to the Atlantic Ocean subjected to higher precipitation than more western sites.

2.2 | Preparation of tree growth data

Of the 537 cross-dated tree-ring collections—distributed across 390 distinct locations—gathered for the study, only 157 were extracted

from the International Tree-Ring Data Bank (ITRDB), the largest database of freely available tree-ring data. The remaining 380 tree-ring collections were previously collected using standard dendrochronological approaches for various research objectives, including hydroclimatic reconstruction as well as ecological research. Potentially suppressed trees (i.e., visually determined by researchers as not dominant or co-dominant in the canopy) were excluded, and tree growth data prior to 1901 was excluded due to the lack of earlier accurate climate data.

In addition to climatic signals, other stand-level factors like disturbances and competition as well as tree-level factors like tree age and size make up a large component of tree-ring width variability. For such reasons, ecological studies that use tree-ring width data typically transform individual, raw tree-ring time series into a dimensionless growth index (thereafter simply referred to as growth index) to remove those low-frequency, nonclimatic effects and emphasize interannual variability associated with climate and allow inter-site comparison (Cook & Kairiukstis, 1990). Therefore, we used a smoothing cubic spline with a frequency response cut-off at 0.50 and a wavelength of 30 years to enhance the climatic signal in tree growth (Cook & Peters, 1997). Ring-width measurements were transformed into dimensionless growth indices by dividing raw values with the spline function estimates (Fritts, 2001). Further, annual growth rings are generally affected by previous-year conditions. Since this autocorrelative structure present in tree-ring series can blur the climatic signal and interfere with several statistical assumptions, autoregressive models of various orders were fitted to each growth index, and the model that minimized the Akaike Information Criterion (Akaike, 1974) was selected by default (Fritts, 2001). Resulting residual series were retained. The resulting growth index fluctuates around one, with lower values when growth is reduced (for a comparative example of raw and standardized growth series, see Figure S1). Such processing of raw ring-width measurements—a standard approach in dendrochronology and dendroecology—was completed using the package 'DPLR' (Bunn et al., 2014) in the R software (R Core Team, 2017).

The statistical quality of each site-species tree-ring collection was evaluated by computing its Expressed Population Signal (EPS), a dendrochronology index sensitive to the sample size and the common signal among trees (Fritts, 2001). Here, we interpret high EPS values as indicative that the associated stand is sensitive to climate, whereas low EPS values indicate that other factors like disturbances or competition may be blurring the common climate response. Eighty-five (15.8% of 537) collections with EPS values less than 0.8, or with less than eight trees, were discarded. While the removal of climate insensitive tree-ring collections can overestimate the ecosystem consequences of drought, this practice is necessary to avoid under-estimating drought sensitivity by sampling trees whose growth is most strongly determined by nonclimatic factors (e.g., pests and pathogens).

The final 452 tree-ring collections are distributed across 346 locations (Figures 1 and S2), have a range of replication from 8 to 196 trees (median = 20), a mean intertree correlation ranging from

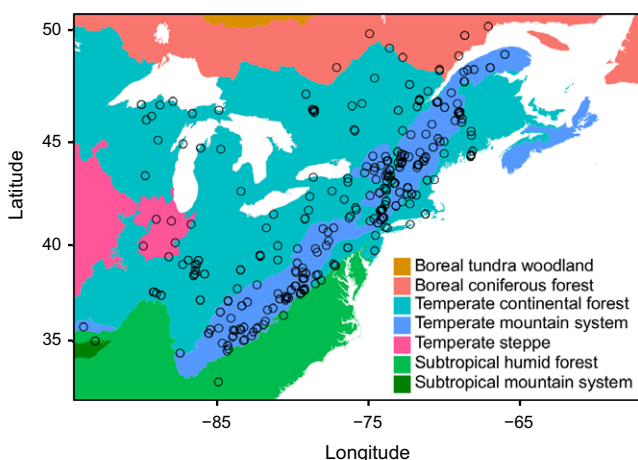


FIGURE 1 Location of the 346 study sites across the different ecoregions of Eastern North America. Ecoregions are areas with similar ecosystems and environmental resources (Commission for Environmental Cooperation, 1997)

0.34 to 0.82 (mean = 0.59), an average EPS of 0.91 and were sampled between 1971 and 2015 (median year = 2000). They represent a total of 24 species, 10 conifers and 14 broadleaves and are composed of trees 120 ± 3 (median \pm SE) years of age. Compared to ITRDB collections which are often 200 years-old or more, this median age is closer to the mean age structure in the region (50–80 years old in northeastern United States, 80–120 years old in eastern Canada; Pan et al., 2011b). According to the U.S. Forest Service Forest Inventory and Analysis, this study comprises 16 of the 18 most abundant tree species of northeastern United States. (Landscape Change Research Group, 2014). For these reasons, we consider the tree-ring collection used here as highly representative of the trees occurring in ENA temperate forests.

2.3 | Determination of historical droughts and tree sensitivity

One-, three- and six-month values of Standardized Precipitation-Evaporation Index (SPEI), extracted from the Global SPEI database (Beguería, Vicente-Serrano, Reig-Gracia, & Latorre Garcés, 2014), were used to estimate historical droughts at each location for the 1901–2015 period (Vicente-Serrano, 2015). SPEI estimates water availability from both precipitation and PET (modeled from the Penman–Monteith method) and converts it to standard deviations from the historical mean and is a good estimator of low water anomalies at various time scales (Beguería et al., 2014). In comparison with the more commonly studied 3-month or 6-month droughts, 1-month droughts exclude temporal autocorrelation between monthly anomalies and can be used to compare the effects of drought timing on tree growth. Further, droughts of short duration can reduce growth substantially in humid forests like the current study area (Vicente-Serrano et al., 2013). Nonetheless, we also analyzed 3- and 6-month droughts. Droughts were defined here as years with 1-, 3-month or 6-month SPEI values below -1.5 , equivalent to droughts with a 15-year recurrence interval. The threshold value of -1.5 was found to be an optimal compromise between intensity and replication of drought events.

Drought sensitivity for each tree was determined as the growth index during years with a drought event, averaged per month when the drought was detected (from March to October). For instance, sensitivity of an individual tree to a drought occurring in May corresponded to the average growth index of that tree during all years containing a May drought. Low correlations between monthly SPEI values for drought years allowed us to compare drought sensitivity between months. For instance, the average SPEI during the month following a June drought (SPEI < -1.5) across all sites was -0.3 , -0.2 and 0.0 for 1-, 3- and 6-month SPEI, respectively.

2.4 | Phenology of radial growth

To account for latitudinal differences in the duration of the growing season, the start of the growing season at each site was estimated by averaging the 1980–2010 First Leaf Spring Index (USA National Phenology Network) extracted for each US study location and

rounded to the closest first of the month to match with the monthly scale of the SPEI values. This index predicts spatial differences in timing of leaf out using historical observations (Ault, Schwartz, Zurita-Milla, Weltzin, & Betancourt, 2015) and closely matches the latitudinal gradient. Being unavailable for the 58 Canadian sites, this information was extrapolated from site latitude using a linear regression model as this variable is an excellent predictor of leaf out ($R^2 = .92$, see Figure S3).

Maximal intraseasonal radial growth rates were estimated from all published and nonpublished data that could be found across the entire range of the temperate forest of ENA. Data were collected at continuous to bimonthly frequencies, using electronic or manual dendrometer bands on mostly dominant or codominant trees covering 16 of the 24 species studied here (Table 1).

2.5 | Environmental variables

Edaphic conditions (clay and sand content, terrain slope, in percent) were included in the analysis because of their obvious control over soil water availability. Data were extracted for US plots from the SSURGO database using site coordinates. The SSURGO database contains soil information collected at scales ranging from 1:12,000 to 1:63,360 by the National Cooperative Soil Survey (Soil Survey Staff, 2016). Soil data from the SSURGO were available for 351 out of the 452 site species.

Summer (May to July) and annual long-term PET and precipitation averages (1960–1990), in mm, were computed because they can help compare the absolute intensity of the water deficiency between sites during a drought, while SPEI values define droughts as anomalies relative to the site normal. Average monthly minimum and maximum temperatures and precipitation data were extracted for each location from the high resolution (30 arc-second) interpolated database WORLDCLIM version 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and used with site latitude to compute monthly PET over the 1960–1990 period with a simplified Hargreaves algorithm. Summer PET and precipitation were summed monthly for each period and averaged over 1960–1990.

Because resource limitation and stand developmental stage can affect the drought susceptibility of a given tree, we calculated tree age and relative basal area increment (bai) as indices of vigor and successional stage during each drought event (Young et al., 2017). Tree age was computed as the sum of tree-rings of each tree up to the year of the drought, from the pith to the bark of the tree. We acknowledge that this variable is probably underestimated because increment cores sometimes fail to reach the center of the tree, or because of missing rings due to pith decay. However, tree size measurements were largely missing, precluding any approach to correct age estimates. Relative basal area increment was estimated annually as the annual increase in basal area (in mm^2/year) divided by corresponding the tree size (in mm^2). Relative bai was then averaged over the 5 years prior to each drought.

Two drought-coping traits—minimum rooting depth and vulnerability to cavitation or ψ_{50} —were extracted from the TRY database

TABLE 1 Location, species and methods used to estimate intraseasonal growth rates

Site	Name	Location	Latitude	Longitude	Species	Trees (DBH)	Years	Method	Sampling frequency	References
SERC	Smithsonian Environmental Research Center	Maryland, US	38.89°N	76.56°W	LITU, QUAL, FAGR, <i>Liquidambar styraciflua</i>	20 (mean: 36 cm, range: 6–103 cm)	2010	Manual dendrometer bands	Weekly	McMahon and Parker (2015)
WBW	Walker Branch Watershed	Tennessee, US	35.97°N	84.28°W	ACRU, LITU, QUAL, QUMO	170 (>20 cm)	1994–1999	Manual dendrometer bands	Biweekly	Hanson, Todd, and Amthor (2001)
WHMF	William L. Hutcheson Memorial Forest	New Jersey, US	40.50°N	74.57°W	ACRU, ACSH, CYOV, FAGR, QUAL, QURU, QUVE	≥14	1956–1958	Dial-gauge manual dendrometers	Weekly	Buell, Buell, Small, and Monk (1961)
MMSF	Morgan-Monroe State Forest	Indiana, US	39.35°N	86.43°W	ACSH, FAGR, LITU, QUAL	107 (>10 cm)	2014–2016	Manual dendrometer bands	2 weeks	Brzostek et al. (2012)
LacDup	Lac Duparquet	Quebec, Canada	48.47°N	79.28°W	BEPA, ABBA, THOC, PCGL, MCPA, PIRE, <i>Pinus banksiana</i>	40 (range: 12.5–27.5 cm)	1997	Automatic dendrometer bands	Continuous	Tardif, Flannigan, and Bergeron (2001)
MontFor	Forêt Montmorency	Quebec, Canada	47.33°N	71.13°W	ABBA	3 (>10 cm)	2004–2010	Automatic point dendrometers	Continuous	Duchesne, Houle, and D'Orangeville (2012)

and from published data (Choat et al., 2012; Kattge et al., 2011). We used a single mean species value for both traits (rooting depth: one replicate per species; ψ_{50} : two to eight replicates per species). While trait data was unavailable for a subset of species, we were able to generate trait data for 345 out of 452 site-species. Other available traits were not retained because of their limited availability for the species studied here.

2.6 | Statistical tests

Linear mixed models (LMM) were used to investigate how environmental conditions, species and drought characteristics affect drought sensitivity. Because 3-month droughts and 6-month drought often contain 1-month droughts, we fitted separate models for 1-, 3- and 6-month droughts. After careful examination of data (Figure 2a), we limited drought sensitivity to the months of May, June, July, and August when drought sensitivity is highest across the entire study gradient. The site-level start of the growing season was not included in the model because of its high correlation to PET (Pearson $r = .87$) and the general synchrony in drought sensitivity across the study area (Figure 2a).

The predictor terms were site edaphic conditions (soil sand and clay contents, slope), long-term average climate (1960–1990 mean summer PET and precipitation), tree characteristics during the drought (tree age and relative basal area increment), drought timing (May, June, July or August, transformed into dummy variables using May as the reference level), drought intensity (SPEI of drought event) and species hydraulic traits (rooting depth and ψ_{50}), while sites crossed with species were included as random terms. Predictors were scaled prior to analysis. Normality of model residuals was also verified graphically. The model equation takes the form:

$$Y_i = A + \sum_{p=1}^{N_p} B_p z_{p,j} + \sum_{q=1}^{N_q} B_q w_{q,k} + \sum_{r=1}^{N_r} B_r x_{r,i} + \epsilon_j + \epsilon_k + \epsilon_{jk} + \epsilon_i$$

where A is the overall intercept, p is the index for the N_p site-level variables z (i.e., PET, precipitation, sand, clay, slope, drought timing, and severity), q is the index for the N_q species-level variables w (i.e., rooting depth and ψ_{50}), k is the number of species, r is the index for the N_r tree-level variables x (i.e., tree age and relative basal area increment), i is the number of individual trees, j is the number of sites, B are the slopes for the fixed effects, and ϵ are the random effects.

Initially, multispecies models were fitted on data from 259 site-species representing 13 species for which all predictor variables (notably soil factors and species traits) were available. However, species traits were found to have nonsignificant, marginal explanatory power ($p > .1$, data not shown). Following this initial result, we tested for site-specific trait effects (by including a random, site-specific effect to each trait factor), with similar nonsignificant results. Thus, species traits were excluded from the final models in order to increase the number of site-species and species to 351 and 22, respectively.

To confirm the general results from the multispecies models (one for 1-, 3- and 6-month drought) including all species and sites,

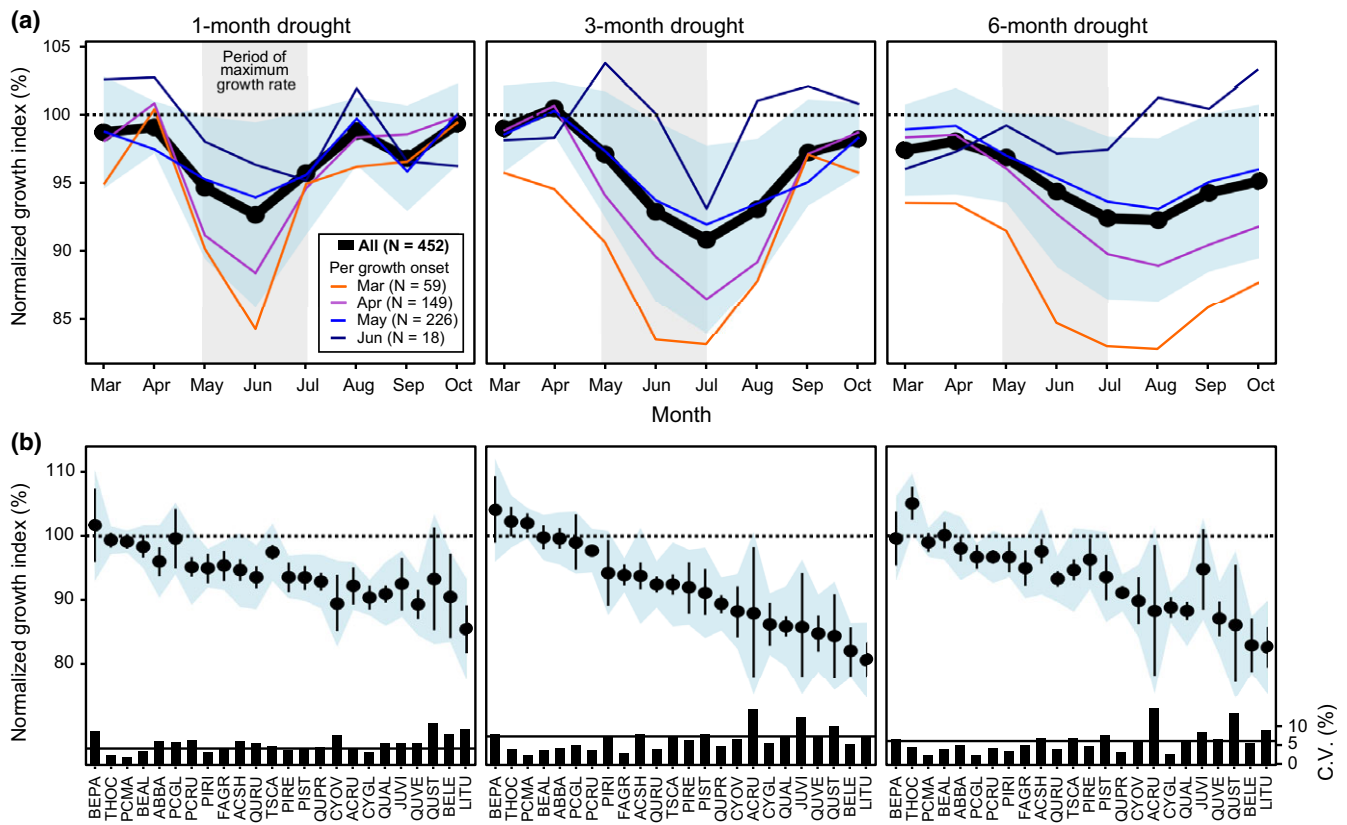


FIGURE 2 Differences in drought sensitivity across species and throughout the growing season for 1 to 6-month drought. (a) Effect of March to October drought (SPEI < −1.5) on same-year normalized growth index averaged across 24 tree species (bold line) and by growing season onset (coloured lines; N = number of sites). The light blue area represents the standard deviation of the average across species and growing season onset. The vertical gray area represents the period of maximum radial growth determined from dendrometer studies (see Figure 3). (b) Species average growth and coefficient of variation (C.V.) during June and July 1-, 3- and 6-month drought (SPEI < −1.5). May was excluded because growth is not yet started at certain northern sites. Error bars are bootstrapped (N = 1,000) confidence intervals (95%) of the mean, while the light blue area represents the standard deviation of the average across sites. ABBA: *Abies balsamea*; ACRU: *Acer rubrum*; ACSH: *A. saccharum*; BEAL: *Betula alleghaniensis*; BELE: *B. lenta*; BEPA: *B. papyrifera*; CYGL: *Carya glabra*; CYOV: *C. ovata*; FAGR: *Fagus grandifolia*; JUVI: *Juniperus virginiana*; LITU: *Liriodendron tulipifera*; PCGL: *Picea glauca*; PCMA: *Picea mariana*; PCRU: *Picea rubens*; PIRE: *Pinus resinosa*; PIRI: *Pinus rigida*; PIST: *Pinus strobus*; QUAL: *Quercus alba*; QUMO: *Q. montana*; QURU: *Q. rubra*; QUST: *Q. stellata*; QUVE: *Q. velutina*; THOC: *Thuja occidentalis*; TSQA: *Tsuga canadensis*

species-specific models were fit separately on data for the eight species with the greatest number of stands (310 out of 452 site-species) to look for species-specific differences. Specifically, we were interested to see if the large timing and PET effects found in multi-species models would hold true within species. In the species-specific models, only sites were included as random terms, and species hydraulic traits were obviously removed. All analyses were conducted using the 'lme4' package in R Software (R Core Team, 2017).

2.7 | Future drought sensitivity

To predict how future changes in PET associated with global warming may affect drought sensitivity, baseline (1976–2005) and future (2070–2099) PET were calculated from 20 general circulation models for a Representative Concentration Pathways (RCP) of 8.5 W·m^{−2} from the NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP) dataset (resolution is 0.25°). Potential evapotranspiration was calculated with a simplified Hargreaves algorithm using

minimum and maximum temperatures, latitude and precipitation. The 50th percentiles of the 20 model simulations per RCP were retained to provide a reasonable estimate of future changes. Because the Hargreaves algorithm tends to overestimate future changes in PET (Dewes et al., 2017; Sheffield, Wood, & Roderick, 2012), and because current PET projections contain a large amount of uncertainty, we used that median projected PET increase (23 ± 5%) as the upper-limit for three scenarios of PET increases (+12%, +17%, +23%). We used the estimates from the multispecies LMM fitted using unscaled predictors to estimate the effects of projected PET changes on drought-induced growth reductions while controlling for other variables in the model (set to their median value).

3 | RESULTS

Overall drought sensitivity displayed a strong seasonal behavior. Trees displayed the highest growth reductions when 1-month

drought occurred in May ($5.3 \pm 5.2\%$; mean \pm SD), June ($7.3 \pm 6.8\%$), and July ($4.3 \pm 4.5\%$; Figure 2a). A similar pattern emerges from tree responses to 3-month droughts, with the highest growth reductions in July ($9.1 \pm 6.9\%$), which also represent droughts from May, June, and July combined. The seasonal effect of 6-month droughts is less obvious as this drought metric integrates a longer time period, although the largest declines are observed in July ($7.6 \pm 6.0\%$) and August ($7.7 \pm 6.0\%$), which also include effects from May, June, and July droughts.

Accounting for latitudinal differences in the growing season length (i.e., the start of the growing season ranges from March, south, to June, north), stands with an earlier onset of the growing season did not experience drought sensitivity earlier in the growing season, suggesting a strong synchrony in the timing of the drought response across forests of ENA (see Figure S4 for species-specific results). Average 1-month drought sensitivity peaked in June for stands where the growing season starts in March, April or May ($N = 434$), with growth index reductions ranging from $15.7 \pm 6.7\%$ in sites with a growth onset in March to $6.1 \pm 6.7\%$ in sites with growth onset in May (Figure 2a). We observe even higher synchrony with 3-month droughts, where all trees show peak drought sensitivity in July, with growth index reductions ranging from $16.8 \pm 6.0\%$ (March growth onset) to $6.9 \pm 9.2\%$ (June growth onset). Six-month drought growth reductions are also synchronized across stands with growth onsets in March, April or May (Figure 2a). These general trends do not exclude some species-specific variations. For instance, the drought sensitivity of chestnut oak tends to be higher in July for trees with later growth onsets (May). Also, sugar maple trees with late growth onsets (May or June) appear less sensitive than those with earlier onsets (Figure S4).

The comparison of intraseasonal radial growth rates of many temperate species from electronic or manual dendrometer bands reveals a remarkable synchrony in maximal growth rates, with peaks in growth occurring around the middle of June across the range of sites (Figure 3). Given that June also reflects peak sensitivity to drought (Figure 2a), our results indicate that drought impacts are most consequential when they occur during periods of peak cambial growth, and least consequential (at least in terms of the current

year's growth) when they occur late in the growing season. In comparison, sensitivity to prior-year drought was lower and associated with late-season prior-year droughts in August, September, and October (Figure S5). Growth reductions associated with prior-year 1-month, 3-month or 6-month droughts ranged between $3.1 \pm 4.3\%$ and $5.4 \pm 4.9\%$.

Mixed modeling confirmed the importance of drought timing on growth during drought, but also revealed significant effects from PET (negative effects), sand fraction in the soil (positive effects), terrain slope (negative effects), drought intensity (negative effects), tree age (positive effects) and relative growth rate (positive effects; Table 2). However, drought timing was the single most important predictor of drought sensitivity. Moreover, mean species "drought-coping traits" (rooting depth and xylem water potential at 50% cavitation, ψ_{50}) had marginal, nonsignificant effects on drought sensitivity, as intraspecific variation in sensitivity to 1-, 3-month or 6-month drought was greater than interspecific variation for 17 of 24 species (Figure 2b).

The mixed model also revealed that along with drought timing, local long-term atmospheric demand for water (PET) was the strongest predictor of drought sensitivity (Table 2). Estimated here from local temperature and solar radiation, PET is the maximum amount of water that would be evaporated and transpired if enough water was available, and typically used as a proxy in conjunction with precipitation to predict the water balance of ecosystems (high PET = high atmospheric water demand). Species found at high latitudes with typically lower PET (*Betula papyrifera*, *Thuja occidentalis*, *Picea glauca*, and *P. mariana*) tended to display lower average sensitivity to drought than species commonly occurring at southern latitudes (*Liriodendron tulipifera*, *B. lenta*, *Quercus velutina*, *Carya ovata*; Figure 2b, see Figure S2 for maps of species ranges). The control exerted by PET over growth sensitivity is also detected during non-drought years. For instance, growth response in July to sensitivity to SPEI in nondrought years (years when values did not fall below -1.5) is highly correlated to PET ($R = .51$; data not shown).

Controlling for differences in soil, stand and species characteristics, drought timing and drought intensity, average growth reductions following 1-, 3-month or 6-month drought increase two-fold with

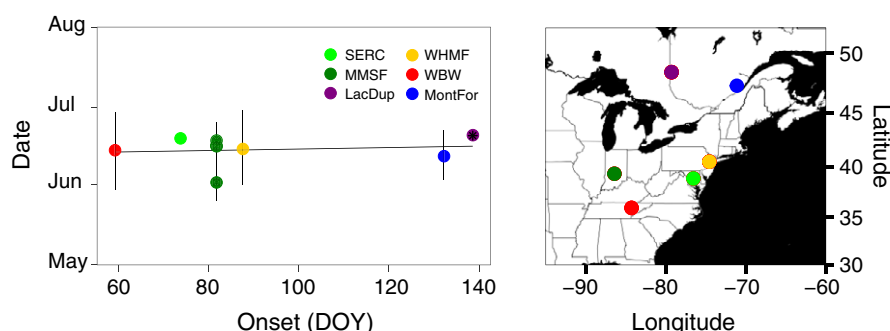


FIGURE 3 Annual peak in radial growth for 16 out of the 24 species from 6 mature stands along a gradient of mean growth onset for 1980–2010 (in Day of Year). Vertical lines represent the range of interannual means, while the blue line represents the slope of the linear regression model between annual peak and onset. When known, species annual peaks are presented separately. Map indicates stand location. See Table 1 for stand characteristics

TABLE 2 Fixed-effect estimates and standard error (SE) of the multispecies linear mixed model predicting tree growth in response to 1-, 3- and 6-month drought

Resolution	Variable	1-month drought			3-month drought			6-month drought		
		Estimate \pm SE	t value	Prob (> t)	Estimate \pm SE	t value	Prob (> t)	Estimate \pm SE	t value	Prob (> t)
Site-level	Intercept	0.931 \pm 0.005	173.6	≤ 0.001	0.966 \pm 0.008	122.8	≤ 0.001	0.966 \pm 0.007	139.51	≤ 0.001
	Drought timing (June)	0.002 \pm 0.002	1.00	ns	-0.037 \pm 0.001	-26.34	≤ 0.001	-0.023 \pm 0.001	-16.69	≤ 0.001
	Drought timing (July)	0.003 \pm 0.002	1.95	≤ 0.05	-0.078 \pm 0.001	-54.96	≤ 0.001	-0.051 \pm 0.001	-36.79	≤ 0.001
	Drought timing (August)	0.048 \pm 0.002	31.76	≤ 0.001	-0.040 \pm 0.001	-27.68	≤ 0.001	-0.046 \pm 0.001	-32.91	≤ 0.001
	Long-term PET	-0.013 \pm 0.003	-3.57	≤ 0.001	-0.025 \pm 0.004	-6.37	≤ 0.001	-0.033 \pm 0.004	-7.91	≤ 0.001
	Long-term prec	-0.002 \pm 0.002	-0.72	ns	0.001 \pm 0.002	0.29	ns	0.001 \pm 0.003	0.43	ns
	Sand fraction	0.009 \pm 0.003	3.08	≤ 0.01	0.006 \pm 0.003	2.01	≤ 0.05	0.006 \pm 0.003	1.76	ns
	Clay fraction	0 \pm 0.003	0.05	ns	0.003 \pm 0.003	0.88	ns	0.004 \pm 0.004	1.01	ns
	Slope	0.003 \pm 0.002	1.28	ns	-0.007 \pm 0.003	2.01	≤ 0.05	-0.003 \pm 0.003	-0.87	ns
	Drought intensity (SPEI)	0.010 \pm 0.001	17.9	≤ 0.001	0.014 \pm 0.001	27.15	≤ 0.001	0.013 \pm 0.001	25.3	≤ 0.001
Tree-level	Tree age	0.014 \pm 0.001	16.4	≤ 0.001	0.018 \pm 0.001	21.67	≤ 0.001	0.020 \pm 0.001	23.36	≤ 0.001
	Tree relative growth rate	0.016 \pm 0.001	20.7	≤ 0.001	0.015 \pm 0.001	19.79	≤ 0.001	0.019 \pm 0.001	23.79	≤ 0.001

Predictor terms are drought timing (May, June, July or August, transformed into dummy variables using May as the reference level), long-term average climate (1960–1990 mean summer PET and precipitation), site edaphic conditions (soil sand and clay fractions, slope), drought intensity (SPEI of drought event; SPEI values are negative, thus positive estimates indicate negative growth responses.) and tree characteristics during the drought (tree age and relative growth rate). After initial tests, species-level variables (ψ_{50} and rooting depth) were excluded from multispecies models due to their lack of explanatory power and nonsignificance ($p > .1$) and to increase the number of species and sites included in the analysis (from 259 sites and 13 species to 351 sites and 22 species). Predictors were scaled prior to analysis.

T-tests use Satterthwaite approximations to degrees of freedom and probability values (package 'lmerMod' in R).

PET (PET range: 286–538 mm; Figure 4) while the influence of PET on May to August drought sensitivity increases with drought duration. Following 1-month drought, average growth decreases of $2.8 \pm 0.8\%$ with every 100-mm increase in summer PET, for a total growth variation of $7.1 \pm 2.0\%$ (Table 2). Following 3-month drought, average growth decreases of $5.6 \pm 0.9\%$ with every 100-mm increase in summer PET, for a total growth variation of $14.1 \pm 2.2\%$. Following 6-month drought, average growth decreases of $7.6 \pm 1.0\%$ with every 100-mm increase in summer PET, for a total growth variation of $19.1 \pm 2.4\%$ (Table 2). Species-specific hierarchical mixed models also reveal significant PET effects on drought sensitivity for six of the eight tested species (Table S1).

Given the sensitivity of tree growth in ENA to changes in PET, an important question arises: how might predicted PET changes influence future forest sensitivity to drought? Controlling for other variables in our model, drought-induced growth declines could be exacerbated by 28%–111% in 2070–2099 depending on future PET scenarios and drought duration (Figure 5). South of 35°N, growth declines are predicted to reach 7.6–18.5% compared to observed reductions of 6.5–12.3%, depending on PET scenario and drought duration. North of 45°N, although stands display historically lower growth declines of 2.8–3.2%, they will be subjected to relatively stronger changes, reaching 5.6–10.6% reductions depending on PET scenarios (Figure 5). Note that these projections are for a single-

drought event, and do not account for an increase in the frequency of drought events (i.e., SPEI < -1.5) associated with increasing PET.

4 | DISCUSSION

Using decades of climate-growth relations archived in tree-ring collections, we found strong environmental controls over drought sensitivity and large-scale synchronization between peak growth and peak drought sensitivity. Our study provides an empirical comparison of biotic and abiotic drivers of drought sensitivity over an extensive area (ENA) for a large number of species, stands, and individuals. The widespread sensitivity to drought observed here for 24 tree species confirms that drought is a significant driver of tree growth in the temperate forests of ENA (Cook, 1991; Martin-Benito & Peder-son, 2015). This includes species and individuals that were rarely studied from a dendrochronological perspective, although they are significant components of the ENA ecosystem.

The finding that sensitivity to 1-, 3-month or 6-month water deficit is highest during the short period of cambial growth across tree species is coherent with radial growth patterns in temperate and boreal trees, which follow a positive exponential growing phase followed by a decline in growth rate (Rossi et al., 2006). Conifers in northern Europe and North America, for example, have maximum

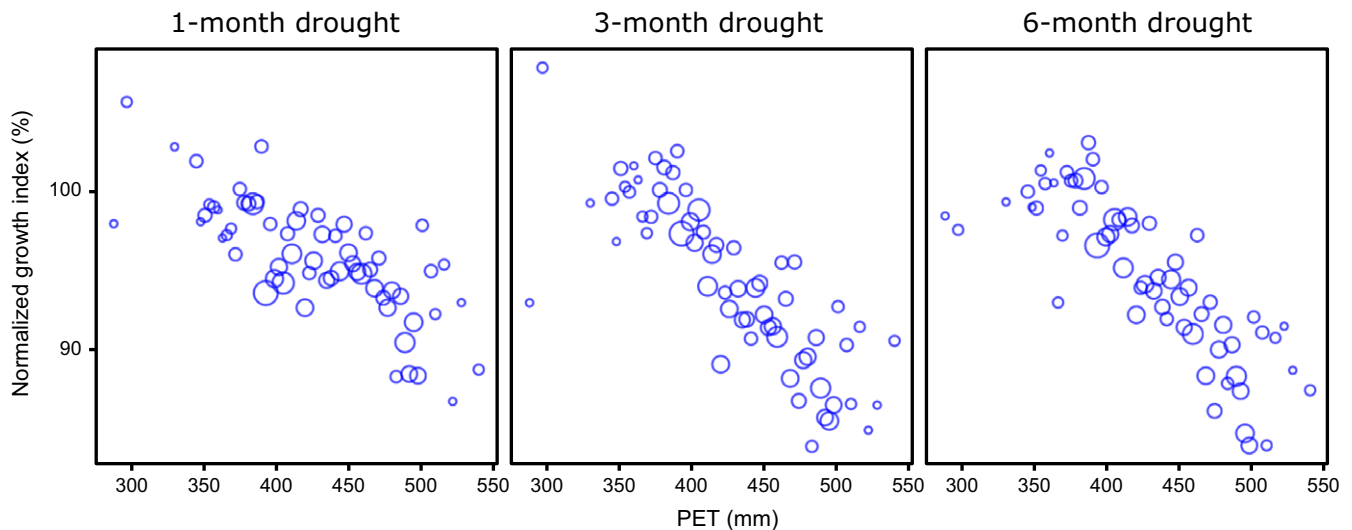


FIGURE 4 Sensitivity to 1-, 3- and 6-month drought across a gradient of long-term (1960–1990) summer PET (MJJ). Droughts occurred from 1901 to 2015 during the May to August period. Growth values (circles) are averaged by 3 mm-width PET bins with point sizes reflecting the number of sites (range: 1–32). [Colour figure can be viewed at wileyonlinelibrary.com]

growth during the period of maximum day length (June 21), which ensures xylem maturation before winter (Rossi et al., 2006). Previous local-scale tree-ring and eddy-covariance studies also report higher tree sensitivity to early and mid-season droughts (i.e., May and June) in deciduous broadleaf forests (Delpierre, Berveiller, Granda, & Dufrêne, 2016; Foster et al., 2014; Schwalm et al., 2010). The low sensitivity to late-season drought (August and later) is probably because radial growth is already completed, although secondary cell wall lignification may exceed that period (Delpierre et al., 2016; Rossi et al., 2006). Instead, late-season droughts can reduce growth in the following year because of their potential impact on growth drivers like carbohydrate and water reserves (Babst et al., 2012). The degree to which the magnitude and duration of such legacy effects vary among species and sites in the ENA is unknown and suggests that the growth reductions estimate here may be conservative.

The large difference in resolution between trait values and environmental factors, added to the unbalanced species representation in our data, could explain the observed lack of significant trait effects on drought sensitivity reported here. However, such results may also indicate that mean species trait values have limited value for predicting broad-scale drought impacts on tree growth, as local-scale factors may represent too great a control on intraspecific trait variation. The high within-species variability observed here supports the hypothesis that the influence of drought-coping traits is subordinated to the environmental context (Clark, 2016; Gazol, Camarero, Anderegg, & Vicente-Serrano, 2017). This subordination may be scale-dependent, as species differences are often highlighted in fine-scale studies covering short environmental gradients (Brzostek et al., 2014), while broad-scale studies generally report a dominant role for environmental factors over species traits (Anderegg, 2015; Gazol et al., 2017; Martin-Benito & Pederson, 2015). It is also possible that trait co-variations and trade-offs yield similar functional responses despite strong intraspecific variability in individual traits, thereby

weakening the effect of single traits on drought sensitivity. For instance, the ring-porous wood structure of oak (*Quercus*) species allows them to maintain higher hydraulic conductivity (partly thanks to relatively more negative ψ_{50}) during a drought than diffuse-porous trees (e.g., *L. tulipifera*, *A. rubrum*) or gymnosperms (Vose et al., 2016). The relatively high drought sensitivity reported here for oak species (*Q. alba*, *Q. velutina*, *Q. montana*), however, suggests that such hydraulic characteristics are at least partially uncoupled from the whole plant C gain and allocation strategies. Notably, growth reductions (i.e., high sensitivity) may be an efficient way to reallocate C resources toward other metabolic processes like respiration, osmoregulation or root growth and promote survival. Such explanation would support our finding that trees from drier, warmer areas are more sensitive to drought and water availability in general. In addition, a cavitation-sensitive xylem (less negative ψ_{50}) does not necessarily imply high drought sensitivity. High sapwood area-to-leaf area ratio or deep roots can compensate for xylem sensitivity, effectively de-coupling drought responses at the plant level from tissue-level traits (Phillips et al., 2016). Similar uncoupling between eco-physiological measurements and whole-plant responses occur for example between leaf-level photosynthesis and growth for temperate species (Abrams, Ruffner, & Morgan, 1998). These contrasting responses across scales might explain why a single tissue-level trait (ψ_{50}) is not a significant predictor of drought sensitivity.

The primary role of PET over soil or stand characteristics found here using either 1-, 3-month or 6-month drought as well as multi-species and species-specific models is in line with earlier reports of temperature control over drought stress in southwestern US forests (Fritts et al., 1965; Williams et al., 2013), in certain broadleaf species of ENA (Martin-Benito & Pederson, 2015) including *Quercus alba* (LeBlanc & Terrell, 2001), and with vapour pressure deficit control on C fluxes during a drought (Novick et al., 2016). As described by Fritts et al. in drier Arizona forests (1965), we show that the

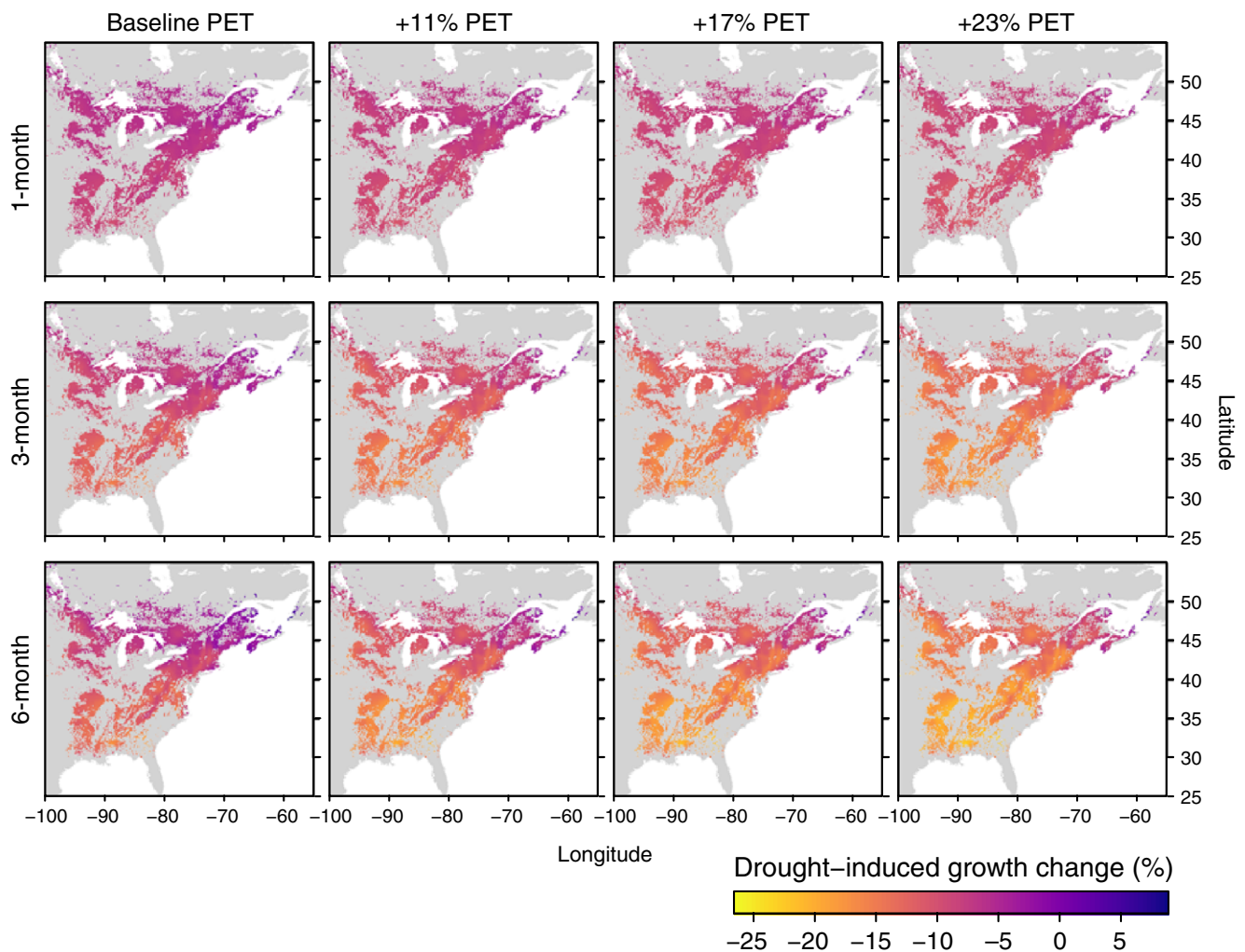


FIGURE 5 Isolated effects of baseline and future PET changes on growth across the temperate forest of ENA following drought. Effects of 1-, 3- and 6-month drought are displayed according to current (1976–2005) and future (2070–2099) PET scenarios. Future PET scenarios are relative changes from baseline PET data (1976–2005) computed here as the 50th percentile PET value from 20 general circulation models for 2070–2099 (see Section 2). Changes in growth are mean estimates from our multispecies mixed model from May to August, controlling for other variables in the model (Table 2). The temperate forest areas regroup deciduous broadleaf and mixed forests as determined by 1-km resolution MODIS land cover classification (Hansen, Defries, Townshend, & Sohlberg, 2000)

sensitivity to water deficit also increases toward the warm edge of the eastern temperate forest biome.

During the severe drought of 2003 in Europe, the reduction in GPP turned European ecosystems to net C source, canceling out the equivalent of 4 years of C sequestration (Ciais et al., 2005). The conclusion that climatic factors and drought characteristics (timing, intensity, and duration) can predict drought sensitivity across ENA forests can help model forecasts better estimate future drought-related vulnerabilities in this forest C sink. Current vegetation models already account for abiotic effects on growth (primarily via stomatal regulation), and the data presented here could offer a new regional-scale benchmark for model predictions, allowing to test if fine temporal scale responses predicted by models result in reliable predictions of growth reductions at the annual time scale. This test of vegetation models is especially important to improve the projected impacts of projected greater drought frequency (Cook et al.,

2015; Dewes et al., 2017) on C sequestration by temperate tree species. Coupled carbon-climate Earth System Models project that warm temperature anomalies could reduce annual GPP by 1.4%–3.2% in mixed and broadleaf forests under global warming (Williams, Torn, Riley, & Wehner, 2014). However, considerable sources of uncertainty remain regarding future GPP changes. For one, the increasing atmospheric CO_2 concentration is likely to increase the water-use efficiency of trees as has been shown with grasslands (Roy et al., 2016), which could reduce the water losses (due to higher PET) and limit negative growth impacts. Also, in addition to our findings that soil texture, tree age, growth rates, and drought intensity can affect drought sensitivity, other co-varying factors such as disturbances, drought-induced mortality and cumulative drought impacts may also interact with forest drought sensitivity. Finally, general circulation models vary in their projections of the magnitude of summertime PET change owing to uncertainty in atmospheric

CO₂ concentration levels and how PET is calculated (Dewes et al., 2017). Nonetheless, the combination of potentially higher PET and drought frequency could significantly offset the potential increases in C sequestration due to changes in growing season length, CO₂ levels, land-use or N deposition.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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