

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-out^{1–3} and commencement of CO₂ uptake^{1,3} in temperate deciduous forests, resulting in a tendency towards increased growing season length³ and annual CO₂ uptake^{1,3–7}. However, less is known about how spring temperatures affect tree stem growth^{8,9}, which sequesters carbon in wood that has a long residence time in the ecosystem^{10,11}. Here 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, using dendrometer band measurements from 440 trees across two forests. 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 spring temperatures^{4,5} does not significantly contribute to increased sequestration in long-lived woody stem biomass. Rather, contradicting projections from global carbon cycle models^{1,12}, 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 approximately 1.6 Gt carbon per year offsets approximately 20% of anthropogenic emissions¹³, dramatically slowing the pace of atmospheric CO₂ accumulation and climate change. Of this important carbon sink, approximately 47% occurs in temperate forests¹³, with temperate deciduous forests sequestering more than 0.3 Gt carbon per year¹⁴. The future behaviour of this carbon sink will have an important yet uncertain role in influencing atmospheric CO₂ and climate change^{15–17}.

In temperate deciduous forests, spring warming generally lengthens the period over which trees have photosynthetically active leaves^{1,3,18} and that over which the ecosystem is a net CO₂ sink^{1,18}. On the basis of these observations, current terrestrial ecosystem models represent warm spring temperatures and longer growing seasons as contributing positively to annual gross primary productivity (GPP) and net CO₂ uptake (that is, net ecosystem exchange (NEE))^{2,12,15}. However, the long-term persistence of this extra carbon 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 centuries^{10,11}, as opposed to being rapidly released

back to the atmosphere through respiration^{19,20}. Model representation of carbon allocation to stem growth—or woody aboveground net primary productivity (ANPP_{woody}) on the ecosystem level—does not capture known decoupling of stem growth from photosynthate production^{9,17,21}. As a result, the consequences of rising spring temperatures on stem growth may not be accurately represented in models^{9,17}. Understanding the sensitivity of ANPP_{woody} to spring temperatures is central to predicting the future of the temperate deciduous forest carbon 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 growth^{22,23} and increased annual growth in mesic climates^{24,25}. By contrast, little evidence exists as to how stem growth and ANPP_{woody} respond to warmer spring temperatures in deciduous forests^{8,9}. Close coordination of budburst and initiation of xylogenesis⁹ suggest that warm spring temperatures should shift the onset of growth earlier alongside observed advances in leaf phenology^{1–3}. However, earlier initiation of growth would not necessarily translate to earlier, faster or greater stem growth; rather, stem growth is dependent on environmental conditions on hourly to daily timescales^{26,27}, and

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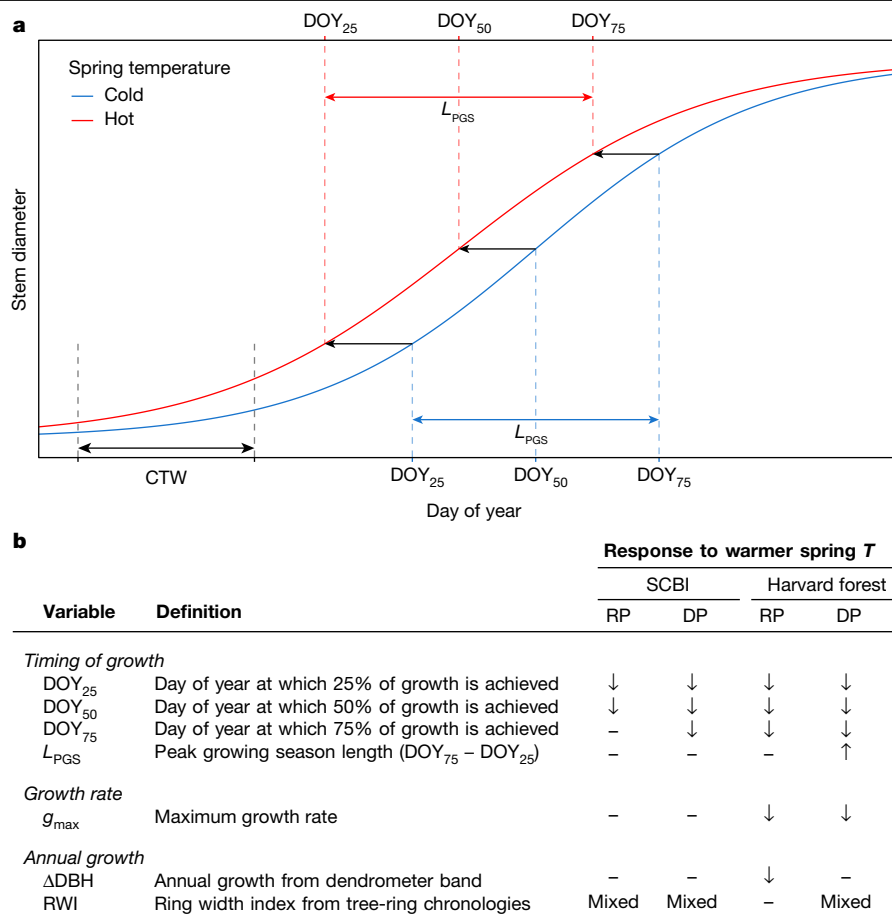


Fig. 1 | Summary of temperate deciduous tree growth responses to warmer spring temperatures. **a**, Schematic illustrating parameters of interest and summarizing predominant responses of each to warmer maximum temperatures during a critical temperature window (CTW), defined as the period with the strongest temperature control over DOY₂₅. **b**, Variable definitions and summary of responses to warmer spring temperatures at two

temperate forests—SCBI and Harvard Forest—and for two groups of broadleaf deciduous species. The up and down arrows indicate increases and decreases, respectively, that are significant both statistically ($P < 0.05$) and biologically (effect size $> 3\%$ per $^{\circ}\text{C}$); ‘—’ indicates no significant correlation; and ‘mixed’ indicates a mix of significant and non-significant correlations, often in different directions. DP, diffuse porous; RP, ring porous.

annual growth is more closely linked to conditions within the growing season than to growing season length²⁸, GPP²¹ or NEE²¹. Furthermore, growth of broadleaf deciduous trees may be sink-saturated^{17,29}, such that longer growing seasons with more carbon fixation do not necessarily augment growth^{21,30,31}. 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 summer^{32,33}, with some evidence that warmer spring temperatures may have a modest positive effect on growth^{25,33}. These observations do not necessarily align with the finding that warming spring temperatures increase annual forest CO₂ uptake in temperate deciduous forests^{1,18}. 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 spring temperatures 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 warm spring temperatures consistently increased annual radial increments, we analysed 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; VA, USA; $n = 119$ trees from 2011 to 2020) and Harvard Forest (MA, USA; $n = 321$ trees from 1998 to 2003), we fit a logistic growth model³⁴ to determine the days of year (DOYs) when 25%, 50% and 75% annual diameter growth were achieved (DOY₂₅, DOY₅₀ and DOY₇₅), the peak growing season length ($L_{pgs} = \text{DOY}_{75} - \text{DOY}_{25}$), the maximum growth rate (g_{max}) and the total annual increment in diameter at breast height (ΔDBH ; Fig. 1). This analysis was performed separately for ring-porous and diffuse-porous species (Extended Data Table 1), which differ in the seasonal timing of growth^{27,35} (Extended Data Table 2 and Extended Data Fig. 1). These milestones in stem growth were compared with canopy foliage phenology (measured at the 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 (T_{max} or T_{min}) throughout the spring, but the strongest effects on the timing of stem growth were found using T_{max} during a critical temperature window (CTW). The CTW was identified by assessing the correlation between weekly T_{max} and DOY₂₅ for all combinations of consecutive weeks from 1 January to mean DOY₂₅ for each xylem architecture–site combination (Extended Data

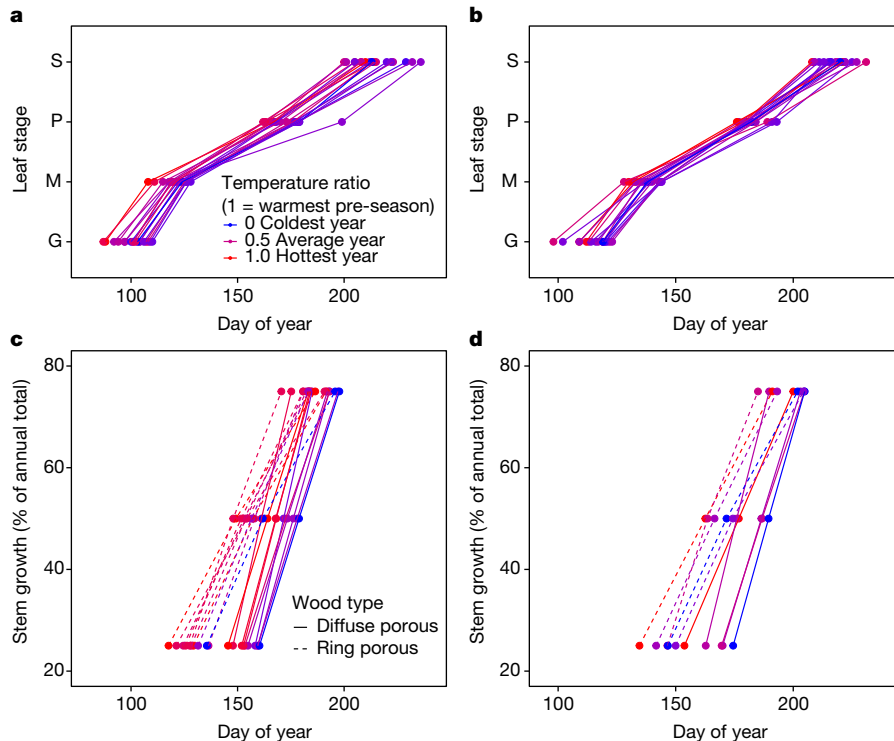


Fig. 2 | Responses of foliage phenology and stem growth timing to spring temperatures at SCBI and Harvard Forest. **a, b**, Ecosystem-level canopy foliage phenology from 2001 to 2018 at SCBI (**a**) and Harvard Forest (**b**), obtained from the MODIS Global Vegetation Phenology product (MCD12Q2.006) for a single pixel at the centre of each ForestGEO plot. G, greenup; M, mid-greenup; P, peak; S, senescence (that is, beginning of greendown). **c, d**, Dates at which stem growth milestones were achieved, on average, for sampled populations of ring-porous and diffuse-porous trees at SCBI (2011–2020; **c**) and Harvard Forest (1999–2003; **d**).

Fig. 2). The CTW was defined as the weeks for which this correlation was strongest, and mean T_{\max} during this period (CTW T_{\max}) was used as our independent variable.

For ring-porous and diffuse-porous species at both sites, warmer CTW T_{\max} resulted in earlier achievement of seasonal milestones. Consistent with findings from previous studies, leaf phenological milestones advanced at both sites (Fig. 2a,b and Extended Data Table 2), with greenup (DOY when the enhanced vegetation index (EVI2) first crossed 15% of the segment EVI2 amplitude) advancing 3.5 days per °C at SCBI ($P = 0.016$) and 2.4 days per °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 T_{\max} (Figs. 1 and 2c,d and Extended Data Figs. 3 and 4). Specifically, DOY₂₅, DOY₅₀ and DOY₇₅ advanced 0–1.7 days per °C for ring-porous species and 2.8–2.9 days per °C for diffuse-porous species at SCBI, and 10.3–12.3 days per °C for ring-porous species and 0.9–4.2 days per °C for diffuse-porous species at Harvard Forest (Extended Data Table 2).

Whereas the length of time between canopy greenup and senescence (that is, the day when greenness dropped below 90% of its peak) increased with the CTW T_{\max} of the porosity group containing the dominant canopy species at each site (diffuse porous at SCBI and ring porous at Harvard Forest; Fig. 2a,b), there was no consistent lengthening of L_{pgs} (Fig. 1 and Extended Data Figs. 3 and 4).

In contrast to the pronounced effects of CTW T_{\max} on the timing of growth, its effects on g_{\max} and ΔDBH were inconsistent and usually weak (Fig. 1 and Extended Data Figs. 3 and 4). Specifically, g_{\max} , 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 T_{\max} for ring-porous and diffuse-porous species. ΔDBH displayed a weak positive relationship (+0.003–0.008 cm per °C) with CTW T_{\max} at SCBI and a weak negative relationship (–0.02 to 0.003 cm per °C) at Harvard Forest (Extended Data Fig. 3).

Tree-ring analysis

To understand how annual radial stem growth increments have responded to spring temperatures at the centennial scale, we analysed tree-ring chronologies of 12 species at SCBI³³ and four species at Harvard Forest (Extended Data Table 1), plus an additional 191 chronologies from 106 sites (Fig. 3, Extended Data Table 3 and Extended Data Fig. 5). 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 T_{\max} . Across all chronologies, the standardized ring-width index (RWI) was significantly (95% confidence interval did not include 0) positively correlated with April T_{\max} 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 T_{\max} : 0% and 1%, respectively (Extended Data Table 3). By contrast, RWI was frequently negatively correlated with T_{\max} during peak growing season months (May–August), with significant correlations for 52% (45 of 141 (May), 107 of 141 (June), 91 of 141 (July) and 53 of 141 (August)) and 46% (10 of 66 (May), 52 of 66 (June), 36 of 66 (July) and 23 of 66 (August)) of species–site–month

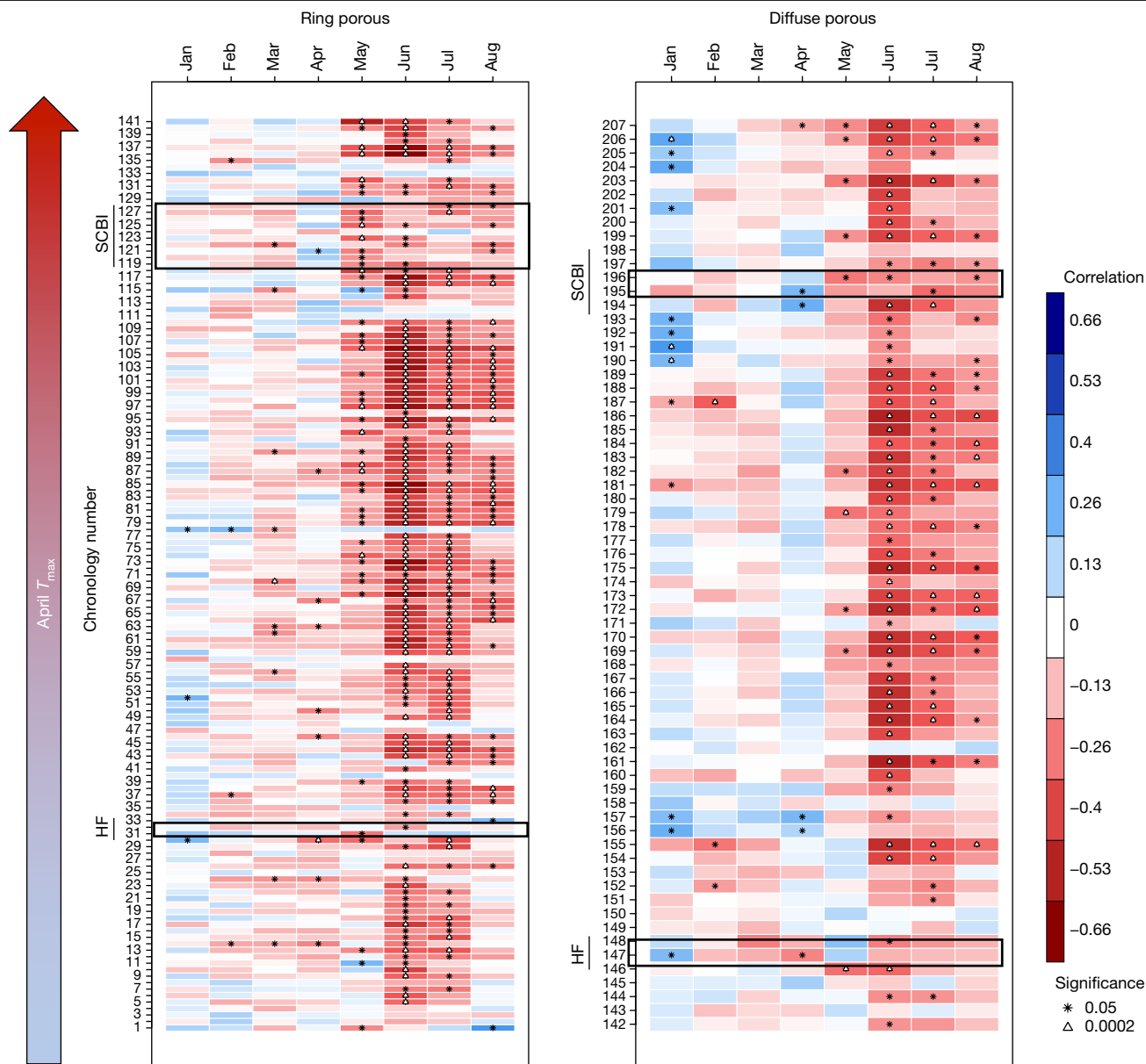


Fig. 3 | Sensitivity of annual growth, as derived from tree rings, to monthly mean T_{\max} , for 207 chronologies from 108 sites across eastern North America. Colours indicate the bootstrapped correlation between monthly T_{\max} and a dimensionless RWI derived from the multiple trees that form each chronology and emphasizing interannual variability associated with climate. Chronologies are grouped by xylem porosity and ordered by mean April T_{\max} .

combinations for ring-porous and diffuse-porous species, respectively. T_{\min} generally exhibited weaker relationships to annual growth than T_{\max} , with few significant correlations between spring T_{\min} and RWI (Extended Data Fig. 6).

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

Plots are annotated to highlight records from our two focal sites: SCBI and Harvard Forest (HF; Extended Data Table 1). Sites included are mapped in Extended Data Fig. 5, species analysed and numbers of significant correlations to T_{\max} are summarized in Extended Data Table 3, and chronology details are provided in Supplementary Table 1.

summer temperatures, we tested for the joint effects of April and June–July T_{\max} on RWI. Results were qualitatively similar to the univariate correlations (Fig. 3), with significant ($P \leq 0.05$) positive correlations to April T_{\max} for only 4% of chronologies and significant negative correlations with June–July T_{\max} 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 spring temperatures parallels advances observed for canopy foliage phenology^{1,3} (Fig. 2a,b) and NEE^{1,3}. However, inconsistent with

the concept that an earlier start to growth would increase ANPP_{woody}, we demonstrate that warmer spring temperatures 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 in mid-summer near the time of peak canopy greenness^{3,28} (Extended Data Fig. 1), is driven by cues other than photosynthate limitation, such as water stress^{21,26,28}, nutrient limitation³⁷, day length²⁸ or sink saturation^{21,29}. This adds to a growing body of evidence for a sink limitation of stem growth^{17,21,31}, in which global change factors known to enhance photosynthesis, such as longer growing seasons or elevated levels of CO₂, do not cause a corresponding increase in stem growth^{19,28}.

Combined with widespread observations that warming spring temperatures tend to lengthen the season of CO₂ uptake^{3,18} and increase net annual CO₂ uptake^{1,3–7}, 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 carbon allocated to functions other than stem expansion in the current or following year. It remains theoretically possible that warm spring temperatures could augment ANPP_{woody}, which, although routinely calculated based on stem growth, can be partially decoupled from it through differences in wood density or carbon content²¹. Extra carbon fixed in years with warm spring temperatures could potentially be allocated to the formation of more carbon-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, whereas warm spring temperatures have a neutral or negative effect on the width of latewood^{39–41}. Thus, it is unlikely that warm spring temperatures have a positive effect on total carbon content of annual rings or ANPP_{woody}.

The fate of any additional carbon fixed during years with warm spring temperatures remains unresolved, but possible destinations—including respiration, non-structural carbohydrate 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 enrichment of CO₂, ANPP_{woody} remained unchanged, whereas additional carbon was released back to the atmosphere on relatively short timescales through enhanced respiration¹⁹. Consistent with this, it has been observed that carbon gains from an earlier spring can be offset through autumn or winter respiration²⁰, although even the carbon in shorter-lived pools would often be carried over into the following year⁴². Thus, observed augmentation of NEE by warm spring temperatures^{1,6,7} 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 ANPP_{woody}. 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, ANPP_{woody} (ref. ⁴⁵) and NEE⁴⁶. 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 ANPP_{woody} is allocated to functions that relieve limitations on woody growth—for example, by enhancing nutrient and water acquisition through enhanced allocation to roots^{30,47}—it is possible that warming spring temperatures could ultimately increase ANPP_{woody} through indirect mechanisms. Understanding how warming spring temperatures are influencing carbon allocation within ecosystems remains a key outstanding question.

Regardless of the influence of spring temperatures on carbon 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 and Extended Data Fig. 7), when increased atmospheric demand associated with high temperatures can limit both leaf-level gas exchange and stem growth^{21,26,28,48}. Indeed, the timing of peak growth in June and July (Extended Data Table 2 and Extended Data Fig. 1) coincides with the timing of the greatest sensitivity of annual growth to T_{max} (Fig. 3 and 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 season^{24,32,33,44}. Warm spring temperatures may also amplify summer drought stress in some times and places, effectively cancelling out any positive effects of an extended growing period^{2,49,50}. Although such an interaction was unlikely to have had 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 and Extended Data Table 3). Thus, warm spring temperatures 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 carbon sequestration in woody biomass and ensuant negative climate change feedback that is anticipated in most climate forecasting models^{1,2,12,31}. Rather, the dominant effect of rising temperatures on temperate deciduous forest woody productivity will be a negative effect of high summer temperatures¹⁵ (Fig. 3), which constitutes a positive feedback to climate change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-022-05092-3>.

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Methods

Dendrometer band analysis

Dendrometer band measurements were collected at SCBI⁵¹ and Harvard Forest^{3,35}, both part of the Forest Global Earth Observatory (ForestGEO)^{52,53}. SCBI (38.8935° N, 78.1454° W; elevation 273–338 metres above sea level (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, VA, USA. The forest is secondary and mixed age, having established in the mid-nineteenth 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 the 1950–2019 mean annual precipitation of 1,018 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 T_{\max} ; source: CRU v.4.04 (ref. ⁵⁴)) and the summer standardized precipitation evapotranspiration index (SPEI)⁵⁵ values (4-month value of August) were similar to the average climate before the study period (1970–2010). Specifically, average spring T_{\max} was 16.9 ± 1.4 °C (mean \pm 1 s.d.) before the study period (range: 14.1–19.9) and 17.6 ± 1.7 °C (range: 15.6–20) during the study period, whereas the summer SPEI was -0.06 ± 1.02 (range: -1.7 to 2.4) before the study period and 0.5 ± 0.8 (range: -0.8 to 1.6) during.

Harvard Forest (42.5388° N, 72.1755° W; elevation 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 twentieth 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 the 1950–2019 mean annual precipitation of 1,104 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 T_{\max} ; source: CRU v.4.04 (ref. ⁵⁴)) and summer SPEI values (4-month value of August) were similar to the average climate before the study period (1970–1998). Specifically, average spring T_{\max} was 10.9 ± 1.5 °C before the study period (range: 8.0–13.2) and 11.2 ± 1.0 °C (range: 10.1–12.2) during the study period, whereas the summer SPEI was 0.1 ± 0.9 (range: -1.8 to 1.7) before the study period and 0.2 ± 0.9 (range: -1.0 to 1.1) during. The driest summer during the study period (1999) had the fifth lowest SPEI value (-1.0) in the period 1970–2003, with precipitation of 52 mm per month in June–August compared to average monthly precipitation of 100 mm or more³⁵.

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). Although we do not estimate the ages of the 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 calliper approximately every 1–2 weeks within the growing season from 2011 to 2020 at SCBI and 1998 to 2003 at Harvard Forest. The number of bands measured at each site fluctuated slightly as trees were added or dropped from the census (for example, 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 14 April, which was adjusted forward when early leaf-out of understory vegetation was observed, with the earliest start date being 30 March (in 2020). Measurements were continued through to fall leaf senescence, with the median end date being 17 October and the latest end date being 26 November (in 2012). At Harvard Forest, all measurements from 1998 were dropped because

of a late start date (26 May). Among the remaining years, the median start date was 21 April and the median end date of 27 October. 1999 was an anomalous year in which initial measurements were taken on 5 January, but were not taken again until 15 April. The latest end date was 11 November 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 modelled curves. Specifically, we removed tree-years with small or negligible total growth ($\Delta\text{DBH} \leq 0.005$ cm; SCBI = 26, Harvard Forest = 253) and tree-years in which 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 2,701 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 modelled the observed DBH on a given DOY (that is, Julian days) as:

$$\text{DBH} = L + \frac{K - L}{1 + 1/\theta \cdot \exp[-r(\text{DOY} - \text{DOY}_{\text{ip}})/\theta]^{\theta}}$$

Here, L and K are lower and upper asymptotes of the model. DOY_{ip} is the DOY during which the inflection point in growth rate occurs, r shapes the slope of the curve at the inflection point, and θ is a tuning parameter controlling the slope of the curve towards the upper asymptote. This allows an asymmetric fit to the data, in which the onset of growth can be estimated independent of the cessation of growth. When $\theta = 1$, g_{\max} occurs on DOY_{ip} . 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 DOY. An advantage of this approach is that short-term shrinkage and swelling associated with rain events^{34,56} 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 modelled 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 modelled growth parameters were outliers, which were commonly indicative of unrealistic fits (for example, 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). Modelled fits for tree-years were removed under two conditions: (1) g_{\max} was 2.5 or more standard deviations away from the mean for each site–xylem architecture group combination (SCBI = 3, Harvard Forest = 11), and (2) timing variables (DOY_{ip} , DOY_{25} , DOY_{50} and DOY_{75}) were 2.5 or more 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 2,392 tree-year records deemed appropriate for analysis, leaving a total of 2,203 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 with others. This process was repeated using 2 and 3 standard deviations as the cut-off 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 (that is, MODIS Global Vegetation Phenology product)⁵⁷ via Google Earth Engine. For each year at each site, we extracted data from the pixel (500-m resolution) containing the centre of each forest plot. Using the daily MODIS 2-band EVI2 data, the product yields the timing of phenometrics (vegetation phenology) over each year, including timing of greenup, mid-greenup, 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 more than 3 standard deviations away from yearly means, which were labelled 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, VA, USA (<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 on the basis of other local records, were obtained from the Harvard Forest weather station^{60,61}. For each site, we used records of daily maximum (T_{\max}) and minimum (T_{\min}) temperatures. SPEI⁵⁵ values were obtained from the ForestGEO Climate Data Portal v1.0 (<https://forestgeo.github.io/Climate/>)^{55,58,62}.

The CTW (Fig. 1), defined as the period over which T_{\max} was most strongly correlated with DOY₂₅, was determined using the R package *climwin*⁶³. 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 timeframe. It does so by reporting the correlation and ΔAICc , 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 (T_{\max} and T_{\min}) and biological outcome variable DOY₂₅ over the timeframe from 1 January to the mean DOY₂₅ for the species group (by xylem porosity) and site (Extended Data Table 2). The time period yielding the lowest ΔAICc 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 T_{\max} 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 T_{\min} . 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 and Extended Data Figs. 6 and 7), we also ran analyses in which we fixed the CTW identified by *climwin* to be the month with the most days in the CTW (Extended Data Table 2) for each critical window. The months identified were March and April for ring-porous and diffuse-porous species at SCBI, respectively, and April and May for ring-porous and diffuse-porous species at Harvard Forest, respectively.

Correlation between the dendrometer band-derived growth parameters (DOY₂₅, DOY₅₀, DOY₇₅, L_{pgs} , g_{\max} and ΔDBH ; Fig. 1) and CTW T_{\max} (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 T_{\max} and T_{\min} , with qualitatively similar results, but we present only results for T_{\max} , which had an overall stronger correlation with growth parameters. Mixed-effect models were used to test the response of growth parameters to fixed effects of xylem porosity and mean T_{\max} (or T_{\min}) 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 T_{\max} (or T_{\min}). 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^{64,65}. In all cases, unless otherwise specified, all prior distributions were 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-month, 6-month and 12-month SPEI values of June, July and August versus April T_{\max} to determine whether warm spring temperatures were associated with greater summer drought stress in our dataset. No significant correlations were found (all $P > 0.05$).

Tree-ring analysis

We analysed 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 methodologies^{66,67}.

Dominant tree species were cored at both SCBI^{33,51} and Harvard Forest^{3,68,69} following sampling designs that covered a broad range of DBH. We analysed records for the ring-porous and diffuse-porous species at each site (Extended Data Table 1), but excluded semi-ring-porous species (for example, *Juglans nigra* L. at SCBI) and conifers (for example, *Tsuga canadensis* at Harvard Forest). We studied a total of 976 cores, which included 12 species at SCBI and four 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 America^{32,70,71}. For the majority of sampled populations (that is, site-species combinations), sampling focused on canopy trees (typically more than 20 trees per population)^{32,70,71}, whereas approximately 15% of the total 207 chronologies came from plot-level collections in which trees above a certain diameter (typically 10-cm DBH) were censused and cored^{33,69}. Again, analyses were limited to broadleaf deciduous species with clearly defined xylem porosity (that is, excluding semi-ring porous).

For each species-site combination, we converted tree-ring records into the dimensionless RWI to emphasize interannual variability associated with climate⁷². A two-thirds 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 series^{72,73}. An adaptive power transformation, a process that also stabilizes the variance over time⁷⁴, 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 records⁷⁵. The one-thirds spline method was chosen when replication in the inner portion of each chronology (the earliest approximately 30–50 years of each record depending on the 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 (\bar{r}) method. The robust biweight mean chronology (RWI) for each species-site combination was calculated from the ring-width indices following variance stabilization⁷³. We defined chronology start year (Extended Data Table 1) as the year in which subsample signal strength passed a threshold of subsample signal strength = 0.8, or where 80% or more of the population signal was captured in the chronology.

For the analysis of correlation between RWI and climate variables, we obtained monthly T_{\max} and T_{\min} data for 1901–2019 from CRU v.4.04 (ref. ⁵⁴). Correlations between monthly climate and RWI were assessed in R v 4.0 (ref. ⁷⁶) using the packages *dplR*⁷⁷ and *bootRes*⁷⁸. Reported correlations and significance were determined using bootstrapped confidence intervals. Summary figures were created using the package *dplR*⁷⁷ (Fig. 3 and Extended Data Figs. 6 and 7).

Our analysis focused on assessing correlations of RWI to months spanning January to September of the current year (presented in Fig. 3

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and Extended Data Fig. 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 Fig. 7). Correlations and significance levels for months March–August are given in Supplementary Table 1.

We used a multivariate model to test for joint effects of April and summer T_{\max} on RWI. We focused on April to represent spring temperatures because it was the month with the greatest overall alignment with the CTWs 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 T_{\max} over three summer windows: June, June–July and May–August. Having determined that, among these, June–July explained the most variation, we then analysed the joint effects of April T_{\max} and June–July T_{\max} on RWI for each chronology independently using the base `lm()` function in R. Slopes and P values for each chronology are given in Supplementary Table 1. Although some models may have benefitted from data transformations, we determined that assumptions of normality and homoscedasticity were sufficiently met for the purposes of this analysis.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets generated and analysed during the current study are available via GitHub in the growth_phenology repository of the ForestGEO Ecosystems & Climate Lab at SCBI (https://github.com/EcoClimLab/growth_phenology) and archived in Zenodo (<https://doi.org/10.5281/zenodo.6632090>). Master versions of the dendrometer band data are available for SCBI via GitHub in the Dendrobands repository of the SCBI ForestGEO plot (<https://github.com/SCBI-ForestGEO/Dendrobands>), which is archived in Zenodo (<https://doi.org/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 (<https://doi.org/10.5281/zenodo.3958215>), and the NCEI weather station located in Front Royal, VA, USA (<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 (<https://doi.org/10.5281/zenodo.3958215>). The SPEI 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 (<https://doi.org/10.5281/zenodo.3958215>). Canopy foliage phenology data were extracted from the MCD12Q2 V6 Land Cover Dynamics product (that is, 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 the repository for this project, many tree-ring datasets are archived in the International Tree-Ring Data Bank (<https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>), the Dendro-Ecological Network (<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 Supplementary Table 1. Original tree cores are archived at the institutions of various members of

the author team (Harvard Forest, SCBI, Indiana University and University of Idaho) and will be made available on reasonable request.

Code availability

Data were analysed in the open source statistical software R (version 4.0). We used the packages `climwin` v.1.2.3 (<https://cran.r-project.org/web/packages/climwin/index.html>), `dplR` v.1.0.2, `bootRes` v.1.2.4, `rstanarm` v.2.21.1 and functions from `Rdendrom` v.0.1.0 (<https://github.com/seanmcm/Rdendrom/>). We used `climpack` software v.1.2.8 (see www.climpack-sci.org). Mixed-effect models were 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 codes are available through the EcoClimlab GitHub repository (https://github.com/EcoClimLab/growth_phenology) and archived in Zenodo (<https://doi.org/10.5281/zenodo.6632090>).

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Additional information

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