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Research paper

Drought elicits contrasting responses on the autumn dynamics of wood formation in late successional deciduous tree species

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Research on wood phenology has mainly focused on reactivation of the cambium in spring. In this study we investigated if summer drought advances cessation of wood formation and if it has any influence on wood structure in late successional forest trees of the temperate zone. The end of xylogenesis was monitored between August and November in stands of European beech and pedunculate oak in Belgium for two consecutive years, 2017 and 2018, with the latter year having experienced an exceptional summer drought. Wood formation in oak was affected by the drought, with oak trees ceasing cambial activity and wood maturation about 3 weeks earlier in 2018 compared with 2017. Beech ceased wood formation before oak, but its wood phenology did not differ between years. Furthermore, between the 2 years, no significant difference was found in ring width, percentage of mature fibers in the late season, vessel size and density. In 2018, beech did show thinner fiber walls, whereas oak showed thicker walls. In this paper, we showed that summer drought can have an important impact on late season wood phenology xylem development. This will help to better understand forest ecosystems and improve forest models.

Keywords: beech, cessation of wood formation, drought, oak, xylogenesis.

Introduction

Studying phenological events is important for understanding ecosystem functioning, especially in the context of global change (Forrest and Miller-Rushing 2010, Liu et al. 2016). Most phenological studies on deciduous forest ecosystems have focused on spring phenology (Gallinat et al. 2015). Nevertheless, autumn phenology is equally important. In fact, during autumn, leaf senescence allows trees to recover leaf nutrients before leaf shedding (Estiarte and Peñuelas 2015), while the last xylem cells finish cell wall-thickening to complete the seasonal wood formation (Plomion et al. 2001). Since autumn wood phenology is even less studied than autumn leaf phenology, we focus here on the dynamics of the cessation of wood formation. We studied late successional deciduous trees because they represent a significant proportion of the temperate forests of the northern hemisphere (e.g., for Europe, 70% of the deciduous forests are dominated by late successional species (Brus et al. 2012)) and comprise many economical important species (e.g., beech, oak).

In spring, the cambium reactivates producing new xylem cells inwards and phloem cells toward the bark. As xylem cells are formed they undergo the process of differentiation, including cell expansion and cell wall-thickening (i.e., the deposition of a secondary cell wall and lignification of the cell walls) followed by programmed cell death (Plomion et al. 2001, Rathgeber et al. 2016) in the sclerenchyma cells (i.e., vessels and fibers). When the xylem cell production stops at the end of the growing season, differentiation of the last formed xylem cells continues for a few weeks to maximum 2 months until the last produced cells become mature (Prislan et al. 2009, Cuny and Rathgeber 2016, Rathgeber et al., 2016). Therefore, carbon allocation to developing xylem cells will still occur after the cell production stops (Cuny et al. 2015, Rathgeber et al. 2016). Since xylogenesis consists of a succession of different phases, changes in a stage can affect the subsequent phases. For example, a higher cell production means more cells have to differentiate and could consequently result in a prolonged wood growing season (Gričar et al. 2005, Lupi et al. 2010).

Soil water content and temperature are known to influence wood formation (Hsiao 1973, Guillemot et al. 2014, Balducci et al. 2016, Saderi et al. 2019). For conifers, it has already been shown that drought stress affects cambial activity (CA), and thus cell production, and the length of the growing season (Swidrak et al. 2014, Liang et al. 2016). Therefore, soil water deficit can reduce or stop xylem growth (Eilmann et al. 2009, Cabon et al. 2020, Peters et al. 2020). Moreover, in both conifers and deciduous species, drought can alter wood anatomy (Arend and Fromm 2007, Galle et al. 2010, Fernández et al. 2012). However, the effect of drought on the end of xylogenesis of deciduous trees in the temperate zone has not been studied thoroughly. In particular, it is not clear yet what magnitude or legacy effects (if any) a summer drought might have on the final stages of xylogenesis in deciduous trees. A better understanding of these effects is important to help predicting the impacts of increased water deficit due to climate change. For beech and oak, we tested the hypothesis that a summer drought can advance the cessation of CA and also of wood formation (differentiation) because fewer cells would have to go through the wall-thickening phase (Lupi et al. 2010). Furthermore, we hypothesized that drought would decrease the fiber percentage and the cell wall thickness of the cells maturing in the late season because less carbon would be available for the formation (Delpierre et al. 2016a, Larson 1994, Verbančič et al. 2018). These two hypotheses were addressed by examining a stand of European beech and a stand of pedunculate oak in Belgium over two consecutive years (2017 and 2018), with a severe drought occurring in the early summer of 2018.

Materials and methods

Site characteristics and tree selection

Dominant and codominant healthy individuals of European beech (*Fagus sylvatica* L.), a diffuse-porous species, and pedunculate oak (*Quercus robur* L.), a ring-porous species, were selected in typical stands for these species within the vicinity of Antwerp, Belgium (51°20′N, 4°30′E; 15 m above sea level; Figure 1). The stands were located in the Park of Brasschaat (PB), on a sandy soil with a deep humus layer. The stands were planted, but have been subjected to only limited management in the last decades. The age of the stands is about 70 and 115 years, for beech and oak, respectively. Four trees per species were selected for the monitoring of xylogenesis by the end of the summer in 2017 (21 August). In 2018, observations were performed on the same individuals, but, in order to more accurately assess intertree variability, four additional individuals were sampled. Because of the focus on the later part of the season, xylogenesis observations were not made for spring–early summer 2017. However, for both species, xylogenesis was monitored throughout the growing season on four trees in 2018. The diameter at breast height of the selected individuals was 45 ± 3 cm (mean ± standard error) and 56 ± 3 cm for beech and oak, respectively. Weather data for both sampling years was provided by the Research Institute for Nature and Forest (INBO, Belgium). The weather station was located about 2.5 km from the studied forest stands.

Sample collection and preparation

During the autumn (late August until late November) of 2017 and 2018, microcores of stem tissue were collected on a weekly basis at breast height with a Trephor (Rossi et al. 2006*a*). To avoid wound reactions, sampling followed an upward spiral and a distance of 30 cm was kept between consecutive years. The samples were immediately stored in 1.5-ml Eppendorf microtubes containing a 50:50 ethanol/water solution for conservation. In the laboratory, the microcores were cut to contain the most recently created xylem rings (at least two), the cambium and the inner phloem. The microcores were then dehydrated in a series of rising ethanol concentration, infiltrated with a clearing agent (UltraClear, J.T. Baker, Avantor Performance Materials, Center Valley, PA, USA) and paraffin (Paraplast plus, ROTH, Karlsruhe, Germany) and embedded in paraffin blocks. The paraffin blocks were cut into 5–10 μm slices with a microtome (Leica Microsystems, Wetzlar, Germany). Next, the paraffin was removed with a clearing agent (UltraClear) and ethanol. The sections were then stained in an aqueous solution of safranin (Merck, Darmstadt, Germany) and Astra blue (Sigma–Aldrich, Steinheim, Germany). Finally, the sections were fixed by mounting in Euparal (Waldeck, Munster, Germany) (Gričar et al. 2017).

Microscopic observations of xylogenesis and xylem anatomy

The anatomical sections were examined under a light microscope (Leica DM 4000 B/M) to estimate the date when wood formation was completed. The cessation of CA has been determined as the time when there was any cell in enlarging phase, i.e., indicating that the cambium is not dividing anymore. Xylem cells in the wall-thickening phase (wall-thickening cells) were recognizable by a blue cell wall, whereas cells that had completed wall-thickening had a completely red wall through the safranin/Astra blue staining. Possible presence of tension wood makes the analysis harder as tension wood also turns blue after staining. For each tree, measurements of cell wall-thickening

Figure 1. Location of the stands on the map of (a) Europe, (b) Belgium and (c) Antwerp area. Blue: beech (PB); yellow: oak (PB).

were performed on samples where CA already ceased, no cell production or enlargement was present anymore, but the last formed cells had not yet completed cell wall formation and lignification. As cells in hardwood species (angiosperms) are not organized in straightforward radial rows like in softwood species (gymnosperms), it is not possible to count the number of thickening cells. Therefore the layer of wall-thickening cells was measured in three radial rows in each histological section. The three selected measurements were approximately representing the minimum, maximum and mean width of the thickening zone (Figure 2). These data were used to evaluate the dynamics of the completion of latewood formation.

Width of the current year ring was also measured for all samples collected in 2017 and 2018. Measurements were done with image analysis software Leica Application Suite. In the Results section we present the percentage of the wall-thickening cells within the growth ring. This was calculated as the width of the layer of thickening cells, divided by the width of the current year ring. The width of the layer of thickening cells is displayed in Figure S1 available as Supplementary data at *Tree Physiology* Online. For 2018, the widths of the enlargement, thickening and mature zone were also measured (see details in Dox et al. 2020).

To evaluate the impact of drought conditions on xylem anatomy we measured vessel characteristics, fiber wall thickness and fiber percentage on transverse sections in the terminal part (i.e., last 25% of the ring) of completely differentiated xylem growth rings. Vessel characteristics in beech (vessel lumen area, radial cell lumen diameter and tangential cell lumen diameter) were measured using image analysis software Image Pro Plus and ROXAS (von Arx et al. 2016, Figure S2 available as Supplementary data at *Tree Physiology* Online). Vessel characteristics in oak and fiber cell wall thickness in both species were measured using Leica Application Suite by applying the area and distance measuring tool, respectively. Thickness of libriform fibers in oak and fibers (fiber tracheids) in beech was measured in three radial rows for two sampling events per tree and year (October and November). In beech, fiber percentage was evaluated by subtracting total vessel and ray area from the measured area of interest (i.e., last 25% of the xylem ring width). In case of pedunculate oak the area occupied by libriform fibers was measured within the area of interest (Figure 2c). Fiber content and fiber wall thickness were only measured in the four individuals that were observed in both years.

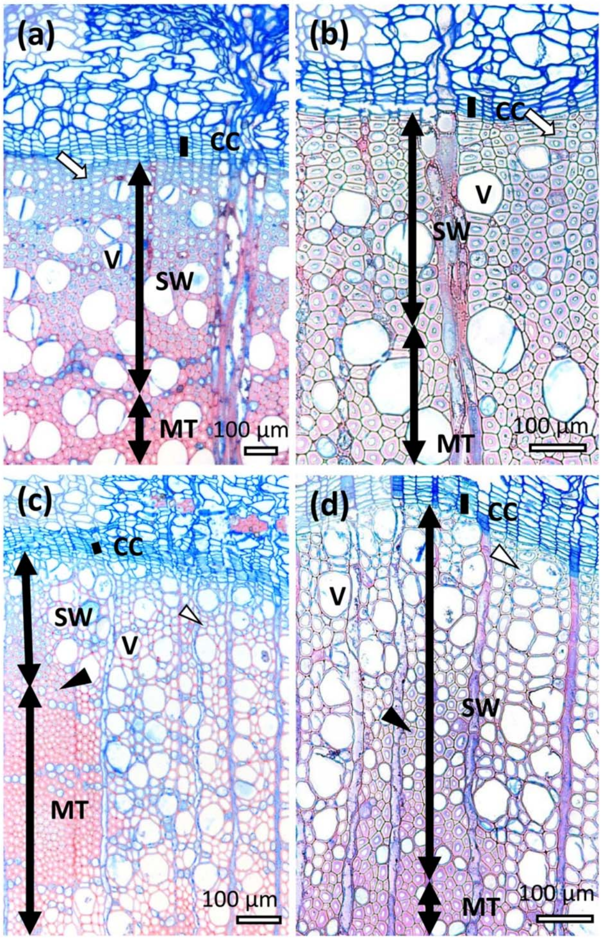

Figure 2. Cross-sectional images of beech (a, b) and oak (c, d) samples collected after the cessation cell production in cambium (CC). Fibers and vessels in the phase of secondary wall formation (SW) in beech and oak at the beginning (a, c) and at the end (b, d) of September 2018. Differentiating fiber tracheids (white arrows) in beech (a, b) are characterized with blue colored inner part of secondary cell walls. Latewood vessels (V) in oak (c, d) are surrounded by differentiating vasicentric tracheids (white arrowhead) and libriform fibers (black arrowhead). Mature xylem fibers (MT) have thick cell walls, which are stained completely red.

Tension wood is formed to adjust trunk position (if the tree is growing in a slope, for instance) or to reorient stems displaced by wind or other environmental forces (Groover 2016). Tension wood can accelerate cell division, prolong CA and, related to this, increase the tree-ring width (Groover, 2016, Jourez et al. 2001, Abedini et al. 2015). Therefore, to detect possible anomalies induced by tension wood, we also tested the difference in tension wood presence between years. On the cross-sections taken at the end of each growing season (2017 and 2018), the proportion of tension wood was measured on the final widths of xylem increments. For this purpose, the measurement frame was determined; the tangential width of the frame was about 2 mm and the radial width was the width of the final xylem ring. Within the frame (F), areas with tension wood were marked (TV_A), and then the proportion of tension wood ($TV_{\%}$) was calculated as follows:

$$TV_{\%} = \left(TV_A {}^*100\right)/F \tag{1}$$

Loss of canopy greenness

Loss of canopy greenness at day t (x_t) in late-summer and autumn was determined following the method of Vitasse et al. (2011) using data on the percentage of leaves that had changed color (α_t) and had fallen (β_t) (Eq. (2)):

$$x_t = \frac{\alpha_t \times (100 - \beta_t)}{100} + \beta_t \tag{2}$$

α_t and β_t were estimated weekly from late August until late November by visual assessment, except during the first half of the assessment in 2017, when a combined rating of α_t and β_t was used (for details see Mariën et al. 2019 and Dox et al. 2020).

Estimation of photosynthetic uptake, relative extractable water and drought stress with CASTANEA

Daily values of photosynthetic uptake (gross primary production, GPP) and relative extractable water (REW, the ratio of actual to maximum plant extractable water) were estimated with the CASTANEA model (Dûfrêne et al. 2005). CASTANEA is a stand process-based model which simulates seasonal dynamics at a half-hourly or daily scale, comprising also REW and the relationship between REW and photosynthesis or wood growth (Guillemot et al. 2014). CASTANEA has been used extensively for modeling photosynthesis and productivity (Delpierre et al. 2012, Guillemot et al. 2014), and also for simulations of seasonal wood growth and its relationship with GPP (Guillemot et al. 2014), in deciduous temperate species. CASTANEA has been validated for beech and oak stands growing on sites with similar climate to our study sites (Davi et al. 2008, Delpierre et al. 2012, Guillemot et al. 2014). However, note that CASTANEA has not been specifically validated at the study sites reported here. The model was run using two parameterizations for the plant maximum extractable water, namely 80 and 200 mm, in order to obtain a range of plausible REW values. For beech and oak, GPP and transpiration are typically affected by drought stress when REW is below 0.4 and more severely when REW drops below 0.2 (Breda et al. 2006, Granier et al. 1999). Wood growth is also more sensitive to drought than GPP (Delpierre et al. 2016a, Guillemot et al. 2014). Site meteorological and environmental data were used as model input. The CASTANEA model was also used to simulate stomatal conductance and a yearly cumulative index of the daily intensity of water stress applied to stomata named diffstress:

$$\text{diffstress} = \max(0, (0.4 - \text{REW})/0.4 \tag{3}$$

The higher the yearly cumulative index of diffstress is, the more the stomata were closed due to soil water shortage.

Data analysis

Determination of cessation of wood formation We defined the timing of completed wood formation as the date when the percentage of thickening cells was <0.5% and such percentage stayed below this threshold for the subsequent period of at least 3 weeks. Tests on a large dataset (Dox et al. 2020) showed that lower thresholds (e.g., 0.1%) were less suitable as they enhanced the impact of outliers, noises (e.g., caused by heterogeneous growth patterns of the sampled tree stem) and the very marginal role played by sporadic cells still active in late autumn. The consideration of a 3-week period with thickening cells <0.5% avoids associating cessation of wood formation with temporary short periods of limited growth due to the current environmental conditions.

Statistics All statistical analyses were performed in R version 3.2.2 (R Development Core Team 2013). If not otherwise specified, the analyses performed met the normality and variance homogeneity criteria.

The date of the cessation of wood formation for a stand was obtained by averaging data from the different trees. To test for significant difference in the cessation of wood formation date for the same species between the 2 years, a repeated measurements ANOVA was performed. Differences between species were tested for each year separately. The residuals were not normally distributed, therefore a Wilcoxon test was used. Statistically, it might have been preferable to derive a confidence interval by performing a nonparametric bootstrap for each stand. However, this method was inadequate for 2017 because we only measured four trees in that year, with multiple trees ceasing their wood formation on the same date. A comparison between our conservative method and the nonparametric bootstrap was done on the eight trees in 2018. This exercise showed that the latter method gave very similar confidence intervals (CI) for beech (24 vs 23 days) and slightly smaller CI for oak (15 vs

19 days) (Table S1 available as Supplementary data at *Tree Physiology* Online).

To check for significant differences in the percentage of wall-thickening cells between consecutive sampling events within 1 year in the period between late August and late November, for the same species, we used pairwise t-test to correct for nonhomogeneity of variances or pairwise Mann–Whitney U tests when the residuals were not normally distributed. Repeated measurements ANOVAs (in 18% of the cases after a log-transformation to ensure normality of the residuals and homogeneity of variances) were performed to compare the percentage of wall-thickening cells for each sampling week in 2017 and 2018, separately. This comparison was made only for those dates when >90% of the trees finished CA.

A one-way repeated measurements ANOVA was used to check for significant difference in wood traits, namely year ring width, percentage of fibers, fiber wall thickness, percentage of tension wood, vessel size and density between the years 2017 and 2018.

Results

Weather data and drought stress

The average daily temperature was very similar over the 2 years with 11.1 and 11.8 °C in 2017 and 2018, respectively. Both years were warmer than the long-term average of 10.5 °C (period 1981–2010; Royal Meteorological Institute (RMI) Antwerp). Compared with a long-term average of 16.1 °C, the average temperature from May to July was 17.8 and 18.8 °C in 2017 and 2018, respectively. Compared with a long-term average of 14.7 °C, the average temperature from August to October was 15.2 and 15.8 °C in 2017 and 2018, respectively (RMI Antwerp).

The total precipitation in 2017 was 846 mm and in 2018 723 mm compared with the long-term of 852 mm (period 1981–2010; RMI Antwerp). The difference in precipitation between years is more pronounced when analyzed seasonally. From May to July, the precipitation was 215 mm in 2017 and 112 mm in 2018. From August to October, the precipitation was 217 mm in 2017 and 179 mm in 2018. The precipitation in the months May, June and July 2018 was extraordinarily low (RMI Antwerp). Solar radiation was 10.3 MJ m^{-2} and 13.9 MJ m^{-2} in 2017 and 2018, respectively (Figure 3). The severe drought of 2018 was not only evident from the meteorological data (see above), but also from the modeled yearly cumulative index of water stress intensity to the stomata (Figure 3). In 2018, this index was the highest in the last 22 years (since 1996, excluding 2015 and 2016 when meteorological data were not available to run the model; Figure 4). Relative extractable water showed a sharp decline in mid-June in 2018 and in late May in 2017. In 2018, REW dropped below 0.4 in mid-July and was maintained below this threshold throughout the summer until mid-November. In July–August 2018, the REW went below 0.2. On the other hand, in 2017, REW was below 0.4 for only a few days in July and between late August and mid-September, and was never below 0.2. The REW values in 2018 are very similar to the REW values during the record drought of 2003 (Figure S3 available as Supplementary data at *Tree Physiology* Online).

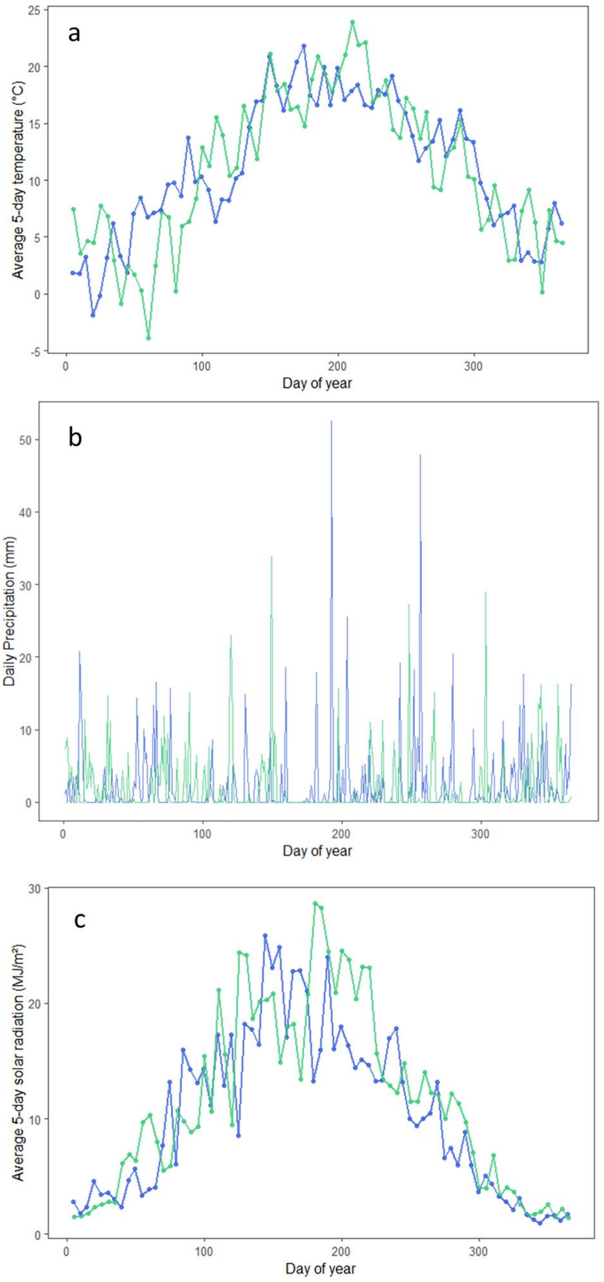

Figure 3. (a) Average 5-day temperature, (b) average 5-day solar radiation and (c) daily precipitation. Temperature, precipitation and radiation are from measurements.

Cessation of CA

For beech, the timing of cessation of CA (early September) was similar for both years. For oak, the date when all trees had ceased CA was different between years, with 2018 showing earlier cessation. In fact, all trees had ceased CA by early September in 2018 and by late October in 2017 (Figure 5). The very prolonged CA in 2017 was due to only one tree. However, the same tree stopped CA 50 days earlier in 2018, showing a very clear difference in behavior between years. No clear relationship was observed between the modeled REW and the CA of the trees (Figure S4 available as Supplementary data at *Tree Physiology* Online).

Late season decline in wall-thickening cells

In 2017, the first sampling after >75% of trees had completed CA ($n \geq 3$) was associated with a low percentage of wall-thickening cells, varying from 3.5% for beech to 5.4% for oak (Figure 6). For the following sampling dates, the percentage of wall-thickening cells remained constant until late September in beech, with a significant decline only afterwards. In contrast, oak presented higher percentage of wall-thickening cells (ca 2%) till the end of October, with full differentiation in mid-November. In 2018, the first sampling (after >75% of trees had completed CA) for oak was associated with a lower percentage of wall-thickening cells than in 2017 (ca 27 September; $P = 0.039$, Table S2 available as Supplementary data at *Tree Physiology* Online). For beech, the difference in percentage of wall-thickening cells between years for the first sampling (after >75% of trees had completed CA) was not significant (ca 7 September; $P = 0.40$) (Table S2 available as Supplementary data at *Tree Physiology* Online). In contrast to 2017, both species presented a more gradual decline in percentage of wall-thickening cells in 2018. Overall, very similar results were obtained when using the width of the layer of wall-thickening cells instead of the percentage (Figure S1 available as Supplementary data at *Tree Physiology* Online).

Growing season xylogenesis for 2018

The enlargement zone started to be visible in early May for beech and early April for oak. For both species, the wall-thickening period started 2 weeks afterwards. The progression of the enlarging cell width was similar for the two species, with decline in July and disappearance in August. The only difference was a peak in enlarging cell width for oak in early season, around the end of April, whereas the peak in enlarging cells in beech was near the end of May. A similar pattern was observed for the progression of the wall-thickening period. Whereas the wall-thickening development was similar between species in the second half of the growing season (with completion of wall cell thickening in late September for beech and early October for oak), oak showed an early season peak, with larger width of the wall-thickening area in May and early June. Similarly, an early activity for oak was observed in the progression of the matured zone. For oak, the latter started and stopped to increase in end May and early August, respectively. For beech, the same occurred in early June–July and the end of September, respectively (Figure 7).

Cessation of wood formation and tree-ring width

In the year 2017, cessation of wood formation was first observed in beech at the beginning of October and a month later ($P = 0.032$) in oak. In 2018, the order stayed the same. However, wood growth ceased earlier in both species: at the end of September for beech and at the beginning of October for oak ($P = 0.027$). The difference between years was only significant for oak (Table 1, Table S3 available as Supplementary data at *Tree Physiology* Online). Interindividual variability in timing of cessation of wood formation was very high. If we consider data from 2018 (when the number of replicates was 8), we observe a range of 29 and 42 days for beech and oak, respectively. This resulted in larger CI for oak than for beech. For both species, no significant differences in tree-ring width were found between 2017 and 2018 (Table 2). No clear relationships between cessation of wood formation and REW was found (Figure S4 available as Supplementary data at *Tree Physiology* Online).

Fiber wall thickness, fiber percentage, vessel size and density, tension wood

For both species, no significant difference was found in fiber percentage in the terminal part of the growth ring increment between 2017 and 2018 (Table 3). There was a significant difference in fiber cell wall thickness of the last 25% formed cells of the year ring for both species. The fiber cell wall thickness of beech was smaller in the year 2018 ($P < 0.0001$). In contrast, the fiber cell walls of oak were thicker in the year 2018 compared to 2017 ($P = 0.0001$) (Table 2). The percentage of vessel area over the whole annual ring in oak was 17.3 ± 1.3% in 2017 and 16.2 ± 1.5% in 2018 ($P = 0.71$). The mean percentage of conductive area within the xylem in beech was 32.5 ± 1.5% in 2017 and 31.0 ± 2.7% in 2018 ($P = 0.91$) (Figure S5 available as Supplementary data at *Tree Physiology* Online). For beech, the mean vessel area did not change between 2017 and 2018 ($P = 0.82$; comparable data for oak were not available). We also did not observe a significant difference in percentage of tension wood between years in either species ($P = 0.6546$ for beech and $P = 0.22511$ for oak; Figure S6 available as Supplementary data at *Tree Physiology* Online).

Photosynthetic uptake and loss of canopy greenness

For both species and years, GPP increased sharply around day of year (DOY) 100–122 (i.e., following bud-burst) and reached its maximum in early June. In 2017, GPP decreased for both species (independently of the plant's extractable water parameterization) in late June and early July, and recovered in early August (Figure 8). In 2018, GPP decreased significantly from early July, reaching a minimum in early August. Such

Table 1. Dates (expressed as DOY, day of year) of cessation of wood formation in 2017 and 2018 for individiual trees of the beech and oak stands, with confidence interval (CI) and level of significance for comparison between years.

Species	Year	Tree	Wood formation cessation (DOY)	Range wood formation cessation (DOY)	Mean date (DOY)	SE. date	Sign. diff. between years
Beech	2017	1	300	298–303	278	8	0.73
		2	268	263–271			
		3	268	263–271			
		4	274	271–277			
	2018	1	272	268–276	268	3	
		2	287	283–290			
		3	272	268–276			
		4	258	255–262			
		5	265	262–268			
		6	272	268–276			
		7	265	262–268			
		8	258	255–262			
Oak	2017	1	300	291–303	305	1.8	0.012
		2	307	303–311			
		3	307	303–311			
		4	307	303–311			
	2018	1	287	283–290	282	5	
		2	283	276–290			
		3	279	276–283			
		4	272	268–276			
		5	272	268–276			
		6	279	276–283			
		7	314	311–318			
		8	272	268–276			

Table 2. Mean ring width (in μm) and standard error for each stand in 2017 (n=4) and 2018 (n=8) with the significance level (p) of their difference. Data in parenthesis represent values when considering only the same trees (n=4) in both years.

Stand	Mean width 2017	SE width 2017	Mean width 2018	SE width 2018	*P*-value
Beech	1499	406	1767 (1422)	247.6 (408.7)	0.83 (0.90)
Oak	1724	158	1412 (1468)	455.1 (232.5)	0.21 (0.37)

Table 3. Mean and standard error of observed fiber percentage and fiber-wall thickness in the last 25% portion of the year ring per stand (n = 4 in 2017 and 2018).

Species	Year	Measurement	Mean and SE (% or nm)
Beech	2017	Fiber %	67.59 ± 1.49
	2018	Fiber %	68.10 ± 2.65
Oak	2017	Fiber %	30.69 ± 2.27
	2018	Fiber %	33.90 ± 4.25
Beech	2017	Cell wall thickness (nm)	4.24 ± 0.73
	2018	Cell wall thickness (nm)	4.04 ± 0.68
Oak	2017	Cell wall thickness (nm)	3.88 ± 0.55
	2018	Cell wall thickness (nm)	4.16 ± 0.65

minimum was characterized by very low values of daily GPP (almost reaching zero with the 80 mm plant extractable water parameterization) and lower than the minimum values in 2017 (Figure 8). In 2018, normal values were recovered from late August when small rain events rewetted the upper part of the soil profile enough to reopen stomata (Figure 3c). For both years, the end-of-season decline of GPP progressed gradually till early November (Figure 8). Also, for both years, the GPP reductions in June, July and August closely matched the seasonal decline of REW, with no marked differences between species (Figure 8). Simulations of stomatal conductance also showed that stomatal regulation of both species closely followed the

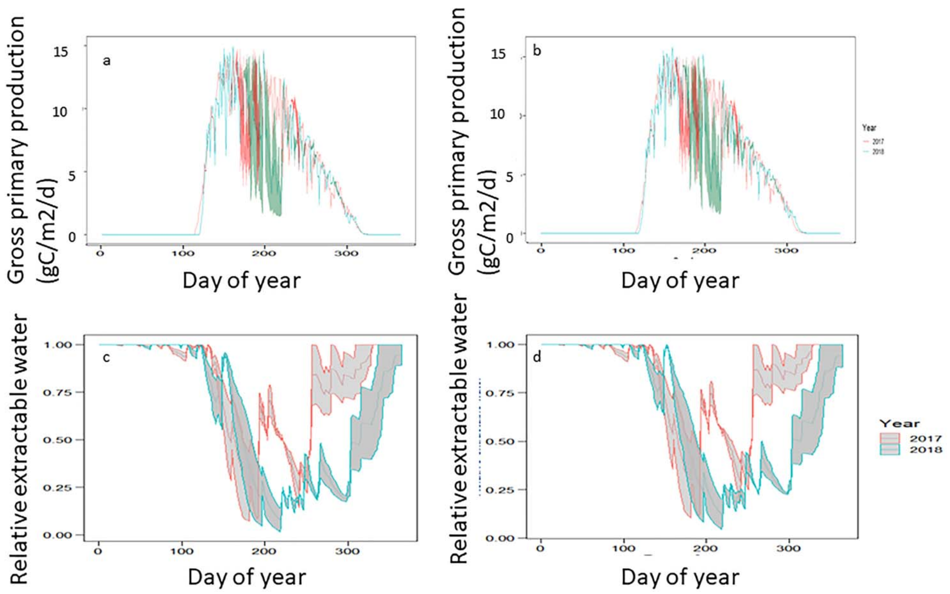

Figure 4. The yearly cumulative index of water stress intensity to the stomata for the beech stand simulated by the CASTANEA model. The error bars represent the variability according to the model parameterization of the soil extractable water reserve (see text).

temporal pattern of REW (Figure S7 available as Supplementary data at *Tree Physiology* Online). The only noticeable difference is that beech appears to have slightly larger values of stomatal conductance both in case of ample water availability (e.g., for 2017, mean values of canopy stomatal conductance for second half of May were 16,900,000 and 14,400,000 mmol(H_2O) m^{-2} day^{-1},for beech and oak, respectively; Figure S7 available as Supplementary data at *Tree Physiology* Online) and drier conditions (e.g., for 2017, mean values of stomatal conductance for second half of August were 12,800,000 and 11,900,000 mmol(H_2O) m^{-2} day^{-1}, for beech and oak, respectively; Figure S7 available as Supplementary data at *Tree Physiology* Online). It is important to note that, for both species, GPP in 2017 was up to 15% larger than in 2018 (Table S4 available as Supplementary data at *Tree Physiology* Online).

For both species and years, the loss of canopy greenness was low (<25%) until the end September, but it increased sharply afterwards, particularly in November. Differences between species were minor in 2017. In 2018, differences between species were also not substantial except a period of ca 3 weeks in late September and early October, when beech showed a range of about +10% and + 25% in loss canopy greenness compared to oak (Figure 9).

Discussion

Our key hypothesis stated that autumn xylogenesis of late successional deciduous species of the temperate zone would be influenced by early-summer drought (e.g., late June, July and early August), resulting in advanced cessation of CA and wood formation. The results obtained suggest to accept the hypothesis for oak, but not for beech.

Oak

An earlier cessation of CA due to drought was observed in oak in 2018, resulting in an earlier cessation of wood formation that year. In fact, cessation of CA and of wood formation were 3 weeks earlier in 2018 compared with 2017. Our key hypothesis is further supported by our observation of percentage of wall-thickening cells, which was lower in the late summer of 2018 compared with 2017. No clear relationship could be found between the REW and both cessation of CA, or cessation of wood formation, but this might be due to the fact that only 2 years were investigated, and to the lack of site measurements of plant extractable water to parameterize the model. Wood formation is hampered by reduced water potential (Hsiao 1973, Guillemot et al. 2014, Körner 2015). Furthermore, an earlier cessation of wood formation under drought could be promoted by changes in carbon allocation toward bud formation, fine root growth or storage (Eilmann et al. 2011, Campioli et al. 2013, Delpierre et al. 2016*b*, Fernández-de-Uña et al. 2017). Reduced growth due to carbon limitation might also be possible because GPP was lower in 2018.

Contrary to our key hypothesis, our complementary hypothesis proved not to be true for oak. The earlier cessation of wood formation was not associated with lower fiber percentage or thinner fiber cell walls in the year 2018, because no difference was found in fiber percentage between the years and we even observed a thicker fiber cell wall in 2018. We consider the

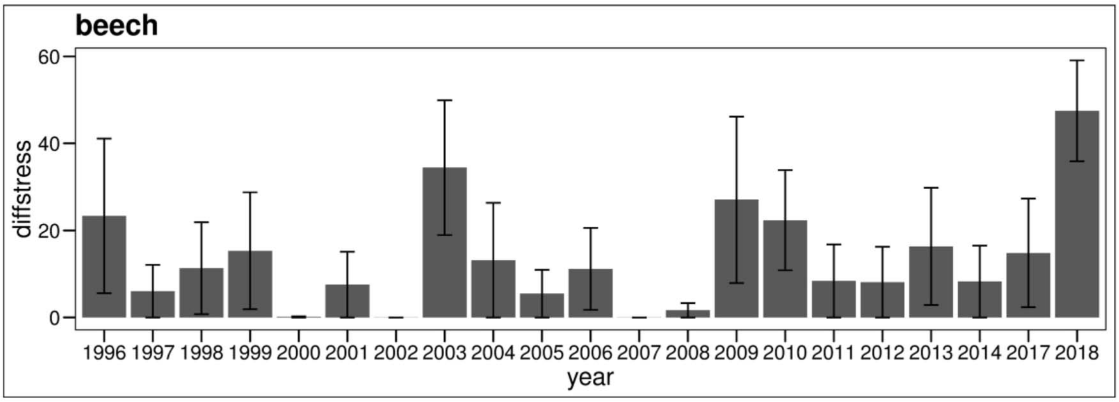

Figure 5. Percentage of trees still in cambial activity (CA) for 2017 (blue) and 2018 (red) for (a) beech and (b) oak. Percentages are based on observations on four trees in 2017 and eight trees in 2018, except that during the first sampling event of beech in 2018 also only four trees were sampled. Data for beech around DOY 220 are not available (NA) for 2017.

possibility that the observed thicker fiber walls in the last part of the xylem increment (i.e., 25% of the last formed cells) in the 2018 ring of oak was the result of an earlier maturation of these cells (early autumn, compared with late autumn) when temperatures were still high (Begum et al. 2012, Gricar et al. 2015).

Beech

For beech, CA stopped in both years around the same date (ca DOY 250). The cessation of wood formation occurred about 10 days earlier in the year 2018. However, this difference was not significant. It is possible that such lack of significant difference was related to the low statistical power due to the large intertree variability for this phenophase (Table 1). Such high variability is not uncommon in xylogenesis studies (Sass-Klaassen et al. 2011).

On the other hand, the complementary hypothesis appeared to be partially true for beech as cells in 2018 were thinner than in 2017. This has already been observed in coniferous species. Eilmann et al. (2011) found that nonirrigated Scots pine (*Pinus sylvestris*) had thinner cell walls compared with irrigated trees. However, in that study the nonirrigated individuals still had a shorter period of wood formation and a lower increment compared with the control group.

There is also the possibility of a drought lag effect to 2019, influencing the growth of the next year. The more severe the drought, the larger the lag effect (Kannenberg et al. 2020). Dendroecological studies have found smaller tree-rings than the climate would predict in a year after a drought (Bréda 2004). However, different species have a different recovery response, which is linked to physiological trade-off (Peltier et al. 2016). For beech, a lag response could be due to hydraulic reasons, especially because beech relies on the vessels of the previous year (which could be damaged by cavitation) in next spring. Also, beech could present a carry-over effect on next year growth due to lower carbohydrate production in the dry year (Bréda et al. 2006, Vanhellemont et al. 2019).

Interspecies differences

It is not unexpected that the drought effect on autumn wood formation was most prominent in oak, as pedunculate oak is among the species less competent in dealing with summer droughts. The pedunculate oak, as a ring-porous species, stops CA as a result of drought and does not resume it afterwards (van der Werf et al. 2007). Resumption of CA has been observed in the evergreen Holm oak (*Q. ilex*) (Campelo et al. 2007), however, this is a semi-ring-porous species in the Mediterranean climate (Campelo et al. 2010). To our knowledge, no observations of cambial reactivation after drought have been made on ring-porous trees in the temperate zone. On the other hand, our study shows that, even if the drought started in early July, CA only stopped in early September. This indicates that wood formation dynamics in the pedunculate oak can withstand extended drought stress. Although cessation of CA and wood formation occurs earlier in beech than in oak, beech (which is also not considered a drought tolerant species) appeared less affected than oak by the 2018 drought when considering late season wood phenology. The larger drought sensitivity of oak in our study might simply be due to its ring-porous character and larger vulnerability to cavitation of the early wood vessels (Taneda and Sperry 2008), precluding water transport and triggering an earlier cessation of CA and wood formation, even if drought does not affect vessel size and density of current year, as we have shown. However, contrasting reports exist on this, showing higher drought tolerance for oak rather than beech in both ecophysiological branch studies on loss of hydraulic conductivity (Hajek et al. 2016, Lobo et al. 2018) or dendroecological studies on growth decline after a severe drought (Meyer et al. 2020). Carry-over effects

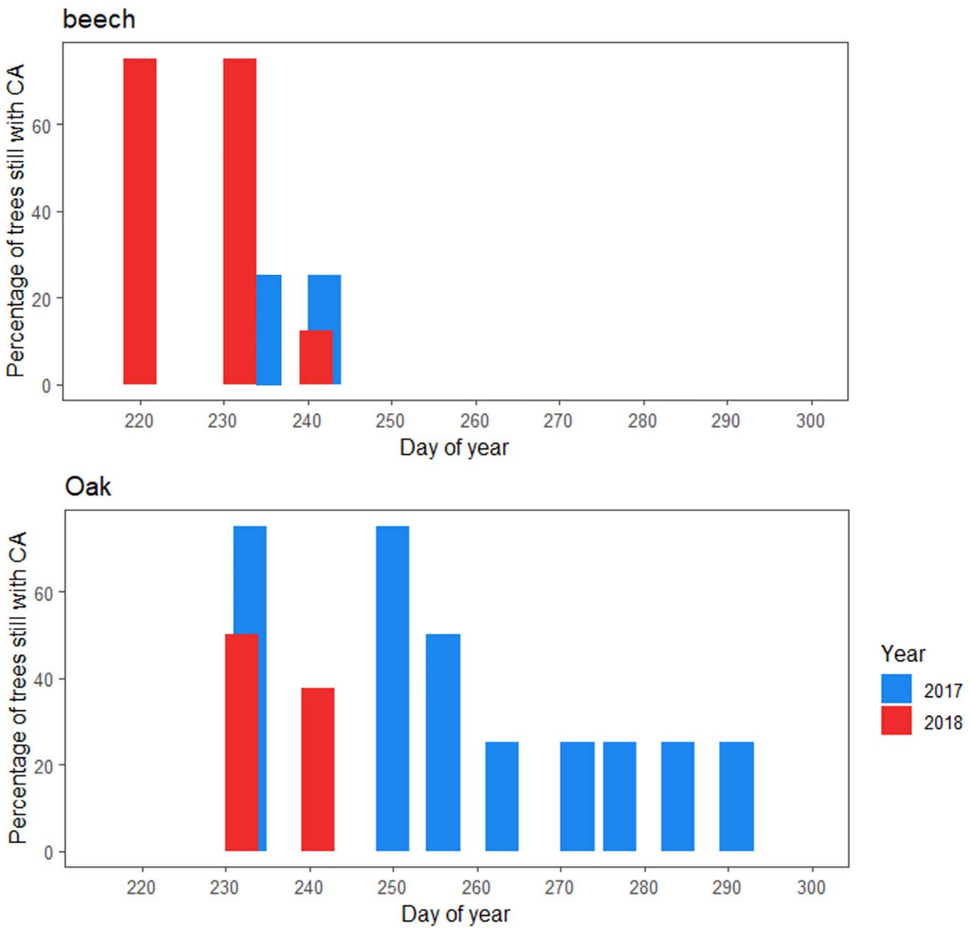

Figure 6. Percentage of xylem cells in the wall-thickening phase in late summer and autumn (points represent the mean and error bars represent the standard error of the mean) and the timing of cessation of wood formation for (a, c) beech and (b, d) oak in 2017 (blue) and 2018 (red). The vertical lines (with standard error of the mean as bands) represent cessation of wood formation for the 2 years. The gray zone on the left indicates the period when >25% of the trees still showed cambial activity. The inner panels provide details for the key period with $n \geq 3$ (before not all trees were measured as the cambium was still forming xylem cells). Different letters indicate significant differences in the percentage of xylem cells in the wall-thickening phase among the sampling events.

on the next year growth (see above) might be more relevant for beech than oak. Also, it is possible that the larger drought effects observed here for oak might not be due to differences in drought sensitivities between species but to the fact that oak, having a longer growing season (see data for 2017), might simply be more negatively impacted because of longer exposure to the drought (note that drought stress was simulated to be present until early November in 2018, see above).

The fact that autumn phenology in beech is more conservative across years also suggests that this species might be more responsive than oak to light characteristics (e.g., photoperiod, Fu et al. 2019), which indeed do not vary across years. The fact that the 2018 drought had no impact on tree-ring width can be explained by the good starting conditions and a very fast cell production in early spring, late March and April (D'Orangeville et al. 2013, van der Werf et al. 2007). A previous study, conducted in the Netherlands for both the European beech and pedunculate oak during the drought of 2003, did not find unusually narrow rings either (van der Werf et al. 2007). Furthermore, a study on dendrometer growth of the DendroGlobal consortium found that the 2018 European heatwave led to stem dehydration, but not to consistent growth reductions (Salomon et al. 2020).

Concerning differences in carbon assimilation between years, the slightly larger values of stomatal conductance for beech might support a more anisohydric behavior for this species than for oak (Tulik 2014, Cocozza et al. 2016). However, the two species show in general similar photosynthetic activity. Because of this, the larger values of annual GPP observed for oak might therefore be due solely to the different spring phenology and earlier start of photosynthetic uptake for oak. CASTANEA did not capture the earlier loss of canopy greenness recorded for beech in late September–early October. However, during this

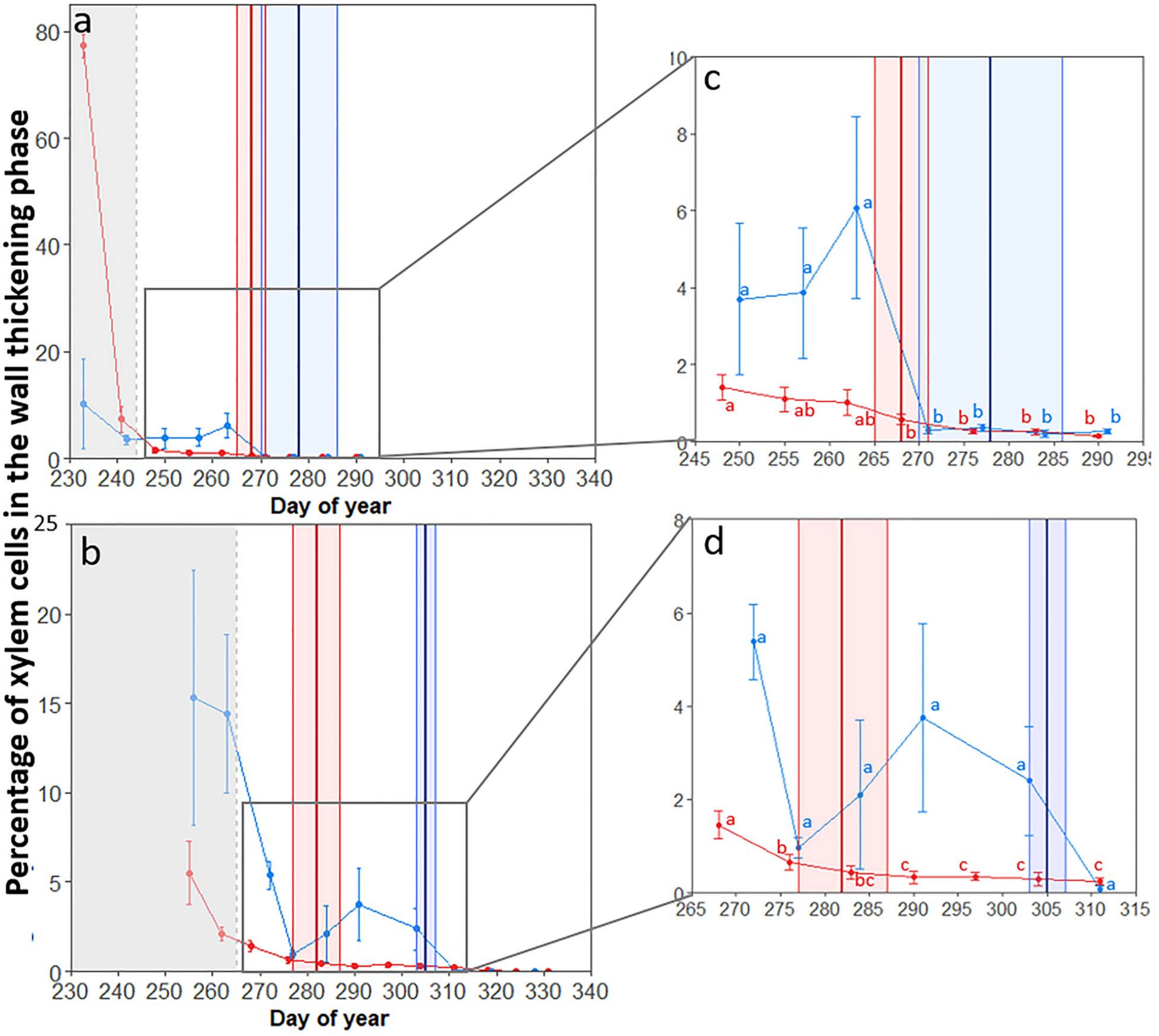

Figure 7. Band width of enlarging, wall-thickening and mature zones over the 2018 growing season of (a) European beech (*Fagus sylvatica*) and (b) pendunculate oak (*Quercus robur*) in Belgium. In red: the width of the current forming ring section with enlarging cells (enlarging zone); in green: the width of the wall-thickening zone; and in blue: the width of the matured cells. Points are means ($n = 4$) and the associated error bars represent the standard errors of the means.

period, photosynthetic rate is low, on average 25% of the annual maximum (Way et al. 2017). Therefore, in this period, we do not expect major influences of leaf shading (possibly associated with cavitation) on assimilation.

Legacy effects of spring xylogenesis

The CASTANEA model provided also simulations of bud-burst for both years. For beech, bud-burst occurred on DOY 114 and 120 for 2017 and 2018, respectively. For oak, for the same years, it occurred on DOY 100 and 109, respectively. The relationship between bud-burst and cambial reactivation is not expected to vary significantly among years for the study species. For beech, bud-burst and cambial reactivation are concurrent (Prislan et al. 2013) even for years with different meteorological conditions (Andrianantenaina 2019). For pedunculate oak, cambial reactivation occurs at our site four weeks before bud-burst (Marchand et al. 2020), which is similar to what observed for other temperate oak species (Gričar et al. 2017). Therefore, we can assume that, compared with 2017, wood growth started around 1 week later in 2018 for beech and 10 days later for oak, which might be related to the colder conditions in late March 2018 (Figure 3). A later start of xylogenesis might result in less cambial cells formed and

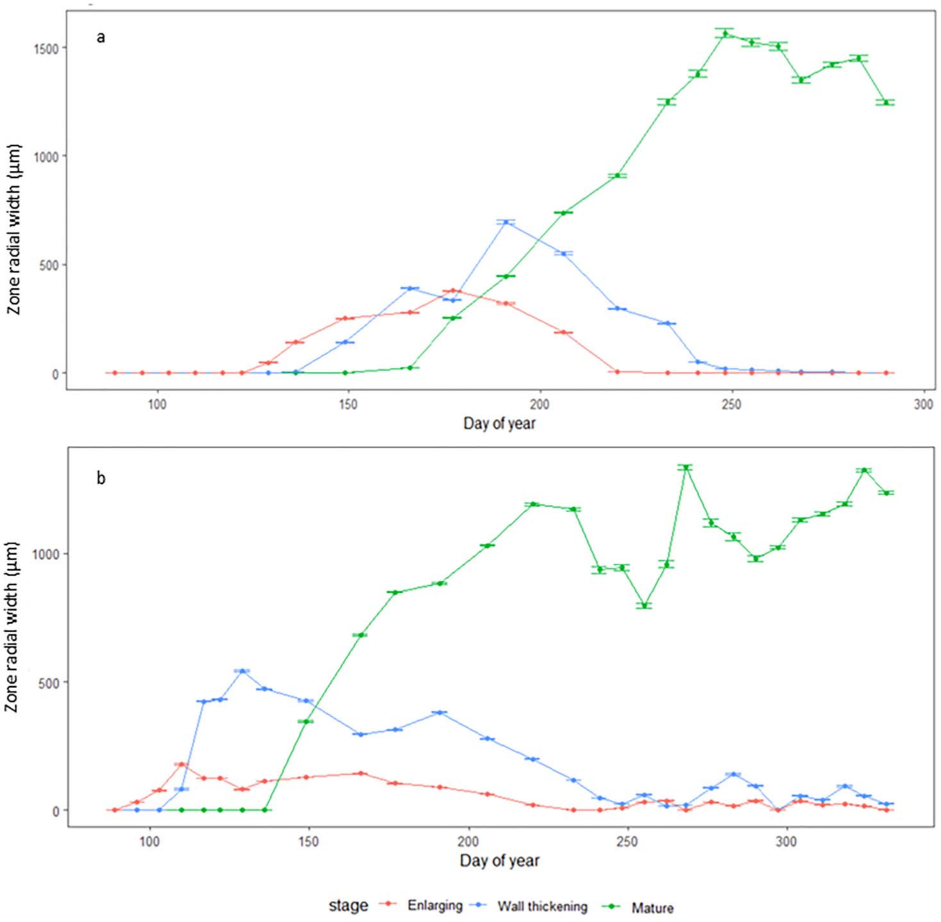

Figure 8. (a) Gross primary production (GPP) of beech in 2017 (red) and 2018 (green); (b) GPP of oak in 2017 and 2018; (c) relative extractable water (REW) of the beech site in 2017 and 2018; (d) REW of the oak site in 2017 and 2018. The gray zone shows the value range obtained using simulations with extractable water reserve of 200 and 80 mm, whereas the line shows the mean.

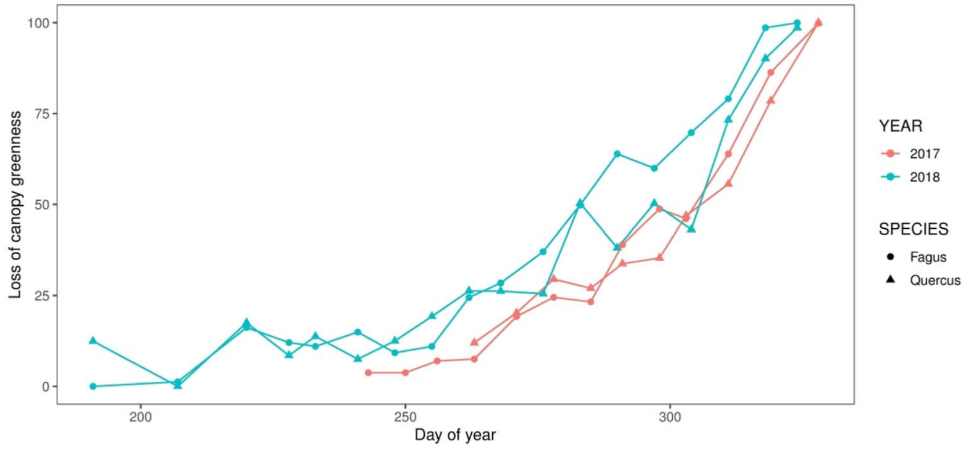

Figure 9. Loss of canopy greenness estimated through the percentage of leaves that had changed color and the percentage of fallen leaves following Vitasse et al. (2011). Circles: beech; triangles: oak; 2017 is displayed in red, 2018 in green.

a shorter maturation period. Although this might explain the nonsignificant advance of wood formation cessation in beech, it would not explain alone the 3 weeks advance in wood formation cessation recorded for oak. Moreover, this argument would also not explain why CA stopped earlier in oak in 2018. Therefore, the evidence provided supports the fact that the autumn differences observed between 2017 and 2018 could not be explained solely by possible legacy effects due to interannual differences in the spring xylogenesis. In other words, the effect of summer conditions (drought) must have played a key role in any case (D'Andrea et al. 2020).

Conclusions

In late season, ring-porous species might be more sensitive to drought legacy for timing of both cessation of CA and cessation of wood formation, but maintain (and even promote) fiber wall thickness. On the other hand, diffuse-porous species subjected to drought do not advance timing of cessation of CA and wood formation but reduce fiber wall thickness. This pattern might indicate contrasting life strategies: favoring fewer but thicker xylem cells for ring-porous species, whereas more but thinner cells for diffuse-porous species.

Supplementary data

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

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Conflict of interest

None declared.

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References

Abedini R, Clair B, Pourtahmasi K, Laurans F, Arnould O (2015) Cell wall thickening in developing tension wood of artificially bent poplar trees. IAWA J 36:44–57.

Andrianantenaina A (2019) Dynamiques intra-annuelles de la séquestration du carbone dans le bois des feuillus et des résineux en forêts tempérées PhD thesis. AgroParisTech.

Arend M, Fromm J (2007) Seasonal change in the drought response of wood cell development in poplar. Tree Physiol 27:985–992.

von Arx G, Crivellaro A, Prendin AL, Čufar K, Carrer M (2016) Quantitative wood anatomy—practical guidelines. Front Plant Sci 7:781.

Balducci L, Cuny HE, Rathgeber CBK, Deslauriers A, Giovannelli A, Rossi S (2016) Compensatory mechanisms mitigate the effect of warming and drought on wood formation. Plant Cell Environ 39:1338–1352.

Begum S, Nakaba S, Yamagishi Y, Yamane K, Islam MA, Oribe Y, Ko J-H, Jin H-O, Funada R (2012) A rapid decrease in temperature induces latewood formation in artificially reactivated cambium of conifer stems. Ann Bot 110:875–885.

Bréda N (2004) Understanding time lag effects of the drought 2003 on physiological and phenological behaviour in oak and beech trees. In: Impacts of the drought and heat in 2003 on forests.

Bréda N, Huc R, Granier A, Erwin D (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 62:625–644.

Brus DJ, Hengeveld GM, Walvoort DJJ, Goedhart PW, Heidema AH, Nabuurs GJ, Gunia K (2012) Statistical mapping of tree species over Europe. Eur J For Res 131:145–157.

Cabon A, Peters R, Fonti P, Martinez-Villalta J, De Cáceres M (2020) Temperature and water potential co-limit stem cambial activity along a steep elevational gradient. New Phytol 226:1325–1340.

Campelo F, Gutiérrez E, Ribas M, Nabais C, Freitas H (2007) Relationships between climate and double rings in *Quercus ilex* from Northeast Spain. Can J For Res 37:1915–1923.

Campelo F, Nabais C, Gutiérrez E, Freitas H, García-González I (2010) Vessel features of *Quercus ilex* L. growing under Mediterranean climate have a better climatic signal than tree-ring width. Trees Struct Funct 24:463–470.

Campioli M, Verbeeck H, Van den Bossche J, et al. (2013) Can decision rules simulate carbon allocation for years with contrasting and extreme weather conditions? A case study for three temperate beech forests. Ecol Model 263:42–55.

Cocozza C, de Miguel M, Pšidová E, Ditmarová L, Marino S, Maiuro L, Alvino A, Czajkowski T, Bolte A, Tognetti R (2006) Variation in Ecophysiological Traits and Drought Tolerance of Beech (Fagus sylvatica L.) Seedlings from Different Populations. Ecological letters 7:886.

Cuny HE, Rathgeber CBK (2016) Xylogenesis: coniferous trees of temperate forests are listening to the climate tale during the growing season but only remember the last words! Plant Physiol 171: 306–317.

Cuny HE, Rathgeber CBK, Frank D et al. (2015) Woody biomass production lags stem-girth increase by over one month in coniferous forests. Nat Plants 1:1–6.

Davi H, Ibanez T, Gillmann M, Gillmann M, Cailleret M, Amm A, Cecchini S, Ulrich E (2008) Budburst of european beech in Ventoux forest: a modelling approach of trade-off between carbon input and frost risks. IUFRO International Beech Symposium, Sep 2008, Hokkaido, Japan. 4 p. ffhal-02818124f.

D'Andrea E, Rezaie N, Prislan P, Gričar J, Collalti A, Muhr J, Matteucci G (2020) Frost and drought: Effects of extreme weather events on stem carbon dynamics in a Mediterranean beech forest. Plant, Cell & Environment 43(10):2365–2375.

D'Orangeville L, Côté B, Houle D, Morin H (2013) The effects of throughfall exclusion on xylogenesis of balsam fir. Tree Physiol 33:516–526.

Delpierre N, Berveiller D, Granda E, Dufrêne E (2016*a*) Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest. New Phytol 210: 459–470.

Delpierre N, Vitasse Y, Chuine I, Guillemot J, Bazot S, Rutishauser T, Rathgeber CBK (2016*b*) Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. Ann For Sci 73:5–25.

Dox I , Gričar J, Marchand L. J, Leys S, Zuccarini P, Geron C, Prislan P, Mariën B, Fronti P, Lange H, Peñuelas J, Van den Bulcke J, Campioli M (2020) Timeline of autumn phenology in temperate deciduous trees. Tree Physiology 00:1–13.

Duchesne L, Houle D (2011) Modelling day-to-day stem diameter variation and annual growth of balsam fir (*Abies balsamea* (L.) Mill.) from daily climate. For Ecol Manage 262:863–872.

Dûfrêne E , Davi H, François C, leMaire G, LeDantec V, Granier A (2005) Modelling carbon and water cycles in a beech forest: Part I: Model description and uncertainty analysis on modelled NEE. Ecological Modelling 185(1–4):407–436.

Eilmann B, Zweifel R, Buchmann N, Fonti P, Rigling A (2009) Drought-induced adaptation of the xylem in scots pine and pubescent oak. Tree Physiol 29:1011–1020.

Eilmann B, Zweifel R, Buchmann N, Graf Pannatier E, Rigling A (2011) Drought alters timing, quantity, and quality of wood formation in Scots pine. J Exp Bot 62:2763–2771.

Estiarte M, Peñuelas J (2015) Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. Glob Chang Biol 21:1005–1017.

Fernández ME, Gyenge JE, De Urquiza MM, Varela S (2012) Adaptability to climate change in forestry species: drought effects on growth and wood anatomy of ponderosa pines growing at different competition levels. For Syst 21:162.

Fernández-de-Uña L, Rossi S, Aranda I, Fonti P, González-González BD, Cañellas I, Gea-Izquierdo G (2017) Xylem and leaf functional adjustments to drought in *Pinus sylvestris* and *Quercus pyrenaica* at their elevational boundary. Front Plant Sci 8:1–12.

Forrest J, Miller-Rushing AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. Philos Trans R Soc 365:3101–3112.

Fu YH, Piao S, Zhou X, Geng X, Hao F, Vitasse Y, Janssens IA (2019) Short photoperiod reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but not in horse chestnut. Glob Chang Biol 25:1696–1703.

Galle A, Esper J, Feller U, Ribas-Carbo M, Fonti P (2010) Responses of wood anatomy and carbon isotope composition of *Quercus pubescens* saplings subjected to two consecutive years of summer drought. Ann For Sci 67:809.

Gallinat AS, Primack RB, Wagner DL (2015) Autumn, the neglected season in climate change research. Trends Ecol Evol 30: 169–176.

Granier A, Bréda N, Biron P, Villette S (1999) A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol Model 116:269–283.

Gričar J, Čufar K, Oven P, Schmitt U (2005) Differentiation of terminal latewood tracheids in silver fir trees during autumn. Ann Bot 95:959–965.

Gričar J, Zupančič M, Čufar K, Koch G, Schmitt U, Oven P (2006) Effect of local heating and cooling on cambial activity and cell differentiation in the stem of Norway spruce (*Picea abies*). Ann Bot 97: 943–951.

Gricar J, Prislan P, De Luis M, Gryc V, Hacurová J, Vavrčík H, Cufar K (2015) Plasticity in variation of xylem and phloem cell characteristics of Norway spruce under different local conditions. Front Plant Sci 6:1–14.

Gričar J, Lavrič M, Ferlan M, Vodnik D, Eler K (2017) Intra-annual leaf phenology, radial growth and structure of xylem and phloem in different tree parts of *Quercus pubescens*. Eur J For Res 136:625–637.

Groover A (2016) Gravitropisms and reaction woods of forest trees – evolution, functions and mechanisms.. New Phytologist 2113):790–802.

Guillemot J, Delpierre N, Vallet P, François C, Martin-StPaul NK, Soudani K, Nicolas M, Badeau V, Dufrêne E (2014) Assessing the effects of management on forest growth across France: insights from a new functional-structural model. Ann Bot 114:779–793.

Hajek P, Kurjak D, von Wühlisch G, Delzon S, Schuldt B (2016) Intraspecific variation in wood anatomical, hydraulic, and foliar traits in ten European beech provenances differing in growth yield. Front Plant Sci 7:791.

Hsiao TC (1973) Plant responses to water stress. Annu Rev Plant Physiol 24:519–570.

Jourez B, Riboux A, Leclercq A (2001) Comparison of basic density and longitudinal shrinkage in tension wood and opposite wood in young stems of Populus euramericana cv. Ghoy when subjected to a gravitational stimulus. Canadian Journal of Forest Research 3110):1676–1683.

Kannenber SA, Schwalm CR, Anderegg WRL (2020) Ghosts of the past: how drought legacy effects shape forest functioning and carbon cycling. Ecological letters 23(5):891–901.

Körner C (2015) Paradigm shift in plant growth control. Current Opinion in Plant Biology 25:107–114.

Larson P (1994) The vascular cambium – development and structure. Springer-Verlag, Berlin Heidelberg.

Liang E, Balducci L, Ren P, Rossi S (2016) Xylogenesis and moisture stress. In: Secondary xylem biology: origins, functions, and applications, pp 45–58.

Liu Q, Fu YH, Zhu Z, Liu Y, Liu Z, Huang M, Janssens IA, Piao S (2016) Delayed autumn phenology in the northern hemisphere is related to change in both climate and spring phenology. Glob Chang Biol 22:3702–3711.

Lobo A, Torres-Ruiz JM, Burlett R et al. (2018) Assessing inter-and intraspecific variability of xylem vulnerability to embolism in oaks. For Ecol Manage 424:53–61.

Lupi C, Morin H, Deslauriers A, Rossi S (2010) Xylem phenology and wood production: resolving the chicken-or-egg dilemma. Plant Cell Environ 33:1721–1730.

Marchand LJ, Dox I, Gričar J, Prislan P, Van den Bulcke J, Fonti P, Campioli M (2020) Timing of spring xylogenesis in temperate deciduous tree species relates to tree growth characteristics and previous autumn phenology. Tree Physiol (revisions).

Mariën B , Balzarolo M, Dox I, Leys S, Marchand L. J, Geron C, Portillo–Estrada M (2019) Detecting the onset of autumn leaf senescence in deciduous forest trees of the temperature zone. New Phytologist 221(1):166–176.

Meyer BF, Buras A, Rammig A, Zang CS (2020) Higher susceptibility of beech to drought in comparison to oak. Dendrochronologia 64:125780.

Peltier D, Fell M, Ogle K (2016) Legacy effects of drought in the southwestern United States: a multi-species synthesis. Ecol Monogr 86:262–390.

Peters R, Steppe K, Cuny H, de Pauw D, Frank DFC, Schaub M, Rathgeber CBK, Cabon A, Fonti P (2020) Turgor - a limiting factor for radial growth in mature conifers along an elevational gradient. New Phytol 229:213–229.

Plomion C, Leprovost G, Stokes A (2001) Wood formation in trees. Plant Physiol 127:1513–1523.

Prislan P, Koch G, Cufar K, Gričar J, Schmitt U (2009) Topochemical investigations of cell walls in developing xylem of beech (*Fagus sylvatica* L.). Holzforschung 63:482–490.

Prislan P, Gričar J, de Luis M, Smith K, Cufar K (2013) Phenological variation in xylem and phloem formation in *Fagus sylvatica* from two contrasting sites. Agric For Meteorol 180:142–151.

R Development Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rathgeber CBK, Cuny HE, Fonti P (2016) Biological basis of tree-ring formation: a crash course. Front Plant Sci 7:1–7.

Rossi S, Anfodillo T, Menardi R (2006*a*) Trephor: a new tool for sampling microcores from tree stems. IAWA J 27:89–97.

Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R, Borghetti M (2006*b*) Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol 170:301–310.

Royal Meteorological Institute (RMI Antwerp). http://www.meteo.be/nl/antwerp.

Saderi M, Rathgeber C, Rozenberg P, Fournier M (2019) Phenology of wood formation in larch (*Larix decidua* Mill.) trees growing along a 1000-m elevation gradient in the French Southern alps. Ann For Sci 76.

Salomon et al. (2020) The 2018 European heatwave led to stem dehydration but not to consistent growth reductions. In preparation for *Nat Clim Change*.

Sass-Klaassen U, Sabajo CR, den Ouden J (2011) Vessel formation in relation to leaf phenology in pedunculate oak and European ash. Dendrochronologia 29:171–175.

Swidrak I, Gruber A, Oberhuber W (2014) Xylem and phloem phenology in co-occurring conifers exposed to drought. Trees Struct Funct 28:1161–1171.

Taneda H, Sperry JS (2008) A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. Tree Physiol 28:1641–1651.

Tulik M (2014) The anatomical traits of trunk wood and their relevance to oak (*Quercus robur* L.) vitality. Eur J For Res 133:845–855.

Vanhellemont M, Sousa-Silva R, Maes S et al. (2019) Distinct growth responses to drought for oak and beech in temperate mixed forests. Sci Total Environ 650:3017–3026.

Verbančič J, Lunn JE, Stitt M, Persson S (2018) Carbon supply and the regulation of cell wall synthesis. Mol Plant 11:75–94.

Vitasse Y, François C, Delpierre N, Dufrêne E, Kremer A, Chuine I, Delzon S (2011) Assessing the effects of climate change on the phenology of European temperate trees. Agric For Meteorol 151:969–980.

Vitasse Y, Bottero A, Cailleret M et al. (2019) Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob Chang Biol 25:3781–3792.

Way D, Stinziano J, Berghoff H, Oren R (2017) How well do growing season dynamics of photosynthetic capacity correlate with leaf biochemistry and climate fluctuations? Tree Physiol 37:879–888.

van der Werf GW, Sass-Klaassen UGW, Mohren GMJ (2007) The impact of the 2003 summer drought on the intra-annual growth pattern of beech *Fagus sylvatica* and oak (*Quercus robur* L.) on a dry site in the Netherlands. Dendrochronologia 25:103–112.