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Research paper

Peak radial growth of diffuse-porous species occurs during periods of lower water availability than for ring-porous and coniferous trees

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Climate models project warmer summer temperatures will increase the frequency and heat severity of droughts in temperate forests of Eastern North America. Hotter droughts are increasingly documented to affect tree growth and forest dynamics, with critical impacts on tree mortality, carbon sequestration and timber provision. The growing acknowledgement of the dominant role of drought timing on tree vulnerability to water deficit raises the issue of our limited understanding of radial growth phenology for most temperate tree species. Here, we use well-replicated dendrometer band data sampled frequently during the growing season to assess the growth phenology of 610 trees from 15 temperate species over 6 years. Patterns of diameter growth follow a typical logistic shape, with growth rates reaching a maximum in June, and then decreasing until process termination. On average, we find that diffuse-porous species take 16–18 days less than other wood-structure types to put on 50% of their annual diameter growth. However, their peak growth rate occurs almost a full month later than ring-porous and conifer species (ca. 24 ± 4 days; mean \pm 95% credible interval). Unlike other species, the growth phenology of diffuse-porous species in our dataset is highly correlated with their spring foliar phenology. We also find that the later window of growth in diffuse-porous species, coinciding with peak evapotranspiration and lower water availability, exposes them to a higher water deficit of 88 ± 19 mm (mean \pm SE) during their peak growth than ring-porous and coniferous species (15 ± 35 mm and 30 ± 30 mm, respectively). Given the high climatic sensitivity of wood formation, our findings highlight the importance of wood porosity as one predictor of species climatic sensitivity to the projected intensification of the drought regime in the coming decades.

Keywords: wood porosity, water deficit, temperate forest, ring-porous, diffuse-porous, diameter growth, dendrometer band.

Introduction

Global change represents a growing threat for many dominant processes that drive the dynamics of forests (Bonan 2008). Among these processes, wood growth controls ecosystem carbon (C) sinks (Pan et al. 2011), timber production, and is closely related to other demographic processes such as mortality and fecundity (Wyckoff and Clark, 2000, Wyckoff and Clark, 2002, Berdanier and Clark 2016, Buechling et al. 2017, Cailleret et al. 2017). A growing number of studies document climate change impacts on tree growth related, in particular, to increased water deficits under global warming (Dai 2013, Cook et al. 2015). Negative impacts of water deficit on tree growth and health has been shown to vary according to a wide array of stand-level conditions including soil characteristics (Buckland et al. 1997, West et al. 2012, Phillips et al. 2016), stand diversity (Grossiord 2018), local precipitation and evaporative demand (Williams et al. 2013, McDowell and Allen 2015, D'Orangeville et al. 2018) and competition for resources (Martin-Benito et al. 2011, D'Amato et al. 2013, Bottero et al. 2017, Gleason et al. 2017). In addition, many tree-level traits also affect individual vulnerability under altering environmental conditions such as carbon allocation strategies (Trugman et al. 2018), previous disturbance history (Itter et al. 2019), rooting depth (Padilla and Pugnaire 2007, Phillips et al. 2016), water-use efficiency (Peters et al. 2018) or wood structure (Elliott et al. 2015, Kannenberg et al. 2019). Multiple studies also suggest that larger trees may be more vulnerable to drought with serious implications for carbon sequestration (Bennett et al. 2015). Despite this ever-growing understanding, the vulnerability of forests to hotter droughts remains uncertain and may be greatly underestimated (Allen et al. 2015).

The timing of drought may strongly influence drought vulnerability of trees, due to the highly seasonal nature of cambial activity (i.e., cambial cell division) and its acute sensitivity to water availability (Gruber et al. 2010, Foster et al. 2014, Lempereur et al. 2015). Recent observations at the global scale (Huang et al. 2018) as well as in dry Mediterranean forest systems (Forner et al. 2018) support these general concepts. In temperate forests of Eastern North America, drought impacts on current-year radial growth were reported to reach their peak in June (D'Orangeville et al. 2018, Kannenberg et al. 2019), coinciding with the period of maximal cambial activity (Rossi et al. 2006, Deslauriers et al. 2007). This relatively short seasonal window for diameter growth is mainly driven by climate (Rossi et al. 2008b), but may also be modified by water deficit (Gruber et al. 2010, D'Orangeville et al. 2013). Tree size and canopy position have also been reported to affect diameter growth phenology. In timberline conifer stands, older and larger trees display a shorter growing period (Rossi et al. 2008a), while in temperate

stands, overstory fir trees start their growth earlier and end it later than understory trees (Rathgeber et al. 2011). Species differences in wood structure also have a large influence on the phenology of diameter growth. Earlier cambial reactivation and wood cell lignification in ring-porous species relative to diffuse-porous species was first reported in a temperate forest in England (Priestley and Scott 1936). This pattern has since been documented in other temperate forests of Europe (Michelot et al. 2012a) and Asia (Takahashi et al. 2013), and in the Acadian forest of North America (Lavigne et al. 2004). Earlier growth in ring-porous species is likely due to the winter embolism of their large xylem vessels requiring restoration of the water transport pathway before new leaves can unfold and begin transpiring (Zimmermann and Brown 1971, Sperry et al. 1994). Differences in phenology may explain why the diameter growth of ring-porous *Quercus robur* and *Q. rubra* in Belgium is more sensitive to spring droughts, while the diffuse-porous species *Fagus sylvatica* reacts more strongly to summer drought (Vanhellemont et al. 2019). Accounting for the seasonal window of climate sensitivity in diameter growth, which appears distinct from that of leaf phenology (Seftigen et al. 2018), may significantly improve our ability to predict future changes in forest productivity. However, our comprehension of diameter growth phenology is limited for most temperate species, and nearly all eastern North American species (Delpierre et al. 2016).

Contrary to diameter growth phenology, leaf phenology is more easily measured using non-intrusive techniques such as cameras (Richardson 2019) or repeated seasonal observations (Denny et al. 2014). Monitoring diameter growth phenology requires more time-consuming approaches. Cellular monitoring uses frequent collection of wood samples and extensive laboratory processing, leading to low sample replication (D'Orangeville et al. 2013). Dendrometer bands, permanently attached to trees, offer a low-cost method to monitor diameter growth over a large number of trees. Mostly used to study annual growth, they are not suited to track xylem maturation phases, but can register volumetric changes in stem diameter and provide valuable estimates of intraseasonal growth dynamics and phenology (Deslauriers et al. 2007) using standardized methods that can be reproduced across trees, species and sites (McMahon and Parker 2015). Here, we utilized a dendrometer band network comprising 610 trees in a secondary-growth, temperate mesic forest to provide a first comparison of diameter growth phenology between 15 different tree species in the northeastern USA. Our objectives were (1) to compare the importance of tree vigor, size and wood porosity as drivers of seasonal growth phenology in diffuse-porous, ring-porous and nonporous tree species and (2) to relate differences in diameter growth phenology to leaf phenology and seasonal climate, specifically seasonal variations in water deficit.

Materials and methods

Site location

This study uses a 6-year data collection (1998–2003) from within the footprint of the Environmental Measurement Site (EMS) eddy-covariance flux tower at the Harvard Forest in central Massachusetts, USA (42°30' N, 72°10' W). The Harvard Forest is a mixed deciduous broadleaf-dominated forest located in the temperate mesic region of Eastern North America with stony to sandy loam soils derived from glacial till. Forests are dominated by northern red oak (*Q. rubra* L.) and red maple (*Acer rubrum* L.), with a smaller representation of American beech (*F. grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* L. Carrière), eastern white pine (*Pinus strobus* L.) and yellow birch (*Betula alleghaniensis* Britton). Climate in the study area is temperate continental, with warm summers (19 °C in July) and cold winters (on average −12 °C in January). Mean annual precipitation is 1,120 mm, a total that is rather evenly distributed over the year. On-site weather records indicate that the study period included the driest summer (1999) over a 26-year period (1991–2017), with monthly precipitations of 52 mm relative to a monthly average of 111 mm from June to August. The last two decades, however, represent a regional wet period with increased frequency of rainfall events during the summer (Bishop and Pederson 2015).

A total of 40 circular, 10-m radius biometric plots were randomly placed during the summer of 1994 within 100-m increments along eight 500-m transects that extended from the EMS eddy-flux tower (Figure 1). All live trees of diameter at breast height (DBH) ≥ 10 cm were tagged and their DBH measured. Six plots that became flooded by a beaver pond or were affected by selective harvest operation in 2001 have been excluded from analysis. In 1998, the tagged trees were resampled and manual dendrometer bands were installed (Barford et al. 2001). From 1998 to 2003, gap increments in dendrometer bands were recorded approximately every 1–2 weeks during the growing season using digital calipers (resolution ~0.01 mm). During this period, 881 trees were monitored across 34 plots, including three ring-porous species (white ash, *Fraxinus americana* L.; northern red oak; black oak, *Q. velutina* Lam.), four conifers (white spruce, *Picea glauca* (Moench) Voss.; red pine, *P. resinosa* Aiton; eastern white pine; eastern hemlock) and eight diffuse-porous species (striped maple, *Acer pennsylvanicum* L.; red maple; yellow birch; black birch, *B. lenta* L.; white birch, *B. papyrifera* Marshall.; gray birch, *B. populifolia* Marshall.; American beech; black cherry, *Prunus serotina* Ehrh.). All species but striped maple were found in multiple plots, with red maple, northern red oak and eastern hemlock being the most common species (36, 21 and 13% of sampled trees, respectively).

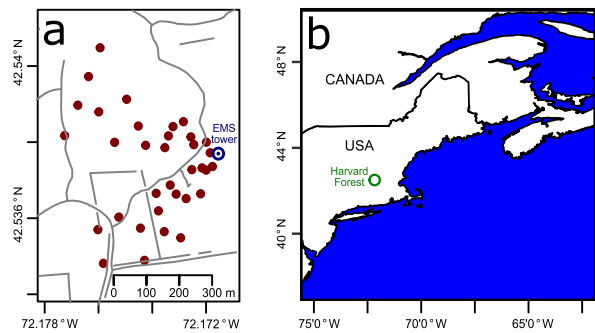


Figure 1. Location of the 34 study plots and the EMS eddy-flux tower at Harvard Forest (a) and within eastern North America (b). Linear features (e.g., roads, former agricultural stone walls) are in gray.

Modeled growth phenology

Dendrometer measurements were converted to an arc to account for the circular nature of the dendrometer band, using measured tree DBH, then translated into diameter values. After removal of tree-years with <10 measurements during the growing season, 52,512 diameter measurements were used for modeling, corresponding to 3286 tree-years spread over 698 trees (on average 5 year of data per tree). A five-parameter logistic model was fitted using an existing function for the R statistical computing environment on each year-tree combination (McMahon and Parker 2015):

$$dbh_{doy} = L + \frac{K - L}{1 + 1/\theta * \exp\left(-r\left(doy - doy_{ip}\right)/\theta\right)}$$

where dbh_{doy} is the measured DBH, r represents the maximum growth rate, L and K are initial and end-of-year DBH, doy_{ip} is the day of year (doy) when maximum growth rate occurs and θ is a tuning parameter adjusting the approach to the upper asymptote. Given the fitted function provides accurate characterization of growth, but less accurate starting and ending diameter sizes, a likelihood ratio test was used to further constrain the estimation of these values following McMahon and Parker (2015). Following a preliminary analysis that indicated growth rates peaked in June (see Results), we noted that the lower early-season sampling effort—compared to the frequency of sampling later in the season—impeded the model capacity to accurately estimate the initial diameter value. To avoid this potential bias as well as the confounding effect of stem rehydration in the spring (Kozłowski and Winget 1964, Deslauriers et al. 2007), the upper asymptote from the prior-year model was used as the starting diameter of a tree. We therefore excluded from our analysis each tree's first-year intra-annual model (743 out of 3286 tree-years, i.e., 23% of all tree-years).

Negative or null growth was detected in 9% of the annual observations. They were disproportionately associated with red

Table 1. Summary of sampled trees. Diffuse-porous, non-porous and ring-porous represent 49, 26 and 25% of trees, respectively.

Species	No. of trees	No. of plots	Tree size (mean biomass in kg C) [5th,95th]	Vigor (%) [5th,95th]	Wood structure
Striped maple	5	1	21 [16–27]	2.3 [0.9–4.5]	Diffuse-porous
Red maple	222	34	89 [19–245]	1.3 [0.1–3.3]	Diffuse-porous
Yellow birch	33	15	79 [21–228]	1.8 [0.1–4.1]	Diffuse-porous
Black birch	9	6	173 [29–623]	2.4 [0.6–3.8]	Diffuse-porous
White birch	5	4	158 [60–346]	0.7 [0.1–1.8]	Diffuse-porous
Gray birch	7	2	107 [55–178]	1.0 [0.2–2.1]	Diffuse-porous
American beech	8	6	89 [25–180]	2.8 [0.9–5.4]	Diffuse-porous
Black cherry	13	7	291 [35–768]	0.7 [0–1.5]	Diffuse-porous
White spruce	23	4	48 [22–86]	0.5 [0–0.9]	Non-porous
Red pine	31	3	211 [81–353]	1.1 [0.3–2.0]	Non-porous
Eastern white pine	27	10	170 [25–455]	1.7 [0.3–3.3]	Non-porous
Eastern hemlock	77	14	113 [14–334]	2.2 [0.2–4.8]	Non-porous
White ash	12	5	249 [67–433]	0.9 [0.1–1.9]	Ring-porous
Northern red oak	125	31	418 [88–1,204]	1.7 [0.5–2.9]	Ring-porous
Black oak	13	10	275 [54–548]	2.3 [0.7–5.3]	Ring-porous
TOTAL	610	34	180 [20–631]	1.5 [0.1–3.8]	

maple trees (55% of observations), while no other species comprised more than 8% of such observations. Observations of trees with no growth were excluded from the analysis. Another 11% of the annual growth models displayed poor fits with abnormal model parameters (e.g., winter growth peak, staircase growth increments) and were excluded. The large majority of these poor fits were represented by small, suppressed trees with low growth rates potentially confounded with stem swelling and shrinking or measurement uncertainty. Indeed, 82% of these trees displayed lower-than-average vigor, and 67% displayed lower-than-average DBH. The final dataset used in the analysis contains up to 5 years of growth for 610 trees from 15 species distributed across 34 plots, for a total of 1992 models (Table 1). The most abundant species were red maple, northern red oak and eastern hemlock. On average, each tree was represented with 4 years of growth.

Growth models fitted using frequently collected dendrometer data provide accurate predictions of the main period of diameter growth due to both high sampling frequency and high growth rates (Deslauriers et al. 2007). The use of dendrometers to determine the onset and cessation of secondary growth is much less accurate, because of the low growth rates and potentially confounding effects of stem swelling and shrinking (Tardif et al. 2001, Deslauriers et al. 2003). We, therefore, limited our analysis to the seasonal window of rapid growth. Three phenological indices were derived from individual growth models: W25, W50 and W75, which correspond to the day of year when 25, 50 and 75% of cumulative annual diameter growth is reached, respectively (Figure 2).

Bud break phenology

During the same sampling years (1998–2003), bud and leaf characteristics were documented at 3–7 day intervals from

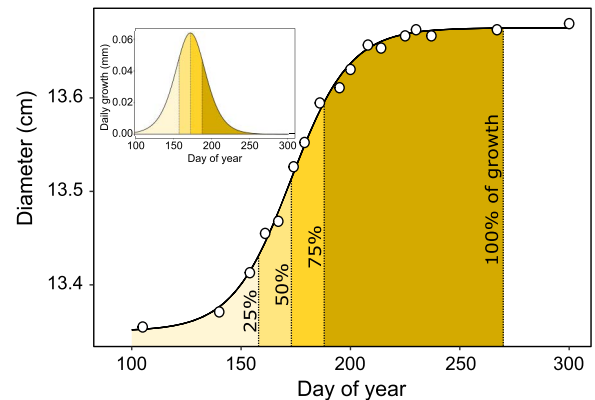


Figure 2. Example of the logistic growth model fitted on diameter measurements (DBH) taken on a yellow birch in 1999. The dotted lines indicate the day of year when modeled growth reached 25, 50, 75 and 100% of its cumulative annual value. The inset figure shows the daily growth rate for that tree derived from the fitted model.

April to June on one to five permanently tagged understory and overstory individuals outside of the study plots but within a 1.5-km radius (Richardson and O'Keefe 2009). The monitored species comprised all species with manual dendrometer bands except red pine and white spruce. We interpolated the timing of bud break and leaf development for each tree and each year. Bud break was defined as the occurrence of 50% of the buds on an individual having recognizable emergent leaves, while leaf development was defined as the occurrence of at least 75% of the leaves on an individual having reached 75% of their final (mature) size. This point was used rather than 'fully developed' because the leaves are functional but still developing rapidly during this period, which permits better estimation of a date between observations.

Tree characteristics

Cambial growth rates and tree size can impact the beginning, duration and end of stem growth (Rathgeber et al. 2011). We used the logistic growth model to interpolate the dendrometer data over time and generate fine temporal resolution estimates of tree DBH. We converted these estimates to above-ground biomass estimates, referred to as tree size therein, using species-specific allometric equations (Smith and Brand 1983, Jenkins et al. 2004). Tree vigor was calculated as the ratio of modeled annual biomass increment over tree biomass at the start of the growing season. Given that tree canopy position was not available, we assume that tree vigor should be related to canopy position, with dominant and suppressed trees displaying higher and lower growth rates, respectively.

Climate

Daily temperature and precipitation were measured at the Harvard Forest weather station. Radiation prior to 2002 did not include global horizontal irradiance (GHI), required by our model to predict potential evapotranspiration (PET), a measure of moisture demand. Half-hourly radiation data was therefore extracted for the study site (4-km resolution) from the National Solar Radiation Data Base (Physical Solar Model 2) - plus space (Sengupta et al. 2018). The Turc algorithm was used to compute daily PET based on temperature and radiation data (Dyer 2009). A Climate Moisture Index (CMI) was then calculated by subtracting PET from daily precipitation.

Analysis

A multivariate mixed model was used to estimate the effects of wood structure, tree size and vigor on the phenological indices W25, W50 and W75. The inclusion of size and vigor in the model allowed us to control for potential biases induced by the larger average size of ring-porous trees compared to nonporous and diffuse-porous species (Table 1). Specifically, the joint phenological response defined as $\mathbf{y}_{it} = (W25_{it}, W50_{it}, W75_{it})'$ where i and t index the individual tree and year of the observation, respectively ($i = 1, 2, \dots, n; t = 1, 2, \dots, T$) was modeled using a multivariate normal likelihood. Note that each \mathbf{y}_{it} corresponds to vector of length three, the total number of phenological indices. The effects of species, year and sample plot were controlled for by including each variable as an additive random effect to the mean response. Specifically for each observation,

$$\mathbf{y}_{it} = \mathbf{B}\mathbf{x}_{it} + \mathbf{u}_{s(i)}^{(\text{species})} + \mathbf{u}_t^{(\text{year})} + \mathbf{u}_{l(i)}^{(\text{plot})} + \boldsymbol{\epsilon}_{it},$$

where $\mathbf{B}\mathbf{x}_{it}$ defines the fixed effects in the model (\mathbf{x}_{it} includes observations of wood structure, tree size and tree vigor, while \mathbf{B} includes three sets of regression coefficients for each covariate—one for each phenological index), the \mathbf{u} terms define species, year and plot random effects (note, $s(i)$ and $l(i)$

indicate the species and plot corresponding to the i th tree) and $\boldsymbol{\epsilon}_{it}$ is the residual error, $\boldsymbol{\epsilon}_{it} \sim \text{Normal}(\mathbf{0}, \boldsymbol{\Sigma})$, where $\boldsymbol{\Sigma}$ is a three-dimensional covariance matrix.

Model parameters were estimated as part of a broader Bayesian hierarchical framework (Gelman et al. 2013). Additional information on the prior distributions and Bayesian inferential approach including the MCMC sampler is provided in the Supplementary Information Note S1.

Results

Diameter growth phenology

Averaged across trees and years, model-derived diameter growth rates peaked on 19 June, with interannual variability ranging between 10 June (in year 2001) and 25 June (in year 2003; 95% credible interval, $\text{CI}_{95\%}$: 0.001 to 0.06 $\text{mm}\cdot\text{day}^{-1}$; Figure 3). However, we observed large variations in the phenology of growth among trees based on their wood porosity, with conifers (i.e., nonporous species) and ring-porous oaks having consistently earlier windows of peak stem growth than diffuse-porous black cherry, American beech, birches and maples (Figure 3).

Bud break in diffuse-porous species preceded the modeled 25% stem growth threshold by an average of 36 ± 6 days. In contrast, bud break in ring-porous species was simultaneous with their 25% stem growth threshold (within 3 ± 7 days), while conifer leaf phenology lagged behind it by 26 ± 7 days on average (Figure 3).

Controlling for size and vigor differences across trees as well as random plot, year and species effects, our multivariate model confirms the observed striking difference in growth phenology with wood porosity: on average, diffuse-porous trees completed 25% of their annual diameter growth later than coniferous and ring-porous trees by 29 days ($\text{CI}_{95\%}$: 14–43) and 35 days ($\text{CI}_{95\%}$: 20–51), respectively (Figure 4). These differences diminish over the growing season due to higher growth rates in diffuse-porous trees: they completed 75% of their stem growth only 12 days ($\text{CI}_{95\%}$: 0–27) and 17 days later ($\text{CI}_{95\%}$: 3–33) than coniferous and ring-porous species, respectively. Such pattern results in diffuse-porous species having higher growth rates during the period of 25 to 75% of annual growth and a shorter duration in peak stem growth period versus coniferous and ring-porous species, lasting only 38 days ($\text{CI}_{95\%}$: 25–52) in diffuse-porous species, compared to 54 days ($\text{CI}_{95\%}$: 39–69) and 56 days ($\text{CI}_{95\%}$: 39–72) in coniferous and ring-porous species, respectively (Figure 4).

Compared with wood porosity, our multivariate model indicates relatively smaller effects of biomass and vigor on the seasonality of diameter growth (Figure 5). The peak diameter growing period of larger and more vigorous trees tended to extend later in the season, but only by a few days. Controlling for all other variables including wood structure, the largest trees

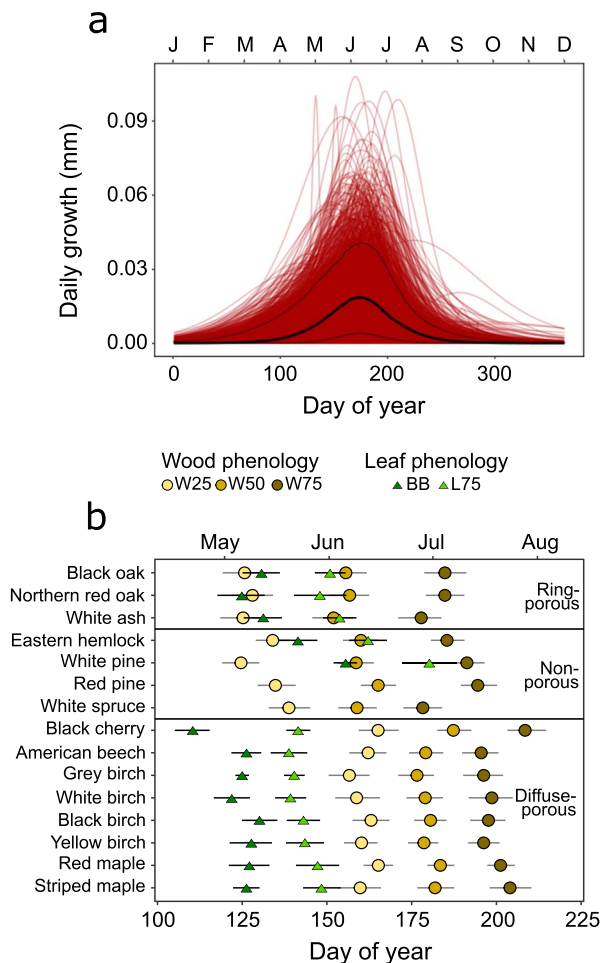


Figure 3. Wood and leaf phenology over 1999–2003 across individuals (red curves) and averaged per species (colored symbols). Error bars indicate 95% credible intervals (stem phenology) or standard deviation (leaf phenology). W25: 25% of annual diameter growth; W50: 50% of annual diameter growth; W75: 75% of annual diameter growth; BB: bud break; L75: leaf out. (a) Daily modeled growth of all 1992 tree-years. The black lines indicate 10th, 50th and 90th quantiles of daily growth rates. (b) Posterior mean estimates of wood phenology per species. Average leaf phenology measured at the site for corresponding species and years is also presented when available.

completed 25, 50 and 75% of their annual diameter growth on an average of 9, 6 and 5 days later than the smallest trees, respectively (Figure 5a). Similarly, the most vigorous trees completed 25, 50 and 75% of their annual diameter growth only 14, 10 and 7 days later than the slowest growing trees, respectively (Figure 5b).

Linking diameter growth with leaf phenology

The five diffuse-porous species used in this analysis display large, positive correlations between leaf and diameter growth phenology across years (Figure 6). The largest correlations are observed between bud break and the point when 25% of annual diameter growth is completed (W25). These relations are

equally strong within and across diffuse-porous species. Intra-species Pearson correlations range between 0.64 (white birch) and 0.95 (black birch), while correlation across all diffuse-porous trees reaches 0.81. The correlations between bud break and diameter growth tend to diminish over the season in diffuse-porous trees, with correlations of 0.69 for W50 and 0.39 for W75. High correlations are also observed between leaf development (i.e., when at least 75% of the leaves on an individual have reached 75% of their final size) and diameter growth in diffuse-porous trees, although the largest correlations are observed for W50 ($r = 0.83$) and W75 ($r = 0.81$) rather than W25 ($r = 0.69$; Figure 6). In contrast to diffuse-porous species, we observe a weaker relationship between leaf and diameter growth phenology in ring-porous trees. Despite a relatively simultaneous bud break with W25, overall correlations for ring-porous species range between 0.30 and 0.52. The limited leaf phenology data did not allow for a robust assessment of this relationship for coniferous species, although there does not appear to be any visible synchrony (Figure 6).

Diameter growth phenology and seasonal water balance

Striking differences in moisture availability were observed during peak diameter growth (period ranging from W25 to W75) according to wood porosity. While all trees experienced the same water deficits (Figure 7a), diffuse-porous trees were subject to a higher water deficit during their period of peak diameter growth compared to ring-porous and coniferous trees (29 ± 17 mm vs 0 ± 19 mm and 5 ± 18 mm, respectively; values are mean \pm SE; Figure 7c). In addition, diffuse-porous trees were the only group of species with diameter growth occurring under water deficit (negative CMI) during all 5 years of study (Figure 7b). This trend for lower moisture availability during peak diameter growth in diffuse-porous species is likely related to their later growth, occurring concurrently with seasonal peaks in evapotranspiration (Figure 7d). For context, these relations occurred during substantially high interannual variation in moisture, documented here with the CMI (see Methods). The annual sum of negative CMI, calculated here as the cumulative annual water deficit, ranged between 232 mm (year 2003) and 409 mm (year 1999; Figure 7a). The year 1999 displayed an unusually dry month of June (CMI = -90 mm) compared to other years (CMI ranging between -4 and 44 mm; Figure 7a).

Discussion

Species differences in diameter growth phenology remain poorly studied despite their important repercussions on stand-scale processes such as seasonal carbon sequestration and drought vulnerability. Here, we found a significant later window of peak growth in diffuse-porous species versus ring-porous and nonporous species. Maples, birches and other diffuse-porous species complete 25% of their diameter growth ca. 1 month

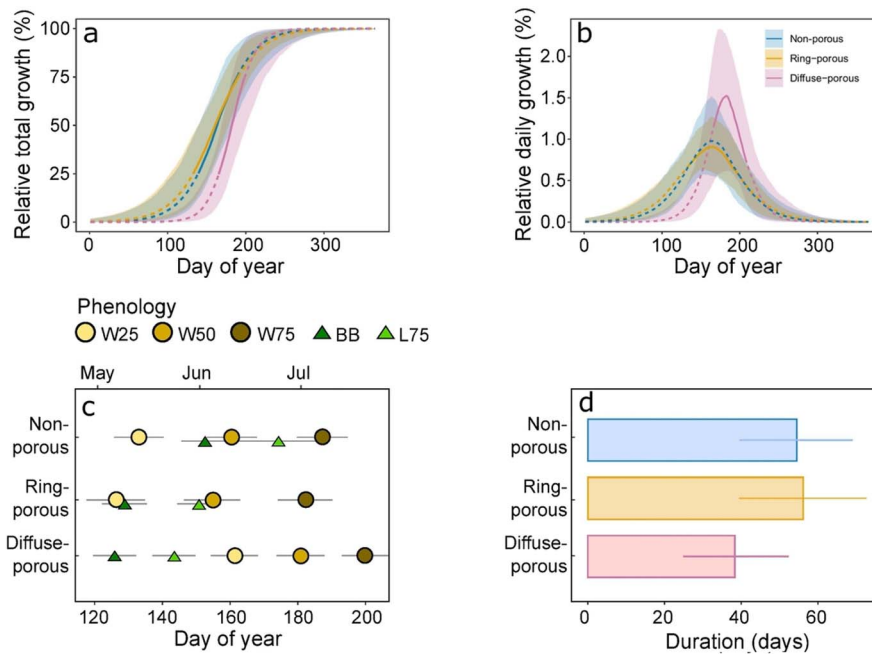


Figure 4. Wood and leaf phenology averaged per diffuse-porous, ring-porous or nonporous wood type. Error bars indicate 95% credible interval (stem phenology) or standard deviation (leaf phenology), while ribbons indicate 10th and 90th percentile values. The continuous and dashed lines indicate growth inside and outside of the W25-W75 period, respectively. W25: 25% of annual diameter growth; W50: 50% of annual diameter growth; W75: 75% of annual diameter growth; BB: bud break; L75: leaf development. (a) Standardized diameter increment. (b) Standardized daily growth rate. (c) Posterior mean estimates of wood phenology. Corresponding leaf phenology averaged over the study period is also presented. (d) Posterior mean estimates of growth duration (days between 25 and 75% growth).

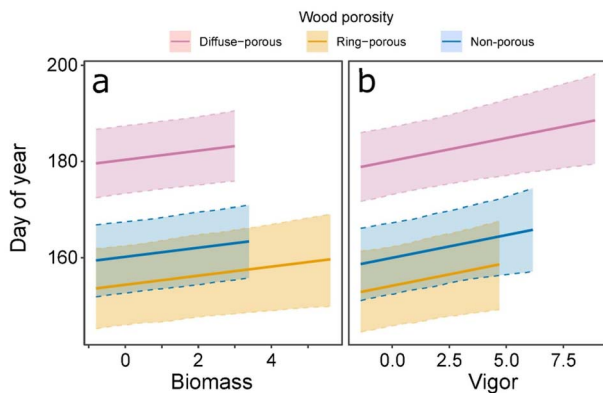


Figure 5. Posterior mean estimated effect of tree biomass (a) and vigor (b) on the day of year when 50% of growth is completed according to wood structure, with all other variables held constant at their median value. Units are standardized. Colored ribbons indicate 95% credible intervals for the posterior mean.

later than other species, but such delay in growth is partially compensated by higher growth rates, so that diffuse-porous species complete 75% of their diameter growth only 2 weeks later than other species.

The later window of peak growth in diffuse-porous species derives from physiological differences in reactivation in the region of the cambium. In diffuse-porous trees, the first vessels are formed when leaves are developing or mature, while the first

vessels of ring-porous species are formed several weeks before bud break (Larson, 1962, Larson, 1994, Suzuki et al. 1996, Zweifel et al. 2006, Sass-Klaassen et al. 2011, Takahashi et al. 2013), although ring-porous vessels only become functional after bud break (Kitin and Funada 2016). The mechanisms driving these difference have been studied for a long time (Wareing 1951), but are still debated (Frankenstein et al. 2005). Auxin (indole-3-acetic acid) is an important promoter of cambium reactivation and has long been thought to originate from developing leaves (Larson 1962, Aloni 1987). This assertion is supported by the high correlation values recorded here between spring leaf and diameter growth phenology in all eight diffuse-porous species studied here, but does not match with the capacity of ring-porous species to form new xylem and phloem before bud break (Prislan et al. 2013, Lavrič et al. 2017). The bimodal rates of cambial activity reported in ring-porous species (Pérez-de-Lis et al. 2017, Guada et al. 2018) may also have reduced the accuracy of our diameter growth phenology results, contributing to the lower correlations observed here between leaf and diameter growth phenology for these species. Our results nonetheless confirm the important synchronicity between leaf flushing and the period of rapid diameter growth in a wide array of broadleaf tree species. In ring-porous species, auxin or auxin precursors have been found in the cambial area prior to bud break (Savidge and Wareing 1981). Debudding experiments also suggest the existence of alternative auxin

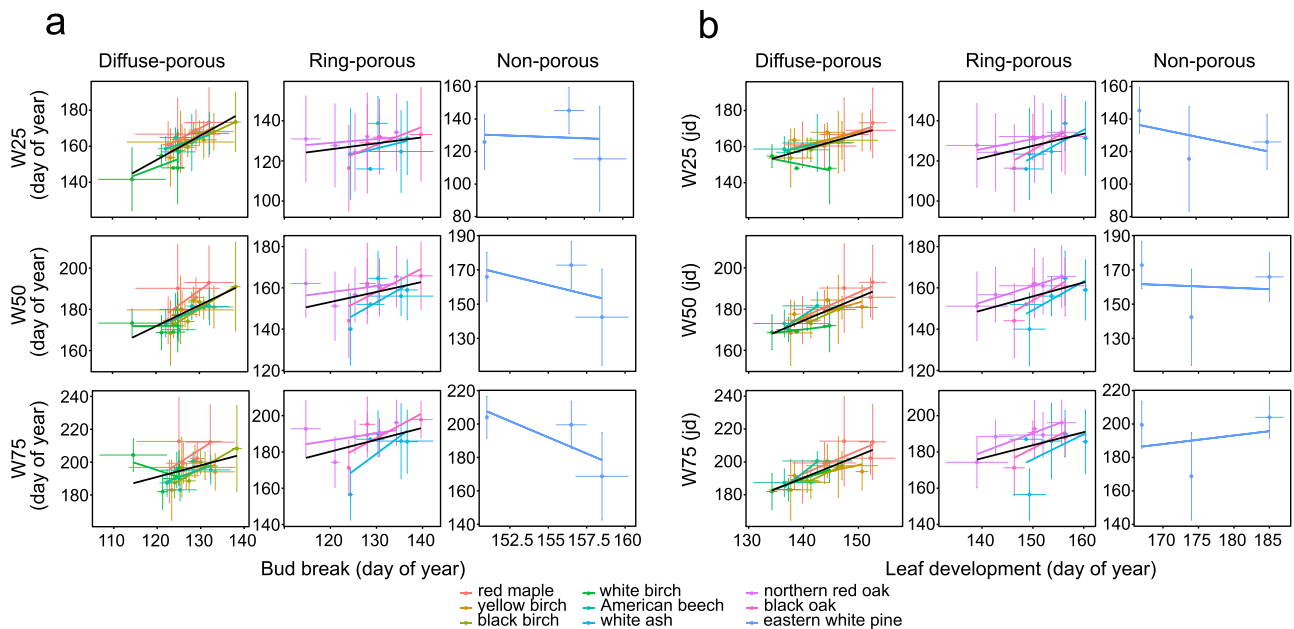


Figure 6. Covariation between wood phenology indices and (a) bud break and (b) leaf out among (black) and within (colored) species per wood structure types. Error bars indicate standard deviation from the mean. W25: 25% of annual diameter growth; W50: 50% of annual diameter growth; W75: 75% of annual diameter growth. The leaf phenology of the species included in the analysis is averaged over 3–5 individuals (species represented by a single individual were excluded).

sources readily available in dormant stem tissues of conifers (Little and Wareing 1981, Sundberg and Uggla 1998). Indeed, the diameter growth onset of co-occurring ring-porous *Quercus* species and coniferous *P. sylvestris* or *P. abies* in Europe revealed only small differences between ring-porous and coniferous trees ranging between 1 and 2 weeks (Zweifel et al. 2006, Michelot et al. 2012a), similar to our observations.

The presence of wide earlywood vessels offers an enhanced water conductive capacity in spring relative to diffuse-porous and nonporous species, albeit at the cost of a higher risk of cavitation when water becomes scarce. Such trade-off suggests that ring porosity is a hydraulic strategy adapted to seasonal temperate climates (Gilbert 1940, Lechowicz 1984, Baas and Wheeler 2011). Baas and Wheeler (2011) note an increasing number of ring-porous and semi-ring-porous species in the Northern Hemisphere since the Cretaceous, coincidental with the increasing seasonality of the climate in the area. Thus, early diameter growth in ring-porous species is a probable adaptation to the severe loss of hydraulic conductivity suffered during late-summer water deficits and winter freeze–thaw events (Sperry et al. 1994). Contrary to other species, the large earlywood vessels of ring-porous trees become nonfunctional after one growing season, while the smaller latewood cells can remain active for several years (Kitin and Funada 2016, Kudo et al. 2018). Severe loss of hydraulic conductivity requires the formation of newly functional xylem cells to restore transpiration capacity prior to leaf-out (Sperry et al. 1994, Hacke and Sauter

1996). Compared with ring-porous species, conifer tracheids and diffuse-porous vessels are very resistant to embolism. In the case of conifers, such resistance is required by their evergreen foliage which increases winter water losses (Hinckley and Lassoie 1981). Conifers also differ from diffuse-porous species in that they can start photosynthesizing using their existing foliage and reactivate their cambium as soon as spring conditions are suitable for growth (Hunter and Lechowicz 1992, Wang et al. 1992, Barbaroux and Bréda 2002). The capacity of conifers to use older foliage is consistent with their later bud break, as observed here and documented in earlier studies (Hoch et al. 2003, Michelot et al. 2012a). Diffuse-porous species also display a low vulnerability to embolism, limiting the need for early cambial reactivation (Hunter and Lechowicz 1992, Sperry et al. 1994). Compared to ring-porous species, the later cambial activity of diffuse-porous trees enables them to avoid using their stored carbohydrates for leaf flush (Barbaroux and Bréda 2002), which may be better adapted to their indeterminate shoot growth pattern (Lechowicz 1984). However, because wood growth in diffuse-porous species occurs later, this more conservative strategy of stored carbon use often coincides with seasonal maxima in evapotranspiration and water deficit.

We found that peak growth in diffuse-porous trees occurred during several-fold higher levels of evapotranspiration and water deficit than other species. In contrast, peak growth in co-occurring ring-porous and coniferous species was completed before this period. Such phenological differences between

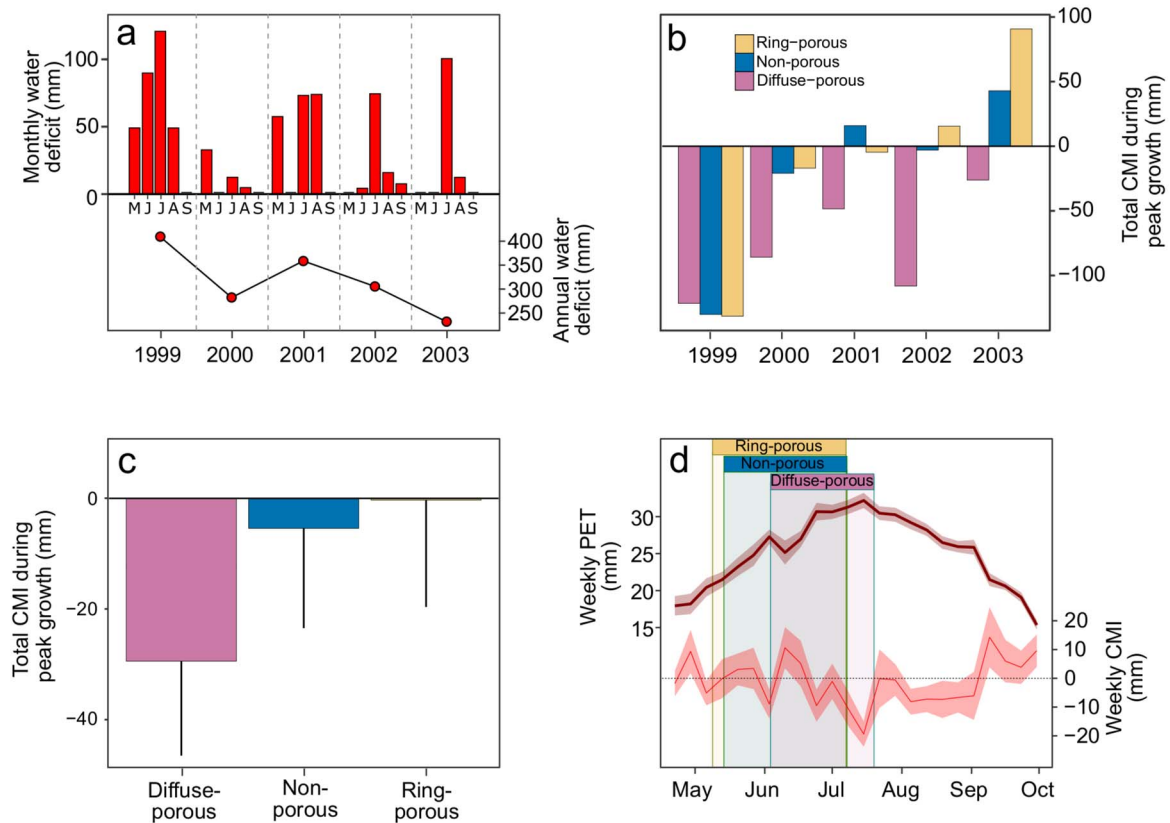


Figure 7. Climatic conditions at our study site (a) over the 1999–2003 study period where negative values of climatic moisture index (CMI) indicate monthly (May to September) and annual atmospheric water deficit, during modeled peak growth averaged per wood structure type (b) per year and (c) over the study period and (d) over a longer period, 1998–2014. The ribbons indicate standard deviation of the weekly averages in CMI and potential evapotranspiration (PET).

species of different wood porosity highlight the importance of wood porosity as a predictor of species responses to climatic conditions, particularly water stresses occurring at different periods of the growing seasons. For instance, ring-porous *Q. robur*, *Q. rubra* and *Q. petraea* were found to be mainly sensitive to spring drought, while diffuse-porous *F. sylvatica* was especially sensitive to summer drought in Europe (Michelot et al. 2012b, Vanhellefont et al. 2019). In the Eastern USA diffuse-porous species have also been repeatedly reported to display stronger reductions in radial growth during and following years of extreme water deficit, as compared with ring-porous or nonporous species (Brzostek et al. 2014, Elliott et al. 2015, Kannenberg et al. 2019). Similar patterns of response to interannual climate variability among ring-porous *Quercus* and *Carya* species also support the use of ring porosity as a functional group to help predict plant response to drought (Martin-Benito and Pederson 2015). However, the lagged growth strategy of diffuse-porous species is only one of the multiple aspects of the overall drought sensitivity of species, which include stomatal regulation, resistance to embolism or rooting depth. The projected increase in drought frequency

and intensity (Dai 2013, Cook et al. 2015) could amplify the consequences of the different growth strategies between wood structure types on their respective drought sensitivity.

Despite the reputation that manual dendrometer bands provide poorly resolved growth estimates, our methodological approach, combined with the high sampling frequency and replication, provides a valid protocol to monitor intra-seasonal growth dynamics. In addition to the phenological observations discussed earlier, we also found a relatively high proportion of red maple trees displaying little to no annual diameter growth. Such result confirms earlier observations of frequent missing growth rings for that species (Pederson 2005, Pederson et al. 2017). We also note the relatively weaker effect of tree size and vigor on the phenology of growth, relative to the genetically driven wood porosity. It is possible that traditional dendrometer bands could factor into these results. Our analytical approach, however, controlled for size and vigor effects on relative growth phenology, which masks the potential effect of phenological delays on total growth. Increased diameter growth has been previously observed to delay the ending of xylem maturation, thus extending the duration of wood formation (see Lupi et al.

2010). While our results do not discriminate between cellular stages in wood formation, they do also suggest that larger or more vigorous trees display a later peak in stem growth than smaller or more suppressed trees. We should also point out that manual dendrometer bands measure girth increment, which is mostly influenced over the growing season by the phase of xylem cell enlargement, along with xylem and phloem cell division, new phloem enlargement and likely phellogen activity (Zweifel et al. 2010). Studies investigating high-resolution growth of these species, such as conducted through microcoring (Deslauriers et al. 2017), are vital to further understanding and refining the new results reported here.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Data and Materials Availability

The data that support this study are available online (datasets HF003 and HF069) at <https://harvardforest.fas.harvard.edu/harvard-forest-data-archive>.

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Conflict of Interest

The authors declare no conflict of interest.

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Authors' contribution

LD and NP designed the research; JWM led the collection of dendrometer band data, while JMD provided the estimates of atmospheric water demand; LD and MI conducted data analysis; LD and NP wrote the manuscript with significant input from all co-authors.

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