**Title:** Warm springs alter timing but not total growth of temperate deciduous trees

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**As the climate changes, warmer spring temperatures are causing earlier leaf-out1,2,3 and commencement of carbon dioxide (CO2) uptake1,3 in temperate deciduous forests, resulting in a tendency towards increased growing season length3 and annual CO2 uptake1,4,5,3, 6,7.** **However, less is known about how spring temperatures affect tree stem growth8,9, which sequesters carbon (C) in wood that has a long residence time in the ecosystem10,11.** **Using dendrometer band measurements from 440 trees across two forests, we show that warmer spring temperatures shifted stem diameter growth of deciduous trees earlier but had no consistent effect on peak growing season length, maximum growth rates, or annual growth.** **The latter finding was confirmed on the centennial scale by 207 tree-ring chronologies from 108 forests across eastern North America, where annual ring width was far more sensitive to temperatures during the peak growing season than in the spring.** **These findings imply that any extra CO2 uptake in years with warmer springs4,5 does not significantly contribute to increased sequestration in long-lived woody stem biomass.** **Rather, contradicting projections from global C cycle models1,12, our empirical results imply that warming spring temperatures are unlikely to increase woody productivity enough to strengthen the long-term CO2 sink of temperate deciduous forests.**

In recent decades, tree growth in Earth’s forests has more than offset losses from deforestation and other disturbances, such that a net forest CO2 sink of ~1.6 Gt C yr-1 offsets ~20% of anthropogenic emissions13, dramatically slowing the pace of atmospheric CO2 accumulation and climate change. Of this important C sink, ~ 47% occurs in temperate forests13, with temperate deciduous forests sequestering >0.3 Gt C yr-1.14 The future behavior of this C sink will play an important yet uncertain role in influencing atmospheric CO2 and climate change15–17.

In temperate deciduous forests, spring warming generally lengthens the period over which trees have photosynthetically active leaves1,3,18 and that over which the ecosystem is a net CO2 sink1,18. Based on these observations, current terrestrial ecosystem models represent warm springs and longer growing seasons as contributing positively to annual gross primary productivity (*GPP*) and net CO2 uptake (i.e., net ecosystem exchange, *NEE*)2,12,15. However, the long-term persistence of this extra C in the ecosystem, and the associated negative feedback to climate change1, will depend on the extent to which it is allocated to woody growth and therefore resides in the ecosystem for decades to centuries10,11, as opposed to being rapidly released back to the atmosphere through respiration19,20. Model representation of C allocation to stem growth – or woody aboveground net primary productivity (*ANPPwoody*) on the ecosystem level – does not capture known decoupling of stem growth from photosynthate production9,17,21. As a result, the consequences of rising spring temperatures on stem growth may not be accurately represented in models9,17. Understanding the sensitivity of *ANPPwoody* to spring temperatures is central to predicting the future of the temperate deciduous forest C sink.

Most studies on tree stem growth responses to warmer spring temperatures have focused on boreal or temperate conifers, which tend to respond to warmer spring temperatures with an earlier start to growth22, 23 and increased annual growth in mesic climates24, 25. In contrast, we have little evidence as to how stem growth and *ANPPwoody* respond to warmer spring temperatures in deciduous forests8,9. Close coordination of budburst and initiation of xylogenesis9 suggests that warm springs should shift the onset of growth earlier alongside observed advances in leaf phenology1,2,3. However, earlier initiation of growth would not necessarily translate to earlier, faster, or greater stem growth; rather, stem growth is dependent upon environmental conditions on hourly to daily time scales26,27, and annual growth is more closely linked to conditions within the growing season than to growing season length28, *GPP*21, or *NEE*21. Furthermore, growth of broadleaf deciduous trees may be sink-saturated17,29, such that longer growing seasons with more C fixation do not necessarily augment growth21,30,31. Tree-ring records, which can be used to examine annual growth but not growth seasonality, reveal that growth of temperate deciduous trees tends to be most sensitive to temperature or potential evapotranspiration between late spring and early summer32,33, with some evidence that warmer springs may have a modest positive effect on growth25,33. These observations do not necessarily align with the finding that warming spring temperatures increase annual forest CO2 uptake in temperate deciduous forests1,18. Characterizing responses of stem growth to warming spring temperatures is critical to bridging this conceptual disconnect and understanding how forest biomass growth is likely to change as the climate warms.

Here, we evaluate how spring temperatures affect the timing, rates, and annual increments of stem diameter growth of temperate deciduous trees across eastern North America. To test whether warmer springs advance the timing and extend the duration of stem diameter growth, we used dendrometer band measurements on 440 trees across two mid-latitude forests. To test whether spring temperatures consistently increased annual radial increments, we analyzed 207 tree-ring chronologies from 108 forests.

## Dendrometer band analysis

Using dendrometer band measurements taken throughout multiple growing seasons at the Smithsonian Conservation Biology Institute (SCBI; Virginia, USA; n = 119 trees from 2011-2020) and Harvard Forest (Massachusetts, USA; n = 321 trees from 1998-2003), we fit a logistic growth model34 to determine the days of year (DOY) when 25, 50, and 75% annual diameter growth were achieved (*DOY25*, *DOY50*, *DOY75*), peak growing season length (*Lpgs = DOY75 - DOY25*), the maximum growth rate (*gmax*), and total annual increment in diameter at breast height (*∆DBH*; Fig. 1). This analysis was performed separately for ring- and diffuse porous species (Extended Data Table 1), which differ in the seasonal timing of growth (Extended Data Table 2, Extended Data Figure 1)27,35. These stem-growth milestones were compared to canopy foliage phenology (measured at ecosystem level via remote sensing).

Both canopy foliage phenology and the timing of stem growth shifted earlier as spring temperatures increased (Fig. 2). We found a consistent effect of temperature (*Tmax* or *Tmin*) throughout the spring, but the strongest effects on stem growth timing were found using *Tmax* during a critical temperature window (*CTW*). *CTW* was identified by assessing the correlation between weekly *Tmax* and *DOY25* for all combinations of consecutive weeks from January 1 to mean *DOY25* for each xylem architecture-site combination (Extended Data Figure 2). The *CTW* was defined as the weeks for which this correlation was strongest, and mean *Tmax* during this period (*CTW* *Tmax*) used as our independent variable.

For ring- and diffuse- porous species at both sites, warmer *CTW* *Tmax* resulted in earlier achievement of seasonal milestones. Consistent with findings from previous studies, leaf phenological milestones advanced at both sites (Fig. 2a-b, Extended Data Table 2), with greenup (DOY when EVI2 first crossed 15% of the segment EVI2 amplitude) advancing 3.5 days/°C at SCBI (p=0.016) and 2.4 days/ °C at Harvard Forest (p=0.1). Similarly, with the exception of ring porous *DOY75* at SCBI, the stem growth milestones *DOY25*, *DOY50*, and *DOY75* decreased with *CTW* *Tmax* (Figs. 1, 2c-d; Extended Data Figures 3-4). Specifically, *DOY25*, *DOY50*, and *DOY75* advanced 0-1.7 days/ °C for ring porous species and 2.8-2.9 days/ °C for diffuse porous species at SCBI, and 10.3-12.3 days/ °C for ring porous species and 0.9-4.2 days/°C for diffuse porous species at Harvard Forest (Extended Data Table 2).

Whereas the length of time between canopy greenup and senescence (*i.e.,* the day when greenness dropped below 90% of its peak) increased with the *CTW* *Tmax* of the porosity group containing the dominant canopy species at each site (diffuse porous at SCBI, ring porous at Harvard Forest; Fig. 2a-b), there was no consistent lengthening of *Lpgs* (Fig. 1, Extended Data Figures 3-4).

In contrast to the pronounced effects of *CTW* *Tmax* on the timing of growth, its effects on *gmax* and *∆DBH* were inconsistent, and usually weak (Fig. 1, Extended Data Figures 3-4). Specifically, *gmax*, which occurred on average within 5 days of *DOY50*, displayed extremely small negative changes (Harvard Forest) or changes in opposite directions (SCBI) in relationship to *CTW* *Tmax* for ring- and diffuse- porous species. *∆DBH* displayed a weak positive relationship (+0.003-0.008 cm/ °C) with *CTW* *Tmax* at SCBI and a weak negative relationship (-0.02-0.003 cm/ °C) at Harvard Forest (Extended Data Figure 3).

## Tree-ring analysis

To understand how annual radial stem growth increments have responded to spring temperatures at the centennial scale, we analyzed tree-ring chronologies of 12 species at SCBI33 and 4 species at Harvard Forest (Extended Data Table 1), plus an additional 191 chronologies from 106 sites (Fig. 3; Extended Data Figure 5; Extended Data Table 3). In total, our analysis included 207 chronologies representing 24 broadleaf species at 108 sites distributed from Alabama (34.35°N latitude) to Michigan (45.56°N latitude) and spanning a 15 °C range in April *Tmax*. Across all chronologies, the standardized ring-width index (*RWI*) was significantly (95% confidence interval did not include 0) positively correlated with April *Tmax* for only 2% of chronologies: 1 of 142 ring porous and 4 of 66 diffuse porous species-site combinations (Extended Data Table 3). There were even fewer significant positive correlations with March and May *Tmax*: 0% and 1%, respectively (Extended Data Table 3). In contrast, *RWI* was frequently negatively correlated with *Tmax* during peak growing season months (May-August), with significant correlations for 52% (May: 45/141, Jun: 107/141, Jul: 91/141, Aug: 53/141) and 46% (May: 10/66, Jun: 52/66, Jul: 36/66, Aug: 23/66) of species-site-month combinations for ring- and diffuse-porous species, respectively. *Tmin* generally exhibited weaker relationships to annual growth than *Tmax*, with few significant correlations between spring *Tmin* and *RWI* (Extended Data Figure 6).

To test whether warm springs might result in storage of non-structural carbohydrates (NSC) that would augment growth the following year36, we extended the analysis to examine correlations between *RWI* and *Tmax* in the previous year (Extended Data Figure 7). This revealed little effect of previous spring temperatures on annual growth, with significant positive correlations of *RWI* to previous March or April *Tmax* for 5/142 ring porous chronologies and to previous April or May *Tmax* for 7/66 diffuse porous chronologies.

To test whether there may be an enhancement of growth by warmer spring temperatures that was offset by the negative effect of high summer temperatures, we tested for the joint effects of April and June-July *Tmax* on *RWI*. Results were qualitatively similar to the univariate correlations (Fig. 3), with significant (p ≤ 0.05) positive correlations to April *Tmax* for only 4% of chronologies and significant negative correlations with June-July *Tmax* for 77% of chronologies (Extended Data Table 3).

## Discussion

Together, our results demonstrate that warmer spring temperatures in the temperate deciduous forests of eastern North America advance the timing of stem diameter growth but have little effect on annual increments (Figs. 1-3). The observed advance in stem growth under warmer springs parallels advances observed for canopy foliage phenology (Fig. 2a-b)1,3 and *NEE*1,3. However, inconsistent with the concept that an earlier start to growth would increase *ANPPwoody*, we demonstrate that warmer springs either hasten the deceleration of stem expansion or otherwise fail to translate extended growing seasons into biologically significant increases in stem growth (Fig. 1), and thereby have negligible effect on total annual growth for most species and locations (Fig. 3). Our observations suggest that the deceleration of stem expansion, which occurs mid-summer near the time of peak canopy greenness (Extended Data Figure 1)3,28, is driven by cues other than photosynthate limitation, such as water stress21,26,28, nutrient limitation37, daylength28, or sink saturation21,29. This adds to a growing body of evidence for a sink limitation of stem growth17,21,31, wherein global change factors known to enhance photosynthesis, such as longer growing seasons or elevated CO2, do not cause a corresponding increase in stem growth19,28.

Combined with widespread observations that warming springs tend to lengthen the season of CO2 uptake3,18 and increase net annual CO2 uptake1,4,5,3, 6,7, our findings imply a lengthening of the period from peak stem growth to the cessation of CO2 uptake by the ecosystem and an increase in C allocated to functions other than stem expansion in the current or following year. It remains theoretically possible that warm springs could augment *ANPPwoody*, which, although routinely calculated based on stem growth, can be partially decoupled from it through differences in wood density or C content21. Extra C fixed in years with warm springs could potentially be allocated to formation of more C-dense wood, either through enhanced cell wall thickening (a process that lags behind stem expansion38) or to a higher ratio of high-density latewood to lower-density earlywood. However, existing evidence indicates that vessel features are most strongly controlled by summer drought stress in the previous (earlywood) or current (latewood) year, while warm springs have a neutral or negative effect on latewood width39–41. Thus, it is unlikely that warm springs have a positive effect on total C content of annual rings or *ANPPwoody*.

The fate of any additional C fixed during years with warm springs remains unresolved, but possible destinations – including respiration, NSC storage, and production of foliage, reproductive structures, roots30, or root exudates – generally have shorter residence times than woody growth. Indeed, when *GPP* of a mature forest was increased through experimental CO2 enrichment, *ANPPwoody* remained unchanged, while additional C was released back to the atmosphere on relatively short time scales through enhanced respiration19. Consistent with this, it has been observed that C gains from an earlier spring can be offset through fall or winter respiration20, although even the C in shorter-lived pools would often be carried over into the following year42. Thus, observed augmentation of *NEE* by warm springs1,6,7 is likely to be compensated by increased respiration in subsequent years.

It is possible that as spring warming continues, forests will adjust to directional changes in growing season length with an enhancement of *ANPPwoody*. Across latitudinal gradients, warmer spring temperatures are associated with earlier leaf-out43 and longer growing seasons, which in turn are correlated with greater tree growth44, *ANPPwoody*45, and *NEE*46. Thus, warming spring temperatures are likely to increase the biophysical potential for annual tree growth. If extra photosynthate made available through a growing difference between *GPP* and *ANPPwoody* is allocated to functions that relieve limitations on woody growth – for example, by enhancing nutrient and water acquisition through enhanced allocation to roots30,47 – it is possible that warming spring temperatures could ultimately increase *ANPPwoody* through indirect mechanisms. Understanding how warming spring temperatures are influencing C allocation within ecosystems remains a key outstanding question.

Regardless of the influence of spring temperatures on C cycling within the ecosystem, our results clearly demonstrate that the dominant effects of temperature on deciduous tree growth occur not in the spring, but during the peak growing season of the current or sometimes previous year (Fig. 3, Extended Data Figure 7), when increased atmospheric demand associated with high temperatures can limit both leaf-level gas exchange and stem growth21,26,28,48. Indeed, the timing of peak growth in June and July (Extended Data Table 2, Extended Data Figure 1) coincides with the timing of the greatest sensitivity of annual growth to *Tmax* (Fig. 3, Extended Data Table 3). This finding is consistent with numerous tree-ring studies demonstrating strong sensitivity of growth to drought stress or high temperatures during the peak growing season24,32,33,44. Warm springs may also amplify summer drought stress in some times and places, effectively canceling out any positive effects of an extended growing period2,49,50. While such an interaction was unlikely to have played a major role within the scope of our dendrometer band study, given relatively mesic conditions and lack of significant correlation between spring temperatures and summer drought stress (see Methods), our tree-ring analysis does reveal a higher frequency of negative than positive correlations of annual growth to spring temperatures, particularly for ring porous species in cooler climates (Fig. 3, Extended Data Table 3). Thus, warm springs can have a net negative effect on growth, particularly when water is limiting25.

As spring temperatures become increasingly warmer, growing seasons will start earlier. However, barring rapid acclimation of temperate deciduous forests to the warming conditions, advancement in the timing of stem growth (Fig. 1) is unlikely to provide a sustained augmentation of C sequestration in woody biomass and ensuant negative climate change feedback that is anticipated in most climate forecasting models1,2,12,31. Rather, the dominant effect of rising temperatures on temperate deciduous forest woody productivity will be a negative effect of high summer temperatures (Fig. 3)15, which constitutes a positive feedback to climate change.

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# Methods

## Dendrometer band analysis

Dendrometer band measurements were collected at SCBI51 and Harvard Forest3,35, both part of the Forest Global Earth Observatory (ForestGEO)52,53. SCBI (38.8935° N, 78.1454° W; elevation 273–338 m.a.s.l.) is located in the Blue Ridge Mountains at the northern end of Shenandoah National Park, 5 km south of Front Royal, Virginia. The forest is secondary and mixed age, having established in the mid-19th century after conversion from agricultural fields51. Dominant canopy species within the 25.6 ha ForestGEO plot include tulip poplar (*Liriodendron tulipifera* L.), oaks (*Quercus spp.*), and hickories (*Carya spp.*)33. The climate is humid temperate, with 1950-2019 mean annual precipitation of 1018 mm and temperatures averaging 1°C in January and 24°C in July44. Within the study period for the dendrometer band analysis (2011-2019), spring temperatures (March and April *Tmax*; source: CRU v.4.0454) and summer Standardized Precipitation Evapotranspiration Index (SPEI)55 values (4-month value of August) were similar to the average climate prior to the study period (1970-2010). Specifically, average spring *Tmax* was 16.9 ±1.4°C (mean ± 1SD) prior to the study period (range: 14.1-19.9) and 17.6± 1.7°C (range: 15.6-20) during the study period, while summer SPEI was -0.06± 1.02 (range: -1.7-2.4) prior to the study period and 0.5± 0.8 (range: -0.8-1.6) during.

Harvard Forest (42.5388° N, 72.1755° W, 340-368 m.a.s.l.) is located near the central Massachusetts town of Petersham. The forest is secondary and mixed age, having re-established around the beginning of the 20th century following agricultural use and significant hurricane damage in 1938. Dominant species within the 35 ha ForestGEO plot are hemlock (*Tsuga canadensis* (L.) Carrière), oak (*Quercus spp.*) and red maple (*Acer rubrum* L.). The climate is temperate continental, with 1950-2019 mean annual precipitation of 1104 mm and temperatures averaging -5°C in January and 22°C in July44. Within the study period for the dendrometer band analysis (1999-2003), spring temperatures (March and April *Tmax*; source: CRU v.4.0454) and summer SPEI values (4-month value of August) were similar to the average climate prior to the study period (1970-1998). Specifically, average spring *Tmax* was 10.9± 1.5°C prior to the study period (range: 8.0-13.2) and 11.2± 1.0°C (range: 10.1-12.2) during the study period, while summer SPEI was 0.1± 0.9 (range: -1.8-1.7) prior to the study period and 0.2± 0.9 (range: -1.0-1.1) during. The driest summer during the study period (1999) had the 5th lowest SPEI value (-1.0) in the period 1970-2003, with precipitation of 52 mm mo-1 in June-August compared to average monthly precipitation of 100+ mm35.

Metal dendrometer bands were installed on 941 trees within the SCBI and Harvard Forest ForestGEO plots. Bands were placed on dominant species, including two diffuse- and two ring porous species at SCBI and eight diffuse- and three ring porous species at Harvard Forest (Extended Data Table 1). While we do not estimate the ages of trees in our sample, bands at both sites were placed on individuals of differing sizes in an attempt to measure trees across a range of ages. Bands were measured with a digital caliper approximately every 1-2 weeks within the growing season from 2011-2020 at SCBI and 1998-2003 at Harvard Forest. The number of bands measured at each site fluctuated slightly as trees were added or dropped from the census (e.g., because of tree mortality). Across years, the number of bands sampled averaged 129 (range: 91-138) at SCBI and 717 (range: 700-755) at Harvard Forest.

Measurements were timed to begin before the beginning of spring growth and to continue through the cessation of growth in the fall. At SCBI, the median start date was April 14, which was adjusted forward when early leaf-out of understory vegetation was observed, with the earliest start date being March 30 (in 2020). Measurements were continued through to fall leaf senescence, with the median end date being October 17 and the latest end date November 26 (2012). At Harvard Forest, all measurements from 1998 were dropped because of a late start date (May 26). Among the remaining years,the median start date was April 21 and median end date of October 27. 1999 was an anomalous year where initial measurements were taken on January 5, but not taken again until April 15. The latest end date was November 11, 2002. In our analysis, each band-year was treated independently, with no data overlap from one year to the next.

The raw dendrometer band data were screened to remove records or entire tree-years that were inappropriate for our analysis because of reduced reliability of predicted growth in the modeled curves. Specifically, we removed tree-years with small or negligible total growth (*∆DBH* ≤0.005 cm; SCBI = 26, Harvard Forest = 253) and tree-years where the first intra-annual measurement was later than the first spring survey (trees that were missed in the initial census; SCBI = 22, Harvard Forest = 8). In total, this process removed 309 of the 2701 available tree-year records for 2011-2020 at SCBI and 1999-2003 at Harvard Forest.

We fit a five-parameter logistic growth model34 to dendrometer band data from each tree-year to define stem growth milestones and growth rates (Fig. 1). In particular, we model the observed diameter at breast height (DBH) on a given day of the year (DOY; *i.e.*, julian days) as:

Here, *L* and *K* are lower and upper asymptotes of the model. *DOYip* is the day of year where the inflection point in growth rate occurs, *r* shapes the slope of the curve at the inflection point, and is a tuning parameter controlling the slope of the curve toward the upper asymptote. This allows an asymmetric fit to the data, where the onset of growth can be estimated independent of the cessation of growth. When , *gmax* occurs on *DOYip*. The model outputs two additional variables, *a* and *b*, which represent the beginning and end DBH in each model year and are constrained by the first and last dendrometer band measurements. The model was fit in R v4.0 using the functions developed in the *Rdendrom* package34. These functions take the time-series of manual dendrometer band measurements and return maximum-likelihood optimized values of the above five parameters that best predict DBH for each day of year. An advantage of this approach is that short-term shrinkage and swelling associated with rain events34,56 and measurement errors show up as residual variation and do not unduly influence the parameters of interest. Having fit the model for each band-year of data, we then modeled DBH using these optimal parameter values in our logistic growth model and extracted the intra-annual growth variables of interest (Fig. 1).

After fitting the growth model, we removed tree-years with poor fits. Models were judged to be poorly fit if modeled growth parameters were outliers, which were commonly indicative of unrealistic fits (e.g., growth occurring outside the growing season or over a very short period) and underlain by very slow tree growth or poor data records that passed the initial screening (described above). Modeled fits for tree-years were removed under two conditions: (1) *gmax* was ≥2.5 standard deviations away from the mean for each site-xylem architecture group combination (SCBI = 3, Harvard Forest = 11); (2) timing variables (*DOYip*, *DOY25*, *DOY50*, *DOY75*) were ≥2.5 standard deviations away from the means for their site, xylem architecture group, and year (SCBI = 74, Harvard Forest = 101). In total, this process removed 189 of the 2392 tree-year records deemed appropriate for analysis, leaving a total of 2203 tree-years included in the final analysis (Extended Data Table 1). At both sites the tree-years removed through this method were proportional to the original sample size, indicating that no species or size class was disproportionately removed compared to others. This process was repeated using 2 and 3 standard deviations as the cutoff for defining outliers, yielding qualitatively similar results.

Canopy foliage phenology data for the years 2001-2018 were extracted for SCBI and Harvard Forest from the MCD12Q2 V6 Land Cover Dynamics product (a.k.a. MODIS Global Vegetation Phenology product)57 via Google Earth Engine. For each year at each site, we extracted data from the pixel (500m resolution) containing the center of each forest plot. Using the daily MODIS 2-band Enhanced Vegetation Index data (EVI2), the product yields the timing of phenometrics (vegetation phenology) over each year, including timing of greenup, midgreenup, peak, and senescence as used in this study. Data points were included in the analysis if they were flagged as “good” or “best” quality.

For the dendrometer band and leaf phenology analyses, climate data corresponding to the measurement periods were obtained from local weather stations at each focal site. For SCBI, weather data were obtained from a meteorological tower adjacent to the ForestGEO plot, via the ForestGEO Climate Data Portal v1.0 (<https://forestgeo.github.io/Climate/>)58. The R package *climpact* (see www.climpact-sci.org)59 was used to plot temperatures for visual inspection and to identify readings that were >3 standard deviations away from yearly means, which were labeled as outliers and removed from the dataset. Gaps in the SCBI meteorological tower data were subsequently filled using temperature readings obtained from a National Center for Environmental Information (NCEI) weather station located in Front Royal, Virginia (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00443229/detail>). Daily temperature records for Harvard Forest, which had already been gap-filled based on other local records, were obtained from the Harvard Forest weather station60,61. For each site, we used records of daily maximum (*Tmax*) and minimum temperatures (*Tmin*). Standardized Precipitation Evapotranspiration Index (SPEI)55 values were obtained from the ForestGEO Climate Data Portal v1.0 (<https://forestgeo.github.io/Climate/>)58,62,63.

The critical temperature window (*CTW*, Fig. 1), defined as the period over which *Tmax* was most strongly correlated with *DOY25*, was determined using the R package *climwin*64. This package tests the correlation between one or more predictor climate variable and a biological outcome variable over all consecutive time windows within a specified time-frame. It does so by reporting the correlation and *∆AICc*, the difference in Akaike Information Criterion corrected for small sample size relative to a null model for each window. Here, we tested for correlation between temperature predictor variables (*Tmax*, *Tmin*) and biological outcome variable *DOY25* over the time-frame from January 1 to the mean *DOY25* for the species group (by xylem porosity) and site (Extended Data Table 2). The time period yielding the lowest *∆AICc* was selected as the *CTW*. To avoid spurious correlations that could occur using temperature data at the daily resolution, we ran this analysis with weekly resolution, using temperatures averaged over weekly time periods. Because *Tmax* proved to have a generally stronger influence over *DOY25* and other growth parameters, we focused on this variable in our ultimate model, as opposed to *Tmin*. We defined *CTW* for *DOY25*, as opposed to other parameters describing the timing of growth, because spring temperatures should have the most direct influence on this variable.

To ensure that patterns were robust under an alternative definition of *CTW*, and to parallel the monthly time windows used in our tree-ring analysis (detailed below; Fig. 3, Extended Data Figure 6-7), we also ran analyses where we fixed the *CTW* identified by *climwin* to be the month with the most days in the *CTW* (Extended Data Table 2) each critical window. The months identified were March and April for ring- and diffuse-porous species at SCBI, respectively, and April and May for ring- and diffuse-porous species at Harvard Forest, respectively.

Correlation between the dendrometer band-derived growth parameters (*DOY25*, *DOY50*, *DOY75*, *Lpgs*, *gmax*, and *∆DBH*, Fig. 1) and *CTW* *Tmax* (at weekly or monthly resolution, as described above) were assessed using a linear mixed model in a hierarchical Bayesian framework. Analyses were run for both *Tmax* and *Tmin*, with qualitatively similar results, but we present only results for *Tmax*, which had overall stronger correlation with growth parameters. Mixed effects models were used to test the response of growth parameters to fixed effects of xylem porosity and mean *Tmax* (or *Tmin*) during the *CTW*, along with random effects of species and of individual tree. We ran separate models for each site, and for the response of all growth parameters to *Tmax* (or *Tmin*). This mixed-effect model was run within a hierarchical Bayesian framework and fit using the rstanarm version 2.21.3 R interface to the Stan programming language.65,66 In all cases unless otherwise specified, all prior distributions are set to be the weakly informative defaults.

To rule out the possibility that observed patterns were strongly influenced by summer drought, we examined the relationship between spring temperatures and summer SPEI indices. Linear models were run with 4-, 6-, and 12-month SPEI values of June, July, and August vs April *Tmax* to determine if warm spring temperatures were associated with greater summer drought stress in our data set. No significant correlations were found (all p>0.05).

## Tree-ring analysis

We analyzed tree-ring records for 108 sites, including our focal sites. All cores had been previously collected, cross-dated, and measured using standard collection and processing methodologies67,68.

Dominant tree species were cored at both SCBI33,51 and Harvard Forest3,69,70 following sampling designs that covered a broad range of DBH. We analyzed records for the ring- and diffuse- porous species at each site (Extended Data Table 1), but excluded semi-ring porous species (e.g., *Juglans nigra* L. at SCBI) and conifers (e.g., *Tsuga canadensis* at Harvard Forest). We studied a total of 976 cores which included 12 species at SCBI and 4 species at Harvard Forest (Extended Data Table 1).

The tree-ring records from our focal sites were complemented with a much larger collection spanning 106 deciduous and mixed forest sites in eastern North America32,71,72. For the majority of sampled populations (i.e., site-species combinations), sampling focused on canopy trees (typically >20 trees per population)32,71,72, while ~15% of the total 207 chronologies came from plot-level collections where trees above a certain diameter (typically 10 cm DBH) were censused and cored33,70. Again, analyses were limited to broadleaf deciduous species with clearly defined xylem porosity (*i.e.*, excluding semi-ring porous).

For each species-site combination, we converted tree-ring records into the dimensionless *RWI* to emphasize interannual variability associated with climate73. A 2/3rds *n* spline was applied to each core using ARSTAN V49\_1b to produce standardized ring-width series; *n* is the number of years in each series73,74. An adaptive power transformation, a process that also stabilizes the variance over time75, was used to minimize the influence of outliers in all series. Low series replication, often in the earliest portions of a chronology collection, can also inflate the variance of tree-ring records76. The 1/3rds spline method was chosen when replication in the inner portion of each chronology (the earliest ca. 30–50 yr of each record depending on full chronology length) was less than three trees. When replication was greater than n = 3 trees, we used the average correlation between raw ring-width series (rbar) method. The robust biweight mean chronology (*RWI*) for each species-site combination was calculated from the ring-width indices following variance stabilization74. We defined chronology start year (Extended Data Table 1) as the year where subsample signal strength (SSS) passed a threshold of SSS = 0.8, or where ≥80% of the population signal was captured in the chronology.

For the analysis of correlation between *RWI* and climate variables, we obtained monthly *Tmax* and *Tmin* data for 1901-2019 from CRU v.4.04.54 Correlations between monthly climate and *RWI* were assessed in R v 4.077 using the packages *dplR*78 and *bootRes*79. Reported correlations and significance were determined using bootstrapped confidence intervals. Summary figures were created using the package *dplR*78 (Fig. 3, Extended Data Figures 6-7).  
Our analysis focused on assessing correlations of *RWI* to months spanning January through September of the current year (presented in Fig. 3, Extended Data Figure 6). To test for potential lag effects of spring temperatures on growth the following year, we also ran a version of the analysis extending back to include climate of every month of the previous year (Extended Data Figure 7). Correlations and significance levels for months March-August are given in SI Table 1.

We used a multivariate model to test for joint effects of April and summer *Tmax* on *RWI*. We focused on April to represent spring temperatures because it was the month with greatest overall alignment with the *CTW*’s identified in the dendrometer band analysis and had the highest rate of positive correlations with *RWI* (Extended Data Table 3). We began by testing univariate correlations of *Tmax* over three summer windows: June, June-July, and May-August. Having determined that, among these, June-July explained the most variation, we then analyzed the joint effects of April *Tmax* and June-July *Tmax* on *RWI* for each chronology independently using the base lm() function in R. Slopes and p-values for each chronology are given in SI Table 1. Although some models may have benefited from data transformations, we determined that assumptions of normality and homoscedasticity were sufficiently met for the purposes of this analysis.

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# Author Information

## Contributions

Cameron Dow and Kristina J. Anderson-Teixeira conceived the ideas and designed the study; Cameron Dow, Loïc D’Orangeville, Erika B. Gonzalez-Akre, Ryan Helcoski, Grant L. Harley, Justin T. Maxwell, Ian R. McGregor, William McShea, Neil Pederson, Alan J. Tepley, and Kristina J. Anderson-Teixeira collected or oversaw collection of data; Cameron Dow, Albert Y. Kim, Valentine Herrmann, Justin T. Maxwell, Ian R. McGregor, Sean M. McMahon analyzed the data or provided analytical tools; Cameron Dow and Kristina J. Anderson-Teixeira led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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# Ethics declarations

## Competing interests

The authors declare no competing interests.

# Data Availability Statement

The datasets generated and analysed during the current study are available via GitHub in the *growth\_phenology* repository of the ForestGEO Ecosystems & Climate Lab @ SCBI, (<https://github.com/EcoClimLab/growth_phenology>) and archived in Zenodo (DOI: 10.5281/zenodo.6632090). Master versions of the dendrometer band data are available for SCBI via GitHub in the *Dendrobands* repository of the Smithsonian Conservation Biology Institute ForestGEO plot (<https://github.com/SCBI-ForestGEO/Dendrobands>), which is archived in Zenodo (DOI 10.5281/zenodo.5551143), and for Harvard Forest via the Harvard Forest Data Archive (<https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF149>). Weather data for SCBI were obtained from the ForestGEO Climate Data Portal v1.0 (<https://github.com/forestgeo/Climate/tree/master/Climate_Data/Met_Stations/SCBI>), which is archived in Zenodo (DOI: 10.5281/zenodo.3958215), and the National Center for Environmental Information (NCEI) weather station located in Front Royal, Virginia (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00443229/detail>). Weather data for Harvard Forest are available through the Harvard Forest Data Archive (<https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF001> AND <https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF000>). Climate data were obtained from CRU v.4.04 via the ForestGEO Climate Data Portal v1.0 (<https://github.com/forestgeo/Climate/tree/master/Climate_Data/CRU>), which is archived in Zenodo (DOI: 10.5281/zenodo.3958215). The Standardised Precipitation-Evapotranspiration Index was obtained from the ForestGEO Climate Data Portal v1.0 (<https://github.com/forestgeo/Climate/tree/master/Climate_Data/SPEI>), which is archived in Zenodo (DOI: 10.5281/zenodo.3958215). Canopy foliage phenology data were extracted from the MCD12Q2 V6 Land Cover Dynamics product (a.k.a. MODIS Global Vegetation Phenology product) via Google Earth Engine (<https://developers.google.com/earth-engine/datasets/catalog/MODIS_006_MCD12Q2#description>). In addition to being archived in this project’s repository, many tree-ring data sets are archived in the International Tree-Ring Data Bank (ITRDB;<https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>), the DendroEcological Network (DEN; <https://www.uvm.edu/femc/dendro/>), and/or the Harvard Forest Data Archive (<https://harvardforest.fas.harvard.edu/harvard-forest-data-archive>), as detailed in SI Table 1. Original tree cores are archived at the institutions of various members of the author team (Harvard Forest, Smithsonian Conservation Biology Institute, Indiana University, and University of Idaho) and will be made available upon reasonable request.

# Code Availability Statement

Data were analysed in the open source statistical software R (version 4.0). We used packages *climwin* v.1.2.3 (<https://cran.r-project.org/web/packages/climwin/index.html>), *dplR* v.1.0.2, and *bootRes* v1.2.4, *rstanarm* v.2.21.1, and functions from *Rdendrom* v.0.1.0 (<https://github.com/seanmcm/RDendrom/>). We used *climpact* software v.1.2.8 (see www.climpact-sci.org). Mixed effects models were run with mixed-effect model was run within a hierarchical Bayesian framework and fit using the rstanarm version 2.21.3 R interface to the Stan programming language (source code available at <https://github.com/EcoClimLab/growth_phenology#steps-to-replicate-the-analysis>). Tree-ring chronologies were developed using the program ARSTAN V49\_1b (<https://www.geog.cam.ac.uk/research/projects/dendrosoftware/>). All custom code is available through the EcoClimlab GitHub repository (<https://github.com/EcoClimLab/growth_phenology>) and archived in Zenodo (DOI: 10.5281/zenodo.6632090).

# Additional Information

**Supplementary Information** is available for this paper.

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# Figure Captions

**Figure 1 | Summary of temperate deciduous tree growth responses to warmer spring temperatures.** (a) Schematic illustrating parameters of interest and summarizing predominant responses of each to warmer maximum temperatures during a ‘critical temperature window’, defined as the period with the strongest temperature control over *DOY25*; (b) Variable definitions and summary of responses to warmer spring temperatures at two temperate forests – Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest – and for two groups of broadleaf deciduous species (RP=ring porous; DP=diffuse porous), where up and down arrows indicate increases and decreases that are significant both statistically (p<0.05) and biologically (effect size >3%/ °C), ‘-’ indicates no significant correlation, and ‘mixed’ indicates a mix of significant and non-significant correlations, often in different directions.

**Figure 2 | Responses of foliage phenology (a,b) and stem growth timing (c,d) to spring temperatures at the Smithsonian Conservation Biology Institute (a,c) and Harvard Forest (b,d).** Panels (a-b) show ecosystem-level canopy foliage phenology from 2001-2018, obtained from the MODIS Global Vegetation Phenology product (MCD12Q2.006) for a single pixel at the center of each ForestGEO plot, where G = Greenup, M=Mid-greenup, P=peak, and S=Senescence (i.e., beginning of green-down). Panels (c-d) show the dates at which stem growth milestones were achieved, on average, for sampled populations of ring porous and diffuse porous trees at SCBI (2011-2020) and Harvard Forest (1999-2003). Mean *DOY25*, *DOY50*, and *DOY75* were estimated using the Bayesian model visualized, with confidence intervals, in Extended Data Figure 3. Mean maximum temperature (*Tmax*) was calculated for each xylem architecture/site combination over the respective critical temperature window (*CTW*), then turned into a ratio and assigned a color on a gradient where the coldest year in the sample is blue and the warmest is red. Leaf phenology years are colored according to the *CTW* *Tmax* of the porosity group containing the dominant canopy species at each site (diffuse porous at SCBI, ring porous at Harvard Forest).

**Figure 3 | Sensitivity of annual growth, as derived from tree-rings, to monthly mean maximum temperatures (*Tmax*), for 207 chronologies from 108 sites across eastern North America**. Colors indicate the bootstrapped correlation between monthly *Tmax* and a dimensionless ring width index (*RWI*) derived from the multiple trees that form each chronology and emphasizing interannual variability associated with climate. Chronologies are grouped by xylem porosity and ordered by mean April *Tmax*. Plots are annotated to highlight records from our two focal sites, the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest (HF; Extended Data Table 1). Sites included are mapped in Extended Data Figure 5, species analyzed and numbers of significant correlations to *Tmax* are summarized in Extended Data Table 3, and chronology details are given in SI Table 1.

# Legends for Extended Data Table & Figures

**Extended Data Table 1 | Dominant broadleaf deciduous species at the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest, along with sample sizes included in our final analysis.**

**Extended Data Table 2 | Summary of parameters describing the seasonality and temperature sensitivity of broadleaf deciduous tree woody growth and canopy phenology at the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest.** Temperature sensitivity refers to the sensitivity of a parameter to the mean maximum temperature (*Tmax*) during the critical temperature window (*CTW*, Fig. 1). Because leaf phenology measurements were derived from satellite imagery and included both ring- and diffuse-porous trees, the selection of a critical window was less straightforward. We used the *CTW* of the porosity group containing the dominant canopy species at each site: *Liriodendron tulipifera* (diffuse porous) at SCBI and *Quercus rubra* (ring porous) at Harvard Forest.

**Extended Data Table 3 | Summary of tree-ring chronologies analyzed and number of significant (at significance level = 0.05) positive or negative correlations of ring width index to monthly *Tmax* in univariate and multivariate analyses.**

**Extended Data Figure 1 | Seasonal patterns of forest canopy greenness (top row) and stem growth of ring- and diffuse-porous trees, represented as both relative and cumulative fractions of total annual growth (middle and bottom rows, respectively), at the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest.** In the top row, canopy greenness is characterized using the two band Enhanced Vegetation Index (EVI2), with each line representing a year between 2000 and 2018. For stem growth, each line represents the average growth over one year, as modeled based on a five-parameter logistic growth model to dendrometer band data. Dashed lines represent modeled DBH change which fell outside of the median DOY where predicted starting DBH (a) and predicted ending DBH (b) were reached. Solid lines represent DBH change attributable to stem growth.

**Extended Data Figure 2 | Landscapes of relationships between the day of year on which 25% of annual growth is achieved (*DOY25*) and temperature in prior weeks for ring- and diffuse-porous trees at the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest.** Shown are matrices of coefficients from first-order linear regressions between mean maximum temperature (*Tmax*) and *DOY25*. Window Open and Window Close indicate number of weeks prior to *DOY25* (listed in Extended Data Table 2). Yellow shading indicates neutral relationships, while orange or red shading indicates that *DOY25* advances with increased *Tmax* over the given time window (negative ). Black circles indicate the critical temperature window selected based on minimization of *∆AICc*, the difference in Akaike Information Criterion corrected for small sample size relative to a null model. Critical temperature windows are listed in Extended Data Table 2.

**Extended Data Figure 3 | Response of stem growth timing and rates to mean maximum temperatures (*Tmax*) during the spring critial temperature window (*CTW*) for ring- and diffuse-porous species at the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest.** *CTW* was defined as the period over which *Tmax* was most strongly correlated with the day of year on which 25% of annual growth was achieved (*DOY25*; Extended Data Table 2, Extended Data Figure 2). Shown are relationships between mean *Tmax* over the *CTW* and days of the year on which 25%, 50%, and 75% total stem growth were achieved (*DOY25*, *DOY50*, *DOY75*, respectively; first row); the length of the peak growing season (*Lpgs*; second row); maximum growth rate (*gmax*; third row); and total seasonal radial stem growth (*∆DBH*; fourth row). Posterior predictions of each variable that did not include zero are represented with solid lines, while those that do include zero use dotted lines. The 95% credible intervals are represented by bands centered on the posterior mean for each year. For both species groups at both sites, *DOY25*, *DOY50*, and *DOY75* all declined significantly with mean *Tmax* during their respective *CTW*. Dots represent growth parameter values for individual tree-year combinations, which were derived by fitting a five-parameter logistic growth model to dendrometer band data.

**Extended Data Figure 4 | Response of stem growth timing and rates to mean maximum temperatures (*Tmax*) for the month most closely corresponding to the spring critial temperature window (*CTW*) for ring- and diffuse-porous species at the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest.** *CTW* was defined as the period over which *Tmax* was most strongly correlated with the day of year on which 25% of annual growth was achieved (*DOY25*; Extended Data Table 2, Extended Data Figure 2), and the most closely corresponding month was determined as that with the greatest number of days within the *CTW*. Shown are relationships between monthly *Tmax* and days of the year on which 25%, 50%, and 75% total stem growth were achieved (*DOY25*, *DOY50*, *DOY75*, respectively; first row); the length of the peak growing season (*Lpgs*; second row); maximum growth rate (*gmax*; third row); and total seasonal radial stem growth (*∆DBH*; fourth row). Posterior predictions of each variable that did not include zero are represented with solid lines, while those that do include zero use dotted lines. The 95% credible intervals are represented by bands centered on the posterior mean for each year. For both species groups at both sites, *DOY25*, *DOY50*, and *DOY75* declined significantly with April *Tmax*, with the exception of *DOY25* for ring-porous species at SCBI. Dots represent growth parameter values for individual tree-year combinations, which were derived by fitting a five-parameter logistic growth model to dendrometer band data.

**Extended Data Figure 5 | Map of sampling locations of tree-ring chronologies analyzed in this study.** Sites are colored by the xylem porosity type of species sampled: ring poroous (RP), diffuse porous (DP), or both. Sampling details are provided in SI Table 1. Base map source is ggplot2.

**Extended Data Figure 6 | Sensitivity of annual growth, as derived from tree-rings, to monthly mean minimum temperatures (*Tmin*), for 207 chronologies from 108 sites across eastern North America** (Extended Data Figure 5). Colors indicate the bootstrapped correlation between monthly *Tmin* and a dimensionless ring width index (*RWI*) derived from the multiple trees that form each chronology and emphasizing interannual variability associated with climate. Chronologies are grouped by xylem porosity and ordered by mean April *Tmin*. Plots are annotated to highlight records from our two focal sites, the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest (HF) (Extended Data Table 1). Species analyzed and numbers of significant correlations to *Tmin* are summarized in Extended Data Table 3, and chronology details are given in SI Table 1.

**Extended Data Figure 7 | Sensitivity of annual growth, as derived from tree-rings, to monthly mean maximum temperatures (*Tmax*) of the current and past year, for 207 chronologies from 108 sites across eastern North America** (Extended Data Figure 5). Colors indicate the bootstrapped correlation between monthly *Tmax* and a dimensionless ring width index (*RWI*) derived from the multiple trees that form each chronology and emphasizing interannual variability associated with climate. Chronologies are grouped by xylem porosity and ordered by mean April *Tmax*. Plots are annotated to highlight records from our two focal sites, the Smithsonian Conservation Biology Institute (SCBI) and Harvard Forest (HF) (Extended Data Table 1). Figure presents the same results as main manuscript Fig. 3 but extends back to include the previous year. Species analyzed and numbers of significant correlations to *Tmax* are summarized in Extended Data Table 3, and chronology details are given in SI Table 1.