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Environment Controls Seasonal and Daily Cycles of Stem Diameter Variations in Portuguese Oak (*Quercus faginea* Lambert)

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Abstract: Tree growth takes place at different time scales ranging from hours to days. To understand growth responses to climate, continuous high-resolution measurements of tree diameter variations are needed, which are usually obtained with automatic dendrometers. Here, we monitored stem diameter increment of *Quercus faginea* Lambert growing in central Portugal to determine the effect of climate on daily and seasonal growth dynamics during the 2013 growing season. Stem diameter variation presented a unimodal seasonal pattern characterized by an exponential phase in spring followed by a plateau during summer, interrupted by an abrupt increase in autumn caused by rainfall. Stem diameter increment started in March when the temperature was above 10 °C. Stem diameter variation showed a double climatic constrain, with temperature limiting growth in spring and precipitation in summer. The amplitude of the daily cycles of stem variation was higher in summer, as well as the expansion phase length, meaning that trees needed longer to replenish the water lost through transpiration during the day. The absence of a pronounced stem shrinkage during the summer suggests that *Q. faginea* has access to water over the whole growing season. Our results indicate that this species relies on deep soil water reserves and can be physiologically active during summer drought.

Keywords: dendrometers; growth dynamics; Mediterranean; native forest; stem growth diameter

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1. Introduction

Tree secondary growth is probably the most studied process in forest science, often relying on tree-ring-based methods that investigate the effect of climatic forcing on tree growth in correlative approaches using monthly climate data together with annual tree-ring parameters [1]. However, cambial activity and wood formation take place at different time scales, from hours to days, highlighting a different resolution between tree growth and the analysis of climate forcing. To bridge this gap, studies on the intra-annual dynamics of wood formation are necessary. Xylogenesis studies are based on (bi)-weekly observations of the cambium and developing xylem and have significantly improved the time resolution of tree growth studies and our understanding of the effect of climatic forcing on wood formation [2–5]. Another method frequently used to monitor intra-annual wood formation is monitoring stem variation using dendrometers [6–9].

The variation in stem size measured by dendrometers is caused by irreversible growth due to the addition of new wood and bark cells and by water-related contraction and expansion of the living stem tissues [10–12]. The contribution of xylem tissue to reversible shrinkage and swelling of the stem is species-dependent [13], and although there is still debate on its contribution, most studies report it to be below 10% [14,15]. This low contribution is explained by the higher density of xylem compared to the storage tissues outside xylem. Due to its dual nature, it is difficult to estimate cambial activity and to precisely determine the onset and cessation dates of growth from stem diameter variation [16]. However, by monitoring the reversible variation in the stem diameter, it is possible to infer the tree water balance, gaining insights into the tree's physiological functioning.

The diel variation in stem diameter reflects water movement due to transpiration during the day and the replenishment of the stem tissues during the night [17]. There is a time lag between water loss by leaf transpiration and water uptake by the roots, which is accounted for by an internal reservoir, the water present in the living tissues of the stem [18,19]. This internal reservoir can be depleted and subsequently replenished on a daily basis, causing the stem diameter to shrink and swell accordingly [20,21]. The diel variations in stem diameter also reflect environmental conditions [22,23]. As the growing season progresses and the environment becomes warmer, the daily cycle adjusts its timings and amplitude to current environmental conditions. In a study on *Pinus pinaster* Aiton growing under the Mediterranean climate, Vieira et al. [22] observed that the amplitude of the daily cycles was ten times higher during summer drought. Similar observations were made in *Larix decidua* Mill. and *Picea abies* (L.) H. Karst. across a temperature gradient in Switzerland, where the amplitude of the daily cycle was nine times smaller on rainy days and 40% larger on warmer days [23].

It is undeniable that the climate is changing, and that these changes pose a major challenge to European forests [24]. In the next 100 years, climate projections for the Mediterranean region predict an increase in the mean annual temperature from 3.3 to 4.1 °C, a decrease of 11% to 17% of the total annual precipitation and increased frequency and intensity of extreme events [25]. Determining the effect of a changing climate on tree growth ultimately depends on our understanding of wood formation processes and how they are driven by environmental conditions. In this context, monitoring intra-annual radial growth with high temporal resolution will provide valuable insights into tree physiological functioning that can help predict forest responses under climate change, as they allow the identification of effects of environmental fluctuations on stem growth and tree water balance.

Quercus faginea Lambert, Portuguese or Lusitanian oak, is native to Portugal and Spain and is also found in the Maghreb in Northern Africa. It is a winter deciduous, ring-porous species that is found in mixed forests with other oaks such as *Q. coccifera* L., *Q. pyrenaica* L., *Q. ilex* L. and *Q. suber* L., as well as with other species, e.g., *Castanea sativa* Mill. and *P. pinaster*. *Quercus faginea* can be considered as an example of a deciduous oak adapted to Mediterranean-type climates [26]. *Quercus faginea* is an anisohydric species [27] with 'water-spending' behaviour [28]. Decreased soil water availability during summer drives vegetative activity reductions, making this species highly vulnerable to increased aridity due to global climatic change [29]. Its distribution was abundant in former times, and its wood was used in the industry and shipbuilding. However, extensive usage and replacement by plantation species such as *Eucalyptus* sp. and *Pinus* sp. has led to a decline of this species [30]. The area occupied by *Q. faginea* and *Q. robur* in Portugal represents 6% of the Portuguese forest, corresponding to 224 k hectares [31]. *Quercus faginea* forests are found nowadays in fragmented relics in agricultural and forest landscapes [32]. These relic forests have a high conservation value because they are fragments of the Portuguese native forest and have an important biogenetic value. Thus, the aim of this research is to study *Q. faginea* stem diameter variation to understand the growth dynamics of this species and to predict how climate change might influence the seasonal and daily cycles of stem diameter variation.

In this study we monitored the stem diameter variation of *Q. faginea* trees from a relic Portuguese forest to determine how environmental factors influence the daily and seasonal cycles of stem diameter variation. The Portuguese climate is Mediterranean, characterized by mild winters and a pronounced summer drought. Previous studies have reported a bimodal growth pattern where evergreen trees (*P. pinaster, P. halepensis* and *Q. ilex*) adjust their period of cambial activity and wood formation to avoid the summer drought and to take advantage of favourable conditions in autumn [33–35], but this bimodal pattern may be considered facultative in some sites or species and can even depend on different climate factors [36]. The bimodal growth pattern was also reported in *Q. faginea* trees growing in a mesic site in Spain [37] and in other oaks also growing in Spain [38]. The study of *Q. faginea* stem diameter variation will allow us to understand the growth dynamics of this species and to determine the influence of climate on the seasonal and daily cycles of stem diameter variation. We hypothesize that (i) stem diameter variation responds mostly to water availability; and (ii) the daily amplitude of stem increment cycles increases with decreasing water availability.

2. Materials and Methods

2.1. Study Site and Data Collection

The study was conducted in Santa Olaia, a relic *Q. faginea* forest in central Portugal (40°10′15″ N, 8°43′02″ W; 25 m a.s.l.) with an area of 8 ha. The study site was located at a low elevation surrounded by the agricultural fields of the Baixo Mondego, flood plains of the Mondego River. It is a mature, closed forest stand, with dominant *Q. faginea* trees and *Q. coccifera* and *Rubus* sp. in the understory. The climate is typically Mediterranean, with precipitation in autumn and winter and a pronounced summer drought (Figure 1A). The mean annual temperature is 16.2 °C, and the total annual precipitation is 848 mm (1984–2013). Daily meteorological data were downloaded from the Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl, accessed on 26 July 2021), using the E-OBS v23.1e data set for the closest grid point to the study site (40.12 N; 8.62 W).

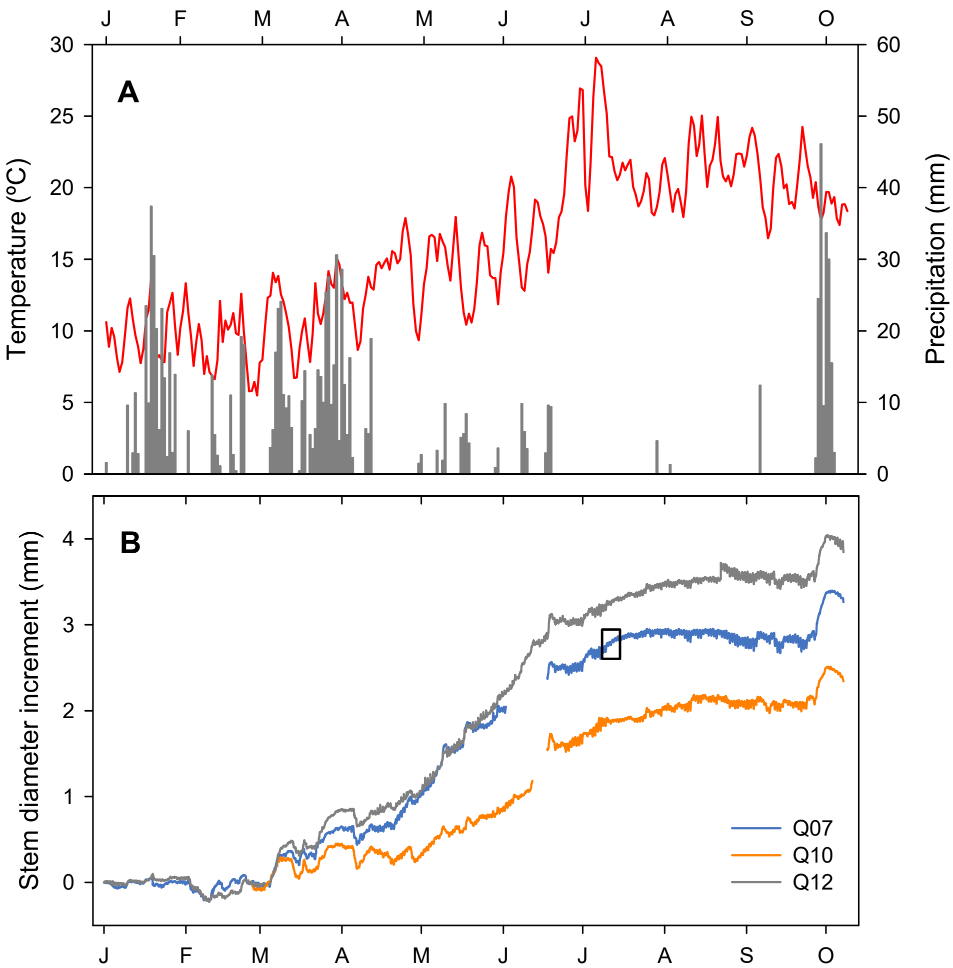

Figure 1. Daily precipitation (grey bars) and mean temperature (red line) (**A**) and seasonal stem diameter increment variation of three *Quercus faginea* Lambert trees growing in Santa Olaia (**B**), from 1 January to 7 October 2013. The square in Q07 corresponds to the period in Figure 2.

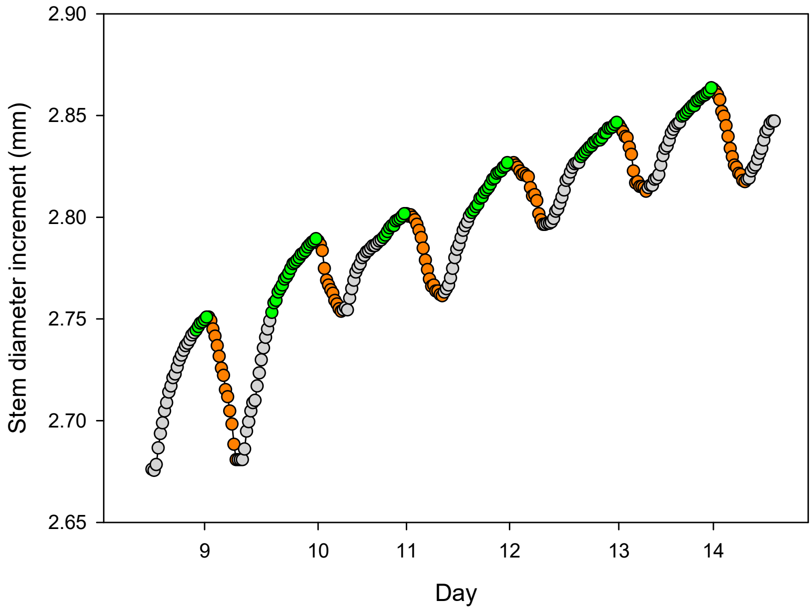

Figure 2. Example of circadian cycles of stem diameter variation. Each cycle is composed of three phases: expansion (white dots), increment (green dots) and contraction (orange dots). Tree Q07 for the week from 9 to 14 July 2013. Period represented by a square in Figure 1B.

From January to October 2013, automatic band dendrometers (UMS, model D6, Munich, Germany) were installed on three *Q. faginea* trees (Q07, Q10 and Q12). Dendrometers were installed in January to allow for a period of adjustment before the start of the growing season. *Quercus faginea* is a winter deciduous species that starts leaf shedding in late summer (August), which is why stem diameter variation monitoring ended in October. The selected trees represented the forest stand in terms of height (15.3 ± 1.1 m), diameter at breast height (33.6 ± 5.5 cm) and age (52.6 ± 0.5 years). The dendrometers were installed on the tree stem, at a height of 3 m, to avoid disturbance by people and animals. Before installing the dendrometers, the outermost tissues of the bark were removed to reduce the influence of hygroscopic swelling and shrinkage of the bark and to ensure a close contact with the xylem. A Teflon net and plate were placed around the tree trunk to avoid friction with the bark, below the measuring cable of the dendrometer. The girth cable is made of INVAR steel, a material that presents a temperature elongation of less than 1 µm per meter and Kelvin. Measurements were collected every 30 min and stored in a datalogger. The final dendrometer series presented missing data due to technical problems that occurred during monitoring.

2.2. Data Analysis

The stem diameter variation time series collected with automatic dendrometers were processed following the stem cycle approach [6,39], using the R package dendrometeR [40] for the R computing environment (R Development Core Team, 2021). This approach divides the daily cycle in three distinct phases: contraction, the period between the first maximum radius and the next minimum; expansion, the period from the minimum until the position of the previous maximum value or when the stem reverts to a contraction phase; and radial increment, which can be positive or negative depending on whether the previous maximum was achieved (Figure 2). A cycle was constituted by a contraction phase, followed by expansion and an increment phase, when present. For each cycle of the stem diameter variation, amplitude and duration of each phase were calculated, for each dendrometer. Daily amplitude and increment were calculated by the difference between the maximum and minimum stem diameter variation observed each day and by the difference between the maximum increment between consecutive days, respectively. Daily increment can be positive, negative or zero.

The effects of climatic forcing on daily amplitude and increment was investigated using Spearman's rank-order correlation analysis between daily amplitude and increment of stem diameter variation (the average of the three dendrometers) and mean temperature and precipitation. The correlation scores were determined for the climatic variables of the day of stem diameter variation (t), the previous day ($t - 1$, the two previous days ($t - 2$) and the five previous days ($t - 5$), from January to September. October was not included in the analysis because there was only one week of data. In addition, 21-day moving Spearman's correlations were performed to investigate the possible seasonal responses to climatic conditions (temperature and precipitation).

3. Results

3.1. Climatic Conditions of the Study Year

The study year, 2013, was a wet year, with a total annual precipitation of 1320 mm, 472 mm above the 30-year historical average (Figure 1A). The winter and spring (January to April) precipitation totalled 828 mm, which is very close to the mean annual precipitation of the long-term mean (848 mm), even though, the summer months had almost no precipitation. The mean annual temperature was 14.9 °C, 1.2 °C below the long-term mean. The spring mean temperature was 13.0 °C, 2.2 °C below average, and the summer mean temperature was 20.7 °C, 1.2 °C below average. Although 2013 was a wet year, in the last 10 years (2009–2020) similar annual precipitation was registered, namely in 2014, 2016 and 2018 (Supplementary Material, Figure S1).

3.2. Stem Diameter Variation

Stem diameter seasonal variation showed positive increment starting in March, followed by an exponential phase until July where increment reached a plateau (Figure 1B). In August there was a period of stem shrinkage, which was more evident in dendrometer Q07. At the end of September there was a pronounced positive increment following the first rain after the summer (Figure 1).

The analysis of monthly hourly amplitude of the stem diameter increment reveals that the hours of maximum (swelling) and minimum (shrinkage) amplitude shifted during the growing season (Figure 3). The hour of maximum amplitude (swelling) was observed at 7 a.m. in June and August, at 8 a.m. in July and at 9 a.m. in April, May and September. The hour of minimum amplitude (shrinking) was observed between 2 and 4 p.m. in April and May, whereas in June, July, August and September it occurred between 5 and 6 p.m. March presented a different pattern, without a marked shrinkage in stem diameter. August was the only month with stem shrinkage, where the amplitude of stem diameter increment at the end of the day was lower than at 0 h, whereas in all other months the amplitude was higher at the end of the day than at 0 h (Figure 3). Oppositely, March and May were the two months with the highest positive increment.

The duration of the stem cycle phases also changed during the year (Figure 4). The longest duration of the increment phase was observed in March. April, May and June presented a similar duration of all three phases. July and August presented a shorter duration of the increment phase and a longer duration of the expansion phase. In September the duration of contraction and expansion was similar, but higher than the increment.

3.3. Climatic Signal

Current-day correlation analysis between amplitude and increment and mean temperature and precipitation revealed than amplitude was negatively influenced by April's precipitation and positively influenced by September's temperature (Figure 5). The stem increment responded positively to January, February and March mean temperatures and to February, March, May, June and September precipitation (Figure 5). When considering previous-day effects, it was observed that current-day climatic conditions presented a stronger influence on stem diameter variation than the previous 1, 2 and 5 days (Figure S2).

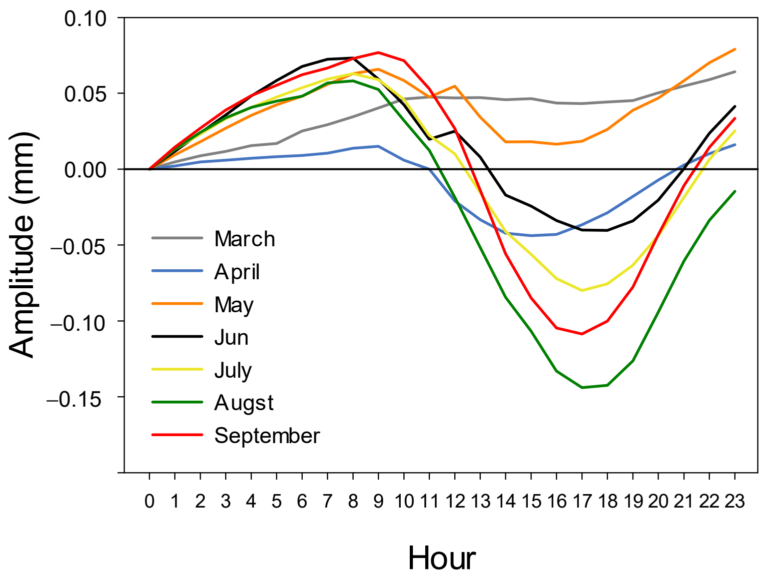

Figure 3. Hourly variation of cumulative stem radius variation starting at 00:00 hours for each month.

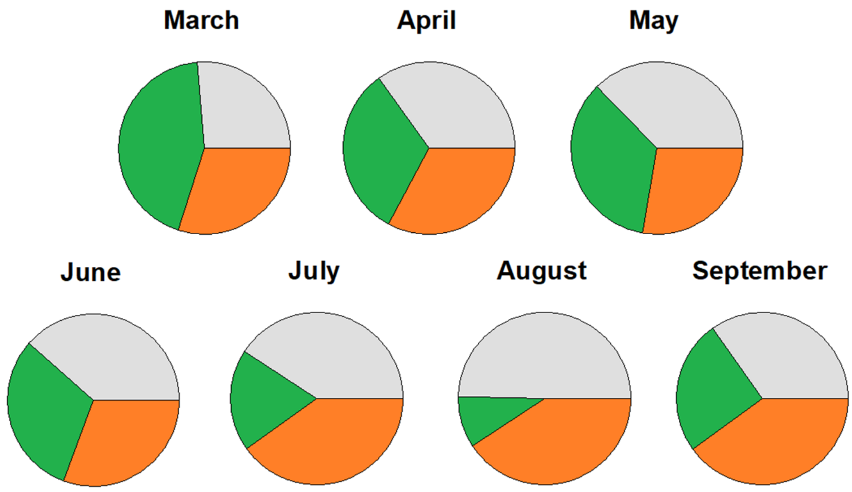

Figure 4. Monthly duration of the three phases of stem radius variation: expansion (grey), increment (green) and contraction (orange).

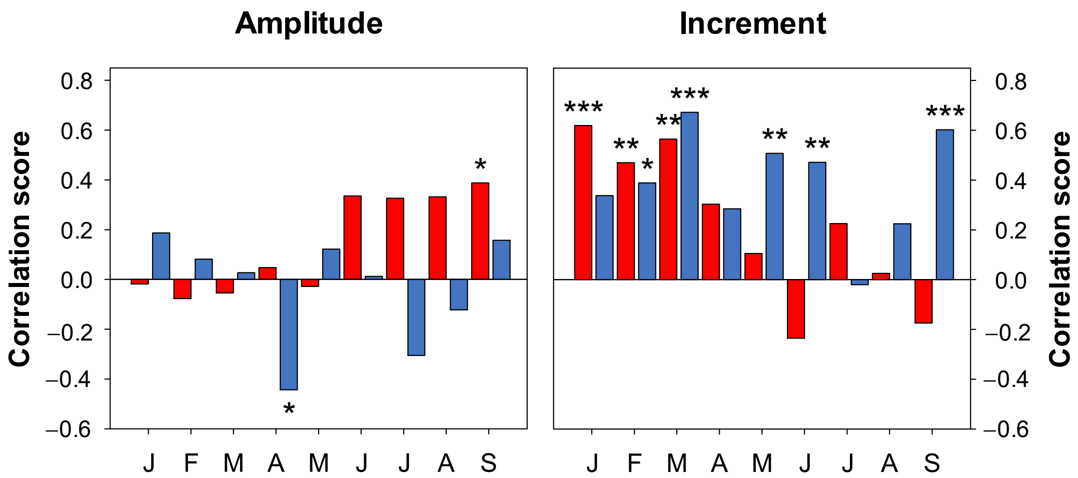

Figure 5. Spearman's rank-order correlations between daily cycle amplitude and increment and mean temperature (red bar) and precipitation (blue bar). Significant correlations are indicated by asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Moving-window correlation analysis detailed the climatic signal obtained in the current-day monthly correlations (Figure 6). Amplitude presented significant positive correlations with February, June and September temperatures and with January, February and May precipitation, and negative ones with January and March temperature and March precipitation. Increment presented a positive response to January, February and June temperatures and to February, March, May, June and September precipitation. September temperature triggered a negative response in increment.

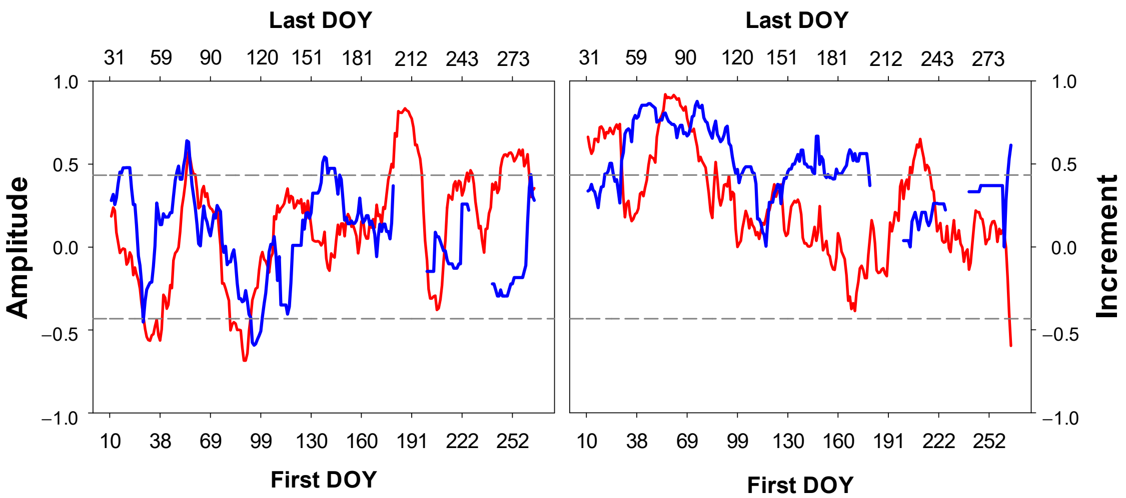

Figure 6. Moving Spearman's correlation analysis between amplitude, increment and mean temperature and precipitation using a 21 day moving window. Red line represents mean temperature, and the blue line represents precipitation. Horizontal dashed lines show the significance level at $p < 0.05$. The x-axis represents the day of the year (DOY), and first (last) day of the moving is indicated in the lower (upper) x-axis.

4. Discussion

Quercus faginea stem increment started in March, when the temperature was above 10 °C. Stem diameter variation was dominated by temperature and precipitation in spring and by precipitation in the summer, presenting a double climatic constrain that rejected our first hypothesis. Amplitude and duration of the stem diameter variation daily cycles changed during the growing season, with wider amplitudes observed in August and September, confirming our second hypothesis.

4.1. Seasonal Pattern

The onset of stem diameter variation was observed in March, when the minimum temperature was above 10 °C. The importance of temperature on cambial activity onset is well described in boreal [3], temperate [41,42] and Mediterranean climate conifers [43]. Although more attention has been given to the study of xylogenesis in conifers, temperature is also the main trigger of cambial reactivation in spring in deciduous tree species [42,44]. Previous studies on the xylogenesis of two ring-porous species (*Q. robur* and *Q. pyrenaica*) growing in northwest Spain [45] have reported the onset of cambial activity and earlywood vessel expansion in mid-March, supporting our findings.

Camarero et al. [37] showed that *Q. faginea* trees growing in a mesic site in Spain had a bimodal growth pattern. In our study site trees seem to present a unimodal growth pattern characterized by an exponential growth phase in spring followed by a plateau in summer. The increment observed in October was probably due to stem and inner bark re-hydration associated with the precipitation events in October. Stem re-hydration following the first rains in late summer and early autumn was also observed in *P. pinaster* growing in central Portugal [22]. However, dendrometer measurements ended in October, and it is not possible to ensure that a second growth peak did not occur.

Contrary to previous findings on *P. pinaster* [22], *Q. faginea* maintained a stable stem diameter variation during the summer months, with no apparent stem shrinkage. *Quercus faginea* is a deep-rooted tree, capable of accessing water not available to other species, namely *Pinus* spp. [46,47]; this capacity allows *Q. faginea* to present high transpiration rates (water-spending strategy) when other species cannot [22]. Compared to evergreen Mediterranean oaks with conservative water-use strategies, this winter deciduous oak is capable of maintaining high water potentials and photosynthetic carbon gains during the summer, extending the period of assimilation until the autumn rains [28].

Although dendrometer monitoring stopped in October, because *Q. faginea* is a winter deciduous tree, it is safe to assume that this species does not present an evident second growth peak in the year of study, as observed in Mediterranean evergreen oaks and pines [34]. However, it is possible that in some years under specific climatic conditions a minor growth peak could be trigger by late-summer and early autumn rains, the so-called facultative bimodal growth pattern [34,36]. Xylogenesis studies in *Q. robur* and *Q. pyrenaica* from northwest Spain reported a minor growth peak in autumn, suggesting the existence of a facultative bimodal pattern [38]. Cambial activity cessation under favourable temperatures for growth suggests that the end of xylem formation is mostly linked to leaf senescence and photoperiod [45]. Leaf senescence can be explained by reduced leaf hydraulic conductance due to cavitation of the vascular system, caused by increased evaporative demand and soil drying or by tyloses deposition in the xylem [48,49]. Although there are several studies emphasizing a link between stem xylem dysfunction and leaf shedding, others have found leaf senescence while stem conductivity remained relatively high, suggesting that other leaf development factors could be responsible for senescence [48].

4.2. Daily Cycles and Its Ecophysiological Meaning

As expected, both the amplitude and duration of stem diameter daily cycle phases changed during the growing season. The highest amplitudes of stem diameter variation were observed in August and September, the warmer and drier months. High amplitudes mean that there is a higher daily variation in stem diameter; the stem shrinks more during the day due to transpiration and expands more during the night, when the internal water storage is re-plenished [20,21]. As previously mentioned, the lack of a stem shrinkage period indicates that the tree could replenish the water lost by transpiration due to its deep root system, despite its water-spending strategy. In fact, although the amplitude of stem diameter variation was higher during the summer, it was not ten times higher, as previously observed in *P. pinaster* [22], *L. decidua* and *P. abies* [23]. The study trees were growing in a relic forest located in a low elevation in the margins of the Mondego River floodplain, which together with a deep rooting system, is indicative of high water availability all year-round. Dendrochronological studies on *Q. faginea* have reported a strong response to previous winter precipitation [50], whereas stem increment studies showed that spring growth rates were influenced by prior winter precipitation and sometimes also by early spring precipitation, indicating the important role of winter precipitation in refilling soil water pools [37].

Although stem shrinkage was only marginally observed in one of the study trees, the duration of the expansion phase was longer in July and August, suggesting that although trees were able to re-plenish the water lost by transpiration, it took longer than in previous months. July and August were the warmest months with the highest potential evapotranspiration rates. In a study comparing stem increment in Mediterranean tree species, Camarero et al. [37] observed that *Q. faginea* growth was very sensitive to spring atmospheric drought, which could explain the longer duration of the expansion phase in the summer months.

4.3. Climate Response

The correlation analysis between climate and stem increment and the amplitude of the daily cycles revealed a double climatic constrain, with temperature dominating growth onset and precipitation spring and summer increment. In winter deciduous trees cambial activity starts before budburst, to ensure efficient water transport before the leaves are fully unfolded and thus before transpiration-induced water transport is reactivated [51]. Cambial onset is mainly triggered by increasing temperature and photoperiod [44], which explains the positive correlations observed between increment and January to March temperatures. The moving correlation analysis highlights the increasing strength of the correlation from February to March, decreasing afterwards when temperatures rise above 10 °C. There is also a positive correlation between increment and February and March precipitation that could be related to the enlargement of the first earlywood vessels [52].

In the second period of stem diameter increment, the summer plateau, correlations between daily increment and precipitation become significant. Our results confirm the observations of Albuixech et al. [53], who reported that *Q. faginea* radial increment, from August to October, responded positively to precipitation. Dendrochronological studies in *Q. faginea* have also shown a positive response of radial growth to January and May precipitation [50].

When considering lagged effects of environmental conditions on stem dynamics, we found that current-day climatic conditions were more important for stem diameter variation than the conditions of the previous 1, 2 and 5 days (Supplementary Material, Figure S2). The daily cycle of stem diameter variation presented maximum and minimum amplitudes between 2 and 6 p.m. and 7 and 9 a.m., respectively, thus, in the current day, which explains why daily amplitude and increment showed stronger responses to current-day climatic conditions than those of the previous days.

5. Conclusions

Quercus faginea stem diameter variation presented a double climatic limitation that is frequent in Mediterranean climates [43], with temperature and precipitation limiting the first part of the growing season and precipitation in the second part. The seasonal growth of *Q. faginea* presented a unimodal pattern, which together with the amplitude and duration of the daily cycle phases, demonstrated that *Q. faginea* has continuous access to deep soil water reserves and can be physiologically active during the summer. *Quercus faginea* once dominated the forests of central Portugal, and although its current distribution is now greatly reduced [32], its potential distribution covers most of central-north Portugal [54]. Further studies are still necessary to characterize the growth and physiology of *Q. faginea* under drought scenarios; however, the high biodiversity, conservation and landscape value of *Q. faginea* woodlands are indicative that this species constitutes an important target for conservation measures. If summer drought becomes more intense and long, as predicted by global change models for the Mediterranean region [25], it is expected that growth and reproductive output would be more negatively affected in winter deciduous species, such as *Q. faginea*, than in evergreen species that could present a second growth peak in autumn [34]. The aridification trend observed in the Mediterranean region could drive competitive exclusion of winter deciduous species by evergreen species and reduce the potential distribution range of deciduous oak species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13020170/s1, Figure S1: Mean annual temperature and total precipitation for the period 2011–2020; Figure S2: Climate lag effect on stem diameter variation.

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