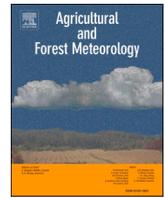


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Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Decoupled leaf-wood phenology in two pine species from contrasting climates: Longer growing seasons do not mean more radial growth

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ARTICLE INFO

Edited by Dr J. William Munger

Keywords:

Cambium phenology
Leaf phenology
Growing season
Radial growth
Vaganov-Shashkin model

ABSTRACT

Climate warming is expected to lengthen the growing season of tree species and enhance radial growth rates. Alternatively, a longer growing season could not lead to improved radial growth if wood production depends more on growth rate than on growing season length. We test these ideas by comparing leaf phenology data and the estimated start and end dates of wood formation predicted by the VS-Lite growth model. We analyzed long-term series of leaf unfolding and fall dates and reconstructed radial growth of two pine species under contrasting climatic conditions: Scots pine (*Pinus sylvestris*) in a Russian boreal site and Aleppo pine (*Pinus halepensis*) in a Spanish Mediterranean site. On average, leaf onset occurred in days 99 and 163 in *P. halepensis* and *P. sylvestris*, respectively, about 40 days earlier than the estimated start date of wood formation. The onset of leaf unfolding advanced 2.1 days per decade in *P. sylvestris* in response to warmer May temperatures. Radial growth was enhanced by warm-wet spring-summer conditions in *P. sylvestris* and by wet soil conditions from prior winter up to current summer in *P. halepensis*. In this species the growing season length and the radial growth rate were not coupled because the growing season length shortened during cool-wet periods whereas growth rates increased. In *P. sylvestris* leaf onset was delayed during years with low growth rates suggesting a potential coupling between warmer spring conditions, earlier leaf onset and enhanced growth whenever soil water content is high enough. Overall, we show that longer growing seasons do not necessarily imply higher radial growth rates.

1. Introduction

Most studies on tree phenology have reported advanced spring events as climate warms, and often delayed fall phenological events, leading to a longer growing season particularly at mid-latitude forested biomes (e.g., Badeck et al., 2004; Menzel et al., 2006a; Menzel and Fabian, 1999; Roslin et al., 2021). Plastic phenological responses to climate warming may increase tree performance in cold regions with short growing seasons, such as boreal forests (Menzel, 2000; Chmielewski and Rotzer, 2001), leading to a longer growing season and, potentially, increasing tree growth and forest productivity (Piao et al., 2011). However, wood production may depend more on meristem

activity (rate of cambial divisions) rather than on growing season length (Cuny et al., 2012; Ren et al., 2019). In addition, fitness trade-offs between maximizing annual carbon assimilation through an early leaf unfolding and reducing the risk of damage caused by spring frost, which favors late leaf unfolding, are predicted by process-based phenological models in boreal forests where the climate warming pace is fast (Chuine, 2010). For instance, an advanced spring green-up of boreal conifers due to warmer conditions increased spring frost damage due to a premature loss of frost hardiness (Richardson et al., 2018).

A contrasting climate scenario applies to seasonal dry regions such as Mediterranean biomes where an earlier growing season could expose tree populations to additional drought stress (Misson et al., 2011).

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<https://doi.org/10.1016/j.agrformet.2022.109223>

Received 24 March 2022; Received in revised form 3 October 2022; Accepted 18 October 2022

Available online 26 October 2022

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There, summer drought could counterbalance the positive effect on forest productivity and tree growth of a longer growing season. Therefore, changing leaf phenology due to climate warming could cause contrasting adaptive responses in different biomes under contrasting climate conditions. Nevertheless, it is unknown how phenological trends would impact tree growth, carbon uptake and climate change mitigation by forests given the high among-population variation in the timing of spring phenological events (Delgado et al., 2020). Such geographical variability in phenological responses to climate warming could depend on local conditions including photoperiod or site temperature (Menzel et al., 2006b; Primack et al., 2009), thus requiring the comparison of different biomes. Furthermore, several xylogenesis studies have compared leaf and wood phenology couplings at intra-annual scales during several years (e.g., Michelot et al., 2012; Ren et al., 2019). However, such time-consuming assessments usually encompass less than 5–10 years of data and cannot fully take into account year-to-year climate variability. Overall, the relationships between long-term data of leaf phenology and radial growth are still understudied in conifers (but see a study on a hardwood species by Čufar et al. (2015)).

Comprehensive, long-term assessments of tree phenology require analyzing leaf and wood phenological phases to disentangle how they respond to climate warming and to figure out how this translates into forest productivity (Delpierre et al., 2016a). However, long datasets of leaf onset dates and xylogenesis or similar records covering wide spatial scales across tree species distribution areas are rare thus limiting our understanding on how trees adapt to changing climate conditions (but see Delpierre et al., 2016b, 2019; Perrin et al., 2017). Process-based growth models, such as the Vaganov-Shashkin (VS) model, are an alternative source of wood phenology data since they allow estimating the dates of start and end of radial growth (Vaganov et al., 2006). These dates of wood development can be compared with ground-based observations of leaf onset or fall or with derived dates based on remote sensing images (Yan et al., 2017). Ground-based observations focused on specific tree species and phenophases (e.g., bud burst, onset of leaf unfolding) may not correspond to assessments based on remote sensing imagery which, despite their wide spatial coverage, capture noisy signals of mixed forests and different species within the same satellite scene (Badeck et al., 2004). Nevertheless, it can be expected some association or coupling between leaf and wood phenology since the start and end of wood formation depends on temperature, as it was found in conifers across the Northern Hemisphere (Rossi et al., 2016). In addition, lagged climate-growth associations are expected since current year wood production also depends on climate and/or carbohydrates synthesis from the previous growing season (Williams et al., 2013).

Here we compare leaf and wood phenology in two pine species dominant in boreal (Scots pine –*Pinus sylvestris* L.– in Siberia, central Russia) and Mediterranean (Aleppo pine –*Pinus halepensis* Mill.– in Catalonia, north-eastern Spain) biomes. Tree growth responses to climate have shown contrasting patterns in these two regions being mainly constrained by cold spring-summer conditions in Russia (Arzac et al., 2021) and dry spring-summer conditions in Spain (Andreu et al., 2007; Sánchez-Salguero et al., 2015). It has been reported an enhancement of growth synchrony across cold-constrained (Siberia, Russia) and drought-constrained (Spain) conifer forests due to climate warming and an earlier start of growth (Shestakova et al., 2016). In contrast, in Spanish Mediterranean forests dominated by drought-tolerant species such as *P. halepensis* the increase of growth synchrony was attributed to an advanced onset of growth and the strengthening of drought-induced growth limitations. However, we lack analyses on how long-term changes in phenology may affect the growing season duration and the radial growth variability of major tree species such as pines in biomes showing contrasting climate conditions and different impacts of climate warming. We capitalized on the existence of long-term leaf phenology data of *P. sylvestris* and *P. halepensis* in boreal and Mediterranean sites, respectively. Then, we developed tree-ring width chronologies for these two sites and species and used the VS-Lite growth model, a simplified

version of the VS model, to infer the dates of start and end of radial growth. These dates were compared with ground observed dates of leaf onset and growing season (difference between dates of leaf onset and leaf fall). We also related phenology and growth data to monthly climate data using correlations and selecting the best-fitted, simple model based on its parsimony and explanatory power. Our main objectives are to determine: (i) how leaf phenology and growth are responding to climate warming in boreal and Mediterranean biomes, and (ii) if warmer conditions are lengthening the growing season and enhancing tree growth. We expect that climate warming is advancing spring leaf unfolding in the boreal *P. sylvestris* site, thus lengthening the growing season and improving growth. However, we expect that climate warming is inducing drought stress in the Mediterranean *P. halepensis* site, where growth should be enhanced by cool-wet conditions which should also lead to a delayed start of leaf onset.

2. Material and methods

2.1. Study sites, climate and phenological data

We selected a Mediterranean *Pinus halepensis* Mill. forest situated in the Observatori de l'Ebre near Roquetes (southern Catalonia, north-eastern Spain) with coordinates 40.821° N, 0.493° E and elevation of 50 m, and a boreal *Pinus sylvestris* L. forest situated in the Krasnoyarsk-Stolby national park (southern Siberia, central Russia) with coordinates 55.883° N, 92.767° E and elevation of 532 m (Fig. S1). These two sites were selected because of the availability of long phenological series for the two study sites. Specifically, we used dates of onset of leaf unfolding covering the periods 1950–2001 (Spain) and 1950–2013 (Russia). In Spain, phenological events were recorded by permanent observers at the Observatori de l'Ebre, which gives these data accuracy and reliability (see Gordo and Sanz, 2005). The Russian data were extracted from Ovaskainen et al. (2020), who collected and checked the accuracy of phenological and climatic events across the former Soviet Union building an extensive database which especially detailed from 1960 onwards. These events were recorded by researchers in protected areas such as national parks, such as Krasnoyarsk-Stolby, who followed a systematic annual protocol included in the Chronicle of Nature of National Parks (Butorina, 1979).

Monthly climate data (mean temperature, total precipitation) were taken from Observatori de l'Ebre (available at the webpage <http://www.obsebre.es>) and Krasnoyarsk meteorological station (56.00° N, 92.88° E). Sunshine duration was also available on the Spanish site and it was used as a proxy of radiation. According to the stations' records (Fig. S2), in the Spanish site the average total annual precipitation was 551 mm, and the average annual temperature was 17.3 °C with a maximum mean monthly temperature of 25.6 °C (June), and a minimum of 10.0 °C (January). Most of the annual precipitation occurred in autumn (37.9% was recorded between September and November) and spring (26.4% was recorded between March and May), while drought lasted from June to August. In the Russian site the average annual temperature was 1.2 °C, with average temperatures in January (coldest month) and July (warmest month) of –16.3 °C and 19.2 °C, respectively. The mean annual precipitation was ca. 600 mm, with a peak in summer (37%) and the lowest precipitation being recorded from January to March (9.5%).

Mean annual temperature showed a significant increase trend in both sites (Fig. S3), with an increase of +0.38 °C per decade in Russia and +0.23 °C per decade in Spain. The “Leaky Bucket” model was used to calculate soil water content (SWC) from temperature and precipitation (Huang et al., 1996). In Spain, a SWC decrease (–0.08 v/v per decade) was detected, whilst no significant trend was observed in the Russian site where SWC increased at a mean rate of +0.05 v/v per decade (Fig. S3).

We selected the phenophase corresponding to the onset of leaf unfolding for pine species available at both sites and provided by local observers. In the *P. halepensis* site, dates of leaf fall were also available

which we used to calculate the growing season length as the difference of dates between leaf unfolding and leaf fall. The growing season is therefore defined as the period between leaf onset and leaf fall throughout the manuscript. Regrettably, leaf fall was not recorded for *P. sylvestris* so the growing season length could not be estimated in this species. Phenological events were reported as days of the year (DOY).

2.2. Tree-ring width data

In each site we selected 14–17 dominant, mature trees of each pine species (Table 1). We sampled them by taking two cores at 1.3 m, separated by 180° and perpendicular to the maximum slope, using Pressler increment borers. Cores were air dried, glued onto wooden supports and sanded with sandpapers of increasing grain until ring boundaries were clearly visible. Then, they were visually cross-dated, scanned at 1200 dpi (Epson Expression 10000XL) and ring widths were measured with a 0.001 mm resolution on images using the CDendro and Coorecorder software (Larsson and Larsson, 2018). The visual cross-dating was further checked using the COFECHA software which calculates moving correlations between individual tree-ring width series and the site mean series (Holmes, 1983).

To remove size- or disturbance-related trends in tree-ring width data and emphasize high-frequency growth variability these series were detrended and standardized using the dplR (Bunn, 2010) and detrendR (Campelo et al., 2012) libraries in the R statistical package (R Development Core Team, 2021). We fitted 32-year cubic smoothing splines to individual ring-width series and obtained ring-width indices by dividing observed by fitted values. Then, the resulting series of dimensionless ring-width indices were averaged using a bi-weight robust mean obtain standardized series or chronologies for each study species (Fritts, 1976).

Lastly, we calculated several statistics to characterize the radial growth data: the mean and standard tree-ring width values, the mean first-order autocorrelation of ring widths which accounts for year-to-year persistence in growth, the mean sensitivity of ring-width indices which measures relative changes in growth between consecutive years, the mean correlation between trees (r_{bt}), and the Expressed Population Signal which is a measure on how coherent and replicated is a species or site chronology (Wigley et al., 1984).

Table 1

Leaf phenology and growth statistics of the *Pinus halepensis* and *P. sylvestris* tree-ring width series. Phenological dates are given as days of the year (DOY; means \pm SD).

	Variable	<i>P. halepensis</i>	<i>P. sylvestris</i>
Leaf phenology	Day of onset of leaf unfolding	99 \pm 4	163 \pm 4
	Day of onset of leaf fall	224 \pm 14	—
	Growing season duration (days)	125 \pm 16	—
	Time span (No. years)	1950–2001 (50)	1950–2013 (58)
Radial growth statistics	No. trees	14	17
	No. cores	27	34
	Mean tree-ring width (mm)	2.23	1.80
	Standard deviation (mm)	1.80	0.44
	First-order autocorrelation	0.72	0.57
	Mean sensitivity	0.35	0.11
	Correlation between trees (r_{bt})	0.58	0.38
	Expressed Population Signal	0.95	0.91
	Time span	1926–2021	1903–2017

2.3. Modeling xylem phenology: the VS-Lite model

The VS-Lite model was used to simulate growth rates (mean series of ring-width indices) as a function of local monthly temperature and soil moisture based on the principle of limiting factors (Tolwinski-Ward et al., 2011, 2013). Tree radial growth rates are modeled as function of temperature (gT) and soil moisture (gM), modulated by insolation (gE), which is estimated from the site latitude without considering inter-annual variability. The gE was adjusted for each species to take into account the specific growth responses to photoperiod, in doing so we consider that *P. halepensis* (*P. sylvestris*) do not growth when photoperiod is lower than 8 (12) hours. The uncertainty associated with the estimation of the soil moisture component is transferred to the soil moisture response parameters M1 and M2 (Tolwinski-Ward et al., 2013). The partial growth responses gT and gM are defined as piece-wise linear functions. Values of gT and gM can take values between zero and one (Tolwinski-Ward et al., 2011). The gM and gT functions have two important parameters. The first parameter represents the threshold (T1 and M1) below which growth will not occur and the second parameter is the first optimal value (T2 and M2). Finally, the VS-Lite model computes the annual ring-width index as the sum of the relative growth between January and December. The window for integration was defined between January and December to make possible the detection of variations in the length of the growing season due to changing climate conditions. The VS-Lite parameters were estimated using the Bayesian approach proposed in Tolwinski-Ward et al. (2011, 2013), with a seed value of 999 to ensure reproducibility. This analysis was conducted using Octave language and the original Matlab code with slight modifications (<https://www.ncdc.noaa.gov/paleo-search/study/9894?siteId=31510>, last access: 4 February 2022). To avoid model over-fitting, a restricted and realistic range of values was defined for each parameter which were adjusted to the species and site's characteristics (Table S1). Each model was evaluated 15,000 times (after 2000 burn-in samples) using three parallel Markov chain Monte Carlo chains with a uniform prior distribution for each parameter and a white Gaussian noise model error. The convergence was checked using the R-hat statistic (Gelman and Rubin, 1996).

2.4. Statistical analyses

Comparisons between non-normal variables such as the dates of leaf unfolding were based on Mann-Whitney *U* tests, whereas *t* tests were used for normal variables. To assess temporal trends of climatic or phenological variables, we used the linear slope of regressions or the Kendall τ statistic in the case of variables following or not following normal distributions, respectively.

To evaluate relationships between monthly climate variables (mean temperature, total precipitation, soil water content and day length), we used the Pearson (*r*) and Spearman (r_s) correlation coefficients in the case of variables following (ring-width indices) or not following (leaf phenology, growing season length) normal distributions, respectively. We considered the common period 1950–2017 and the analyses window from prior to current September.

The correlation analyses were compared with analyses based on the *climwin* software which allows to compare different models with different windows relating response variables (e.g., leaf phenology, growth rate) to climatic variables and selects the model (and therefore the climatic window) with the lowest corrected Akaike Information Criterion (AICc) (Bailey and van de Pol, 2016; van de Pol et al., 2016). The *climwin* package also allows performing randomization tests to test the significance of selected models and may use, among others, linear, quadratic and cubic functions to account for non-linear relationships. This package has been successfully used in dendroecological studies and can reveal stronger and more accurate climate-growth associations as compared to correlation analyses (Rubio-Cuadrado et al., 2022).

3. Results

3.1. Leaf phenology and tree growth: trends and patterns

The onset of leaf unfolding occurred on average 64 days earlier for *P. halepensis* (DOY 99, 14 March) as compared with *P. sylvestris* (DOY 163, 11 June) (Table 1). The *P. halepensis* growing season lasted 125 days with leaf fall peaking in summer (DOY 224, 11 August). The trends of the onset of leaf unfolding and the length of growing season were not significant in *P. halepensis* ($p = 0.56$ and $p = 0.92$, respectively; Fig. 1). However, the slope of the dates of onset of leaf unfolding in *P. sylvestris* was negative and significant ($p = 0.003$). In this species, time explained 15% of the variability of onset of leaf unfolding which advanced at a mean rate of 2.1 days per decade from 1950 to 2013.

The mean tree-ring width in *P. halepensis* (2.23 mm) was significantly ($p < 0.05$) higher than in *P. sylvestris* (1.80 mm) (Table 1). The first species showed also higher first-order autocorrelation of tree-ring width and higher values of mean sensitivity, correlation between trees and Expressed Population Signal. These statistics indicate a higher year-to-year variability in growth and higher growth coherence among trees in the case of *P. halepensis* as compared with *P. sylvestris*.

In *P. halepensis*, the growing season length and growth rate were not significantly correlated ($r_s = 0.07$, $p = 0.63$; Fig. 2). This is so because during cool-wet periods such as 1969–1972, with a 44% higher than average soil water content (Fig. S3), the growing season length shortened (96 days, 23% lower than the average; see Table 1) but growth rates increased (3.2 mm, 39% higher than the average; see Table 1).

The standardized series of ring-width indices showed mean trends of -0.01 and $+0.02$ per decade in *P. halepensis* and *P. sylvestris*, respectively (Fig. 3). Observed and simulated series of ring width indices were positively and significantly correlated (Table 2, Figs. 3 and S4).

3.2. Climate drivers of leaf phenology and tree growth

Leaf unfolding dates in *P. halepensis* advanced as temperatures rise in March, whilst the main climate driver of *P. sylvestris* leaf onset was May to July temperature (Table 3). High March and September snow and rain precipitation were also related to an earlier leaf onset in *P. sylvestris*, whilst the *P. halepensis* growing season was longer in response to prior September warm conditions leading to low soil water content and warm March conditions (Table 3).

In the case of *P. sylvestris* growth was mainly limited by cold March temperatures and also by low soil moisture from June to September (Table 4, Fig. 4), whereas in *P. halepensis* growth was mainly limited by

low precipitation and reduced soil moisture from prior December until September and also by cool January conditions (Table 4, Fig. 4).

The analyses based on *climwin* models found that the onset of leaf unfolding in *P. sylvestris* linearly depended on spring-summer temperatures, but also on soil water content since prior December (Table 5, Fig. S5). In *P. halepensis*, leaf unfolding was non-linearly related to radiation from prior October to February with an earlier onset data for periods with intermediate radiation values. The selected model of *P. sylvestris* growth showed positive and non-linear effects of June–September temperature, whereas *P. halepensis* growth responded in a linear and positive way to precipitation from prior autumn to current summer and April–May soil water content.

3.3. Matching leaf phenology and tree growth

The VS-Lite model was able to successfully reproduce growth rates of the two study species (Fig. 3). The correlations between observed and simulated ring-width series were $r = 0.65$ and $r = 0.44$ in the case of *P. halepensis* and *P. sylvestris*, respectively (Table 2). Using these fits we estimated the dates of radial growth onset. The observed dates of leaf onset occurred from 38 (*P. halepensis*, early March) to 43 days (*P. sylvestris*, late April) days before the dates of radial growth onset (Fig. 5). In *P. sylvestris* we found a significant positive relationship between the date of onset of leaf unfolding and the date of growth onset ($r_s = 0.57$, $p < 0.001$).

The estimated duration of the wood formation period (mean \pm SD) was significantly higher ($U = 1$, $p < 0.0001$) in *P. halepensis* (282 ± 11 days) than in *P. sylvestris* (164 ± 13 days). In both species there is a positive trend towards longer durations of the wood formation period (*P. halepensis*, $\tau = 0.20$, $p = 0.02$; *P. sylvestris*, $\tau = 0.19$, $p = 0.04$). On average, the wood formation period has lengthened 2 days per decade from 1950 to the 2000s.

We did not observe significant differences in the date of leaf onset in *P. halepensis* when comparing the two deciles corresponding to years with lowest and highest growth rates (Fig. S6). There were neither differences in the duration of the wood formation period when comparing years of high and low growth rates in this species ($U = 39$, $p = 0.273$). However, we found significantly delayed dates of leaf onset during years with low growth in *P. sylvestris* (Fig. S6). On average, *P. sylvestris* leaf onset started in DOYs 170 (18 June) and 156 (4 June) during years with low and high growth rates, respectively. Lastly, we found that the dates of maximum growth rate estimated by the VS-Lite occurred later for years with higher growth rate as compared with years of lower growth rate in *P. halepensis* (Fig. S7).

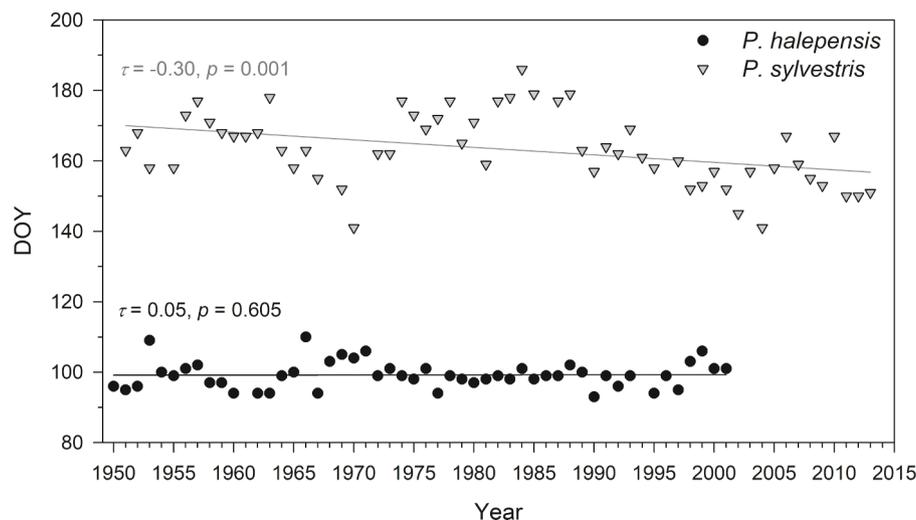


Fig. 1. Temporal series of the day of the year (DOY) corresponding to the onset of leaf unfolding in the two study pine species.

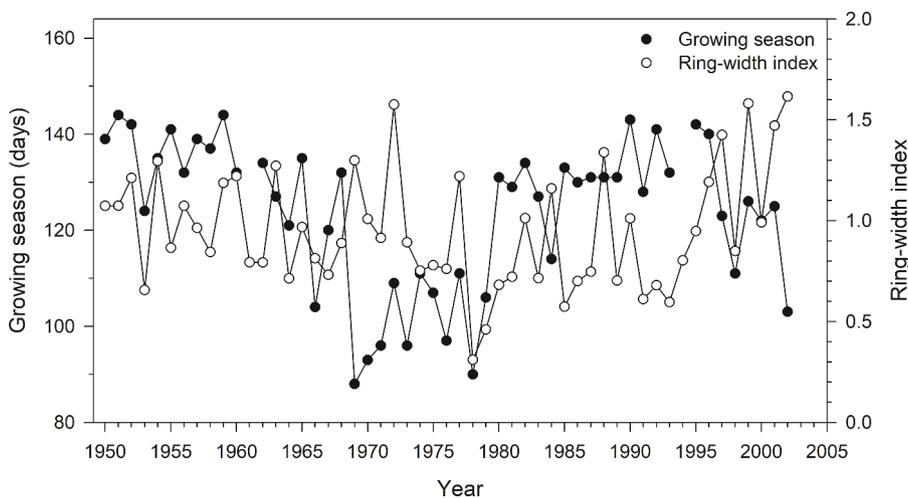


Fig. 2. Growing season (differences between the dates of onset of leaf unfolding and leaf fall) of *Pinus halepensis* pine and radial growth rates (ring-width indices). The plotted values correspond to the period common to both time series (1950–2002).

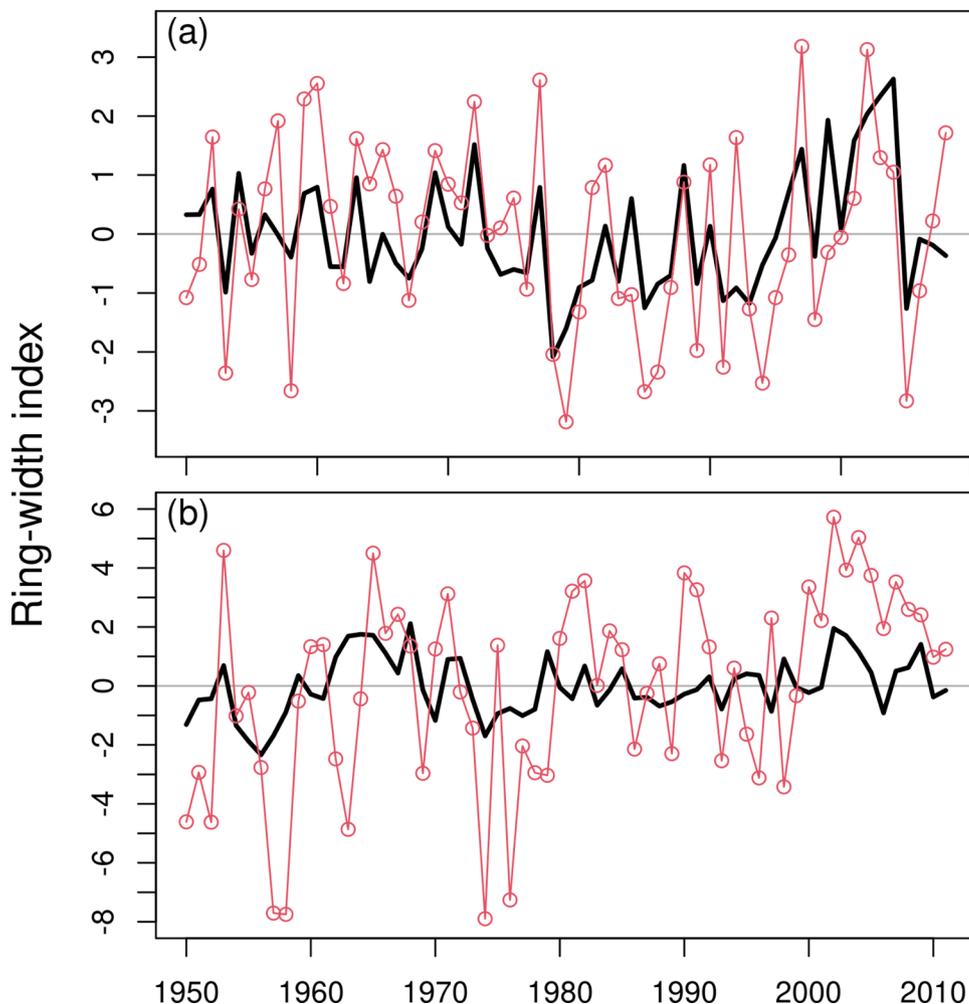


Fig. 3. Observed (black lines) and simulated (red lines) series of standardized ring-width indices in (a) *Pinus halepensis* and (b) *Pinus sylvestris*. In both cases, correlations between observed and simulated series were significant (see Table 2). Note that the plots show the best-replicated period for both sites but tree-ring data were available until 2021 and 2017 in *P. halepensis* and *P. sylvestris*, respectively (see Table 1). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Our overall conclusion that season length and radial growth are decoupled comes directly from field observations and we applied the VS-Lite growth model to better understand the timing of radial growth within the growing season. To validate our results long xylogenesis

series are needed for both study species in the field. There are previous xylogenesis studies on both pine species (e.g., Camarero et al. 2010, Kalinina et al. 2019), but they are still too short to be comparable with long phenological series.

As hypothesized, spring warming advances leaf onset in *P. sylvestris* at the boreal site, but we could not find support there for enhanced

Table 2

Temperature (T1, T2) and soil moisture (M1, M2) parameters used in the fit of the VS-Lite model to simulate the indexed ring-width series of *Pinus halepensis* and *Pinus sylvestris*. The relative volumetric soil moisture content is the relation between the volume of water and the soil volume (v/v). The last four lines show statistics characterizing the relationships between observed and simulated ring-width indices (see Fig. 3): Pearson correlation (*r*) and associated probability; coefficient of determination (*R*²); slope and intercept (standard errors are shown between parentheses).

Parameter	<i>Pinus halepensis</i>	<i>Pinus sylvestris</i>
T1 (°C)	11.309	5.949
T2 (°C)	15.737	12.611
M1 (v/v)	0.0184	0.0234
M2 (v/v)	0.2252	0.2841
<i>r</i> (p)	0.65 (0.0001)	0.44 (0.003)
<i>R</i> ²	0.42	0.19
slope	0.388 (0.039)	0.954 (0.111)
intercept	0.624 (0.002)	0.076 (0.012)

radial growth. In the boreal *P. sylvestris* forest, leaf onset and onset of wood formation both occurred earlier with earlier spring warming leading to a longer growing season, but growth rates were not enhanced. However, we cannot extrapolate this finding to other boreal regions since only one site was studied. In the seasonally-dry Mediterranean site, *P. halepensis* growth was constrained by winter to spring dry conditions as expected but leaf unfolding responded to temperature and radiation. Therefore, in this Mediterranean *P. halepensis* forest leaf phenology and wood production were not related, i.e. they were decoupled. This is confirmed by the positive relationship found between the observed date of leaf unfolding and the estimated date of start of wood formation in *P. sylvestris*, which was not significant in *P. halepensis*.

4.1. Responses of leaf onset and growing season to climate

A previous study on leaf phenology in the study *P. sylvestris* site also recorded an advancement of the leaf onset in response to warmer May conditions (Ovchinnikova et al., 2011). Those findings fully agree with our analyses and concur with phenological observations taken across the former Soviet Union for six decades which detected a pattern of earlier springs, later autumns and longer growing seasons associated to warmer temperatures, particularly at high-latitude sites (Roslin et al., 2021). We could not analyze the growing season length trend for *P. sylvestris*, but data from other coexisting tree species (*Abies sibirica*, *Picea obovata*, *Larix sibirica*) showed similar trends towards and earlier leaf onset (Ovchinnikova et al., 2011). This suggests that their growing seasons are probably longer in the early 21st century than in the mid-20th century. In fact, the estimated period of wood formation in the 1950s and in the 2000s increased, respectively, from 277 to 287 days in *P. halepensis* and from 162 to 175 days in *P. sylvestris*. Inter-specific differences are also remarkable and should be further explored since *P. sylvestris* showed a more pronounced trend towards earlier dates of onset of leaf unfolding than the other mentioned species. The correlations observed between *P. sylvestris* leaf onset and climate conditions after the main period of leaf onset (July temperature, August precipitation, September precipitation and soil water content; Table 3) are spurious and not due to correlations among spring and summer climate variables which were not significant. They could also reflect indirect links between leaf onset and radial growth, which deserve further investigation, since both responded to September soil water content.

The amount of chilling required to break bud dormancy in *P. sylvestris* leads to a wide geographical variation in leaf unfolding trends across the species range (Hänninen and Pelkonen, 1989). Earlier unfolding may be observed at the core of the distribution range where chilling requirements are met and growth rate is high (Duputié et al., 2015). However, later dates could occur in both cold (boreal) distribution margins –where colder temperatures slow down growth and delay

Table 3 Spearman correlations calculated between climate variables and the days of onset of leaf unfolding and leaf fall in *Pinus halepensis* and *Pinus sylvestris* from the Spanish and Russian sites, respectively Months of prior (*t*-1) and current (*t*) years are abbreviated by lowercase and uppercase letters, respectively. Significant (*p* < 0.05) coefficients are shown in bold.

Variable	Species	Phenological phase	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Temperature	<i>P. halepensis</i>	Growing season	0.30	-0.02	0.10	0.08	-0.09	-0.15	0.27	0.09	0.13	0.12	0.13	0.09	0.07
		Precipitation	-0.05	-0.07	0.14	0.01	-0.12	0.21	-0.09	-0.16	-0.16	-0.16	-0.09	0.09	0.20
Soil water content	<i>P. halepensis</i>	Temperature	-0.26	-0.22	-0.13	-0.11	-0.12	-0.04	-0.09	-0.18	-0.24	-0.22	-0.17	-0.04	-0.01
		Onset of leaf unfolding	-0.02	0.21	0.04	-0.15	0.10	-0.05	-0.28	0.01	0.08	0.08	0.02	-0.03	0.11
Precipitation	<i>P. sylvestris</i>	Leaf fall	0.20	0.03	0.18	-0.01	-0.04	-0.17	0.10	0.07	0.14	0.05	0.06	-0.01	-0.05
		Onset of leaf unfolding	-0.11	-0.14	0.04	0.12	0.08	-0.25	-0.27	-0.24	-0.51	-0.27	-0.30	-0.09	0.01
		Onset of leaf unfolding	-0.12	-0.08	-0.09	0.04	-0.07	-0.11	0.21	-0.21	0.10	0.10	-0.03	0.16	-0.33
		Leaf fall	0.04	-0.07	0.09	0.09	-0.04	0.00	-0.01	-0.02	-0.03	-0.11	-0.04	0.19	0.04
Soil water content	<i>P. halepensis</i>	Onset of leaf unfolding	-0.21	0.13	-0.08	-0.01	0.01	-0.11	-0.27	0.09	0.07	-0.26	0.04	-0.17	-0.34
		Leaf fall	0.06	-0.04	-0.08	-0.02	-0.04	-0.12	0.04	0.04	0.11	0.19	0.08	0.13	-0.09
<i>P. sylvestris</i>	<i>P. sylvestris</i>	Onset of leaf unfolding	-0.15	-0.16	-0.10	-0.02	-0.04	0.00	-0.05	-0.04	-0.07	-0.06	-0.05	0.04	0.07
		Onset of leaf unfolding	-0.21	-0.09	-0.07	-0.08	-0.11	-0.13	-0.17	-0.17	-0.10	-0.02	-0.15	-0.06	-0.13

Table 4

Pearson correlations calculated between climate variables and radial growth rates (mean series of ring-width indices) in *Pinus halepensis* and *Pinus sylvestris*. Months of prior (*t*-1) and current (*t*) years are abbreviated by lowercase and uppercase letters, respectively. Significant ($p < 0.05$) coefficients are shown in bold.

Variable	Tree species	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Temperature	<i>P. halepensis</i>	0.09	0.12	0.06	0.07	0.27	-0.02	0.14	0.23	-0.03	0.18	-0.01	0.06	-0.23
	<i>P. sylvestris</i>	0.15	-0.04	0.03	0.10	0.20	0.26	0.29	-0.04	0.25	0.14	0.19	0.05	-0.02
Precipitation	<i>P. halepensis</i>	0.04	0.03	0.24	0.36	0.26	0.01	0.21	0.28	0.31	0.05	0.31	-0.01	0.21
	<i>P. sylvestris</i>	-0.13	0.03	0.22	0.21	0.22	-0.15	0.17	-0.01	0.07	0.33	0.08	0.14	0.06
Soil water content	<i>P. halepensis</i>	-0.04	-0.01	0.11	0.30	0.36	0.36	0.44	0.53	0.60	0.45	0.49	0.42	0.36
	<i>P. sylvestris</i>	-0.04	-0.02	0.08	0.12	0.15	0.13	0.16	0.14	0.13	0.30	0.23	0.27	0.29

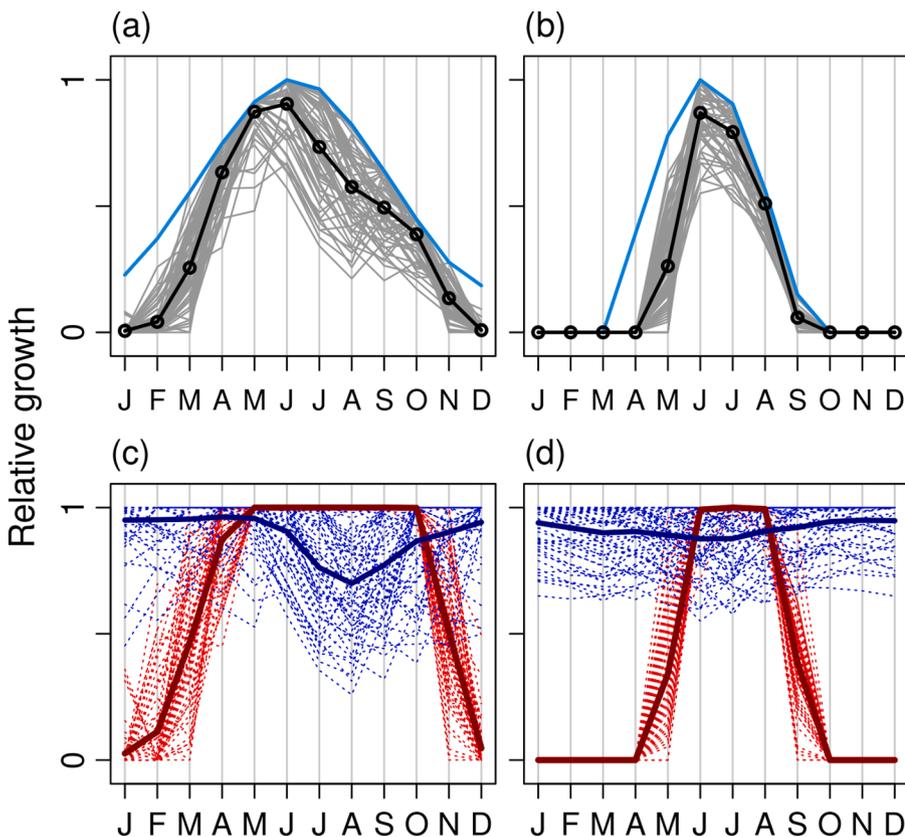


Fig. 4. Simulated monthly partial growth rates of (a) *Pinus halepensis* and (b) *Pinus sylvestris*, modulated by day length (blue line) and corresponding climate limitations of growth (c, *P. halepensis*; d, *P. sylvestris*) due to temperature (red lines) and soil moisture (blue lines). In the upper plots the grey lines indicate individual years whereas the black line is the mean for the whole considered periods. In the lower plots the dotted lines indicate individual years, whereas the thick lines show the mean temperature or soil moisture functions for the whole period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 5

Relationships found between monthly climate variables, leaf phenology and radial growth rates (ring-width indices) based on selected *climwin* models (see Fig. S5). Months with the subscript “t-1” correspond to the year prior to tree-ring formation. $\Delta AICc$ is the corrected Akaike Information Criterion (AICc) of the selected model minus AICc of the null model (van de Pol et al., 2016). Window open and close indicate the beginning and end of the optimum period. *P* value (AIC) is the likelihood of obtaining the model selected by chance (data resulting from the randomization test).

Tree species	Variable	Climate variable	Function	$\Delta AICc$	Window open	Window close	R^2	<i>P</i> value	<i>P</i> value (AIC)
<i>P. halepensis</i>	Radial growth	Precipitation	Linear	-29.43	October _{t-1}	July	0.42	<0.001	<0.001
	Radial growth	Soil water content	Linear	-26.11	April	May	0.39	<0.001	<0.001
	Onset of leaf unfolding	Radiation	Quadratic	-11.45	October _{t-1}	February	0.28	<0.001	0.045
<i>P. sylvestris</i>	Radial growth	Temperature	Cubic	-13.75	June	September	0.29	<0.001	0.010
	Onset of leaf unfolding	Temperature	Linear	-22.61	April	July	0.36	<0.001	<0.001
	Onset of leaf unfolding	Soil water content	Quadratic	-9.28	December _{t-1}	July	0.22	0.001	0.006

leaf unfolding– and warm (Mediterranean) regions –where insufficient chilling delays dormancy break.

In the Mediterranean site, Gordo and Sanz (2005) already reported a positive trend towards a longer growing season due to an earlier leaf unfolding as spring warmed and also a more delayed leaf fall. These local analyses were in agreement with other regional analyses based on long records of phenology showing how warm springs advanced leaf unfolding (Peñuelas et al., 2002; Gordo and Sanz, 2009, 2010). However, they also noted a shortened growing season, associated with a

delay in leaf unfolding and earlier leaf fall, during the wet and cold 1970s when growth rates were high. The high rainfall variability in Mediterranean areas or species-specific responses probably explained why it has been reported a higher explanatory power of temperatures than precipitation for predicting the start of the growing season. Overall, leaf unfolding responses to precipitation variability are complex among Mediterranean species (Peñuelas et al., 2004). In addition, Mediterranean summer drought splits the wet-warm spring and autumn growing seasons leading to bimodal growth patterns (Camarero et al., 2010;

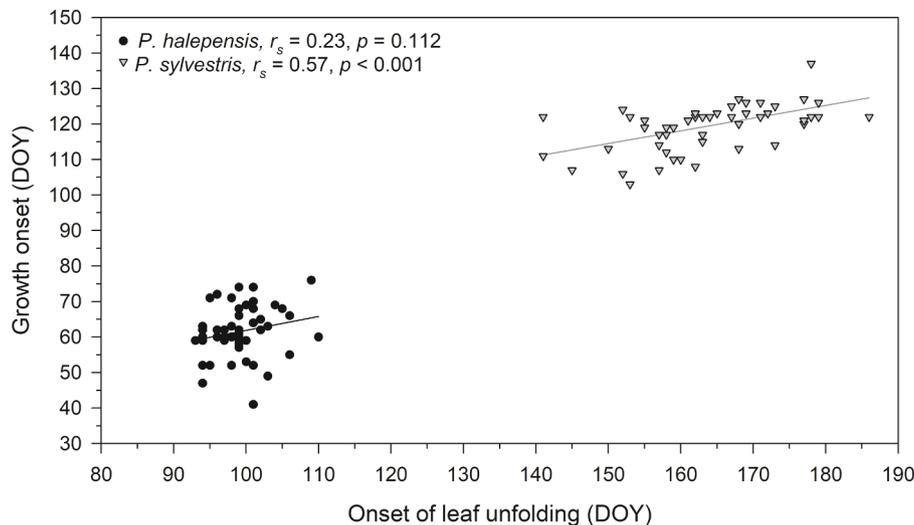


Fig. 5. Relationships observed between the date of onset of leaf unfolding and the growth onset date simulated by the VS-Lite model for both study species. There was a positive and significant correlation in *Pinus sylvestris*.

Campelo et al., 2018), thus complicating phenological responses to climate warming. This could explain why *P. halepensis* growth was enhanced by cool and wet conditions which also delayed leaf onset and the decoupled leaf-wood phenology.

In *P. halepensis* leaf phenology may be constrained by temperature and photoperiod showing a peak of leaf elongation in summer, whilst leaf photosynthesis may show a more plastic response peaking in early spring to avoid the dry summer conditions (Maseyk et al., 2008). This separation between phenological and photosynthesis peaks would allow adjusting to drought and allow high productivity whenever winter-spring conditions are not too dry.

4.2. Linking leaf onset phenology, radial growth and climate

In the Krasnoyarsk-Stolby study site, Kalininia et al. (2019) carried out a xylogenesis study during 2012 on Scots pine and reported that the tree ring started forming between mid-May and early June and finished its development in late September with a range of duration of the growth period of 125–140 days. They also reported maximum growth rates (highest production of radially-enlarging tracheids) between mid-June and early July. Our simulations gave as mean dates of the start and end of growth early May (ranging between mid-April and mid-June) and early October (ranging between late September and mid-October), respectively, giving a duration of the growth period (mean \pm SD) of 164 ± 13 days, i.e. about 32 days longer than the duration observed in 2012. Simulated dates of maximum growth rates corresponded to mid-July. Since the 2012 growing-season was particularly warm and dry in Siberia (cf. Kalininia et al., 2019), it is expected that the simulated growth start would be close to the earliest modeled dates, i.e. mid- to late April. As a comparison, in Finland, at a much higher latitude (66° N) than the Russian study site, wood formation of *P. sylvestris* started between late May and mid-June and ended in mid-August (Schmitt et al., 2004).

At boreal forests, tree growth is limited by low temperatures and earlier bud burst driven by increased temperature could result in longer xylogenesis periods. For instance, Rossi et al. (2011) predicted longer periods of xylem growth at higher temperatures, with an increase of 8–11 days per $^\circ\text{C}$, because of an earlier onset and later ending of growth. Our results indicate earlier leaf onset and higher growth rates under wet summer conditions. In Siberia, *P. sylvestris* growth is not only constrained by cold climate conditions but also by low summer soil moisture (Arzac et al., 2021). These authors indicated that an earlier growing season onset could compensate for warming-triggered drought stress in

those forests, but this would depend on the timings of maximum growth rate and drought stress. In *P. sylvestris*, bud break and cambial resumption in spring depend on surpassing a 5–6 $^\circ\text{C}$ threshold of minimum air temperature (Swidrak et al., 2011; Fajstavra et al., 2019), but drought could also trigger an earlier onset of radial growth (Nezval et al., 2021) or an earlier cessation of wood formation (Oberhuber and Gruber, 2010). In addition, a lasting snowpack due to wetter spring conditions can also reduce root-zone temperatures and delay the spring cambial onset (Kirilyanov et al., 2003).

In some Mediterranean sites, *P. halepensis* may show almost year-round cambial activity if winters are not cold (Liphshitz et al., 1984; Nicault et al., 2001; De Luis et al., 2007). In addition, this species can produce a new flush of leaves and show radial growth in response to wet autumn conditions (Serre, 1976) triggering a second growth peak (Camarero et al., 2010; Pacheco et al., 2018; Campelo et al., 2021). This bimodal pattern was already predicted for *P. halepensis* using the VS (Touchan et al., 2012) and VS-Lite models (Campelo et al., 2021). In general, winter to spring wet conditions improve shoot elongation and wood production in this species (Girard et al. 2012), and warmer winters can also promote an earlier budburst and leaf onset (Vennetier et al., 2011), whereas drying reduces the growing season length and also constrains radial growth (Klein et al., 2012).

The lags observed between the recorded leaf unfolding dates and the estimated dates of start of wood formation agree with the literature. In *P. sylvestris*, wood growth begins ca. 30 days before buds break and needles start unfolding (Michelot et al., 2012; Fajstavra et al., 2019) and a similar delay has been observed in *P. halepensis* (Serre, 1976; Weinstein, 1989; Borghetti et al., 1998; Maseyk et al., 2008). In this species leaf onset depended on spring temperature but also on day length, which means that non-linear associations between phenology or growth and climate should be accounted for. The maximum growth rate of conifers in cold environments is achieved around the summer solstice when day length is highest (Rossi et al., 2006). This is also related to primary growth since long days may also compensate for a lack of chilling during rest break in Scots pine (Jensen and Gatherum, 1965).

4.3. Decoupled leaf phenology and growth responses to climate

In *P. sylvestris* chilling-influenced heat-sum models predicted the onset of wood formation in spring (Delpierre et al., 2019). In this species warmer temperatures promote earlier growth resumption, but they are associated to less chilling, imposing a higher forcing temperature sum to trigger the start of wood formation. Therefore, results presented by

Delpierre et al. (2019) question the predictions that warmer spring conditions would result in an earlier growth onset since warming reduces the number of chilling days. This decoupling between temperatures and tree growth adds to the observed decline in the sensitivity of spring leaf phenology to warm spring temperatures (Fu et al., 2015), which play a major role as climatic cue of leaf out (Flynn and Wolkovich, 2018).

Based on remote-sensing and tree-ring data, it has been observed that an earlier start of the growing season may not lead to enhanced tree growth in dry areas where a longer growing season is associated to increased drought stress (Gao et al., 2022). This would explain why we could not find a positive association between the growing-season length and tree growth in *P. halepensis*. In semi-arid sites, xylogenesis studies revealed that the number of produced xylem cells depends more on growth rate than on the duration of the growing season (Ren et al., 2019). In addition, there could species-specific differences in the phenology-growth links. Way and Oren (2010) found that elevated temperatures enhanced growth in deciduous species more than in evergreen trees. In temperate forests of the deciduous European beech (*Fagus sylvatica* L.), a longer growing season and an earlier spring leaf unfolding (Vitasse et al., 2011) and also higher growth rates (Prislan et al., 2019) were predicted in response to spring warming. However, neither trends nor year-to-year variability in leaf phenology and radial growth were related in this species despite the warming climate (Čufar et al., 2015). These findings concur with our results on pines demonstrating that an earlier leaf unfolding or a longer canopy duration do not mean increased radial growth.

The leaf-wood decoupling may be due to the different climate drivers of leaf phenology and wood formation (Polgar and Primack, 2011). Furthermore, a longer growing season due to warmer conditions may lead to higher carbon losses through respiration or increase the amount of stored carbon pools but not enhance wood formation. At tree level, climatic stressors (cold, drought) constrain first growth (carbon sink) than photosynthesis (carbon source) and carbon sinks determine the activity of carbon sources under sub-optimal conditions (Körner, 2015). Lastly, radial growth rates may be more important for total annual growth than the duration of the growing season. For instance, Cuny et al. (2012) found that 75% of the annual radial increment can be attributed to cambial activity rates and only 25% to the duration of the wood formation period.

Spring phenology depends on several cues (spring forcing, winter chilling and photoperiod), which explains why leaf-onset responses to ongoing climate warming are complex (Heide, 1993; Fu et al., 2015; Chuine et al., 2016; Carter et al., 2017). However, forcing temperature plays a major role as cue of leaf out (Flynn and Wolkovich, 2018), which concurs with our results in both pine species. Further research efforts should focus on jointly modeling leaf and wood phenology (e.g., Delpierre et al., 2016a; Huang et al., 2014) to disentangle how their trends impact on tree growth, productivity and the capacity of forests to mitigate climate warming. This would need field monitoring of leaf and wood formation (e.g., Rossi et al., 2009) and long-term (> 5-10 years) series of xylogenesis data to validate and constrain growth models (e.g., Buttò et al., 2020; Tumajer et al., 2021). Lastly, the VS-Lite model produced a better fit of simulated ring-width indices in the most climatically stressful *P. halepensis* site. Further approaches could use more elaborated versions of the VS model to improve simulations in more mesic sites such as the study *P. sylvestris* stand.

5. Conclusions

We found no support for the idea that an earlier leaf unfolding due to spring warming would lead to increased radial growth. This was more evident in *P. halepensis* at the drought-prone Mediterranean site, where wet-cool conditions delayed leaf unfolding but enhanced growth. In the boreal site, *P. sylvestris* leaf phenology and growth were decoupled, but years with low growth rate were characterized by late dates of leaf onset

suggesting potential relationships between growing-season length and growth rates. Since warmer spring conditions advanced leaf unfolding and enhanced growth in *P. sylvestris*, such potential link between climate, leaf phenology and wood growth should be further investigated in boreal conifer forests. Alternatively, warmer and drier summer conditions could also lead to reduced *P. sylvestris* growth. In the seasonal dry Mediterranean forest, *P. halepensis* growth was mainly constrained by dry winter to spring conditions explaining the decoupled leaf-wood phenology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

We thank the “Ebre Observatory” for providing phenological and climatological data. This study was supported by project FORMAL (RTI2018-096884-B-C31) from the Spanish Ministry of Science, Innovation and Universities. FC was supported by the R&D unit CFE (FCT/UIDB/04004/2020).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109223.

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