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Tree-ring formation dynamics in *Fagus sylvatica* and *Quercus petraea* in a dry and a wet year

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Abstract: European beech *Fagus sylvatica* and Sessile oak *Quercus petraea* are reaching the north-eastern limits of their natural ranges in northern Poland. According to the projected changes in potential ranges in this region, climatic conditions for both species until 2080 will remain stable. On the other hand, a decrease in the vitality of mature trees and a reduction in their radial growth are currently observed. To understand these contradictory findings, we monitored the cambial activity in both species during two vegetation seasons. 2015 was characterized by a negative water balance, while 2017 was wet. This provided an opportunity to compare how the xylogenesis proceeds in diffuse-porous beech and ring-porous oak during contrasting in the summer precipitation seasons. The forming annual increments were sampled with Presler borer at variable time intervals depending on the leaf phenological phases. The cores were prepared using a sledge microtome and double-stained with safranin and astra blue. Observations of the phases of wood formation and measurements of the width of the forming increments were analysed on the microslide digital images. Differences in the dates of the phenological phases were analysed using Two-Way ANOVA, while the dynamics of the formation of annual increments were fitted to the Single and Double Gompertz function for beech and oak, respectively. The beginning of vessel formation started earlier in both seasons compared to previous studies. Inter-seasonal differences in the duration of spring phenological phases were insignificant for both species, while inter-species differences were significant due to physiological diversity between diffuse-porous beech and ring-porous oak. In dry 2015, cambial activity ceased sooner in both species than in 2017. Differences between oak and beech were insignificant in both years, but statistically significant disparities existed within each species due to varying in precipitation seasons. Rainfall significantly elongated the duration of cambial activity and caused wider tree-rings. According to our study, despite predicted maintaining their climatic niche, both species, situated at the north-eastern cooler range boundary, are expected to produce wood at a lower rate due to the projected warmer central European climate with increased heatwaves and summer droughts.

Keywords: climate change, meteorological extremes, wood formation, summer drought, xylogenesis

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Introduction

Knowledge of the seasonal pattern of leaf phenology and tree-ring formation is crucial for understanding how environmental conditions affect the growth processes of trees (Die et al., 2012; Gričar et al., 2020). Under the temperate climate of Europe, the onset of spring vegetation is primarily driven by late winter and early spring temperatures. Thus, winter warming observed in recent decades leads to an acceleration of phenology (Kolářová et al., 2014; Jabłońska et al., 2015), and the extension of the growing season (Gunderson et al., 2012). A warming in the early spring (February to April) by 1°C causes an advanced beginning of growing season of 7 days (Chmielewski & Rötzer, 2000). On the one hand, the extension of the vegetation season means that trees have more time to grow, but on the other hand, it poses the risk of prolonged exposure to extreme weather events. The warming climate causes the onset of cambial activity to be accelerated by several weeks compared to observations made several decades ago (Puchałka et al., 2017; Dow et al., 2022). The studies conducted in southern Europe have revealed that summer droughts lead to the premature cessation of cambial activity and tree mortality (Hacket-Pain et al., 2016; Colangelo et al., 2018; Prislan et al., 2019). On the other hand, severe summer droughts can lead to a delay in leaf senescence (Vander Mijnsbrugge et al., 2016; Dox et al., 2022). So far, there is a lack of studies on the climate warming effect on intra-annual tree-ring formation in deciduous trees at the coldest northern limits of their distribution.

In ring-porous oak, tree-ring formation begins before, and in diffuse-porous beech, simultaneously with leaf development (Hejnowicz, 1990; Guzicka & Hejnowicz, 2006). A species-specific strategy in leaf phenology and cambium activity results in differences in carbohydrate management (Barbaroux & Bréda, 2002; Pérez-de-Lis et al., 2016). Thus, for example, for the development of the first wood cells, storage compounds accumulated in previous growing seasons may be more important in oak than in beech (Michelot et al., 2012b; Richardson et al., 2013). The diffuse-porous beech usually has one growth peak, while two growth peaks are usually present in a healthy oak with wide latewood increments (Michelot et al., 2012b). Oak, is better adapted to the warmest and driest climate than beech (Walentowski et al., 2017; Martinez del Castillo et al., 2022). Hence, there is evidence that species from these two functionally different groups may respond differently to the same meteorological factors during the growing season. Previous, comparative studies of *F. sylvatica* and *Q. petraea* have shown that beech substantially reduces secondary growth under dry conditions compared to oak (Lasermann & Bräuning, 2011; Mette et al., 2013), because oaks (in general) have deeper root systems allowing them to reach water sources more easily during drought events. On the other hand, ring-porous oak wood with large early wood vessels and rare pits is exceptionally susceptible to cavitation (Christman et al., 2012).

Studies on the impact of climate niche availability suggest that the climatic optima of both species will shift north-eastward in Europe (Dyderski et al., 2018). Hence, trees growing in Central Europe should find more favourable climatic conditions (Fréjaville et al., 2020; Wang et al., 2022). However, the climatic changes carry also the risk of damage to the vegetative and generative organs of trees as a result of more frequent extreme climatic events (Puchałka et al., 2017; Strømme et al., 2019; Zohner et al., 2020).

European beech and Sessile oak are among the most important species of the European deciduous temperate forests (Durrant et al., 2016). They have similar distribution ranges, prefers similar soil types and frequently co-occurs in mixed tree-stands (Jones, 1959; Packham et al., 2012; Walentowski et al., 2017). In north-eastern Poland, both species reach the limit of their geographic ranges, resulting from the strong influence of a severe continental climate characterised with a high frequency of the late spring frosts and summer droughts (Boratyńska & Boratyński, 1990; Boratyński et al., 2006).

In this paper, we present the results of monitoring cambium activity in European beech and Sessile oak at locations close to the north-eastern edge of the ranges of both species in two growing seasons contrasting in terms of summer and autumn Standardized Precipitation Evapotranspiration Index (SPEI) values (Fig. S1).

Previous phenological studies on *F. sylvatica* and *Q. petraea* in the lowlands in the northeastern part of the range have focused only on the observations of leaves and generative organs (e.g., Stachak, 1965, 1972a; b; Będkowski, 2018). Hence, our study fills a knowledge gap on the seasonal dynamics of tree-ring formation at the climatic margin of species under extreme weather events. This will contribute to a better understanding of the adaptation of oak and beech to the climate change.

The aim of this study is (i) to evaluate the leaf and xylem formation phenology of European beech and Sessile oak near their north-eastern distribution margins in two contrasting growing seasons (Fig. S1), (ii) to clarify the timing of tree-ring formation of both species and their susceptibility to extreme meteorological conditions, (iii) to determine the differences in tree-ring formation dynamics in response to the climatic factors between these two species.

We hypothesized that (i) under warmer conditions, the onset of tree-ring formation in oak and beech occurs earlier, while the cessation of the cambial activity occurs later than was shown in decades-old studies, (ii) dry season emphasises the species-specific growth response (length of the tree-ring formation period) more than the moderate season does, (iii) the diffuse-porous beech and the ring-porous oak may respond differently to tree-ring formation under the same environmental factors.

Materials and methods

Study sites and tree selection

Study sites selection criteria were similarity in soil condition, age of trees among studied species and their social position in tree stand. We select two different tree stands, oak (N 53.053055; E18.556388) and beech (N53.053611; E18.541388) in distance about 1 km between them (Fig. 1). Both species are growing on similar in moisture and fertility fresh red-podzolic soils. The age of *F. sylvatica* trees was about 63 years, and *Q. petraea* 93 years (Forest Data Bank www.bdl.lasy.gov.pl/). Both are species that grow as co-dominants in mixed stands with *Pinus sylvestris*.

The beech stand near Toruń is located in a climatically marginal area for this species (Mellert et al., 2016) and lies outside the core range of this species. The Sessile oak in the studied site is also located near the edge of the range and further to the north-east, where it is only locally more frequent (Zając & Zając, 2001).

Meteorological data

We used gridded daily averages of precipitation and climate temperatures from the E-OBS 0.1° × 0.1° lat 1923–2019 version 24.0e database (Haylock et al., 2008) to describe study site weather conditions and specifically climatic water balance of observation seasons 2015 and 2017. This dataset contains interpolated values of meteorological variables from the measurements of European weather stations (Cornes et al., 2018). Based on the gridded climatic variables, we calculated the SPEI, a drought index that incorporates actual precipitation and potential evapotranspiration (*PET*) (Begueria et al., 2017). When calculating *PET*, we used the Hargreaves-Samani method (Hargreaves & Samani, 1985) according to Eq. 1

$$PET = 0.0023(T_{mean} + 17.8)\sqrt{T_{max} - T_{min}}\, R_a$$

where T_{mean}, T_{min} and T_{max} are mean, minimum and maximum daily temperatures, respectively, while R_a is daily net radiation at the surface in in MJ/m^2. We calculated the climatic water deficit as the difference between daily precipitation and daily *PET*. Then, we calculated daily SPEI series integrated over 45 days as accumulated drought effects by aggregating climatic water deficits into a log-logistic probability distribution (Klisz et al., 2022).

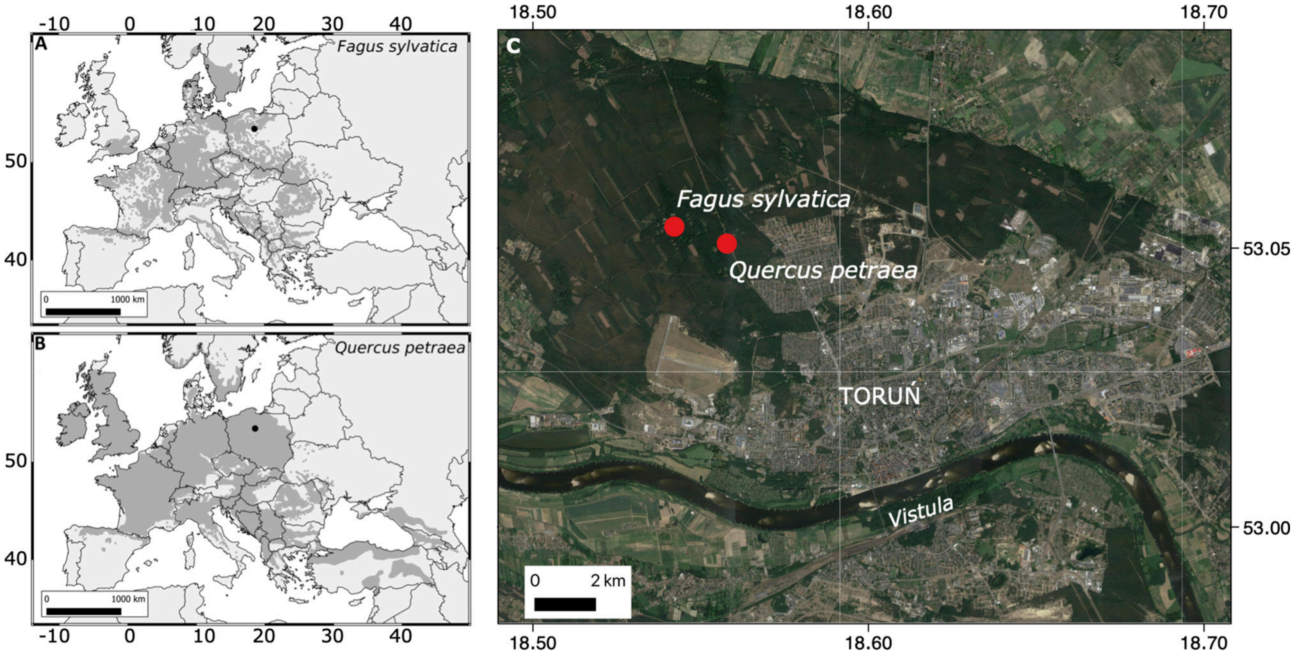

Fig. 1. Location of study sites in relation to the natural ranges of *Fagus sylvatica* (A) and *Quercus petraea* (B) according to Caudullo et al. (2017) and to Toruń (C)

Leaf phenophases observation and microcore sampling

On each study site, we selected five trees per species, which were of similar height, DBH (diameter at breast height) (Table S1 and S2) and co-dominant in the stands, while showing no disease or developmental anomalies symptoms. The monitoring of leaf development in both species was carried out simultaneously with the cores collection, following the commonly used approach (e.g., Derory et al., 2006; Puchałka et al., 2017) (Table 1, S3).

In 2015 and 2017, five trees per species were sampled for growth monitoring. Since the first year of sample collection turned out to be a year of drought (Tukey's test for monthly SPEI values for 2015 and multi-year averages 1923–2019; p-value = 0.049), we decided to pause for a year to avoid the delayed effect of drought, and the next year of collection was conducted in 2017. In both vegetation seasons, the coring was carried out from the early mid-March to the late mid-October. Samples were taken at a height of 120–140 cm above the ground in a helical order using a 5 mm increment borer at a distance of no less than 5 cm to avoid the influence of previous sampling on the anatomical features of the sample (Puchałka et al., 2017). The cores were then taken at intervals of six to twenty-one days (on average every 8.7 days) until the leaves turned yellow and fell. A total of thirty-two cores per tree from both species were collected in 2015, and twenty-five series of samples from beech and twenty-six series of samples from oak in 2017. The cores were stored in formaldehyde-acetic acid-ethanol solution (FAA).

Phenological, observations, sample preparation, measurement and analysis

The samples were placed in to distilled water for 30 minutes, then were clamped in the core holder, and cross-sections of 15–20 μm in thickness were cut using a MC-2 sledge microtome. They were then immersed in a water solution of Safranine and Astra blue mixture for the differentiation of non-lignified, developing xylem cells and cambium (blue stained cell walls) from lignified, mature xylem cells (red stained cell walls). Next, the sections were mounted in Hecht Assistent Histokitt (www.assistent.eu).

We observed tree-ring formation on the microcore cross-section using a light microscope under 400× magnification. The tree-ring width (TRW) increment measurements were performed using ImageJ 1.52a (Schneider et al., 2012) on digital images of cross-sections, captured with a Canon 1300d camera and an Olympus CX33 microscope. The interannual xylem growth was described using the Gompertz function in the case of beech and the Double Gompertz function in the case of oak (Rossi et al., 2003; Michelot et al., 2012b).

The onset of cambium activity was determined by the increase in the number of cambium cell layers compared to the dormant (winter) stage and the beginning of the formation of new xylem cells (Prislan et al., 2011). Next, the beginning of earlywood vessels enlargement was recorded (first vessel detection) (BVE). Then, the secondary wall formation (BSW) of earlywood vessels was determined on the basis of the partially red-stained cell walls. The first mature earlywood vessels (FMV) were also documented and were characterized by fully red-stained cell walls. In the case of oak, the end of production of earlywood cells (EWF) was additionally recorded and was defined with the appearance of small latewood vessels, which were not arranged in rings as typical of earlywood vessels in oak (Gričar, 2010). The cessation of cambial activity (CES) in both species was determined when no new enlarging cells (i.e., cells in the phase of post-cambial growth) were observed. At this phase, the cell walls were red-stained, but the vessel lumina still appeared blue due to the continued viability of the cell protoplasts. Fully formed

Table 1. Observed phenological phases and measured characteristics of annual increments

Abbreviation	Tree-ring parameter	*F. sylvatica*	*Q. petraea*
SWO	Bud swelling	+	+
BRO	Bud breaking and opening	+	+
UNF	Leaf unfolding	+	+
FEX	Leaf fully developed	+	+
TRW	Tree-ring width	+	+
OCA	Onset of cambial activity (increase of count of cambial cells; number of cells in beech >5 and in oak >6)	+	+
BVE	Beginning of earlywood vessels enlargement	+	+
BSW	Beginning of secondary wall formation of earlywood vessels	+	+
FMV	First mature earlywood vessels	+	+
EWF	End of earlywood formation (time of the end of production of earlywood cells	–	+
CES	Cessation of cambial activity	+	+
DUR	Number of days from onset of cambial activity to full maturation of tree-ring	+	+
TRW	Tree-ring width	+	+

xylem increments were considered at the time when the latest formed xylem cells adjacent to the cambium were fully lignified and their cell lumina unfilled, i.e., without living protoplasts (Prislan et al., 2011).

The observations were conducted at intervals of several days (see "Leaf phenophases observation and microcore sampling"**)**. Hence, the observed phenological stages occurred between consecutive observation days. Therefore, the approximate date of the tree-ring formation and leaf development phases was calculated as follows:

$$PD = \frac{D + P}{2}$$

where:

- *PD* – phenophase approximate date,
- *D* – date of given phenophase detection,
- *P* – date of previous observation/sampling (before given phenophase detection).

Based on the established dates of the phenological phases of leaves and xylem, we established their course during two vegetation seasons in 2015 and 2017. Despite the fact that some of the data from phenological observations showed minor incompatibility with the normal distribution giving a Shapiro-Willk test result with a p-value of 0.02–0.05, the differences in the mean DOY of occurrence of phenological phases between species and seasons were analysed with Two-Way ANOVA and post-hoc Tukey test (Table 2, Fig. 3) using R software (R Core Team, 2022). According to Blanca et al. (2017) ANOVA is not very sensitive to non-normal data distribution and gives reliable results even with strongly skewed data. Therefore, we assume that the use of Two-Way ANOVA and post-hoc Tukey test for our data was justified.

Table 2. Results of Two-Way Anova analyses for average DOYs of tree-ring formation phases (OCA, BVE, BSW, FMV, CES) and duration of cambium activity (DUR)

OCA	F	p-value
species	52.888	<0.001
year	1.273	0.276
species:year	3.073	0.099
BVE	F	p-value
species	158.169	<0.001
year	0.367	0.553
species:year	0.207	0.656
BSW	F	p-value
species	33.235	<0.001
year	1.231	0.284
species:year	0.796	0.386
FMV	F	p-value
species	22.141	<0.001
year	0.310	0.585
species:year	0.003	0.955
CES	F	p-value
species	0.001	0.971
year	26.902	0.000
species:year	0.646	0.433
DUR	F	p-value
species	14.659	0.001
year	32.826	<0.001
species:year	0.014	0.908

Descriptive statistics, including minimum, maximum, mean and standard deviation for the time of occurrence of phenological phases in the studied trees are provided in the Results and Table S3.

Tree-ring formation dynamics

We modelled the cumulative growth of the tree-rings for each of the examined trees. In both 2015 and 2017, we adopted the day range from 70 to 300 days of the year (DOY). The curves were fitted by minimizing the residual sum of squares (RSS). We described the curves fitting by the R^2 parameter. Due to the differences between diffuse-porous and ring-porous trees in the dynamics of tree-ring formation, we applied the Gompertz function to beech having a single growth peak and the Double Gompertz function to oak usually having two growth peaks during the vegetation season (Michelot et al., 2012b) (Fig. S2). Growth curves were calculated for each tree and each year. Furthermore, based on the parameters of the Gompertz function, growth rates and the date of maximal cell production were calculated (e.g., Prislan et al., 2013; Gričar et al., 2021). To fit the Gompertz functions, the package *nls2* (Grothendieck, 2022) was used within R software (R Core Team, 2022).

Gompertz function

$$y = A \exp(-\exp(B - kt))$$

where: y – estimated TRW in the given DOY, A – upper asymptote representing maximum TRW, B – estimated place on the x-axis of the onset of tree-ring formation, k – inflection point on the curve, the value of the maximum daily rate of growth, t – DOY – day of the year.

Double Gompertz function

$$y = A_1 \exp(-\exp(B_1 - k_1 t)) + (A_2 - A_1) \exp(-\exp(B_2 - k_2 t))$$

where: y – estimated TRW in the given DOY, A_1 – asymptote representing earlywood formation (fitted value of earlywood width), A_2 – upper asymptote representing maximum TRW, B_1 – estimated place on the x-axis of the onset of tree-ring formation, B_2

– estimated place on the x-axis of the onset of late wood formation, k_1 – rate of change of earlywood formation, k_2 – rate of change of latewood formation, t – DOY – day of the year.

Then, we estimated the TRW values for each DOY for each tree. Based on these values, we calculated the average curve with standard deviation for both species in 2015 and 2017, respectively (Fig. 4).

Results

Tree-ring formation and leaf phenology

In both oak seasons, OCA was detected in mid-March, and the difference in averages from 2015 and 2017 was 2.2 DOY. This is 29.6 and 21.8 days before SWO in 2015 and 2017, respectively. In beech, OCA occurred in 2015 at the end of March, and in 2017 at the beginning of April, 8.3 DOY days later. This is 6.4 and 0.1 days after SWO in 2015 and 2017, respectively (Table S3). Differences in OCA within the species between years were insignificant, but we found statistically significant differences between beech and oak (Table 2, Fig 3).

The BVE in oak in both vegetation seasons was found in the last week of March. In 2017, it occurred about 2.8 days later than in 2015. The corresponding BVE was observed 16.3 and 7.5 days before SWO in 2015 and 2017, respectively. Differences in average in BVE in beech between years were 0.4 days. In both seasons, this phenophase is detected at about 120 DOY. Differences in average in BVE in beech between years were 0.4 days. In both seasons, this phenophase was detected around 30 April. This is an average of 5.6 and 0.0 days after FEX in 2015 and 2017, respectively. We found only statistically significant differences in average BVE between species (Table 2, Fig. 3).

We detected the BSW in oak in the first week of May in 2015 and the second week of May in 2017, 4.2 and 4.4 days after UNF in both growing seasons, respectively. We found BSW in beech in both years around May 20 with a difference in averages of about 0.5 days, that is, 26.5 and 21.0 days after FEX in 2015 and 2017, respectively. The differences in BSW averages were statistically significant between species (Table 2, Fig. 3).

We found FMV in oak in 2015 on May 20 and in 2017 on May 21, with an average of 6.0 and 4.2 after FEX in both seasons, respectively. In contrast, in beech FMV, we found in the first week of June. The difference in averages was 1.6 days. We found statistically significant differences in FEX only in comparisons between species (Table 2, Fig. 3).

EWF in oak was detected in 165.2±8.2 DOY in 2015 and 167.0±1.0 in 2017, and this difference was statistically insignificant ($t = 0.48$, $p>0.05$).

In the moist 2017, CES oak occurred 22.8 and 24.0 beech days later than in the dry 2015. In contrast to the previous phases, the dates of CES were statistically insignificant between species, while significant differences were within species between years (Table 2, Fig. 3).

The average DUR in oak was 31.0, and 32.3 days in beech longer in moist 2017 than in dry 2015. Also, the differences in DUR were statistically significant between years for both species (Table 2, Fig. 3). In both growing seasons, leaf senescence was observed in both species starting around mid-September after CES in both species.

Tree-ring formation dynamics

In beech, radial growth was characterized by a sigmoid growth curve. Therefore, the Gompertz function was used to evaluate growth dynamics, with R^2 values ranging from 0.73 to 0.98 (Table S2). In most of oak trees, radial growth followed a bimodal growth pattern, thus we used a Double Gompertz function to fit the tree-ring width data; in this case, R^2 values ranged from 0.64 to 0.99 (Table S3). In beech in dry 2015, the average slope value determining the rate of TRW growth ($b=5.63$) was lower than in 2017 ($b=7.30$) (Table S1). Similarly, the average slope values in the first growth peak were lower in 2015 ($b_1=18.67$) than in 2017 ($b_1=36.00$). In contrast, in the second incremental peak, the averaged slope value was higher in 2015 ($b_2=9.45$) than in 2017 ($b_2=5.35$) (Table S2).

In 2015, oak trees reached an average of 0.45 mm at the FEX stage, representing about 50% of the width of the annual increment, and about 0.53 mm in 2017, which is about 25% of the tree-ring width. In oak, the time from BRO to FEX was a period of dynamically increasing annual growth width (Fig. 4). During this time, earlywood vessels were produced (Fig. 3). Their lignification was completed about 31.2 days after FEX later in 2015, and 30 days later after FEX in 2017. Accelerated growth in oak was observed around 175 DOY in both years, which was about 40 days after FEX detection, and about a few days after EWF. In contrast, in beech, dynamic radial growth was observed from FEX, and it lagged behind oak by about 26 days in 2015, and about 17 days in 2017.

By the end of May, oak and beech had reached comparable growth rates in both years (Fig 4). In contrast, the two seasons differ in the dynamics of tree-ring formation and final tree-rings widths from the end of spring to autumn. In dry year 2015, the slope of the growth curve from summer to fall was less steep than in wet year 2017. The estimated average annual growth at the end of the growing season, calculated for 300 DOY, is 0.76±04 mm for beech in 2015, 1.92±0.7 mm in 2017, and for oak in 2015 and 0.81±0.3 mm, and 2.1±0.9 mm in 2017.

Discussion

Differences in the tree-ring formation dynamics between species and contrasted summer meteorological conditions

According to our hypotheses, the onset of xylem formation under a warming climate for both species was detected about a few weeks earlier than reported in the literature (Hejnowicz, 1990; Guzicka & Hejnowicz, 2006). Exactly how large this difference is, however, is impossible to estimate due to the lack of previous studies on cambium activity from the region where we conducted our research. The studies cited by Guzicka and Hejnowicz (2006) and Hejnowicz (1990) refer to studies in warmer regions from the central part of the ranges of *F. sylvatica* and *Q. petraea,* where likely phenological phases occur earlier than in the cooler north-eastern parts of the ranges. In both species, a highly uniform leaf development between individuals of the same species is observed (Fig. 4). The even leaf phenology may be due to the fact that the stands may have come from a narrow genetic pool, which may cause a similar reaction to environmental conditions (Osada & Hiura, 2019) or may be due too low resolution in monitoring. It is a

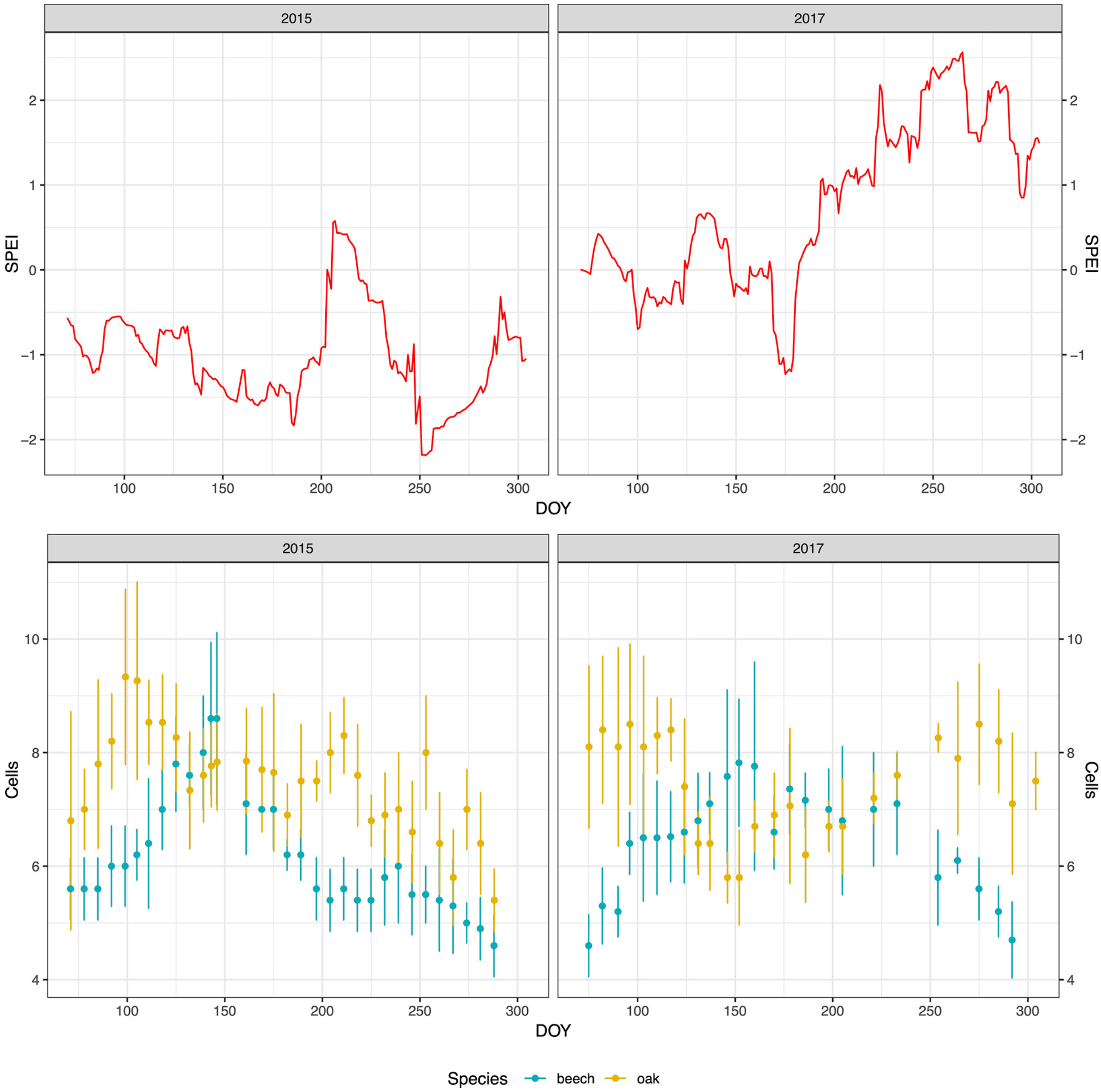

Fig. 2. Number of cambium cells, considered as an indicator of cell division activity and vitality of trees in relation to SPEI (over 45 days)

well-known phenomenon that similarly sized trees have similar phenological phases (Seiwa, 1999; Sayer & Newbery, 2003), while natural populations and size-differentiated trees sometimes are highly phenologically variable (Puchałka et al., 2017; Utkina & Rubtsov, 2018). We have observed a much greater variability in the phenology of tree-ring formation (Fig. 3). The lack of detectable variability in leaf development and the comparatively high variability in the timing of tree-ring formation phases, confirms

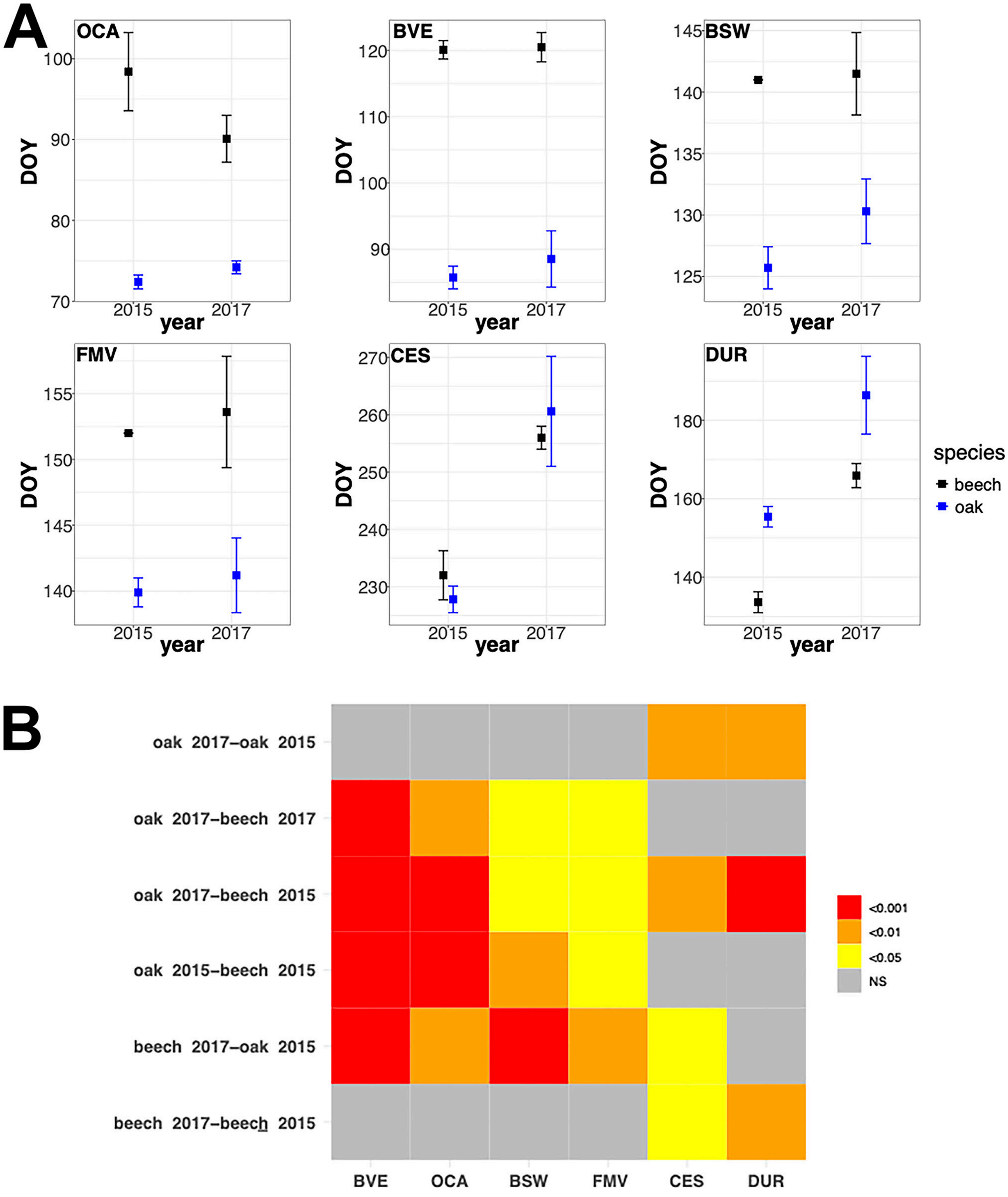

Fig. 3. The differences in mean timing of the phenophases between oak and beech in 2015 and 2017. The whiskers indicate standard error (A). The heat map presents the results of the post-hoc Tukey test for tree-ring formation phases in 2015 and 2017 (B). For phases IDs see Table 1

the results of previous studies showing that spring leaf phenology is not a sensitive proxy for the cambial activity (Sass-Klaassen et al., 2011; Puchałka et al., 2017). According to other studies, variation in leaf phenology does not affect growth rates in beech (Čufar et al., 2015). However, the general pattern (Barbaroux & Bréda, 2002; Takahashi et al., 2013) that cambial activity begins several weeks before leaf development in ring-porous oak and more or less simultaneously with leaf development in diffuse-porous beech is confirmed. Contrary to what is reported in the literature (Guzicka & Hejnowicz, 2006), the completion of the formation of earlywood vessels in oak occurred only after full leaf development (Fig. 4). This is consistent with what we have observed in *Q. robur* (Puchałka et al., 2017).

Differences in the timing of phenological phases and dynamics of tree-ring formation between species are due to different physiology and strategies of carbohydrate management in ring-porous and diffuse-porous species (Barbaroux & Bréda, 2002; Michelot et al., 2012b). In contrast, we observed the lack of significant differences in the early stages of xylem formation (from BVE to FMV) between years in the same species (Fig. 3, Table 2). It is notable that the two species responded differently to the contrasting weather conditions of late summer and autumn. These differences were reflected in the number of cambium cell layers (Fig. 2), which is thought to be a proxy for the secondary meristem activity affecting radial growth (Hejnowicz, 1990; Guzicka & Hejnowicz, 2006). According to Gričar et al. (2014), the number of cambial cell layers can be greatly affected by tree vitality or tree age. For instance, in *Q. robur,* the number of dormant cambial cell layers may vary from 2 to 8. During the summer and autumn droughts of 2015, the radial growth rate and the number of cambial cells decreased in both species, and they responded similarly by slowing growth (Fig. 4). This can be clearly attributed to the limiting effect of water shortage and high temperatures on photosynthetic rate (Teskey et al., 2014). However, individual trees differed within and between species in the timing of CES and DUR (Fig. 3). This may be

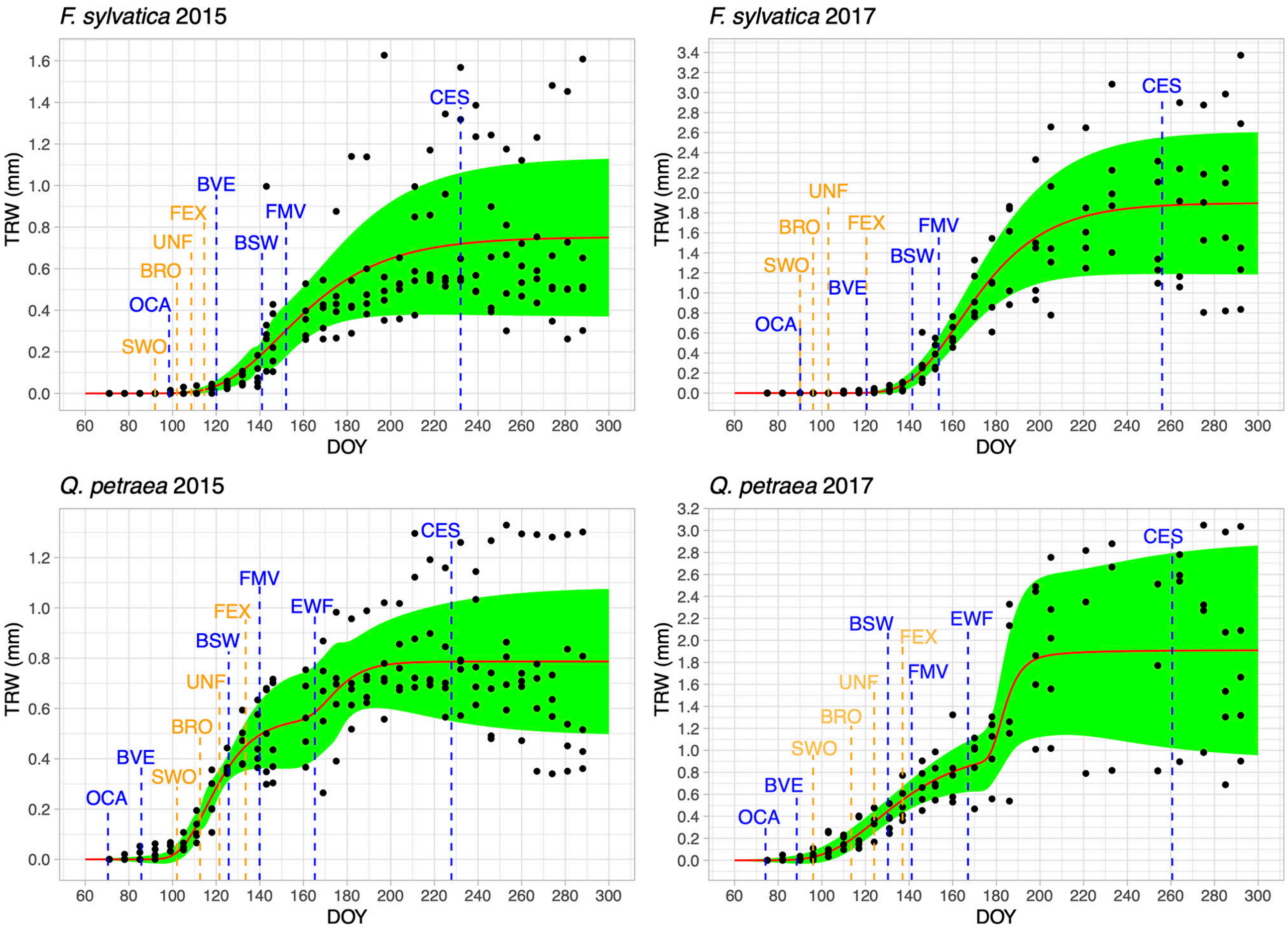

Fig. 4. The seasonal tree-ring growth dynamics and the leaf phenology in *Fagus sylvatica* and *Quercus petraea* in 2015 and 2017. The solid red lines represent the curve fitting for the width measurements of tree rings for all trees of the same species in a given year, calculated from measurements on DOYs (black points). The 95% confidence intervals for the curves are presented as green polygons. For leaf phenology (orange labels) and tree-ring formation phases (blue labels) IDs see chapter 2.3. TRW – tree-ring width, DOY – day of the year

due to the different physiological states of individual trees, or a different shift of carbohydrate allocation from a building to a storage function (Klisz et al., 2020). In the summer and fall seasons of 2017, with high rainfall, the responses of the cambial meristem were different in *F. sylvatica* and *Q. petraea* (Fig. 2). In beech, the number of cambium cells, as in the year with summer drought, decreases from mid-summer, while in oak the high number of cambial cell layers persists until October. Thus, the number of cambium cells does not fully correspond to the dynamics of growth formation, since in both species, the curves describing radial growth do not reach their plateau until mid-September. Hence, cell number may not be a sensitive proxy of cambium activity (Fig. 4). According to previous research, in both species, the offset of the cambial activity occurs in late August (Hejnowicz, 1990; Guzicka & Hejnowicz, 2006). In dry 2015 (Fig. S1), we observed CES in both species, in the middle of this month (Fig. 3). On the other hand, in humid 2017 CES was observed from mid-September, which is about a month later than the literature information suggests (Hejnowicz, 1990; Guzicka & Hejnowicz, 2006). However, given that the summer and autumn of 2017 were characterized by a positive water balance, and that the frequency of summer water deficits is expected to increase in the future, we can assume that despite thermal conditions, CES will probably be observed in the near future at the mid-summer.

Functioning of *F. sylvatica* and *Q. petraea* in a changing climate at the north-eastern end of the range

The lack of previous studies on the formation of the annual increment of *F. sylvatica* and *Q. petraea* in the north-eastern part of their ranges do not allow a clear determination of how much the period of cambium activity in both species has lengthened at the site of our study. However, taking into account previous studies from sites, west of Poland, cited by Guzicka and Hejnowicz (2006) and Hejnowicz (1990), which have a longer growing season, and reported from them a later BVE and earlier CES than observed in 2015 and 2017 in Poland, we can speculate that the growing season of both studied species may have lengthened by up to several weeks. Such a significant prolongation of cambial activity is in line with the general trend of lengthening the growing season observed in recent years in the temperate climate zone of the northern hemisphere (Gunderson et al., 2012; Kolářová et al., 2014). Puchałka et al. (2022) suggest that as the climate continues to warm, the growing season in Europe could start up to one month earlier than today in the coming decades. There will also be a north-eastward shift in the potential range of both species, which is currently strongly limited by thermal conditions (Weigel et al., 2018; Dyderski et al., 2023). Shifting the climatic niche in this direction does not mean that *F. sylvatica* and *Q. petraea* will significantly increase their share in forests and enlarge timber production. An earlier offset of the growing season will be associated with a higher risk of plant damage from late spring frosts, the frequency of which is expected to increase with climate change (Liu et al., 2018; Zohner et al., 2020; Sangüesa-Barreda et al., 2021). Nowadays, in northern Poland, frost damage in spring is also more frequently observed in *Q. robur*, which is better adapted to the numerous meteorological extremes of the continental climate (Puchałka et al., 2016). Another factor shaping the ranges of *F. sylvatica* and *Q. petraea* is the availability of water during the warmest quarter (Dyderski et al., 2023). On the one hand, an earlier start of vegetation may ensure the fulfilment of growth and generative functions before the onset of summer drought, but on the other hand, as in 2015, it may strongly limit the growth of trees and, despite favourable thermal and light conditions, CES may occur earlier due to summer drought. This factor may particularly limit the growth of *F. sylvatica*, which is much less drought-tolerant than *Q. petraea* (Mette et al., 2013). It should also be considered that while the onset of cambium activity is predominantly influenced by thermal conditions (Żelawski, 1954), leaf out, which is the end of photosynthetic activity, is strongly dependent on photoperiod (Fu et al., 2019). With a warming climate, only the photoperiod will not change, and despite the favourable values of other environmental factors it will limit the production of carbohydrates necessary for the formation of annual growth (Richardson et al., 2013). Hence, a shift in climatic niches, allowing species to realize their full life cycles, does not necessarily mean improved conditions for their growth and higher timber production. The occurrence and even dominance of *F. sylvatica* and *Q. petraea* in natural plant communities on sandy, south-facing hot and dry slopes that occur, for example, in the Puszcza Piaskowa (NW Poland) (Puchałka & Płąchocki, 2014), suggests that both species may exist in many other places under conditions of expected warming and greater water deficits. Both species in such habitats grow much more slowly and produce less attractive timber than *P. sylvestris*, which are predicted to be the losers of climate change (Bombi et al., 2017; Dyderski et al., 2018). However, even in the most pessimistic climate change scenarios, where *F. sylvatica* and *Q. petraea* may not provide satisfactory economic outcomes, they may be species that ensure the stability of forest ecosystems (Dyderski et al., 2023). However, the uncertainty about which of the climate change scenarios will occur suggests that there is a need to disperse the risk of species decline by replacing monocultures with mixed stands (Bouwman et al., 2021), and a more diverse genetic and age structure. Stability could be enhanced by growing mixed oak and beech stands, as other studies also show that ring-porous and diffuse-porous trees may respond differently to environmental conditions (Michelot et al., 2012a; Alla & Camarero, 2012; Michelot et al., 2012b). Bonn (2000) proved that on beech/oak mixed stands in dry years, oak as a less sensitive tree species shows, smaller growth reduction than beech.

Conclusions

The shift of the climatic optimum towards the northeast may be favourable for the expansion of *F. sylvatica* and *Q. petraea* in this direction, but this is not synonymous with the fact that these species will have higher timber production. An earlier start of vegetation is associated with the risk of damage by late spring frosts. On the other hand, higher summer temperatures are not necessarily conducive to increased timber production. The offset of the cambial activity may occur earlier as a result of summer water deficits. Conversely, in autumn, even with sufficient water availability, it can be limited by light availability and photoperiod, which are factors affecting the timing of the leaf senescence and leaf fall. However, the final TRW is not only a result of DUR, but also depends on the rate of the divisions of cambial cells. While spring phenological phases are very similar between individuals of the species, the course of autumn phases is less clear, more variable and thus more difficult to predict. The observed increase in the number of cambium cells in *Q. petraea* after tree-ring formation may indicate high tree vitality following favourable meteorological conditions during the period from late summer to early autumn.

However, the high amount rainfall did not significantly prolong the trees' vegetation, despite the fact that thermal conditions also seemed favourable. The results of our study indicate the need to add to our knowledge of the phenology of tree-ring formation, particularly with regard to an offset of the cambial activity, and to estimate growth rates in future climatic conditions. Furthermore, long-term tree-ring formation monitoring would provide key knowledge of trends in the adaptation of growth processes under changing climate conditions.

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