

Are neighboring trees in tune? Wood formation in *Pinus pinaster*

Joana Vieira · Sergio Rossi · Filipe Campelo ·
Cristina Nabais

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Abstract Neighboring trees growing under identical environmental conditions can exhibit different dynamics and periods of growth. Despite the recent advances in cambial biology, the exogenous and endogenous factors generating asynchronous xylem growths still remain undetermined. This study investigated timings and duration of xylem formation in maritime pine (*Pinus pinaster* Ait.) from an even-aged plantation in Portugal growing under Mediterranean climate. Cambial phenology and stem diameter were monitored weekly, from March to December 2010, on two classes of trees divided according to the tree ring widths of the last 15 years, but similar age and size: fast- and slow-growing trees. We tested the hypothesis that differences in tree ring widths result from cell production which in turn affects timings of xylogenesis and that the bimodal growth pattern, typical of the Mediterranean, originates from a double reactivation of the cambium: in spring and autumn. Cambial activity started earlier and ended later in fast-growing trees, confirming that cell production is a key factor determining the duration of xylogenesis. Intra-annual variations in stem diameter recorded by band dendrometers revealed two peaks of increment occurring in spring and late summer. However, the number of cambial cells did not increase in late summer, which

suggested that the second peak of increment was caused by stem rehydration, rather than by a reactivation of cell division. These results demonstrated that the variability in the timings of xylem phenology observed among trees of the same age and size and growing under similar environmental conditions was closely related to cell production and not to age or size per se.

Keywords Cambium · Mediterranean · Xylogenesis · Cell production · Tree age · Tree size

Introduction

The period in which wood formation occurs is the time window when environmental factors can act directly on the cells forming the tree ring and, consequently, on wood characteristics and properties. Thus, understanding the mechanisms of xylem development, namely the environmental factors responsible for the activation and cessation of radial growth, can have a great ecological and economic importance.

Xylem growth is a complex mechanism involving increases in the number of cells produced by the division of initials in the cambial zone, and in the volume of derivatives which undergo differentiation before their complete maturation and functionality. Recently, there have been major steps forward in understanding cambial activity and wood formation (Deslauriers et al. 2009; Fonti et al. 2010; Gruber et al. 2010). In temperate and cold environments, there are evidences that temperature is a key factor for xylem growth, mainly in spring and autumn, as observed in the field (Begum et al. 2008; Deslauriers et al. 2008; Rossi et al. 2007; Seo et al. 2008; Vaganov et al. 2005) or with manipulation experiments (Begum et al. 2007; Gričar et al. 2006; Oribe

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J. Vieira (✉) · F. Campelo · C. Nabais
Centro de Ecologia Funcional (CFE), Departamento de Ciências
Da Vida, Faculdade de Ciências e Tecnologia, Universidade de
Coimbra, Apartado 3046, 3001-401 Coimbra, Portugal
e-mail: joana.vieira@uc.pt

S. Rossi
Département des Sciences Fondamentales, Université du Québec
à Chicoutimi, Chicoutimi, Canada

et al. 2001). Nonetheless, trees living in the same site and subjected to the same climate can exhibit different growing dynamics and periods of growth (Rathgeber et al. 2011). This clearly indicates that factors other than climate can play a role in determining the timings of xylem formation.

In conifers of the Alpine timberline, xylem phenology is not constant throughout the tree's lifespan, with older trees showing shorter and delayed periods of cambial activity and xylem cell differentiation than adult trees (Rossi et al. 2008). However, the older trees considered in that study were also taller and larger, thus the effect of age was not definitively disentangled from tree size. The shorter durations of xylogenesis observed in older trees by Rossi et al. (2008) could then be related to the size effect and not to age *per se*. In another study, Rathgeber et al. (2011) removed the age factor by investigating xylogenesis in an even-aged plantation of silver fir. Trees showed the same age and similar heights, but belonged to different social classes. Cambial activity started earlier, stopped later, lasted longer and was more intense in dominant individuals than in intermediate and suppressed ones. Moreover, variability in tree ring width was mostly explained by the rate of cell production and only partially by the duration of growth. Since dominant trees were those with larger stem diameters and greater annual radial increments, it was unclear whether either or both factors were a significant component of the growth process. Thus, the question whether cambial phenology is age and/or size related still remains unraveled.

The Mediterranean climate is characterized by dry and hot summers and wet and cold winters, both periods unfavorable for growth (Larcher 2000; Mitrakos 1980; Terradas and Save 1992). Trees from these environments have physiological and morphological features (Battipaglia et al. 2010; Cherubini et al. 2003) as well as phenological adaptations (Gratani et al. 2008; Llorens et al. 2003; Monserrat-Martí et al. 2009) to survive in this double-stressed climate. Thus, two physiologically active periods are observed, with photosynthesis, shoot elongation and leaf flushing occurring during the warm and rainy months of spring and autumn. Similarly, adaptations to the Mediterranean climate have been observed in the timings of cambial activity, with the presence of bimodal patterns of xylem growth (Battipaglia et al. 2010; Camarero et al. 2010; de Luis et al. 2011; Gutierrez et al. 2011; Linares et al. 2009). The two periods of growth in spring and autumn are separated by a drought-imposed quiescent period in summer (Cherubini et al. 2003; Larcher 2000). Is the bimodal growth pattern observed in Mediterranean areas generated by an autumnal reactivation of cambium or by a swelling of previously produced cells or by both components? Either process can be monitored with anatomical observations of xylem development or

dendrometers, but to our knowledge, the two techniques are rarely used together (Camarero et al. 2010; Deslauriers et al. 2007; Makinen et al. 2008). The present study investigated timings and duration of xylem formation of maritime pine (*Pinus pinaster* Ait.) using both anatomical observations and band dendrometers. Trees with the same age and size but different annual growth rates in the last 15 years (1994–2009) were selected in a coastal stand in Portugal with the aim of testing the hypotheses that (1) the differences in tree ring width are a result of cell production and that cell production rates affect timings of xylogenesis and (2) the bimodal pattern originates from a double reactivation of cambial activity in spring and autumn.

Materials and methods

Study site and tree selection

The study was carried out in Perimetro Florestal Dunas de Cantanhede (40°21'35.15"N, 8°49'10.06"W; 15 m a.s.l.), a plantation of maritime pine growing on sand dunes in the northwest coast of Portugal (Fig. 1a). Climate is typically Mediterranean with oceanic influence. Precipitation occurs mostly in autumn and winter, and summer is characterized by high temperatures and occasional precipitation events of low intensity (Fig. 2). The long-term (1979–2009) mean annual temperature was 16.2 °C and the total annual precipitation 948 mm (CRU). Meteorological data (daily maximum and minimum temperature and total precipitation) were acquired from the nearest meteorological station (Instituto Português de Meteorologia), located in Figueira da Foz, at 25 km south from the study site.

The selected forest stand had a density of approximately 230 trees per hectare, and trees presented similar characteristics in terms of dominance, height and vigor. All trees were dominant or co-dominant with an average cambial age of 45 years at breast height (Table 1). In December of 2009, 35 trees were sampled with an increment borer. A core was taken at breast height in the south direction. The cores were air-dried and sanded until the tree ring patterns were perfectly visible. Tree ring width was measured to the nearest 0.01 mm using a linear table, LINTAB (Frank Rinn S.A, Heidelberg, Germany) and the program TSAP-Win (Rinn 2003). Based on the tree ring widths from the previous 15 years, the trees were divided into fast- (F-trees) and slow-growing trees (S-trees) (Fig. 3). From the initial 35 trees, 10 were selected for monitoring cambial activity and 25 for diameter variation. At the end of the monitoring season, four trees were excluded from the analysis because no growth was observed in 2010. Thus, 4 F- and 4 S-trees were analyzed for cambial activity, and 12 F- and 11 S-trees were monitored for diameter variation.

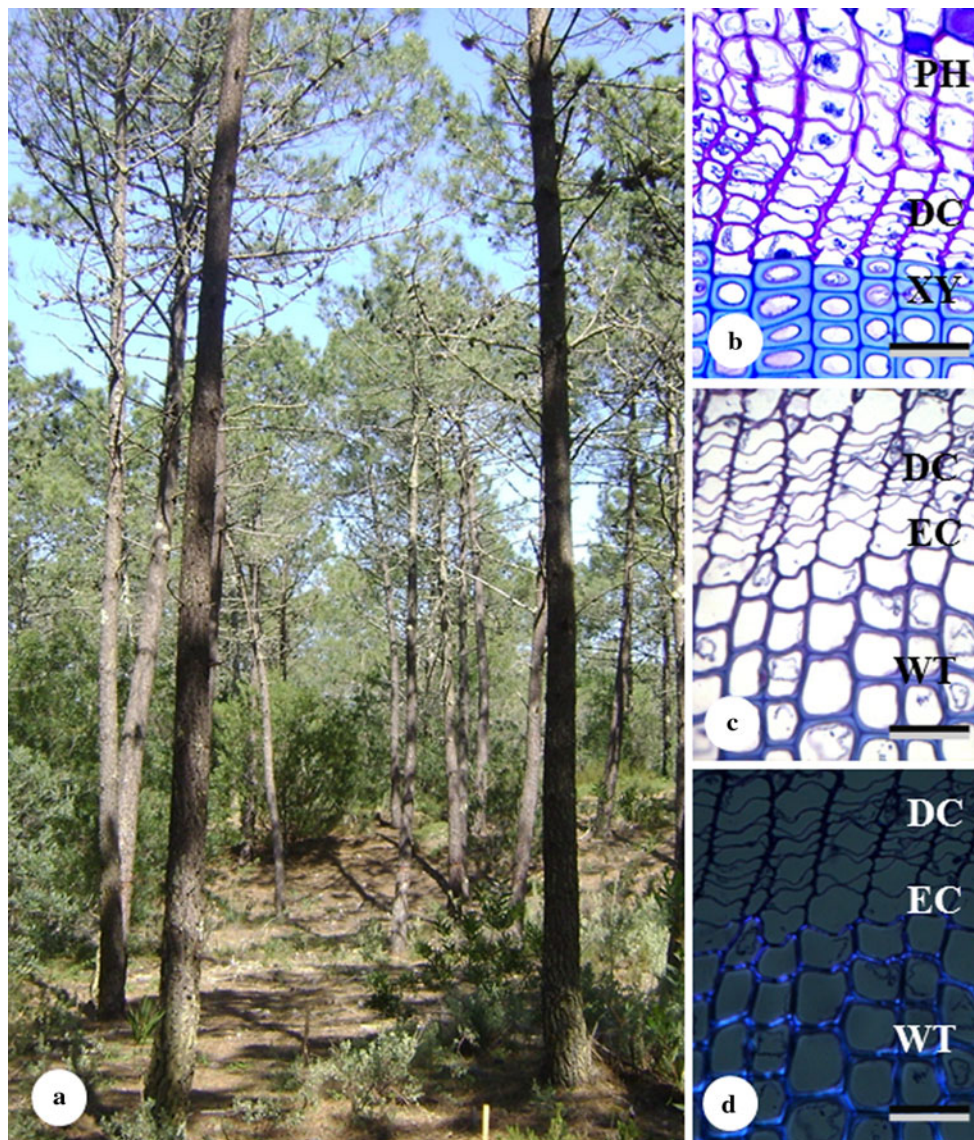


Fig. 1 Maritime pine (*Pinus pinaster*) at the site (a), Perimetro Florestal Dunas de Cantanhede (40°21'35.15"N, 8°49'10.06"W; 15 m a.s.l.); cambial zone transverse sections under visible (b, c) and

polarized light (d). DC dormant cambium, XY xylem, PH phloem, EC enlarging cells, WT wall-thickening cells. Scale bar = 50 μm

For each tree, height and crown diameter were measured in 2009. Diameter at breast height (DBH) was measured in the wood cores, from the last ring to the pith. Tree height was measured with an electronic clinometer and crown diameter calculated as twice the quadratic mean of the four cardinal radii of the projected crown.

Xylem formation

Sampling was performed from March to December 2010, [62–349 Day of the Year (DOY)] by weekly collecting microcores on the stem using a Trephor (Rossi et al. 2006). The microcores were collected from 30 cm below and

above breast height, in a spiral pattern on the south-facing side of the tree stem. Before sampling, bark was removed in order to reach the living tissues. Between two successive sampling dates, microcores were collected at least 5 cm apart to prevent getting resin ducts from adjacent sampling points. The microcores were placed in eppendorfs filled with alcohol (50 % in water) and stored at 5 °C to avoid tissue deterioration. In the laboratory, the microcores were dehydrated through successive immersions in alcohol and D-limonene and embedded in paraffin (Rossi et al. 2006). Transverse sections 6–10 μm thick were cut from the samples with a rotary microtome, stained with cresyl violet acetate (0.16 % in water) and immediately observed in a

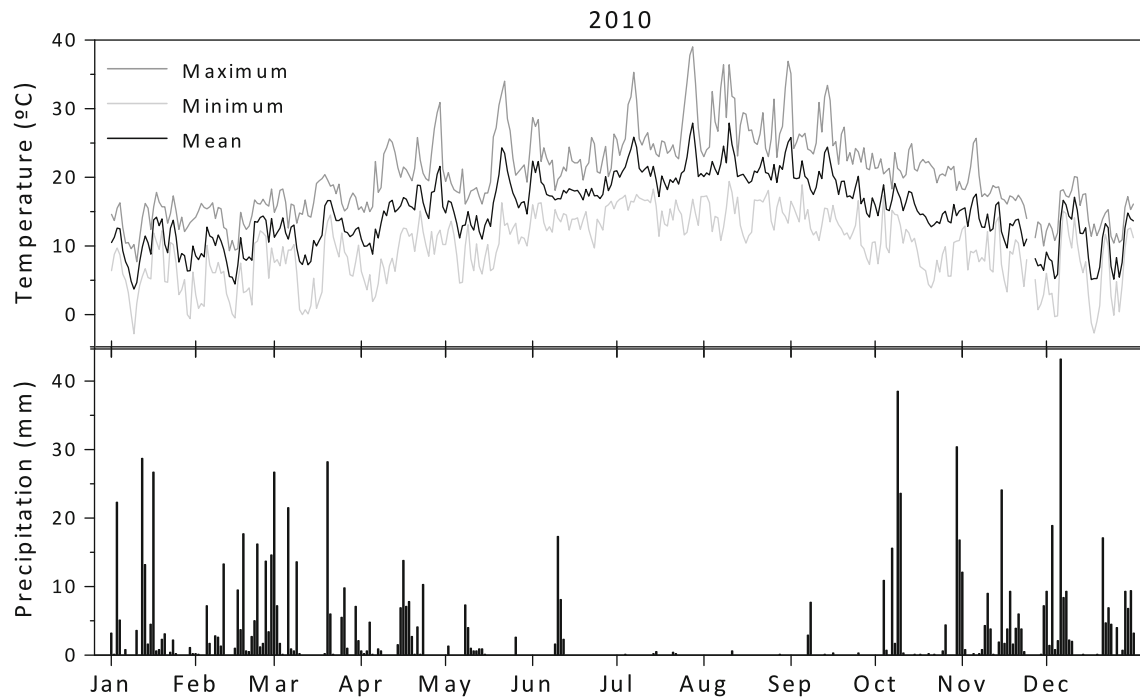


Fig. 2 Daily temperature and precipitation in Figueira da Foz during 2010, at 25 km south from the study site (data from Instituto Nacional de Meteorologia, Portugal)

Table 1 Diameter at breast height (DBH), height and crown diameter of fast-(F-trees) and slow-growing trees (S-trees) (mean \pm standard deviation)

Class	Xylogenesis		Dendrometers	
	F-trees	S-trees	F-trees	S-trees
DBH (cm)	12.97 \pm 1.15	12.05 \pm 1.28	23.58 \pm 4.77	24.64 \pm 3.09
Height (m)	15.42 \pm 0.92	15.02 \pm 0.32	15.18 \pm 0.85	15.45 \pm 0.68
Crown diameter (m ²)	10.68 \pm 0.26	9.82 \pm 1.33	10.74 \pm 1.46	7.62 \pm 1.66

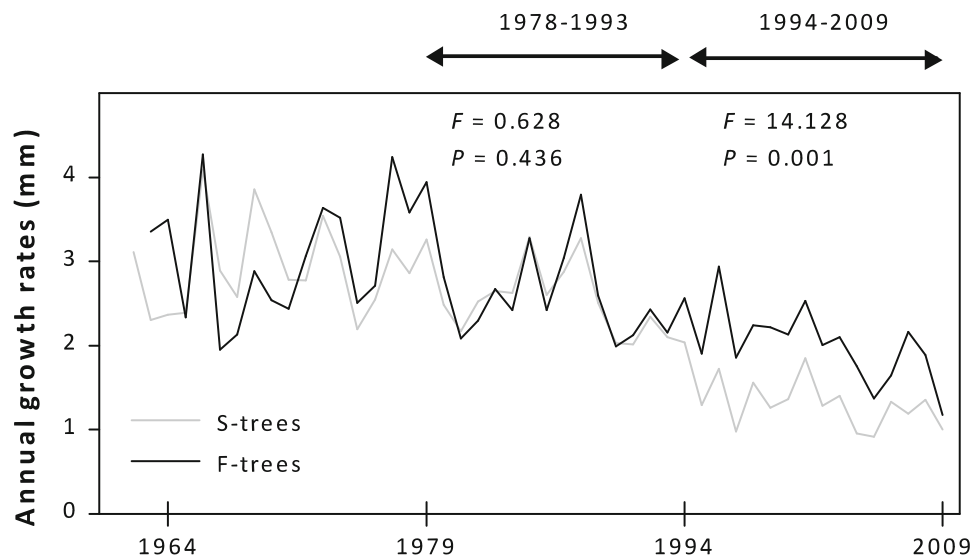


Fig. 3 Annual time series of slow- (S-trees) and fast-growing trees (F-trees) used for anatomical investigation and dendrometer measurements in 2010. F values are the values of the two-way ANOVA

analysis of variance in each 15-year window period (1978–1993: synchronized period/1994–2009: different growth rate period)

microscope (400–500× magnification), under visible and polarized light to distinguish the developing xylem cells. Cambial and enlarging cells only have primary cell walls, which, unlike secondary walls, do not shine under polarized light (Fig. 1b–d). Cambial cells are characterized by thin cell walls and small radial diameters, while enlarging cells have a diameter at least twice that of a cambial cell (Fig. 1c). Wall-thickening cells shine under polarized light and show a light violet coloration changing to dark violet at the end of maturation (Fig. 1d). When the entire cell wall presents a blue coloration, lignification is complete and tracheids reach maturity (Gričar et al. 2005). In each sample, the number of cambial and developing cells was counted along three radial rows and averaged per class. Xylem formation was considered to have begun when an average of at least one enlarging cell was observed in each class. Xylem differentiation was considered complete when no cells were observed in cell wall-thickening phase.

Band dendrometers

To estimate the changes in diameter, band dendrometers made of astralon (model D1-L, UMS, Munich, Germany) were installed on the stem of 25 trees at breast height. Installation was performed in January 2010, which allowed for a period of adjustment before the beginning of the growing season (Linares et al. 2010). Before dendrometer installation, bark was carefully removed with a chisel to better adjust the band dendrometer to the stem and to reduce as much as possible the non-xylematic sources of swelling and shrinking (Zweifel et al. 2006). Band dendrometers were read weekly to the nearest 0.1 mm. To avoid biases due to the circadian rhythms of water storage and depletion (Vieira et al. 2013), all measurements were done in early morning.

Statistical analysis

The characteristics of the F- and S-trees (diameter, height and crown diameter) selected for the xylogenesis and dendrometer analyses were compared using a two-way analysis of variance (ANOVA). Tree ring width was divided into two 15-year periods and compared using a two-way ANOVA to test for differences between the S- and F-trees and between both periods. Mean cell distribution was compared between F- and S-trees using the nonparametric Kruskal–Wallis test (χ^2). Cumulative and increment data from dendrometers were compared throughout the growing season using a PROC MULTTEST of the software package SAS version 9.2 (SAS Institute, Cary, NC). When performing many hypothesis tests on the same data set, this procedure excludes the probability of declaring false

significances by adjusting the P values using 10,000 bootstrap resamplings with replacement.

Results

Temperature and Precipitation in 2010

The minimum temperature in 2010 fell below zero in only three occasions, on 9th and 29th January and on February 14th (Fig. 2). Mean daily temperature in January and February ranged between 3 and 13 °C, with an average minimum temperature of 8 °C measured during the week prior to the beginning of sampling. In spring and summer, temperature raised reaching a maximum of 39 °C in mid-July. In September, temperature started gradually to decrease, but mean temperatures were still above 15 °C. Temperature only dropped below 10 °C in mid-November. Precipitation was more frequent in January–March and October–November. In April, precipitation started to decrease and very few precipitation events were observed from June to September, with a total of 43 mm of rain recorded during that period. The first precipitation event in autumn occurred at the beginning of October, with a total of 90 mm of rain in 1 week.

Tree characteristics

Tree ring width measurements showed that in the last 15 years F- and S-trees were significantly different ($F = 14.128$; $P = 0.001$) despite the fact that in the previous period (1978–1993) this difference was not observed ($F = 0.628$; $P = 0.436$; Fig. 3). DBH ranged from 20 to 27 cm, tree height between 15 and 16.5 m and crown diameter between 7.62 and 10.74 m² (Table 1). No significant statistical differences were observed between F- and S-trees concerning tree height ($F = 0.0157$; $P = 0.901$), DBH ($F = 0.333$; $P = 0.569$) and crown diameter ($F = 3.036$; $P = 0.093$).

Xylem phenology

The overall pattern of the differentiating tracheids showed a clear variation during the year in terms of number of cells (Fig. 4). Cells in cambium, enlargement and cell wall thickening followed the typical bell-shaped distribution, although there were still cells in wall thickening when the sampling stopped (DOY 349). Mature cells exhibited a growth curve with a plateau achieved at the end of summer. The number of cells in F-trees was always higher than in S-trees for all differentiation phases, except for cambium in spring. Statistics confirmed these observations, with the frequency distribution of the number of cells in enlargement ($\chi^2 = 6.97$, $P < 0.01$), cell wall-thickening

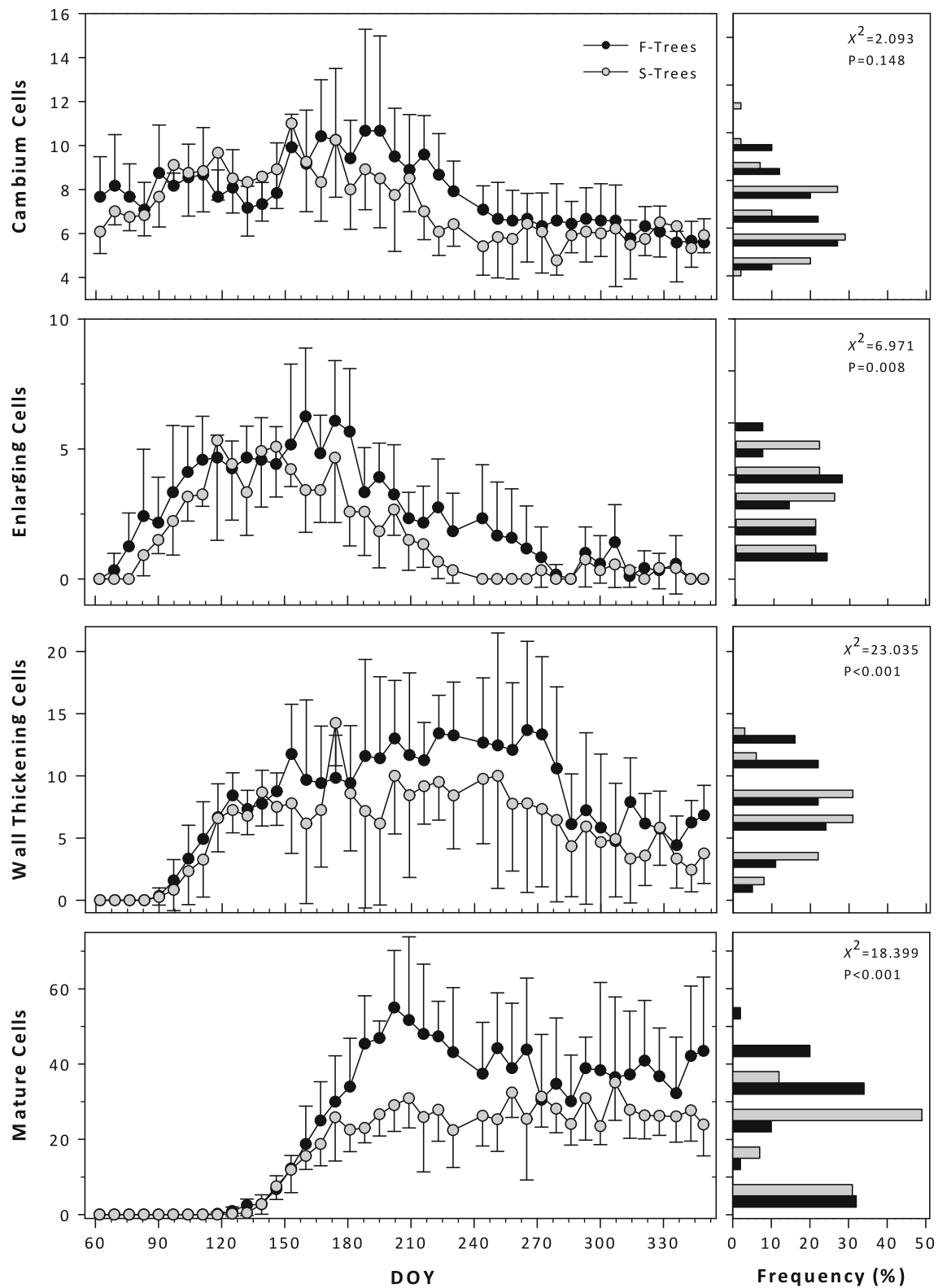


Fig. 4 Number and frequency of cambial, enlarging, cell wall-thickening and mature cells in fast- (F-trees) and slow-growing trees (S-trees). Vertical bars represent standard deviation; χ^2 : Kruskal–Wallis test between F- and S-trees

($\chi^2 = 23.03$, $P < 0.001$) and mature cells ($\chi^2 = 10.39$, $P < 0.001$) being significantly different between the two groups of trees.

Winter samples revealed that there were 5–7 cells in the dormant cambium (Fig. 4). The first samples taken in March (DOY 62) had 6–9 and 5–7 cambial cells in F- and S-trees, respectively. The maximum number of cambium cells occurred in June, followed by a slow decrease until October. The first tangential row of enlarging cells was observed in F-trees on DOY 76 (mid-March), and a week later in S-trees. The last enlarging cells were observed in December (DOY 336) in F- and S-trees. Cell wall thickening and lignification was observed in April, 21 days after the beginning of enlargement, and started first in F-trees on DOY 97 and was observed one week later on S-trees (Fig. 4). Since mid-July, S-trees exhibited a gradual reduction in the number of cells in wall thickening and lignification, while this reduction was observed in F-trees only in mid-October. The first mature cells were observed in May, on DOY 125, in F-trees and 2 weeks later in S-trees. In December, the last sampling month, cells under lignification were still observed in both groups of trees and the end of the maturation phase could not be determined. At the end of sampling, F-trees produced 40 cells, about 15 more than those produced by S-trees.

Dynamics of diameter increment (Dendrometers)

Trees of both groups showed annual diameter increments with a clear bimodal pattern characterized by a pronounced first period of increment in spring, followed by a decrease in summer and a second less marked period of increment in autumn (Fig. 5, top graphics). Stem diameter increment started in mid-March (DOY 83) for both groups, but F-trees presented higher increment rates than S-trees. The maximum increment was reached at the beginning of May, followed by a decreasing trend and a stem variation close to zero in August–September. The second period of positive increment was observed in October–December and corresponded with the first rainy event of autumn (compare Fig. 5 with Fig. 2). Several false significant probability scores were calculated for both weekly and cumulative increments (Fig. 5, lower graphics). The high variation in diameter increment among trees hid all differences between the two groups of trees, and bootstrapped differences were only significant for the measurements performed at the end of May, on DOY 146 (Fig. 5a). More marked differences were detected using cumulative data (Fig. 5b), with patterns of F- and S-trees diverging since mid-April when the bootstrapped adjusted P values became significant ($P < 0.05$).

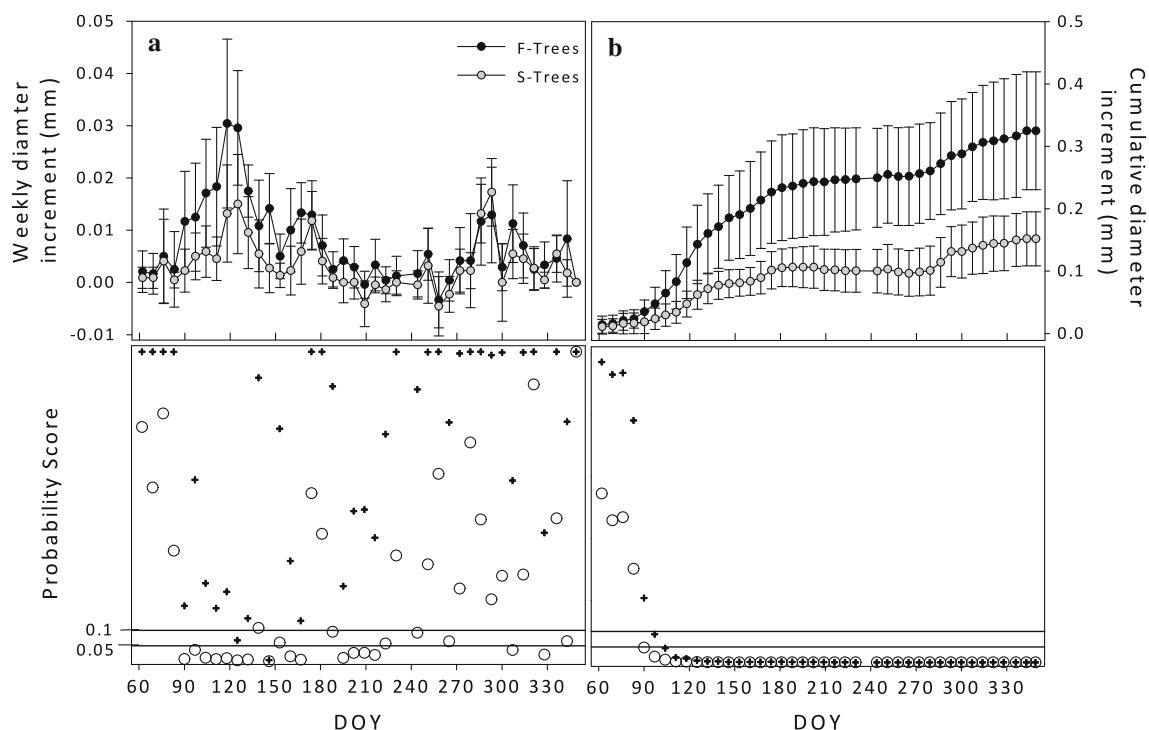


Fig. 5 Weekly (a) and cumulative (b) increments by band dendrometers and probability scores comparing fast- (F-trees) and slow-growing trees (S-trees). Circles and crosses represent normal and adjusted P values calculated by 10,000 bootstrap iterations with replacement, respectively

Discussion

The present study investigated timings and duration of cambium phenology and dynamics of xylem growth in fast and slow trees, growing in a Mediterranean climate with oceanic influence. Trees had the same age, similar height, crown diameter and DBH despite the differences in annual growth rates in the last 15 years. Earlier onsets of cell enlargement in spring and the presence of a higher number of cells in cell wall thickening in winter were observed in F-trees. Also, F-trees showed faster growth rates than S-trees since mid-April, accumulating a higher number of cells in differentiation and mature xylem, confirming the hypothesis that cell production affects timings of xylogenesis. Although there was a clear bimodal pattern with two periods of increment in spring and autumn, no marked increase in the number of cambial cells was observed in autumn, suggesting that the second increment peak involved mainly changes in stem size. Consequently, the hypothesis that the bimodal growth pattern originates from a double period of cambial activity was not supported by the current findings.

Differences in xylem growth have already been described in trees of different age, size and vitality, and growing in different climatic conditions (Gričar et al. 2009; Linares et al. 2009; Lupi et al. 2010; Rathgeber et al. 2011; Rossi et al. 2008). However, the differences in the growing season observed in these studies could result from a number of different factors, such as size, age or dominance (Rossi et al. 2008). Also, the comparison of wood formation in even-aged trees by Rathgeber et al. (2011) was not completely conclusive since trees belonged to different social classes and had different sizes. For the first time, an experimental design maintaining constant age and size was applied in trees growing in the same forest stand. The observed differences between F- and S-trees in the period of xylogenesis showed that cell production, and not age or size, played an important role determining timings of xylem phenology. Rossi et al. (2012) demonstrated that cell production is closely interconnected with the phenological phases of xylem according to a complex causal link. The date of onset and the rate of cambial division affect the number of cells produced by the cambium which, in turn, influences the ending of cell differentiation (Lupi et al. 2010; Rossi et al. 2012). Although cambial activity started 1 week earlier in F-trees, the wider tree ring formed in F-trees was caused by a higher rate of cell division, rather than by a longer period of xylogenesis. The higher number of cells produced by the cambium of F-trees lead to a larger accumulation of cells in the developing xylem, which prolonged the differentiation phase and delayed the end of wood formation.

The analysis of the annual radial growth showed that F- and S-trees consistently diverged after 1994. A severe drought occurred in 1995, which might have reduced the competitive ability of some trees, causing the different growth rates observed afterward. During periods of low precipitation, better-adapted trees can maintain higher growth rates and also recover faster (Martinez-Vilalta et al. 2012; Metsaranta and Lieffers 2008). F-trees could have recovered faster from the 1995 drought due to genetic, morphological (e.g., rooting depth), physiological and/or microclimatic differences. Further studies are necessary to understand why, after 1995, trees with the same age and size showed different growth rates.

Trees presented a clear bimodal pattern of diameter increment with two peaks, in spring and autumn, and a quiescent period in summer, which is characteristic of the vegetation in Mediterranean areas (Camarero et al. 2010; Gutierrez et al. 2011). Trees respond to water stress by closing the stomata and reducing leaf transpiration, which causes a progressive decline of CO₂ uptake (Cochard et al. 2000). The change in CO₂ uptake alters the proportion of carbon allocated to the different metabolic processes, which results in a decreased availability of carbon for those processes with lower priorities, such as cambial activity and secondary growth, which slow down or even cease (Oribe et al. 2003). In an early state of water deficit, cell expansion is restricted by the decline in turgor pressure, but if water stress persists, cambial cell division can also be affected (Abe et al. 2003). De Luis et al. (2011) showed that water availability after the summer drought was the determining factor to increase the number of cambial cells of *P. halepensis* saplings subjected to different irrigation regimes. However, in our case, the autumnal growth period did not correspond to a second period of cell division in the cambium. The autumnal recovery occurred shortly after the first rains and consisted mainly in a swelling of the outermost tissues of the stem and in the achievement of the pressure potential required for enlarging the few remaining undifferentiated cells more likely produced by cambium during early summer (Abe et al. 2003; Rossi et al. 2009).

The second increment period was more evident on stem diameter variation than on cell anatomy studies. Diameter increment consists of several components including cell accumulation, and swelling and shrinking of the outermost tissues of stem due to water absorption and thermal variations (Zweifel et al. 2006). In areas with long dry periods, swelling and shrinking of the xylem and phloem can cause drastic changes in stem dimensions that exceed growth (Forster et al. 2000; Vieira et al. 2013). In our study, the association between dendrometers and anatomical observations showed that the second increment period was due to variation in tree water status rather than new cell production by the cambium. Also, a 3-week delay was observed

between the beginning of xylem differentiation (corresponding to the date of appearance of the first enlarging cell) and diameter increment. The resolution of dendrometers is probably not suitable to record microscopic variations caused by the first increases in cell number (Gruber et al. 2009). Other studies which have also compared band dendrometers and cellular analysis showed that indirect measurements fail in assessing the start of growth in spring (Camarero et al. 2010; Linares et al. 2009; Makinen et al. 2008). Nonetheless, unlike anatomical observations, dendrometers are a non-destructive method of measuring stem diameter fluctuations and can provide suitable estimates of xylem growth, after the non-xylematic sources of cyclic rhythms of water storage and depletion are removed (Vieira et al. 2013; Turcotte et al. 2011; Zweifel et al. 2006).

As far as we know, this is the first study where cambial phenology was monitored in trees with the same age and size and different tree ring widths. The results showed that F- and S-trees exhibited different rates of cell production and durations of xylogenesis. F-trees presented a higher rate of cell production which led to a prolonged xylem differentiation and the formation of wider tree rings. Thus, we can also conclude that the observed differences in xylogenesis resulted from cell production rather than age or size. The divergence in the annual growth rates of these trees started after a severe drought, with F-trees showing a faster recovery rate than S-trees. Also, the combined analysis of anatomical observations and dendrometers demonstrated that the bimodal pattern of maritime pine in 2010 was related to changes in stem size rather than an autumnal resumption of cambial activity.

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