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Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest

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Summary

• The climate sensitivity of forest ecosystem woody productivity ($ANPP_{stem}$) influences carbon cycle responses to climate change. For the first time, we combined long-term annual growth and forest census data of a diverse temperate broadleaf deciduous forest, seeking to resolve whether $ANPP_{stem}$ is primarily moisture- or energy-limited and whether climate sensitivity has changed in recent decades characterised by more mesic conditions and elevated CO_2.

• We analysed tree-ring chronologies across 109 yr of monthly climatic variation (1901–2009) for 14 species representing 97% of $ANPP_{stem}$ in a 25.6 ha plot in northern Virginia, USA.

• Radial growth of most species and ecosystem-level $ANPP_{stem}$ responded positively to cool, moist growing season conditions, but the same conditions in the previous May–July were associated with reduced growth. In recent decades (1980–2009), responses were more variable and, on average, weaker.

• Our results indicated that woody productivity is primarily limited by current growing season moisture, as opposed to temperature or sunlight, but additional complexity in climate sensitivity may reflect the use of stored carbohydrate reserves. Overall, while such forests currently display limited moisture sensitivity, their woody productivity is likely to decline under projected hotter and potentially drier growing season conditions.

Introduction

Forests globally sequester *c.* 1/3 of anthropogenic CO_2 emissions from fossil fuel combustion (Le Quéré *et al.*, 2017), therefore slowing atmospheric CO_2 accumulation and consequent climate change. Yet, the persistence of this global forest carbon (C) sink is threatened by climate change, including the increasing risk of severe drought (Trenberth *et al.*, 2014; Clark *et al.*, 2016), and its future course remains one of the largest uncertainties in global climate models (Friedlingstein *et al.*, 2006). To predict the future C balance of forests, it is necessary to understand the climate sensitivity of aboveground woody net primary productivity, that is the portion of C fixed through photosynthesis that is preserved long term in woody stems ($ANPP_{stem}$). The challenge to doing so is that this requires multidecadal records of annual growth for all tree species that contribute substantively to $ANPP_{stem}$. Tree rings are invaluable for disentangling the multiple interacting factors that influence growth, including climatic variation. However, traditional dendrochronological methods, in which only targeted canopy trees are sampled, are not optimal for characterisation of the climate sensitivity for entire forest stands (Babst *et al.*, 2018).

Moreover, they may overestimate climate sensitivity (Klesse *et al.*, 2018b). There has been limited use of tree rings to estimate $ANPP_{stem}$ (Graumlich *et al.*, 1989; Davis *et al.*, 2009; Babst *et al.*, 2014; Dye *et al.*, 2016; Klesse *et al.*, 2016; Teets *et al.*, 2018a) and its climate sensitivity (Woolley *et al.*, 2015; Klesse *et al.*, 2018a; Teets *et al.*, 2018b).

Temperate forests are an important C sink (*c.* $0.8\,Pg\,C\,yr^{-1}$; Pan *et al.*, 2011), with *c.* 0.2 Pg C sequestered annually by the broadleaf deciduous forests of eastern North America (Albani *et al.*, 2006). Despite being among the best-studied ecosystem types on Earth (Martin *et al.*, 2012), there remains large uncertainty to the climate sensitivity of temperate broadleaf forests and how they will respond to future climate change. Notably, of the >4000 collections in the International Tree-Ring Databank, only 19% are of broadleaf species; of that small proportion, 67% are *Quercus* species (Zhao *et al.*, 2019).

The broadleaf deciduous forests of eastern North America are generally mesic and conventionally considered to be more markedly limited by energy (temperature or solar radiation) than by water (Running *et al.*, 2004). Over relatively short time scales, gross primary production (GPP) and transpiration are reduced

under cloudy, cool conditions (Barford, 2001; Anderson-Teixeira *et al.*, 2015b). Growing season length (shaped by spring and fall temperatures) appears to be a primary driver of interannual variability in net ecosystem exchange of CO_2 (NEE; Baldocchi *et al.*, 2018). Tree ring-based records of radial growth covering most of the 20th century have indicated that most of the dominant canopy species in the region respond positively to water availability and negatively to high temperatures (Elliott *et al.*, 2015; Martin-Benito & Pederson, 2015; Charney *et al.*, 2016; Levesque *et al.*, 2017; D'Orangeville *et al.*, 2018). However, it is unknown whether the whole forest ecosystem follows the trends observed in tree rings from canopy trees or whether codominant and subdominant individuals or smaller statured species alter the response of $ANPP_{stem}$ to climatic variation (that is a niche complementarity effect; Isbell *et al.*, 2015). Therefore, it remains unclear how the whole-ecosystem $ANPP_{stem}$ responds to interannual variability in growing season climate.

Beyond the influence of current growing season conditions, $ANPP_{stem}$ is almost inevitably influenced by conditions in the preceding year. This is because early-season stem growth is partially fuelled by nonstructural carbohydrate (NSC) reserves, particularly in ring-porous species (Trumbore *et al.*, 2002; Kagawa *et al.*, 2006; Zweifel *et al.*, 2006; Michelot *et al.*, 2012; Richardson *et al.*, 2013). While NSC reserves can be decades old, the active ('fast') pool that fuels new growth is typically composed of C that was fixed within the past 1–2 yr (Carbone *et al.*, 2013; Richardson *et al.*, 2013, 2015), suggesting a lagged relationship between current year growth and previous years' climate conditions. These lags are common in temperate deciduous species, although their direction and strength is somewhat variable (Pederson *et al.*, 2012; Charney *et al.*, 2016; D'Orangeville *et al.*, 2018; Hacket-Pain *et al.*, 2018). Despite the high probability that $ANPP_{stem}$ is sensitive to climate conditions before the current growing season, this sensitivity has not been characterised in most ecological studies. Characterising the long-term sensitivity of $ANPP_{stem}$ to current and previous years' climatic conditions requires scaling tree-ring records from a diversity of tree sizes and species to the ecosystem level, and will be critical to predicting temperate forest responses to climate change.

Finally, it remains unclear if and how climate sensitivity has changed over recent decades, during which tree growth in US eastern deciduous forests has been altered by more mesic conditions, increasing atmospheric CO_2, and declines in atmospheric pollutants (SO_x, NO_x). Several studies have found that these changes drove increased tree growth within the biome, but attributed the increased growth to different sets of environmental changes (McMahon *et al.*, 2010; Levesque *et al.*, 2017; Mathias & Thomas, 2018). It remains unknown how such changes have affected climate sensitivity in eastern US forests. In other forest biomes around the world, there have been observations of reduced climate sensitivity in recent decades (Briffa *et al.*, 1998a, b; Knapp *et al.*, 2001; Soulé & Knapp, 2006; Leal *et al.*, 2008; Wyckoff & Bowers, 2010; Maxwell *et al.*, 2016), although the pattern is not universal (Biondi, 2000; Carrer & Urbinati, 2006). The reductions in climate sensitivity found in some species may be attributable to increased water use efficiency driven by elevated

CO_2 (Briffa *et al.*, 1998a; Knapp *et al.*, 2001; Soulé & Knapp, 2006; Leal *et al.*, 2008; Wyckoff & Bowers, 2010), although other factors are also at play, for example in the Midwest USA there has been a reduction in the strength of droughts in recent decades (Maxwell *et al.*, 2016).

Here, we analyse 109 yr of annual woody growth for 14 species within a temperate deciduous forest in Virginia, USA to understand how multiple climate drivers influence individual species growth and $ANPP_{stem}$. We test the hypothesis that woody growth of most species and $ANPP_{stem}$ are primarily water limited as opposed to energy limited, that is growth responds positively to growing season moisture and negatively to increased temperatures or potential evapotranspiration (PET). We evaluate this hypothesis across more than a century of historical climate variation (1901–2009) and for three consecutive 30-yr periods namely 1920–1949, 1950–1979 and 1980–2009.

Materials and Methods

Study site

Our study site was the 25.6-ha large forest dynamics plot at the Smithsonian Conservation Biology Institute (SCBI) in the Blue Ridge Mountains of northern Virginia, USA (Supporting Information Fig. S1; 38°53′36.6″ N, 78°08′43.4″W; elevation 273–338 m; Bourg *et al.*, 2013), which is part of the Forest Global Earth Observatory (ForestGEO) network (Anderson-Teixeira *et al.*, 2015a). The climate is humid temperate. From 1901 to 2009, January and July, temperatures averaged 1°C and 24°C, respectively, with mean annual precipitation of 998 mm distributed fairly evenly throughout the year (Table 1; Fig. S2). Bud break typically occurs in April, and leaf senescence begins in September and extends into November. Stem expansion is typically most rapid between May and July. The plot is a mature secondary mixed deciduous forest that developed after agricultural abandonment in the mid-19th century. Canopy trees are primarily 65–145 yr old with some individuals > 240 yr old (Fig. S3a).

Plot census and $ANPP_{stem}$ calculations

The plot was censused in 2008 and 2013 using standard ForestGEO protocols, in which all woody stems ≥ 1 cm in diameter at breast height (DBH) were identified, mapped, tagged, and measured in DBH (Condit, 1998; Bourg *et al.*, 2013). Census data, which were last updated in 2014, were obtained through the ForestGEO data portal (www.forestgeo.si.edu).

Census data were used to calculate mean annual $ANPP_{stem}$ from 2008 to 2013. Specifically, we first identified individuals that were alive in both 2008 and 2013 and estimated their aboveground biomass for both years using the allometries identified in Gonzalez-Akre *et al.* (2016) and recorded in our database of allometric equations, allodb (https://github.com/forestgeo/allodb; Gonzalez-Akre, pers. comm.). The growth rate of each individual was calculated as the difference between these values divided by the time interval, using exact census dates for each tree. To identify and deal with outliers, trees were grouped into DBH bins

Table 1 Climate variables analysed here, along with their January and July means.

Variable	Code	Units	1901–2009 mean ± SD	
			January	July
Average daily maximum temperature	TMX	°C	7.0 ± 2.7	31.2 ± 1.2
Average daily mean temperature	TMP	°C	1.1 ± 2.6	24.2 ± 1.0
Average daily minimum temperature	TMN	°C	-4.8 ± 2.5	17.3 ± 0.9
Diurnal temperature range	DTR	°C	11.7 ± 0.9	13.9 ± 1.1
Potential evapotranspiration	PET	mm d^{-1}	1.3 ± 0.2	4.4 ± 0.4
Potential evapotranspiration–precipitation	PET-PRE	mm month^{-1}	-31.2 ± 35.3	31.4 ± 44.5
Palmer Drought Severity Index[1]	PDSI	–	-0.19 ± 2.01	0.08 ± 1.94
Precipitation	PRE	mm month^{-1}	71 ± 33	104 ± 37
Wet day frequency	WET	month^{-1}	12.8 ± 2.7	11.2 ± 1.9
Cloud cover	CLD	%	69 ± 3	62 ± 6

Values were prewhitened for analysis.
[1]Higher values indicate wetter conditions.

(1–5, 5–10, 10–50, >50 cm) and the annual biomass increment of trees deviating from the size bin mean by more than ± 4 standard deviations (SD) were replaced with that mean. Individual biomass growth rates were then summed across species, using minimum DBH thresholds of both 1 and 10 cm.

Comprehensive estimation of $ANPP_{stem}$ requires accounting for the growth of trees that recruit into the census or die between censuses (Clark *et al.*, 2001). For trees that grew into the ≥ 1 or ≥ 10 cm DBH size class between 2008 and 2013, growth was calculated as the difference between 2013 biomass and the biomass of an individual of the minimum size threshold. We assumed minimal $ANPP_{stem}$ contributions of stems that died between 2008 and 2013, because trees at this site and elsewhere typically have greatly reduced growth rates for several years before dying (Gonzalez-Akre *et al.*, 2016; Cailleret *et al.*, 2017). We considered the $ANPP_{stem}$ estimates, including recruitment, as the authoritative values for this site and used these to calculate total

$ANPP_{stem}$ and contributions of each species (Table 2). However, to compare census- and tree ring-based estimates of $ANPP_{stem}$, we excluded recruitment, as it was not included in tree ring-based estimates (Table S3).

Tree core collection and chronology building

We collected increment cores from a subset of trees distributed throughout the plot in either 2010–2011 or 2016–2017 (Tables 2, S1; Fig. S1). All cores were taken at breast height (137 cm). In 2010–2011, cores were taken from randomly selected live individuals from each species with at least 30 trees ≥ 10 cm DBH. Most trees were subsequently measured (Bourg *et al.*, 2013). In 2016 and 2017, we collected cores from all trees found dead in our annual mortality census (Gonzalez-Akre *et al.*, 2016). Cores were dried, mounted, and sanded with a belt sander or by hand when necessary to see the cell structure

Table 2 Species analysed here, their contributions to aboveground woody net primary productivity ($ANPP_{stem}$) within the Smithsonian Conservation Biology Institute (SCBI) ForestGEO plot (stems ≥ 10 cm; 2008–2013), and key features of their chronologies.

Species	Species code	Ring porosity	$ANPP_{stem}$		Chronology		
			Mg C ha^{-1} yr^{-1}	%	n cores	$\overline{DBH}_{2008}$ (min, max)	SD of RWI
Liriodendron tulipifera	LITU	Diffuse	1.349	47.61	109	32.7 (10.0, 97.6)	0.14
Quercus alba	QUAL	Ring	0.305	10.77	66	42.9 (11.3, 76.7)	0.12
Quercus rubra	QURU	Ring	0.288	10.17	71	49.4 (10.1, 137)	0.10
Quercus velutina	QUVE	Ring	0.217	7.66	83	50.6 (16.0, 109)	0.13
Quercus montana	QUPR	Ring	0.136	4.80	67	38.1 (10.2, 84.6)	0.14
Fraxinus americana	FRAM	Ring	0.107	3.77	69	33.3 (5.8. 93.0)	0.10
Carya glabra	CAGL	Ring	0.103	3.62	39	26.6 (10.2, 52.3)	0.10
Juglans nigra	JUNI	Semi-ring	0.060	2.12	31	43.4 (20.4, 76.2)	0.18
Carya tomentosa	CATO	Ring	0.055	1.95	17	24.0 (12.0, 44.4)	0.18
Carya cordiformis	CACO	Ring	0.055	1.93	18	23.9 (10.4, 60.5)	0.13
Fagus grandifolia	FAGR	Diffuse	0.040	1.43	81	19.9 (10.1, 103)	0.15
Carya ovalis	CAOVL	Ring	0.031	1.10	24	32.9 (15.1, 60.3)	0.11
Pinus strobus	PIST	–	0.007	0.25	36	28.8 (15.0, 51.0)	0.16
Fraxinus nigra	FRNI	Ring	0.005	0.18	16	19.4 (6.9, 38.4)	0.15
All other species	–	–	0.075	2.64	–	–	–

$\overline{DBH}_{2008}$, mean diameter at breast height of tree species in 2008; SD of RWI refers to the SD of Ring-Width Index.

during periods of strong growth suppression (Speer, 2010). Rings were measured using a TA Unislide Velmex (0.002 mm precision; Velmex Inc., Bloomfield, NY, USA) for cores collected in 2011 and 2016. For cores collected in 2017, we used WINDENDRO (Regent Instruments Inc., Québec, QC, Canada), having verified that these methods gave extremely similar results. Ring-width measurements were crossdated and verified using the program COFECHA (Holmes, 1983).

We built crossdated chronologies for all species contributing $> 1\%$ of $ANPP_{stem}$ ($n = 12$) and two additional species, *Pinus strobus* and *Fraxinus nigra* (Table 2), which ranked 18th and 20th in terms of productivity contributions. Species in the top 20 contributors to $ANPP_{stem}$ for which we were unable to develop accurate chronologies included *Acer rubrum, Platanus occidentalis, Tilia americana, Nyssa sylvatica, Cercis canadensis* and *Ulmus rubra*, which each contributed $< 0.5\%$ of $ANPP_{stem}$ and ranked 13th to 17th and 19th in productivity, respectively. Because we were interested in ecosystem-level climate sensitivity, all trees were included in our final chronology, that is we included trees whose correlations to the master chronology for its species were lower than series typically used for other dendro-ecological applications, such as climate reconstructions. We did not include cores from our chronologies if they were degraded by decay or damaged such that deciphering ring boundaries increased uncertainty in crossdating accuracy. Chronologies of trees cored live and dead were pooled following analyses showing similar climate sensitivity at least up to 2009 (that is excluding 7–8 yr before death) for all four species with ≥ 10 cores in each category (LITU, QURU, QUVE, FRAM; comparison plots available at https://github.com/SCBI-ForestGEO/climate_sensitivity_cores/tree/master/results/live_vs_dead).

To remove or reduce nonclimatic factors related to growth (for example geometric constraints on ring width) or the influences of stand dynamics (for example individual tree growth release and suppression), all ring-width series for each species were standardised via ARSTAN using a 2/3 n spline, where n is the number of years in each series (Cook, 1985; Cook & Kairiukstis, 1990). We also tested a 50-yr fixed-width spline, which gave extremely similar results, indicating that our findings were not sensitive to variable-width vs fixed-width detrending. The influence of outliers in all series was reduced using the adaptive power transformation, which also stabilises the variance over time (Cook & Peters, 1997). Next, each series was stabilised using either the average correlation between raw ring-width series (rbar) method or a 1/3rds spline method to adjust changes in variance as series replication decreased towards the earlier portion of each chronology (Jones *et al.*, 1997). The 1/3rds spline method was chosen when replication in the inner portion of each chronology (*c.* the inner 30–50 yr of each record depending on full chronology length) dropped below three trees. Once that step was complete, a robust biweight mean chronology for each species was calculated from the ring-width indices (Cook, 1985). We chose to use residual chronologies because the autoregressive standardisation process in creating them removes much of the tree-level autocorrelation in growth and these chronologies would most likely contain the most conservative information on drivers of interannual growth

(Cook, 1985). We defined the chronology start date as the year the subsample signal strength (SSS) exceeded 0.75 (Table 2; Fig. S3b), and the end date as 2009 (therefore buffering mortality events by 7–8 yr). We used SSS instead of the expressed population signal (EPS) because EPS can be saturated with high series replication (Buras, 2017) and we were interested in climatic sensitivity, not 'quality of the tree-ring chronology' per the traditional paleoclimatic approach.

Analyses

We characterised the sensitivity of growth to monthly variation in 10 climate variables (Table 1) from 1901 (or chronology start date, as late as 1938; Table S1) to 2009 and over three 30-yr periods covering the last 90 yr of this time period (1920–1949, 1950–1979, 1980–2009). The years 1901–1919 were excluded from the analysis of shorter time periods because the chronologies of several species, including the dominant *Liriodendron tulipifera*, did not reach SSS ≥ 0.75 until 1910–1920.

Climate data were obtained from the ForestGEO Climate Data Portal (https://github.com/forestgeo/Climate) in August 2018, including Climatic Research Unit monthly data for eight variables from 1901 to 2016 (CRU TS v.4.01; Harris *et al.*, 2014) and NOAA Divisional Data's Palmer Drought Severity Index (PDSI) from 1895 to 2017. Atmospheric CO_2 data, used as context for comparing the two time periods, was obtained from a publicly available NASA data set that includes historical ice core data and NOAA ESLR atmospheric data (Etheridge *et al.*, 1996; Keeling & Whorf, 2012; National Aeronautics and Space Administration, 2017; NOAA/ESRL/Global Monitoring Division, 2018). Analyses of climate–growth relationships were conducted using 'dplR' (Bunn, 2008) and 'bootRes' (Zang & Biondi, 2013) in R v.3.5.1 (R Core Team, 2017), which correlated functions and bootstrapped confidence intervals for the relationships between annual growth and monthly climate variables following Biondi & Waikul (2004).

To scale from the species-level chronologies to the whole stand, we first developed species-specific allometries between the average tree ring-based radial growth increment from 2007 to 2009 and DBH measured in the 2008 census (Table S2). We then applied these allometries to predict radial increment for every stem ≥ 10 cm DBH (focal species), filling in 2008–2013 census growth measurements for species for which we did not have chronologies (3% of $ANPP_{stem}$). Next, we combined our radial growth estimates with species-specific allometries to estimate tree biomass growth and $ANPP_{stem}$. Estimates of $ANPP_{stem}$ for the entire stand and for each species were compared with estimates derived from 2008 to 2013 census data, indicating close correlation ($R^2 > 0.99$; Table S3). Finally, we estimated the change in $ANPP_{stem}$ that would be expected under a $+ 1$ SD increase (calculated for 1901–2009) in the monthly values for each climate variable ($\Delta ANPP_{stem}$). Pearson correlations between climate and each tree-ring chronology were converted to linear slopes as in Charney *et al.* (2016) and then used to predict the change in radial increment for a 1 SD increase in each monthly climate variable. This coefficient was expressed relative to mean

radial increment for the species (Table S1) to calculate per cent change under + 1 SD of the climate variable. Radial increment under a + 1 SD increase in the climate variable was then predicted by applying this % change to the radial increment predicted from allometry. For species without chronologies, we assumed no climate response. Although unrealistic, this assumption is likely to have minimal impact on our estimates of $ANPP_{stem}$ given the small contribution of these species to plot-level $ANPP_{stem}$ (2.6%; Table 2). We computed $\Delta ANPP_{stem}$ as the difference between $ANPP_{stem}$ under altered climate and that derived for baseline climate conditions, in both cases calculating $ANPP_{stem}$ as described above.

All data, R code, and results are available through the SCBI-ForestGEO organisation on GitHub (https://github.com/SCBI-ForestGEO: SCBI-ForestGEO-Data and climate_sensitivity_cores repositories), with static versions corresponding to data and analyses presented here archived in Zenodo (DOIs: 10.5281/zenodo.2649302 and 10.5281/zenodo.2656633, respectively).

Results

In total, our chronologies consisted of 728 trees from 14 species and seven genera with 16–109 cores per species (Table 2). From 2008 to 2013, these species represented 97.4% of $ANPP_{stem}$ (with recruitment) for stems ≥ 10 cm DBH (2.83 Mg C ha^{-1} yr^{-1};

Table 2), or 96.9% of $ANPP_{stem}$ for all stems ≥ 1 cm DBH (2.87 Mg C ha^{-1} yr^{-1}).

The 14 species had fairly consistent interannual signals and differed modestly in their variability (Fig. 1). Correlations between species-level residual chronologies averaged 0.41 and ranged from 0.86 between *Quercus alba* and *Q. montana* to −0.032 between *Fraxinus americana* and *Pinus strobus* (Fig. S4). Correlations between the dominant species, *Liriodendron tulipifera and* other species averaged 0.44 and ranged from 0.19 (*Fraxinus nigra*) to 0.63 (*Carya covalis*). Standard deviations of the ring-width index averaged 0.136 and ranged from 0.10 (*Quercus rubra, Fraxinus americana*) to 0.18 (*Juglans nigra, Carya tomentosa*; Table S1).

Over the centennial time scale, species' climate responses were broadly indicative of water-, as opposed to energy-, limitation (Figs 1, 2, S5–S14; Tables S4–S13). Species generally responded positively to current peak growing season (May–August) moisture (rain day frequency, precipitation, PDSI) and cloudiness, while responding negatively to temperature (max, mean, min), daily temperature range, PET and potential evapotranspiration–precipitation (PET-PRE). This held true for 92.7% of all climate variable−month combinations, with 36% of the relationships significant at $P < 0.05$. Species also responded positively to April temperatures (max, mean, min) and PET (82.1% of species-variable combinations, 11% significant). Responses to previous

Fig. 1 Residual chronologies of 14 tree species, including the 12 largest contributors to aboveground woody net primary productivity ($ANPP_{stem}$) in the Smithsonian Conservation Biology Institute (SCBI) ForestGEO plot, from 1901 to 2009. Also shown is mean May–July potential evapotranspiration (PET; mm month^{-1}) and precipitation (PRE; mm month^{-1}), with dashed vertical lines indicating the 10 yr in which the difference between the two was greatest (1911, 83 mm; 1914, 82 mm; 1930, 112 mm; 1936, 85 mm; 1944, 89 mm; 1964, 84 mm; 1966, 83 mm; 1977, 87 mm; 1999, 80 mm; 2007, 82 mm). Species are shown in descending order of their contributions to $ANPP_{stem}$. Chronologies are shown starting when subsample signal strength (SSS) ≥ 0.75 Supporting Information (Table S1). Refer to Table 2 for species-specific code information.
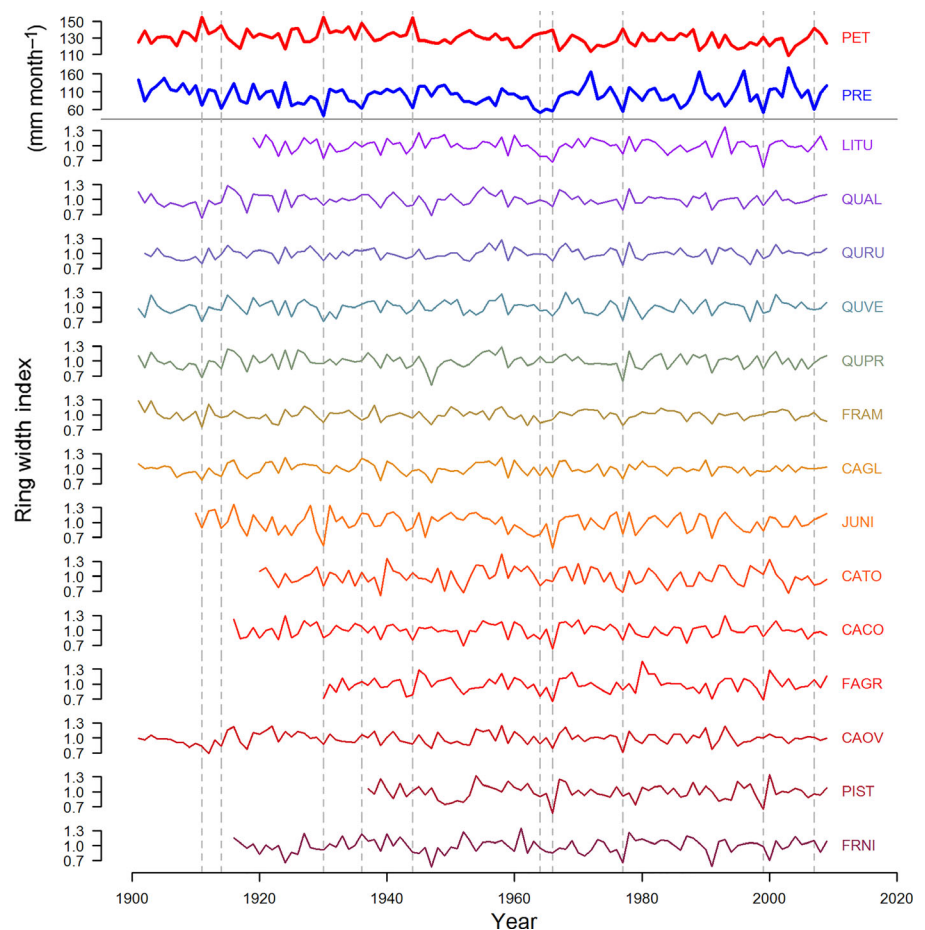
May–July conditions tended to be opposite those of the current growing season (75.7% of species-variable-month combinations, 19% significant), tending to be most pronounced in *Quercus* spp. (Figs 2, S5–S14). However, responses to conditions in August and September of the previous growing season were more similar to those of the current growing season; growth was generally higher under cloudy, wet conditions with favorable water balance (CLD, PRE, WET, PDSI; 74.1% of species−variable−month combinations), but responses of energy variables (temperature, diurnal temperature range (DTR), PET, PET-PRE) were not consistent (56.5% of species−variable−month combinations). The species deviating most commonly from the above-described patterns were the two contributing < 1% of $ANPP_{stem}$: *Fraxinus nigra*, most individuals of which grow along streams or in other persistently wet microsites, and *Pinus strobus*, a conifer and also the species with the shortest chronology (Fig. 1).

The climate sensitivity of each species' growth and $ANPP_{stem}$ – that is % change in individual growth or $ANPP_{stem}$ for + 1 SD change in climate – mirrored the observed Pearson correlations while also scaling with the SD of chronologies (Fig. 2). In other words, for the same strength of correlation with a climate variable under current climate, the growth and $ANPP_{stem}$ of species with higher growth variability (for example *Juglans nigra*, *Carya tomatosa*) was more sensitive to increases in the climate variable than those with low growth variability (for example *Quercus rubra*, *Fraxinus americana*). Growth sensitivities ranged up to c. ± 5% for each species−climate variable−month combination, but on average were much less, including for the dominant species, *Liriodendron tulipifera* (Fig. 2). While < 5% is a modest response, we note that it applies to only a + 1 SD change in one climate variable for 1 month, whereas a notably hot or dry growing season may involve changes > 2 SDs over several months, resulting in a larger growth response.

Scaled to the ecosystem level, $ANPP_{stem}$ reflected the dominant climate responses described above (Figs 2, 3) – particularly those of *Liriodendron tulipifera*, which contributed by far the most to stand-level $ANPP_{stem}$ (Fig. 2i). $ANPP_{stem}$ was generally most sensitive to conditions in the current peak growing season and to moisture of the previous May. The most influential variables (by month) included current May PET-PRE, PET, and wet day frequency, ± 1 SD variation in which affected $ANPP_{stem}$ by > 0.05 Mg ha^{-1} yr^{-1} (> 1.8% of total; Fig. 3). Responses were somewhat buffered relative to those of *Liriodendron tulipifera*, for which the strongest responses were slightly greater than ± 2.5%.

The three 30-yr time periods selected for comparison differed somewhat in climatic and atmospheric conditions. Climatically, 1950–1979 was most similar to the average conditions over 1901–2009, with more drought in the early 20th century (1920–1949) and more mesic conditions in recent decades (Figs 1, S2). Specifically, 1980–2009 was characterised by slightly higher than average cloud cover and PDSI and a narrower range of daily temperatures, whereas the reverse was true of 1920–1949 (Fig. S2). Of the 10 yr with the largest difference between PET and precipitation during May–July, two occurred in 1980–2009 (ranked 8th and 10th in magnitude), with three each in the other time periods (ranked 1st to 6th in magnitude with the two largest in 1920–1949; Fig. 1).

Atmospherically, recent decades were characterised by higher atmospheric CO_2 (average of 361 ppm) compared with previous periods (308 ppm for 1920–1949, 322 ppm for 1950–1979) and the full time period (325 ppm) (Keeling & Worf, 2012).

Over recent decades (1980–2009), species' climate responses were more variable and less pronounced compared with both the full time period (1901–2009) and the two earlier 30-yr time periods (1920–1949, 1950–1979; Figs 4, S5–S14; Tables S4–S13). Most notably, from 1980 to 2009, there were fewer positive species' responses to moisture (CLD, WET, PRE, PDSI) and fewer negative responses to temperatures, DTR, PET and PET-PRE (70% of species−variable−month combinations, 5% significant; compared with 83–93% in the other three time periods; Fig. 4a). The average strength of these correlations was also notably reduced in recent decades relative to earlier decades and the full 110-yr time frame (Figs 4, S5–S14; Tables S4–S13). Consistency of responses to April temperatures and PET and previous May–July conditions were similarly reduced (59% and 41% with same sign of correlation coefficients as the trends described above, respectively; Fig. 4a). Also, over the last 3 decades, responses to conditions in August and September of the previous growing season switched from moisture dominated to temperature dominated (Fig. 4a); growth was not consistently higher under cloudy, wet conditions (54% of species−variable−month combinations), whereas temperature and PET responses were predominantly negative (72% of species−variable−month combinations).

Similarly, $ANPP_{stem}$ was generally less responsive to climate over recent decades (1980–2009) than during 1920–1949, 1950–1979, or the entire 109 analysis time frame (Figs 3, 5). This largely reflected the responses of *Liriodendron tulipifera* (LITU; 48% of $ANPP_{stem}$; Fig. 2i), which tended to have relatively weak responses to growing season climate from 1980 to 2009 compared with some other species (Figs S5–S14), but was also consistent with the overall weakening of climate sensitivity across species (Fig. 4).

Discussion

In the first study to scale from species level to the climate sensitivity of $ANPP_{stem}$ (ecosystem level) in a diverse broadleaf-dominated temperate deciduous forest, we show that radial growth of 14 tree species and ecosystem-level $ANPP_{stem}$ respond positively to cool, moist growing season conditions for > 92% of month−variable combinations over 109 yr of variable climatic conditions (Figs 1–3). These responses generally remained the same in structure across three 30-yr periods, but were more variable and less pronounced during recent decades (1980–2009) at both individual and ecosystem scales ($ANPP_{stem}$; Figs 4, 5). There was also a tendency, again less consistent over recent decades, for the lagged relationship between the current year's growth and climate during the previous May–July to be opposite that of the current growing season (Figs 2, 3, 5). That is, growth was reduced by cool, moist conditions during the previous May–July. This pattern, together with commonly negative responses to high temperatures from late summer of the preceding year through
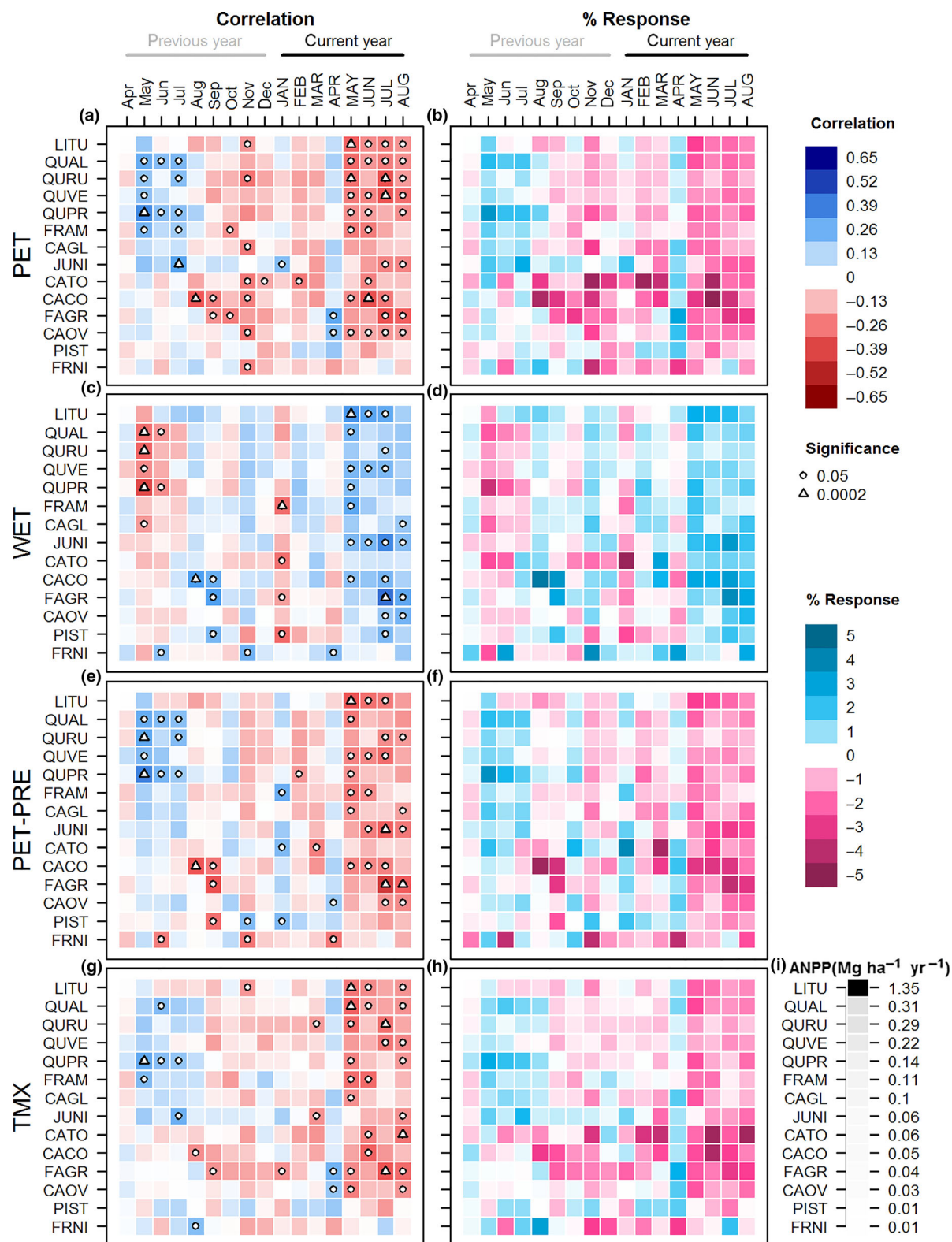
Fig. 2 Species' responses to four of the most influential climate variables analysed here – potential evapotranspiration (a, b) wet day frequency (c, d), the difference between potential evapotranspiration and precipitation (e, f), and maximum temperature (g, h). Shown are Pearson correlations between ring-width index and monthly climate variables (left panel) and per cent response of growth and aboveground woody net primary productivity ($ANPP_{stem}$) to + 1 SD in the climate variable (right panel). Also shown is $ANPP_{stem}$ of each species (i). Refer to Table 2 for species-specific code information.
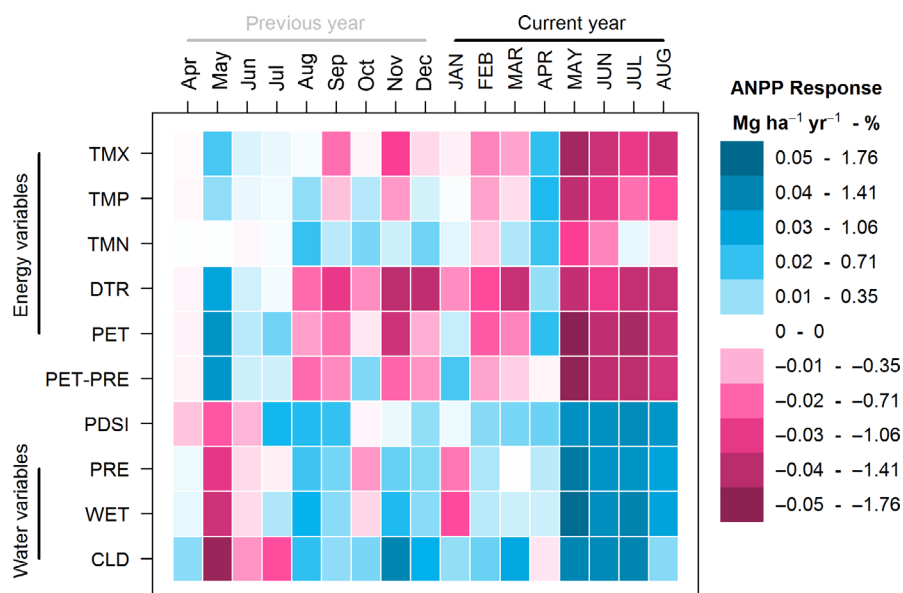
Fig. 3 Sensitivity of aboveground woody net primary productivity ($ANPP_{stem}$) to 10 climate variables from 1901 to 2009. Shown is change in $ANPP_{stem}$ (Mg C ha^{-1} yr^{-1} and % of total) with + 1 SD in climate variable, as predicted based on the responses of individual species and the 2008 census of the Smithsonian Conservation Biology Institute (SCBI) ForestGEO plot.
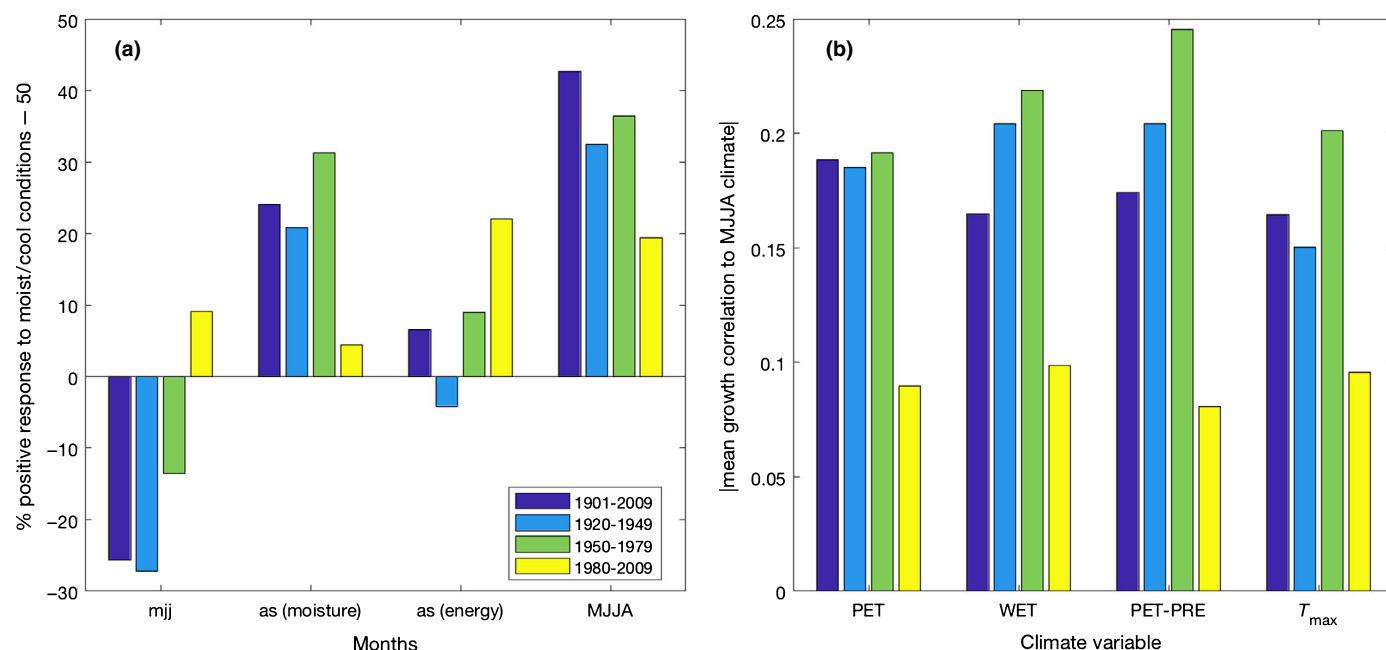

Fig. 4 Comparison of the (a) consistency and (b) average strength of climate correlations across the time periods analysed here. (a) Percent of species-climate variable−month combinations for which Pearson correlations are positive for moisture variables (PRE, WET, PDSI, CLD) and negative for energy variables (TMAX, TMP, TMIN, DTR, PET, PET-PRE) in each of three time periods: previous year's early growing season (mjj), previous year's late growing season (as), and current peak growing season (MJJA). (b) Mean absolute correlation of growth to several climate variables of all species over MJJA. Refer to Table 1 for explanations of moisture and energy variables.

current early spring (Figs 2, 3, 5, S5–S7), could indicate a key role of NSC reserves. Therefore, building from species-level research, we show that $ANPP_{stem}$ of a humid temperate forest is also primarily limited by moisture, as opposed to temperature or sunlight, but that carbohydrate reserves from the previous year contribute to a more complex climate sensitivity.

Responses to the 10 climate variables analysed were largely consistent across species (Figs 1, 2), and therefore the climate sensitivity of $ANPP_{stem}$ (Fig. 3) reflected that of most individual species.

There was a modest niche complementarity effect (Figs 2, 3), implying that, in this forest, species diversity slightly increases the stability of $ANPP_{stem}$ under fluctuating climate conditions, as has been observed in other plant communities worldwide (Isbell *et al.*, 2015; Anderegg *et al.*, 2018). However, the similar responses across species imply that biophysical constraints have bound species' climate sensitivities within a relatively narrow range and limited the potential for biodiversity to buffer substantially against climate extremes. An additional implication is that in forests such
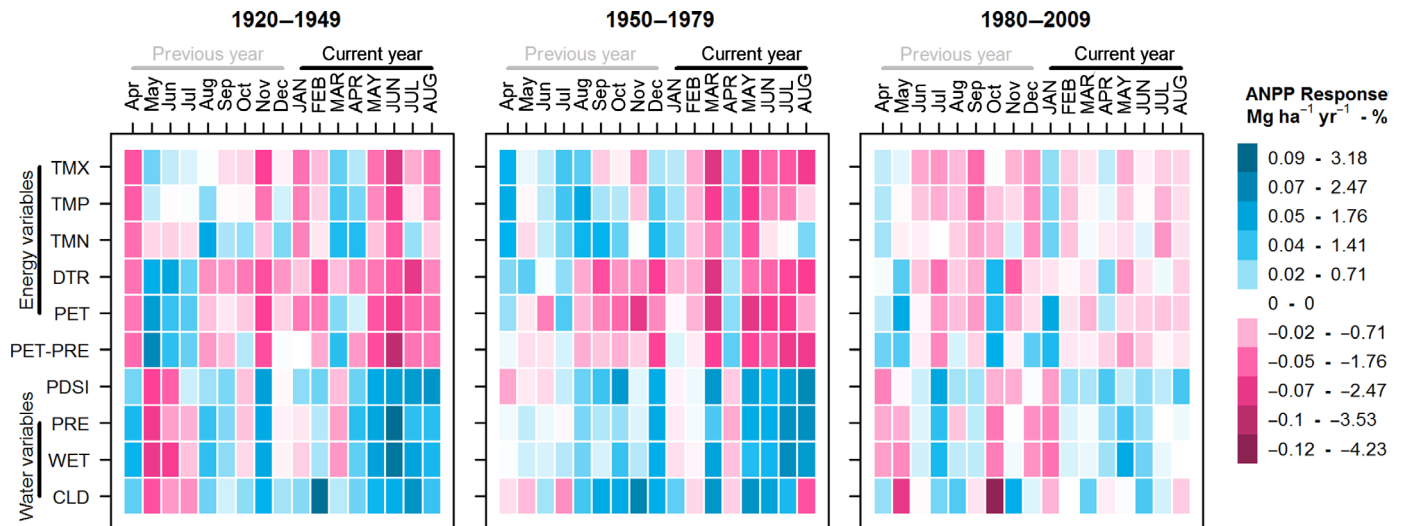
Fig. 5 Predicted response of aboveground woody net primary productivity ($ANPP_{stem}$) to + 1 SD change in 10 climate variables, as predicted based on the responses of individual species over three 30-yr time periods and the 2008 census of the Smithsonian Conservation Biology Institute (SCBI) ForestGEO plot.

as this with relatively low topographic complexity and the majority of $ANPP_{stem}$ concentrated within several dominant species (here, five species account for 80% of $ANPP_{stem}$; Table 1), the climate sensitivity of $ANPP_{stem}$ can be satisfactorily characterised based on tree-ring chronologies of those dominant species.

Forest woody productivity ($ANPP_{stem}$) was strongly influenced by current growing season conditions, being highest under relatively cool, low-PET, cloudy conditions with frequent precipitation (Figs 2, 3). This agrees with other tree-ring studies across eastern US deciduous forests showing positive moisture responses of tree growth (Belmecheri *et al.*, 2014; Elliott *et al.*, 2015; Martin-Benito & Pederson, 2015; Charney *et al.*, 2016; Levesque *et al.*, 2017). Physiologically, the observed positive response of radial growth to wet conditions is consistent with the fact that the proximate driver of stem growth is hydraulically driven cell expansion (Zweifel *et al.*, 2006), with most rapid stem diameter increases on rainy days (Herrmann *et al.*, 2016). Subsequent C sequestration associated with cell wall thickening can lag by more than a month (Cuny *et al.*, 2015), implying that the climate sensitivities of stem growth and photosynthesis are at least partially decoupled in time within the current growing season. Therefore, observations of negative responses of temperate moist deciduous forest GPP (Barford, 2001) and sap flow (Anderson-Teixeira *et al.*, 2015b) to cool, wet conditions over time scales of days to months are not inconsistent with the observed positive response of annual stem growth to interannual variation in moisture.

By contrast with the negative impact of temperature during the growing season, tree growth and $ANPP_{stem}$ responded positively to high April temperatures, indicative of thermal limitations to the start of the growing season and consistent with other tree-ring observations in the central Appalachians (Mathias & Thomas, 2018) and with findings that GPP and NEE (White *et al.*, 1999; Baldocchi *et al.*, 2018) are sensitive to growing season length. However, the influence of April temperatures on $ANPP_{stem}$ was quite modest relative to conditions in May–August and even the previous early growing season (Fig. 3).

The relationship between current year's growth and climate before the current growing season is likely to be due to spring and early summer stem growth being partially fuelled, at least in part, by NSC reserves – particularly in ring-porous species (*c.* 48% of $ANPP_{stem}$ in our plot; Table 2; Zweifel *et al.*, 2006; Michelot *et al.*, 2012). We suggest three possible mechanisms behind the observed inverse responses to past May–July conditions (Figs 2, 3, S5–S14). First, at this site, tree transpiration, and by extension photosynthesis, are reduced on humid, cloudy days (Anderson-Teixeira *et al.*, 2015b), whereas stem expansion is essentially twice as rapid on rainy days than rainless days (Herrmann *et al.*, 2016). Therefore, on the time scale of one to a few days, GPP and $ANPP_{stem}$ respond differently to climatic conditions, but it remains unknown how these climate sensitivities scale to monthly or annual time scales. Second, wet conditions early in the growing season may drive greater stem expansion and, subsequently, higher C demand for cell wall thickening, potentially resulting in less surplus C for NSC storage and lower growth the following year. Finally, NSCs may be preferentially allocated to other functions (for example, reproduction) – and away from stem growth – based on the previous year's growing conditions (Hacket-Pain *et al.*, 2018). Research will be needed to test the hypotheses that NSC reserves at the beginning of the growing season may influence $ANPP_{stem}$ and its climate sensitivity. Regardless, the dependency of stem growth on prior climate implies that, while tree-ring analysis is invaluable for inferring the climate sensitivity of $ANPP_{stem}$, these relationships must be combined with physiological data and models to characterise climatic drivers of total forest C sequestration.

In recent decades, we have observed two notable shifts in the climate sensitivities of woody growth and $ANPP_{stem}$. First, the consistency of the relationship between tree growth and moisture became muted compared with that found over the full 109-yr record (Figs 4, 5). This weakening of the climate–growth relationship was, at least partially, driven by slightly more mesic conditions with fewer strong droughts (Figs 1, S2), with a similar

trend noted across several sites in the Midwest USA (Maxwell *et al.*, 2016) and evidence that more mesic conditions have been associated with increased growth in the Northeast USA (Levesque *et al.*, 2017). It is also possible that elevated CO_2 has an interactive effect on climate sensitivity, buffering growth responses in drought years by increasing water-use efficiency (Levesque *et al.*, 2017; Mathias & Thomas, 2018), while having less or no impact on growth during wet years (Knapp *et al.*, 2001; Soulé & Knapp, 2006; Wyckoff & Bowers, 2010; Levesque *et al.*, 2017). Further research will be required to fully understand the mechanisms driving the observed declines in the strength of climate–growth relationships. However, whatever the mechanism, this observation is significant for our understanding of the ecophysiology of North American temperate deciduous forests in that they appear to be less moisture limited at present than they have been in the past or are likely to be in the future (Clark *et al.*, 2016). Current ecophysiological research on these forests (for example, eddy-covariance studies, extensive forest monitoring, model parameterisation and evaluation) is therefore capturing a period of low drought stress and are likely to be underestimating the importance of moisture for forest ecosystem productivity.

At least on the ecosystem level ($ANPP_{stem}$), the relative importance of climatic conditions before the start of the growing season appears to have increased, in part because of decreasing influence of current growing season conditions (Figs 4, 5). This also points to increasing decoupling between the climate sensitivities of $ANPP_{stem}$ and GPP, implying that responses of woody growth to current growing season climatic conditions are not currently a reliable indicator of the climate sensitivity of ecosystem C sequestration.

Our results suggest that the woody productivity of forests such as ours is likely to decline under expected future climate conditions. Future projections for the region include increased temperatures (*c.* 1–5°C by 2100, depending on emissions; IPCC, 2014), with associated increases in PET and evaporative demand likely to more than offset the predicted slight ($\leq 10\%$) increases in precipitation (IPCC, 2013, 2014, US Global Change Research Program, 2014; Cook *et al.*, 2015). The negative effects of high temperatures and PET on growth (Figs 2, S5–S9) and $ANPP_{stem}$ (Fig. 3) indicate that increasing temperatures will be likely to reduce forest productivity by increasing evaporative demand and water limitation, aligning with the conclusions of other temperate deciduous forest tree-ring studies (Charney *et al.*, 2016; Klesse *et al.*, 2018a,b). Moreover, our finding that wet day frequency had an overall greater importance than total precipitation implies that any shift in precipitation distribution into fewer, larger storms is also likely to have a negative impact on tree growth (Elliott *et al.*, 2015). These effects could be somewhat buffered by increased water-use efficiency under elevated CO_2, and understanding the extent to which this may be occurring remains an important open question. While the CO_2 effect on growth overall may be weak in eastern US deciduous forests (Levesque *et al.*, 2017) and globally (Peñuelas *et al.*, 2011), this does not rule out a meaningful impact during drier years – as has been observed in other regions (Knapp *et al.*, 2001; Soulé & Knapp, 2006; Wyckoff & Bowers, 2010). However, even if the weakening of

climate–growth relationships in recent decades observed here (Figs 4, 5) is attributable to increased water-use efficiency under elevated CO_2, the effect is unlikely to be sufficient to prevent productivity declines under projected future climate conditions (Charney *et al.*, 2016).

Our pairing of tree-ring analyses with plot data yields a long-term perspective on climate sensitivity of $ANPP_{stem}$. Without such long-term data, it is impossible to disentangle the some-times-subtle influence of climate on tree growth. As we show, the longer time frame can reveal sensitivities that are not being detected by contemporary high-resolution forest measurements (for example eddy flux, dendrometer bands) that serve as the basis for most forest ecosystem−climate models. Importantly, the processes that appear to be governing growth in this study are not well represented in current models, most of which forecast an overall enhancement of forest productivity with projected climate change (Albani *et al.*, 2006; Ollinger *et al.*, 2008; Duveneck & Thompson, 2017). We have yet to characterise interactive effects among climate variables (Foster *et al.*, 2016) or variables known to influence climate sensitivity, including tree size (Bennett *et al.*, 2015), canopy position (Teets *et al.*, 2018b), topographic position (Elliott *et al.*, 2015), and competition (D'Amato *et al.*, 2013). Incorporating these factors in future analyses will further strengthen predictions of $ANPP_{stem}$ and its responses to climate variability and change.

Acknowledgements

Author contributions

KAT, RH, AT and NP designed the research. Cores were collected and measured by JM (2010–2011), VM (2016), and RH (2017) under guidance of JRT (2010–2011), KAT and AT (2016–2017). Chronologies were developed by RH under guidance of AT and NP. Data analyses were performed by performed by VH under guidance of KAT, AT and NP. KAT, RH, AT and NP interpreted the results. RH and KAT wrote the first draft of manuscript, and all authors (RH, KAT, AT, NP, JM, VM, JRT and VH) contributed to revisions.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Map of trees cored in the 26-ha SCBI-ForestGEO plot and analysed in this study.

Fig. S2 Monthly means ± SD of climate variables over the four time frames analysed here.

Fig. S3 Numbers of cores and SSS through time for chronologies analysed here.

Fig. S4 Matrix of correlation between species chronologies.

Fig. S5 Species responses to daily maximum temperature (TMX).

Fig. S6 Species responses to daily mean temperature (TMP).

Fig. S7 Species responses to daily minimum temperature (TMN).

Fig. S8 Species responses to diurnal temperature range (DTR).

Fig. S9 Species responses to potential evapotranspiration (PET).

Fig. S10 Species responses to potential evapotranspiration–precipitation (PET-PRE).

Fig. S11 Species responses to Palmer Drought Severity Index (PDSI).

Fig. S12 Species responses to precipitation (PRE).

Fig. S13 Species responses to wet day frequency (WET).

Fig. S14 Species responses to cloud cover (CLD).

Table S1 Chronology details, including *n* cores and chronology statistics.

Table S2 Species-specific allometries between radial increment and diameter at breast height (DBH).

Table S3 Comparison of ANPP_stem estimates from census data and cores.

Table S4 Summary of Pearson correlations with daily maximum temperature (TMX) for all species.

Table S5 Summary of Pearson correlations with daily mean temperature (TMP) for all species.

Table S6 Summary of Pearson correlations with daily minimum temperature (TMN) for all species.

Table S7 Summary of Pearson correlations with diurnal temperature range (DTR) for all species.

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Table S13 Summary of Pearson correlations with cloud cover (CLD) for all species.

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