ORIGINAL ARTICLE

Spring precipitation effects on formation of first row of earlywood vessels in *Quercus variabilis* at Qinling Mountain (China)

Yiping Zhang[1] · Junliang Xu[1] · Wei Su[1] · Xiping Zhao[1] · Xiaoli Xu[1]

Abstract

Key message Under drier spring conditions, *Q. variabilis* might slow the FEV growth rate but will not produce narrower FEVs. FEV size might be a trade-off between hydraulic efficiency and hydraulic safety.

Abstract Wood anatomical features can encode tree reactions to fluctuating environmental conditions. The first row of earlywood vessels (FEV) has proven to be very promising with respect to the inter-annual climate variability. However, knowledge of how intra-annual FEV formation reflects climate is still limited. We observed wood formation of *Quercus variabilis* in a warm temperate–subtropical climate transition at Qinling Mountain, China. Using micro-cores, growth of six trees was monitored at weekly/biweekly intervals February–December in 2015 and 2016, of which 2016 had a drier spring. Cambial activity and xylem cell differentiation were documented by microscopic observation. The FEV diameter and ring width were measured. The onset of xylem growth, which significantly differed between the years, occurred 8 days earlier in 2016, in mid-March. However, the completion of FEV was synchronized in mid-April over the 2 years. This delayed completion of FEV in 2016, when precipitation increased and Standardized Precipitation Evapotranspiration Index changed from a negative to positive value. The cessation of xylem formation was 3 weeks earlier during the drought year (September 5, 2016) compared to the moist year (September 29, 2015) because of the drought conditions in late summer. This finding was supported by evidence that a positive and significant correlation between precipitation and xylem growth was found only in 2016. The ring width differed significantly between the years, but the FEV diameter did not. Our results suggest that the drought-induced delayed formation of FEV and earlier cessation could be a strategy for oak trees to adapt to water stress.

Keywords Chinese cork oak · Earlywood vessels of first row · Drought · Xylogenesis · SPEI

Introduction

Wood anatomical features (e.g., conduit size and density) are regarded as a useful proxy that records environmental signals (Fonti et al. 2010). For conifers, tracheid lumen size and cell wall thickness are the main potential proxies for recording environmental signals (Eilmann et al. 2006; Vaganov

---

✉ Junliang Xu
xujunliang@haust.edu.cn

[1] College of Forestry, Henan University of Science and Technology, No. 263 Kaiyuan Avenue, Luoyang 471023, China

et al. 2006). Intra-annual density fluctuations (IADFs) are identified as the key parameter for understanding tree responses to water stress (Battipaglia et al. 2014). For angiosperms, the vessel area and the vessel density are the main focus of attention in ring-porous species (Fonti and García-González 2004) and diffuse-porous species (Sass-Klaassen and Eckstein 1995). Notably, in ring-porous trees, the sizes (diameter/area) of the first row of earlywood vessels appear to be particularly sensitive to the local environment (García-González and Fonti 2006). At the intra-specific level, narrower earlywood vessels (EV) were reported to reduce the risk of cavitation under both dry and wet conditions (Corcuera et al. 2005; Fonti et al. 2009). Nevertheless, recent work has challenged this paradigm (Eilmann et al. 2011; Fernández-de-Uña et al. 2017), as similar EV diameters in *Quercus robur* were found under two different flood regimes (Gričar et al. 2013). The environment influences the EV diameter by inducing changes to the process of cambial cell division

and earlywood differentiation, both in the growth rate and duration (Hacke et al. 2017). Therefore, it seems that not only the size of EV but also its formation process (rate and duration) may provide a better understanding of the tree's performance under drought conditions.

Analysis of the intra-annual dynamics of wood formation can provide related information on xylem anatomy. The dynamics of wood formation describe the process of cambial phenology and cell production throughout the growing season, with specific growth timing, rate and duration (Cuny et al. 2012; Lupi et al. 2010), which reflect the effects of different climatic factors on trees with a high time resolution (Rossi et al. 2014).

The key role of temperature in cambial reactivation and cell production has recently been demonstrated (Deslauriers et al. 2008). The predicted increase in temperatures is expected to enhance xylem formation (King et al. 2013) by starting earlier and prolonging the growing season. However, the influence of temperature may weaken during the course of the growing season since wood formation is not completed at same time each year and the duration of formation is variable (Rossi et al. 2008). Several recent studies have proven that precipitation in late spring can also play a critical role in the onset of xylogenesis under cold drought-prone regimes (Ren et al. 2015; Zhang et al. 2018). Thus, recovering the appropriate cell turgor by water uptake is necessary to resume tree growth (Kozlowski and Pallardy 2002). Furthermore, long and severe drought in summer may slow down or even stop wood formation (Eilmann et al. 2011) since xylem cell differentiation (division and expansion) is also sensitive to water potential (Stojanović et al. 2017). Therefore, a deeper understanding of the environmental factors controlling the intra-annual progress of wood formation and wood anatomy would be useful to evaluate the impact of the predicted climate change on future tree growth.

Chinese cork oak (*Quercus variabilis* Blume) plays a key role in the development of the regional economy and ecosystem, which produces wood, cork, charcoal, and edible fungi. This ring-porous species is a common and widespread deciduous broad-leaved tree in eastern Asia, which grows in temperate–subtropical climate conditions (19°–42°N and 97°–140°E) (Ma et al. 2013). Due to its wide distribution, *Q. variabilis* is a good candidate for studying the influences of environmental factors on wood formation. Based on a previous dendrochronology analysis, the radial growth response of the oak can record climatic variations and is especially sensitive to precipitation in the early spring/summer (Ferrio et al. 2003; Lyu et al. 2017).

In this study, the wood formation of *Q. variabilis* was monitored at weekly/biweekly intervals, and the wood anatomy features were measured. Our study was conducted in two consecutive growing seasons (2015 and 2016), with different levels of monthly and seasonal dryness, in which 2016

was a warmer year with a drier spring. Therefore, the aims of this study were (1) to monitor the timing of intra-annual cambial phenology and the xylem differentiation dynamics of *Q. variabilis*; (2) to analyze the environmental influence on wood formation, especially the formation of the first row of earlywood vessels exposed to spring drought; and (3) to verify whether the first row of earlywood vessels could be a stable climate proxy in this monsoon-dominated region since most previous studies were conducted in Mediterranean climates with dry growing seasons. We hypothesized that (1) drought would induce a shorter growing season and that (2) the first row of earlywood vessels would be a sensitive indicator of the climate conditions, especially in the spring.

Materials and methods

Study site

The study area was located at Xiong'er Mountain (Central China, 33° 54′N–34° 31′N, 111° 10′E–112° 09′E, Fig. 1), in the Western Henan Mountain region. This mountain region is an extension of Qinling Mountain in Henan Province and transitions from a warm temperate zone to a subtropical zone, which is one of the most suitable habitats for *Q. variabilis* (Zhang et al. 2010). The mean annual temperature is 12.6 °C. The mean annual precipitation is 636 mm (1953–2014), and over 72% of this precipitation falls between May and September. These data were obtained from the nearest State standard meteorological station in Lushi (34° 03′N, 111° 02′E, 568 m a.s.l., linear distance *ca.* 30 km from the study site).
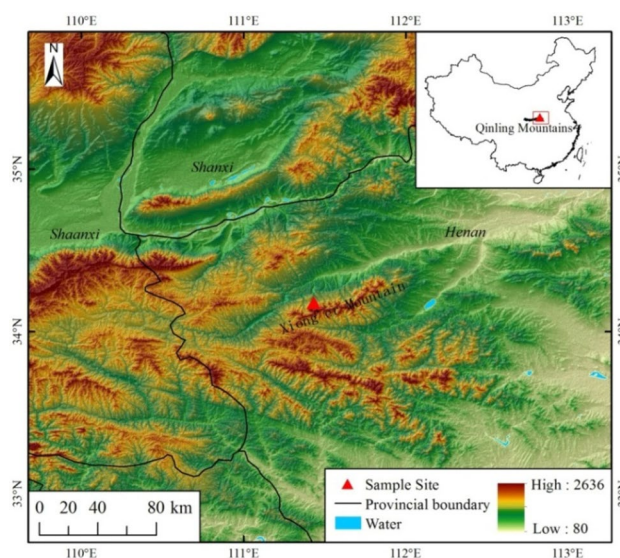

Fig. 1 Geographical location of the study area in Central China

The research was conducted on an uneven-aged Chinese cork oak secondary forest (Cao et al. 2003). *Q. variabilis* is the dominant woody species at low and middle elevations (< 1600 m a.s.l.), with an average height of 15 m and occupying more than 80% of the canopy coverage. The main soil type is sandy brown soil with an average soil depth of *ca.* 50 cm. The site is on a south-facing slope (20–30%) at an elevation of 970 m a.s.l.

Tree selection and section preparation

Intra-annual radial growth was monitored from late February until early December 2015 and 2016. Each year, we selected six healthy *Q. variabilis* sample trees without any visible injuries on the stems, branches or roots. To avoid wound effects from previous samplings, sampling positions on each tree were kept at least 5 cm apart in both horizontal and vertical direction. Thus, sampling could not be continued on the same trees in the second year, due to the high frequency of sampling dates and the need for multiple samples on some dates. The latter owed much to the high level of hardness in oak Chinese cork (level IV–V), which made it difficult to obtain intact samples. Trees sampled in 2015 and 2016 were distinct but with no significant differences (by *T* value test) in age, height and diameter at breast height (DBH), which were 31 ± 6 and 25 ± 4 years ($p = 0.304$), 16 ± 0.7 and 17 ± 2.3 m ($p = 0.188$), 20 ± 1.2 and 17 ± 1.5 cm ($p = 0.465$), respectively.

Micro-cores were initially collected at weekly intervals from late February to early June. Due to the slower growth rate of trees in summer, samples were processed at biweekly intervals from June to early December (González-González

et al. 2013). Overall, *ca.* 1000 samples were collected using a Trephor tool (Rossi et al. 2006). Samples were stored in a solution (30% water and 70% equal parts ethanol and glycerol) at 4 °C to avoid tissue deterioration. After 1 month, the samples were dehydrated with increasing concentrations of ethanol and xylene and embedded in paraffin blocks (Paraplast Plus, ROTH, Karlsruhe, Germany). Transverse sections were cut to a thickness of 10–15 µm with a Leica RM 2235 rotary microtome (Leica Microsystems, Wetzlar, Germany). All sections were stained with 1% safranin (Solarbio, Beijing, China) (in water) and 0.5% fast green (Sigma-Aldrich, Steinheim, Germany) (in 95% ethanol). They were observed using a Nikon Ni-U light microscope (Tokyo, Japan) under a bright field and polarized light.

Cambial phenology and xylem growth

Stained sections for each tree were examined to distinguish the phenological phases of cambial activity and xylem cell differentiation as follows: (1) the onset of cambial cell production; (2) the onset of the enlargement of the first row of earlywood vessels (FEV); (3) the completion of FEV; (4) the transition from earlywood to latewood; (5) the end of cambial cell production; and (6) the end of xylem formation. Phases were assessed for each tree, which were calculated and expressed as the day of the year (DOY).

The observed phases were defined as follows (Plomion et al. 2001): (1) the onset of cambial cell production was defined as an increased number of thin-walled cambial cells compared to the dormant cambium (Fig. 2c) (Prislan et al. 2011); (2) the onset of FEV enlargement was characterized by large vessel cells and thin, non-lignified cell walls, which
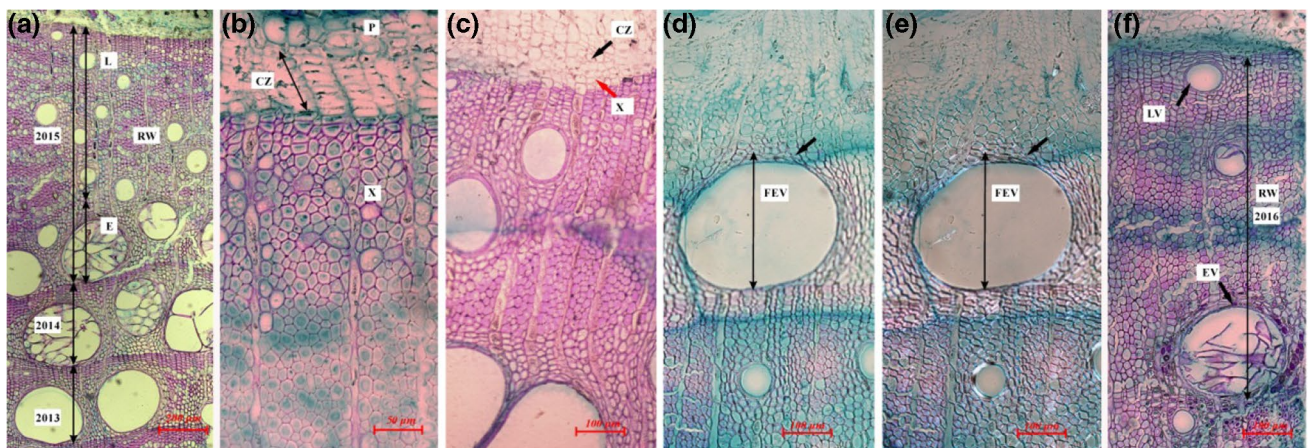

Fig. 2 Phases of cambial phenology in Quercus variabilis in 2016. **a** The structure of xylem rings in *Q. variabilis*. **b** The cambial zone was dormant on February 25; no new xylem cell production was observed. **c** Active cambium (black arrow) and newly formed xylem cells (enlargement, red arrow) on March 10. **d, e** Full completion of the first row of earlywood vessels on April 20; observed under a bright field (**d**) and polarized (**e**) light, respectively. **f** Newly formed xylem ring on September 5, 2016. **a, b** and **c–f** magnification of 50X, 200X and 100X, respectively. *RW* radial width, *L* latewood, *E* earlywood, *CZ* cambial zone, *P* phloem, *X* xylem, *FEV* the first row of earlywood vessels, *LV* latewood vessel, *EV* earlywood vessel

were generally located near the previous year's growth ring boundary (González-González et al. 2014); (3) the completion of FEV was identified as the complete lignification of the FEV, which was indicated by completely red cell walls stained by the safranin–fast green procedure (Fig. 2d, e) (Gričar et al. 2017); (4) the transition from earlywood to latewood was defined as when small latewood vessels were no longer present in the rings (Gričar 2010); (5) the end of cambial cell production was determined as the time at which no new thin-walled cambial cells were observed in the cambium, and the number of cambial cells was comparable to the number before its reactivation in spring (Gričar et al. 2017); and (6) the end of xylem formation was identified by the complete lignification of the last formed latewood cells, which was indicated by completely red-stained cell walls (Fig. 2f). The duration of xylem formation was calculated as the number of days between the onset of cambial cell production (phase 1) and the end of xylem formation (phase 6) since cells in the enlargement phase were difficult to distinguish for *Q. variabilis* (Michelot et al. 2012).

Intra-annual xylem growth monitoring and fitting

The number of cambium cells was counted and the widths of xylem (µm) at each cell development phase were monitored and measured along three radial rows. This was accomplished with Nikon NIS-Elements D software (Tokyo, Japan).

The dynamics of the intra-annual cumulative xylem width per tree were fitted by the Gompertz function, which has proven its effectiveness in describing cellular-level growth (Lupi et al. 2014). Based on the estimated parameters from the Gompertz function, the date of the maximum rate of the new xylem width (t_p, DOY) and the average new xylem width growth rate (r_m, µm·day^{-1}) were computed. The growth-fitting procedures are given in detail in the Supplement.

Wood anatomy

The first row of earlywood vessels (FEV) has been found to contain the strongest record of environmental signals (García-González and Fonti 2006). The FEVs were considered to be (1) all vessels that were close to the ring boundary, and (2) those vessels whose front edges (i.e., the edges toward the pith) were radially positioned inward of the center of the vessels close to the ring boundary (González-González et al. 2014). The mean diameter of the first row of earlywood vessels (DFEV) and ring width (RW) on an inter-annual scale (2009–2016) were measured based on the micro-cores taken from every monitored tree in November 2016 (Table 1). Considering the substantially higher contribution of large conduits to hydraulic conductivity, only

Table 1 Several anatomical variables in the tree rings of *Quercus variabilis*

Abbreviation	Full name
EV	Earlywood vessels
FEV	First row of earlywood vessels
DFEV	Diameter of the first row of earlywood vessels
RW	Ring width

earlywood vessels with a lumen area > 7500 µm^2 were considered to be FEVs (González-González et al. 2014). Anatomical sections were photographed with a Nikon Ni-U light microscope (Tokyo, Japan), and measurements were carried out using NIS-Elements D software.

Environmental factors

To assess the cumulative heat exposure before xylem formation, the cumulative growing degree days (GDD) from $Date_{Ta>5}$ (see below) to the date of cambial cell production onset and FEV completion were calculated. GDD was computed by a modified sine wave model based on daily air temperature (maximum and minimum) and threshold temperature (Seo et al. 2008). Here, 5 °C was chosen as the threshold temperature according to previous results performed on temperate species (Rossi et al. 2008). The date of $Date_{Ta>5}$ is defined as the first date on which a daily mean air temperature was warmer than 5 °C for five consecutive days.

To quantify environmental drought, we used the monthly Standardized Precipitation Evapotranspiration Index (SPEI). SPEI was calculated as the monthly difference between precipitation and potential evapotranspiration for the 1953–2016 period (Vicente-Serrano et al. 2010) using the SPEI package in R 3.4.2 (R Core Team 2017). Positive and negative SPEI values represent periods of wetness or dryness, respectively.

To produce corroborative environmental data from our study site, we measured the soil temperature (T_s, °C) and soil volumetric water content (SWC, m^3 m^{-3}) at a soil depth of 10 cm using a HOBO data logger (Onset Computer Corp, Bourne, MA, USA) from 2015 to 2016. The recording frequency was every 2 h.

Data analysis

The differences in the timing and duration of cambial phenological phases between years (2015 and 2016) were determined using the Mann–Whitney *U* test (SPSS Inc., Chicago, IL, USA). Because the assumption of normality was not met by all parameters of critical dates and durations,

analyses between years were followed by non-parametric Mann–Whitney U tests.

To investigate the effects of year and cambial age on DFEV and RW, we used linear mixed-effect models with the "lme4 package" in R 3.4.2 (Bates et al. 2012). The proposed models included the tree as a random effect and the year and cambial age as fixed effects. If year/cambial age had a significant influence on DFEV and RW ($p < 0.05$), we tested the differences using Tukey's test. Additionally, we used Pearson correlations to assess the relationship between DFEV and RW.

The environment–xylem growth relationships were analyzed using Pearson correlation coefficients (Ren et al. 2015). Five environmental factors were included, i.e. daily mean air and soil temperatures, precipitation, relative humidity and soil volumetric water content. All factors were calculated as averaged (except for precipitation) or summed (precipitation) values between successive sampling dates (7–10 days). Xylem growth was measured by xylem width increments between successive samples, in which the xylem widths were predicted by the Gompertz model. Time-lag effects were also considered (Deslauriers and Morin 2005); however, the correlation coefficients between the environment and xylem growth gradually weakened when the lag time shifted from 0 to 7 days before each sampling date.

Results

Cambial phenology and xylem growth

The onset of cambial cell production occurred during the third week of March in 2015 (March 19, DOY 78), while it was *ca.* 1 week earlier in 2016 (March 10, DOY 70, Fig. 2c),

with significant differences between the years (Table 2, $p < 0.01$). 7–10 days after the onset of cambial activity, the FEV became enlarged. Notably, the complete formation of FEV was nearly concurrent in 2015 (April 19, DOY 109) and 2016 (April 20, DOY 111, Fig. 2d), with no significant differences between the years ($p = 0.734$). However, the end of cambial cell production in 2015 was almost 3 weeks later than in 2016 (DOY 218), which was found as late as late-August (DOY 240). The end of xylem formation was detected on September 29 and September 5 (DOY 272 and 249, Fig. 2f) in 2015 and 2016, respectively.

Thus, the duration of FEV formation was significantly different between the years ($p < 0.05$), which lasted an average of 31 days and 41 days in 2015 and 2016, respectively. Similarly, the duration of cambial cell production in 2015 lasted 163 days, compared with the shorter period of 148 days in 2016. As a result, the duration of xylem formation in 2015 was greater than 6 months (184 days), which was longer than the 172 days in 2016.

Dynamics of intra-annual xylem growth

Four to six cambium cells were present during the dormancy period, and after activity initiated, the number increased to a peak of 9 to 11 cells in May. The Gompertz function adequately fitted the intra-annual growth of Chinese cork oak ($R^2 = 0.88 \pm 0.07$, $N = 12$, $p < 0.001$; Fig. 3). During the two study years, >60% of xylem growth was produced from May to July. The average width of xylem was 4311 ± 445 μm (min = 3896 μm; max = 5076 μm) and 3752 ± 891 μm (min = 2686 μm; max = 4952 μm) in 2015 and 2016, respectively (Fig. 3a, c). The date of maximum xylem growth rate (t_p) occurred on June 1 in 2015 (DOY 152) and June 10 in 2016 (DOY 162). However, the average xylem width growth

Table 2 Phases of cambial phenology and xylem growth of *Quercus variabilis* in 2015 and 2016

	2015	2016	Z	sig
Wood formation phases (DOY ± standard deviation)				
Onset of cambial cell production (phase 1)	78 ± 0^a	70 ± 5^b	− 3.146	**0.002**
Onset of FEV enlargement (phase 2)	88 ± 0^a	77 ± 7^b	− 2.739	**0.006**
Completion of FEV (phase 3)	109 ± 4	111 ± 4	− 0.339	0.734
Transition from earlywood to latewood (phase 4)	151 ± 6^a	155 ± 7^b	− 1.185	0.236
End of cambial cell production (phase 5)	240 ± 4^a	218 ± 6^b	− 3.035	**0.002**
End of xylem formation (phase 6)	272 ± 4^a	249 ± 6^b	− 3.035	**0.002**
Duration of different phases (days ± standard deviation)				
Duration of cambial cell production (phase 1–5)	162 ± 4^a	148 ± 11^b	− 2.978	**0.003**
Duration of FEV formation (phase 2–3)	31 ± 4^a	41 ± 4^b	− 2.374	**0.018**
Duration of xylem formation (phase 1–6)	184 ± 4^a	172 ± 9^b	− 2.454	**0.014**

Significant difference ($p < 0.05$) are marked bold

DOY day of the year, *FEV* first row of earlywood vessels

Letters (a, b) indicate significant differences between two years based on Mann–Whitney rank-sum Test ($p < 0.05$)
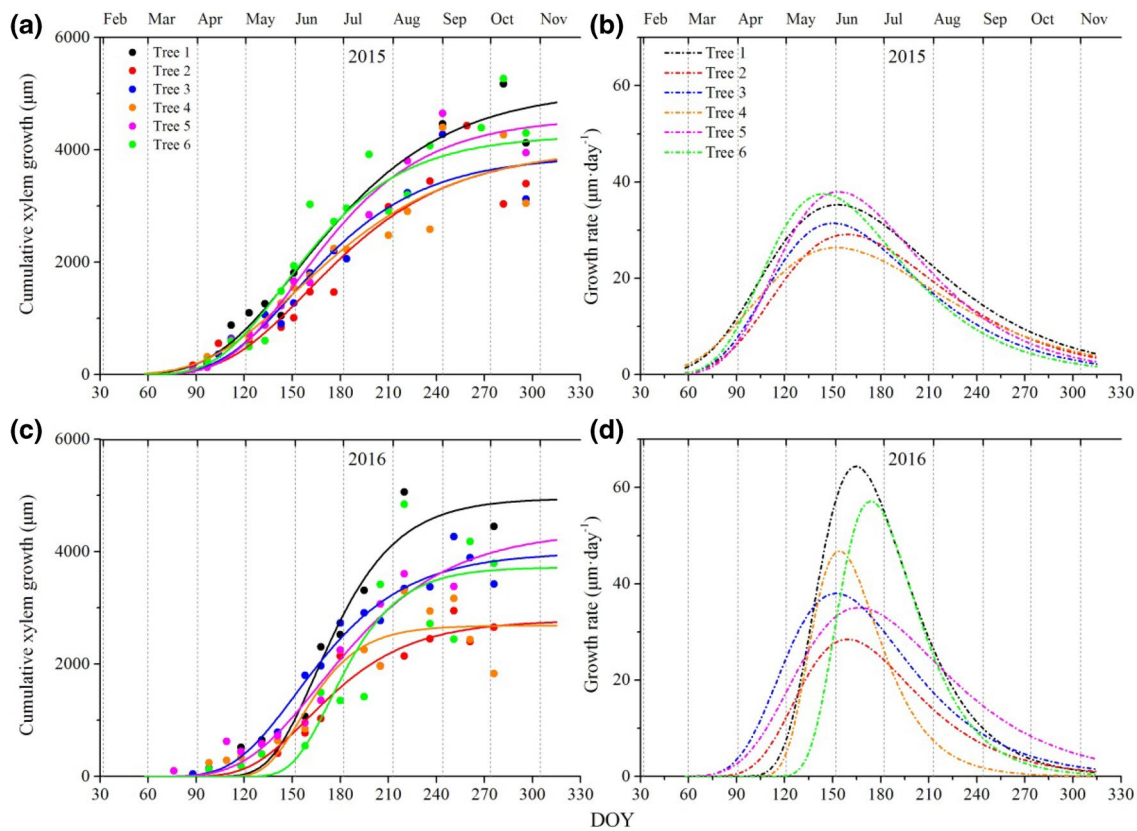
Fig. 3 Xylem growth modeled by the Gompertz function for *Quercus variabilis* in 2015 and 2016. **a, c** Cumulative xylem growth (solid line), and **b, d** daily xylem width growth rate (dashed line). Dots rep-resent micro-core data from six monitored trees in the 2015 and 2016 growing seasons

rate (r_m) was 20 ± 2.9 μm day^{-1} in 2015, which was less than 28 ± 8.4 μm day^{-1} in 2016. Additionally, greater dif-ferences among the six trees were observed in 2016 than in 2015, which showed in both the date and the value of the maximum growth rate.

Wood anatomy

No differences were found between the years ($p = 0.235$) or cambial ages ($p = 0.159$) in DFEV (Table 3), which were 390 ± 68.8 μm and 375 ± 82.3 μm in 2015 and 2016, respectively. In contrast, significant differences were found between years in RW ($p < 0.01$) but not for cambial ages ($p = 0.114$). RW in 2015 and 2016 was 2597 ± 1034.7 μm and 2583 ± 1207.0 μm, respectively. Moreover, the correla-tion coefficient between DFEV and RW was significant and positive ($r = 0.326$, $N = 74$, $p < 0.01$).

Environmental conditions in 2015 and 2016

The environment in 2015 and 2016 showed distinct differ-ences at the start of the growing season in spring (Febru-ary–April), and 2016 had a warmer but drier spring than

Table 3 Contribution of the year, cambial age, and their interaction on the mean diameter of the first row of earlywood vessels (DFEV) and ring width (RW) for *Quercus variabilis* (2009–2016)

	df	chisq	*p* value
(a) DFEV			
Year	5	1.410	0.235
Cambial age	5	1.981	0.159
Year × Cambial age	6	0.205	0.651
(b) RW			
Year	5	7.018	**0.008**
Cambial age	5	2.504	0.114
Year × Cambial age	6	1.884	0.170

Significant difference ($p < 0.05$) is marked bold

2015, including 0.4 and 2.2 °C higher monthly mean daily air temperatures in March and April, respectively, compared to 2015 (Fig. 4). Meanwhile, an extended drought period from December 2015 to early April 2016 (Fig. 5) caused an SPEI with continuously negative values that reached a minimum value of − 1.9 in March, when precipitation was only 0.5 mm. In contrast, 2015 had a much moister spring,

Fig. 4 Standardized precipitation evapotranspiration index (SPEI), soil water content (SWC), precipitation and air temperature on a monthly scale in 2015 and 2016
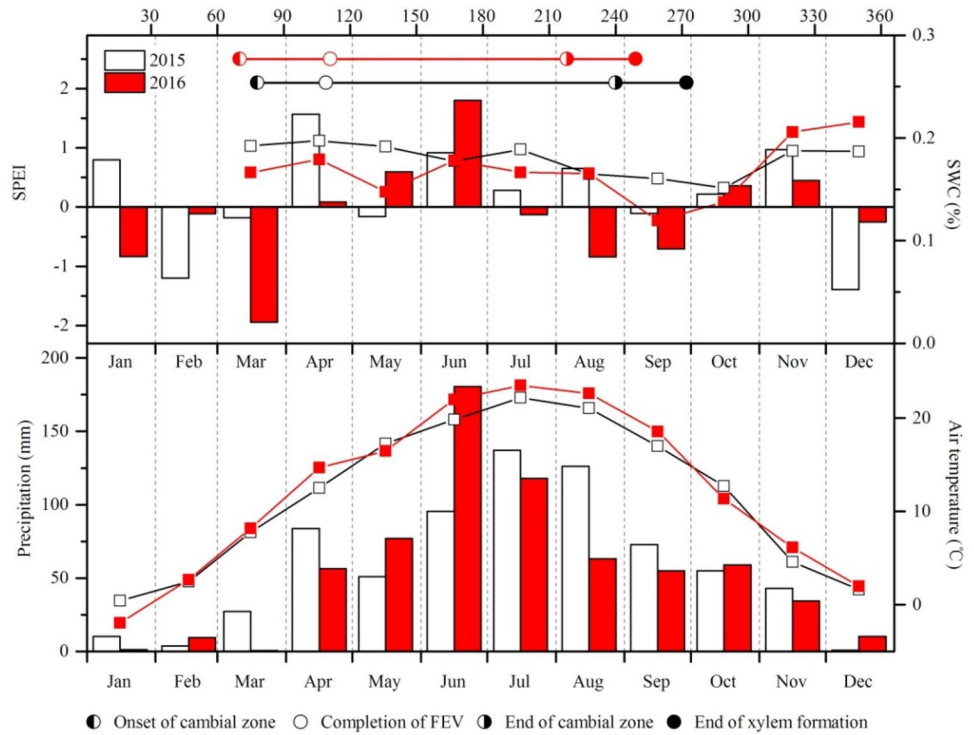

Fig. 5 Daily environmental parameters at the study site in 2015 and 2016, including mean air and soil temperature (T_a, T_s), the sum of precipitation (P), mean relative humidity (RH), and mean soil water content (SWC). Data in **a, c** and **d** were obtained from the nearest State standard meteorological station in Lushi. Data in **b** and **e** were recorded by HOBO in the study site at Xiong'er Mountain. Vertical lines in (**a**) represent the $Date_{Ta>5}$ (the first date on which the daily mean air temperature was warmer than 5 °C for five consecutive days) in 2015 (black line) and 2016 (red line)
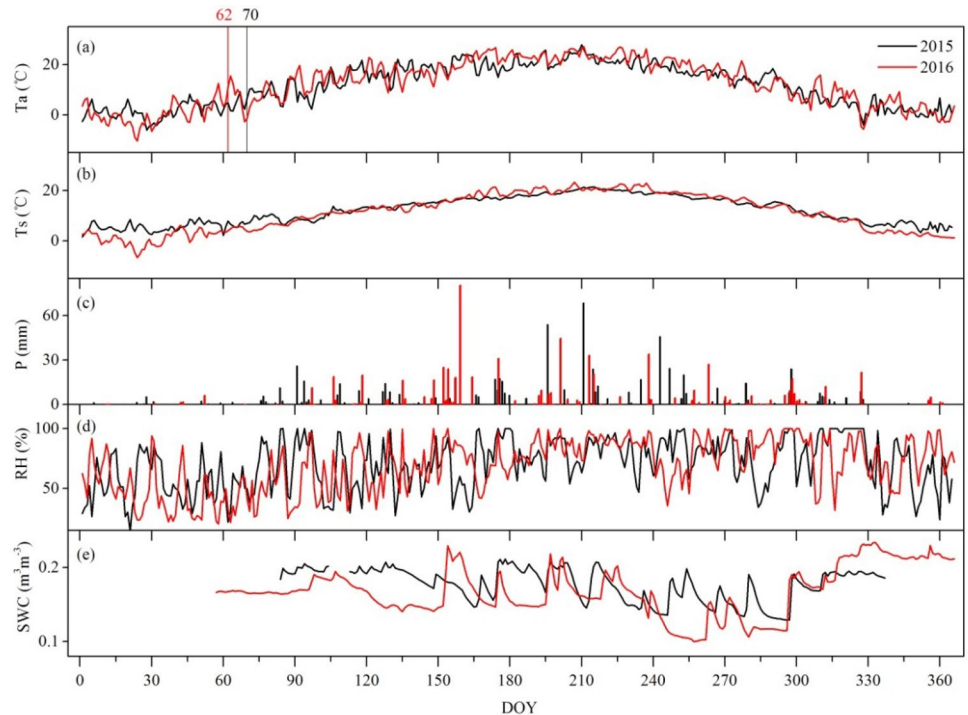
with near-positive SPEI and a higher SWC value (*ca*. 20%) in March and April.

In the main growing season (May–July), precipitation was slightly higher in 2016 (375.5 mm) than in 2015 (283.5 mm). However, its distribution was more uneven in 2016, in which 27% of the annual precipitation fell in June

2016 (14% in June 2015). High evaporation and low precipitation in August and September 2016 caused a negative SPEI value and lower SWC (Fig. 4).

$Date_{Ta>5}$ in 2015 and 2016, which represent the thermal condition, appeared on March 11 and March 2, respectively (Fig. 5a). Thermal requirements (GDD) for the onset

of cambial cell production were similar in 2015 and 2016 ($GDD_{2015} = 30.8 \pm 0$; $GDD_{2016} = 37.0 \pm 2.5$; $p = 0.050$). However, different GDD requirements for FEV completion were observed between the 2 years ($GDD_{2015} = 186.9 \pm 34.0$; $GDD_{2016} = 266.0 \pm 50.3$; $p < 0.05$).

Environment–xylem growth relationship

Xylem growth showed positive and significant responses to air temperature, soil temperature and precipitation in 2016 (Table 4). However, xylem growth responded differently to precipitation between the years. In 2015, no significant correlation was observed with precipitation ($r = 0.335$, $N = 23$, $p > 0.05$), whereas positive and significant correlations were found only with air and soil temperature.

Discussion

Impact of thermal conditions on the onset of xylogenesis

Chinese cork oak exhibited similar thermal requirements for the onset of cambial cell production between the 2 years ($GDD_{2015} = 30.8 \pm 0$; $GDD_{2016} = 37.0 \pm 2.5$; $p = 0.050$), in spite of the warmer air temperature in 2016. $Date_{Ta>5}$ in 2015 and 2016 occurred at different times, March 2 (DOY 70) and March 11 (DOY 62), respectively (Fig. 5b). Interestingly, 8 days after $Date_{Ta>5}$, trees began synchronous cambial cell division in both years (Table 2).

This is consistent with some previous works that found thermal conditioning drives xylem growth resumption for similar oak species (Pérez-de-Lis et al. 2016). Temperature has been identified as the dominant environmental factor in triggering tree phenology at high altitudes/latitudes (Jiang et al. 2015; Körner 2006). However, some studies challenged this general belief that temperature is the only driver of growth reactivation. Various studies have demonstrated that thermal conditioning (Seo et al. 2008), precipitation (Ren et al. 2015) and/or photoperiod (Maurya and Bhalerao 2017) could determine the onset of cambial activity. On the other hand, an interaction between these environmental factors for the onset of xylogenesis was further reported, such as thermal status and precipitation in cold and drought-prone regions (Ren et al. 2018), and photoperiod and temperature in humid extra-tropical climates (Basler and Körner 2014). However, counterbalancing of thermal and precipitation factors during the onset was not confirmed in our study, as cambial cell division started under different precipitation conditions in the 2 years, probably suggesting weak precipitation influence on the onset of xylogenesis.

Linkage between spring precipitation and FEV formation

The earlier onset but delayed completion of FEV in 2016 led to the synchronous end of formation in 2015 and 2016 ($Z = -0.339$, $p = 0.734$, Table 2). This probably suggests a weak thermal influence on the completion of FEV compared to the onset of cambial cell divisions because different GDD requirements for FEV completion were observed between the 2 years ($GDD_{2015} = 186.9 \pm 34.0$; $GDD_{2016} = 266.0 \pm 50.3$; $p < 0.05$).

In the drought year, *Q. variabilis* finished FEV formation in mid-April, when precipitation increased and SPEI changed from negative to positive ($SPEI_{March\,2016} = -1.9$, $SPEI_{April\,2016} = 0.1$, Fig. 4). Our results provide support for the hypothesis that the FEV, especially its duration, is sensitive to spring climate conditions since the secondary wall formation of FEV in 2016 completed 1–2 weeks after two moderate rain events (11.6 mm on April 5 and 18.8 mm April 14). As previously reported, to some extent, trees may slow down the growth rate of EV formation according to the moisture condition (Lavrič et al. 2017). Once EV formed, most of them are available to contribute to the water transport (Takahashi et al. 2013). Thus, under warm but severe water-deficit conditions, the earlier formation of EV would add to the risk of drought-induced embolisms in trees.

Besides the duration of FEV formation, the relationship between the diameter of FEV and precipitation has been widely studied. In drought-prone areas, narrow vessels are formed to reduce the risk of cavitation (Borghetti et al. 2017). However, recent work has challenged this paradigm by pointing out that similar or even larger size of EV was found under drought conditions (Gričar et al. 2013; Pérez-de-Lis et al. 2018). The size of vessels under drought stress may be a consequence of the duration and rate in the period of cell enlargement, rather than the period of secondary wall deposition (Cuny et al. 2014). This may explain why the mean diameter of FEV was similar in our study under different spring precipitation conditions. In the warmer spring of 2016, the larger the vessels due to the earlier reactivation, the more effective they are at water transport, but drought stress would impede growth rates, resulting in narrower

Table 4 Pearson correlation coefficients between environmental factors and xylem formation of *Quercus variabilis* in 2015 and 2016

Year	$T_{a\,mean}$	$T_{s\,mean}$	P	RH	SWC
2015	**0.805**[**]	**0.673**[**]	0.335	0.242	0.174
2016	**0.600**[**]	**0.544**[*]	**0.621**[**]	0.369	0.158

SWC soil water content, *P* precipitation, T_a air temperature, T_s soil temperature

* and ** represent the significance level of 0.05 and 0.01, respectively, and are marked as bold; $N = 23$ and $N = 21$ for 2015 and 2016, respectively

vessels that are safer in hydraulic conductivity (Pérez-de-Lis et al. 2016). Therefore, vessel size is the trade-off between hydraulic efficiency and hydraulic safety (Zanne et al. 2006), which highlights the potential of vessel features (width/structure) time series for the study of intra-annual variation in climatic conditions (Verheyden et al. 2005).

Impact of drought on the end of xylem formation

As hypothesized, drought conditions in late summer/early autumn caused early completion of cambial cell production, which led to a shorter growing season in 2016. Significantly earlier cessation of cambial cell production and xylem formation in 2016 compared to 2015 ($p < 0.05$, Table 2) can be related to lower precipitation amounts occurring during late summer 2016. In the environment–xylem growth relationship analysis, precipitation was the main environmental factor driving xylem growth in the drought year (Table 4). Meanwhile, in the moist year, no significant correlation could be detected between precipitation and xylem growth, which may imply that precipitation in 2015 was appropriate for tree growth, without apparent limitations. On the other hand, June was the main growing period, during which 33.5% of xylem growth occurred in rainfall-abundant conditions in 2016 (180.5 mm), in contrast with the 21.6% growth observed in 2015 (95.5 mm).

Many studies have observed that water deficits during summer cause early cessation of cambial activity in conifers and broadleaves trees (Oberhuber et al. 2014; Scharnweber et al. 2011). The environmental factors controlling xylem formation at the beginning and the end of tree growth were different (Thibeault-Martel et al. 2008). The temperature at cessation is obviously still advantageous to growth, which indicates that different physiological mechanisms are involved in the onset and cessation periods. Several studies have revealed that tree growth cessation is mainly controlled by the photoperiod since simultaneous cessations are found along different altitudes (Moser et al. 2010) or in different years (Gruber et al. 2009). However, our results conflict with this synchronous cessation pattern, which likely means that the growth cessation of *Q. variabilis* is seldom determined by the photoperiod.

With respect to oak phenology, Hill et al. (1995) pointed out that oak trees rely on the stored carbohydrate resources (starch) from the previous year to initiate the radial growth before any leaves are present to produce new photosynthate for growth. Therefore, when under severe summer droughts, oak trees may trigger an earlier cessation of growth in response to decreased carbon gain (Bréda et al. 2006), and to adjust carbon reserves for the following year (Barbaroux and Bréda 2002). The impact of drought on the amount of carbohydrate reserve available for the growth of Chinese cork oak is, however, largely unknown but may also exist

since earlier end of xylem growth under summer drought was observed.

High variability of growth among trees in drought year

Higher growth variability among six trees was observed in 2016 (Fig. 3), especially for the growth rate, which may be an adaptation of trees to different stress factors. According to other studies, these between-tree growth differences can be attributable to both abiotic and biotic factors (Lupi et al. 2014). Under drought conditions, water availability strongly affected tree growth and led to considerable variability between the trees (Jochner et al. 2017). We observed a significant correlation between precipitation and xylem growth in the 2016 drought year but not in the 2015 moist year. A similar result was observed by Latreille et al. (2017), who found no significant variability among individuals except for the response to summer precipitation in the current year.

On the other hand, tree genetics, cambial age, social status or neighborhood interaction, are also associated with the among-tree growth variability. As reported, species interaction was considered as a major factor in controlling the treeline dynamics of the Tibetan Plateau (Liang et al. 2016). Compared to intermediate and suppressed trees, dominant trees have a faster growth rate and produce more xylem cells (Rathgeber et al. 2011). In this study, these trees were selected from an even-aged group and were dominant or co-dominant; thus, the effects of cambial age or social status were expected to be very limited. However, the difference in selected trees between the 2 years may partly explain the differences in growth. Younger cambial-age trees were selected in 2016, the year when greater growth variations were shown.

Conclusions

To our knowledge, this is the first study to address the effect of spring precipitation on the formation of the first row of earlywood vessels (FEV) in ring-porous species under a monsoon climate. The results mainly confirmed our hypothesis that the growth rate of FEV in *Q. variabilis* is probably an adaptive response to water-stress conditions since there was an early onset of FEV formation, but completion was delayed until the spring drought was alleviated. However, the FEV diameter did not significantly differ under different spring precipitation conditions, suggesting that vessel size may be a trade-off between hydraulic efficiency and hydraulic safety. Earlier reactivation under warm temperature is expected to produce wider vessels, which are more efficient, whereas drought stress would impede growth rates, resulting in narrower vessels, which have greater hydraulic safety. Our

results suggest that *Q. variabilis* has the ability to shift the process of earlywood formation under drought. However, to better understand how ring-porous species may respond to climatic instability, longer temporal and spatial monitoring is still needed.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

References

Barbaroux C, Bréda N (2002) Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. Tree Physiol 22:1201–1210

Basler D, Körner C (2014) Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. Tree Physiol 34:377–388

Bates DM, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4

Battipaglia G, De Micco V, Brand WA, Saurer M, Aronne G, Linke P, Cherubini P (2014) Drought impact on water use efficiency and intra-annual density fluctuations in *Erica arborea* on Elba (Italy). Plant Cell Environ 37:382–391

Borghetti M, Gentilesca T, Leonardi S, van Noije T, Rita A (2017) Long-term temporal relationships between environmental conditions and xylem functional traits: a meta-analysis across a range of woody species along climatic and nitrogen deposition gradients. Tree Physiol 37:4–17

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625–644

Cao XX, Ding SY, Li HM (2003) A study on vegetation in the State-owned tree farm of Quan bao Mountain in Luoning, Henan province. Henan Sci 21:183–186 (in Chinese with English abstract)

Corcuera L, Camarero JJ, Sisó S, Gil-Pelegrín E (2005) Radial-growth and wood-anatomical changes in overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape. Trees Struct Funct 20:91–98

Cuny HE, Rathgeber CB, Lebourgeois F, Fortin M, Fournier M (2012) Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France. Tree Physiol 32:612–625

Cuny HE, Rathgeber CBK, Frank D, Fonti P, Fournier M (2014) Kinetics of tracheid development explain conifer tree-ring structure. New Phytol 203:1231–1241

Deslauriers A, Morin H (2005) Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. Trees Struct Funct 19:402–408

Deslauriers A, Rossi S, Anfodillo T, Saracino A (2008) Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. Tree Physiol 28:863–871

Eilmann B, Weber P, Rigling A, Eckstein D (2006) Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. Dendrochronologia 23:121–132

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, Pannatier EG, Rigling A (2011) Drought alters timing, quantity, and quality of wood formation in Scots pine. J Exp Bot 62:2763–2771

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 8:12

Ferrio JP, Florit A, Vega A, Serrano L, Voltas J (2003) Δ^{13}C and tree-ring width reflect different drought responses in *Quercus ilex* and *Pinus halepensis*. Oecologia 137:512–518

Fonti P, García-González I (2004) Suitability of chestnut earlywood vessel chronologies for ecological studies. New Phytol 163:77–86

Fonti P, Treydte K, Osenstetter S, Frank D, Esper J (2009) Frequency-dependent signals in multi-centennial oak vessel data. Paleogeogr Paleoclimatol Paleoecol 275:92–99

Fonti P, von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytol 185:42–53

García-González I, Fonti P (2006) Selecting earlywood vessels to maximize their environmental signal. Tree Physiol 26:1289–1296

González-González BD, García-González I, Vázquez-Ruiz RA (2013) Comparative cambial dynamics and phenology of *Quercus robur* L. and *Q. pyrenaica* Willd. in an Atlantic forest of the northwestern Iberian Peninsula. Trees Struct Funct 27:1571–1585

González-González BD, Rozas V, García-González I (2014) Earlywood vessels of the sub-Mediterranean oak *Quercus pyrenaica* have greater plasticity and sensitivity than those of the temperate *Q. petraea* at the Atlantic-Mediterranean boundary. Trees-Struct Funct 28:237–252

Gričar J (2010) Xylem and phloem formation in sessile oak from Slovenia in 2007. Wood Res 55:15–22

Gričar J, de Luis M, Hafner P, Levanič T (2013) Anatomical characteristics and hydrologic signals in tree-rings of oaks (*Quercus robur* L.). Trees-Struct Funct 27:1669–1680

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

Gruber A, Baumgartner D, Zimmermann J, Oberhuber W (2009) Temporal dynamic of wood formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables. Trees Struct Funct 23:623–635

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspect. Plant Ecol Evol Syst 4:97–115

Hacke UG, Spicer R, Schreiber SG, Plavcova L (2017) An ecophysiological and developmental perspective on variation in vessel diameter. Plant Cell Environ 40:831–845

Hill SA, Waterhouse JS, Field EM, Switsur VR, Rees TA (1995) Rapid recycling of triose phosphates in oak stem tissue. Plant Cell Environ 18:931–936

Jiang Y, Zhang Y, Guo Y, Kang M, Wang M, Wang B (2015) Intra-annual xylem growth of *Larix principis-rupprechtii* at its upper and lower distribution limits on the Luyashan mountain in north-central China. Forests 6:3809–3827

Jochner M, Bugmann H, Notzli M, Bigler C (2017) Among-tree variability and feedback effects result in different growth responses to climate change at the upper treeline in the Swiss Alps. Ecol Evol 7:7937–7953

King G, Fonti P, Nievergelt D, Büentgen U, Frank D (2013) Climatic drivers of hourly to yearly tree radius variations along a 6 °C natural warming gradient. Agric For Meteorol 168:36–46

Körner C (2006) Significance of temperature in plant life. In: Morison JIL, Morecroft MD (eds) Plant growth and climate change. Blackwell Publishing Ltd, Oxford, pp 48–69

Kozlowski TT, Pallardy SG (2002) Acclimation and adaptive responses of woody plants to environmental stresses. Bot Rev 68:270–334

Latreille A, Davi H, Huard F, Pichot C (2017) Variability of the climate-radial growth relationship among *Abies alba* trees and populations along altitudinal gradients. For Ecol Manage 396:150–159

Lavrič M, Eler K, Ferlan M, Vodnik D, Gričar J (2017) Chronological sequence of leaf phenology, xylem and phloem formation and sap flow of *Quercus pubescens* from abandoned karst grasslands. Front Plant Sci 8:11

Liang E, Wang YF, Piao SL, Lu XM, Camarero JJ, Zhu HF, Zhu LP, Ellison AM, Ciais P, Penuelas J (2016) Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. Proc Natl Acad Sci USA. 113:4380–4385

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

Lupi C, Rossi S, Vieira J, Morin H, Deslauriers A (2014) Assessment of xylem phenology: a first attempt to verify its accuracy and precision. Tree Physiol 34:87–93

Lyu S, Wang X, Zhang Y, Li Z (2017) Different responses of Korean pine (*Pinus koraiensis*) and Mongolia oak (*Quercus mongolica*) growth to recent climate warming in northeast China. Dendrochronologia 45:113–122

Ma C, Zhang W, Wu M, Xue Y, Ma L, Zhou J (2013) Effect of aboveground intervention on fine root mass, production, and turnover rate in a Chinese cork oak (*Quercus variabilis* Blume) forest. Plant Soil 368:201–214

Maurya JP, Bhalerao RP (2017) Photoperiod- and temperature-mediated control of growth cessation and dormancy in trees: a molecular perspective. Ann Bot 120:351–360

Michelot A, Simard S, Rathgeber C, Dufrêne E, Damesin C (2012) Comparing the intra-annual wood formation of three European species (*Fagus sylvatica, Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. Tree Physiol 32:1033–1045

Moser L, Fonti P, Büentgen U, Esper J, Luterbacher J, Franzen J, Frank D (2010) Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. Tree Physiol 30:225–233

Oberhuber W, Gruber A, Kofler W, Swidrak I (2014) Radial stem growth in response to microclimate and soil moisture in a drought-prone mixed coniferous forest at an inner Alpine site. Eur J Forest Res 133:467–479

Pérez-de-Lis G, Rossi S, Vázquez-Ruiz RA, Rozas V, García-González I (2016) Do changes in spring phenology affect earlywood vessels? Perspective from the xylogenesis monitoring of two sympatric ring-porous oaks. New Phytol 209:521–530

Pérez-de-Lis G, Rozas V, Vázquez-Ruiz RA, García-González I (2018) Do ring-porous oaks prioritize earlywood vessel efficiency over safety? Environmental effects on vessel diameter and tyloses formation. Agric For Meteorol 248:205–214

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

Prislan P, Schmitt U, Koch G, Gričar J, Čufar K (2011) Seasonal ultrastructural changes in the cambial zone of beech (*Fagus sylvatica*) grown at two different altitude. IAWA J 32:443–459

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rathgeber CBK, Rossi S, Bontemps J-D (2011) Cambial activity related to tree size in a mature silver-fir plantation. Ann Bot 108:429–438

Ren P, Rossi S, Gričar J, Liang E, Čufar K (2015) Is precipitation a trigger for the onset of xylogenesis in *Juniperus przewalskii* on the north-eastern Tibetan Plateau? Ann Bot 115:629–639

Ren P, Rossi S, Camarero JJ, Ellison AM, Liang E, Penuelas J (2018) Critical temperature and precipitation thresholds for the onset of xylogenesis of *Juniperus przewalskii* in a semi-arid area of the north-eastern Tibetan Plateau. Ann Bot 121:617–624

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

Rossi S, Deslauriers A, Gričar J, Seo J-W, Rathgeber CBK, Anfodillo T, Morin H, Levanic T, Oven P, Jalkanen R (2008) Critical temperatures for xylogenesis in conifers of cold climates. Glob Ecol Biogeogr 17:696–707

Rossi S, Girard M-J, Morin H (2014) Lengthening of the duration of xylogenesis engenders disproportionate increases in xylem production. Glob Change Biol 20:2261–2271

Sass-Klaassen U, Eckstein D (1995) The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. Trees-Struct Funct 9:247–252

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schroeder C, Wilmking M (2011) Drought matters-declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. For Ecol Manag 262:947–961

Seo J-W, Eckstein D, Jalkanen R, Rickebusch S, Schmitt U (2008) Estimating the onset of cambial activity in Scots pine in northern Finland by means of the heat-sum approach. Tree Physiol 28:105–112

Stojanović M, Sánchez-Salguero R, Levanič T, Szatniewska J, Pokorný R, Linares JC (2017) Forecasting tree growth in coppiced and high forests in the Czech Republic. The legacy of management drives the coming *Quercus petraea* climate responses. For Ecol Manage 405:56–68

Takahashi S, Okada N, Nobuchi T (2013) Relationship between the timing of vessel formation and leaf phenology in ten ring-porous and diffuse-porous deciduous tree species. Ecol Res 28:615–624

Thibeault-Martel M, Krause C, Morin H, Rossi S (2008) Cambial activity and intra-annual xylem formation in roots and stems of *Abies balsamea* and *Picea mariana*. Ann Bot 102:667–674

Vaganov EA, Hughes MK, Shashkin AV (2006) Growth dynamics of conifer tree rings: images of past and future environments (ecological studies). Springer, Berlin, Heidelberg, Germany

Verheyden A, De Ridder F, Schmitz N, Beeckman H, Koedam N (2005) High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. New Phytol 167:425–435

Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J Clim 23:1696–1718

Zanne AE, Sweeney K, Sharma M, Orians CM (2006) Patterns and consequences of differential vascular sectoriality in 18 temperate tree and shrub species. Funct Ecol 20:200–206

Zhang YM, Xiao FJ (2010) Study on precipitation and temperature change in western Henan Mountain area. J Nat Res 25:2132–2141 (in Chinese with English abstract)

Zhang Y, Jiang Y, Wang B, Jiao L, Wang M (2018) Seasonal water use by *Larix principis-rupprechti*i in an alpine habitat. For Ecol Manage 409:47–55