**Title:** Warmer spring temperatures in temperate deciduous forests advance the timing of tree growth but have little effect on annual woody productivity

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**As the climate changes, warmer spring temperatures are causing earlier leaf-out1–6 and commencement of net carbon dioxide (CO2) sequestration2,4 in temperate deciduous forests, resulting in a tendency towards increased growing season length1,4,5,7–9 and annual CO2 uptake2,4,10–14.** **However, less is known about how spring temperatures affect tree stem growth15,16, which sequesters carbon (C) in wood that has a long residence time in the ecosystem17,18.** **Using dendrometer band measurements from 440 trees across two forests, we show that warmer spring temperatures shifted the peak stem growth of deciduous trees earlier but had no consistent effect on peak growing season length, maximum daily 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 growth 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 springs10–12 does not significantly contribute to increased sequestration in long-lived woody stem biomass.** **Rather, contradicting current projections from global C cycle models2,3,19,20, our empirical results imply that warming spring temperatures are unlikely to increase woody productivity or 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 emissions21, dramatically slowing the pace of atmospheric CO2 accumulation and climate change. Of this important C sink, ~47% occurs in temperate forests21, with temperate deciduous forests sequestering >0.3 Gt C yr-1.22 The future behavior of this C sink will play an important yet uncertain role in influencing atmospheric CO2 and climate change23,24.

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In temperate deciduous forests, spring warming generally lengthens the period over which trees have photosynthetically active leaves1,7–9,25 and that over which the ecosystem is a net CO2 sink2,25. Based on these observations, current terrestrial ecosystem models effectively assume that longer growing seasons lead to sustained increases in annual net CO2 uptake (i.e., net ecosystem exchange, *NEE*)2,3,19,20. However, model representation of C allocation to stem growth – or woody aboveground net primary productivity () on the ecosystem level – and its seasonality is simplistic relative to *known decoupling of photosynthate production and stem growth16,26*. Given that the C allocated to woody growth has the longest residence time in the ecosystem**refs?**, understanding whether warming spring temperatures will lead to sustained increases in forest C sequestration requires understanding the sensitivity of to spring temperatures.

We have little evidence as to how stem growth and respond to warmer spring temperatures in deciduous forests15,16. Most studies on tree 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 growth27–29 and increased annual growth in mesic climates30,31,**more\_conifer\_refs?**. Much less is known about how deciduous broadleaf tree growth responds to spring temperatures. While close coordination of budburst and initiation of xylogenesis16 suggests that warm springs should shift the timing of growth earlier alongside leaf phenology1–6, it has been observed that annual growth is more dependent on conditions within the growing season then on growing season length32. Furthermore, recent evidence suggests that growth of broadleaf deciduous trees may be sink-saturated, such that longer growing seasons with more C fixation do not necessarily augment growth**refs?**. Tree-ring records, which can be used to examine relationships of annual growth to temperature but not to understand growth seasonality, reveal that growth of temperate deciduous trees tends to be most sensitive to temperature or potential evapotranspiration between late spring and early summer33,34, with some evidence that warmer springs may have a modest, but usually insignificant, positive effect on growth30,34. These observations do not necessarily align with the finding that warming spring temperatures increase annual forest CO2 uptake in temperate deciduous forests2. 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**refs?**.

*points to make in new version*:

* stem growth is routinely used to estimate woody productivity (but wood density partially decouples them)26 and refs therein
* stem growth and woody productivity are decoupled from GPP26 and refs therein

~~~~ ( old version starting here)

In temperate deciduous forests, spring warming generally lengthens the period over which trees have photosynthetically active leaves1,7–9,25 and that over which the ecosystem is a net CO2 sink2,25. Current terrestrial ecosystem models, which have a rudimentary treatment of tree growth phenology16, effectively assume that longer growing seasons lead to increasing annual net CO2 uptake (i.e., net ecosystem exchange, *NEE*)2,3,19,20. However, recent experimental and observational findings show that annual stem growth is not correlated with growing season length32, *but rather can be limited by sink factors19,26,35,36*, and that positive effects of warm springs can be compensated by negative effects of accumulation of seasonal water deficits3. These studies suggest that warmer spring temperatures may not have the expected positive effect on forest CO2 sequestration.

~~While responses of leaf phenology and seasonal~~ *~~NEE~~* ~~to warming spring temperatures have been documented in the temperate deciduous biome and beyond,~~~~1–4,7–9~~ ~~little is known about how the longest-lived component of fixed C in trees, the woody stem growth, is responding to warming spring temperatures in deciduous forests~~~~15,16~~ ~~(but see Refs.~~~~27–29~~ ~~for influence of spring temperatures on timing of growth in conifers).~~ The timing of stem growth and its climate sensitivity is linked to annual growth26,32,37–39; however, the role of spring temperatures in shaping the timing and amount of growth remains unclear15.

Three cambial processes drive the relationship between stem growth and woody productivity: cell differentiation, cell enlargement, and cell wall thickening. Irreversible stem expansion occurs as a result of differentiation (20% of stem growth) and expansion (80% of stem growth), and accounts for ~10% of annual woody productivity40. The remaining 90% of woody productivity is caused by cell wall thickening. It would stand to reason that years with identical stem growth have a similar number of cells which are similarly sized (increased latewood can be an issue here, as you acknowledge). If we assume that cell wall thickness is controlled by processes within the tree (ie. hormonal responses instead of external climate drivers), then we can predict that cell wall thickness is relatively uniform within each cell type (early wood and late wood). Therefore, years with a similar amount of stem growth would sequester a similar amount of carbon during cell wall thickening, and we can say that stem growth equates to woody productivity.

~~Tree-ring records, which can be used to examine relationships of annual growth to temperature~~~~30~~ ~~but not to understand growth seasonality, reveal that growth of temperate deciduous trees tends to be most sensitive to temperature or potential evapotranspiration between late spring and early summer~~~~33,34~~~~, with some hints that warmer springs may have a modest positive effect on growth~~~~34~~~~. Thus, tree-ring evidence does not necessarily align with the finding that warming spring temperatures increase annual forest CO~~~~2~~ ~~uptake~~~~2~~~~. 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.~~

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Here, we evaluate how early spring temperatures affect peak stem growth timing, growth rates, and annual growth of temperate deciduous trees across eastern North America. To test whether warmer springs extend the period of peak stem growth, we used dendrometer band measurements on 440 trees across two mid-latitude forests. To test whether spring temperatures consistently increased annual growth, 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 = 123 trees from 2011-2020) and Harvard Forest (Massachusetts, USA; n = 340 trees from 1998-2003), we fit a logistic growth model41 to determine the days of year (DOY) when 25, 50, and 75% annual growth were achieved (, , ), peak growing season length (-), the maximum daily growth rates (; occurs on average within 5 days of ), and total annual increment in diameter at breast height (; Fig. 1). This analysis was performed separately for ring- (67 trees at SCBI and 138 trees at Harvard Forest) and diffuse porous (52 trees at SCBI and 183 trees at Harvard Forest) species, which differ in the seasonal timing of growth37,38. These stem-growth milestones were compared to canopy foliage phenology (measured at ecosystem level via remote sensing).



**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 control over ; (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-1), ‘-’ indicates no significant correlation, and ‘mixed’ indicates a mix of significant and non-significant correlations, often in different directions.

Seasonal milestones for both canopy foliage phenology and stem growth occurred 3-16 days earlier at SCBI than at Harvard Forest (Fig. 2, Extended Data Table 2). Consistent with the results of Ref37, ring porous species began growing earlier, reaching the benchmark earlier (by 27 days at SCBI and 22 at Harvard Forest), and their growth was spread over a longer growing season (average 22 and 17 days longer at SCBI and Harvard Forest, respectively; Fig. 2, Extended Data Figure 2, Extended Data Table 2). Peak growing season length was similar across sites, with being, on average, only six days longer at SCBI for ring porous species and less than one day longer for diffuse porous species (Extended Data Table 2).



**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 , , and were estimated using the Bayesian model visualized, with confidence intervals, in Extended Data Figure 4. Mean temperature was calculated for each xylem architecture/site combination over the respective critical window, 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 temperature in the critical window which had the best correlation with timing of greenup (ring porous window at HF and diffuse porous at SCBI).

Both MODIS-derived canopy foliage phenology and dendrometer band measurements of stem growth timing generally shifted backwards as spring temperatures increased (Fig. 2, Extended Data Figures 4-5). We found a consistent effect of temperature ( or ) throughout the spring, but the strongest effects on stem growth timing were found using during a critical temperature window (CTW). CTW was identified by measuring the correlation between all combinations of weekly and from January 1 to mean for each xylem architecture-site combination (Extended Data Figure 3). The CTW was defined as the week(s) which had the strongest correlation with .

For ring- and diffuse- porous species at both sites, warmer in the CTW resulted in earlier achievement of seasonal milestones. Consistent with findings from previous studies9,42,43, 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 3.45 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 at SCBI, the stem growth milestones , , and decreased with mean during the critical temperature window (Figs. 1, 2c-d; Extended Data Figures 4-5). Specifically, , , and 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 in years with warmer temperatures during the critical temperature window compared to those with cooler temperatures (Fig. 2a-b), there was no consistent lengthening of (Fig. 1, Extended Data Figures 4-5).

In contrast to the pronounced effects of on the timing of growth, its effects on and were weak and inconsistent (Figs. 1, Extended Data Figures 4-5). Specifically, , which occurred very close to , displayed extremely small negative changes (HF) or changes in opposite directions (SCBI) in relationship to mean during the critical temperature window for ring- and diffuse- porous species. displayed a weak positive relationship (+0.029-0.08 mm/ C) with mean during the critical temperature window at SCBI and a weak negative relationship (-0.2-0.03mm/ C) at HF (Extended Data Figure 4).

## Tree-ring analysis

To understand how annual growth increments have responded to spring temperatures at the centennial scale, we analyzed tree-ring chronologies of 12 species at SCBI34 and 4 species at Harvard Forest (Extended Data Table 1), along with an additional 191 chronologies from 106 sites (Fig. 3; Extended Data Figure 1; Extended Data Table 3)33. In total, our analysis included 207 chronologies representing 24 broadleaf species at 108 sites distributed from Alabama (Lat = 34.35) to Michigan (Lat = 45.56) and spanning a 15 C range in April . Across all chronologies, the standardized ring-width index (RWI) was significantly (at p 0.05) positively correlated with April for only 2% of chronologies: 1 of 142 ring porous and 4 of 66 diffuse porous species-site combinations (Extended Data Table 3). In contrast, RWI was frequently negatively correlated with 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 porous and diffuse porous species, respectively. generally exibited weaker relationships to annual growth than , with few significant correlations between spring and RWI (Extended Data Figure 6).

To test whether the negative effect of summer temperatures might offset an enhancement of growth by warmer spring temperatures, we tested for the joint effects of April and June-July on RWI. Results were qualitatively similar to the univariate correlations (Fig. 3), with significant (at p = 0.05) positive correlations to April for only 4% of chronologies and significant negative correlations with June-July for 77% of chronologies, supporting that summer temperatures were the more important driver of annual stem growth (Extended Data Table 3).



**Figure 3 | Sensitivity of annual growth, as derived from tree-rings, to monthly mean maximum temperatures (), for 207 chronologies from 108 sites across eastern North America** (Extended Data Figure 1). Colors indicate the correlation between monthly 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 . 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 are summarized in Extended Data Table 3, and chronology details are given in SI Table 1.

## Discussion

Together, our results demonstrate that warmer spring temperatures in the temperate deciduous forests of eastern North America advance the timing of stem growth but have little effect on total annual growth (Figs. 1- 3). The observed advance in stem growth under warmer springs parallels phenological advances observed for canopy foliage (Fig. 2a-b)2,4,5, which makes sense given close coordination of budburst and xylogenesis16, and *NEE*2,4. **However, inconsistent with the concept that an earlier start to growth would increase annual woody productivity, we demonstrate that warmer springs either hasten the deceleration of stem expansion or otherwise failed to translate extended growing seasons into biologically significant increases in stem growth, and thereby have negligible effect on total annual growth for most species and locations (Fig. 3).** We find statistically, but not biologically, significant relationships between total growth and spring temperature at both sites in our dendrometer band analysis (schematic\_summary). However, the slope of the relationships are in opposite directions, with warming causing decreasing stem growth at Harvard Forest but increasing stem growth at SCBI (EDT\_phenology\_parameters). We believe this difference is due to severe drought conditions in 1999 which obviously caused abnormal growth patterns in that year (Extended Data Figure 4). Therefore, we suggest that our two sites represent two scenarios: 1. A forest which had no significant summer drought, but was only influenced by warming temperatures (SCBI). 2. A forest which experienced spring warming along with severe summer drought (Harvard Forest).

At SCBI, we see a very small increase in total stem growth (on average +0.05mm/C), suggesting that even in the absence of drought or inclement climate conditions during the growing season, spring warming does not enhance stem growth in a meaningful way. At Harvard Forest, we see a decrease in total growth with warmer temperatures in the CTW (-0.15mm/C on average). We speculate that this result is likely a product of reductions in total stem growth related to drought effects in 1999. Due to the method of selection for CTW, years with significant departures from the norm can influence the analysis to a greater extent. Stem growth in 1999 was clearly impacted by climate conditions (Extended Data Figure 4), and so the CTW selected by climwin maximizes the effect of these impacts (most likely the effects of drought) on stem growth. To examine this further, we reran our dendrometer band analysis using the month of May as the CTW. When we change the CTW to the month of May, we see results much closer to those found at SCBI, with a similar advancement in growth timing but a much less pronounced effect of on total growth (-0.015mm/C on average, a tenfold decrease compared to the CTW optimized around the drought year;EDF\_pheno\_Tmax\_AprilMay). Once again see that there was no meaningful influence of spring temperature on total growth. In fact, the magnitude of the effect of the summer drought compared to the effects of spring illustrates the point that conditions during the peak growing season are much more influential to stem growth than conditions during the Spring. **We demonstrate that warmer springs either have little effect on, or even hasten, the deceleration of stem expansion and thereby have negligible effect on total annual stem growth for most species and locations (Fig. 3).** Our observations suggest that the deceleration of stem expansion (starting around ), which occurs mid-summer near the time of peak canopy greenness (Extended Data Figure 2)4,32, is likely driven by cues other than photosynthate limitation, such as water stress, daylength, or sink limitation16,19,26,32,35,39,44. Our tree-ring analysis (Fig. 3) demonstrates that the primary effect of warming temperatures on annual ring-width is not an augmentation through an earlier start to growth, but rather a reduction associated to drought stress during the peak growing season32,33. Warm springs may also amplify summer drought stress in some times and places, effectively canceling out any positive effects of an extended growing period3,45. However, we did not find evidence that higher spring temperatures were correlated with summer drought stress in our dendrometer band analysis, implying that the effects of warm spring temperatures on stem growth elucidated here (Fig. 1) were not attributable to summer drought.

Our finding that interannual variation in stem growth is more strongly linked to conditions during the peak growing season than to the length of the season of active stem growth aligns with recent studies on annual stem growth26,32,38 and with parallel findings for *NEE*13,14. However, there is also a disconnect with findings that *NEE* is at least modestly greater in years with warm springs2 or long growing seasons4,13,14. Warming advances spring phenology and may advance or delay autumn senescence depending on timing of warming and water availability12,46,47, with delays more common across eastern North America,2–4 implying that warming temperatures are lengthening the period from peak stem growth to the cessation of CO2 uptake by the ecosystem. We show that the extra C fixation in years with warm springs does not substantially augment stem growth, but it remains unclear how it is allocated within the ecosystem. There are two main possibilities, which hold contrasting implications for the response of forest C balance to rising spring temperatures.

One possibility is that extra photosynthate in years with warm springs may be allocated to woody growth without affecting diameter growth in the current year. It is theoretically possible that extra C is allocated to cell wall thickening, a process that lags behind stem expansion40, or to a thicker layer of higher-density latewood, resulting in formation of more C-dense wood in years with warm springs. However, existing evidence indicates that warm springs have a neutral or negative effect on latewood width48–50, which is more strongly controlled by summer drought stress48,49, suggesting that a positive effect of warm springs on the total C content of annual rings is unlikely. Extra C could also be saved within trees as non-structural carbohydrates (NSC) and used towards growth the following year51,52, potentially including an earlier start to growth44. Extension of our tree-ring analysis revealed weak correlation between April and growth the following year (sig. pos. correlations for 5/142 RP and 3/66 DP species-site combinations, Fig. Extended Data Figure 7), although predominantly positive (non-significant) correlations in RP species suggests that this dynamic may weakly influence their annual growth. Thus, warm springs are unlikely to provide substantial, sustained C sinks under warming spring temperatures.

A second possibility is that any additional C fixed during years with warm springs may be allocated to plant functions other than stem growth, including respiration, NSC storage, reproduction, and production of foliage, roots36, or root exudates. Much of this C would have a relatively short residence time within the ecosystem, and C loss through fall or winter respiration may offset gains from an earlier spring3,53. However, C allocated to nonstructural carbohydrates or relatively short-lived plant tissues would typically remain in the ecosystem beyond the end of the year51, such that the long-term effect of warm springs on the forest C balance would not be captured in analyses of interannual variation2,13,14. Studies within or including the temperate deciduous biome that examined long-term trends in growing season length and ecosystem C uptake2,4,10,11 – as opposed to their interannual variation – showed increasing trends in both variables, suggesting that the C not allocated to woody productivity within the current year has a multi-year residence time within the ecosystem. However, given our finding that warm springs do not significantly enhance woody productivity, this C is likely to have a relatively short residence time within the ecosystem.

Thus, a distinction between interannual variation and directional change may be critical when considering how directional climate change is likely to affect tree growth and ecosystem C dynamics. As discussed above, temporal lags between C uptake and release imply that the full effects of warm spring temperatures on forest woody productivity and C cycling are unlikely to be apparent in analyses of interannual variation (including this analysis)54. Moreover, acclimation of trees to warming temperatures55 and, on longer time scales, species adaptations and shifts in community composition56 are likely to alter the seasonality of forest C cycling. If we look across spatial gradients where the latter have had time to play out, we see that warmer spring temperatures are associated with earlier leaf-out6 and longer growing seasons, which in turn are correlated with greater tree growth31, woody productivity57, and *NEE*58. Thus, warming spring temperatures are expected to increase the biophysical potential for annual tree growth, but that potential is not being realized on an interannual time frame.

As climate change accelerates and 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 the sustained increase in CO2 sequestration in woody biomass and ensuant negative climate change feedback that is anticipated in most climate forecasting models2,3,19,20. Rather, the dominant effect of rising temperatures on forest woody productivity will be a negative effect of high summer temperatures (Fig. 3), which constitutes a positive feedback to climate change.

# Methods

## Dendrometer band analysis

Dendrometer band measurements were collected at SCBI59 and Harvard Forest4,37, both part of the Forest Global Earth Observatory (ForestGEO)60,61. 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 fields59. Dominant canopy species within the 25.6 ha ForestGEO plot include tulip poplar (*Liriodendron tulipifera* L.), oaks (*Quercus spp.*), and hickories (*Carya spp.*)34. 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 July31.

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 July31. The summer of 1999 was abnormally dry. Records indicate that in 1999 only 52mm of precipitation fell per month June-August compared to average monthly precipitation values of 100mm+.37

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. In total, our analysis included 2210 tree-years (Extended Data Table 1).

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). Timing of measurements at Harvard Forest were similar, with the median start date of April 23 and median end date of October 30. 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 manually inspected before analysis. We screened the data for three classes of errors. First, when a measurement was drastically different from previous and following measurements, it was assumed to be a human error and removed. Second, when measurements remained essentially unchanged for several readings, followed by a sudden jump then return to a normal growth pattern, this was assumed to be a case where the band was stuck on the tree bark and then released. In these cases, the full annual record for the tree was removed. Third, data points that deviated substantially from normal growth patterns, but for unknown causes, were removed. If a majority of the data points fell into this class within a tree-year, the entire year was removed from the analysis. We also removed tree-years with small or negligible total growth ( mm; SCBI = 26, Harvard Forest = 253), and tree-years where first intraannual measurement was later than the first spring survey (trees that were missed in the initial census; SCBI = 22, HF = 8). These were removed because they reduce the reliability of predicted growth in the modeled curves.

We fit a five-parameter logistic growth model41 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, and are lower and upper asymptotes of the model. is the day of year where the inflection point in growth rate occurs, 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 , occurs on . The model outputs two additional variables, and , which represent the beginning and end DBH in each model year. We used the first and last manual dendrometer band measurements as starting points to calculate these two variables. With this method, initial measurements too late in the growing season which miss the start of the growing season can cause incorrect estimations of and . The 1998 survey at Harvard Forest recorded first measurements on May 26, which is less than 2 weeks away from the average DOY25 at this site. This late start made the calculation of timing and total growth variables unreliable, so we removed tree years in 1998 from our analysis. The model was fit in R v4.0 using the functions developed in the *Rdendrom* package41. 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 events41,62 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. Modeled fits for tree-years were removed under two conditions: (1) was standard deviations away from the mean for each site-xylem architecture group combination (SCBI = 3, Harvard Forest = 11);  
(2) timing variables (, , , ) were standard deviations away from the means for their site, xylem architecture group, and year (SCBI = 74, Harvard Forest = 101). 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)63 via Google Earth Engine. For each year at each site, we extracted data from the pixel containing the center of each forest plot (resolution of 500m). 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/>)64. The R package *climpact* (see www.climpact-sci.org)65 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 station66,67. For each site, we used records of daily maximum () and minimum temperatures ().

The critical temperature window (CTW, Fig. 1), defined as the period over which was most strongly correlated with , was determined using the R package *climwin*68. 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 , 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 (, ) and biological outcome variable over the time-frame from January 1 to the mean for the species group (by xylem porosity) and site (Extended Data Table 2). The time period yielding the lowest was selected as the CTW. Because proved to have a generally stronger influence over and other growth parameters, we focused on this variable in our ultimate model, as opposed to . We defined CTW for , 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 to be the month of April. This was consistent with the periods identified by *climwin* for ring- and diffuse porous species groups at both sites, all of which included all or part of April (Extended Data Table 2).

Correlation between the dendrometer band-derived growth parameters (, , , , , and }, Fig. 1) and spring temperatures were assessed using a linear mixed model in a hierarchical Bayesian framework. Analyses were run for both and , with qualitatively similar results, but we present only results for , 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 (or ) 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 (or ). This mixed-effect model was run within a hierarchical Bayesian framework and fit using the rstanarm R interface to the Stan programming language69,70. 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 Standardized Precipitation Evapotranspiration Index71. The latter was obtained from the ForestGEO Climate Data Portal v1.0 (<https://forestgeo.github.io/Climate/>)64,72,73. Linear models were run with 4-, 6-, and 12-month SPEI values of June, July, and August vs April 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 methodologies74.

Dominant tree species were cored at both SCBI34,59 and Harvard Forest4,75,76 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 America33,77. Again, records 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 climate.78 A 2/3rds *n* spline was applied to each core using ARSTAN to produce standardized ring-width series; *n* is the number of years in each series78,79. An adaptive power transformation, a process that also stabilises the variance over time80, 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 records81. The 1/3rds spline method was chosen when replication in the inner portion of each chronology (ca. inner 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 stabilisation79. 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 and data for 1901-2019 from CRU v.4.04.82 Correlations between monthly climate and were assessed using *dplR*83 and *bootRes*84 in R v 4.0 (R Core Team, 2020), which correlated functions and bootstrapped confidence intervals for these relationships85. We analyzed these correlations for 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 April-August are given in SI Table 1.

We used a multivariate model to test for joint effects of April and summer on RWI. We began by testing univariate correlations of 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 and June-July 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 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 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.

# 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 *[TBD]*). 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>), downloaded on [DATE]. 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>). Original tree cores are archived at the institutions of various members of the author team 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* (<https://github.com/seanmcm/RDendrom/>). We used *climpact* software v.1.2.8 (see www.climpact-sci.org). All custom code is available through the EcoClimlab GitHub repository (<https://github.com/EcoClimLab/growth_phenology>) and archived in Zenodo (DOI: *[TBD]*).

# Additional Information

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

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